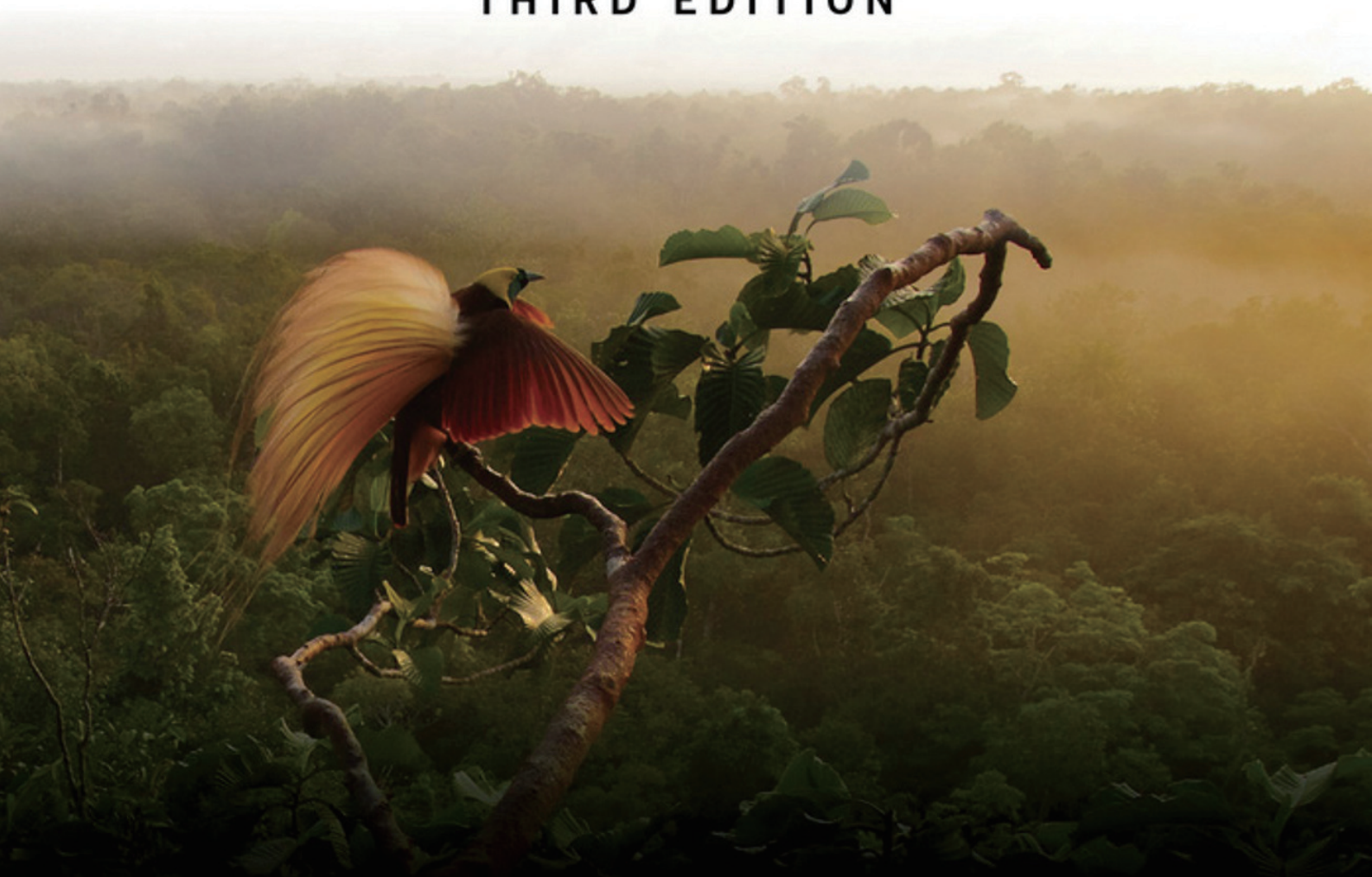
THE CORNELL LAB OF ORNITHOLOGY

HANDBOOK OF BIRD BIOLOGY

THIRD EDITION



EDITED BY
IRBY J. LOVETTE AND JOHN W. FITZPATRICK

The Cornell Lab of Ornithology

WILEY

HANDBOOK OF BIRD BIOLOGY

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WILEY

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Cover image: Displaying male Greater Bird-of-Paradise (*Paradisaea apoda*). Photograph by Tim Laman © Tim Laman.

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Preface

At this very moment, somewhere on earth, the sun is rising and a dawn chorus of birdsong welcomes the new day. This never-ending avian symphony has been performed non-stop for millions of years, yet our scientific understanding of avian biology still improves with every passing year. This third edition of the *Handbook of Bird Biology* is intended as a current and helpful guide into the spectacular richness of bird diversity and the wonderful and varied ways that birds look, behave, display, function, and evolve.

The third edition of the *Handbook* extends a tradition that began in 1972 when the Cornell Lab of Ornithology first offered a Home Study Course in Ornithology to the general public. That early correspondence course comprised nine seminars on different topics, all written by the Cornell Lab's Director at the time, Dr. Olin Sewall Pettingill, Jr, an ornithologist known for helping connect recreational birdwatchers with scientific advances in avian biology. The first Home Study Course students received nine units of mimeographed sheets sent through the mail. Over the subsequent two decades, the materials increased in length and sophistication as the Home Study Course evolved and expanded. More than 10,000 students successfully passed their mailed-in exams and completed the course.

This material was expanded and modernized as it was incorporated into the 2004 second edition of the *Handbook*, which was produced as an impressively hefty single-volume book co-published by the Cornell Lab of Ornithology and Princeton University Press. It became a multi-authored endeavor with 11 chapters written by experts in their respective fields, each of whom lent their own personal style to explaining why birds look, act, and function in the ways that they do. The second edition remained the foundation of the continuing Home Study Course, used by an additional 5000 students from 65 countries. The book was likewise adopted as a textbook for many college-level ornithology courses and enjoyed as a general reference by many individuals interested in learning more about birds, even outside of any formal or informal coursework.

This third edition, published in 2016, represents an even more extensive overhaul of the content, presentation, and coverage of the *Handbook of Bird Biology*. The new edition's 15 chapters have been authored by 18 expert ornithologists, including five authors who extensively revised their well-regarded chapters from the second edition and 13 who contributed entirely new material. The new content includes extensive and expanded coverage of hundreds of recent discoveries and insights about avian ecology, behavior, evolution, physiology, anatomy, and conservation.

Given that birds are so visually appealing, it is appropriate that the new edition be presented in full color, a first for any general textbook of Ornithology. The 1150 photographs, illustrations, and figure elements depict hundreds of bird species, along with graphs and tables that explain intriguing facets of their underlying biology. The *Handbook* editors and authors express their deep thanks to the many individuals—credited in the figure legends—who generously contributed photographs or artwork to this edition.

Readers familiar with the earlier additions may notice that this edition is now global in its coverage of the world's birds and the people who study and conserve them. It includes examples featuring bird species that are collectively found literally everywhere on earth that birds occur. In addition to the venerable traditions of ornithological research in North America and Europe, exciting new discoveries are now constantly being made by ornithologists from the rest of the Americas, Africa, Asia, Australia, and islands around the world. Our hope is that readers of this book—wherever they might be—will enjoy finding out more about some of the most familiar birds that live around their homes, while also being inspired by learning about species that occur in far-away places.

A special new feature of the third edition is that it is complemented and supplemented by a wealth of online

materials found on the Bird Academy website of the Cornell Lab of Ornithology (web link: **birdbiology.org**). These resources include interactive learning modules on topics ranging from feathers to sexual selection; high-quality video and audio clips chosen to represent behaviors or phenomena discussed in the text; animations that illustrate fundamental concepts in ornithology; longer feature-length coverage of special topics; and much more. The resources are conveniently organized in reference to the corresponding chapters of this *Handbook*. We encourage all readers to use this online material to supplement their readings here. This is especially helpful for the chapters on bird song (Chapter 10) and mating behavior (Chapter 9) where there is no better way to understand these behaviors than to hear or see examples of living birds in action.

In addition to the 18 chapter authors, the creation of this third edition was possible only through the dedicated efforts of the skilled editorial and production teams at the Cornell Lab of Ornithology and Wiley. The Editors express a debt of gratitude to their Cornell colleagues whose expertise and energy brought this book to completion, including Myrah Bridwell (Permissions Editor), Rebecca Brunner (Development Editor), Alexandra Class Freeman (Art Program Editor), Kevin McGowan (Advising Science Editor), Nancy Trautmann (Education Program Director), Mya Thompson (Online Content Manager), and Megan Whitman (Project Manager). We are likewise deeply appreciative of the wise input and skillful management of this project from the editorial group at Wiley, from our initial discussions with Alan Crowden and Ward Cooper and ultimate project oversight by Kelvin Matthews, through to the production oversight by Emma Strickland and David McDade, hundreds of artistic contributions to figures by Debbie Maizels, production management by Rosie Hayden, skillful project management by Jane Andrew and indexing by Terrence Halliday. We feel extremely fortunate to have had the opportunity to work with such dedicated and professional individuals and teams from both organizations.

About the Cornell Lab of Ornithology

This *Handbook* is an educational resource created by the Cornell Lab of Ornithology, a unit of Cornell University located in Ithaca, New York, USA. The Cornell Lab is a world leader in the study, appreciation, and conservation of birds. Our hallmarks are scientific excellence and technological innovation to advance the understanding of nature and to engage people of all ages in learning about birds and protecting the planet. Our mission—which we take to heart and which guides all of our endeavors—is *to interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds.*

Founded in 1915, the Cornell Lab has grown over the past century into an unusual amalgam of a university department, conservation organization, technology and engineering think-tank, and communications agency. Our staff and faculty number nearly 200 individuals, complemented by almost as many undergraduates, graduate students, and postdoctoral scholars from Cornell and from visiting institutions worldwide. Our vibrant broader community includes 400,000 citizen science participants from all walks of life and 14+ million bird enthusiasts of all ages who connect with us online at birds.cornell.edu.

The Cornell Lab is located in the Johnson Center for Birds and Biodiversity and surrounded by the Sapsucker Woods preserve. We invite all readers of this book to come and enjoy our visitor center and to go birding on our trails. If you cannot visit us in person, be sure to take advantage



The Cornell Lab of Ornithology. Located in the Johnson Center for Birds and Biodiversity, the Cornell Lab is both a unit of Cornell University and an international membership organization. Our mission is *to interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds.* (Photograph by Diane Tessaglia-Hymes © Cornell Lab of Ornithology.)

of our web resources, not only the companion site to this book but also our All About Birds website (**allaboutbirds.org**), our live cameras at active bird nests around the world (**cams.allaboutbirds.org**), our award-winning magazine *Living Bird* (**allaboutbirds.org/living-bird-latest-issue**), and our many citizen science projects (**birds.cornell.edu/citsci**) where you can get involved in collecting information that adds to our ornithological knowledge base to inform bird conservation and management.

We especially encourage all birders—from beginners to experts—to discover and use eBird. At ebird.org you can upload your own checklists and access a rich suite of resources designed to enhance your ability to find and identify birds, all at no cost. eBird is a truly global resource with web portals and partners in many languages and most countries.

We also invite all users of this book to become members of the Cornell Lab at **birds.cornell.edu**. As a nonprofit organization, we depend on our members, donors, research, and our other programs for 99% of our operating budget. These resources support the continued development of this *Handbook* and its online enhancements, along with our many other endeavors in science, conservation, education, and outreach. Your engagement supports the advancement of ornithological science and the informed conservation of birds and their habitats worldwide.

Irby J. Lovette
Fuller Professor of Ornithology
Cornell Lab of Ornithology

For additional online material please visit the
Bird Academy website of the Cornell Lab of Ornithology at **birdbiology.org**

Bird Academy Web Resources

This *Handbook* is complemented by extensive online learning resources hosted on the Bird Academy site of the Cornell Lab of Ornithology. Be sure to visit **birdbiology.org** to access the web content associated with each *Handbook* chapter. These include hundreds of videos of wild birds, interactive learning modules and features, animated and annotated sound recordings, and in-depth articles on topics of particular importance about birds and their conservation.

We particularly encourage all readers to use the Bird Academy site when reading *Handbook* Chapter 10 on Avian Vocal Behavior. The spectrogram figures seen as static images in the printed chapter are playable on the Bird Academy site as animated recordings: you can hear the actual sounds and watch the visual display of the sonogram. The direct link to that enhanced Chapter 10 content is: **birdbiology.org/vocalbehavior**.

How to report errors and offer suggestions

We encourage all readers of this *Handbook* to visit **birdbiology.org/suggestions** to let us know if you find errors in the text or have other critiques to offer. At that same web link we also welcome suggestions about additional content that could be covered in future editions, newly published studies with relevant findings and discoveries, and all other kinds of feedback that can help the *Handbook* remain a useful and current resource for individuals interested in avian biology. We pay close attention to this feedback and thank all respondents for offering their input.

For additional online material please visit the
Bird Academy website of the Cornell Lab of Ornithology at **birdbiology.org**



Chapter 1 Why Study Birds?

Irby J. Lovette and John W. Fitzpatrick
Cornell Lab of Ornithology

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Birds have a special place in human science and culture: they capture our hearts, arouse our curiosities, and inspire a sense of wonder. We may revel in the diversity and simple beauty of their forms, but birds also fuel fascinations that drive us towards deeper scientific inquiries into their varied ways of life. Every student of ornithology—from recreational birders to career scientists—will find much to learn and appreciate in the extraordinary physical and behavioral adaptations of birds, their rich evolutionary history, and their commanding global presence.

One of the wonderful aspects of enjoying birds is that they are found nearly everywhere. Given that these outwardly delicate creatures must maintain an internal body temperature even higher than our own, their capacity to live in almost every environment on earth is staggering. Birds occupy windswept arctic tundra and harsh antarctic ice, fog-shrouded mountaintops and tropical rainforest understories, the world's driest deserts, and storm-swept high seas. They live amongst us in the most urbanized cities, in suburban backyards, and in the most remote wildernesses. Wherever we travel, birds are our constant companions, and by discovering more about the birds we find around us, we can come to understand many other aspects of the natural world and our relationship to it.

Birds are endlessly fascinating partly because they are so diverse. Birds make use of their myriad habitats with an almost bewildering array of foraging strategies, performing important ecological functions in the process. Many birds capture and eat other animals, from tiny insects to large vertebrates, sometimes including other birds. Some birds hunt by night, and a few even navigate by echolocation. Others hunt high in the sky with eyes far keener than our own, diving down with incredible speed and agility at a moment's notice; many are equally skilled in detecting insects on leaves or worms under the ground. Still others specialize in scavenging, thus speeding up the process of decomposition. Many birds eat nectar, seeds, or fruits, sometimes aiding in plant reproduction by serving as pollinators and seed dispersers.

The breeding strategies of birds are just as varied as their ecological roles. Many engage in complex choreography as a precursor to mating, often presenting highly decorative displays and intricate vocal performances. Some birds pair together for many years or live in extended families, while others mate only for an instant, never to see one another again. Some bird chicks are raised by groups of relatives, some by both parents, others by only their father or their mother, and a few receive no parental care at all. Some birds attempt to raise just one offspring in every alternate year, while other species can raise large broods of chicks several times within a single season. Bird nests come in a dazzling variety of forms, from simple scrapes on the ground, to intricately woven baskets, to messy piles of sticks that may weigh several tons.

Birds flap, hover, soar, glide, stoop, swim, dive, burrow, walk, hop, and even sprint. To us, they often appear—and quickly vanish—as a burst of motion and color. Through their longer movements, birds create living links among the

Opposite: This flock of Greater Flamingos (*Phoenicopterus roseus*) includes both colorful adult birds and whiter juveniles. (Photograph by Ian Davies.)

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Fig. 1.01 Conifer needles are the principle food of the Spruce Grouse (*Falcipennis canadensis*). (Photograph by Christopher Wood.)

earth's continents, oceans, and hemispheres. Migratory species know the planet as a north-south stage to be traversed twice each year, generating one of the most remarkable global migration spectacles on earth. The annual return of individual birds to their precise breeding or winter territory seems almost miraculous, and this homing ability is a testament to their underlying adaptations for orientation as birds move across vast distances. Other kinds of birds are nomadic, sometimes wandering in great flocks in search of super-abundant food or prime breeding sites; yet other birds are home-bodies, remaining very close to their hatching site throughout their entire adult lives.

The songs of some birds are among nature's most evocative sounds. Birds make sounds primarily to communicate with other birds, but they do so in a great variety of ways and across a great range of auditory frequencies. For human birders and scientists, learning bird calls and songs is often the key to discovering what species are present in a habitat or location. Going further, we can eavesdrop on the more detailed lives of birds by learning how they use songs to defend territories, advertise to mates, warn of potential dangers, and communicate about their own status.

Beneath all this behavioral and ecological diversity of birds lies a remarkable vertebrate body structure and physiological potential. Birds have unique skeletons: every bird is equipped with specialized forelimbs and fused hand bones that together form a wing. Some birds' wings are proportionally too small for flight; others have wings that are modified into flippers for swimming. All birds have beaks, lay eggs, and breathe via a system of one-way airflow, which permits more efficient capture of oxygen than the in-and-out breathing pattern of mammals. Yet despite these similarities, birds have a wondrous variety of physical forms—from the smallest of hummingbirds to the towering ostriches—that are adapted to different ways of life. Their internal body processes are similarly multifarious: some birds can dive deep into water and remain submerged for minutes, others can fly at great heights where the air is thin and oxygen correspondingly poor. Different birds can extract energy and nutrients by digesting a great range of foods, from tough leaves to fluid nectar, and from tiny invertebrates to rodents swallowed whole. Some birds time their breeding based on subtle shifts in day length that cause cascading effects on their hormones and reproductive systems. Others use specialized areas of their brains to remember the locations of thousands of seeds that they have hidden for later consumption.

The external beauty of birds is enriched by their variety of feathers, which are magnificent in function as well as form.



Fig. 1.02 Scimitar-billed Woodcreepers (*Drymornis bridgesii*) are among the many bird species in which male–female pairs coordinate their songs to produce a synchronized duet. (Photograph by Ian Davies.)



Fig. 1.03 The Rufous-tailed Jacamar (*Galbula ruficauda*) uses its long bill to capture butterflies and other agile flying insects. (Photograph by Benjamin G. Freeman.)



Fig. 1.04 Penguins, like this Gentoo Penguin (*Pygoscelis papua*), have many morphological and physiological adaptations for their aquatic lifestyle. (Photograph by Christopher Wood.)

Feathers are an adaptation found in no other animal group today, but we now know that birds are the living descendants of otherwise extinct dinosaurs that also sported a great variety of feathered plumage. Feathers provide birds with thermal insulation, waterproofing, and, in many cases, facilitate their flight. Feathers come in bold or cryptic patterns, ornamental shapes, incredible shades of color, pure tones, impressive lengths, or, in just the right light, brilliant iridescence. Many birds offer a combination of these features that play a large role in both mate choice and camouflage.

There are enough species of living birds—10,000 or so—to keep the most ardent birders questing after new sightings throughout their lives. This rich diversity has evolved over 150 million years, creating the panoply of avian orders and families that populates our field guides. Over the smaller timescales that can be addressed in field studies, birds have provided some of the best examples of how evolutionary forces play out in time. Scientists have carefully documented how natural selection can change bird populations in just a few generations, and how intense sexual selection can drive the evolution of gaudy plumage and elaborate displays. Birds have therefore played a central role in our general understanding of these most basic processes by which species arise and change through time.

Birds have a similarly influential standing in our efforts to conserve the natural world. Birds serve as flagships for imperiled habitats and ecosystems, and as early warning systems for environmental toxins or other destructive forces. Conservation efforts focused on birds often help preserve many other less conspicuous organisms. And owing to their charisma and popularity with humans, birds can help inspire all of us towards being better stewards of natural systems and biodiversity.

This book is about all of these aspects of avian biology, and more. Thanks to a fortuitous combination of diversity, accessibility, and charisma, birds through the ages have taught humans an extraordinary amount about natural history. Nearly everyone on earth has seen and wondered about a bird, and this familiarity helps give birds their special inspirational power—birds capture our imagination and curiosity by simply being in our presence. Researchers over the years have harnessed this same accessibility of birds to answer questions in the laboratory and in the field with relative ease, especially compared with the challenges of studying most other animals. Dozens of principles in evolution, ecology, biogeography, behavior, neurobiology, life history theory, natural resource management, and conservation biology have been—and continue to be—discovered and refined through studies of birds. This book is intended as a tool to help all of its readers find further inspiration in the birds that form an important part of our lives.

1.1 Engaging with birds in the twenty-first century

Whether we study them as students, casual observers, lifelong learners, or professional scientists, birds can be mesmerizing any time we stop and simply watch them. At the bird feeder, at the city park, in a parking lot, at the beach, or in the woods, these creatures share the planet with us largely in disregard of our fascination with them. Pausing to observe birds employ their adaptations—those that allow them to fly, catch a fish in a flash, or show off gorgeous songs and plumage—is one of the most satisfying ways to connect personally with the details and the larger workings of the natural world. The more we watch them, the more we are likely to want to know about birds.

Today our intrinsic interest in birds can go further than ever before. We can learn, observe, and contribute to a

dynamic and unprecedented collection of knowledge about birds. Significant gaps still exist in our understanding, but by simply by watching and recording birds—even the most common ones—individuals and communities can make a big difference. Birds are extremely sensitive indicators of ecosystem conditions and quality. As humans continue to alter the natural world, the status of bird populations can provide clues about the type and scale of our impacts. Which bird species are declining, and which are increasing? Which species are successfully adapting to human-modified habitats, and why? As the planet warms, are birds changing their migratory routes, or spending the winter in different places?

Among all of the ways that we can engage with birds, "citizen science" projects deserve special mention owing to the benefits they generate for both their human participants and the avian subjects of their observations. Many local and regional citizen science endeavors provide enjoyable ways to enhance your engagement with the birds in your area. On a global scale, eBird (**ebird.org**) is the most geographically widespread avian citizen science initiative of all; it is based at the Cornell Lab of Ornithology, the same organization that developed this book, with partnering organizations in many countries and resources available in most of the world's major languages. The eBird project involves simple checklists of bird sightings submitted online by birders from every country in the world. The aggregation of this vast amount of information on bird distributions allows researchers to address questions that have, until now, been impossible to pursue. By sharing observations in the same database, people from all professions and walks of life directly increase global understanding of bird populations, movements, use of habitats, and relationships with humans.

Such studies are particularly crucial as we develop strategies to facilitate the coexistence of human cultures with stable and functioning natural systems. When we take the time to listen and understand them, birds become more than captivating creatures—they reveal themselves as indicators of environmental health. All over the world, humans are taking the pulse of the planet through their interactions with birds.

1.2 A short note on the names of birds

Depending on your place of origin, you may find that some familiar birds mentioned in this book have unfamiliar names, as there is some regional variation in the "official" English names of birds, and even greater variation in their colloquial names. Similarly, there are several authoritative lists of the world's bird species that are generally in high agreement with one another, but that differ in the way they "lump" or "split" a handful of species or higher taxonomic groups. All English and scientific names of birds used in this book follow the eBird/Clements Checklist version 6.9, which includes taxonomic updates through to August 2014. This Checklist and its more recent updates are freely accessible at **birds.cornell.edu/clementschecklist/**.

In this book, we treat the full English names of bird species as capitalized proper nouns. Group names and other variants are regular nouns and not capitalized. Thus you might read a sentence like: "Among all of the world's species of chickadees and tits, the Great Tit (*Parus major*) is one of the most widely distributed and best studied." The two-word Linnaean name (*Genus species*) is included every time a bird species is mentioned within the text in a new context or as a new example.

1.3 Birds and ornithology are both worldwide

This book is international in scope: birds are found worldwide, and ornithologists have conducted important studies of thousands of species in all of the major habitats and biomes of the earth. The discipline of ornithology is similarly global, as the scientific process of investigation is unconstrained by national boundaries and new discoveries about birds are constantly being published in scientific journals by researchers from all parts of the world.

In choosing examples to be included in this book, the authors and editors have purposefully selected species and studies that span this global breadth. If a particular example



Fig. 1.05 The Red-billed Leiothrix (*Leiothrix lutea*) is native to Asia, but its popularity as a cage-bird has led to introduced populations in other areas of the world. (Photograph by Ian Davies.)

treats a bird that is unfamiliar to you, consider whether any of the species that you know from your own region might exemplify a similar trait or phenomenon. More generally, we hope that this global breadth of examples helps inspire you to learn about the full range of avian diversity in all of its worldwide glory.

Although ornithological expertise is now truly global, in past times the scientific study of birds was centered largely in Europe and North America, and these regions still have more academic ornithologists than do some other areas of the world. The editors and authors of this book are primarily based in North America, with a few from Europe, although most of us have done field studies elsewhere. For these two reasons—ornithological history and our own familiarity—North American and European birds are somewhat overrepresented in this book in comparison to their total fraction of avian diversity. Nonetheless, readers from every other corner of the globe are sure to find examples in this book featuring birds found in their local area.

1.4 Web resources beyond this handbook

We hope that you feel excited and empowered with this book in your hands. We encourage you to treat it as an entry point into the lives of birds, for there is so much more to bird biology than we could squeeze into these chapters. This book is a product of the Cornell Lab of Ornithology, where our scientists and outreach experts have assembled a wealth of supplemental materials that accompany this book and which are free to access online. Using this book in combination with these web resources will enhance your learning about avian biology and simultaneously be a lot of fun. These online resources include video and audio files related to the material covered in each chapter; interactive, visually compelling modules that bring to life many of the principles outlined here; and much more.

Before reading further, be sure to access additional online content for this book at birdbiology.org.








Chapter 2 Avian Diversity and Classification

Irby J. Lovette
Cornell Lab of Ornithology

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The nearly 10,000 species of modern birds share a common ancestor, a bird that probably lived about 130 million years ago (Fig. 2.01). The evolutionary tree that stretches back through time to connect present-day birds with their avian ancestors provides the basis for classifying birds into a series of hierarchical groups, from the Class Aves, which includes all birds, down to the species that form the tips of the tree's branches. These nested groups are important because they provide a system of classification that helps organize avian diversity in a way that is both evolutionarily correct and useful to birders and ornithologists.

This is a particularly exciting time for people interested in the evolutionary relationships of birds. Rapid advances in genetic technologies make it possible to access the entirety of avian genomes, providing a wealth of comparative information about living birds that can be used to reconstruct their evolutionary relationships and learn how their genes control aspects of avian physiology, behavior, and ecology. Meanwhile, spectacular fossil discoveries continue to expand our understanding of ancient birds and their affinities both to one another and to other dinosaurs. A comprehensive picture of the relationships of all living birds, and a good understanding of where they came from, is now within reach.

This chapter concludes with an overview of all orders and families of living birds. These categories are essential tools for organizing avian diversity for both scientists and birders.

2.1 Classifying avian diversity

Today there are slightly more than 10,000 species of living birds, according to the most commonly accepted classifications of worldwide avian diversity. The scientists who study this diversity are called systematists. The field of systematics involves two general pursuits. One is the **classification** of birds and other organisms into a hierarchy of taxonomic levels, such as species and families. This endeavor focuses on describing newly discovered species and on understanding the distinctions between species. The other task of systematics is to uncover the relationships between taxonomic groups and to look back through time to reconstruct their evolutionary histories. Most commonly, this historical investigation involves creating an underlying evolutionary tree, or **phylogeny**.

Classification: in an evolutionary context, the process by which scientists name organisms and assign them into larger groups based on their evolutionary relatedness.

Phylogeny (or phylogenetic tree): a diagram that depicts the evolutionary relationships connecting a set of organisms.

Opposite: Stunning *Tangara* tanager diversity. Many species in this neotropical genus frequently forage together in mixed flocks. (Photographs by: top left, Andy Johnson; top right, João Sérgio Barros Freitas de Souza; middle left, Frank Shufelt; middle right, Dario Sanches; bottom left, Juan Ignacio Zamora Mora; bottom right, Almir Cândido de Almeida.)

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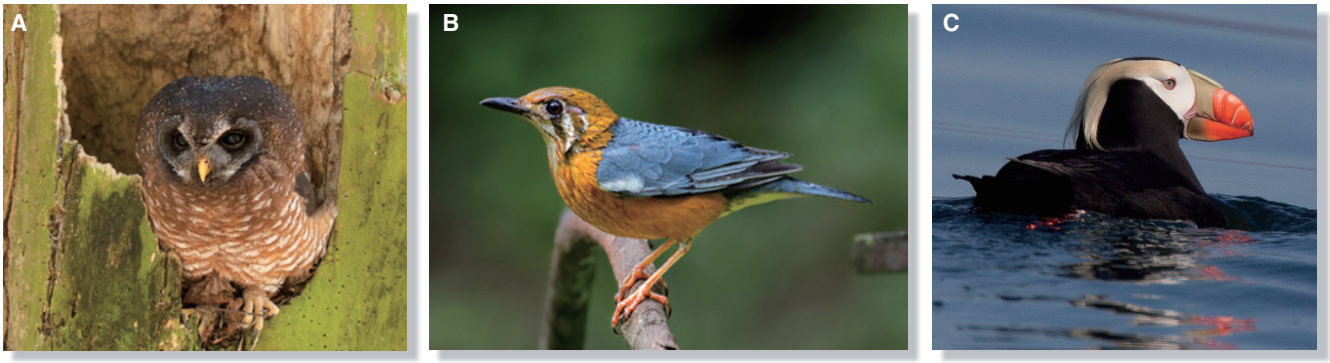


Fig. 2.01 All living birds share a common ancestor. Despite their incredible diversity in forms and ways of life, all living birds—including the (A) African Wood-Owl (*Strix woodfordii*), (B) Orange-headed Thrush (*Geokichla citrina*), and (C) Tufted Puffin (*Fratercula cirrhata*)—descend from a common avian ancestor that lived about 150 million years ago. (Photographs by: A, Roger Wasley; B, Shashi Shankar Hosur; C, Christopher Wood.)

These two endeavors are fundamentally linked to one another. For example, an avian systematist who discovers a bird that could be a new species will likely describe the particular characteristics that help define it as a distinct entity, while also placing the new species within a broader evolutionary tree that includes other related species. Our understanding of both the classification and phylogeny of birds has improved greatly in recent years, in part because of new discoveries and in part because of technological advances.

2.1.1 Avian classification

A quick flip through a typical bird field guide will reveal that the birds in it are organized meaningfully: for example, the ducks and geese are grouped together, and they are clustered separately from other superficially similar waterbirds such as loons, grebes, or cormorants (Fig. 2.02). These groupings are based primarily on studies of museum specimens over the past 150 years (Boxes 2.01 and 2.02; Chapter 6), and they reflect our understanding of bird evolution and the way it has played out over time as a branching, hierarchical process. For example, the ducks and typical geese are all more related to one another than they are to any members of other groups, and they are therefore classified together in the family Anatidae. Within this family, species that are even more closely related to each other are then placed within the same genus; for example, the genus *Anas* includes several dozen species of dabbling ducks, including the Mallard (*Anas platyrhynchos*) and related species of teals, wigeons, shovelers, and pintails. This classification structure allows us to place birds into increasingly inclusive categories, as shown in Fig. 2.03, in which each level includes all the members of the previous ranks, going back to the common shared ancestor of all birds. Most field guides and other references on bird diversity follow this organizational practice of putting the most closely related species together, usually by grouping together birds in the same family.

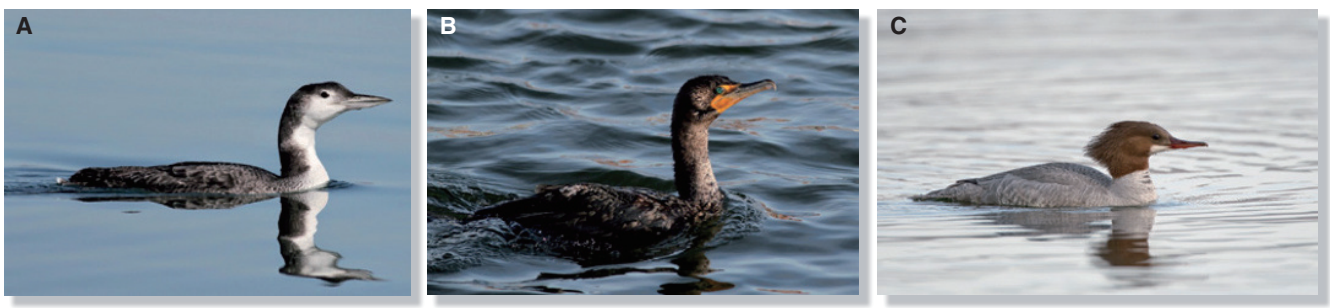


Fig. 2.02 Similar-looking birds in different taxonomic groups. Despite their superficially similar appearances, the (A) Common Loon (*Gavia immer*), (B) Double-crested Cormorant (*Phalacrocorax auritus*), and (C) Common Merganser (*Mergus merganser*) are only distantly related—each belongs to a different order. (Photographs by: A and B, Jay McGowan; C, Christopher Wood.)

Box 2.01 The importance of scientific collecting

Our understanding of living birds is founded on studies of specimens that have been collected and prepared over the past two centuries, and which now are curated in museums around the world. Some of the largest museums hold more than 1 million bird specimens, others only a handful, but all are important for the record of avian diversity they preserve.

A collection of specimens is a physical archive of actual biodiversity that records which birds were present in particular times and places, along with a great variety of information about the birds themselves, such as the habitat they were found in, detailed features of their internal and external anatomy, and the DNA content of each bird's genome. Bird specimen collections therefore are an irreplaceable resource used by a wide range of ornithological researchers and conservation professionals, as well as by students, teachers, and artists.

Although museum curators frequently salvage birds that die from other causes—such as birds that hit windows or cars, or that are caught in commercial fishing nets—and turn them into specimens, most specimens in the world's museums were collected intentionally for that purpose. The era of intense scientific collecting spanned the late 1800s into the mid-1900s, but this endeavor continues today. No ornithologist enjoys intentionally sacrificing birds, but many would argue that when done responsibly, the value of new specimens is high enough to justify the endeavor. Others disagree, and emotions can run high on both sides of the pro-collecting and anti-collecting debate.

One question often asked by first-time visitors to a large museum collection is: "Why do you need so many specimens? Wouldn't one or a few specimens of each species be enough?" For some kinds of research, one specimen is adequate, but for most studies it is important to be able to measure the degree of variation within each species. This broader sampling is especially essential in any study that uses statistics to compare different groups of birds.

A natural related question is: "You have so many specimens already; why do you keep collecting more?" One answer is that birds and their distributions change over time, and having new specimens allows researchers to study these changes. Another answer is that we can glean more data from new specimens than from older material. Current specimen preparators are careful to record every aspect they can about a bird they convert into a specimen, whereas a label on a specimen from the nineteenth century might indicate only the country in which it was obtained. Modern specimens also are accompanied by new types of materials, such as frozen tissue samples, which allow types of analyses that are impossible with older samples.

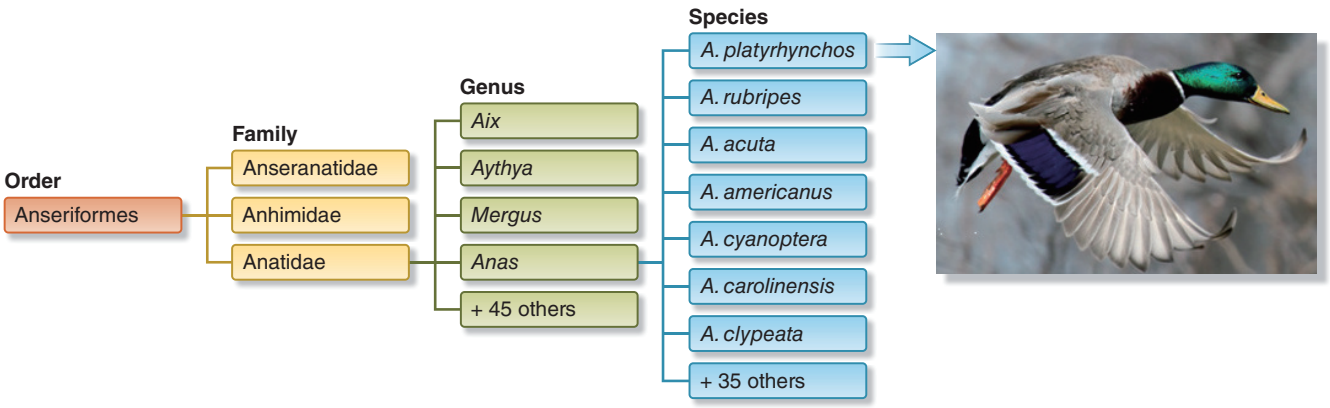


Fig. 2.03 Avian classification. The Linnaean system categorizes organisms within hierarchical levels based on their relatedness to other taxa, down to the principle unit of species—as illustrated here with the Mallard (*Anas platyrhynchos*). (© Cornell Lab of Ornithology; photograph by Randy E. Crisp.)

Box 2.02 Preparing bird specimens

When people think of bird specimens in a museum, they often envision the taxidermy mounts in exhibit displays that show birds in realistic postures. Specimens made for research purposes, however, almost never take on this life-like appearance. Instead, scientific bird specimens traditionally have been prepared in one of three ways: round skins, wet specimens, or skeletons.

Most specimens are in the form of round skins, in which most of the bird's internal parts are removed and replaced with stuffing (Fig. 2.B2.01). The specimen then is dried in a standard stretched-out orientation, with the wings folded at the side and the bill pointing forward. Advantages of round skins include the ease of taking many standard measurements of structures such as the bill, wing, and tail, and the practical utility of fitting many specimens together in one museum drawer.

Making a beautiful round skin requires practice and skill. The parts of the bird that could rot must be removed, and, in the process, the entire skin is turned inside-out, stuffed, and then sewn back together. Once dried, round skins are generally stable: on opening a specimen drawer, it can be difficult to distinguish round skins that are more than a century old from those that were recently collected. Moisture and insects are the greatest threats to round skins.

Museum collections also may include wet specimens, entire birds that are first fixed using formalin—which helps keep their tissues hard—and then stored in jars full of alcohol. Wet specimens are particularly useful for studies of avian anatomy because they preserve the internal structures and organs that are destroyed when making a round skin.

Skeletons are a third common type of bird specimen (Chapter 6). To make a skeleton, first the skin and feathers are removed, along with the organs and largest muscles. Then the remaining carcass often is put into a bin containing dermestid beetles that eat the remaining fleshy tissues but not the bones. The cleaned bones later are numbered and stored in a small box.

Most specimen preparators try to maximize the information that can be gleaned from each specimen, so they also freeze bits of tissue for genetic and other biochemical analyses, and they may also preserve the contents of the crop and stomach for diet analysis.

Laws about possessing and transporting dead birds vary widely around the world. Although some museums are happy to receive carcasses of birds that have died from natural causes, it is critically important to check with them in advance to ensure that no regulations are violated in the process. In any situation in which a dead bird might become a specimen, it is essential to record exactly where and when the dead bird was found. This procedure usually is done by writing these data on a slip of paper and bagging it securely together with the bird before placing it in a freezer.



Fig. 2.B2.01 Round skins in avian research collections. This common type of museum specimen preserves the bird's external anatomy, including the plumage. When kept dry and away from destructive insects, round skins remain useful indefinitely. These specimens—including some that are more than a century old—are from the Cornell University Museum of Vertebrates collection. (Photograph by Jennifer Campbell-Smith.)



Fig. 2.04 Distinctive variants of the same species. Despite their different coloration, these two male Asian Paradise-Flycatchers (*Terpsiphone paradisi*) are members of the same species. Individuals of both forms often occur and interbreed at the same location. (Photographs by: left, Manish Panchal; right, Dr. George Mothi Justin.)

Within this classification system, the **species** is the most fundamental and broadly used unit of avian diversity. As covered later in this chapter, ornithologists have devised many definitions for what exactly constitutes a bird species, but in general terms each bird species looks or behaves differently from related species, tends not to interbreed with members of other species, and has a past history of being evolutionarily distinct from other species.

Below the species level, ornithologists may describe **subspecies**, populations that differ in subtle attributes from other populations of the species. In situations where subspecies are readily distinguished by plumage differences or other distinctive traits, they may be illustrated separately in field guides. For example, the single Barn Swallow subspecies that breeds in North America (*Hirundo rustica erythrogaster*) has reddish underparts, whereas the subspecies that breeds across much of Europe and Asia (*Hirundo rustica rustica*) has snowy white underparts (Chapter 3). Although some bird subspecies have been defined carefully and show distinctive traits, such regional variants are not sufficiently different to cause them to be treated as fully separate species. Many named subspecies, however, are the result of older studies that do not meet modern standards because of limited sampling, obsolete criteria, or a focus on subjective differences among the subspecies. Still other subspecies are known to have fuzzy boundaries, with one subspecies blending into the next where their ranges overlap; sometimes birds showing this kind of geographical variation are instead referred to as being of different *races* of the same species. Often it is convenient to be able to give a name to a truly distinctive bird population, but many birds can be assigned to a particular subspecies or race only by knowing where they were observed. At an even finer scale, some birds show distinctive variants even within a single location; the forms of these species with distinctive plumage or markings are termed *morphs* (Fig. 2.04).

Species: the basic unit of biological classification for birds. Criteria for defining bird species vary, but they generally group into a single species the individuals and populations with very similar traits, a history of recently shared ancestors, and the continued ability to fully interbreed.

Subspecies: in birds, a distinct population or group of populations within a more widespread species that is distinguishable from other subspecies on the basis of one or more diagnostic traits.

Monophyletic group: in evolutionary terms, any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

Clade: a synonym for a monophyletic group, referring therefore to any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

Above the species level, avian taxonomy is somewhat more straightforward. When the classification is correctly assigned, every higher grouping, from a particular genus—such as the genus *Anas* into which the Mallard falls—all the way to the Class Aves—which includes all birds—includes an ancestral bird species and all of its descendants. This important criterion means that every named group of birds reflects a true evolutionary unit and that these units can be assembled into a hierarchy representative of the underlying evolutionary tree of all birds. In technical terms, these categories each represent **monophyletic groups**, or **clades**. These interchangeable terms refer to the complete

collection of evolutionary lineages past and present that share a common ancestor.

In theory, every split in the evolutionary tree of birds could be used to define one of these taxonomic categories, and some avian systematists argue for exactly this approach. Unfortunately, giving a name to every such split would result in many thousands of avian groups, and the names would change with every advance in our understanding of the evolutionary tree of birds. Instead, most traditional and current avian classifications use a much smaller group of hierarchical categories, such as the familiar levels of genera, families, and orders. Although the placement of the boundaries between these higher ranks is somewhat arbitrary and is highly influenced by past practices and our own organizational convenience, this approach leads to a manageable number of taxonomic categories. As described later in this chapter, our understanding of avian relationships is improving rapidly, so even the traditional taxonomic hierarchy of birds is being modified to reflect new discoveries about how these groups and their constituents are related to one another.

2.1.2 Naming bird species

The concept of hierarchical classification actually predates our modern understanding of evolution. The hierarchical classification system still in use today—the Linnaean System—is named after Carl Linnaeus, the Swedish biologist who in the 1830s developed and popularized a system of nomenclature in which each organism is given a two-word scientific name indicating its genus and species. For example, the scientific name of the House Sparrow is *Passer domesticus*. The first word in this type of **binomial name** refers to the genus in which the species is placed: the House Sparrow is in the genus *Passer* along with more than 20 other Old World sparrow species with which it shares a common ancestor (Fig. 2.05). In a Linnaean binomial name, the first letter of the genus name is capitalized. The second word in the name—*domesticus*—is the species name, which refers only to the House Sparrow; the species part of the binomial is never capitalized.

Although birds are most commonly referred to using this two-word naming system, technical publications on avian diversity sometimes use more elaborate versions with additional levels. For example, a reference to "*Passer domesticus rufidorsalis* Brehm 1855" includes an additional word—*rufidorsalis*—that refers specifically to the subspecies of House Sparrow found in the Nile Valley of Africa, as well as a reference indicating that this subspecies was formally described in an 1855 paper by the German ornithologist Alfred Brehm.

Every bird species is given a scientific binomial name when it is first described formally in a publication. A standardized set of rules set by the International Commission on Zoological Nomenclature (ICZN), the governing body charged with setting the criteria for animal nomenclature, must be followed by the person or team describing the new species. As explorers penetrate the last remote areas of the world, the naming of new bird species is becoming increasingly rare, with only a few such discoveries each year. Sometimes, however, new birds are found in less remote areas, as in the recent discovery of the Cambodian Tailorbird (*Orthotomus chaktomuk*) in the highly populated floodplain of the Mekong River (Mahood et al. 2013) (Fig. 2.06). In contrast to the earlier days of exploration, when it was common to name a species for oneself or in recognition of a sponsor, the scientific names of new species now are based most often on the new bird's region, the local language, a distinctive trait of the species, or the name

Binomial name: a naming system in biology in which each species is assigned a unique name consisting of two parts, the name of the genus and the name of the species, as in the scientific name of the House Sparrow: *Passer domesticus*.



Fig. 2.05 Binomial nomenclature. As indicated by their scientific names, (A) the House Sparrow (*Passer domesticus*), (B) the Eurasian Tree Sparrow (*Passer montanus*), and (C) the Cape Sparrow (*Passer melanurus*) all belong to the same genus, *Passer*. (Photographs by: A, Jay Diaz, KoolPix; B, Johan van Beilen; C, Ian White.)



Fig. 2.06 New birds are still being described. The Cambodian Tailorbird (*Orthotomus chaktomuk*) was first discovered in 2009 as a serendipitous outcome of a research program on avian influenza. (Photograph by James Eaton, Birdtour Asia.)

of an influential scientist. The species name *chaktomuk* of the Cambodian Tailorbird, for example, is based on a Khmer language term for the region near the city of Phnom Penh where the bird was discovered.

In addition to discoveries of previously unknown species, we are steadily gaining a better understanding of variation within and among previously described species. This improved understanding can lead to the **lumping** together of two species formerly considered distinct species into one single species. More commonly, however, populations within a described species are found to be more different than previously thought, leading to the **splitting** of one former species into two or more species. For example, the widespread bird known in Eurasia as simply the Wren and in North America as the Winter Wren was long considered to be the same species (*Troglodytes troglodytes*), but studies of genetic and song differences (Drovetski et al. 2004; Toews and Irwin 2008) recently led to a three-way split that divided the Eurasian Wren (*Troglodytes troglodytes*) from two species in North America, the western Pacific Wren (*Troglodytes pacificus*) and the eastern Winter Wren (*Troglodytes hiemalis*) (Fig. 2.07). As with the split of these wren species, changes in bird classification are usually first motivated by scientific studies that present new information on the underlying biology of the species being lumped or split. The formal decision about which species to recognize (and the names they are given) then usually rests with regional committees of professional ornithologists, who weigh the evidence for each potential change.

Lumping: informal term for changes in classification that involve merging into one species two or more taxa that were previously each considered to be a separate species.

Splitting: informal term for changes in classification that involve separating into different species populations that were previously considered to be part of a single species.

2.1.3 English and local names

Although every bird species has a formal scientific name, most people who enjoy birds—including professional ornithologists—refer to a bird by its common name in their local language. Although lists of worldwide common bird names exist in several languages, the most comprehensive common name systems for birds are in English. Worldwide, every bird species has a common English name, and occasionally more than one if it has varying names in different parts of the world. For example, the species scientifically known as *Gavia immer* has long been known as the Common Loon in North America but as the Great Northern Diver in Eurasia. An international group of ornithologists has proposed a standardized list of English names for all birds in order to reduce these regional naming discrepancies (Gill and Wright 2006). In their system, for example, the English name of *G. immer* is a compromise between the North American and Eurasian variations: the Great Northern Loon. Although nobody enjoys changing long-standing and familiar names, the general goal of improving worldwide communication about birds through consistent terminology is laudable.

Bird species often have additional names in local dialects or languages that reflect a direct understanding of that bird's ecology or behavior. For example, in Jamaica, the Snowy Egret (*Egretta thula*) is known as "Golden Slippers," a reference to the bright yellow feet at the base of its black legs (Chapter 8). Likewise, several cuckoos from Jamaica are known as "rainbirds," because they often call before or after downpours (Downer and Sutton 1990).

Comparisons of local names used by indigenous communities with the scientific names given by ornithologists usually reflect very similar patterns of classification. Both groups of observers recognize very similar sets of species and often distinguish nearly each species with a different name. This suggests that both indigenous and scientific communities fundamentally categorize avian diversity very similarly, probably in response to the real biological differences that separate bird species from one another.

2.1.4 Defining species

Ornithologists who classify bird species follow standard criteria to judge whether two bird populations are members of the same or different species. These boundaries usually are obvious and uncontroversial, but sometimes different scientists reach opposing conclusions about where

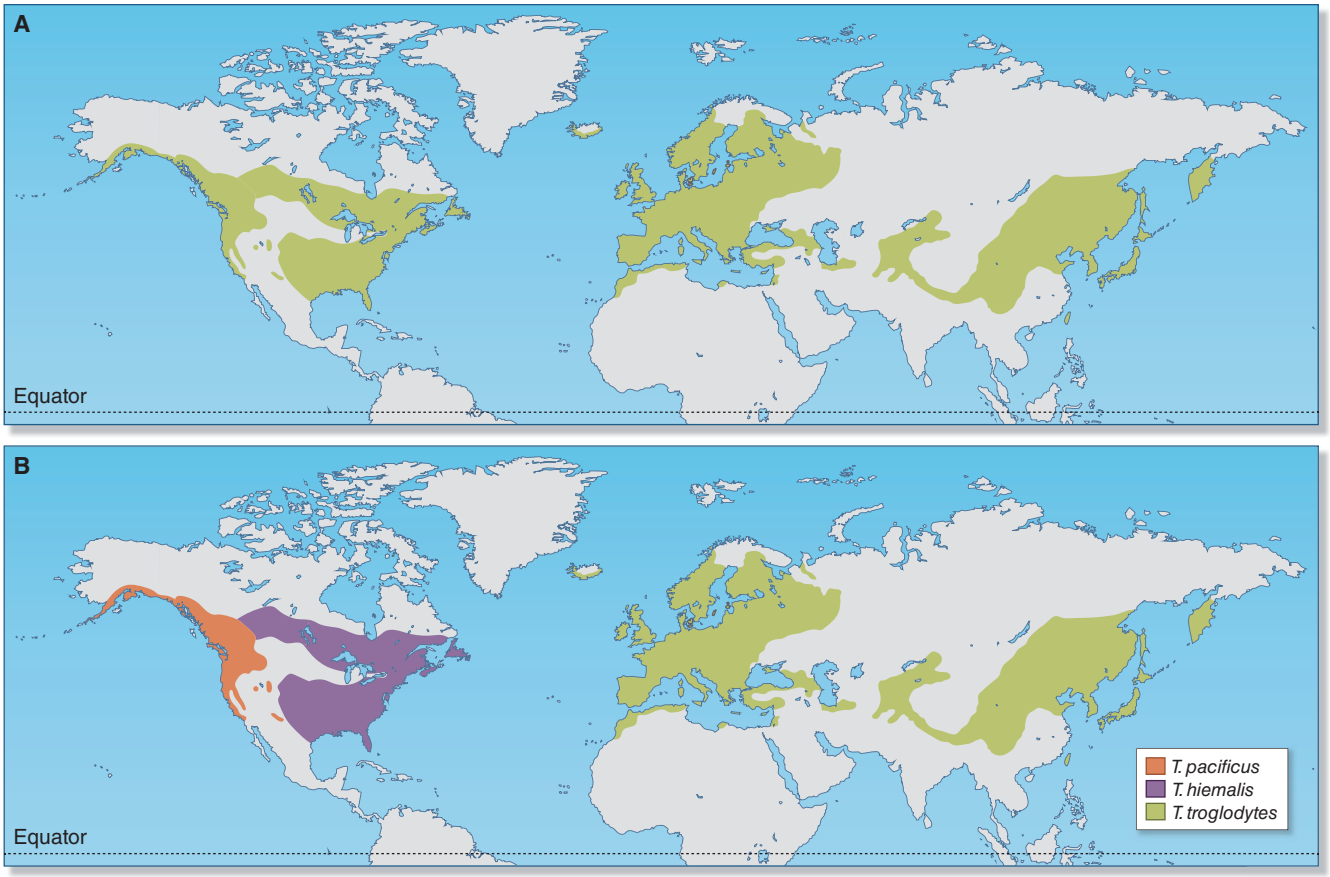


Fig. 2.07 Splitting species based on new evidence. (A) The Winter Wren was once considered to be one species (*Troglodytes troglodytes*) with an extremely broad range (green). (B) On the basis of new behavioral and molecular evidence, these birds have been divided into three separate species: the Eurasian Wren (which kept the original scientific name, *Troglodytes troglodytes*; green), the Pacific Wren (*Troglodytes pacificus*; orange), and the Winter Wren (*Troglodytes hiemalis*; purple). (© Cornell Lab of Ornithology.)

to draw the biological lines delineating different species. In these more complicated scenarios, it is important to remember that the entities we now classify as distinct species all formed over time through the gradual evolutionary process of **speciation** (Chapter 3). Because the speciation process involves one ancestor species gradually splitting into two or more descendant species, it is not surprising that there are points along that evolutionary pathway where conflicting classifications can be drawn, depending on what kind of evidence is considered.

Most birds occur in discrete **populations**, groups of individuals that breed in locations that may be separated in space from other similar populations. Imagine that you have to make a decision about whether the bird populations on two nearby islands belong to the same or different species. The birds from these two islands are generally very similar and clearly closely related, but they also differ in some subtle aspects of their plumage and courtship behavior. What evidence should you examine and what criteria should you use to decide whether they are one or two species?

To define species, biologists refer to **species concepts** that highlight the most important criteria used to decide whether two populations belong to the same or different species. The two most prevalent species concepts in

Speciation: the evolutionary process by which one ancestor lineage splits into two or more descendant species.

Population: in ornithology, a group of interbreeding birds of the same species that live in the same place at the same time.

Species concept: the precise sets of criteria that systematists use when deciding whether two populations are members of the same species, or two separate species. Different species concepts tend to emphasize different such criteria, sometimes leading to disagreements about classification.

ornithology are the **biological species concept** and the **phylogenetic species concept**. Their respective criteria focus on different aspects of the speciation process. In essence, the biological species concept focuses on current mating compatibility and what might happen in the future. In contrast, the phylogenetic species concept focuses on the history of populations and whether they have been evolutionarily separated in the past.

2.1.5 Birds and the biological species concept

The biological species concept has been adopted broadly across the field of biology, but its roots are in ornithology, as it was first formalized by the ornithologist and evolutionary biologist Ernst Mayr, an expert on South Pacific birds. Mayr's classic definition of a biological species is especially useful because it is both concise and descriptive of a fundamental aspect of biology: a biological species comprises "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). This definition places the emphasis on interbreeding: when populations can no longer interbreed owing to their biological differences, they are considered different species.

The biological species concept is easy to apply when birds found in the same location clearly either interbreed fully (thereby showing that they are the same biological species) or completely fail to interbreed (indicating that they are different biological species). However, individual birds of two species occasionally mate with one another in nature and produce hybrid offspring, and even more can do so when kept together in captivity (Chapter 3). One challenge in applying the biological species concept to birds is deciding what level of hybridization to accept between two populations that are otherwise considered distinct species. In the mid-twentieth century, a small amount of hybridization was considered enough to lump populations into a single species, even when those populations had other distinctive traits. For example, collections made in the 1950s showed that the species known as Baltimore (*Icterus galbula*) and Bullock's (*I. bullockii*) Orioles hybridize in a narrow region of the North American Great Plains (Chapter 3). This evidence of consistent hybridization led to their official reclassification into one species, the Northern Oriole, in 1983. However, subsequent research showed that these forms do not exchange genes as effectively as their levels of hybridization might suggest, as the hybrids appear to have lower fitness than non-hybrids and therefore are poor conduits for the exchange of genes between the two species. On a continent-wide scale, these two orioles therefore remain essentially genetically isolated, and since 1995 they have once again been formally classified as two separate species despite their ability to hybridize.

Biological species concept: a classic species concept that is still widely used in ornithology; it places the greatest emphasis on whether or not the members of two populations retain the ability to interbreed.

Phylogenetic species concept: a species concept that focuses on the history of a related set of organisms, in which a species is usually defined as the smallest group descended from a common ancestor that shares some kind of distinguishing feature that separates them from other such groups.

Allopatric: populations that occur in separate regions with no geographic overlap.

Similar populations that live in separated places, such as populations of landbirds on islands separated by wide stretches of ocean, pose another practical challenge to the application of the biological species concept. Their isolation means that they cannot interbreed with one another, even if they would otherwise be reproductively compatible. In theory, ornithologists could test whether these populations are different species by introducing birds from one island to the other, and watching to see if the immigrants breed with the residents. For a host of practical and ethical reasons such experiments are rarely conducted, and, instead, ornithologists generally use other, more indirect, forms of evidence to predict what would happen if the populations somehow came together. In such cases, alternative criteria are used to delineate species, including differences in plumage and song traits that are important to mate choice, and the degree of genetic difference relative to other populations that are known to be distinct biological species (Box 2.03). Demarcating species' boundaries in these situations usually requires judgment calls about the divergence between **allopatric** populations relative to that between reproductively isolated populations that occur together.

2.1.6 Birds and the phylogenetic species concept

The phylogenetic species concept is an alternative way of defining species that considers their past evolutionary histories. Under this approach, a species is the smallest cluster of individuals in an evolutionary tree in which all members share at least one distinctive, inherited trait that is absent in other groups. The shared trait provides evidence of the common ancestry of the individuals grouped together into one species, whereas the absence of the trait in other organisms provides evidence that they have diverged along a different branch of the avian evolutionary tree. The phylogenetic species concept thereby focuses on past levels of

Box 2.03 Birds with complicated distribution patterns

Some bird species, particularly those in tropical regions, have a complicated mosaic of populations with widely varying traits. Often, in such situations it is difficult to determine whether forms should be considered variants within one species or, alternatively, as separate and distinct species. Ornithologists often refer to such groups as "species complexes" to reflect this uncertainty.

The White-browed Brush-Finch (*Arremon torquatus*) forms one such complex along its distribution from Costa Rica south to Argentina. Plumage traits in this group vary dramatically, particularly with regard to the presence and extent of a white superciliary stripe on the head, and the presence or absence of a black band on the breast. In some cases, similar-looking brush-finch populations are found in widely separated locations, but interspersed in between are brush-finch populations that look quite different (Fig. 2.B3.01). This "leapfrog pattern" of plumage variation is seen also in other birds with long distributions along the Andes mountain

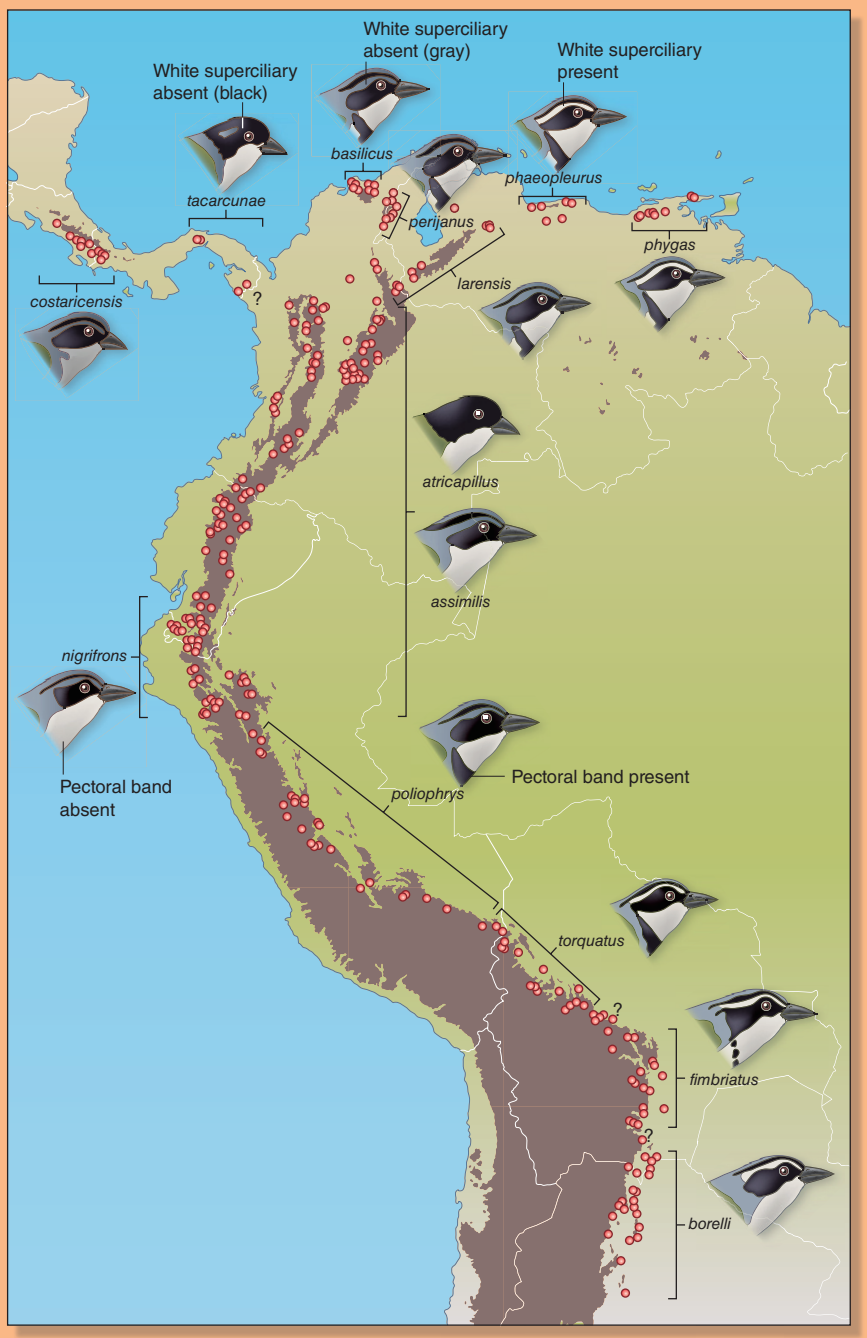


Fig. 2.B3.01 Distribution and plumage variation in a species complex. Various populations of White-browed Brush-Finches (*Arremon torquatus*) show great variation in plumage traits, including the presence/absence of the black pectoral band and white superciliary feathers. Gray shading indicates range; Latin names paired with illustrations refer to subspecies. (Cadena et al. 2011. Reproduced with permission from John Wiley and Sons.)

range. Researchers have long wondered about how this pattern originated: did the similar but separated populations evolve those plumage types independently, or are they similar because they are more closely related to each other than they are to their adjacent but differently plumaged neighbors?

The Colombian ornithologist Carlos Daniel Cadena and his collaborators used a combination of techniques to test these hypotheses in brush-finches. Using DNA sequences, they reconstructed a phylogeny for the different populations and found that each population had evolved its particular combination of plumage traits independently and that these plumage changes occurred at a relatively fast rate during the complex's evolution (Cadena et al. 2007, 2011). Similar-looking populations are therefore not particularly closely related to one another, suggesting that the leapfrog pattern arises when distant populations separately evolve similar appearances. Additional comparisons of habitat preferences and song variants in these populations suggest that the populations are in the process of diverging into as many as eight distinct species (Cadena and Cuervo 2010).

genetic connection, an intrinsically historical perspective, rather than on reproductive compatibility, an intrinsically biological perspective.

The phylogenetic species concept has both advantages and disadvantages. One benefit lies in its fine-grained approach, which demands high levels of specificity and thereby avoids lumping together as one species the larger groups that share traits inherited from a more ancient common ancestor. For example, among living organisms, all birds share the trait of having feathers, but clearly the trait of *has feathers* is not useful in defining the breakpoints among individual bird species. More problematically, however, any bird populations that have been geographically isolated—especially small populations—are likely to develop some distinctive traits fairly quickly. A strict application of this species concept in birds would result in the recognition of far more than 10,000 living bird species, because many geographic populations of the same biological species have subtle but distinctive shared traits that could be used to classify them as separate phylogenetic species. Despite these challenges, the phylogenetic species concept has a solid basis in evolutionary theory, and it has many proponents among professional ornithologists.

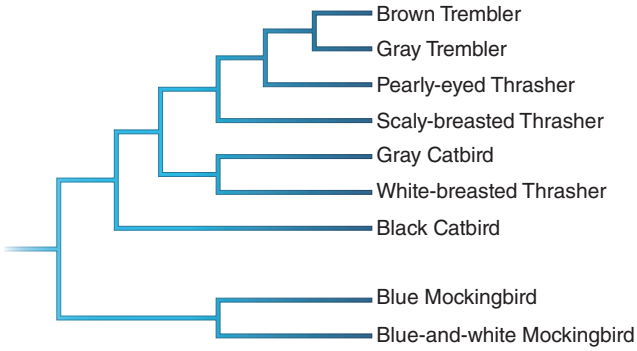


Fig. 2.08 Evolutionary trees. Also called phylogenies, these trees represent hypotheses about the historical relationships among past and present birds. Based on evidence from DNA, this phylogeny depicts the evolutionary relationships among nine of the many living species in the family Mimidae. Branches convey levels of relatedness within a clade: for example, the Brown (*Cinclocerthia ruficauda*) and the Gray (*Cinclocerthia gutturalis*) Tremblers are sister taxa, followed by the Pearly-eyed Thrasher (*Margarops fuscatus*), which is equally related to them both. (From Lovette et al. 2012. Reproduced with permission from Elsevier.)

2.2 Phylogenetics: the evolutionary tree of birds

All birds, living or extinct, are connected in a master evolutionary tree—a phylogeny—that reaches back to their common ancestor, which (as described later in this chapter) was probably a theropod dinosaur. The avian phylogeny therefore is the result of many millions of years of evolutionary change, speciation, and extinction. It has thousands of connected branches, some of which lead ultimately to the species that exist today, and others that terminated in the past in lineages that have gone extinct without leaving any descendants. A primary goal of avian phylogenetics is to reconstruct this evolutionary history to produce a complete picture of how and when bird diversity originated.

2.2.1 What is a phylogeny?

At one level, a phylogeny is a diagram that represents the history of evolutionary connectedness among a group of organisms. For example, Fig. 2.08 shows a phylogeny for a group of nine species within the avian mockingbird and thrasher family, Mimidae. Although there are many other living species in this family, genetic and other evidence demonstrate that these nine species are each other's closest living relatives, thereby forming a monophyletic group, or clade.

Phylogenies are depictions of evolutionary connections. Although any one phylogeny can be drawn in many alternative orientations, phylogenies typically comprise lines

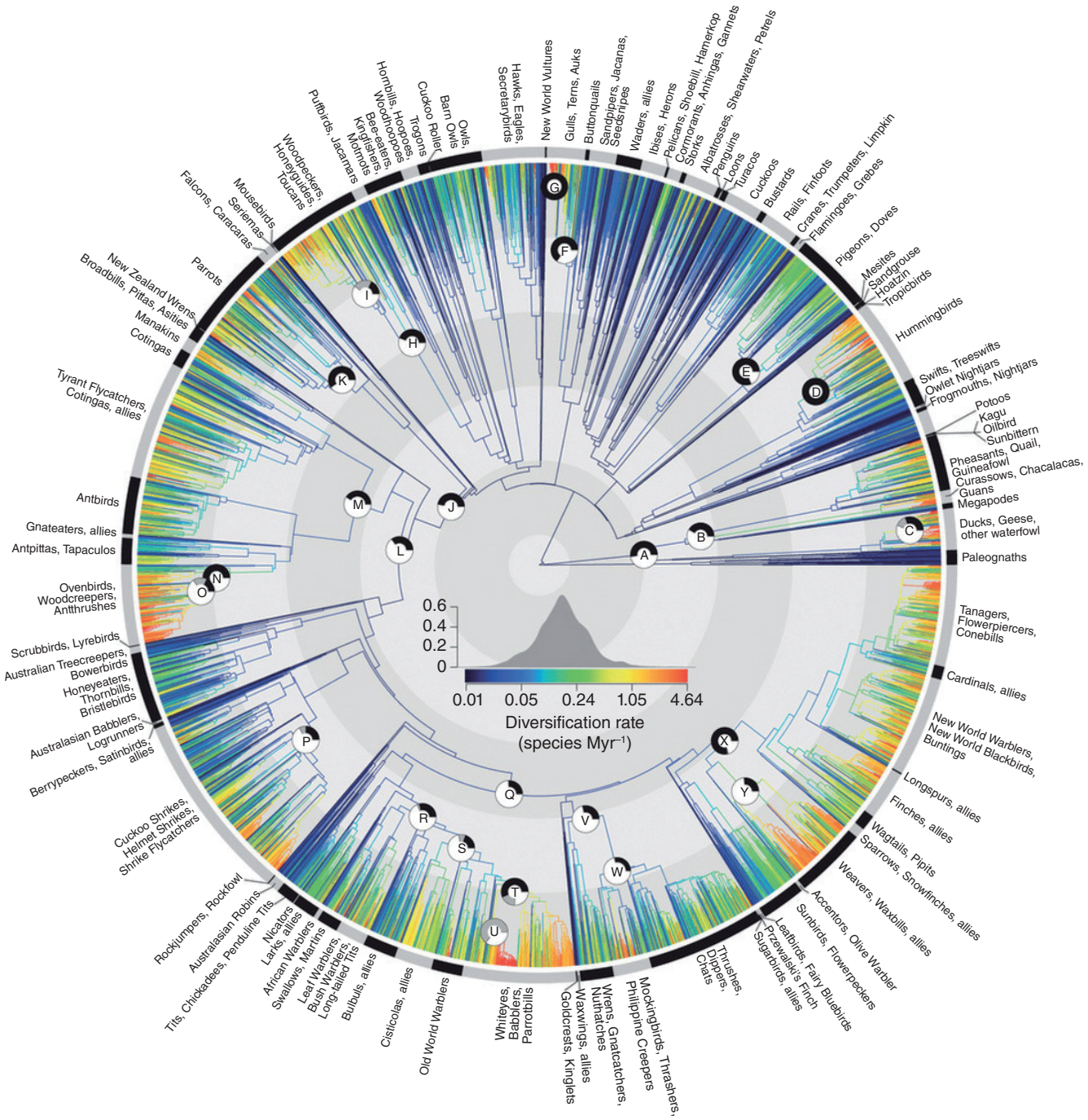


Fig. 2.09 Diversification of all modern bird groups. This circular evolutionary "tree" tracks rates of speciation across space and time, and is one of the first to include all recognized species of extant birds. Reddish branches indicate groups with particularly high speciation rates. (From Jetz et al. 2012. Reproduced with permission from Macmillan Publishers Ltd.)

called **branches** that join together at points termed **nodes**. The branch lines represent evolutionary lineages that have persisted through a period of time, and nodes represent points in the past when one ancestral lineage split into two or more descendant lineages. Though there are phylogenies that include nearly every living species of bird (Jetz et al. 2012) (Fig. 2.09), most phylogenies of birds show the

Branches: the lines on a phylogeny that trace the pathway of evolutionary lineages through time.

Nodes: the points on a phylogeny where branches separate, usually representing points where an ancestral lineage splits into two or more descendant lineages.

relationships only of a certain group—the species within a particular genus, the families within an order, and so on. For example, the phylogeny in Fig. 2.08 shows only the connections between a group of living species; although there are likely to have been additional species in this clade that are extinct and unknown to us, they cannot be shown in the phylogeny. The phylogeny's branches connect bird species and illustrate their level of evolutionary relatedness, as in the tree in Fig. 2.08 where the Gray Catbird (*Dumetella carolinensis*) is most closely related to the White-breasted Thrasher (*Ramphocinclus brachyurus*). In that tree, these species therefore represent **sister taxa**, a pair of species with no closer relatives.

2.2.2 Phylogenetic data and techniques

Historically, early experts on avian relationships drew phylogenies based on their general perceptions of how bird groups were related. In modern studies, however, avian phylogenies are based on careful analyses of specific characters that are shared or variable among groups. Many kinds of traits can serve as useful characters, including the presence of a particular patch of plumage, a distinctive behavior, or a DNA variant at a particular location in the genome. Before genetic technologies became available, all avian systematists studied morphological **characters**, and much of our understanding of avian relationships derives from their early insights. Today, systematists who study living groups of birds most often use genetic characters because genomes of different birds vary at millions of points in their DNA sequences, and these differences can be used to infer their relationships. Despite science fiction movies that show scientists working with ancient dinosaur DNA, most genetic characters cannot be recovered from fossils, because DNA molecules degrade over time. The oldest bird DNA successfully analyzed thus far is less than 20,000 years old and comes from the bones or eggshells of extinct moas from New Zealand (Box 2.04). Therefore, avian systematists who study fossil birds still most commonly analyze and compare morphological characters measured from preserved bones or feathers.

Technological advances make it increasingly easy to generate and analyze large datasets of genetic characters from samples taken from extant birds (Box 2.05). Most research museums maintain collections of frozen tissues taken when specimens are collected, and these well-preserved tissues are excellent starting material for genetic studies. Newer laboratory techniques also make it possible to perform genetic studies with older museum materials, such as bits of dried tissue snipped from traditional museum skin specimens.

The genetic characters targeted in these phylogenetic studies have changed as laboratory methods have grown more powerful. The first large-scale phylogenetic studies of avian genetic characters were conducted in the 1960s through the early 1980s and were based on differences in egg-white proteins, as those proteins were relatively easy to isolate from recently laid eggs. These protein investigations were followed in the 1980s by an important series of studies that used a technique called DNA-DNA hybridization, influentially synthesized by ornithologists Charles Sibley and Jon Ahlquist (1990). The phylogenies generated using this method were far more comprehensive than any earlier genetic surveys of birds, and led to many discoveries about previously unsuspected avian relationships; for example, the DNA-DNA hybridization work showed for the first time that the Old World starlings are most closely related to the New World mockingbirds and thrashers. Today, however, the technical limitations of the DNA-DNA hybridization method along with methodological controversies about its application to birds have rendered it obsolete.

In the late 1980s it became possible to determine the precise sequence of DNA building blocks (the four **nucleotides** abbreviated as A, G, C, and T) within a region of DNA (Box 2.06). Many studies of avian phylogenetics conducted since then have been based on relatively short **DNA sequences** from the genes found in **mitochondrial DNA**, a part of the genome passed from a mother bird to her offspring. In the 2000s, many researchers started to include DNA sequences from other regions of the avian genome into their analyses to create evermore robust phylogenetic studies. For example, using DNA characters, one research group produced an influential phylogeny for all major groups of songbirds (Passeriformes) (Barker et al. 2004). Other researchers studying the deeper relationships among avian families and orders similarly generated a tree for 169

Sister taxa: two groups (often but not always two species) that are each other's closest evolutionary relatives.

Character: in avian systematics, any heritable trait that can be compared among different groups of birds.

Nucleotides: the basic molecular building blocks of DNA and RNA.

DNA sequence: the precise order of the nucleotides in a region of the DNA molecule.

Mitochondrial DNA (or **mtDNA**)**:** in birds, the DNA that is found not in the cell nucleus, but rather in the cell's mitochondria, a structure involved in generating energy within the cell. Mitochondrial DNA is passed down only from mother birds to their offspring.

Box 2.04 Ancient DNA and the extinct moas of New Zealand

Approximately 700 years ago, the first humans who traveled to the islands now known as New Zealand encountered a world where birds were the dominant animals. They would have seen an eagle far larger than any known today, as well as its giant prey: the moas, a group of giant birds related to kiwis, ostriches, emus, cassowaries, and the other ratites. Moas had never experienced hunting by a terrestrial predator, and they were highly vulnerable to human exploitation; the entire moa family went extinct shortly after humans colonized New Zealand. Today, physical evidence of moas comes from fragmentary remains found in fossil deposits or old human campsites, and from caves and gullies that have preserved desiccated moa feathers and body parts. Fortunately, these remains often hold moa DNA, which researchers can use to reconstruct the diversity and relationships of this extinct family. DNA from fossil specimens is fragmented and degraded, so laboratory work on ancient DNA must be done very carefully in specially designed facilities to reduce the risk of contamination by modern DNA from bacteria, the researchers themselves, or the lab in which the study is performed.

Using these techniques, researchers have successfully sequenced DNA from hundreds of moa specimens, including bones, eggshells, and skin fragments. Their studies show that at the time of human discovery of New Zealand, there were between 9 and 11 moa species (Fig. 2.B4.01). These species can be clustered into three groups based on their phylogenetic relationships (Baker et al. 2005), and all probably shared a common ancestor about 6 million years ago (Bunce et al. 2009). By using these DNA samples to determine the sex of each of the moas that left these fossil remains, researchers further discovered that some moa species had extreme sexual size dimorphism, with adult females weighing more than twice as much as adult males. Based on this extreme size difference, many moa specialists had previously believed that the large and small moas represented different species (Bunce et al. 2003). Distinctive male moa DNA found on the outer parts of preserved eggshells even suggests that the smaller male moas incubated the eggs, as do males of various other ratites like ostriches (Huynen et al. 2010).

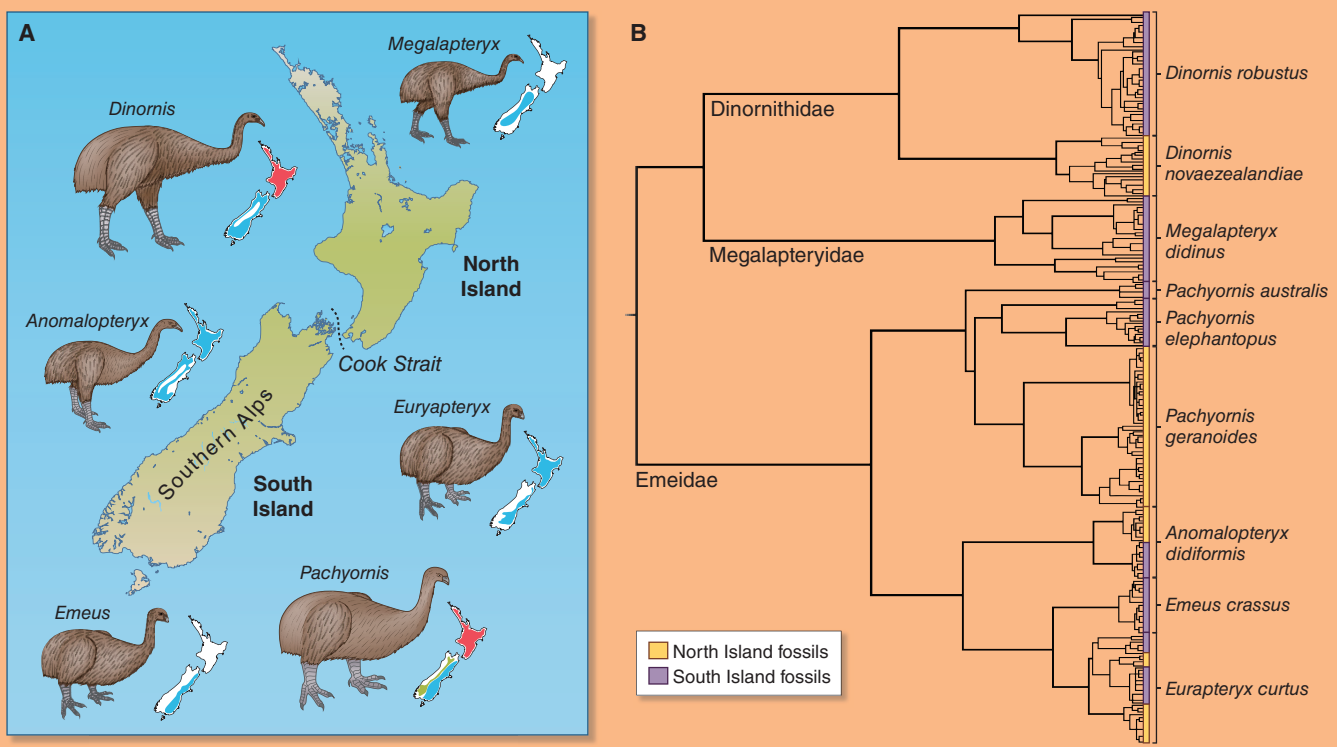


Fig. 2.B4.01 Moa distribution and phylogenetics. (A) The distribution of extinct moa genera on the islands of New Zealand. Species' ranges are depicted on each genus map. If a genus includes more than one species, their distributions are distinguished with different colors. (B) Reconstruction of phylogenetic relationships based on DNA recovered from moa fossil remains. (From Bunce et al. 2009. Reproduced with permission from National Academy of Sciences, USA.)

Box 2.05 The theory behind evolutionary trees

The study of bird relationships has benefited greatly from advances in the way phylogenies are reconstructed from data on morphology, DNA, or other traits. The single greatest innovation was the formalization in the 1960s of an approach termed "cladistics." In an evolutionary tree based on a cladistic analysis, a trait shared by two or more avian lineages provides evidence to group them together, under the assumption that such shared traits are present in those lineages because they were also present in their common ancestor. Only traits that have changed at some point and then been passed down—derived traits—are useful evidence in this cladistic framework, because these "shared derived traits" identify subgroups within the hierarchical nodes of the tree. Cladistic methods had a transformative role because they based phylogenetic analyses on a sound and logical theoretical footing.

Today, many avian phylogenies are made instead using a statistical approach called "maximum likelihood," in which the analysis evaluates the fit between the characters that vary among the species in the phylogeny (nowadays, these characters are usually but not always based on DNA variation), a model of how those characters change over time, and the resulting evolutionary tree. These and related analyses are particularly useful for studies that involve huge datasets that must be analyzed on advanced computer systems.

An ongoing challenge in DNA-based phylogeny studies is that the correct phylogeny based on a particular subset of the genome—termed a "gene tree"—can differ somewhat from the average phylogeny of the entire genome—the "species tree." This discordance can arise from several sources. One is when a part of the genome is inherited differently from the rest; for example, the mitochondrial DNA in birds and most other organisms is passed down only from a mother to her offspring, so mitochondrial DNA gene trees do not reflect any gene flow caused by males dispersing from one area to another. Fortunately, now it is possible to generate thousands of independent gene trees as part of a phylogenetic study and to use statistical approaches to find the overall species tree that is best supported by this abundance of information.

Box 2.06 DNA barcoding of birds

Studies of DNA variation have become central to our modern understanding of bird diversity, as genetic similarities and differences can be used to reconstruct how various lineages of birds are related to one another. Different regions of the avian genome are better suited to different kinds of phylogenetic analysis. At the level of populations and species, genes that evolve quickly are particularly useful, because they are more likely to have evolved distinctive differences even during relative short and recent periods of evolutionary separation.

Genes from the mitochondrial genome have long been the workhorse for studies of recent divergences in birds. An international consortium of scientists is attempting to assemble a database of mitochondrial DNA sequences—which they term "DNA barcodes"—for all bird species (Lijtmaer et al. 2011). By gathering together sequences of the same gene from as many bird species as possible, this DNA barcode database makes it possible to compare and match any new sequence to the archive of known sequences. As demonstrated by hundreds of studies from long before the term "DNA barcode" was coined, mitochondrial DNA is a good genetic starting point for discovering genetic breakpoints within individual species and for assembling phylogenies of closely related species. Hypotheses based on mitochondrial DNA then can be explored in depth with more powerful sources of data from throughout the genome.

DNA barcodes are particularly useful in forensics to identify the source of an unknown avian sample. For example, DNA barcodes have been used to identify the mangled remains of birds that have passed through aircraft engines, as well as the sources of illegally collected live birds or feathers. Avian DNA barcodes recovered from bird blood in the stomachs of midges, mosquitoes, and blackflies have even been used to discover which bird species these insects feed upon under natural conditions.

avian species based on sequences from 19 different genes (Fig. 2.10). The resulting phylogenetic hypothesis generated by this international team was broadly considered to be that decade's most important advance in avian systematics (Hackett et al. 2008). Together with numerous phylogenetic studies of smaller groups of living birds, these new and expansive perspectives on avian diversity inspired ornithologists to address broad-scale questions such as the origins of avian behaviors, and the times and places at which avian diversification has been unusually rapid.

DNA sequencing also has made it possible to determine the affinities of unusual bird species, and has revealed many

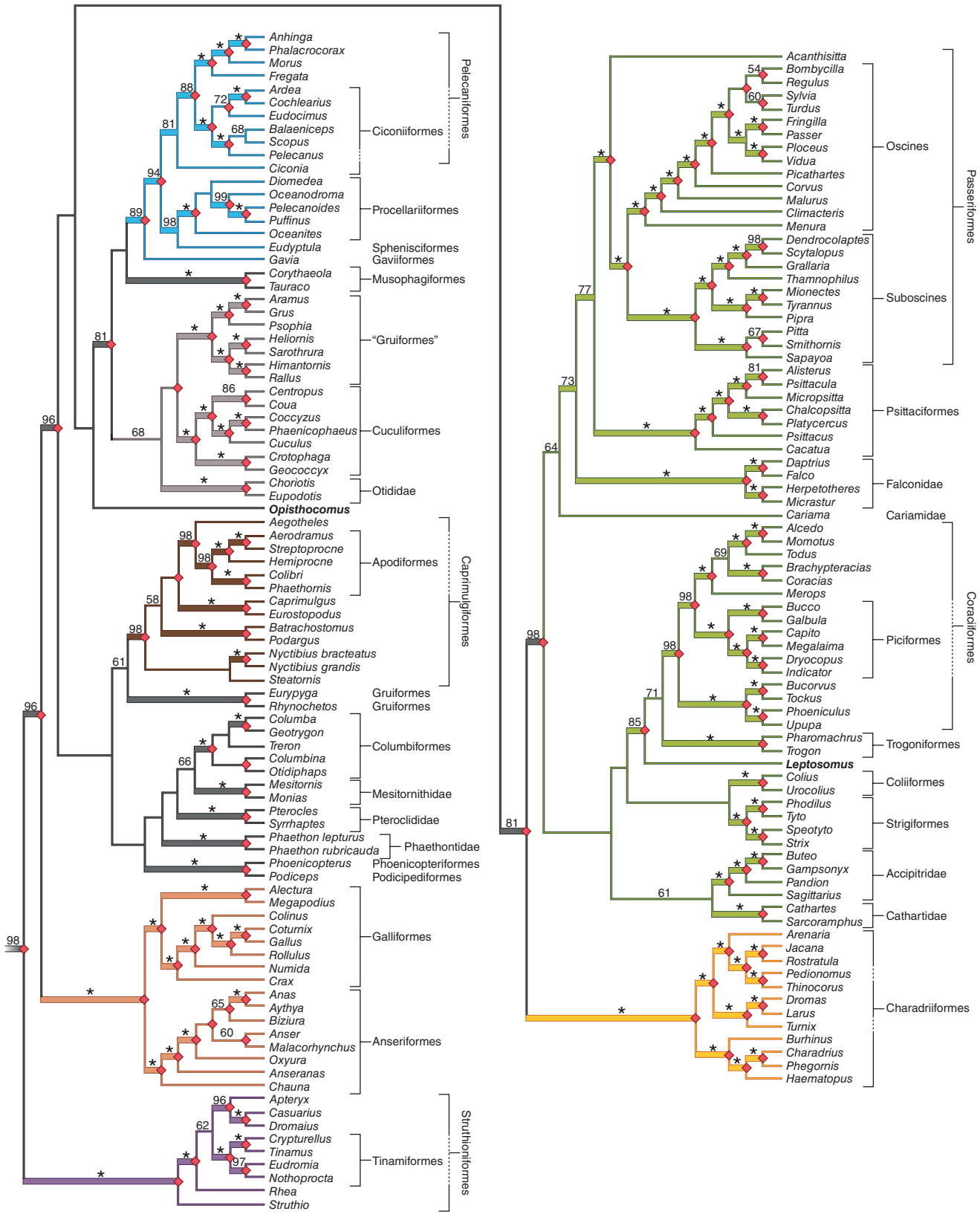


Fig. 2.10 Phylogenies based on DNA. One of the first avian evolutionary trees based on large amounts of DNA sequence data, this phylogeny reconstructs the relationships among 169 species from most major groups of birds using sequences from 19 different genes. (From Hackett et al. 2008. Reproduced with permission from AAAS.)

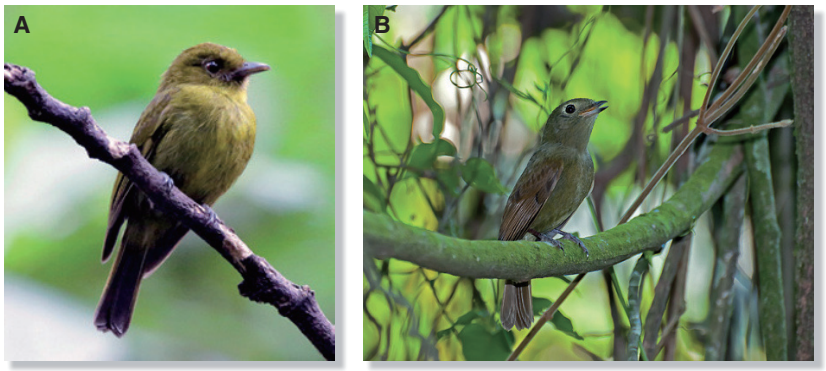


Fig. 2.11 Phylogenetics can reveal surprising relationships. For years, (A) the Sapayoa (*Sapayoa aenigma*) was assumed to be closely related to similar-looking birds that are also found in the neotropics such as (B) the Greenish Schiffornis (*Schiffornis virescens*), until genetic evidence revealed that the Sapayoa is actually more closely related to Asian broadbills. (Photographs by: A, Nicholas Athanas; B, Dario Sanches from São Paulo, Brazil (FLAUTIM (*Schiffornis virescens*). CC-BY-SA 2.0. http://creativecommons.org/licenses/by-sa/2.0.)



Fig. 2.12 Morphology can be misleading. Many bird species were originally named according to morphological similarity to other known species. For example, Hume's Ground-Jay (*Pseudopodoces humilis*) is not actually a jay, but rather an unusual member of the chickadee and tit family. It has since been renamed the Ground Tit. (Photograph by Fung Wai Choy.)

surprises involving birds with previously uncertain relationships. For example, the Sapayoa (*Sapayoa aenigma*) is a drab songbird that nests along lowland streams in Panama, Colombia, and Ecuador (Fig. 2.11A). Based on its general resemblance to other groups of birds found in the neotropics (Fig. 2.11B), the Sapayoa was often thought to be an aberrant manakin or flycatcher. It was therefore notable and surprising when phylogenies based on genetic data showed conclusively that the Sapayoa is instead the sole New World representative of the broadbill radiation, an ancient group of songbirds that is otherwise restricted to Africa and Australasia (Fjeldså et al. 2003; Chesser 2004; Moyle et al. 2006). Similarly, a bird of the high Tibetan Plateau previously called Hume's Ground-Jay (*Pseudopodoces humilis*) (Fig. 2.12) was long considered an unusual member of the crow and jay family, as reflected by its common name. When DNA-based phylogenies showed that really it is an atypical member of the chickadee and tit family, it was accordingly renamed the Ground Tit (James et al. 2003). In a final example, several birds from South Asia—the White-bellied Erpornis (*Erpornis zantholeuca*) and the shrike-babblers (genus *Pteruthius*)—were long thought to be part of the babblers, but DNA-based phylogenies determined them to be the only Old World members of the vireo family (Jønsson and Fjeldså 2006; Reddy and Cracraft 2007), revealing a previously unsuspected connection between the avifaunas of Asia and North America.

This process of phylogenetic discovery continues, and future studies undoubtedly will bolster many of the current phylogenetic hypotheses about avian relationships while refuting others and making new discoveries. We are moving into an era of expanding phylogenetic scope, in which reconstructions of the relationships among living birds will be based on comparisons of their entire genomes and in which giant phylogenies will be assembled that include thousands of bird species (Hugall and Stuart-Fox 2012). An ultimate goal of these advances in analytical methods and resources is to create well-supported phylogenies that include all living birds.

2.2.3 Genetic variation within bird species

In addition to phylogenies that illuminate the connections between species and higher taxa of birds, more subtle genetic variation also exists among populations of the same bird species. Bird populations start to become phylogenetically distinct when they are able to diverge genetically from one another, which most often happens when the populations are separated from one another geographically and few or no individuals move between them, allowing each population to evolve its own set of genetic differences. This process of divergence occurs more readily if the populations are small, and it becomes more and more pronounced when the populations have been geographically isolated for longer periods; ultimately, this same process can lead to full speciation of the two populations. Therefore, recently separated populations are likely to be very similar to one another genetically, whereas long separated populations are likely to show more differences in DNA characters and other traits.



Fig. 2.13 Geography and gene flow. Colored sampling points from a genetic study of Arctic Warblers (*Phylloscopus borealis*) show how populations spanning from northern Europe to Alaska are closely related (blue points), whereas those in the remote Kamchatka region of Russia (yellow points) and more southerly islands of Japan (red points) are each genetically distinct. (From Saitoh et al. 2010. CC-BY-2.0. http://creativecommons.org/licenses/by/2.0.)

When many birds move between two such populations, the high level of gene flow tends to mix the populations genetically, thereby slowing their genetic divergence. For this reason, bird species that undertake movements such as long-distance migration tend to be genetically similar across broad distances. For example, migratory populations of Yellow Warblers (*Setophaga petechia*) sampled from across much of North America are very similar to one another genetically, whereas non-migratory populations of this same species on different tropical islands often are genetically distinct from each other (Boulet and Gibbs 2006; Chaves et al. 2012). A similar pattern is found in the Arctic Warbler (*Phylloscopus borealis*), in which populations spanning northern Europe to Alaska are quite similar, but populations from the remote Kamchatka Peninsula in Russia and the islands of Japan are each genetically distinct (Saitoh et al. 2010) (Fig. 2.13).

Variation among bird populations is particularly obvious in bird species with wide but patchy distributions, because their disjunct populations often have evolved independently for a period of time. **Range disjunctions** are especially prevalent in birds that occur on islands or in birds restricted to habitats that act like islands within a matrix of other habitat types. For example, birds that require high-elevation habitats may be restricted to isolated patches on different mountains, a pattern that occurs in many parts of the world and in many groups of birds. The White-starred Robin (*Pogonocichla stellata*) of central and eastern Africa follows this pattern, breeding only in montane regions above 1500 meters (Fig. 2.14). Populations of this species from different mountain ranges show plumage differences that have led them to be classified as different subspecies, and genetic surveys have confirmed that many of these populations are genetically distinct, although not at the level that that would lead most ornithologists to classify them as separate species (Bowie et al. 2006).

Studies of finer scale geographic variations that use phylogenetic methods to understand past connections within species, either among individuals or populations, fall within the discipline of **phylogeography**. Avian phylogeographers explore relationships among bird populations and test hypotheses about the processes that lead them to diverge. The most powerful such analyses compare phylogeographic patterns across many bird species. For example, Burney and Brumfield (2009) looked at genetic variation within 40 South American bird species, comparing populations from either side of a major barrier such as the Andes Mountains or a wide river (Fig. 2.15). They found that bird species in the forest canopy consistently had fewer genetic differences among their separated populations than did bird species that use lower parts of the forest understory. This finding links a phylogeographic pattern—lower differentiation in canopy birds—with the ecological process that likely generates it: the higher dispersal ability of birds that inhabit

Range disjunction: a pattern of geographic distribution in which two or more occupied areas are separated by substantial intervening areas where the species is not found.

Phylogeography: the scientific study of the evolutionary relationships of populations and species across space, usually as inferred from genetic information.

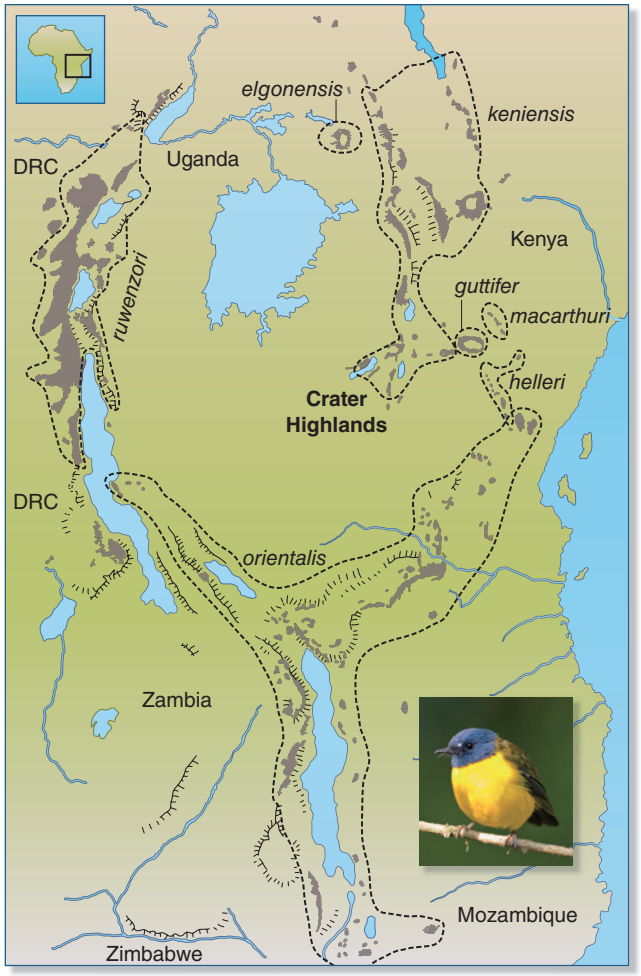


Fig. 2.14 Range disjunctions and genetic divergence. Species with fragmented ranges often show genetic variation among their constituent populations. For example, the White-starred Robin (*Pogonocichla stellata*) breeds only in montane regions above 1500 meters (depicted as the solid gray areas). Populations that occupy different mountaintops have become genetically distinct (dotted lines) over time. (From Bowie et al. 2006. Reproduced with permission from Elsevier. Photograph by Ronan Donovan, www.ronandonovan.com.)

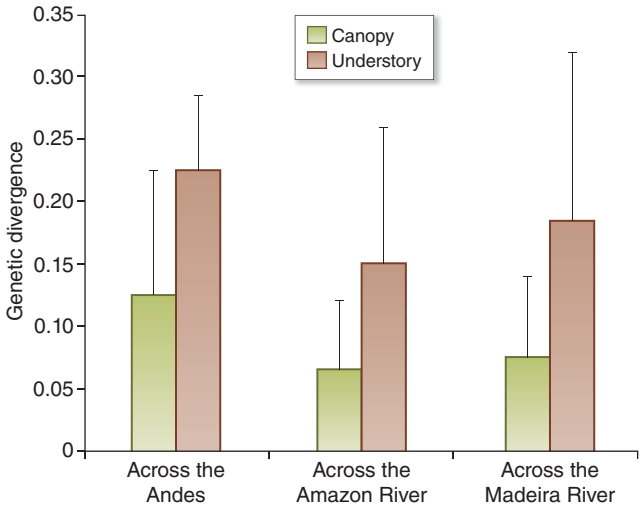


Fig. 2.15 Dispersal ability affects genetic differentiation. In the neotropics, canopy species tend to disperse more readily than birds of the forest understory and thus canopy species generally maintain higher levels of gene flow across potential barriers. For example, understory birds on each side of three major barriers (the Andes Mountains, the Amazon River, and the Madeira River) tend to have higher genetic differentiation than do canopy species. (Adapted from Burney and Brumfield 2009.)

the more open parts of the environment and that are adapted to moving long distances in search of fruit or other widely spaced resources.

2.3 Global patterns of avian diversity

Some of the variation in the diversity of bird communities arises from ecological forces like the availability of niches, competition among species, and the presence or absence of particular resources (Chapter 14), but other patterns occur on a larger biogeographic scale and allow us to make several concrete generalizations about bird diversity worldwide.

First, all else being equal, bird diversity increases with area. As summarized in more detail in Chapter 14, there are multiple reasons for this nearly universal pattern. Larger areas within a region are likely to contain more habitat types, which in turn can host a larger variety of bird species. Larger areas are better targets of colonization, so that bird diversity builds up over time. Larger areas generally support more individuals of each species, thus lowering the risk of local extinction. Finally, large areas can support populations of rare or wide-ranging species that are unable to persist in smaller regions.

Second, bird diversity is greatest near the equator and lowest at the earth's poles, a phenomenon termed the **latitudinal diversity gradient.** This pattern is one of the most conspicuous in avian biogeography, but it has no single cause; rather, it arises from a combination of past and

Latitudinal diversity gradient: the general rule that in most groups of organisms, species diversity is greatest in the tropics and steadily decreases towards the earth's polar regions.

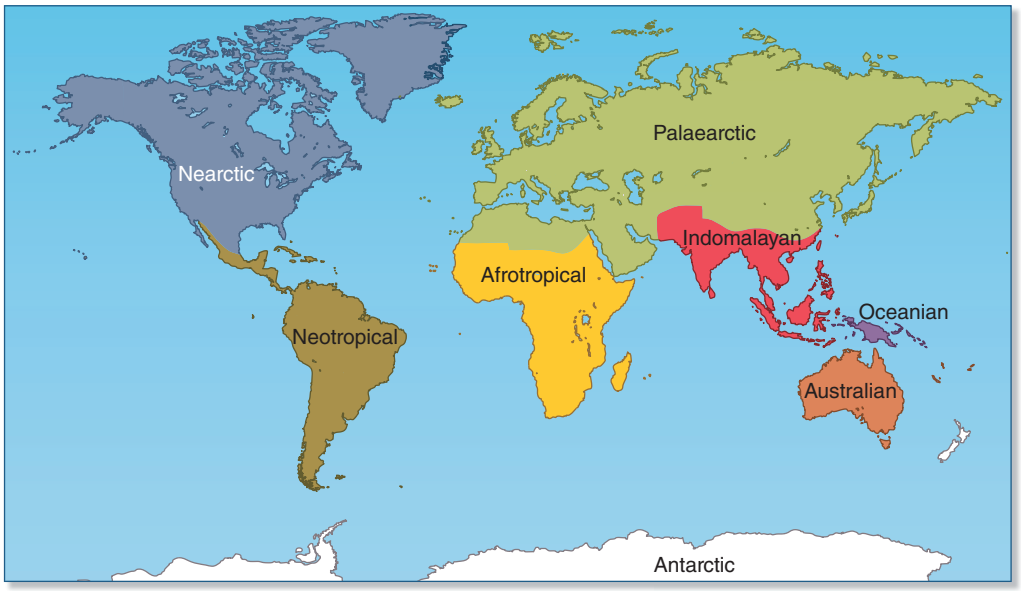


Fig. 2.16 Biogeographic realms. Avian biogeographers traditionally subdivide the world into eight primary realms based on the distributions of birds endemic to each region. (© Cornell Lab of Ornithology.)

present forces. On an evolutionary scale, the tropics are more diverse because they have a higher overall ratio of speciation to extinction than areas at higher latitudes, so that the number of tropical species increases over time. At an ecological scale, the tropics are more diverse because a given area of habitat can support more bird species, probably because tropical habitats typically have a higher diversity of plants, insects, and other resources important to birds. Furthermore, as discussed in Chapter 14, there is more turnover in bird species across tropical habitats, a pattern that boosts diversity when it is measured regionally rather than at a single point in space.

Third, islands support fewer breeding bird species than continental areas of the same size. This phenomenon is a manifestation of the same processes that cause bird diversity to scale with area more generally. Further, not all types of birds can colonize islands successfully, and extinction rates on islands are higher because their isolated populations are not as readily replenished by dispersal from other populations (Chapter 13).

2.3.1 Birds and biogeographical realms

Avian biogeographers have traditionally divided the world into eight primary **biogeographic realms** based on bird distributions (Fig. 2.16). Although similar systems have been developed for other organisms, this type of classification was first suggested in the 1850s by the British ornithologist Philip Sclater, the leading expert of his time on songbird classification and diversity. As Sclater and his successors recognized, each biogeographic realm has a distinctive avifauna with a unique mix of avian families and orders.

Not surprisingly, the boundaries of each realm coincide with general barriers to the dispersal of birds. Many families of birds are found in only one of the eight biogeographic realms and a visit to a new realm often provides the first chance for a birder or ornithologist to see entirely new branches of the avian evolutionary tree. At the same time, many groups of birds that are good at dispersing are found in two or more biogeographic realms. The realm system is therefore more relevant for landbirds, because waterbirds and seabirds tend to disperse more easily across the water barriers that often separate different realms.

The most famous barrier between biogeographic realms occurs at the shared boundary of the Australasian and Indomalayan realms (Fig. 2.17), where there is a sudden change in faunas at the junction known as "Wallace's Line." Alfred Russel Wallace, the biologist who first proposed it, was a founding figure in biogeography. Wallace's Line runs along a deep sea channel that separates the island of Sulawesi from Borneo and the island of Lombok from Bali. The channel is so deep that, even during past periods of low sea levels, there was no land bridge connecting these nearby islands.

Biogeographic realms: a traditional classification of the earth's terrestrial regions that groups them by their broadly similar faunas, floras, and evolutionary histories.

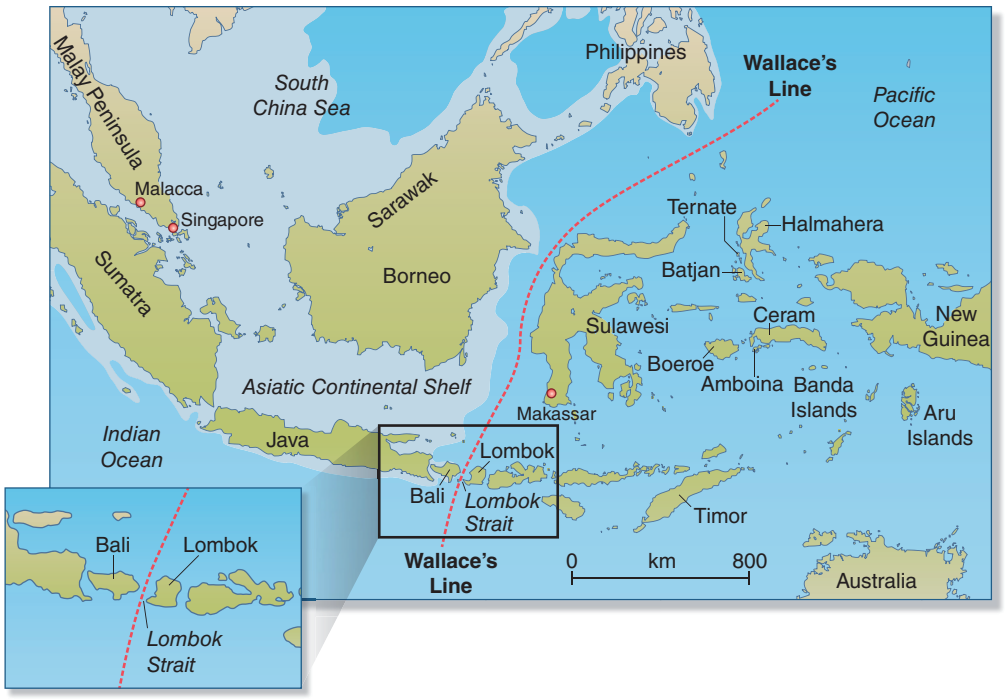


Fig. 2.17 Wallace's Line. The most famous barrier to dispersal between distinct biogeographic realms, this line occurs at the shared boundary of the Australasian and Indomalayan tectonic plates. (Map by Leanne Olds, in *Into the Jungle* by Sean Carroll (2008), courtesy of the author.)

Many families of birds found to the north have distributions that stop at Wallace's Line, whereas bowerbirds (Ptilonorhynchidae), owlet-nightjars (Aegothelidae), birds of paradise (Paradisaeidae), and others are found only to the south.

Past isolation has resulted in some realms having unique families and orders. However, a number of broadly dispersing bird lineages cross between realm boundaries and are represented in multiple realms. For example, the nearctic and neotropical realms have exchanged many birds, and today there is no single, clear breakpoint to indicate where their bird faunas diversified. Topographically, one might expect this breakpoint to occur at the Isthmus of Panama, a land bridge connecting North and South America that emerged from the sea about 3 million years ago. The formation of the Panama land bridge had a profound effect on non-flying animals such as most mammals, because it allowed the previously isolated faunas to mix rapidly, a phenomenon known as the **Great American Interchange**. Genetic studies, however, have shown that its effect on birds was more varied: members of avian groups that disperse easily over water had moved between these continents many times previously and were relatively unaffected by the advent of the land bridge, but the new dispersal corridor created opportunities for birds such as antbirds and woodcreepers that do not normally disperse across water (Weir et al. 2009).

Great American Interchange: the exchange of animals that commenced about 3 million years ago when a land bridge first connected the previously isolated continents of North and South America.

2.3.2 Avian distributions and their limits

No bird species can be considered to have a truly worldwide distribution since no species is found on every continent. The Peregrine Falcon (*Falco peregrinus*), which is found on all continents except Antarctica, has the broadest natural breeding distribution of any landbird. Runners-up include the Barn Owl (*Tyto alba*), which is found on five of the seven continents, and the Barn Swallow (*Hirundo rustica*), which breeds on four, and visits two more during other parts of the year. Among waterbirds, the Wilson's Storm-Petrel (*Oceanites oceanicus*) (Fig. 2.18A), Arctic Tern (*Sterna paradisaea*) (Fig. 2.18B), and Sooty Shearwater (*Aedenna grisea*) are among the most wide-ranging species; all have annual migration cycles that span most of the world's five major oceans.

It can be surprisingly difficult to define the precise geographic range of a particular bird species. The easiest

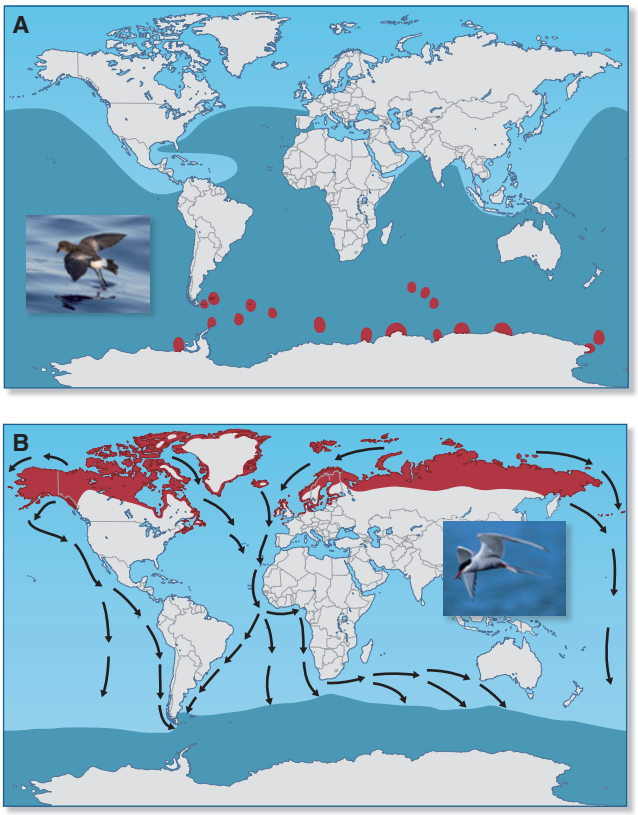


Fig. 2.18 Seabirds with worldwide distributions. Some pelagic seabirds spend much of their lives away from land, such as (A) Wilson's Storm-Petrel (*Oceanites oceanicus*) and (B) the Arctic Tern (*Sterna paradisaea*). Their expansive ranges cover most of the world's oceans. Wintering areas are shown here in darker blue; breeding areas are depicted in red. (A, Shyamal, https://en.wikipedia.org/wiki/File:OceanitesDistribution.svg. CC0 1.0; photograph by Olli Tenovuo. B, Andreas Trepte, http://en.wikipedia.org/wiki/File:Sterna_paradisaea_distr_mig.png. CC-BY-SA 2.5; photograph by Arto Hakola.)

situations occur when a bird is found exclusively on a small island or in a very specific type of habitat; in these cases, the bird's distribution corresponds directly to the area of the island or the distribution of its specialized habitat. More commonly, however, birds have complex distributions, with populations that vary in abundance in both time and space. Nomadic birds might be common in a region one year but completely absent the next. Migratory birds similarly move around during their annual cycle. Many bird species are relatively common in a core part of their breeding distribution but then become increasingly rare towards the edges of their range. Even within a region, a bird is likely to be present in certain habitats but absent from others. Distribution maps therefore are particularly sensitive to the scale at which they are drawn, as discussed in Box 2.07.

Some factors that determine the limits of a particular bird's distribution are readily apparent. Range limits often are dictated by where the species' preferred habitat occurs or by the availability of other fundamental resources such as particular foods or nesting sites. Similarly, many birds are physiologically adapted to certain climate conditions and are found only in areas with appropriate temperatures and water availability. Changes in climate therefore may cause changes in avian range limits, both over evolutionary timescales and during recorded history. One clear example comes from surveys conducted 100 years apart in the Sierra Nevada Mountains of California (USA), where changes in temperature and rainfall patterns over the course of a century are well documented. Of the 53 bird species surveyed, 48 showed range shifts that corresponded to these long-term changes in temperature and rainfall, demonstrating that the distributions of these birds are determined at least in part by these fundamental environmental attributes (Tingley et al. 2009).

In many settings, range limits can be mysterious, and it is common for a bird species to be absent from areas where it may seem well suited. In these cases, the range limits may be a legacy of the past, for example if the species has gone locally extinct or never had the opportunity to disperse into the region. Alternatively, a species might be limited by hidden environmental features, such as the presence of parasites, diseases, or predators. Or it might be generally suited to the local environment but unable to compete successfully with other species that are even better adapted to those conditions. Many birds have range limits that are dictated by several factors simultaneously. For example, studies of range limits in birds of the Himalayas have suggested that climate variation and the presence or absence of competitors all strongly influence the distribution of each individual bird species (Price et al. 2011).

2.3.3 Variation in the diversity of living birds

Bird groups demonstrate an enormous range in their levels of diversity. For example, the largest order of birds—Passeriformes—includes more than half of all living bird species, whereas several other orders that have existed for equivalent lengths of time contain only a few species. Ancient but low-diversity lineages include the strange Hoatzin (*Opisthocomus hoazin*) of South America, the only member of its order (Opisthocomiformes), and the three species of mesite from Madagascar, which together form the order Mesitornithiformes.

There are several complementary explanations for why some groups of birds are richly diverse while others have only a few species. Fossil evidence demonstrates that some groups with low diversity today were once far more widespread and numerous. For example, all six species of living mousebirds (which together form the order Coliiformes) are restricted to Africa, but the fossil record shows that

Box 2.07 Bird distributions from far and near

The geographic breeding distribution of a particular bird species often is complex, particularly when observed in fine detail. Birds that breed in colonies, such as many seabirds, may range widely when foraging or during the non-breeding season, but their breeding sites usually are highly localized. Non-colonial landbirds usually have a more even distribution across space, but even these species usually are restricted to a particular set of habitats. Indeed, no widespread bird species occurs everywhere within its range.

Classic distribution maps for birds, such as those found in many field guides, do not capture much of this heterogeneity in bird distributions. Such maps usually use shading to indicate the outline of the entire region in which a particular species might be found. Colors can be used to distinguish areas where the species is a permanent resident, migratory breeder, migrant, or non-breeding visitor. For mapmakers, the boundaries of these colored zones often are challenging to draw, because many species become rarer at the edges of their range. Deciding exactly where to place the distribution lines therefore becomes a matter of judgment, and map users need to consider their knowledge of each species' habitat use when looking for birds at a particular location.

With advanced mapmaking techniques, ornithologists can create atlases of bird distributions on a much finer scale than ever before. These approaches take advantage of huge, worldwide datasets derived from satellite observations, climate measurements, and land-use assessments. They also integrate precise information on locations where bird species are found, as recorded on museum specimens or reported by birders. The power of this approach is that it is not necessary to know every location where a bird species occurs. Instead, sophisticated mathematical models are created to determine what environmental parameters best predict these locations, and then the predictions are expanded to determine a species' entire range. Because these predictions are expressed as probabilities, it is possible to generate a probability map of each species' distribution (Fig. 2.B7.01) in which the intensity of the color on the map codes the probability that the species occurs at that point. These more detailed maps are of obvious interest to birders, but they also have great utility in any setting where fine-scale knowledge of a species' distribution is important for conservation, management, or land-use decisions.

The quality of these predictive maps is highly dependent on the quantity of bird observations that underlie them. Birders have contributed hundreds of millions of observations to this endeavor by participating in citizen science projects such as eBird (www.ebird.org), the source of the heatmaps shown here. However, many places still exist where observations are sparse, and additional observations will improve maps even for well-covered areas. Anyone with an interest in birds can make valuable contributions to our scientific knowledge by participating in this kind of citizen science project, while simultaneously improving resources for birders and aiding bird conservation.

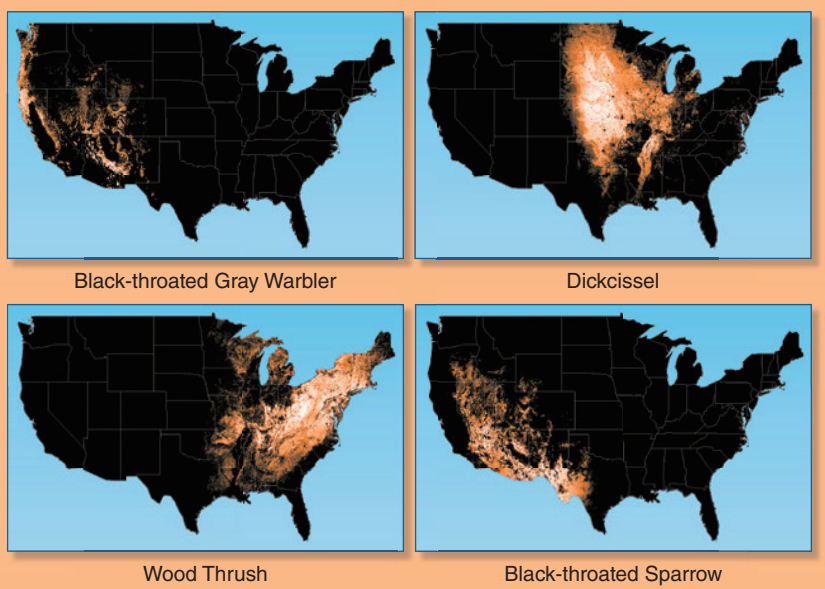


Fig. 2.B7.01 Heatmaps of bird abundance. These breeding distribution maps of four North American bird species were generated from bird counts submitted by bird watchers to the eBird website. Lighter/whiter colors indicate a greater likelihood of a particular species occurring at that location. (© Cornell Lab of Ornithology.)

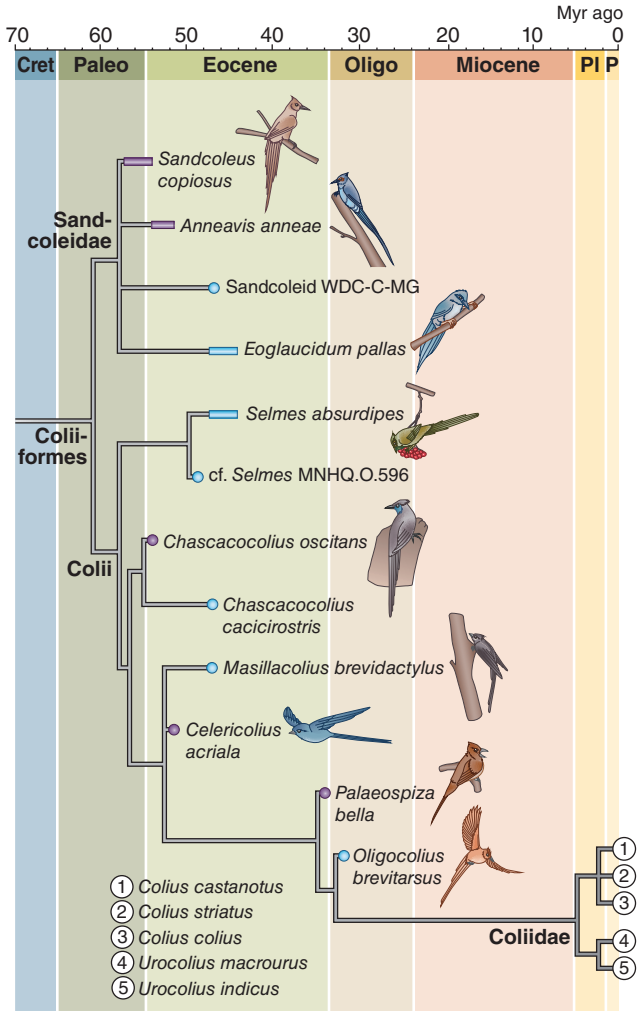


Fig. 2.19 Evolutionary expansion and contraction. Fossil evidence reveals that mousebirds were once extremely diverse with a worldwide distribution. Only five mousebird species (bottom right) occur today, all in Africa. (From Ksepka and Clarke 2010. Reproduced with permission of John Wiley and Sons.)

other lineages of mousebirds were once very diverse components of North American and European bird faunas. It is not clear why mousebirds eventually died out everywhere except Africa (Ksepka and Clarke 2010) (Fig. 2.19).

A more complete fossil record would allow us to track such changes in detail for all groups of birds and to study how their patterns of diversity have waxed and waned over time. In the absence of such a detailed record of the past, diversity can be explored by comparing groups of living birds with high and low diversity to determine whether certain aspects of their biology are associated with their differing levels of diversity. Biologists often have wondered if **key innovations** drive diversity; that is, whether the occasional evolution of an important new trait allows a lineage to diversify as new species expand into additional locations or avail themselves of new resources. Most obviously, the ability to fly almost certainly was a fundamental key innovation that contributed to the diversity and long-term success of birds in general. Potential key innovations for particular groups of birds include the ability to learn songs and other mate-attracting or territory-protecting behaviors, the presence of high levels of sexual dimorphism and sexual selection, and behaviors related to migration and dispersal ability.

Phylogenetic data can be used to compare the pace of diversification in different groups of birds. The fastest rates of generation of new species often occur when birds colonize island archipelagos, as has happened in the Galápagos finches and Hawaiian honeycreepers (Chapter 3). White-eyes in the genus *Zosterops* are another instructive example of just how fast avian diversification can occur, given favorable circumstances. These birds are distributed across much of tropical and semitropical Africa and Asia, including many islands in the Indian and Pacific Oceans. Phylogenetic studies show that birds in this family have diversified steadily over the past 10 million years, but the approximately 80 species of the *Zosterops* group result from a notable explosion of diversification during only the past 2 million years (Moyle et al. 2009). One cause of the diversification of *Zosterops* is this small bird's propensity for colonizing new and often remote locations, where small, isolated populations can diverge quickly to become new species.

Many groups of living birds share a common pattern of diversification: a pulse of early and rapid speciation followed by a decreasing pace of further speciation over time (Phillimore and Price 2008). There are at least two potential explanations for this pattern. One starts with the dispersal of the group into new and somewhat isolated areas: the colonization of new places initially provides these populations with the raw material for speciation, but eventually the newly available locations are all colonized, and the rate of speciation slows. The *Zosterops* white-eyes exemplify this pattern, since their pulse of speciation seems to have followed from one very widespread wave of dispersal 2 million years ago, after which fewer new species were generated (Fig. 2.20). These geographic opportunities and limits on speciation are most prominent in allopatric groups, in which new species form in different locations. The second possible reason involves the eventual competition among the resulting species. Particularly in settings where many existing bird species within a group occur

Key innovation: a newly evolved trait that allows a lineage to take advantage of new ecological opportunities, and which results over time in that lineage diversifying into multiple species that are specialized for those new ecological niches.

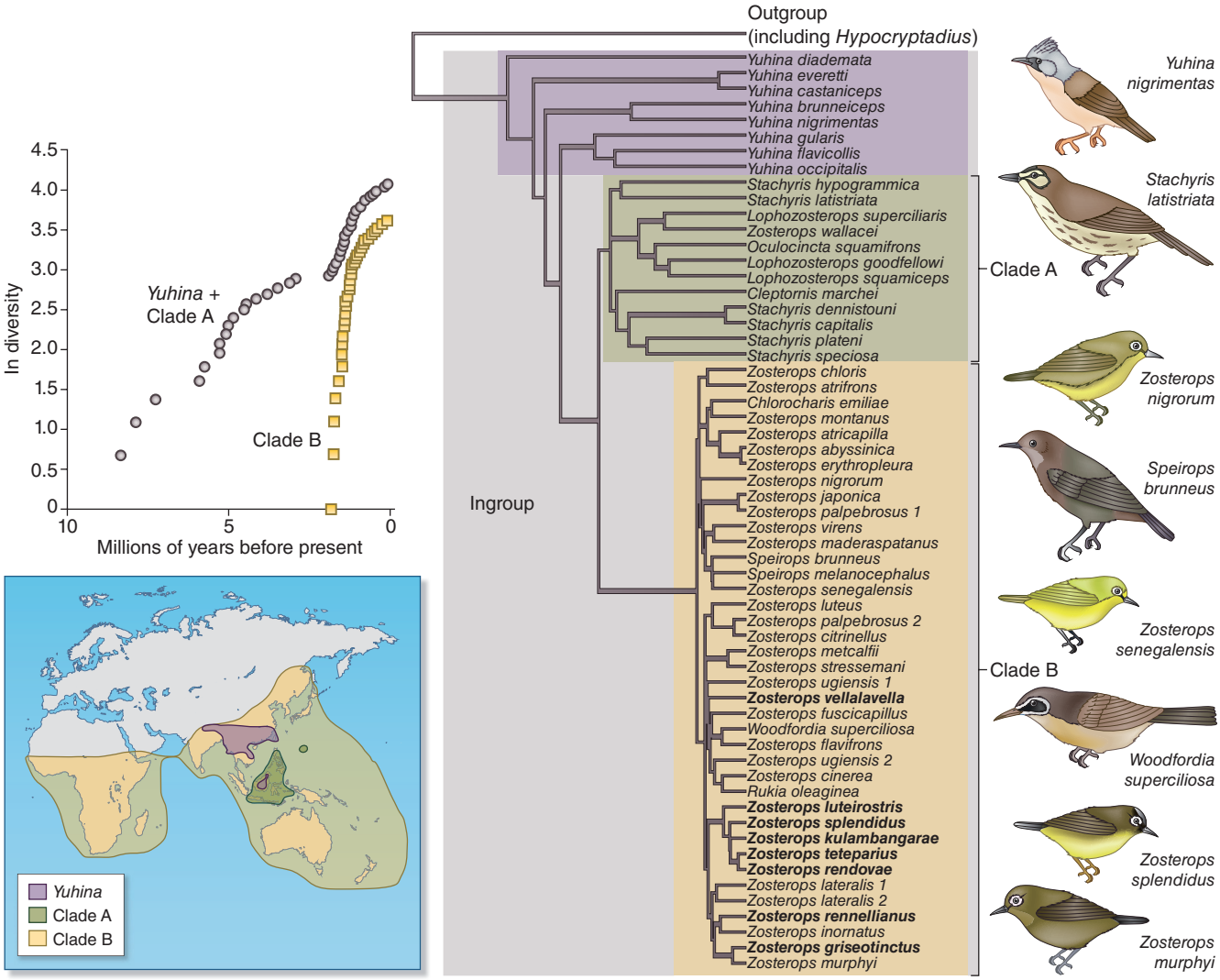


Fig. 2.20 Rapid speciation. This evolutionary tree for the genus *Zosterops* and its close relatives can be used to plot the increase of white-eye species through time. Several pulses of diversification occurred as this group spread through continental regions and colonized many isolated groups of islands. Colors on the map depict the areas inhabited by the groups with the same color codes on the evolutionary tree. (From Moyle et al. 2009. Reproduced with permission from National Academy of Sciences, USA.)

together in **sympatry**, their ecological competition with one another can place limits on their opportunities to diversify further. For example, many species in the North American wood-warbler *Setophaga* group likely diverged during past periods of geographic separation, but many breed in the same places and habitats today, and phylogenetic studies show that speciation in this group has slowed markedly since its origin (Rabosky and Lovette 2008). This pattern of diversification slowing through time suggests that there is feedback between existing diversity and the origin of new species—especially when the species that occur together are in competition with one another: the more species present, the less likely it is that new species will arise. This general phenomenon is termed **density-dependent diversification**, and its prevalence and potential causes across different groups of birds are intriguing yet not fully understood.

Sympatry: refers to organisms or groups of organisms that occur in the same place.

Density-dependent diversification: the somewhat controversial concept of a feedback loop in which speciation within a group slows down over time as the number of species increases, since the presence of existing species blocks opportunities for new species to arise.

2.4 Origin of birds

Few topics in all of ornithology have engendered more debate than the origin of birds, and those arguments continue today. Fortunately, new information from both fossils and DNA has helped to clarify the relationship between birds and other dinosaurs and defined the timescale over which birds most likely originated and diversified.

2.4.1 Birds are theropod dinosaurs

Nearly all experts now feel confident that birds are the living descendants of dinosaurs, a diverse group of reptiles that originated about 230 million years ago and which subsequently became the dominant group of land animals until the mass extinction at 66 million years ago that ended the Cretaceous Period. Earlier researchers often suggested that birds might be more closely related to various non-dinosaur groups of reptiles or that birds represent a very early offshoot of the dinosaurs. Many lines of evidence—including traits seen in fossils and shared aspects of their inferred physiology and behavior—now strongly support the idea that birds form a subgroup of the dinosaurs, one that arose fairly late from within the broader dinosaur radiation (Fig. 2.21).

Even though birds are traditionally classified into a Class Aves that is separate from the reptile Class Reptilia, in evolutionary terms dinosaurs and birds are both more correctly considered a subset of the reptiles, a group that also includes living turtles, crocodiles, snakes, and lizards. Reptile diversity was even higher in the past, because the group includes not only all dinosaurs but also a number of other long extinct lineages such as plesiosaurs, ichthyosaurs, and the flying pterosaurs. Therefore, it is technically correct to say that "birds are living dinosaurs" or that "birds are reptiles," but it is incorrect to claim—as still happens in the popular media—that these statements are scientifically controversial.

The evolutionary affinity between birds and dinosaurs was first recognized in the 1860s, when British biologist Thomas Huxley popularized the idea that the fossil *Archaeopteryx* (covered later in this chapter in more detail), which had been recently discovered, represented an evolutionary transition between these groups. In the early 1900s, however, influential scientists challenged the dinosaur–bird link, emphasizing specific differences in a small number of traits seen in fossils. Their cornerstone argument was based on the idea that dinosaurs had lost the fragile bones called clavicles, which are present in more ancient groups of reptiles and also in birds, which have fused clavicles that

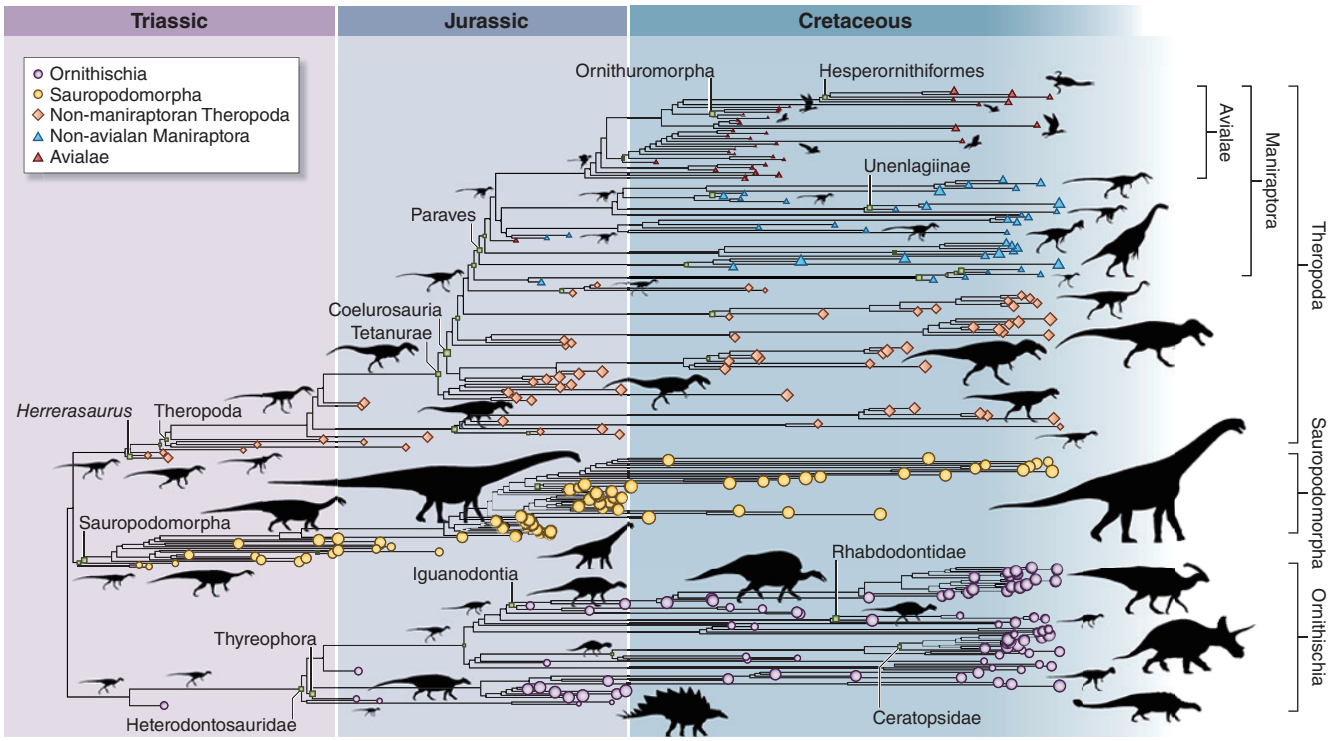


Fig. 2.21 Birds form a subgroup of dinosaurs. This phylogenetic tree shows one widely accepted view of how modern birds (top right) might have evolved from carnivorous dinosaurs. Key evidence for this version of the avian evolutionary tree comes from late Jurassic fossils unearthed in China and South America. (From Benson et al. 2014.)



Fig. 2.22 *Tyrannosaurus rex* was a theropod dinosaur. This spectacular specimen in the Field Museum (Chicago, USA) is the largest and most complete *T. rex* fossil ever found. (Photograph by Connie Ma, http://en.wikipedia.org/wiki/File:Sues_skeleton.jpg. Used under CC-BY-SA 2.0.)

form the furcula, or wishbone (Chapter 6). Under the assumption that birds would not have re-evolved a complex structure that was lost in their immediate ancestors, birds were thought to be descended from one of the older, non-dinosaur reptile groups with clavicles. For 50 years, this targeted focus on clavicles and a few other similar traits distracted researchers from the many other features shared by dinosaurs and birds.

Researchers started to adopt a more synthetic view of bird origins in the late 1960s, sparked in part by advances in the reconstruction of evolutionary relationships based on the similarities and differences between organisms. Based initially on the insights of paleontologist John Ostrom, many other morphological traits were identified that revealed evidence for the shared ancestry of birds and dinosaurs. At the same time, new fossil discoveries expanded our knowledge of the diversity of both dinosaurs and early birds. A critical later finding was that dinosaurs did have clavicles after all, and that the fusion of clavicles into a furcula is a trait found not only in birds but also widely in the theropod group of dinosaurs that includes the well-known tyrannosaurs, among others (Nesbitt et al. 2009). The presence of clavicles was overlooked previously because these fragile bones do not fossilize well, and because some dinosaur clavicles were misidentified.

Debate has persisted longer over which subgroup within the dinosaurs gave rise to birds. One possibility is that birds originated relatively early in the radiation of the **archosaurs**, the group that includes all of the dinosaurs and crocodiles, as well as birds. Previously it was thought that birds were more closely related to crocodiles than to dinosaurs, but this possibility has been refuted by newer fossil evidence. Alternatively, birds might be embedded deeply within the dinosaurs, within the theropod dinosaurs, or within or near one of the other dinosaur groups. Variants of this latter possibility have long been championed by the paleontologist Alan Feduccia (2012) and his colleagues, but among most other avian paleontologists there now is nearly universal agreement that birds originated from within the theropods (Dyke and Kaiser 2011).

The earliest theropod dinosaur fossils date from the Late Triassic Period about 225 million years ago, when several major groups of dinosaurs first arose. Throughout the subsequent 160 million years of the Jurassic and Cretaceous Periods, theropods were the dominant terrestrial carnivores. The most famous theropod species was the fearsome *Tyrannosaurus rex* (Fig. 2.22). However, although many theropods were huge meat eaters, the theropods also included a diverse range of smaller-bodied dinosaurs, some of which were likely herbivores or insectivores. Within the bipedal theropods, birds probably arose within a group termed the **Maniraptora**, which was distinguished by bird-like features such as long arms. Fossil evidence suggests that some non-avian maniraptorans could also fly

Archosaurs: a large group of reptiles that includes the non-avian dinosaurs, pterosaurs, crocodiles, and birds.

Maniraptora: a group that includes birds and their closest relatives within the theropod dinosaurs.



Fig. 2.23 Maniraptorans likely gave rise to birds. These dinosaurs had many bird-like features, suggesting that the earliest birds might have arisen within this group. (Illustration by Jane Kim, Inkdwell.)



Fig. 2.24 Present-day archosaurs. Crocodiles are the nearest living relatives of modern birds; these two groups represent the only extant archosaurs. (© Shane Moore/Animals Animals.)

or glide; indeed, because of their similarities to birds, there is still debate about whether some maniraptoran fossils should perhaps be reclassified as early birds. More generally, however, it is likely that the lineage that ultimately gave rise to modern birds was just one of many similar maniraptoran lineages that had features once thought to be found only in birds and their direct ancestors (Fig. 2.23).

From the broader archosaur group that once included the non-avian dinosaurs and other extinct groups, only birds and crocodiles have survived to the present day. Therefore, among living organisms, birds and crocodiles are each other's closest present-day relatives (Fig. 2.24).

2.4.2 Feathers and other dinosaur traits in birds

Birds and theropod dinosaurs share many traits, some of which are also found in other dinosaur groups. From a historical perspective, feathers are one of the most surprising features that birds and other dinosaurs have in common, because the presence of feathers was long thought to be a trait that unambiguously distinguished birds from all other animals. Starting in the 1990s, an important series of fossil discoveries produced increasingly clear evidence that most lineages of theropod dinosaurs sported feather-like quills and plumes (Chapter 4). Many of these new discoveries came from exceptionally well-preserved dinosaur and early bird fossils found in Liaoning Province, China, where fine volcanic ash fell about 125 million years ago and preserved not only bones but also impressions of soft external parts of the animals entombed in the ash deposits (Fig. 2.25). Evidence of feathers now has been found in dozens of fossil theropods from China as well as a few from North America and Europe; feather-like structures also have been identified in some non-theropod dinosaur fossils. Although today feathers are a feature restricted to living birds, in the past feathers were widespread among the dinosaur ancestors and relatives of birds.

In addition to feathers, birds and theropod dinosaurs share many other morphological traits, including the furcula formed by fused clavicles. Like birds, some theropods had bones that were tube-shaped and hollow, or **pneumatized**. Feathers and pneumatized bones were long considered avian adaptations arising from selection for flight, but we now know that these features evolved in non-flying dinosaurs, the ancestors of birds. Instead, the hollow bones of theropods may be evidence of a respiratory system in which the spaces within the bones serve as part of the air-sac network, similar to that of modern birds (Chapter 6). Comparative studies suggest that pneumatized bones evolved separately in different groups of theropods; in the largest such dinosaurs, these bones may have served to reduce the weight of the huge skeletal structures needed to support their massive bodies. In the non-avian theropod lineages related to birds, these air spaces and the lighter bones were more likely related to an active, fast-moving lifestyle (Benson et al. 2012).

Although no ancient dinosaur DNA survives to be analyzed, fossil evidence suggests that birds and the other theropod dinosaurs share the trait of having a small **genome** relative to most other vertebrates. In an elegant paleontological detective story, researchers realized that in living

Pneumatized: filled with small air cells.

Genome: the complete set of genetic material—DNA—within an individual bird.

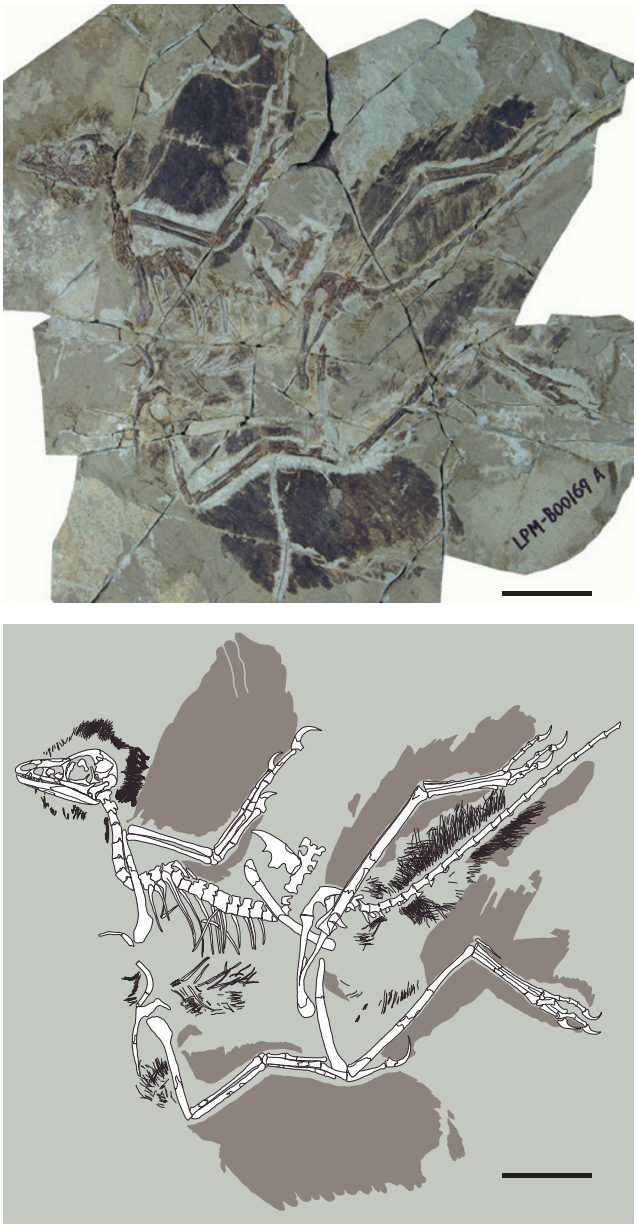


Fig. 2.25 Feather impressions in fossils. Numerous fossils of non-avian dinosaurs include preserved impressions of feathers. This fossilized theropod dinosaur from Liaoning Province, China has visible remains of feathers around the tail and limbs, indicated by the dark gray areas in the illustration. Scale bar = 5 cm. (From Hu et al. 2009. Reproduced with permission from Macmillan Publishers Ltd.)

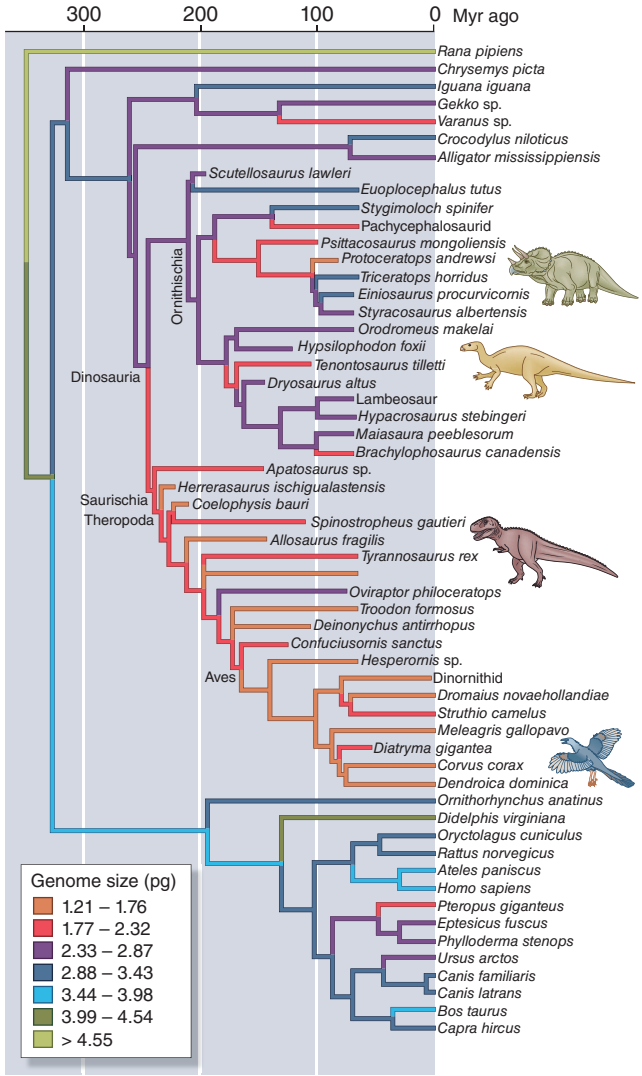


Fig. 2.26 Birds and other theropod dinosaurs have small genomes. The colored branches on this evolutionary tree indicate the genome sizes of various groups of tetrapod vertebrates. The orange and red branches indicate the smallest genomes and are found in birds and their theropod dinosaur relatives. Genome size here is measured in picograms (pg), or one-trillionth of a gram. (From Organ et al. 2007. Reproduced with permission from Macmillan Publishers Ltd.)

vertebrates, the size of certain bone cells correlates strongly with the size of an animal's genome: larger genomes result in larger bone cells. The diameter of these bone cells can be measured in some particularly well-preserved dinosaur fossils, which shows that genome size became reduced during the early evolution of theropods. This reduction is therefore another trait that birds probably inherited from their theropod ancestors (Organ et al. 2007) (Fig. 2.26).

Birds and the other theropod dinosaurs further share many physiological and behavioral traits: an upright, bipedal posture; the rapid growth rate of young individuals; and details of the structures of their calcified eggs. Fossil trackways of dinosaur footprints and fossilized theropod nest sites show that at least some theropods were social and that they likely guarded or incubated their eggs, similar to most modern birds. Debate persists about whether these other theropods, like modern birds, were endothermic—metabolically able to maintain their core body temperature at a level higher than their surroundings—but it is possible that they also share this trait.

2.4.3 *Archaeopteryx*, the earliest known bird

The fossil bird *Archaeopteryx* is one of the most famous of all extinct organisms. *Archaeopteryx* fossils are known only from 150-million-year-old limestone deposits in southern Germany. The species name of *Archaeopteryx lithographica* derives from the fact that most specimens come from rock quarries that were mined for use in lithography, a printing process. Fossils of *Archaeopteryx* and thousands of other Jurassic Period organisms were discovered when quarry workers split slabs of this stone to make lithographic plates.

Several of the earliest *Archaeopteryx* specimens found in the 1860s and 1870s were nearly complete skeletons, with clear impressions of feathers surrounding the arms and body. One of the most spectacular of these fossils is now in the natural history museum at Humboldt University in Berlin, Germany; it accordingly is referred to as the "Berlin specimen" (Fig. 2.27). Another famous exemplar known as the "London specimen" is in the British Museum. The limestone sediments in which all *Archaeopteryx* fossils have been found were formed in a shallow, tropical sea dotted with islands. Other flying vertebrates coexisted there with *Archaeopteryx*, including a variety of the flying reptiles known as pterosaurs. Pterosaur fossils are much more common in these deposits than are *Archaeopteryx* fossils.

The early *Archaeopteryx* fossils were—and remain—sensational finds because they reveal an organism with a mosaic of traits showing linkages to both theropod dinosaurs and modern birds. Bird-like traits in *Archaeopteryx* include the structure of its plumage, its relatively large brain, and many details of its skeletal anatomy. Features that link it to its non-avian theropod relatives include its many small teeth, a long tail with a bony midline, claws on the ends of its three finger bones in the wings, and additional skeletal details.

There is still great debate about the behavior and flying ability of *Archaeopteryx*. The largest specimen of this species had a wingspan of about half a meter, and various features of its feather and wing anatomy suggest that it could fly, but it is not clear how well (Fig. 2.28). The claws



Fig. 2.27 *Archaeopteryx*, an early bird. One of the most famous of all fossilized organisms, this Berlin specimen of *Archaeopteryx lithographica* provided early evidence that modern birds are derived from dinosaurs. (Photograph by H. Raab, http://commons.wikimedia.org/wiki/File:Archaeopteryx_lithographica_(Berlin_specimen).jpg. Used under CC-BY-SA-3.0.)

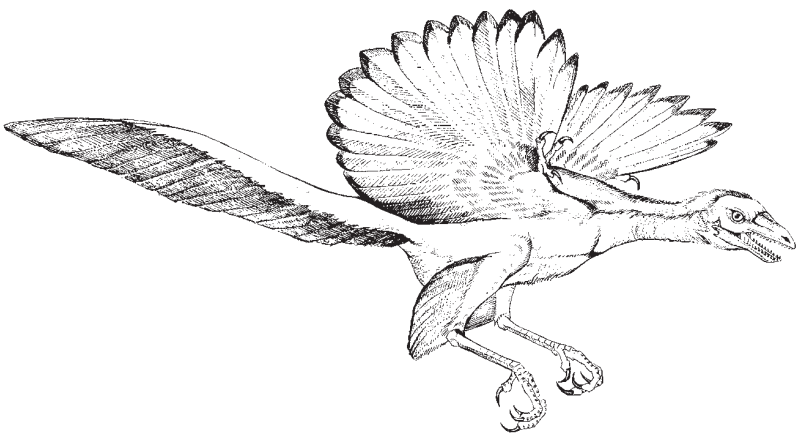


Fig. 2.28 *Archaeopteryx* reconstruction. An illustration depicting how *Archaeopteryx* may have appeared in life. (Illustration by Jane Kim, Inkdwell.)

on its wings have featured prominently in reconstructions of *Archaeopteryx* as a climbing, arboreal specialist, but other anatomical features suggest that it may have spent much of its time on the ground (Chiappe 2007).

Despite the clear affinities of *Archaeopteryx* to both modern birds and extinct groups of dinosaurs, we now understand that *Archaeopteryx* is not a direct missing link between these groups. This is because *Archaeopteryx* is not a direct ancestor of modern birds, but rather a representative of an extinct evolutionary offshoot of early birds, a side branch of the large diversity of early birds that originated earlier in the Jurassic Period. A different—and presently unknown—early bird present at this time was more likely the direct ancestor of all modern birds. Nonetheless, *Archaeopteryx* is generally considered to be the oldest known organism that is clearly a bird (Lee and Worthy 2012). New discoveries of contemporaneous theropods with avian attributes highlight the great diversity of such lineages in the late Jurassic fauna. As in all situations where diverse lineages occur at a time of great evolutionary transition, and because all fossils are inherently incomplete, it can be challenging to distinguish the early birds from non-avian theropods with many similar traits (Xu et al. 2011).

2.4.4 Other early birds from the Mesozoic

Animals that were unquestionably birds exploded in diversity during the last part of the Mesozoic Era, in the Cretaceous Period from 66 to 145 million years ago. However, most of the fossil birds from this time are not the direct ancestors of birds alive today; instead, they are offshoots of the avian evolutionary tree that left no direct descendants. Of the dozens of avian groups present in the Cretaceous that are now extinct, four merit special mention.

Discovered in 1993, the crow-sized *Confuciusornis* is now one of the best understood Mesozoic birds due to the exquisite level of anatomical detail preserved in some fossils. Although they are known only from the Liaoning deposits in China that date to about 120–135 million years ago, hundreds of *Confuciusornis* specimens have been studied by avian paleontologists; unfortunately, hundreds, or perhaps thousands, of additional specimens have been sold (often illegally) to collectors and are not available for research. The skeletal anatomy of *Confuciusornis* has many avian characters but lacks adaptations seen in later birds, such as an extensive keel on the sternum (Chapter 6). Its wings were long and pointed, and its wing feathers were highly asymmetrical, as seen in modern flying birds. Instead of the long, bony tail seen in earlier birds such as *Archaeopteryx*, *Confuciusornis* had a pygostyle, the knot of fused vertebrae that support the tail feathers in modern birds (Chapter 6). Although *Confuciusornis* did not have the full, fan-shaped tail seen in most living birds, many specimens preserve two dramatically long tail plumes (Fig. 2.29). These feathers are reminiscent of sexually selected ornaments seen in many groups of living birds and suggest that female birds of various species have been selecting mates with long tails for at least 140 million years.

Some groups of Mesozoic birds, including *Hesperornis* and its relatives in the order Hesperornithiformes, have



Fig. 2.29 *Confuciusornis* reconstruction. An illustration depicting *Confuciusornis* (120–135 MYA), an early bird known from Mesozoic deposits in China. (Illustration by Jane Kim, Inkdwell.)

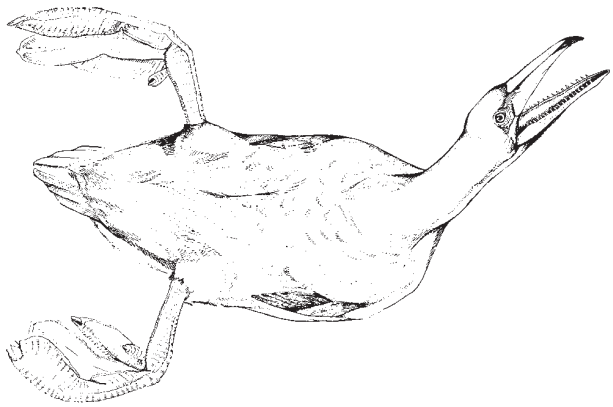


Fig. 2.30 *Hesperornis* reconstruction. An illustration depicting *Hesperornis* (80 MYA), a waterbird of the Campanian that left no close living relatives. (Illustration by Jane Kim, Inkdwell.)

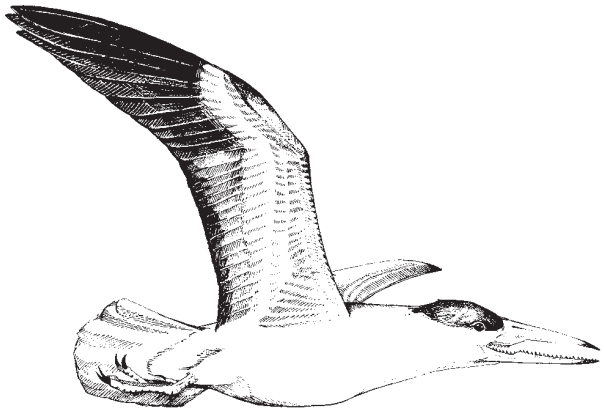


Fig. 2.31 *Ichthyornis* reconstruction. An illustration depicting *Ichthyornis* (85–93 MYA), a tern-like bird of the Cretaceous that may be closely related to the ancient lineage that gave rise to modern birds. (Illustration by Jane Kim, Inkdwell.)

been known to paleontologists for much longer than *Confuciusornis*. *Hesperornis* fossils were discovered in western North America in the 1880s. These birds were all highly specialized swimmers with long, torpedo-shaped bodies (Fig. 2.30). Their reduced wings indicate that, like modern penguins, they had lost the ability to fly. With large, lobed feet and strong leg muscles, they could move swiftly underwater to catch fish in their long, toothed jaws. More fragmentary remains of related species suggest that *Hesperornis* is but one representative of a larger radiation of birds with similar features that went extinct at the close of the Cretaceous Period.

Fossils of one of the most diverse and successful groups of Mesozoic birds, the Enantiornithes, are found on all modern continents except Antarctica. The diversity of enantiornithine birds may have rivaled the varied morphologies and foraging specializations seen in modern songbirds. Enantiornithes were similar in body size to today's songbirds, and details of their skeletons suggest that many were strong fliers. Although their finger bones had claws, the general structure of enantiornith wings shares many features—including the presence of an alula (Chapter 4)—with modern birds. Considered as a group, the Enantiornithes had diverse ecologies, including both aquatic and terrestrial lineages. Fossil evidence from tiny droplets of amber indicates that at least one species had an unusual diet: fossilized tree resin found in the bird's digestive tract suggests that this enantiornithine species fed directly on tree sap (Dalla Vecchia and Chiappe 2002).

Ichthyornis is another well-known bird from the Mesozoic (Fig. 2.31). Compared with Enantiornithes, *Confuciusornis* (Fig. 2.29), and *Hesperornis* (Fig. 2.30), *Ichthyornis* is probably more closely related to the lineage that gave rise to modern birds, although it too is not their direct ancestor. *Ichthyornis* was a strong flier, a fish-eating equivalent of modern seabirds, and was the size of a modern tern. Its wing structure and breastbone with a large keel were similar to those of modern birds. Many *Ichthyornis* specimens were collected in western North America in the late 1800s, and, along with *Hesperornis*, these discoveries of early birds with teeth became well known. In 1880, Charles Darwin wrote a letter to an American paleontologist noting that these archaic birds provided some of "the best support to the theory of evolution" since his publication of his *Origin of Species* (Clarke 2004).

Despite the recent dramatic discoveries in fossil lineages of Mesozoic birds, we have only fragmentary evidence for the full diversity of early birds and other bird-like dinosaurs from this time period. Only a single lineage from the entire radiation survived until the present day to become the lineage of modern birds.

2.4.5 Mass extinction and the origin of modern birds

There is ongoing debate as to when the lineages of birds living today originated and started to diversify from one another. The devastating mass extinction event that ended the Cretaceous Period at 65.5 million years ago is most famous for causing the extinction of all dinosaurs except for birds (Fig. 2.32). This end-Cretaceous event also caused the demise of many other groups of terrestrial and marine organisms, and it may have sparked the diversification of many of the bird lineages that still exist today.

Although the causes of this mass extinction are long obscure, evidence suggests that the impact of a huge asteroid, which produced the Chicxulub crater near Mexico's Yucatan Peninsula, resulted in sudden shifts in climate worldwide. However, independent events happening at the same time, such as sharp rises in volcanic activity and sea levels, may have contributed to the mass extinction.

Fossil deposits from just before the asteroid impact are particularly important for pinpointing whether the extinction was rapid—as would be expected if it resulted primarily from the asteroid impact—or more gradual, as would be expected if there were multiple factors. The few deposits with avian fossils from just before 65.5 million years ago suggest that the asteroid impact was devastating to the birds present in the late Mesozoic. For example, analyses of avian bones from sites in North America and Madagascar have revealed a wide diversity of Mesozoic birds, including representatives of the Hesperornithiformes and Enantiornithes, and *Ichthyornis*, that persisted until the very end of this period but not beyond (O'Connor and Forster 2010; Longrich et al. 2011). In contrast, these surveys did not identify any bones that could be assigned to orders of birds still living today, suggesting that the diversification of most modern groups of birds started after the mass extinction event.

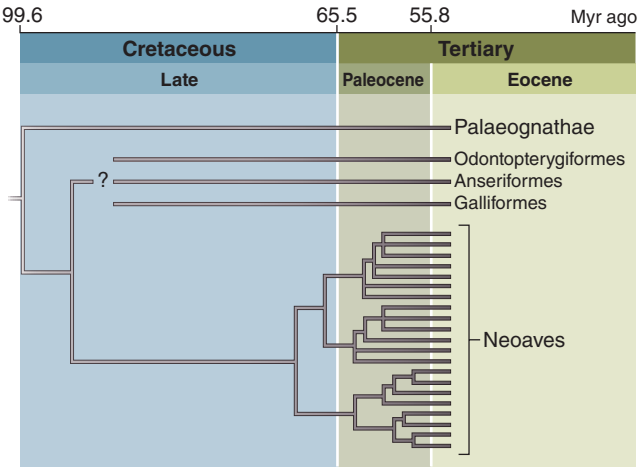


Fig. 2.32 Bird diversity before the Tertiary Period. Substantial uncertainty still exists regarding how many groups of living birds originated before the mass extinction at the end of the Cretaceous Period. Few fossils of modern birds have been found in Cretaceous deposits, but dates derived from DNA comparisons often suggest that many modern birds had Cretaceous origins. This tree shows one hypothesis in which a few modern lineages had Cretaceous origins, but most radiated later on in the Tertiary. (From Dyke and Kaiser 2011. Reproduced with permission from John Wiley and Sons.)

In fact, there is only one known fossil from the entire Cretaceous that unambiguously falls within a group of still living birds: the fossil duck relative *Vegavis* (order Anseriformes). Many other Cretaceous fossils from sites around the world have been linked tentatively to groups of living birds, but these associations usually are uncertain and often based on single bones. In contrast, the *Vegavis* fossil specimen is a nearly complete skeleton, except for the skull. The *Vegavis* fossil was found in Antarctica in 1992, but was not recognized as a waterfowl until detailed analyses were conducted a decade later (Clarke et al. 2005). The presence of a duck relative in the late Cretaceous has important implications, because we know from other phylogenetic evidence that ducks, geese, and their relatives in the Anseriformes split from the group that includes living chickens, grouse, and pheasants (order Galliformes) after an earlier split that divided the paleognaths (ostriches, emus, kiwis, tinamous, and their relatives) and all other living birds. The fossil *Vegavis*, therefore, shows that these two earlier splits must predate the end of the Cretaceous, despite the current lack of fossil evidence for these modern lineages during the Mesozoic (Slack et. al. 2006) (Fig. 2.33).

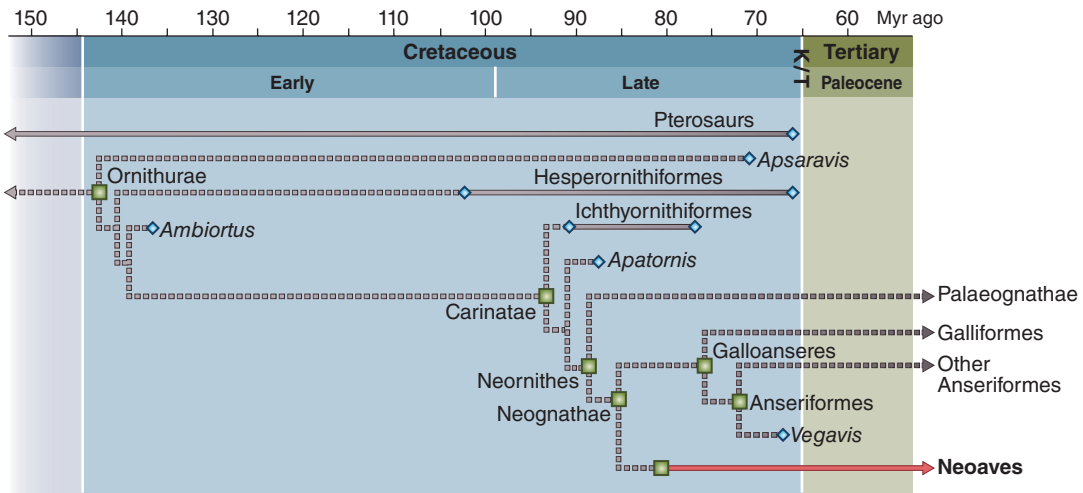


Fig. 2.33 One hypothesis of modern bird origins. This avian phylogeny shows the possible placement of lineages that likely went extinct at the K/T boundary at the end of the Cretaceous, along with the few known early fossils of modern birds, including the early duck *Vegavis*. (From Slack et al. 2006. Reproduced with permission from Oxford University Press.)

Fossils representing many modern orders are found in subsequent deposits from the early Tertiary Period, after the mass extinction. However, many archaic bird lineages that were common in the late Cretaceous are absent in the Tertiary. This pattern of sudden turnover in the avian fossil record further suggests that nearly all bird lineages were wiped out in the mass extinction at the junction between the Cretaceous and Tertiary. Under this line of reasoning, the few groups of surviving birds then diversified rapidly in the very early part of the Tertiary as the environment became more hospitable, refilling many avian ecological niches (Chapter 13) opened up by the mass extinction. This period of very rapid radiation in the early Tertiary gave rise to many modern orders and families.

In contrast to the later, Tertiary radiation implied by the near absence of most modern birds from the earlier fossil record, studies based on genetic comparisons consistently point to a much earlier origin of modern birds. These DNA dates are based on evolutionary trees calibrated using fossils from deposits of known age. Dates from a few well-documented fossils can help calibrate the timescale for more extensive phylogenies that are mostly based on DNA comparisons among still living species. This **molecular clock** method is useful for back-calculating the point in the past when two bird lineages diverged from one another. Different mutations accumulate over time in each descendant lineage once they separate from their common ancestor; therefore, if you know the overall average rate of mutational change, you can use the amount of DNA difference between two living species to estimate the time when their ancestors separated. In practice, this process is not very precise, in part because different parts of the genome have different average mutation rates, because well-dated fossils are absent for many groups of living birds, and for other technical reasons. Many of these procedural issues can be addressed through statistical analyses that take these underlying sources of variation into account to provide a window of the most likely time for each evolutionary split, rather than pinpointing one exact age.

Using the molecular clock approach to date the origins of groups of organisms was originally controversial when the method was introduced several decades ago, but today it is widely applied and broadly accepted among evolutionary biologists. Controversies involving the outcomes of molecular clock analyses still exist, however, including the general discrepancy between the fossil and DNA dates for the origins of most groups of modern birds. For reasons that remain uncertain, dates estimated using molecular tools are almost always much earlier than the corresponding earliest fossils known for those groups. Even the most advanced DNA-based estimates suggest that the earliest split within the evolutionary tree of living birds—the split between the paleognaths and all other living birds—occurred in the earlier part of the Cretaceous, at roughly 130 million years ago (Cooper and Penny 1997; Haddrath and Baker 2012). Some studies further suggest a Cretaceous origin for many living orders, yet the earliest equivalent fossils of nearly all of these groups are from much later in the Tertiary Period.

When both the fossil and genetic evidence are considered, it seems clear that at least a few lineages of modern birds arose before the mass extinction at the Cretaceous–Tertiary boundary. The extent of the Cretaceous radiation of modern birds remains uncertain, but future fossil discoveries may provide direct evidence for the existence of the **ghost lineages** in the Cretaceous whose existence currently is inferred from phylogenies but which are physically missing from the known fossil record. Additional genome-wide DNA data, analyzed in concert with improved molecular clock analyses and calibration, alternatively might show that most of the diversification in modern birds occurred in the Tertiary, as these lineages expanded into niches opened during the previous mass extinction. Reconciling these two possibilities remains an important challenge in avian systematics.

2.4.6 Diversification of living birds

The groups of birds that diversified just after the mass extinction at the close of the Cretaceous Period include representatives of most extant avian orders. Few fossils from this early part of the Tertiary can be linked to modern birds at the family level, however, because most avian diversity in this early period occurred in families that later went extinct.

At the family level for living birds, fossils clearly assignable to **crown groups**—groups that consist of the common ancestor of living representatives and all its descendants—generally date to the Eocene Epoch (55 to 33 million years ago). Fossils assignable more specifically to genera of living birds are younger, generally originating 2–25 million years ago.

A dramatic feature of the Eocene avian fossil record is the surprisingly broad distribution of some groups that later became restricted to certain parts of the globe. Some

Molecular clock: the idea that DNA changes accumulate at a relatively steady rate, and that the genetic differences among organisms can therefore be used to estimate the time in the past when they started to diverge from one another.

Ghost lineages: an evolutionary lineage that is inferred from a phylogeny, but for which no fossil evidence has been found.

Crown group: a special type of monophyletic group (i.e., clade) that includes all organisms descended from the last common ancestor of all *living* members of a larger clade.

Box 2.08 Ancient hummingbirds in surprising places

All 335 living species of hummingbirds are found exclusively in the Americas. These birds astounded the European naturalists who first encountered them zipping about the tropics. Ever since, the logical assumption has been that this family of tiny, hovering birds originally evolved in the New World. Therefore in 2004 it came as a great surprise when fossil bird expert Gerald Mayr recognized that several 30-million-year-old remains from a site in southern Germany were actually fossil hummingbirds. Mayr carefully described those fossils, clearly documenting that hummingbirds occurred in the Old World during an earlier part of their evolutionary history.

Mayr's specimens were conclusively hummingbirds: features of their bone structure showed that they could rotate their wings to hover, and their elongated bills suggested that they fed on flowers. However, these first-known European hummingbirds differed from all present-day hummingbirds in various details of anatomy, suggesting that they were an early part of the hummingbird evolutionary tree.

Another spectacular hummingbird specimen from the same early period was found in southern France (Louchart et al. 2008). The skeleton of this ancient hummingbird is nearly complete, and the rock matrix around its bones even reveals the outline of the bird's feathers, making it possible to discern its wing and tail shape (Fig. 2.B8.01).

The French specimen is more similar to modern hummingbirds than the fossils first discovered by Mayr, providing even stronger evidence that important aspects of hummingbird evolution occurred outside of the Americas. Mayr and his French colleagues point out that the presence of ancient hummingbirds in what is now Europe does more than provide a radically new perspective on our ideas of where and when these birds evolved: because hummingbirds often coevolve with the plants they feed on, some modern plants in Europe and Asia may retain attributes from the time when they evolved to attract hummingbirds as pollinators.



Fig. 2.B8.01 Early Eocene hummingbird fossil from France. Hummingbirds today are restricted to the Americas, but they were more widespread 30 million years ago. (From Louchart et al. 2008. Reproduced with permission from Springer Science + Business Media.)

of the best and most diverse fossil deposits from this period, for example, are found in Europe (Box 2.08). They record the presence of birds closely related to todies, hummingbirds, and New World vultures, yet today these groups are found only in the Americas. Similarly, the deposits contain frogmouths, which now are restricted to Australasia; and relatives of the Secretary-bird (*Sagittarius serpentarius*), mousebirds, ground-rollers, and turacos, all of which are now found only in Africa (Mayr 2005).

The most diverse and widespread order of living birds—the passerines or songbirds (Passeriformes)—is conspicuously absent from most Eocene deposits in the northern hemisphere. The earliest fossil passerines known are a few Eocene-age bones found in Australia (Boles 1994, 1997). This finding parallels other lines of evidence suggesting that passerines first evolved in the southern hemisphere. Passerine fossils appear in northern hemisphere deposits in the Oligocene (34 to 23 million years ago), but do not become common until the Miocene (23 to 5 million years ago), at which point they constitute a major part of most fossil avifaunas (Box 2.08).

2.4.7 Relationships of living avian orders

There is strong phylogenetic evidence that many orders of living birds originated during a brief period, although, as described earlier, the timing of that burst of diversification is uncertain. The rapidity of this diversification has impeded attempts to reconstruct the precise phylogeny connecting these avian lineages, although some parts of that overall tree are well resolved.

The earliest split in the tree of living birds separates the **ratites** (Fig. 2.34) and the tinamous (collectively termed

Ratite: a group of mostly large and flightless birds that includes ostriches, kiwis, rheas, cassowaries, emus, and tinamous, as well as the recently extinct moas and elephantbirds.

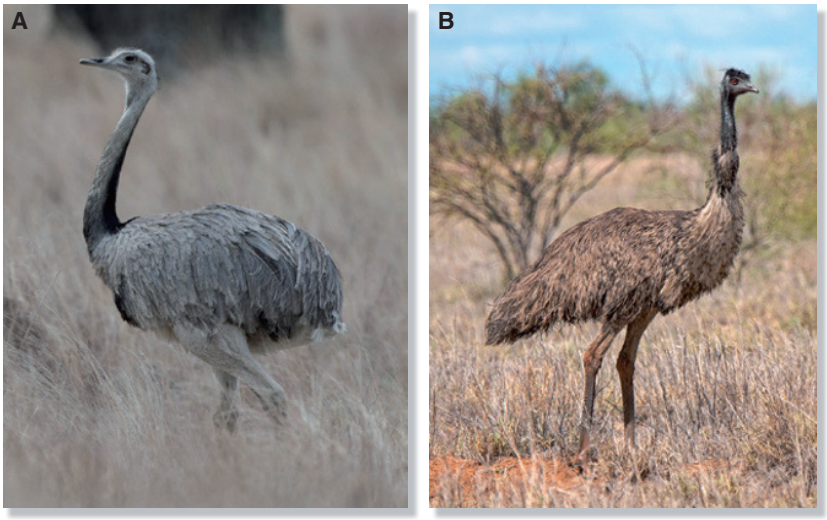


Fig. 2.34 Two examples of living ratites. Tinamous and the large, flightless ratites—including (A) the Greater Rhea (*Rhea americana*) and (B) the Emu (*Dromaius novaehollandiae*)—form the sister group to all other living birds. (Photographs by: A, Christopher Wood; B, Chris Burns.)



Fig. 2.35 Gondwana. A map of the super-continent of Gondwana about 170 million years ago, before it began to break apart into the smaller continents and islands we know today. (From Gibbs 2006. Reproduced with permission from Craig Potton Publishing.)

paleognaths) from all other birds (termed **neognaths**). With the exception of the flying tinamous, the paleognaths are all large and flightless, and exist on current fragments of the ancient supercontinent of **Gondwana**: ostriches in Africa, rheas in South America, emus and cassowaries in Australia, and kiwis and moas in New Zealand. This distribution of heavy, flightless birds was long thought to be the result of their separation when Gondwana broke up into the present-day smaller continents during the Cretaceous Period, because these non-flying, non-swimming birds would have had difficulty dispersing across the seas separating the new continents. Phylogenetic studies have overturned this hypothesis, however, by showing that the common ancestor of these groups lived more recently than the Gondwana breakup (Fig. 2.35). Furthermore, the flighted tinamous fall well within this group as the sister to the moas (Haddrath and Baker 2012; Smith et al. 2013). It now seems most likely that there were multiple losses of flight within the paleognaths after they were present on their respective present-day continents. Under this new scenario, it remains uncertain how the ancestors of today's flightless ratite lineages might have originally dispersed between the continents and islands on which they are now found.

Within the living neognaths, the earliest split separates the group comprising ducks, geese, megapodes, chickens, and their relatives (Galloanseres) from the remaining groups (Neoaves). As described above, the fossil waterfowl *Vegavis* shows that the Galloanseres already had started to diversify before the mass extinction at the end of the Cretaceous. Today, members of this group are found worldwide.

Relationships among the many deep lineages of neognaths remain uncertain. Fig. 2.09 depicts one possible reconstruction of their evolutionary tree, but the details likely will change as we gather more information. In general, however, some traditional groupings find little support in modern DNA-based phylogenies. The list of orders and families in Box 2.09 represents a synthesis of the current phylogenetic information about avian relationships.

Paleognaths: one of the two groups of living birds, containing all ratites as well as the extinct elephant-birds and moas.

Neognaths: one of the two groups of living birds, containing all living birds except the ratites.

Gondwana: the name of the ancient southern super-continent of 180–600 million years ago that included most of present-day Africa, Antarctica, Australia, India, Madagascar, New Zealand, and South America.

Box 2.09 A survey of avian orders and families

Contributed by Shawn M. Billerman

One of the joys of Ornithology is encountering an entirely new group of birds for the first time. An exploration of avian diversity best begins with an understanding of the diversity of living birds that we classify into the various orders and families. Many college-level ornithology courses therefore cover the bird families that occur in the local region, or sometimes even the entire set of bird families from across the world. The remainder of this chapter provides a brief introduction to this worldwide diversity of living birds based on the classification of Winkler et al. (2016), a reference that provides more in-depth coverage of each of these groups.

Struthioniformes. The ratites and tinamous together form this ancient and diverse order of terrestrial birds found primarily in the southern hemisphere. Recently extinct forms include the moas of New Zealand and the elephantbirds of Madagascar. Taken together, the members of this order are the sister group to all other living birds. All except the tinamous have lost the ability to fly.

Struthionidae. The Ostrich (*Struthio camelus*), the largest living bird, is found today only in sub-Saharan Africa. The flightless Ostrich is an extremely fast runner. Males care for the eggs and chicks of many females simultaneously.

Rheidae. The rheas include a pair of species found in the grasslands of South America. Although large and flightless, the rheas are more closely related to the smaller and flighted tinamous than to the other ratites.

Tinamidae. Tinamous are a diverse family of flying but ground-dwelling birds from South America with relatively plump bodies and small heads. Generally secretive, many tinamous are more often heard than seen.

Casuariidae. The cassowaries and the Emu (*Dromaius novaehollandiae*) are a small family of large, flightless birds from Australia and New Guinea. The cassowaries, covered with stiff, black, hair-like feathers, inhabit dense rainforests. The Emu is found in drier parts of Australia.

Apterygidae. The kiwis are a small group of small- to medium-sized, flightless birds found only in New Zealand. Covered in fine, brown, hair-like feathers, kiwis are mainly nocturnal and forage primarily on earthworms. They lay the largest egg proportional to their body size of any living bird.

Galliformes. Members of this large and diverse order of fowl-like birds are found worldwide from the arctic tundra to the tropical rainforest. Galliformes range in size from the tiny quail to the robust turkey. The most familiar species of this group are domesticated, including chickens, turkeys, guineafowl, and quail. Males of many galliform species use elaborate displays or exaggerated plumages to attract females.

Megapodiidae. The megapodes are found in tropical regions of Southeast Asia and Australia. Unlike all other birds, megapodes provide no care to their young after the eggs are laid; instead, megapode eggs are incubated by heat from the decomposing matter of large organic mounds piled up by the males or other sources.

Cracidae. An entirely New World radiation, the tropical guans and curassows are diverse. Many are threatened with extinction caused by over-hunting, and they are especially susceptible to being lost from fragmented habitats. These wary birds can be difficult to see but are often heard.

Numididae. A small family of African upland birds, some species of guineafowl have been domesticated. Their raucous calls, intricately patterned plumage, and bare, colorful heads make them instantly recognizable.

Odontophoridae. A diverse family of small, upland birds that often congregate in large coveys, the New World quail are recognizable by their distinctive calls and bold patterns. They are found in a wide range of habitats, from dry deserts to tropical rainforests.

Phasianidae. The pheasants and their allies are found worldwide and include a number of commonly domesticated species, including the chicken. Species in this family come in a wide range of shapes, sizes, and colors, ranging from the diminutive Old World quail to the large turkey. Many species have intricate and exaggerated plumages and use bizarre displays, including dances and booming calls, to attract females.

Anseriformes. A large, diverse, and very familiar group with three families, Anseriformes are found worldwide, primarily in wetland habitats from the arctic tundra to the tropics. They inhabit bodies of water ranging in size from small inland ponds to the open ocean.

Anhimidae. The large South American screamers are found in wetlands, where—as their name suggests—they fill the air with their loud calls. These birds are an avian anomaly in terms of anatomy: they have no feather tracts but do have air sacs under their skin. They have large, heavy bodies, long legs, and tiny heads, and feed primarily by grazing on vegetation.

Anseranatidae. The Magpie Goose (*Anseranas semipalmata*) of Australia and New Guinea nests in large colonies where one male often has a harem of several females who lay their eggs in a common nest. Magpie Geese may be nomadic in their search for suitable wetland conditions for feeding and nesting.

Anatidae. This familiar group of ducks and geese is found worldwide, usually associated with ponds, lakes, oceans, and other wetlands. Many species have distinctly flattened bills, often with serrations or grooves to help them filter or grasp food.

Podicipediformes. This order contains only one family, the grebes.

Podicipedidae. A diverse family of fish-eating waterbirds, grebes are found worldwide. They are well adapted for their life in the water, with lobed toes and feet set far back on their bodies to enable foot-propelled diving.

Phoenicopteriformes. This order contains only one family, the flamingos.

Phoenicopteridae. Flamingos are found in a range of shallow wetlands, mostly in the tropics. Famous for their pink coloration and oddly shaped bill that is specially adapted for filtering tiny food, flamingos are most closely related to grebes.

Columbiformes. This order contains only one family, the doves and pigeons.

Columbidae. Doves and pigeons are found worldwide in a wide variety of habitats, ranging from dry deserts to urban cities. Feeding mostly on seeds, doves and pigeons feed their chicks "crop milk," a substance comprised of water, proteins, and fats.

Mesitornithiformes. This order contains only one family, the mesites.

Mesitornithidae. The mesites are a small family of largely terrestrial birds endemic to Madagascar. Relatively little is known about their natural history, and their relationships with other birds are similarly unclear.

Pterocliformes. This order contains only one family, the sandgrouse.

Pteroclidae. The sandgrouse are found in some of the most arid environments in the world, throughout sub-Saharan Africa and central Asia. Sometimes forming huge flocks, sandgrouse can fly long distances to find water. Adults carry water to chicks by saturating their feathers.

Caprimulgiformes. This is a large order containing both nocturnal and diurnal families. Nocturnal families include the nightjars, potoos, owlet-nightjars, frogmouths, and the frugivorous, cave-dwelling Oilbird (*Steatornis caripensis*). Diurnal Caprimulgiformes include the aerial, insectivorous swifts and treeswifts, and the highly diverse but mostly nectivorous hummingbirds of the New World.

Steatornithidae. The Oilbird is found in the tropical forests of South America. Roosting primarily in caves, it uses its excellent vision and echolocation to navigate in almost complete darkness. Oilbirds are completely frugivorous and use their excellent sense of smell to locate fruiting trees.

Nyctibiidae. The potoos are found in the tropics of South and Central America. Large and cryptically patterned, they sit motionless on trees, resembling the broken ends of branches. Largely nocturnal, they feed mostly on insects.

Podargidae. The frogmouths are found in the tropics of Southeast Asia and Australia. Large and cryptically patterned, they are difficult to find by day, when they sit motionless, resembling the ends of broken branches. At night, they are more active and feed on a wide variety of insects and small vertebrates.

Caprimulgidae. The nightjars are a diverse and worldwide group of nocturnal, aerial insectivores. They have extremely wide mouths and fly around with their mouths open to capture insects. Cryptically patterned, they nest primarily on the ground. Although difficult to see, many species have vocalizations that can be heard at a great distance.

Aegothelidae. Owlet-nightjars are found in a variety of forested habitats in Australasia. They usually roost in tree cavities during the day, and, at night, feed on insects by picking them from the air.

Hemiprocnidae. The treeswifts are small, aerial insectivores found in the tropical forests of Southeast Asia. Most treeswifts have crests or whiskers, which distinguish them from the similar and closely related swifts. Treeswifts do not build nests but instead simply glue their egg to a branch with their saliva.

Apodidae. The swifts are a large radiation of aerial insectivores with a global distribution. Swifts spend much of their life in the air, and have poorly developed feet and legs. Most species nest on vertical or nearly vertical surfaces, and use their saliva to glue nesting material and eggs to the nesting substrate.

Trochilidae. Hummingbirds, named for their unique hovering flight, are small, often brightly colored birds of the New World. With their long, thin bills, hummingbirds famously feed on the nectar of flowers, but also take many small insects and spiders.

Cuculiformes. This order contains only one family, the cuckoos.

Cuculidae. Cuckoos are a diverse group of birds with a global distribution. They are found in a wide variety of habitats, from deserts to tropical savannas. Some cuckoos are nest parasites and notoriously lay their eggs in the nests of other bird species, but many cuckoo species build nests and care for their own young.

Musophagiformes. This order contains only one family, the turacos.

Musophagidae. Turacos and go-away-birds are found in sub-Saharan Africa in a variety of forested habitats, from acacia savanna to tropical rainforest. They are large birds with long tails, and feed on both fruits and leaves. The feathers of many species are extraordinarily colorful, with some species sporting pigments found only in this family.

Otidiformes. This order contains only one family, the bustards.

Otididae. Bustards are medium-sized to very large terrestrial birds found across open grasslands and savannas of the Old World. The bustards include the world's two heaviest flying bird species: the Great Bustard (*Otis tarda*) of Europe and western Asia, and the Kori Bustard (*Ardeotis kori*) of sub-Saharan Africa.

Opisthocomiformes. This order contains only one species in its own family, the Hoatzin (*Opisthocomus hoazin*).

Opisthocomidae. The Hoatzin of tropical South America is an enigmatic bird in many ways, and its relationship to other birds is still debated. The Hoatzin is the only bird that eats only leaves, which it digests using unique foregut fermentation akin to that found in ruminant mammals.

Gruiformes. The gruiform order includes the cranes, the rails, the trumpeters of South America, the finfoots, and the Limpkin (*Aramus guarauna*). Although much reduced by recent extinction, rails once were the most diverse family in the world, with more than 2000 species. Found worldwide, many species in this order have loud and recognizable vocal displays.

Heliornithidae. The finfoots are a small group of birds with lobed feet. They are found in slow-moving waterways of the tropics, where they are shy and secretive.

Sarothruridae. The flufftails, which consist of the genera *Sarothrura* and *Canirallus*, are highly secretive birds from sub-Saharan Africa. Inhabiting wet woodlands, grasslands, and marshes, the flufftails were long thought to be part of the large rail radiation, but recent data have shown that they are more closely related to the finfoots than to the rails.

Rallidae. An extremely diverse and widespread group, until recently the rails were likely the most speciose family of birds, with a great number of flightless species found on isolated oceanic islands. The 140 or so extant species are found in a wide variety of wetland and terrestrial habitats.

Psophiidae. Trumpeters are a small family of largely terrestrial birds from the Amazon Basin rainforests of South America. Trumpeters are named for their loud call, and their habit of forming large, noisy flocks. Although they forage on the ground, mainly for fruit, trumpeters nest in tree cavities.

Aramidae. The Limpkin is a wading bird found in the marshes of the tropical Americas. Limpkins have a long, decurved bill that is specially adapted for feeding on their main prey, apple snails.

Gruidae. Cranes are a widespread and charismatic group of birds, with some species known for their spectacular courtship dances. Absent only from South America and Antarctica, cranes are found in a variety of open habitats, from drier grasslands to marshes. Many species form huge flocks during migration and on wintering grounds.

Charadriiformes. This extremely diverse order is second only to passerines in number of families and species. Although known by the collective name "shorebirds," members of this group are found in almost every terrestrial habitat in the world, and many also occur in pelagic habitats. With a truly global distribution, the shorebirds are notably varied in their breeding strategies and mating systems. This group includes some of the world's most extreme

migrants: some species fly non-stop for thousands of kilometers. The order also includes the quail-like buttonquail and seedsnipe, the wading shorebirds, the penguin-like auks, and the gulls and terns.

Burhinidae. The thick-knees are a small family of terrestrial "shorebirds" found in tropical and subtropical regions of the world, often in relatively dry, open habitats such as savannas. Thick-knees are cryptically patterned and typically nocturnal.

Chionidae. The sheathbills are a small family of seabirds found in the southern oceans, primarily near offshore islands and coastal Antarctica. Resembling large, white pigeons, the sheathbills feed on penguin eggs and chicks, carrion, and other refuse.

Pluvianellidae. The Magellanic Plover (*Pluvianellus socialis*) is a rare wader that has been placed into its own family based on behavioral and molecular evidence. It is a small shorebird of southern South America with bubblegum-pink legs. Using their short, stout bills, these birds flip small rocks and dig into the ground in search of invertebrate prey.

Pluvianidae. The Egyptian Plover (*Pluvianus aegyptius*), found along freshwater bodies of northern and central Africa, is a boldly patterned shorebird that feeds mainly on invertebrates. Once thought to pick food from the mouths of crocodiles, this habit has never actually been well documented. Nesting on sandbars, Egyptian Plovers must actively cool their nest and chicks.

Haematopodidae. Oystercatchers are a small family of large shorebirds that are found along the coasts of much of the world. They use their long, chisel-shaped, coral-red bills to pry or hammer open shellfish and other marine invertebrates.

Ibidorhynchidae. The sole member of this family, the Ibisbill (*Ibidorhyncha struthersii*), lives along fast-moving mountain streams of central Asia. With its long, decurved bill, the Ibisbill searches for invertebrate prey under large boulders and amidst cobbles.

Recurvirostridae. Stilts and avocets are long-legged shorebirds that have a global distribution. They forage for small invertebrates in both fresh- and saltwater marshes.

Charadriidae. Plovers are a large and diverse group of small to medium-sized shorebirds. Found worldwide in a wide variety of open habitats from tundra to tropical savanna, plovers feed on a variety of terrestrial and benthic invertebrates.

Pedionomidae. The Plains-wanderer (*Pedionomus torquatus*), the only member of this family, is a small, rare, and declining terrestrial shorebird from the outback of Australia. Largely nocturnal, the Plains-wanderer feeds mainly on seeds and insects.

Thinocoridae. A small family of odd shorebirds that resemble grouse and quail more than sandpipers, the seedsnipe are found both above the treeline in the Andes and in the open grasslands of southern South America. Unlike most shorebirds, seedsnipe feed mainly on seeds and other vegetation.

Rostratulidae. Painted snipe are a small group of small shorebirds of tropical and subtropical marshes. Often difficult to detect due to their cryptic patterning, painted snipe feed on a variety of aquatic and benthic invertebrates.

Jacanidae. The jacanas are a small group of medium-sized shorebirds. With their extraordinarily long toes, jacanas can wade across surface vegetation in tropical freshwater marshes as they forage for invertebrates. Unlike most birds, male jacanas provide all parental care for the eggs and chicks.

Scolopacidae. The sandpipers and their allies are the largest and most speciose family of shorebirds. They are diverse in their natural history as this family includes species with a wide variety of mating systems and diverse feeding ecologies. They also have varied migration behaviors, with some species flying non-stop for thousands of kilometers.

Turnicidae. The Old World buttonquail are a small group of tiny groundbirds. Seeming more akin to quail than to their actual shorebird relatives, the buttonquail were a longstanding taxonomic mystery until genetic work clarified that they are members of the shorebird group. Buttonquail are terrestrial, cryptically patterned, and feed primarily on seeds and insects.

Dromadidae. The only member of this family, the Crab Plover (*Dromas ardeola*) is a strikingly patterned black-and-white, medium-sized shorebird that breeds along the coasts of east Africa and the Middle East. Crab Plovers construct burrows in the sand where they nest and roost.

Glareolidae. The pratincoles and coursers are the two distinct groups of this family, both of which feed primarily on insects. Pratincoles are swallow-like and catch insects on the wing. Coursers are terrestrial birds and are usually found in dry, open habitats.

Laridae. Gulls, terns, and skimmers together are a widespread family found on every continent. Although largely associated with water, many species also are found in terrestrial environments, and some have adapted well to urban settings.

Stercorariidae. The skuas and jaegers are seabirds found in oceans worldwide, but they restrict their breeding to high latitudes. They feed primarily by pirating food from other birds, particularly gulls and terns.

Alcidae. The auks are a small but diverse family of seabirds of the northern hemisphere. Unlike penguins, which they superficially resemble, auks are fully capable of flight, although they also are accomplished wing-propelled divers. Some auks have brightly colored bills or ornate feathers around the head.

Eurypygiformes. This new order was formed when the former Gruiformes group was split. It contains only two families, each with a single species. Although both species have characteristically colorful wing patterns, they are otherwise quite different.

Rhynochetidae. The Kagu (*Rhynochetos jubatus*) is a flightless landbird endemic to the remote Pacific island of New Caledonia. Found in dense forest, its population is declining. Males display by erecting their long crest and spreading their wings to expose their striking pattern. A cooperative breeder, Kagu helpers defend the territory while the parents care for chicks.

Eurypygidae. The Sunbittern (*Eurypyga helias*) is a striking bird most often found near streams in the tropical lowlands of Central and South America. Sunbitterns are cryptically patterned until they are threatened, which triggers them to spread their wings to reveal the spectacular plumage for which they are named.

Phaethontiformes. This order contains only one family, the tropicbirds.

Phaethontidae. The tropicbirds are a small family of graceful tropical seabirds with white-and-black plumage and long tail streamers. The tropicbirds were long thought to be related to various other seabird families but instead seem to be relatives of the Eurypygiformes.

Gaviiformes. This order contains only one family, the loons.

Gaviidae. The loons (also known as divers) are a small group of birds found only in the northern hemisphere. They breed on northern lakes and ponds, and winter primarily along the coasts of North America and Eurasia. Loons are specially adapted to an aquatic lifestyle: they feed on fish, and their feet are placed far back on their body for foot-propelled diving.

Sphenisciformes. This order contains only one family, the penguins.

Spheniscidae. The penguins are a group of flightless seabirds that are well adapted for swimming and diving. Penguins are most diverse in the southern oceans near Antarctica.

Procellariiformes. The petrels, shearwaters, albatrosses, and storm-petrels are a diverse order of tubenose seabirds found across the world's oceans. They range in size from the small storm-petrels to albatrosses, which have the largest wingspan of any bird. They feed on a wide variety of prey, from small plankton to fish. Many tubenoses have an acute sense of smell that they use to find food and to locate their nests after being away at sea.

Oceanitidae. The southern storm-petrels are a small family of tubenose seabirds that breed primarily on islands in the southern hemisphere, but may be found in the northern oceans when they are not breeding.

Diomedeidae. Albatrosses are a group of large seabirds that range widely across the world's oceans, returning to land only to breed. At 3.5 meters, the Wandering Albatross (*Diomedea exulans*) has the widest wingspan of any living bird.

Hydrobatidae. The northern storm-petrels are a small family of tubenose seabirds that breed primarily on islands in the northern hemisphere. Like southern storm-petrels, northern storm-petrels feed by fluttering over the water and picking items from its surface.

Procellariidae. The petrels and shearwaters are tubenose seabirds found across the world's oceans. They range in size from small diving-petrels to large giant-petrels. They feed on a wide variety of prey, from small plankton

to fish. They use their acute sense of smell to find their nests when returning from sea.

Ciconiiformes. This order contains only one family, the storks.

Ciconiidae. Storks are wading birds that are most diverse in the Old World tropics. Primarily found in marshes, storks inhabit a variety of open habitats, from dry acacia savanna to urban landscapes. Many species have bare skin on their heads and necks. They feed on a variety of prey, from carrion and insects to fish and small mammals.

Suliformes. Members of this order of seabirds are found throughout the world's oceans. Suliformes lack external nostrils, an adaptation to their aquatic lifestyle. Families in this order employ a variety of foraging techniques: frigatebirds pirate food from other species, gannets and boobies are plunge divers, and cormorants and darters swim underwater to take fish. Many species are colonial breeders, sometimes nesting in huge concentrations.

Fregatidae. Frigatebirds are the pirates of the tropical oceans. Found across all tropical waters, frigatebirds often feed by stealing food from other birds such as terns and gulls. Nesting mostly on islands, males perform elaborate courtship displays in which they inflate their massive, red gular pouch.

Sulidae. Boobies and gannets are large seabirds that capture fish by plunging into the water from the air. Found in all the world's oceans, species in this family often nest in huge colonies, primarily on islands. Gannets are larger than boobies and are found in temperate waters, whereas the slightly smaller boobies are found in tropical waters.

Phalacrocoracidae. Cormorants are a diverse and widespread group of waterbirds. Found worldwide, the cormorants swim and dive for fish in both freshwater and marine environments. Cormorants do not have oil on their feathers and thus must dry their wings by flapping and airing them out after diving.

Anhingidae. Like cormorants, the Anhinga (*Anhinga anhinga*) and darters are waterbirds that swim and dive to catch fish. Found mainly in tropical and subtropical wetlands, this small group of birds stabs their prey with their dagger-shaped bill. Like cormorants, they do not have oil on their plumage and must dry their feathers after being in the water.

Pelecaniformes. This order of wading birds includes the herons, egrets, ibises, and spoonbills. It also includes the pelicans, recently found to be closely related to the Shoebill (*Balaeniceps rex*) and Hamerkop (*Scopus umbretta*). Most pelecaniform species are associated with aquatic habitats, ranging from wet meadows to marine environments, and feed on aquatic vertebrates, implementing a variety of foraging techniques.

Threskiornithidae. A diverse family of wading birds, the ibises and spoonbills include many members with spectacular plumage. Both ibises and spoonbills have specially adapted bills; ibises use their long, decurved bills for probing, and spoonbills use their flattened, spatulate-shaped bills to take prey from water.

Ardeidae. The herons and egrets are a diverse and widespread family of wading birds, found worldwide and in many habitats, from dry grasslands to dense rainforest. Most species feed in or along the water, probing and stabbing prey with their dagger-like bills; others feed on insects picked from grass and other vegetation.

Scopidae. The Hamerkop (*Scopus umbretta*) is a medium-sized, brown wading bird from sub-Saharan Africa that uses its bill to take frogs, fish, and other prey from the water. Hamerkops build the largest nest of any bird, a mass of sticks in a tree with an inner nesting chamber.

Balaenicipitidae. A large wading bird of the marshes of central Africa, the Shoebill (*Balaeniceps rex*) has a large, blocky head and a large bill reminiscent of a wooden clog, which it uses to catch lungfish and other aquatic prey. On hot days, adults may use their bills to scoop up water to cool their chicks.

Pelecanidae. Pelicans are widespread waterbirds mostly found on interior lakes and wetlands; some are found along continental coastlines. They use a large bill with an expandable gular pouch to scoop up many fish at one time.

Cathartiformes. This order contains only one family, the New World vultures.

Cathartidae. New World vultures are a small family of raptorial birds ranging from temperate North America to extreme southern South America. The New World vultures feed primarily on carrion, and some species have an excellent sense of smell. The New World vultures are only distantly related to the Old World vultures.

Accipitriformes. These diurnal raptors include the hawks, eagles, kites, and the long-legged Secretary-bird (*Sagittarius serpentarius*). Members of this order are found worldwide

in almost every terrestrial habitat from the arctic tundra to the tropical rainforest.

Sagittariidae. The Secretary-bird is an odd raptor of sub-Saharan African savannas. With long legs, a long tail, and elaborate crest, the Secretary-bird stalks through the grass searching for mammalian and reptilian prey, which it may kill with sharp kicks.

Pandionidae. The Osprey (*Pandion haliaetus*), the only member of this family, is a large raptor that specializes in eating fish. Found on nearly every continent, the Osprey has adaptations, including rough foot-pads and a reversible outer toe, that help it grasp its slippery prey.

Accipitridae. The hawks, eagles, and kites are a large and diverse family of diurnal raptors that prey on animals from insects to monkeys. Found worldwide in nearly all terrestrial habitats, they range in size from the Tiny Hawk (*Accipiter superciliosus*) to the Great Philippine Eagle (*Pithecophaga jefferyi*).

Strigiformes. The owls and barn owls are typically nocturnal predators found across the world.

Tytonidae. The barn owls are a small family of nocturnal predators with a global distribution. Similar in many ways to the typical owls, barn owls have a distinctive, heart-shaped facial disc.

Strigidae. The typical owls are a large, diverse group of mainly nocturnal predators found across the world. Owls feed on a wide range of prey, from insects to fish. Unmistakable the world over, owls have superb nocturnal vision and acute hearing.

Coliiformes. This order contains only one family, the mousebirds.

Coliidae. Mousebirds are a small group of birds restricted to sub-Saharan Africa. They have soft, gray-brown plumage, fluffy crests, and long tails. Mousebirds are highly social and will huddle together in groups for warmth. When foraging, they may scramble through dense brush, often hanging from branches.

Leptosomiformes. This order contains only one species in its own family, the Cuckoo-Roller (*Leptosomus discolor*).

Leptosomidae. The Cuckoo-Roller is endemic to tropical and subtropical forests in Madagascar. Relatively little is known about this large sit-and-wait predator, which feeds on animals ranging from insects to small vertebrates.

Trogoniformes. This order contains only one family, the trogons.

Trogonidae. Trogons are a diverse family found in tropical and subtropical forests around the world. Fantastically colored in iridescent greens and blues above, and bright reds and yellows below, trogons often sit motionless for long periods.

Bucerotiformes. This small order of three families is found primarily in the Old World tropics; the Eurasian Hoopoe (*Upupa epops*) occurs in Europe and central Asia. These three families are found in a variety of habitats, from dense tropical forest to open savanna.

Bucerotidae. The hornbills are a diverse family of medium to large birds found in tropical and subtropical Africa and Asia. They have bold plumage and large bills, often topped with a horny casque. Most female hornbills are walled into their nest cavities and fed by their mate until their nestlings are well grown.

Upupidae. Hoopoes are found in Eurasia and Africa in a variety of relatively open habitats. With large, movable crests; long, thin, decurved bills; and broad black-and-white patterned wings, hoopoes are highly distinctive. They nest in cavities and forage primarily on insects.

Phoeniculidae. Woodhoopoes are closely related to hoopoes but are restricted to forested and scrubby habitats of sub-Saharan Africa. With long decurved bills, long tails, and glossy black plumage, woodhoopoes probe bark and branches for insects.

Coraciiformes. The Coraciiformes are a diverse order of birds, most of which are brightly colored. Found worldwide, the order includes the rollers, bee-eaters, motmots, todies, and the diverse kingfishers. Species are found in a wide variety of habitats, ranging from marsh to open savanna. They are mostly sit-and-wait predators of vertebrates and insects, and all nest in cavities or burrows.

Meropidae. Bee-eaters are brightly colored and boldly patterned aerial insectivores. Found in the Old World, many species live in relatively open habitats, although some live in dense forests. Many are highly social and nest in burrows, often in large colonies.

Coraciidae. Rollers are a small Old World family of bright, colorful, sit-and-wait predators. Named for acrobatic flight displays during which some species roll their body back and forth, rollers are found in a variety of open habitats where they prey mainly on insects and small vertebrates.

Brachypteraciidae. Ground-rollers are endemic to Madagascar. Boldly marked and patterned, they are found from arid thorn scrub to tropical rainforest. Ground-rollers feed on invertebrates and nest in burrows.

Todidae. The todies are tiny, brightly colored, sit-and-wait insect predators found only in forested habitats on the Greater Antilles islands of the Caribbean. Todies have bright emerald-green backs, but they can be difficult to spot when they sit motionless on a shaded branch.

Momotidae. The motmots are boldly patterned, sit-and-wait predators from Central and South America. Named for their calls, motmots have serrated bills that they use to grasp large insects and small vertebrate prey. Most motmots have long, racquet-tipped tails that they wag back and forth.

Alcedinidae. Kingfishers are a diverse family with worldwide distribution. Although their name suggests that they feed on fish, and many species do, a number of species are found in dry habitats where they feed on insects, small rodents, reptiles, or amphibians. Most kingfishers are boldly patterned, and some are very brightly colored.

Piciformes. The Piciformes use a variety of foraging techniques: woodpeckers drill and probe bark whereas puffbirds and jacamars use a sit-and-wait predation strategy. With a nearly global distribution, the Piciformes are found in a wide variety of habitats and nest exclusively in cavities or burrows. The honeyguides are obligate brood parasites; all other families raise their own young.

Galbulidae. Jacamars, found in the lowland tropical forests of South and Central America, are sit-and-wait predators famous for preying on butterflies and dragonflies. Many species have iridescent green and rufous plumage, and long, pointed bills.

Bucconidae. Puffbirds, closely related to jacamars, are sit-and-wait predators found in the lowland tropical forests of South and Central America. Puffbirds have large heads; are boldly patterned in black, white, and brown; and have heavy bills for catching large insects and small invertebrates.

Capitonidae. New World barbets are found in the tropical forests of South and Central America. Brightly colored and boldly patterned, barbets have large bills and feed primarily on fruits. Like other barbets, New World barbets nest in tree cavities.

Ramphastidae. The toucans are found in the subtropical and tropical forests of Central and South America. Most toucans are boldly patterned and have massive, brightly colored, serrated bills. Although primarily frugivorous, toucans also feed on insects and small vertebrates, and raid the nests of other birds for eggs and nestlings.

Semnornithidae. Prong-billed barbets are represented by only two species, the Toucan Barbet (*Semnornis ramphastinus*) of South America and the Prong-billed Barbet (*Semnornis frantzii*) of Central America. The prong-billed barbets primarily eat fruit and, like other barbets, nest in tree cavities that they excavate themselves.

Megalaimidae. The Asian barbets are found in the tropical and subtropical forests of south and southeastern Asia. Brightly colored and boldly patterned, barbets have large bills and feed primarily on fruits. Like other barbets, Asian barbets nest in tree cavities.

Lybiidae. The African barbets are found in a variety of habitats in sub-Saharan Africa, ranging from acacia scrub to tropical forest. The African barbets vary in size and have diverse features: some have the stout bills typical of other barbets, but others have slim bills and feed more extensively on insects.

Indicatoridae. Honeyguides are an odd family of birds: they are all obligate brood parasites, and they are able to eat and digest beeswax. They are most diverse in sub-Saharan Africa but are also found in Southeast Asia. One species is famous for reportedly leading humans and other large mammals to beehives.

Picidae. Found on most continents, but notably absent from Australia, woodpeckers have a suite of adaptations that allow them to use their chisel-like bills to hammer into trees in search of invertebrate prey.

Cariamiformes. This order contains only one family, the seriemas.

Cariamidae. There are only two species of seriemas, both in central South America. With long legs, curved bills, and short crests, seriemas walk the savannas in search of food, feeding primarily on insects but also taking seeds, fruit, and small vertebrates.

Falconiformes. This order contains only one family, the falcons and caracaras.

Falconidae. Falcons and caracaras are a diverse family of diurnal raptors. Recently found to be closely related to parrots and songbirds, falcons are found worldwide. Most falcons are swift aerial predators that catch their prey in their talons, often in mid-air. Caracaras are restricted to the New World and are largely scavengers.

Psittaciformes. The parrots and cockatoos are largely restricted to tropical and subtropical regions, but are popular the world over as pets. Many species are brightly colored.

Strigopidae. The New Zealand parrots are a small family of large parrots restricted to New Zealand and its small surrounding islands. All species have large, strongly hooked bills. They occupy a wide range of habitats, from forest lowlands to alpine habitats. This family includes the largest parrot, the flightless Kakapo (*Strigops habroptila*).

Cacatuidae. Cockatoos are relatively large parrots restricted to Australia and Southeast Asia. They bear distinct crests and feed primarily on fruit and seeds. Most cockatoos are either white or black, with patches of yellow or pink.

Psittacidae. Parrots are largely restricted to tropical and subtropical regions. Popular as pets, parrots are diverse and many are brightly colored. With strong, hooked bills and strong feet, parrots can easily grasp and feed on a wide variety of fruits, seeds, and nuts.

Passeriformes. This huge order of 137 families contains more than half the bird species in the world. The passerines are found around the world in almost every terrestrial habitat. They are also called the perching birds or, more often, songbirds because many species use complex vocalizations and songs. The passerines are hard to generalize: they range in size from large ravens to small kinglets.

Acanthisittidae. New Zealand wrens are found, as their name suggests, only in New Zealand. With relatively long legs, a thin bill, and hardly any tail, New Zealand wrens are energetic insectivores. They represent the ancient sister lineage to all other songbirds.

Pittidae. The pittas are the most diverse family of Old World suboscines. Largely terrestrial, pittas have relatively long legs, short tails, and an upright posture. Most pittas are spectacularly colorful and intricately patterned in a palette of colors including yellow, blue, green, red, and white.

Philepittidae. The asities are endemic to Madagascar. With widely divergent bill shapes, the asities feed primarily on fruit and nectar. During the breeding season, males sport brilliantly colored sky-blue and apple-green wattles.

Eurylaimidae. The broadbills are brightly colored, boldly patterned birds found in the tropical forests of Africa and Southeast Asia. Broadbills feed mainly on insects caught in sallying flights.

Sapayoidae. The Sapayoa (*Sapayoa aenigma*) is a dull, olive-green bird with a fascinating taxonomic history. Part of an ancient, otherwise Old World, radiation of birds, the Sapayoa is found in the lowland tropical forests of southern Central America and northern South America. Sapayoas forage by sallying from branches for insects.

Calyptomenidae. The green broadbills are perching birds from Southeast Asia and sub-Saharan Africa. Most species have large, rounded heads and iridescent, apple-green plumage. The green broadbills, like other broadbills, sally from perches to catch insects.

Thamnophilidae. Antbirds are an extremely diverse group of songbirds from Central and South America. Many are boldly patterned in black, white, and gray. Some species follow army ant swarms to forage on the insects that the ants flush.

Conopophagidae. Gnateaters are a group of small songbirds from the forested neotropical lowlands. With their brown and black plumage, gnateaters are like tiny antpittas (Grallariidae), but with relatively long legs and small, rounded bodies. They usually forage for invertebrates in the branches of understory shrubs.

Melanopareiidae. The crescentchests are songbirds found in scrubby habitats of South America. Boldly patterned in browns and blacks, crescentchests, like wrens, cock their tails as they forage for invertebrates.

Grallariidae. Found in a variety of forest types in the neotropics, antpittas are the duller, New World equivalent of the Old World pittas (Pittidae). Antpittas have a wide range of body sizes, but all are largely terrestrial. With their long legs and upright posture, they often hop when foraging for terrestrial invertebrates.

Rhinocryptidae. Tapaculos are a moderately diverse group of cryptic songbirds found in a wide variety of habitats across South America. With loud but simple whistled songs, tapaculos are more often heard than seen. They are largely terrestrial, and many nest in tunnels dug into the ground.

Formicariidae. Antthrushes are songbirds of lowland tropical forests in Central and South America. More often heard than seen, antthrushes walk on the forest floor with their short tails cocked as they forage for insects.

Furnariidae. The ovenbirds and their allies are an extraordinarily diverse collection of songbirds from Central and South America. Although not colorful, this family sports an incredible diversity of nest types, bill

shapes, and habitat use, from the altiplano of the Andes to the lowland tropical rainforest of Amazonia.

Pipridae. The manakins are small, colorful birds found in neotropical forests where they feed largely on fruits. Some manakins are famous for their lekking displays in which groups of males gather to perform elaborate courtship dances for females, often accompanied by wing-snapping and other mechanical noises.

Cotingidae. Cotingas are a diverse set of songbirds found primarily in neotropical lowland forests. Most cotingas feed only on fruit. Many species in this family have elaborate lek-based courtship displays in which males use spectacular vocalizations and their bright, often iridescent, plumage to attract females.

Tityridae. The tityras and becards, songbirds found only in the neotropics, feed largely on invertebrates by sallying from a perch. These birds have an upright posture, and many are patterned with gray, white, and black.

Tyrannidae. With more than 300 species, the tyrant flycatchers are the most diverse family of birds in the world. They are found only in the New World but occur there in most terrestrial habitats. Many species feed primarily on insects, but some species also eat fruit.

Menuridae. Lyrebirds are found in the eastern forests of Australia. They are arguably the most accomplished avian vocalists and have been known to mimic chainsaws, camera shutters, and cell phones. Male lyrebirds have long tail plumes that are used in their courtship displays.

Atrichornithidae. Scrubbirds are a small family of songbirds with a very restricted range in the coastal scrub of Australia. Cryptically plumaged in brown with extensive barring on the wings, tail, and flanks, they scramble through the scrub and leaf litter in search of invertebrates. Scrubbirds, unlike most birds, lack a furcula (wishbone) and are very poor fliers.

Ptilonorhynchidae. The bowerbirds are found in a variety of forested habitats in Australia and New Guinea. Male bowerbirds construct elaborate bowers, usually from sticks, and decorate them with shells, flowers, fruit, and other items to impress females. Bowerbirds generally are found in the understory and forage for invertebrates and fruit.

Climacteridae. Australasian treecreepers are found in Australia and New Guinea. Although they lack the stiff tail feathers and sharp, chisel-shaped bill of woodpeckers, these treecreepers fill the general niche of woodpeckers in Australia where they scale trees and glean insects from bark and branches.

Orthonychidae. Logrunners are largely terrestrial songbirds found in Australia and New Guinea. Unlike most birds, the logrunners forage in leaf litter by kicking leaves outward to the side, instead of behind them, in search of invertebrate prey.

Pomatostomidae. The Australasian babblers, found across Australia and New Guinea, are highly social songbirds. With decurved bills, strong legs and feet, and long tails, these babblers forage for invertebrates and seeds on the ground and glean tree bark. Adapted to an arid climate, many species have never been observed drinking and are believed to get most or all of their water from food.

Maluridae. The fairy-wrens and grasswrens are a diverse group of small songbirds in Australia and New Guinea with complex breeding systems. Ranging from the bright colors and bold patterns of the fairy-wrens to the cryptic, brown, streaked plumage of the grasswrens, this family is found from tropical forest to Australian scrub desert.

Dasyornithidae. A small family of dull brown Australian songbirds, the bristlebirds are named for the bristle-like feathers above their eyes. They occur in dry scrubby habitats where they feed primarily on insects and seeds gathered from the leaf litter.

Meliphagidae. Honeyeaters are a diverse family found in Southeast Asia, Oceania, and Australia. With thin, pointed bills and tongues with special, brush-like tips, honeyeaters are well adapted for feeding on nectar, although they also eat invertebrates and fruit. Found in a broad range of habitats, many honeyeaters are brightly colored and boldly patterned.

Pardalotidae. These tiny, brightly colored and intricately patterned birds occupy forested habitats in Australia. With short, stout bills, pardalotes feed primarily on invertebrates and on the sap of trees and plants. Unlike many Australian songbird families, there is no evidence of cooperative breeding in pardalotes.

Acanthizidae. Australasian warblers, like many other warbler-like families of the Old World, are a diverse family of small insectivores found in a wide variety of habitats. Most have relatively dull plumage. Many species are cooperative breeders in which the young from previous nesting attempts help parents raise their younger relatives.

Mohouidae. A small family of three species endemic to New Zealand, the mohouids are small songbirds that inhabit a variety of forested habitats. Long considered part of the whistler family (Pachycephalidae), recent

work has shown that these three songbirds represent their own lineage.

Eulacestomidae. The Wattled Ploughbill (*Eulacestoma nigropectus*), whose genus name means "plough-share bill," is a small songbird from the montane forests of New Guinea. Named for their laterally compressed bill and the male's pink wattles, little is known of the biology of this species.

Neosittidae. The two species of sittellas are found in Australia and New Guinea. Sittellas are small songbirds with strong feet and chisel-shaped bills, which they use to scale trees, often upside-down, as they search for invertebrate prey.

Oriolidae. The Old World orioles and figbirds are found in a variety of habitats ranging from gardens to dense forest. Often brightly colored and boldly patterned in black and yellow, orioles feed mainly on fruits and invertebrates. The figbirds typically have duller, olive plumage. All species weave pendant nests hung from branches.

Paramythiidae. This family containing only two species, the Crested Berrypecker (*Paramythia montium*) and the Tit Berrypecker (*Oreocharis arfaki*), is restricted to the montane forests of New Guinea. Both species feed primarily on fruit.

Oreoicidae. This hodgepodge family consists of three species—the Crested Bellbird (*Oreoica gutturalis*), Rufous-naped Bellbird (*Aleadryas rufinucha*), and Crested Pitohui (*Ornorectes cristatus*)—that are grouped on the basis of phylogenetic studies. The Crested Pitohui, like other distantly related poisonous pitohuis, incorporates toxins into its feathers; neither the bellbird nor whistlers do so.

Cinclosomatidae. The quail-thrushes and jewel-babblers are found in Australia and New Guinea. Quail-thrushes are cryptically patterned in browns, black, and white; jewel-babblers are brightly colored and boldly patterned in blue, black, and white. Feeding mainly on invertebrates and seeds, these species forage in the understory of tropical forests.

Falcunculidae. The Crested Shrike-tit (*Falcunculus frontatus*), once part of the large and diverse whistler family (Pachycephalidae), is found in eucalyptus forests and woodlands in Australia. This distinct and boldly patterned songbird uses its strongly hooked, parrot-like bill to tear bark from trees in search of insect prey.

Pachycephalidae. The whistlers and their allies are an extremely diverse family that has colonized many oceanic islands; they are found through Australia, New Guinea, and Southeast Asia. They are brightly colored and many have beautiful songs. Included in this family are many pitohuis, which sometimes have highly toxic plumage.

Psophodidae. Whipbirds and wedgebills are found from arid scrub to tropical rainforest in Australia and New Guinea. With earth-toned plumage, long tails, and a distinct crest, most species are largely terrestrial. Their distinct, whip-like vocalizations are a characteristic sound of eastern Australia.

Vireonidae. The vireos, shrike-babblers, and White-bellied Erpornis (*Erpornis zantholeuca*) are a diverse family with its core diversity in North and South America. Phylogenetic studies recently found that the shrike-babblers and erpornis of Southeast Asia group into this otherwise New World family. With straight, hooked bills, the vireos and their allies feed primarily on insects and other invertebrates.

Campephagidae. Cuckooshrikes occur in a variety of forest types from sub-Saharan Africa through Southeast Asia and Australia. Their long, sleek body and long, graduated tail give them a general appearance similar to cuckoos, but they have the strong, hooked, predatory bills more characteristic of shrikes.

Rhagologidae. The Mottled Whistler (*Rhagologus leucostigma*) is endemic to the montane forests of New Guinea. Once considered part of the large and diverse whistler family (Pachycephalidae), recent work has shown this species to be more closely related to other songbird groups. Little is known of the biology of this brown, streaked songbird.

Artamidae. The butcherbirds and woodswallows are found in Australia and Southeast Asia. Woodswallows, as their name suggests, are aerial insectivores. Butcherbirds have strong, hooked bills and feed on insects and small vertebrates.

Machaerirhynchidae. Boatbills are a small family of two species of small, flycatcher-like birds with relatively long, straight, flattened bills. Brightly colored and boldly patterned in black and yellow, they are found in the tropical forests of northeastern Australia and New Guinea.

Vangidae. The vangas, helmet-shrikes, and wood-shrikes are a morphologically diverse family found mainly in sub-Saharan Africa, with a small group in Southeast Asia. Vangas are found in Madagascar and have evolved a wide array of bill types, including long, decurved bills; short, chisel-shaped bills; and large, inflated bills.

Platysteiridae. Batises and wattle-eyes are tiny but feisty songbirds from sub-Saharan Africa. Batises are boldly patterned in black and white. The wattle-eyes are named

for the brightly colored, fleshy wattle around their eyes. Species occur in habitats from dry acacia scrub to montane tropical forest.

Aegithinidae. Ioras are yellow and black songbirds found in Southeast Asian forests and gardens. With their sharp, thin bills, ioras forage for insects and other invertebrates by gleaning from branches and foliage.

Pityriasidae. The sole member of this family, the Bornean Bristlehead (*Pityriasis gymnocephala*), is a bizarre songbird from the tropical forests of Borneo with a black body, bright red head, and bare crown with yellow bristles. Traveling in social groups, bristleheads feed mainly on large invertebrates.

Malaconotidae. Bush-shrikes are brightly colored and boldly patterned predators found in sub-Saharan Africa. Usually seen hunting from a perch, they feed mainly on insects but also take small vertebrates. Bush-shrikes are well known for the duets males and females sing back and forth to each other.

Rhipiduridae. With their core diversity in Australia and New Guinea, the fantails stretch into Southeast Asia where they are found in a wide variety of habitats. They are relatively small birds with thin, straight bills, and typically drab brown plumage. Fantails are named for their long tails, which they often spread as they forage in order to startle insects.

Dicruridae. Found in the Old World tropics, the drongos are flycatcher-like birds with glossy black plumage and characteristically ornate tail feathers. Found in a variety of habitats, ranging from forest to acacia scrub, drongos catch their insect prey by sallying from perches.

Ifritidae. This family consists of just a single enigmatic species, the Blue-capped Ifrita (*Ifrita kowaldi*). The Blue-capped Ifrita is endemic to the montane forests of New Guinea, where it forages up and down branches for insects, in a manner similar to the widespread nuthatches (Sittidae). The Blue-capped Ifrita is also one of the few species of bird in the world that is toxic, sequestering compounds in its feathers from insects it eats.

Monarchidae. The monarch flycatchers are a diverse Old World group of tropical insectivorous birds ranging from the streamer-tailed paradise-flycatchers of Africa and Asia to the more subdued black-and-white monarchs of Australasia.

Platylophidae. The Crested Jay (*Platylophus galericulatus*), the sole member of this family, is a striking species from the tropical lowland forests of Southeast Asia. With a superficial similarity to many jays (family Corvidae), the Crested Jay is colored black to dark brown with a distinct white neck patch and long crest.

Laniidae. Colloquially termed "butcherbirds" for their habit of impaling their prey—insects and small vertebrates—on thorns, shrikes are a widespread family of birds. They are most diverse in Africa but also are found in North America and Eurasia. Many species are patterned in gray, black, and white with a distinct, dark mask.

Corvidae. The crows and jays are an extremely diverse family of birds that range in size from the large Common Raven (*Corvus corax*) of the northern hemisphere to the Dwarf Jay (*Cyanolyca nanus*) of Mexico. Found worldwide and in nearly all terrestrial habitats, crows and jays have powerful bills, complex social systems, and varied diets.

Melampittidae. Endemic to the montane forests of New Guinea, the Melampittidae consist of two poorly known species, the Greater Melampitta (*Melampitta gigantea*) and Lesser Melampitta (*M. lugubris*). These black, terrestrial songbirds forage for insects and other small arthropods on the forest floor, digging and tossing leaves aside as they search.

Corcoracidae. The White-winged Chough (*Corcorax melanorhamphos*) and Apostlebird (*Struthidea cinerea*) of Australia are highly social cooperative breeders. Although very different in terms of morphology, both species build highly distinctive bowl-shaped nests of mud. Found in open woodlands, these two species forage on the ground for invertebrates and seeds.

Paradiseidae. Found throughout the forests of New Guinea and northeastern Australia, the birds-of-paradise are an extremely diverse family and are a textbook example of the power of sexual selection to create bizarre plumages and display behaviors.

Callaeidae. The wattled crows comprise two highly distinct species from New Zealand. Both the Kokako (*Callaeas cinereus*) and Saddleback (*Philesturnus carunculatus*) have distinct, colorful, fleshy wattles. These two forest-dwelling species feed on insects, fruits, leaves, nectar, and seeds.

Notiomystidae. The Stitchbird (*Notiomystis cincta*) is small and boldly patterned in yellow and black. Closely related to the wattled crows, the Stitchbird has a bizarre mating behavior. An endangered species, the Stitchbird is currently restricted to predator-free islands off New Zealand.

Melanocharitidae. The berrypeckers are a small family of dark-plumaged songbirds endemic to the forests of New Guinea. Berrypeckers feed mainly on insects, fruit, and nectar; their bills range from short and thin to long and decurved.

Cnemophilidae. The satinbirds are a small family of brightly colored songbirds endemic to montane forests on New Guinea. They have a confusing taxonomic history and previously were placed in several other families. Satinbirds feed mainly on fruit and females build dome-shaped nests and care for the chicks alone.

Picathartidae. Rockfowl are represented by only two species, both restricted to the tropical forests of western Africa. These large songbirds have dull gray plumage, but their heads are completely bare with brightly colored skin. Rockfowl build their mud nests in caves and on cliff faces.

Eupetidae. The sole member of this family—the Malaysian Rail-babbler (*Eupetes macrocerus*)—is a strange, largely terrestrial songbird found in the lowland tropical forests of Malaysia. With a long tail and relatively long legs with strong feet, the Malaysian Rail-babbler is patterned in rich browns. Its bizarre vocal display includes the enlargement of two blue air sacs on its throat as it delivers a single long whistle.

Chaetopidae. A relict lineage, the rockjumpers are represented by only two species, both found among high rocky outcrops in southern Africa. Boldly patterned with black, gray, and cinnamon, rockjumpers scramble among rocks with strong feet in search of invertebrate prey.

Petroicidae. The Australasian robins are a diverse family of small songbirds. Found in a variety of habitats in New Guinea, Australia, and New Zealand, these small songbirds feed mainly on insects. Most are have dark plumage above, but some species are spectacularly colorful below, sporting pink, red, or yellow breasts.

Hyliotidae. The hyliotas are warbler-like songbirds from sub-Saharan African forests and woodlands. These insectivores have dark, often glossy, backs and pale, cream-colored underparts.

Stenostiridae. Fairy flycatchers are small songbirds that occur from sub-Saharan Africa through Southeast Asia. Sallying to catch insect prey, these small, often colorful, birds are found in forested and scrub habitat.

Paridae. The tits and chickadees are small, energetic, and vocal songbirds with boldly patterned plumage found across the northern hemisphere and into Africa and parts of Southeast Asia. They often forage in flocks for seeds, fruit, and invertebrate prey in a variety of forested and shrubby habitats.

Remizidae. Most penduline tits are found in the Old World, with one representative in North America. Small, drab birds with short, sharp bills, the penduline tits are named for their woven, often fuzzy, pendulous nests.

Alaudidae. Larks are a large and diverse family of generally dull-colored, cryptically patterned birds that are found worldwide, typically in dry, open habitats. What larks lack in color, they make up for in song, with many species having elaborate aerial vocal displays. Most larks have thin, straight bills and feed mainly on insects, but also eat seeds.

Panuridae. The Bearded Reedling (*Panurus biarmicus*), the sole member of this family, is a small songbird found in marshes across Europe and Asia. Reedlings have long tails, and males have distinct black plumes on their faces. They are highly social and may forage in large flocks for insects and other invertebrates, as well as seeds in the winter.

Nicatoridae. The nicators are a family of only three species in the forests of sub-Saharan Africa. With relatively large, hooked bills, the nicators feed on a variety of invertebrates and small vertebrates. Patterned largely in olive-green with bright yellow spots on the wings, nicators are more often heard than seen.

Macrosphenidae. The crombecs and African warblers are a small family of small, insectivorous birds of sub-Saharan Africa. Found in a variety of habitats, from rocky scree slopes to tropical forest, this group has been recently recognized based on phylogenetic data.

Cisticolidae. A large and diverse family, the cisticolas are found throughout the Old World but reach their peak diversity in sub-Saharan Africa. Usually small, active, warbler-like insectivores, the cisticolas and their allies range from brown and streaked to boldly patterned with gray, black, and yellow. The family is found in a wide range of habitats, from marsh to arid scrubland.

Acrocephalidae. Reed-warblers are small, warbler-like insectivores found throughout the Old World; one species has reached Hawaii. Many reed-warbler species live in marshes and reed beds, but other species occur in a variety of forested and shrubby habitats. Reed-warblers generally have dull plumage, but many are spectacular singers with elaborate, complex songs.

Pnoepygidae. Cupwings, also known as pygmy wren-babblers, are very small songbirds found in Southeast Asia. Occupying the dense forest understory, cupwings generally have dark brown plumage and a very short tail. With a thin, straight bill, cupwings feed on invertebrates.

Locustellidae. Grassbirds and their allies are small, warbler-like insectivores found throughout the Old World. Occupying more open, shrubby, and grassy habitats than other "warbler" families, the grassbirds and their allies generally are brown, some with bold streaking on their breast and back.

Donacobiidae. The Black-capped Donacobius (*Donacobius atricapilla*), the sole member of this family, is a large and conspicuous bird of the lowland Amazon Basin marshes. Pairs sing loudly together from exposed perches. The Black-capped Donacobius is boldly patterned, dark above and buffy below. With a thin, slightly decurved bill, it feeds mainly on invertebrates.

Bernieridae. A small radiation of small, active, warbler-like insectivores, the Malagasy warblers are endemic to Madagascar. With plumage ranging from drab yellow-olive to brown, they are found in a variety of wooded and forested habitats.

Hirundinidae. Swallows are a large and diverse group of aerial insectivores found worldwide. Boldly patterned, generally dark above and pale below, swallows are fast, agile fliers. Swallows construct and use a wide variety of nest structures, from mud domes on cliff faces to tunnels dug into banks.

Pycnonotidae. Bulbuls and greenbuls are a large and diverse family of songbirds from Africa and southern Asia. Found in a variety of forested habitats, members of this family feed on fruit, seeds, insects, and small vertebrates. With relatively long tails, bulbuls and greenbuls generally have plain plumage in browns and olives, but many have brighter faces or undertail patches.

Phylloscopidae. Small, yellow-olive insectivores, the leaf-warblers are a speciose family of birds that for the most part look much alike. With small, thin bills, the leaf-warblers actively glean insects from leaves and branches. They are found in a variety of Old World forested habitats.

Scotocercidae. Bush warblers are small, brown, secretive insectivores. Like many other "warbler" groups around the world, the bush warblers are active birds with thin, straight bills. They are found in a variety of forested habitats from southern Europe through central and south Asia and northern Africa.

Aegithalidae. The bushtits and long-tailed tits are very small, highly energetic birds with dull black, brown, and white plumage, found from western North America through Europe and Asia. The bushtits and their allies are highly social, foraging for insects in wooded habitats.

Sylviidae. Until recently, the sylviids included many groups that now are assigned to other families. The sylviids still include various small warbler-like birds with thin bills for feeding on insects, and the parrotbills with their thick, seed-crushing bills. Members of this family are found in a wide variety of habitats throughout the Old World; one species occurs in western North America.

Zosteropidae. White-eyes and yuhinas are a radiation of small, active, warbler-like insectivores found from Africa through southern Asia and Australia. Variable in plumage pattern, from bright yellow and olive with bold white eye-rings to duller earth tones, the white-eyes and yuhinas are found in a variety of habitats from forest to arid scrubland. Although they feed primarily on insects, many white-eyes also eat fruit and drink nectar using special brush-tipped tongues.

Timaliidae. The tree-babblers and scimitar-babblers, once part of a much larger "babbler" family that has now been subdivided into multiple families, are found in Southeast Asia. With bills ranging from straight and short to long and decurved, they feed primarily on insects and other invertebrates gleaned from leaves and branches. Most species have earth-toned plumage, and build domed or globular nests.

Pellorneidae. Fulvettas and ground-babblers are a diverse group found in Southeast Asia. Occupying a variety of forested habitats, they forage mainly for insects in dense understory vegetation or on the ground with rather short, straight bills.

Leiothrichidae. The laughing-thrushes and their allies are a diverse group of mainly insectivorous birds found from Africa to Southeast Asia. Ranging in size from warbler-like to thrush-sized, and with a dazzling array of blue, yellow, green, and red colors, the laughing-thrushes and their allies are found in a variety of habitats from forest to open acacia–savanna.

Certhiidae. Small, bark-probing birds, treecreepers scale the trunks of trees in search of insect prey. Although they have bright white bellies, most treecreepers are extraordinarily cryptic, with mottled brown upperparts that resemble lichen-covered bark. Treecreepers are found in forests across the northern hemisphere.

Sittidae. Nuthatches are distributed in forests throughout the northern hemisphere. With straight, chisel-shaped bills, most nuthatches forage for insects by descending tree trunks headfirst. Generally, nuthatches are patterned in grays and blacks, but some species are brighter, with blue and rufous coloration.

Polioptilidae. Gnatcatchers are very small insectivores with thin, squeaky voices found in a variety of forested and scrubland habitats from North America to tropical South America. Largely gray with some black patterns, gnatcatchers are known for decorating their small nests with lichen.

Troglodytidae. The wrens are found largely in the New World; a single species is found in Eurasia. Wrens are largely insectivorous, and most are accomplished singers;

many species are known for their complex duets. Wrens can be boldly patterned with browns, blacks, and whites. They often hold their tails upright.

Buphagidae. The two species of oxpecker are found in the savannas of sub-Saharan Africa. Oxpeckers have stout, bright red or yellow bills. They specialize in foraging on the backs of large domestic and wild mammals, from which they pick ectoparasites such as ticks, and eat skin from around wounds.

Sturnidae. Starlings and mynas are diverse across the Old World, although some species have been introduced elsewhere. They are found in a wide range of habitats, from arid scrubland to dense forest, and have similarly diverse diets including nectar, fruit, seeds, insects, and small vertebrates.

Mimidae. Mockingbirds and thrashers are New World songbirds well known for their vocal mimicry abilities and beautiful songs. Found primarily in open, shrubby habitats, the mockingbirds and thrashers feed on a variety of invertebrates and small vertebrates.

Cinclidae. The dippers are remarkable for being the only songbirds that forage underwater, usually in fast-moving mountain streams of the New World and Eurasia. Relatively fat with short, upright tails, dippers walk on the streambed in search of aquatic invertebrates.

Turdidae. The diverse thrushes are found in a wide variety of terrestrial habitats worldwide. Many thrushes have remarkable songs. With straight, thin bills, thrushes feed on fruit, some seeds, and invertebrates. Many species are largely terrestrial and are patterned in earth tones; others are more arboreal and aerial, and some of these are brightly colored.

Muscicapidae. The chats, Old World flycatchers, and allies are a diverse assemblage of songbirds found mostly in the Old World. With a range of feeding ecologies, from small, sallying birds to terrestrial, thrush-like birds, members of this family typically have thin, straight bills and feed largely on insects and other invertebrates.

Regulidae. Kinglets are very small, highly active insectivores of northern hemisphere forests and woodlands. Generally olive-yellow, most kinglets have bright patches of color in the crown, usually yellow, red, or orange. These tiny, vocal, and aggressive birds are able to overwinter in frigid environments by huddling together at night to keep warm.

Dulidae. The Palmchat (*Dulus dominicus*), the only member of this family, is endemic to the island of Hispaniola, where it constructs huge stick nests high in trees that are occupied by multiple pairs. The Palmchat has brown, streaky plumage and forages in groups, primarily on fruit.

Hypocoliidae. The Hypocolius (*Hypocolius ampelinus*), with its pale, gray-brown plumage and distinct black mask, is endemic to the Middle East. It feeds on fruits and insects. The Hypocolius is the sole species of this family; it breeds in loose colonies and gathers in groups during the non-breeding seasons.

Hylocitreidae. The Hylocitrea, or Olive-flanked Whistler (*Hylocitrea bonensis*), is a little-known bird of Sulawesi (Indonesia). Until recently, it was thought to be a member of other families, but phylogenetic work has shown it to be a distinct lineage. This dull, olive-yellow plumaged bird is found in montane forests.

Bombycillidae. Waxwings are a small family found in various forested and shrubby habitats throughout the northern hemisphere. With their silky brown plumage and distinct crest, waxwings are named for the red, wax-like tips of their secondary feathers. Waxwings feed primarily on fruit during winter months but consume invertebrates during the warmer seasons.

Ptilogonatidae. Silky-flycatchers are found from the southwestern USA through Central America. With upright posture, silky plumage, and distinct crests, the silky-flycatchers occur in forested and shrubby habitats where they feed on fruits and sally for insects.

Elachuridae. This newly described monotypic family is found in dense, broadleaf forests in Southeast Asia. Once part of the large babbler family, the Spotted Elachura (*Elachura formosa*) is more often heard than seen, spending much of its time in dense underbrush, where it forages for insects.

Promeropidae. Sugarbirds are endemic to the fynbos habitats of southern Africa, where they specialize in feeding on the nectar from *Protea* flowers with their long, slightly decurved bills. Generally dull brown with faint streaking and yellow on the rump, male sugarbirds have spectacularly long tails.

Modulatricidae. An odd collection of three species without a collective common name, the Spot-throat (*Modulatrix stictigula*), Dapple-throat (*Arcanator orostruthus*), and Gray-chested Illadopsis (*Kakamega poliothorax*) are found in montane regions of sub-Saharan Africa. These three species forage mainly for invertebrates in the dense undergrowth.

Irenidae. Fairy-bluebirds are mid-sized songbirds from the tropical forests of Southeast Asia. Male fairy-bluebirds are spectacularly colored, with bright patches of pale blue contrasting with black and brown. Commonly kept in zoos and aviaries, fairy-bluebirds feed mainly on fruit, but also take insects.

Chloropseidae. Leafbirds are found in the forests of Southeast Asia. As their name suggests, leafbirds generally

have green plumage and spend their time in the treetops. Like other birds that feed on nectar, leafbirds have specialized brush-tipped tongues.

Dicaeidae. The flowerpeckers are small, colorful songbirds of the woodlands and forests in southern Asia and Australia. Typically having short, stout bills, many flowerpeckers feed primarily on fruit and nectar; however, some species are the primary seed dispersers of plants such as mistletoe.

Nectariniidae. The sunbirds of Africa and southern Asia are the Old World equivalent of hummingbirds. Sunbirds have bright, iridescent plumage and long, thin, usually decurved bills that allow them to probe into flowers to drink nectar. Being somewhat nomadic so that they can track the blooming cycle of flowers, sunbirds sometimes gather in mixed-species flocks that forage actively in trees and bushes.

Prunellidae. Accentors are small, largely terrestrial songbirds with relatively drab brown and gray plumage that are found across Europe and Asia. With thin, pointed bills, accentors largely feed on insects and small seeds. The accentors have extraordinary variation in their breeding biology, with one species alone—the Dunnock (*Prunella modularis*)—having four mating strategies.

Peucedramidae. The Olive Warbler (*Peucedramus taeniatus*) is a small, insectivorous songbird found in the pine–oak forests of Mexico and the southwestern United States. Long a taxonomic mystery, the Olive Warbler has now been shown to be most closely related to a group of Old World birds, not to the warblers of the New World that it closely resembles.

Urocynchramidae. Przevalski's Rosefinch (*Urocynchramus pylzowi*), an enigmatic songbird from central China, is found in montane shrubland. This small songbird, with a long, pink tail and a rosy pink wash on its face and breast has long been a taxonomic puzzle, variously placed with the Old World buntings and finches, until recent genetic data showed that is not closely related to any of these groups.

Ploceidae. Weavers are diverse songbirds found in sub-Saharan Africa and southern Asia. Often brightly colored and boldly patterned with yellows, reds, and blacks, weavers are famous for the nests that the males of some species construct from woven grass. The family also includes the widowbirds and bishops, which sport elaborate plumage and courtship displays.

Estrildidae. The waxbills, munias, and their allies are found from Africa through southern Asia and Australia. Although not exhibiting great diversity in size and bill type, these small, seed-eating birds are extremely diverse in plumage and often have brilliant colors and patterns, ranging through yellows, reds, oranges, greens, and purples.

Viduidae. The indigobirds and whydahs are small, colorful, finch-like birds found in sub-Saharan Africa. Similar in many ways to the closely related waxbills and allies, the indigobirds and whydahs are all obligate brood parasites, laying their eggs in the nests of waxbill species. Many males have elaborate songs or plumages used in courtship.

Passeridae. The Old World sparrows and snowfinches have heavy, conical, seed-crushing bills and generally are patterned in shades of brown, black, and white. Birds in this family range from rocky alpine areas to arid desert, as well as urban and rural habitats. Although this group is native to the Old World, the House Sparrow (*Passer domesticus*) has been introduced worldwide.

Motacillidae. Pipits and wagtails are largely terrestrial songbirds that reach their highest diversity in the Old World. Pipits have cryptic plumage, and most are brown with streaks. Many wagtails are boldly patterned with black, white, and yellow. Largely found in open habitats, from tropical savanna to tundra, pipits and wagtails feed mainly on insects.

Fringillidae. This family includes the typical finches, which are small songbirds with conical, seed-cracking bills. It also includes the amazingly diverse radiation of Hawaiian honeycreepers, as well as the colorful and frugivorous euphonias and chlorophonias of South and Central America.

Calcariidae. Found in open habitats across northern North America and Eurasia, the longspurs and snow buntings are strikingly patterned sparrow-like birds with conical, seed-crushing bills. Breeding from arid prairies to tundra, the longspurs are named for their long hind claws.

Rhodinocichlidae. The sole member of this family, the Rosy Thrush-Tanager (*Rhodinocichla rosea*), is a secretive bird with a disjunct range spanning Mexico, Panama, Colombia, and Venezuela. With dark brown to gray plumage, males have a bright pink throat, but they are difficult to see as they forage for invertebrates on the ground within dense thickets.

Emberizidae. The Old World buntings are brightly colored and boldly patterned sparrow-like birds with conical, seed-crushing bills. Occurring across Europe, Asia, and Africa, most Old World buntings are found in open habitats.

Passerellidae. The New World sparrows are a large and diverse family of songbirds, including many conical-billed, seed-eating species. It also includes a number of tanager-like birds, including the bush-tanagers, which feed mainly on fruit. The New World sparrows are found throughout the Americas in nearly all terrestrial habitats.

Zeledoniidae. This family consists of just a single species, the skulking Wrenthrush (*Zeledonia coronata*), which is found in the highlands of Costa Rica and Panama. A difficult bird to see, the Wrenthrush spends much of its time in the dense understory where it forages for insects and other small invertebrates.

Teretistridae. Endemic to Cuba, these two species of warbler-like birds are found in a variety of forested habitats. Foraging mainly on insects and other small invertebrates, the Yellow-headed Warbler (*Teretistris fernandinae*) and Oriente Warbler (*Teretistris fornsi*) are important members of flocks of mixed species.

Icteridae. Breeding from the far northern boreal forest to Patagonia, the blackbirds and allies are medium-sized songbirds that include the bright, colorful New World orioles, raucous grackles, and burbling oropendolas. With diets ranging from seeds and fruit to small vertebrates, species in this family—including the brood-parasitic cowbirds—demonstrate a wide range of breeding strategies.

Parulidae. The New World warblers are similar in ecology and structure to many Old World warbler-like birds with thin, straight bills. They breed in a wide range of habitats throughout the Americas. Unlike their Old World counterparts, many New World warblers are spectacularly patterned and colored with blues, greens, yellows, reds, and pinks.

Phaenicophilidae. The Hispaniolan tanagers, as their name suggests, are endemic to the island of Hispaniola. These four species of tanager- and warbler-like birds, found in a range of forest types, feed mainly on insects and other invertebrates. They generally are white and gray on the undersides with olive green upperparts.

Spindalidae. A family of similar songbird species found on many of the larger Caribbean islands, the spindalises are tanager-like birds that feed primarily on fruit and invertebrates. These species were called "stripe-headed tanagers" previously, and indeed, males in this family are extremely colorful, with striking black-and-white head patterns and yellow, orange, and rufous coloration on the breast.

Nesospingidae. The sole member of this family, the Puerto Rican Tanager (*Nesospingus speculiferus*), is endemic to its namesake island in the Caribbean. Dark brown above and white below, the Puerto Rican Tanager feeds mostly on invertebrates in humid montane forest.

Calyptophilidae. The two species of chat-tanagers are endemic to the Caribbean island of Hispaniola. Previously considered part of the large tanager family, these skulking, difficult-to-see birds of the dense understory are largely brown with a white throat and dusky breast and belly. They spend their time foraging on the forest floor.

Mitrospingidae. There is, as yet, no common name for this recently recognized group of four tanager-like species found in forested habitats from Central America through tropical South America. Feeding on fruits and invertebrates, these species range in color from dull olive-green to bold black-and-white patterns.

Cardinalidae. Cardinals and their allies are found across North and South America. With varied diets ranging from seeds to insects, cardinal species have varied bill types adapted to their specialized diets. Found in a wide range of habitats, many species are very brightly and boldly patterned with reds, greens, blues, and yellows.

Thraupidae. Found throughout Central and South America, the tanagers and their allies are extraordinarily diverse in bill shape and size. They fill many specialized niches, feeding on nectar, fruits, seeds, and insects. Along with many spectacularly colorful and patterned tanagers, this family includes the Galápagos finches and many of the "finches" of South America.

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Chapter 3 How Birds Evolve

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The world of birds abounds with species that seem precisely attuned to their particular way of life. Barn Owls (*Tyto alba*) have such acute hearing that they can localize and catch prey in total darkness. Emperor Penguins (*Aptenodytes forsteri*) have special traits that allow them to swim underwater for more than 10 minutes; Bar-headed Geese (*Anser indicus*) routinely fly over the world's highest mountains. The females of many ground-nesting birds, such as snipe and woodcocks, have such camouflaged plumage that they seem nearly invisible as they sit motionless on their nests. Similarly, some nocturnally active birds, like the potoos of the New World tropics and the frogmouths of the Old World tropics, have feather patterning that matches the bark of the trees in which they roost during the day (Fig. 3.01). These birds even adopt branch-like body postures reinforcing the illusion that they are nothing more than a broken-off stub on a tree.

Choose your favorite group of birds, and you can easily identify other amazing **adaptations**, specialized features molded by evolution. Soaring birds, such as albatrosses and vultures, deploy wing-locking structures that allow them to hold their wings outstretched for hours with little muscle strain. The length and curvature of hummingbirds' beaks usually closely match the shapes of the flowers on which they feed. Jacanas of tropical marshes have greatly elongated toes that help them stroll across floating vegetation. Birds that hide seeds for storage—like many jays, chickadees, and tits—have an unusually large hippocampus, the part of the brain that is essential for remembering locations.

A list of avian adaptations could fill this entire book. Each bird species confronts the challenges of survival and reproduction in a unique way. It is no coincidence, then, that every group of birds has specialized traits that are advantageous in particular settings. At its core, ornithology is fueled by the fascination of the spectacular diversity of avian morphologies and behaviors that match the fundamental challenges faced by birds. The evolutionary process called **natural selection** links these fine-tuned adaptations to their matching environments. Understanding the evolutionary diversity of birds also requires that we explore other kinds of selection, along with the various ways that avian lineages can split apart over time to form new species.

Adaptation: any heritable trait in an individual that has evolved by past natural selection to make birds with the trait more successful at survival and reproduction. All kinds of traits—from subtle aspects of internal physiology to complicated avian behaviors—are potentially adaptations.

Natural selection: an evolutionary process in which the higher survival and reproduction of individuals with favorable inherited traits causes those traits to increase in the population over time.

Opposite: A classic example of adaptive radiation. From a single common ancestor, the vanga group has diversified into 15 genera, each strikingly different in appearance and habits. This Madagascarene species, the Sickle-billed Vanga (*Falculea palliata*), uses its long bill to probe into crevices in trees. (Photograph by Robert Lewis.)

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Fig. 3.01 Adaptations for camouflage. The wondrously crypic plumage of the Great Potoo (*Nyctibius grandis*) combines perfectly with its erect, dead-branch posture—a predator avoidance behavior. This species has also evolved two small notches in its eyelids, an adaptation that permits it to glimpse its daytime surroundings without revealing its huge, night-adapted eyes. (Photograph by Linda S. Martin.)

3.1 Natural selection

Natural selection provides the underlying evolutionary explanation for how these various adaptations have arisen in birds and all other forms of life on earth. As first and famously outlined by Charles Darwin and Alfred Russel Wallace in the late 1850s, natural selection is popularly referred to as "the survival of the fittest." Under the process of natural selection, individual birds with advantageous traits will, on average, have more offspring than individuals without these traits. If these beneficial traits are inherited, the traits will become increasingly common in the population over multiple generations. In relative terms, individual birds that are favored by natural selection to produce the most and best quality offspring are said to have the highest **fitness**. Individual birds with the highest fitness leave the most descendants, thereby passing along their genetic traits to future generations. Although "survival of the fittest" holds true in most cases of natural selection, the process also can operate as "death of the least fit," so that the individuals most poorly suited for the environment or with the least advantageous traits are weeded out of the population.

3.1.1 Four conditions for natural selection

Considered in a bit more detail, natural selection is an inevitable outcome when four basic biological conditions are met. First, natural selection can act only when differences exist among individual birds in a population. Because every wild bird is genetically unique (Box 3.01), this condition is always met. When closely observing a group of birds (Fig. 3.02), differences among individuals oftentimes are readily apparent—for example, in any flock of starlings feeding on a lawn, individual birds will differ in plumage pattern, body and beak size, state of molt, and behavior, among other characteristics. Researchers who study wild bird populations often amass large databases on these types of individual differences, because even subtle variations can be critical components of a bird's ability to survive or reproduce.

The second condition for natural selection requires that at least some of this individual variation must be **heritable** so that it can be passed down to future generations of birds. Only some of the differences among individuals are inherited, because some variation is generated by environmental conditions or by various experiences during a bird's lifetime. This dichotomy often is termed "nature versus nurture," with "nature" being inherited variation and "nurture" being the variation caused by the environment. This distinction is important because the environment can have a substantial impact on an individual's development and overall survival. For example, the bills of Eurasian Oystercatchers (*Haematopus ostralegus*) will abrade into a range of different shapes depending on an individual's diet and foraging technique (van de Pol et al. 2009). Oystercatchers that mostly probe the mud for worms experience the least abrasion; their bills remain long and pointed. A different individual may instead hunt shellfish via stabbing, quickly wearing its bill into a chisel-like shape. Preferring brute force, still other oystercatchers hammer shellfish open, inadvertently forming short and blunt bills. In many places, oystercatchers with these various bill shapes forage side by side. However, they do not pass along their particular bill type to their offspring, as the bill shape itself is a product of an individual's reaction to its environment. In fact, when an oystercatcher's diet is changed in captivity, its bill shape shifts to match the new conditions—and the foraging behaviors themselves are learned and not inherited. Therefore, the various bill shapes in oystercatchers are not heritable; they are the product of "nurture" rather than of "nature" and are not directly influenced by natural selection.

Although some of the characteristics measured in wild birds are affected by the bird's environment, many traits have high heritability. Studies of wild birds show that

Fitness: the relative success of an individual—compared with other individuals in their population—in passing along their own genes to later generations.

Heritability: the proportion of the variation in a trait that is due to underlying genetic variation.

Box 3.01 Is every bird unique?

Reproduction in birds requires that a female mate with a male. In some birds, the fathers contribute little more to their offspring than their sperm, but this basic genetic contribution is essential. The offspring inherit half of each parent's total genetic material; because each chick gets a different mix of its parents' DNA, each one is genetically unique, just like most human siblings.

There are two exceptions to these rules, but both are very rare. Twin birds, which develop within the same egg, have been reported from a broad range of bird species. Although twin embryos almost always die before the egg hatches, two chicks have hatched successfully from the same egg on occasion. Only one such case—a pair of captive hatchlings that emerged from one unusually large egg on an Emu (*Dromaius novaehollandiae*) farm in New Zealand—has been investigated genetically; test results revealed that the birds were identical rather than fraternal twins. Both Emu twins survived and grew, although initially they were smaller than typical chicks of the same age (Bassett et al. 1999).

On a few extremely rare occasions, female birds have reproduced via parthenogenesis, without any sperm from a male at all. Parthenogenetic development occurs regularly in a few breeds of domestic turkeys and chickens, and it has been documented rarely in captive Zebra Finches (*Taeniopygia guttata*) and Rosy-faced Lovebirds (*Agapornis roseicollis*). Surviving offspring (an uncommon phenomenon in and of itself) in all these cases inherit a subset of their mother's total genetic variation, but they are not her exact clones; in fact, these offspring usually are male. No case of avian parthenogenesis has yet been documented in the wild.



Fig. 3.02 Individual variation. A flock of Budgerigars (*Melopsittacus undulatus*) demonstrates how individuals may appear indistinguishable at first glance. A closer look reveals discernable individual variation in the plumage of different birds. The same generalization is true of other traits, including genetic variation. (Photograph by Irby Lovette.)

genetics often accounts for 50–90% of the variation in morphological features such as bill size, wing length, and adult body weight; that is, much of the variation in those traits is passed down from parent to offspring. Perhaps more surprisingly, many bird behaviors also have a strong heritable component. For example, in the Western Bluebird (*Sialia mexicana*) of North America, levels of aggression toward other bluebirds (Duckworth and Kruuk 2009) and the propensity to engage in helping at a relative's nest (Charmantier et al. 2007) (Chapter 9) are substantially



Fig. 3.03 Heritable behavioral traits. Useful in nest defense, aggression can be heritable. Here, a Western Bluebird (*Sialia mexicana*) pair attacks a simulated territorial intruder (a Tree Swallow, *Tachycineta bicolor*, in the wire cage). (Photograph by Alex Badyaev, tenbestphotos.com.)

heritable behavioral traits (Fig. 3.03). In Great Tit (*Parus major*) populations studied in Europe, behaviors with a well-documented heritable basis include the willingness to explore new environments (van Oers et al. 2004) and the timing of egg laying (Garant et al. 2008).

A third condition underlying natural selection is the difference in how many offspring individuals produce, or their **reproductive success**. Individual birds within a population differ in their ability to produce viable offspring. In evolutionary terms, this reproductive disparity among individuals is the most direct measure of their variation in lifetime fitness. This variability is another precondition for natural selection that probably is always in operation for natural bird populations, because reproductive success always varies among individuals. Reasons include both chance events (e.g. a storm that kills a bird before it has a chance to breed) and intrinsic quality differences among individuals (e.g. good body condition in a male that helps him attract several mates).

Reproductive success: the number of viable offspring produced by an individual over their lifetime.

Lek: an aggregation of males that engage in competitive mating displays towards visiting females.

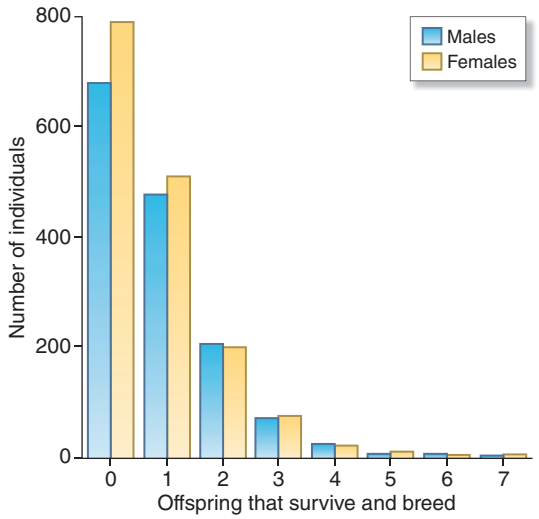


Fig. 3.04 Lifetime reproductive success. In Collared Flycatchers (*Ficedula albicollis*), most males (blue) and females (gold) produce zero or one offspring during their lives that survive to become breeders themselves; only a few exceptional birds of this species produce five or more successful offspring. (From Merilä and Sheldon 2000. Reproduced with permission from University of Chicago Press.)

For logistical reasons, it often is extremely difficult to track the reproductive success of an individual wild bird throughout its entire lifetime. Ornithologists therefore often measure fitness in units of "successful nests" or "number of chicks fledged" in one or several years. Nonetheless, a better way to measure fitness is to track how many of an adult's total offspring survive to reproduce as adults themselves, because this is the most accurate index of this original parent's direct genetic contribution to future generations.

Despite the challenges in gathering this type of information, individual birds have been monitored throughout their lifetimes in some decades-long studies. One such long-term study has tracked reproduction in the Collared Flycatchers (*Ficedula albicollis*) that breed on the island of Gotland in Sweden (Merilä and Sheldon 2000) (Fig. 3.04). Lifetime data on nearly 2000 of these flycatchers show how reproductive success varies among individuals: almost half of all adult flycatchers ultimately failed to produce even a single offspring that went on to breed itself; about half of the flycatchers reared one to three successful offspring that reproduced successfully; and only a tiny fraction of breeders—those with the highest fitness of all—produced four or more offspring that later had chicks of their own.

Individual Collared Flycatchers differ substantially in their lifetime reproduction, but other birds show even greater variation in this fundamental measure of evolutionary success. For instance, variation in individual fitness is taken to the extreme in lekking species (Chapter 9). In a **lek**, many males display to females, generally in close

proximity to one another. Depending on the species, a lek consists either of one space where multiple males congregate in order to impress visiting females or multiple, spaced-out display areas that double as a particular male's breeding territory. Each visiting female generally chooses the single most attractive male as her mate. Lekking birds include the Ruff (*Calidris pugnax*) of Eurasia, many grouse species in North America, most manakins in Central and South America, and New Guinea's birds-of-paradise. In most avian leks, the dominant male mates with nearly all the visiting females. This creates a great disparity between his high reproductive success and the negligible success of the less dominant males. Commonly, male dominance at a lek is associated with longevity: the male who displays at the lek for the greatest number of years rises to the top position. In these situations, the lifetime reproductive success of a dominant male is closely related to his ability to survive.

The fourth and final condition necessary for natural selection integrates the previous three: higher reproductive success must be associated, on average, with heritable differences among individuals. In other words, fitness is not random; instead, it relies on heritable traits that help some individuals survive and reproduce better than others.

Under these four conditions, any traits that create a fitness advantage for an individual are more likely to be passed along. As they are passed down through multiple generations, these beneficial traits become more and more prevalent in the population. This process of natural selection occurs at all times in subtle ways, and over an evolutionary timescale it produces the wondrous adaptations that match different birds to their ways of life.

3.1.2 Avian examples of natural selection

Birds provide countless examples of natural selection acting on wild populations, often during the short timeframe of a single research project. Without a doubt, the most comprehensive study of natural selection in birds focuses on the finches living on one tiny island in the Galápagos Archipelago (Box 3.02), where a long-term field study has become a

Box 3.02 Natural selection in Darwin's finches

Natural selection is simple in principle and pervasive in nature, but documenting natural selection with absolute certainty in the wild remains a challenge. In any field study, there usually are practical or logistical barriers to the collection of important data, including the heritability of relevant traits, the survival and entire lifetime reproduction of all individuals in a population, or other prerequisites of evolutionary processes.

One of the most famous of all field studies of birds has been led by Peter and Rosemary Grant of Princeton University (Grant 1986). Since 1973, the Grants and their many students and colleagues have followed the fates of the populations of Darwin's finches on the tiny Isla Daphne in the center of the Galápagos Archipelago. The environment on that island is highly cyclical: in rainy years, food is both abundant and varied, and the finches follow with high survival and reproduction. In contrast, during occasional droughts, which may span several years, very few seeds or insects are available, and many finches die of starvation.

Over the past four decades, the Grants have banded and measured all the finches on Isla Daphne: the tens of thousands of birds hatched there, and the few that have flown in from nearby islands. They have monitored the survival and reproduction of every individual finch for its entire lifetime, allowing them to associate each bird's fitness with the particular traits that have made it more or less successful at surviving and producing offspring. As generations of finches have hatched and died, the researchers also monitored the climate of the island, along with the types and abundance of seeds and other food available to the finches in each season.

An early and now classic outcome of this work is clear documentation of strong natural selection acting upon the most common finch species on the island, the Medium Ground-Finch (*Geospiza fortis*) (Fig. 3.B2.01), during a severe drought in 1976 and 1977. In periods of low rain, most of the vegetation on Isla Daphne withers; the finches then subsist on seeds that they find in the soil. As the harsh conditions continued into 1977, seeds became more and more scarce. Many birds died of starvation, and the finch population plummeted from 1400 birds to a mere 200 survivors. The scavenging finches ate the smaller, more easily cracked seeds first; by the end of the drought, the few remaining seeds were mostly large and tough, and therefore difficult for most finches to open.

Because the Grants measured the finches both before and after the drought, they were able to show conclusively that the surviving finches had larger bills than the ones that died. The overall size change was subtle—the average finch bill depth increased just under 1 millimeter—but experiments showed that even this modest increase in bill size is enough to make a life or death difference when finches must crack large seeds in order to survive. In the years just after the drought, these relatively large-beaked surviving finches bred with one another, and the increased beak size

Continued



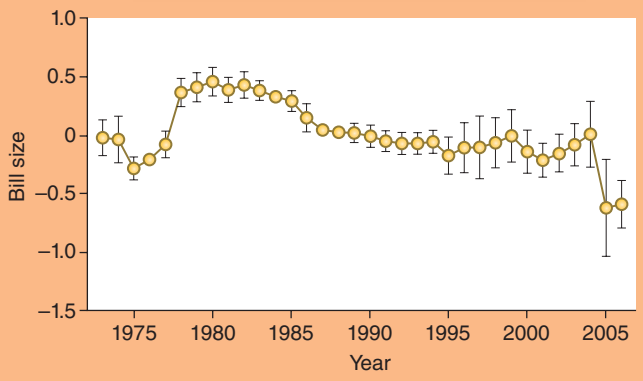


Fig. 3.B2.01 Documenting natural selection. Bill size (a combination of several measurements, including width and length) among Medium Ground-Finches (*Geospiza fortis*) on tiny Isla Daphne in the Galápagos is plotted from 1973 through 2006. Increases and decreases in bill size often correspond to periods of varying natural selection on this trait. (From Grant and Grant 2006. Reproduced with permission from AAAS. Photograph by Oleg Chernyshov.)

caused by this bout of natural selection was inherited by the following generation of finches.

The natural selection on finches during the 1977 drought now has become a textbook case study of natural selection, but the story continues to the present day. It turns out that the variable environment of Isla Daphne imposes different selection pressures at different times. For example, during wet periods tiny seeds are most abundant; then the smallest-beaked finches have high fitness, and the average beak size decreases accordingly via natural selection. The Grants now have documented a series of natural selection cycles in which the average finch beak size has tracked the changing nature of the seed crop on the island.

Sometimes the pressures on Isla Daphne change in even more complicated ways (Grant and Grant 2006). In 1982, a substantially larger-beaked species called the Large Ground-Finch (*Geospiza magnirostris*) colonized Isla Daphne; these appropriately named birds are adept at cracking even the largest seeds, and their population on the island grew steadily. Harsh conditions in 2004–2005 closely resembled those of the famous 1976–1977 drought, but this time the Medium Ground-Finches were in competition for the largest seeds with the now numerous Large Ground-Finches. Accordingly, the beak sizes of the Medium Ground-Finches did not increase as seen in 1977, but rather declined sharply via natural selection, because the individuals who survived this more recent drought were the ones that could specialize on the tiniest of the remaining seeds.

model for evolutionary investigations of all types of organisms. A tale of avian natural selection with an even more venerable history dates back to 1898, when 136 stunned and nearly frozen House Sparrows (*Passer domesticus*) were gathered by hand from the campus of Brown University in Rhode Island (USA) following a particularly cold and wet winter storm. Moved into the warmth of the laboratory of professor Harold Bumpus, more than half of the sparrows recovered, but the rest died. Comparing measurements of the surviving and deceased sparrows, Bumpus (1898) found that the survivors generally had body shapes that were near the average for the population, whereas the dead sparrows tended to have body measurements that were either larger or smaller than average (Fig. 3.05). He interpreted this pattern as evidence for an episode of natural selection in which the unusually cold conditions culled individuals with the more extreme traits. Subsequent analyses of his original data have challenged some of Bumpus' bolder conclusions, but his study remains famous as the first detailed exploration of natural selection in any wild bird population.

Similar episodes of natural selection on traits such as body size have been documented using modern study techniques. In 1996, Cliff Swallows (*Petrochelidon pyrrhonota*) returning to breed in the Great Plains region of North America encountered a long, late spring storm that grounded the flying insects on which these swallows feed. More than half the adult swallows perished of starvation; the survivors had, on average, larger bodies and accordingly greater reserves of stored fat. This increase in body size was maintained over at least the subsequent decade (Brown and Brown 1998, 2011). Similar processes of natural selection can occur even in the absence of extreme weather conditions. For example, Social Weavers (*Philetairus socius*) in South Africa breed in huge colonies. In some years, the weavers with the highest survival are those with intermediate body size: smaller birds suffer a higher risk of starvation, but the larger birds have difficulty maneuvering and thus are captured more often by predators such as the Gabar Goshawk (*Micronisus gabar*) (Covas et al. 2002).



Fig. 3.05 Survival and body size. An early study of natural selection found that House Sparrows (*Passer domesticus*) of medium size tended to survive better during periods of unusually cold temperatures than did atypically larger or smaller birds of the same species. (Photograph by Susumu Kishihara.)

Changes likely resulting from natural selection have been seen in bird populations that have recently colonized new areas. For example, in 1957 a group of about 200 Great Kiskadees (*Pitangus sulphuratus*) was captured in their native Trinidad and released on the island of Bermuda. Although these predatory flycatchers failed in their hoped-for role of controlling previously introduced lizards, they quickly became one of the most common birds on Bermuda. Later comparisons of the Bermudian and Trinidadian Great Kiskadees showed that the Bermuda birds evolved larger body sizes in only a few generations (Mathys and Lockwood 2009). Similar increases in the body size of birds that have colonized new islands have been documented many times, including the Capricorn Silver-eye (*Zosterops lateralis*) on islands off the east coast of Australia (Clegg et al. 2008).

3.1.3 Kin selection and indirect fitness

The number of offspring an individual bird produces—its lifetime reproductive success—determines its direct genetic contribution to the next generation and hence its **direct fitness**. There are also indirect ways that a particular bird's genes can be represented in future generations, because its relatives share a substantial portion of the same genetic material. The math works in birds just as it does in humans: a given parent shares 50% of its DNA with each of its chicks; full siblings also share 50%, half-siblings 25%, first cousins 12.5%, and so on. Birds can gain substantial **indirect fitness** if their close relatives produce many offspring. Thus, when measured in a genetic context, a bird's **total fitness** is the sum of its direct fitness (via the offspring it produces itself) and its indirect fitness (via the portion of its genetic material that is passed down by its relatives to their chicks).

This concept of indirect fitness was formalized in the mid-1960s by theoretical biologist William Hamilton, who realized that it provides a powerful explanation for why some animals forgo reproduction of their own, expending their time and energy to help their relatives reproduce instead. **Hamilton's Rule** describes this concept: a bird should help its relatives—even if it loses direct fitness—as long as its behavior results in an overall gain in its total fitness.

The various ways in which birds indirectly pass along their genes fall within a subset of natural selection termed **kin selection**. Related topics, such as altruism and cooperative breeding behaviors, are covered in more detail in Chapter 9, but one example here illustrates the basic concept. Florida Scrub-Jays (*Aphelocoma coerulescens*), found only in their namesake Florida (USA), defend territories within a unique—and increasingly uncommon—type of oak scrub habitat. Most jay territories host a group of relatives, usually a breeding pair and some of their offspring from previous years. During the nesting season, "stay-at-home

Direct fitness: the fitness an individual bird gains through its own production of offspring; direct fitness is usually measured via a bird's lifetime reproductive success.

Indirect fitness: the component of an individual's fitness that results not from their own reproduction, but rather by the aid they give to relatives that then enhances their relative's reproductive success.

Total fitness: the sum of direct fitness via the individual's own reproduction plus their indirect fitness via their relative's reproduction. Sometimes also termed "absolute fitness."

Hamilton's Rule: the formula that describes when an individual should forgo its own reproduction and instead help its relative reproduce. One formulation of this idea suggests helping should be favored when $rB > C$, where r is the genetic relatedness of the individual and its breeding relative, B is the additional number of offspring this helping behavior will add to the relative's reproductive success, and C is the cost to the helper in the form of offspring that they cannot produce themselves if they invest instead in helping their relative.

Kin selection: natural selection arising through indirect fitness, via the reproduction of relatives that are aided by an individual.

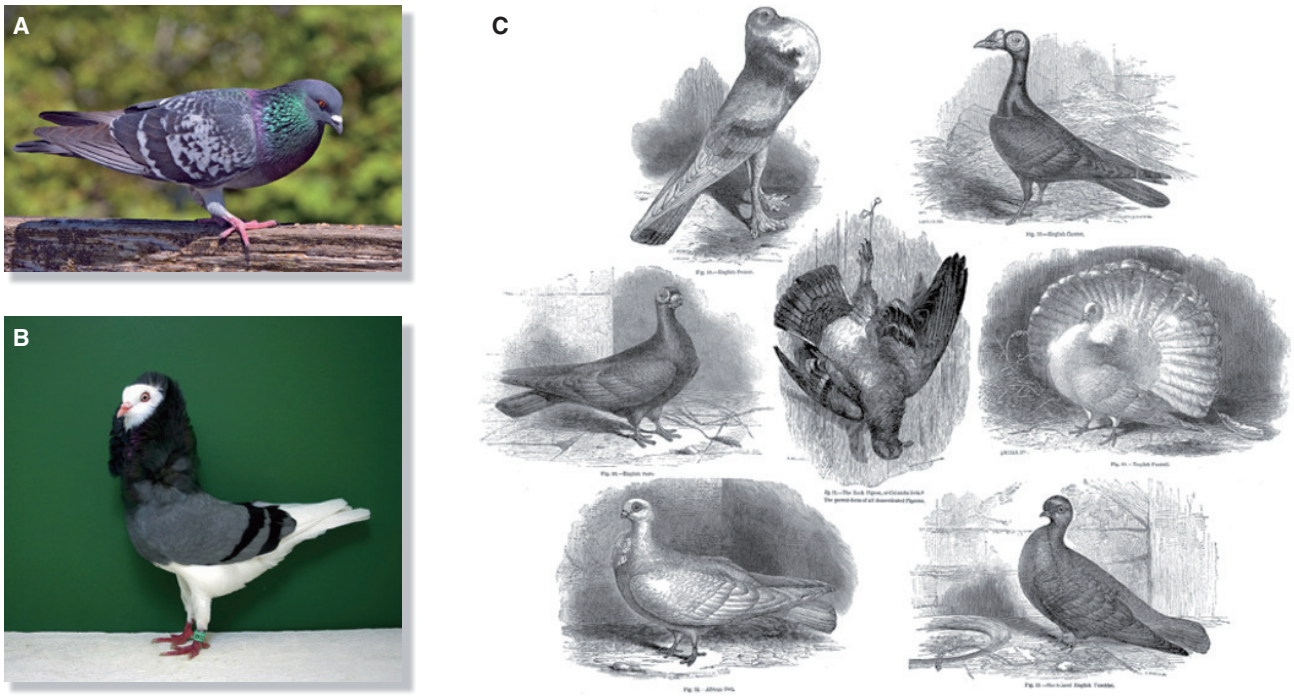


Fig. 3.06 Elaborate plumage through selective breeding. (A) From just one species, the wild Rock Pigeon (*Columba livia*), humans have selectively bred over 350 distinct domestic pigeon varieties. (B) Each such domestic breed is prized for a suite of elaborate and sometimes bizarre plumage characteristics, body shapes, bill formations, and vocalizations. (C) Charles Darwin used artificial selection (or selective breeding) of pigeons as an example of how selection for specific genes can dramatically change the phenotype of an organism. (Photographs by: A, Elaine R. Wilson; B, Layne Gardner; C, from Darwin 1868, public domain.)

jays" aid their parents by defending the boundaries of the territory against neighboring groups of jays, mobbing predators, and bringing food to the nestlings. Genetic studies show that these Scrub-Jay helpers never receive direct fitness (Townsend et al. 2011); they do, however, receive indirect fitness via every younger relative that they help raise. Because jay territories usually fill the limited scrub habitat, and because breeding vacancies arise only rarely, it makes evolutionary sense for these jays to stay at home and help their relatives unless they are unusually fortunate in finding a breeding territory of their own.

3.1.4 Artificial selection in birds

In his book *On the Origin of Species* (1859), Charles Darwin highlighted the many parallels between natural selection as it occurs in the wild and the **artificial selection** that animal breeders have imposed on domesticated species, consciously or unconsciously, for millennia. In assembling his evidence for natural selection, Darwin became fascinated by the dozens of breeds of domestic pigeons that amateur fanciers had produced through selective breeding for traits such as elaborate plumage, homing ability, and unusual body shapes (Fig. 3.06). Darwin kept more than 20 such breeds himself, and he noted that their differences were so extreme that, had the pigeons been wild birds, ornithologists likely would have described each breed as a unique species—or, in some cases, even a distinct genus (Chapter 2). However, Darwin also recognized that all of these remarkably diverse pigeon breeds traced their ancestry back to the wild Rock Pigeon (*Columba livia*), and that their differences had arisen over only a few thousand years as human breeders selectively mated male and female pigeons to enhance particular traits.

Artificial selection: the evolutionary process analogous to natural selection that results when humans are the selective agent that determines which individuals are allowed to reproduce; often this occurs when humans selectively breed individuals for desirable traits.

This process of artificial selection on pigeons continues, and now there are even more distinct pigeon breeds than Darwin saw. Other familiar birds also have been subject to intense artificial selection, perhaps none more so than the domesticated chicken. Chickens trace their ancestry back to the Red Junglefowl (*Gallus gallus*), which was domesticated in Southeast Asia and China by 3200 BC (Kanginakudru et al. 2008) and perhaps even as early as 8000 BC. As with pigeons, selective breeding of chickens has produced



Fig. 3.07 A sexually selected trait. The ornamental secondary flight feather extensions of a male Standard-winged Nightjar (*Caprimulgus longipennis*) hinder its foraging efficiency. A male's ability to survive with this burden likely demonstrates his quality to potential mates and rival males. (Photograph by Paul Cools, https://commons.wikimedia.org/wiki/File:Standard-winged_Nightjar_1.jpg. CC-BY-SA-3.0.)

hundreds of distinct breeds, each with a characteristic suite of traits. In modern times, chicken breeders have imposed extremely intense artificial selection on traits that enhance economic returns from the breeds that are farmed commercially. For example, Sue Jackson and Jared Diamond (1996) raised chicks of wild junglefowl and commercial broiler chickens under identical conditions. They found that domesticated chicken hatchlings were three times heavier than just hatched junglefowl chicks and that the young chickens also grew much faster. This difference highlights the outcome of past artificial selection on the domesticated ancestors of chickens, which favored traits such as large breast muscles, large body size, and rapid growth. Anatomically, this selection also increased the size of the chickens' digestive tracts, but it decreased the size of the chickens' brains and leg bones, as compared with their wild junglefowl relatives, which had experienced a history of very different selection pressures imposed by the challenges of finding food, attracting mates, and avoiding predators.

The results of artificial selection also are evident in pet stores that sell other species of birds commonly bred in captivity. Wild Budgerigars (*Melopsittacus undulatus*) in their native Australia have bright green underparts and mottled yellow upperparts (Fig. 3.02), but artificial selection on captive Budgerigars has produced birds in a rainbow of plumage colors. Similarly, other popular cage birds such as Zebra Finches (*Taeniopygia guttata*) and Rosy-faced Lovebirds (*Agapornis roseicollis*) have been bred selectively to produce a variety of plumage colors and patterns.

3.2 Sexual selection

The process of **sexual selection**, a special type of natural selection driven by access to mating opportunities, has produced some of the most conspicuous and spectacular traits of birds. In many ways, a bird's level of fitness depends on how well it can attract mates or compete for them with other members of its sex, and often both these avenues of sexual selection play an interconnected role in the failure or success of an individual's attempt to mate. Male Indian Peafowl (*Pavo cristatus*) are rightly famous for their enormous and dazzling tails. In the breeding season, male Standard-winged Nightjars (*Caprimulgus longipennis*) from the savannas of central Africa grow giant, flag-like extensions of their secondary flight feathers (Fig. 3.07)—a remarkably costly ornament for a bird that feeds on aerial insects. Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) in Australia weave elaborate display arenas, which they decorate with seashells, scavenged feathers, and (nowadays) brightly colored bits of plastic. Andean Cock-of-the-rock (*Rupicola peruvianus*) males gather together in leks where they perform energetic displays for visiting females. Male Brown Thrashers (*Toxostoma rufum*) in eastern North America have repertoires of thousands of distinct song types that they sing throughout the breeding season. These are all conspicuous examples of traits that likely have arisen via the process of sexual selection.

Sexual selection may involve traits seen in both male and female birds, but there are underlying biological reasons that explain why most highly conspicuous such traits—like the Indian Peafowl's (*Pavo cristatus*) train of showy tail feathers—reach their extremes in males rather than females. The constraints of reproduction set up a fundamental difference

Sexual selection: a special form of natural selection that involves the differential reproductive success of individuals that arises specifically from competition over mating opportunities; this can involve direct competition with members of the same sex or competition to attract members of the opposite sex.

between the sexes: the reproductive output of a female bird is most fundamentally limited by the number of eggs she can produce and chicks she can rear, whereas the reproductive output of a male is typically limited instead by the number of females with whom he can mate. This difference explains why, in most bird species, the male rather than the female performs elaborate songs or mating dances, acquires and defends resources, or boasts conspicuous plumage.

Even the exceptions to this pattern serve to illustrate the general rule. About 1% of all birds adopt a polyandrous mating system (Chapter 9) in which males provide most or all of the post-laying care to the eggs and chicks, and females mate with multiple males in the same breeding season. Under this reversal of the typical avian sex roles, females must compete to attract males, often more than one within a single breeding season. These polyandrous females therefore are subject to relatively intense sexual selection via mate choice; as a result, in most polyandrous bird species the typical trend is reversed, with the females being larger or more conspicuously colored than the males. Well-studied birds with this type of **reverse sexual dimorphism** include the Spotted Sandpiper (*Actitis macularius*) (Oring and Lank 1982) and the three phalarope species (genus *Phalaropus*) of North America (Reynolds 1987) (Fig. 3.08), the Bronze-winged Jacana (*Metopidius indicus*) of India (Butchart 2000), the Wattled Jacana (*Jacana jacana*) of Central America (Emlen and Wrege 2004), and the Black Coucal (*Centropus grillii*) of Tanzania (Goymann et al. 2004).

3.2.1 Sexual selection and mate attraction

The general phenomenon of sexual selection often is divided into two subcategories, both of which are widespread and important in birds. The first, which involves one sex choosing individuals of the other sex, is called **intersexual selection**. Because female birds are often the "choosy" sex, this subcategory also is sometimes referred to as "female choice," but the use of this terminology is waning because males sometimes are choosy as well. However, because females usually are the choosier sex in birds, much of the discussion below (and in Chapter 9) approaches this phenomenon from a choosy female perspective (Box 3.03).

Some males prove their worth by providing **direct benefits**: when a female mates with a high-quality male, she often obtains various types of resources that increase her own fitness. For example, in a large aggregation of communally nesting birds, the nesting sites at the center of the colony are often less exposed to predators. Females prefer to pair with the males that can best defend a central position because they benefit directly from this. Likewise, for birds that defend large territories, the territories with the most food, densest cover, or optimal nesting locations are often in short supply. Females choose to pair with males that can monopolize the best area of habitat. In practice, it is often difficult for field biologists to determine exactly what these females are selecting: are they choosing the most attractive male, the highest quality territory, or basing their choice on some combination of this and other information?

Sometimes the direct benefits for females are more readily defined. Many birds engage in **courtship feeding**,

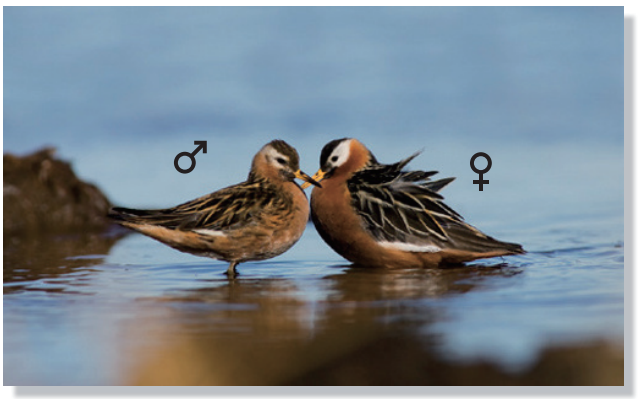


Fig. 3.08 Reverse sexual dimorphism. In some species, females exhibit more elaborate plumage and larger body size. For example, Red-necked Phalarope (*Phalaropus fulicarius*) females have more striking coloration than males. (© Roy Mangersnes, naturepl.com.)

Reverse sexual dimorphism: a situation in which the sex that is usually smaller or less ornamented is the larger or more conspicuous sex in a particular species. In birds, sexual selection is usually stronger on males, so reverse sexual dimorphism refers to species where females are the flashier sex.

Intersexual selection: a subset of sexual selection, one involving the reproductive success of individuals that depends on the actions of the opposite sex. In birds, intersexual selection often (but not always) involves mate choice by females who are selecting among potential male mates.

Direct benefits: the tangible benefits that a mate derives directly from their partner, such as food, access to a good territory, protection from predators, or a high-quality nest site.

Courtship feeding: a behavior in which one member of a pair (usually the male) presents his potential partner with food during courtship or before mating. The food item is sometimes termed a "nuptial gift" and this behavior is an important part of pair bonding in some bird species.

Box 3.03 Sexual selection in Barn Swallows

Barn Swallows (*Hirundo rustica*) are the world's most naturally widespread songbird. In part because they nest on buildings and therefore are relatively easy to monitor, these swallows have become a model species for studying the interactions between natural and sexual selection.

Anders Møller (1988) conducted an extensive series of selection studies on Barn Swallows in Europe. Through a series of observations and experiments, Møller has shown that sexual selection strongly dictates the tail length of male swallows, because females prefer to mate with longer tailed males. These birds feed only on aerial insects; therefore it is important for them to be fast, highly maneuverable fliers. Because the tail of male European Barn Swallows is longer than the aerodynamic optimum, males pay a maneuverability price for the trait that helps them attract mates.

Barn Swallows in other places face different selection pressures, and this species has strong geographic variation in tail length and other plumage traits. For example, male Barn Swallows in North America have substantially shorter tails than their European counterparts (Fig. 3.B3.01A, B). In addition, in place of the snowy white breast feathers seen in European Barn Swallows, North American birds are reddish brown when viewed from below. Studies by Rebecca Safran and her colleagues (2005) show that in North America, females do not strongly select for male tail length. Instead, female North American Barn Swallows prefer males with the darkest breast feathers.

Even more intriguingly, Barn Swallows in Israel have both long tails and richly colored underparts (Fig. 3.B3.01C). There, females pay attention to both breast coloration and tail length (Vortman et al. 2013). Considered in concert, these discoveries illustrate how the traits targeted by sexual selection can differ even among bird populations of the same species.

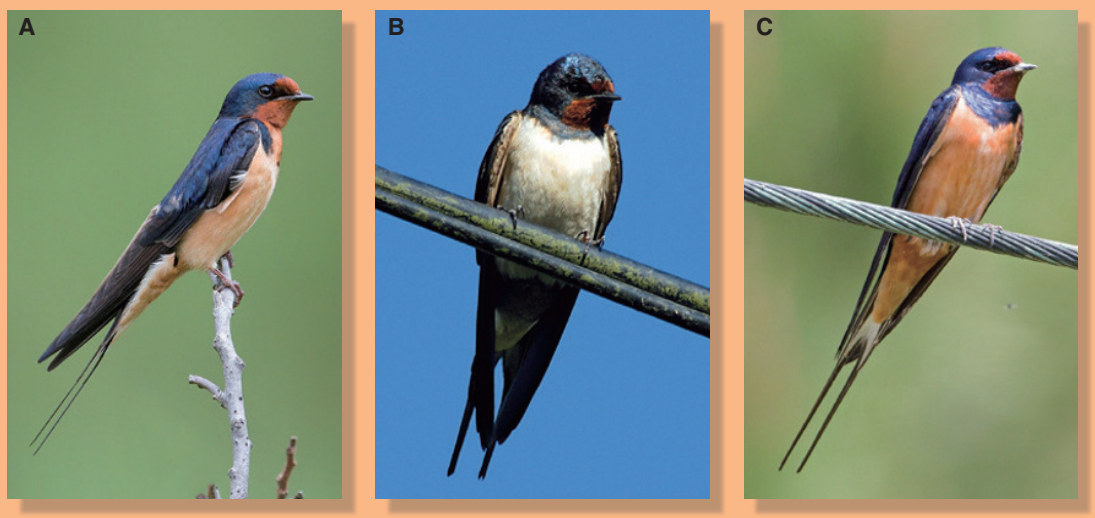


Fig. 3.B3.01 Phenotypes vary in different populations. Barn Swallows (*Hirundo rustica*) from (A) North America, (B) Europe, and (C) Israel differ in the reddishness of their plumage and the lengths of their tails. Females in these different populations prefer mates with different combinations of these traits. (Photographs by: A, Anupam Dash; B, Alan Cherry; C, William Vivarelli.)

in which the male presents food items to the female as part of a pair-bonding or precopulation display (Fig. 3.09). These rituals give the female a direct input of calories and nutrients at a time when she is investing in her developing eggs; this behavior also may provide her with information about the male's potential as a future provider to their offspring. For example, Piotr Tryjanowski and Martin Hromada (2005) observed this behavior in Northern Shrikes (*Lanius excubitor*) at their field site in Poland: in the early breeding season, male shrikes frequently presented food items—small birds, voles, lizards, or insects—to females. In return, the females often would copulate with the male. These post-feeding matings were more likely when the gift presented by the male was relatively large.

Many of the spectacular plumages, complex displays, and intricate songs of male birds also have arisen via the process of intersexual selection. Some of these intersexually selected traits seem truly bizarre, and sometimes it is difficult to imagine how they have come to be involved



Fig. 3.09 Courtship feeding. Beyond its pair-bonding function, providing food during courtship—as demonstrated in these Forster's Terns (*Sterna forsteri*)—yields a nutritional advantage. Female terns lay larger and heavier clutches when their mates supply quality food before and during egg laying. (Photograph by Mark F. Schwall.)



Fig. 3.10 Dramatic plumage dimorphism. (A) The male Golden Pheasant (*Chrysolophus pictus*) exhibits elaborate, sexually selected plumage that appears especially dramatic compared with (B) the camouflaged female. (Photographs by: A, Tracey Fandre; B, Chang Tuck Wah.)

in mate selection. What could possibly make the pendulous wattles of the male Long-wattled Umbrellabird (*Cephalopterus penduliger*) of South America attractive to females? What about the incredible vocal repertoire and elaborate courtship display of the Superb Lyrebird (*Menura novaehollandiae*) of Australia? When considering the evolutionary consequences of mate choice, it is instructive to approach these puzzles from the perspective of the sex doing the choosing: what might those individuals gain by selecting a particular mate?

Although impressive in their own right, the elaborate plumages, songs, and displays of male birds can all function as indicators of a male's general quality. Many bird species exhibit plumage dimorphism, with the male and female differing in plumage. Most of the time, males claim the most beautiful coloration or most exaggerated plumes (Fig. 3.10). The most extreme cases of such dimorphism are found in avian groups such as hummingbirds, birds-of-paradise, grouse, and manakins; that the extremes are seen in these birds makes evolutionary sense, given that the males in these species provide no help to the female in nest building, incubation, or care of the chicks. Therefore, in these birds, a male's fitness depends entirely on his besting his rivals in the mate attraction contest.

However, some of the traits brought about by intersexual selection still may remain puzzling because of their exaggerated nature. How can even the most intense sexual selection drive traits like the peafowl's tail or the plumes of a bird-of-paradise to such extremes, especially when that degree of elaboration poses real costs to the male bird?

The **handicap principle** may help explain the existence of these super-elaborated traits. First proposed by Amotz Zahavi (1975), it is based on the idea that when traits are costly to produce and maintain, they are more likely to serve as reliable indicators of individual quality than are traits that are easier to produce and maintain. In effect, the costs involved in developing an elaborate trait limit the ability of low-quality males to cheat by masquerading as higher quality males. For example, a male bird in overall poor condition that sports a long tail or bright plumage is likely to attract unwanted attention from predators or from rival males that are in better shape. Under these conditions, only the best quality individuals can afford to invest in the most showy ornaments or most complex songs. Females then can use these hyper-elaborated traits as honest indicators of each male's relative condition.

Another explanation for ultra-elaborate traits involves a process called **runaway sexual selection**, a feedback loop between female preferences and male traits. Under the runaway scenario, because females are predisposed to select mates with a particular trait, males with that trait have a higher likelihood of siring offspring. In turn, these matings produce a new generation of females with the same preference, and males with the trait. When these traits are all under similar genetic control, this process intensifies selection for the trait, exaggerating it to an ever greater extent, until it is balanced by equally strong natural selection against it.

It is beneficial for males to indicate their quality to females because females also obtain indirect benefits, often termed **good genes benefits**, from their mates in the form of genetic material passed along to their mutual offspring. Although the male's genes do not aid her directly, they nonetheless increase the female's fitness by enhancing the fitness of her offspring. High-quality males might have particular genes or gene combinations that are advantageous—hence "good genes"—which they pass along to their descendants. For example, a male Galápagos finch may contribute to his offspring the genes for large bill size—an advantageous trait in some times of drought (Box 3.02).

Other kinds of genetic benefits are a bit more complicated, in that sometimes it is not the particular genes themselves but rather the mix of genes that matters. For example, in the Superb Starlings (*Lamprotornis superbus*) that Dustin Rubenstein (2007) has studied in Kenya, females often choose to mate with males that are unusually genetically dissimilar to them, thereby increasing the genetic diversity of their offspring (Fig. 3.11). Among other potential benefits, this heightened genetic medley may give offspring a greater diversity of genetic variants for resistance to various diseases. This interpretation is supported by the opposite fitness effects seen in situations where birds produce offspring with unusually low genetic diversity. In such situations involving **inbreeding**, when relatives breed together, the offspring may suffer severe fitness consequences. For example, when closely related American Crows (*Corvus brachyrhynchos*) mate and produce chicks, those offspring have a much higher probability of dying from disease than non-inbred chicks (Townsend et al. 2009). The low genetic diversity caused by inbreeding also can pose a problem for conservation, as in captive-breeding programs involving small numbers of breeding birds or when endangered species are reduced to a handful of remaining individuals.

Mating benefits can arise even from the genetic compatibility of a particular female with a particular male. For practical reasons, it is notoriously difficult to detect whether specific pairings of individuals affect fitness, but some studies have found evidence for this phenomenon. For example, Tim Birkhead and his collaborators (2004) artificially inseminated female chickens with the sperm from two males, carefully controlling for factors such as the number of individual sperm and the reproductive state of the female. They discovered large differences in the number of eggs each male's sperm fertilized, but these differences were not consistent across females: a given male's sperm had a high fertilization rate with a particular female but did poorly in fertilizing the eggs of a different female. It remains an open question whether this kind of between-individual variation in genetic compatibility is common in wild birds, and, if so, whether birds have ways of choosing the mates that they are most genetically compatible with.

When considering sexual selection involving mate choice, it is important to keep the difference between social and genetic pairings in mind. Females may pair bond with

Handicap principle: the hypothesis that females of some species have evolved mating preferences for males who display very costly and exaggerated ornaments or behaviors, since these costs ensure that only particularly high-quality males can afford these so-called handicaps.

Runaway sexual selection: a hypothesis for how extremely exaggerated ornaments or behaviors might evolve, via a feedback loop that involves females choosing males with the extremes of that trait, the resulting generations of male offspring having more and more elaborate variants of the trait, and the resulting female offspring having ever stronger preference for males with the trait.

Good genes benefits: the fitness advantage that individuals (usually females) gain by selecting mates on the basis of the genetic qualities that they will pass on to their mutual offspring.

Inbreeding: the offspring resulting from matings between individuals who are more closely related than would be expected by chance within a population.



Fig. 3.11 Benefits of genetic diversity. Individual Superb Starlings (*Lamprotornis superbus*) tend to choose mates with dissimilar genes, thereby providing their offspring with a greater resilience to environmental unpredictability. (Photograph by Judith Nicolai.)

a particular social mate but copulate and produce chicks with other genetic mates as well. In fact, in some bird species, each egg in the same clutch may have a different father. It is now easy to conduct genetic paternity tests on wild birds, and hundreds of studies have assessed **extra-pair fertilization** rates within specific species. These investigations have uncovered much variation among bird species in this otherwise largely invisible mating behavior. However, in general, extra-pair offspring within a clutch are the norm rather than the exception. As discussed more fully in Chapter 9, this alternative route to gaining the benefits of good genes outside the social pair bond may have important consequences for the fitness of both males and females.

3.2.2 Sexual selection and competition

The second type of sexual selection, termed **intrasexual selection**, involves competition among members of the same sex over access to mating opportunities. Because of the different fundamental reproductive limits that apply to males and females, males often are subject to greater intrasexual selection. Historically, this process has been referred to as male–male competition. However, this male-biased phrasing is falling out of fashion, because field studies reveal that many female birds also compete for access to the best mates.

One of the most pervasive types of intrasexual selection in birds involves competition over resources important for reproduction, such as a high-quality territory, a safe nesting site, or a central display location within a lek. Many migrating songbirds, for example, are under intense pressure to arrive at their breeding sites early in the spring, when the best quality territories remain unoccupied. In American Redstarts (*Setophaga ruticilla*) breeding in Michigan (USA), males and females arrive at roughly the same time, but older, more dominant birds of both sexes arrive earlier than the younger breeders (Smith and Moore 2005). These "early birds" benefit by obtaining territories in the densest shrub patches—optimal redstart habitat—and go on to produce not only more nestlings but heavier, healthier ones as well. American Redstarts also defend territories in the non-breeding season, but with a different arrival pattern: in Jamaica, young birds tend to arrive first in the early fall, often settling in prime habitat. Then, as the older and more dominant birds return, they evict the younger birds from the best territories (Marra 2000). Whether in spring or fall, it pays to be an older redstart in good condition.

Intrasexual selection also affects the various advertisements and displays that birds use to signal their dominance status to competitors of the same sex. Male songbirds often use specific song types when countersinging with males on adjacent territories (Chapter 10). Likewise, the size or intensity of prominent plumage patches often is associated with dominance. You can observe this status signal while sitting in most outdoor urban cafes around the world, where the House Sparrows (*Passer domesticus*) at your feet squabble over dropped crumbs: in these birds, the size of the black "bib" on the breast of the male sparrow serves as a prominent badge of his overall status and condition.

Extra-pair fertilization: the fertilization of eggs resulting from matings between two members of a population who are not pair bonded.

Intrasexual selection: a subset of sexual selection, one involving the reproductive success of individuals that depends on competition with members of the same sex. In birds, intrasexual selection often (but not always) involves competition among males over access to females.

Box 3.04 The strange dimorphism of Eclectus Parrots

The Eclectus Parrot (*Eclectus roratus*) provides an unusual example of avian sexual dimorphism that arises from strong selection pressures acting differently on the two sexes. Males and females of these medium-sized parrots have very different coloration: males are bright green with scarlet wing linings, whereas females are a striking mix of red and blue (Fig. 3.B4.01). These plumages are so distinct that early ornithologists thought that male and female Eclectus Parrots were different species.

Rob Heinsohn (2008) has intensively studied the breeding biology of Eclectus Parrots in Australia's Cape York Peninsula. It turns out that suitable nest cavities in tall trees are rare in this rainforest habitat: ideal cavities must be high in the canopy to limit access by predators and must remain dry, even during torrential tropical downpours. Female Eclectus Parrots compete aggressively for the few appropriate nest sites, sometimes even battling to death. Once she has ownership of a good cavity, a female guards it assiduously, literally never leaving the nest tree for periods as long as 11 months.

Meanwhile, male Eclectus Parrots group together and travel long distances in search of the fruits on which they feed. These groups of males return to bring food to a nest-guarding female; in return, she copulates with most of them. A particular group of males may visit and mate with several females during a given breeding season.

Heinsohn's studies suggest that the different coloration of these sexes is related to both natural and sexual selection. The bright red and blue females are subject to extremely intense competition with other females, and their striking coloration may help signal their presence and ownership of their nest cavity. These females are particularly conspicuous when viewed from above, the perspective another female would have when flying in and prospecting for an unoccupied nest site. At the same time, despite being conspicuous, these females are relatively safe from predators; because their food is delivered to them by males, they can afford to spend a lot of time being vigilant and can dive into the protection of their nest cavity when threatened.

Male Eclectus Parrots, on the other hand, are exposed to predators such as Peregrine Falcons (*Falco peregrinus*) and Rufous Owls (*Ninox rufa*) as they commute among fruiting trees. Their green coloration likely helps camouflage them in this leafy setting. Back at the nest tree, however, this same green coloration provides much greater contrast when the males are offset against the wood of a tree trunk. The green coloration of the males also is likely to be a conspicuous signal of its own when seen through a female parrot's eyes.

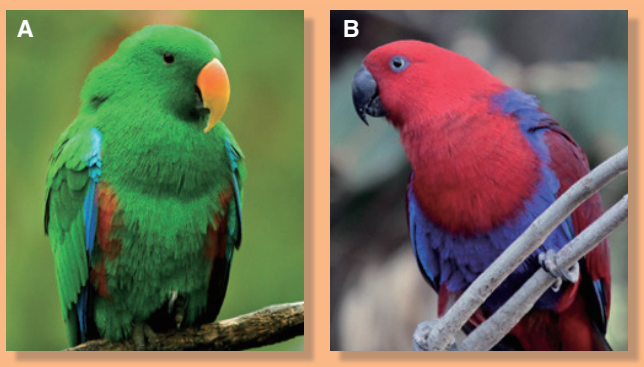


Fig. 3.B4.01 Dimorphism driven by natural and sexual selection. Eclectus Parrots (*Eclectus roratus*) have evolved extreme plumage color dimorphism, as each sex faces very different selection pressures. (A) The green coloration in males serves as camouflage while foraging, but also helps them stand out against tree trunks when courting females. (B) The striking red-and-blue female plumage signals ownership of nesting cavities to competing females, while also advertising their location and status to interested males. (Photographs by: A, Tim Collins, http://commons.wikimedia.org/wiki/File:Male_Eclectus_Parrot.jpg. CC-BY-SA-3.0; B, www.animalphotos.me.)

House Sparrows with larger bibs are more aggressive, higher in dominance, and have greater reproductive success over their lifetimes (Jensen et al. 2004).

Intrasexual competition sometimes can escalate into actual fighting, although damage from combat is relatively rare in birds. However, as discussed in Box 3.04, female Eclectus Parrots (*Eclectus roratus*) in Australia may battle over ownership of nest cavities, sometimes leading to the serious injury or death of one combatant. Likewise, male Common Loons (*Gavia immer*) breeding on small lakes in Wisconsin (USA) often battle ferociously when one male tries to take over another male's territory. Loon bills are sharp and pointed, so death by bill spearing and other fighting-related trauma is a major source of breeding season mortality for that species (Piper et al. 2008).

Competition among males also can occur through **sperm competition**, a less obvious but arguably more clear-cut version of intrasexual selection. In many bird

Sperm competition: in birds, a form of intrasexual selection that arises after more than one male has copulated with the same female, and therefore the sperm of multiple males are in competition to fertilize an egg within the female's reproductive tract.

species, females have the opportunity to copulate with multiple males during their fertile, egg-laying period. Because the oviducts of female birds have specialized structures that can store sperm for up to several weeks, the sperm from these multiple partners are rivals long after the actual copulations have occurred. Sperm competition has been particularly well studied in captive Zebra Finches (*Taeniopygia guttata*). It turns out that a female finch can bias paternity toward a particular male by copulating with him during an hour-long time window just as the developing egg begins to move down through her oviduct. If a female finch fails to copulate during that period, the egg is fertilized by stored sperm, and the sperm stored from the most recent copulation has the best chance at fertilization (Birkhead 1998).

Studying sperm competition in the wild requires researchers to develop unusual techniques. In a study of Collared Flycatchers (*Ficedula albicollis*) breeding in the oak woodlands of Hungary, a research team caught male flycatchers just before their paired females began to lay eggs. They placed rubber bumpers around the cloaca of some of the males, preventing them from transferring sperm to the females. Subsequently, some eggs proved to be fertilized by sperm stored from earlier copulations with these males; others were fertilized by non-treated males from the population (Michl et al. 2002).

3.2.3 Sexual selection in widowbirds: a case study

African widowbirds provide a particularly elegant case study of how inter- and intrasexual selection can simultaneously influence the showy traits of male birds. The eight species of widowbird breed in grassland habitats. Each species is polygynous: one male often mates with multiple females. During the breeding season, all males molt to assume a dark black plumage, but different species vary dramatically in two plumage traits: the breeding males in some species grow spectacularly long tail feathers and/or develop bright yellow or red patches on their wing or body feathers.

A group of Swedish biologists has conducted a series of experiments designed to tease apart the sexual selection pressures acting on different male widowbirds. Their earliest and now classic study focused on the Long-tailed Widowbird (*Euplectes progne*) (Fig. 3.12), a well named species in which the breeding male's tail is so elongated that flying seems almost out of the question. In Central Kenya, Malte Andersson (1982) manipulated male tail lengths within a population of Long-tailed Widowbirds to determine whether females were choosing mates based on this conspicuous trait. He first mapped the territories of the males and counted the number of nests in each territory as an indication of how many females each male had attracted before the experiment began. He then caught the males and changed their tails: he trimmed some tails to shorter lengths and lengthened others by gluing on parts of additional feathers. As a control, he simply cut the tails of another set of males and glued them back together at the original length.

This experiment had clear-cut results: the males with shortened tails lost many of their females, and the males with lengthened tails gained additional mates. Female Long-tailed Widowbirds do choose mates based on tail length, supporting the idea that the extremely long tails of these males evolved in response to intersexual selection. Similar results have since been revealed in several other

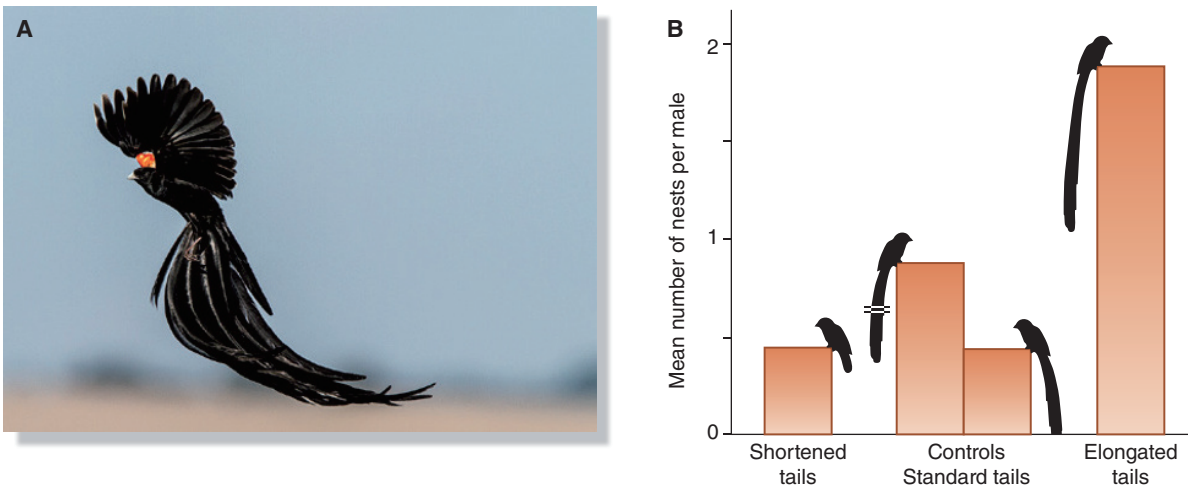


Fig. 3.12 Elaborate traits and sexual selection. (A) The tail of the male Long-tailed Widowbird (*Euplectes progne*) results from intense sexual selection. (B) A classic study manipulated the tail lengths of different widowbird males, shortening some and lengthening others (both control groups included males with average tail length, but group one had their tails cut and glued back on to ensure that the process itself did not have an effect). Males with the longest tails attracted the most females to their nesting territories. (A, photograph by Bradley Webb. B, from Andersson 1982. Reproduced with permission from Macmillan Publishers Ltd.)



Fig. 3.13 Plumage reveals breeding strategy. In Red-collared Widowbirds (*Euplectes ardens*), plumage signals male status: (A) duller red (or orange) males tend to roam around while seeking opportunistic mating opportunities, whereas (B) males with dark red plumage defend stable territories to which they attract nesting females. (Photographs by: A, Kurt Wedberg; B, Fran Trabalon.)

widowbird species with very long male tails, demonstrating that female selection for long tails is a general trend in this group of birds.

However, long tails are just one component of the widowbird story. In most widowbird species, the males have both long tails and bright plumage patches. Staffan Andersson, Sarah Pryke, and their collaborators (2002) worked on the Red-collared Widowbird (*Euplectes ardens*) in South Africa, where they found that males adopt one of two breeding strategies: some males defend territories, but others become "floaters" who forgo a territory and try to copulate with females as they move about the grassland (Fig. 3.13). Through both field observations and a series of experiments, these researchers discovered that the size and intensity of a male's red collar is related to his territory-holding ability. In other words, this colorful collar serves as a badge of a male's status in relation to other males. Female Red-collared Widowbirds, on the other hand, do not seem to care much about a male's collar, preferring instead males with longer tails. The red collar in this species has therefore evolved largely in response to intrasexual selection via male–male competition over status and territory ownership.

It turns out that both red collars and long tails are costly for male Red-collared Widowbirds to produce. Each male is forced into a trade-off between being a strong contender against other males and appearing attractive to females: a territorial male must invest enough in his collar to deter his rivals and enough in his tail to attract females. In contrast, floater males are able to invest more in their tails, because they do not even try to hold a territory. As a consequence, even though territorial males are the males in the best condition overall, they tend to have slightly shorter tails than the floaters. Thus these Red-collared Widowbirds offer a particularly clear demonstration of how sexual selection on each male results from a balance of intersexual (via female choice) and intrasexual (via male–male competition) pressures. Natural selection undoubtedly plays a role also, because having bright red plumage and a long streaming tail must increase a male's vulnerability to predators such as hawks and falcons.

How did this female preference for elaborate traits arise in the first place, in widowbirds and in all other species for which this selection occurs? A study on a third species of widowbird addresses this issue. Sarah Pryke and Staffan Andersson (2002) conducted a tail length manipulation much like the classic experiment described above, on the Fan-tailed Widowbird (*Euplectes axillaris*), the one widowbird species in which all males have relatively short tails. By giving some male Fan-tailed Widowbirds an unnaturally long super-tail, they determined that widowbird females universally have an intrinsic preference for long-tailed mates, even within a species in which the males normally have short tails (Fig. 3.14). In evolutionary terms, the female preference for long tails may have arisen before the male trait became so exaggerated in any widowbird species.

3.2.4 What about choosy males?

In the literature on sexual selection, from Darwin to the present day, there has been a strong tendency to overlook the potential for selection imposed by males selecting among females. This bias stems in part from the fundamental biological tendency that access to females is usually the factor that limits how many offspring a male can sire, and hence females usually are the sex that can afford to be choosier when selecting a mate. Nonetheless, there is an increasing awareness that males often may benefit by selecting the fittest females as mates, and ornithologists recently have become interested in the topic of male-choice sexual selection.

Male choice is expected in polyandrous species, such as the phalaropes and jacanas mentioned earlier in this chapter, in which each female tries to attract multiple males. Male choice also is likely to be important in monogamous species in which the reproductive fates of both members of the mated pair are closely linked. This prediction has been

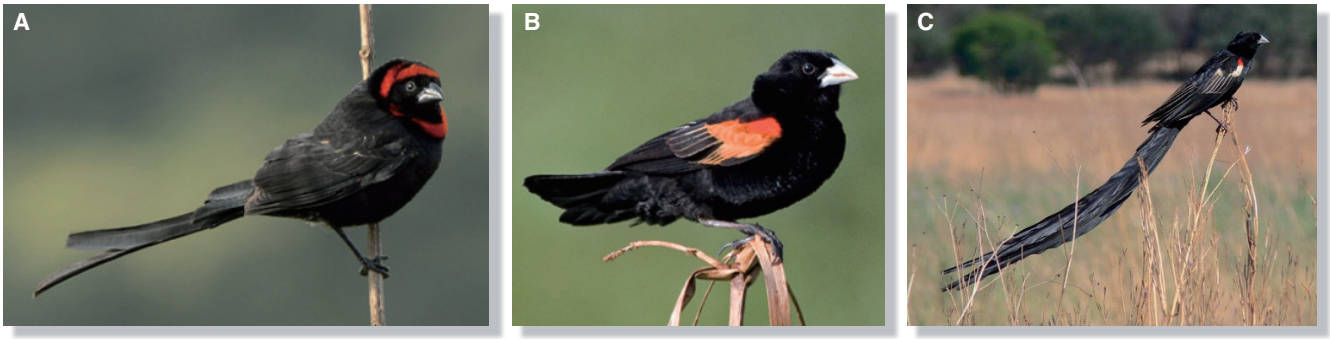


Fig. 3.14 Intrinsic preference for elaborate traits. Females of (A) Red-collared Widowbirds (*Euplectes ardens*), (B) Fan-tailed Widowbirds (*Euplectes axillaris*), and (C) Long-tailed Widowbirds (*Euplectes progne*) all prefer males with experimentally lengthened tails—even females of species B, in which males have naturally short tails. (Photographs by: A, Krzysztof Blachowiak; B, Robert Wienand Photography; C, Dr. Ron Matson.)

supported by experiments on a number of bird species, including Crested Auklets (*Aethia cristatella*) breeding in Alaska, in which males display more enthusiastically to the females with the largest crests (Jones and Hunter 1993) (Fig. 3.15). Similarly, male Barn Owls (*Tyto alba*) in Switzerland prefer females with greater black spotting on their feathers (Roulin 1999): male owls provided less food to nestlings after some of their mate's spots were trimmed off. Male Bluethroats (*Luscinia svecica*) in Norway court females with bright plumage more attentively than dull females; because the bright females tend to be in the best body condition, males direct their attraction efforts to the females with the higher fitness (Amundsen et al. 1997). Finally, female Rock Petronias (*Petronia petronia*) in Spain receive less male attention, mate later in the season, and produce fewer offspring when the patches of yellow on their breasts are experimentally reduced (Griggio et al. 2005).



Fig. 3.15 Male and female choice. Sexual selection works both ways in Crested Auklets (*Aethia cristatella*), as both sexes prefer mates with the largest crests. (Photograph by Hector Douglas.)

Male choice is particularly strong in the Gouldian Finch (*Erythrura gouldiae*) of Australia. Wild Gouldian Finches assume three color morphs: yellow, red, or black heads (Fig. 3.16). Both under natural conditions and in aviaries, these finches tend to pair up based on head color. Sarah Pryke and Simon Griffith (2007) discovered that this pairing tendency is driven primarily by the male's preference for females whose head color matches his own, because females exhibit much less of a preference. It turns out that there is a good reason for a male to prefer females with his own head color: offspring produced from the pairing of



Fig. 3.16 Choosy males. Gouldian Finches (*Erythrura gouldiae*) have three naturally occurring head color variants: yellow, red, and black. Males strongly prefer females with the same head color. This preference makes sense given that there is a genetically linked condition that causes decreased survival of offspring of dissimilarly colored parent finches. (Photograph by Sarah Pryke.)

differently colored parents suffer from a genetic incompatibility that substantially decreases their survival. Natural selection therefore has favored males who pair up with similarly colored mates.

These and other studies documenting male choice in birds may help resolve a longstanding paradox in bird morphology: why do so many female birds have the same bright plumage exhibited by males? For example, in the New World tropics, most tanager species are notably brightly colored, with females usually looking nearly identical to males. Likewise in the bee-eaters of the Old World, males and females of most species sport the same bright plumages and long tail feathers. Traditionally, these similarities between females and males have been explained away as having little to do with female quality, and instead have been thought to be genetically "carried over" as a by-product of the strong selection acting on males. It now seems likely, however, that many such female traits are also subject to intersexual selection through choosy males.

3.3 Speciation

Nearly 10,000 species of living birds exist in the world today. Each one came about through the process of **speciation** in which different groups of one ancestor species gradually changed and eventually split into two or more descendant species. The ways in which we define species are covered in Chapter 2; here we explore the underlying processes that create new avian diversity.

When two types of bird cannot interbreed, they are said to be reproductively isolated from one another. **Reproductive isolation** is the gold standard for defining avian species. With this standard in mind, ornithologist Ernst Mayr (1942) coined the leading definition of "species" which has been learned by generations of high school and college biology students. By Mayr's definition, "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." As covered in the following sections, new species achieve reproductive isolation in a number of ways. Furthermore, reproductive isolation sometimes is not absolute, as demonstrated by the existence of hybrids between species that usually do not interbreed. These situations of partial reproductive isolation provide valuable insights into how species originate.

3.3.1 Reproductive barriers that arise before birds mate

In almost all situations, individual birds benefit when they mate with other members of their own species. These benefits have created a variety of adaptations that help birds avoid cross-species pairings. Even when several closely related species are present in an area, each species typically has unique songs or other courtship displays that attract mates of their own species. This form of separation among species is termed **behavioral isolation**, because different bird species' behaviors and mate choice preferences keep them separated from one another.

Behavioral isolation is particularly important for groups of closely related bird species that breed in the same location at the same time. In seasonal environments, most male birds use some kind of vocalization to advertise themselves to potential mates (Chapter 10). Song therefore plays a particularly important isolating role for many birds. This isolating effect is evident when a bird enthusiast plays a recorded bird song to lure in a particular species: usually only individuals of the same species are attracted to a song playback.

Researchers similarly use song playback experiments to discover whether birds recognize each other as members of the same species. The great variety of bird song results in part from selection that favors the divergence of related species' songs, but female birds often are sensitive to tiny nuances of song that encode information about the singer's identity, even when songs sound incredibly similar. For example, in the Madre de Díos region of Peru, two closely related species of antbirds—the Peruvian (*Hypocnemis peruviana*) and Yellow-breasted (*Hypocnemis subflava*) Warbling-Antbirds—occur together in the same habitat. These species have songs that are so similar that they are indistinguishable even to many experienced field researchers, but careful playback studies show that females of each antbird species are attracted only to male songs of their own species (Seddon and Tobias 2010).

Behavioral isolation helps birds avoid mating with different species when they occur in the same location, but other forms of reproductive isolation act by physically

Speciation: the evolutionary process by which one ancestor lineage splits into two or more descendant species.

Reproductive isolation: a mating incompatibility that occurs when some kind of behavioral, physiological, or genetic barrier prevents successful interbreeding among individuals from two different populations even where they occur together.

Behavioral isolation: a form of reproductive isolation involving incompatibilities in behavior that prevent the interbreeding of two populations. These can include behaviors involved in recognizing members of the same species, specialized courtship displays, or any other behaviors necessary for successful mating.

separating a species in space. **Geographic isolation** occurs when species occupy different regions or are separated by some kind of barrier, such as a mountain range or river, that they cannot easily cross. Geographic isolation is common among closely related species of birds; as discussed later in this chapter, it is thought to play an important role in most avian speciation events.

Habitat isolation is similar to geographic isolation, but it occurs on a smaller scale. If closely related bird species occur in the same region but tend to occupy different habitats, males and females of the different species have fewer opportunities to mate. This kind of habitat separation is common in many groups of birds, and experienced birders often are well aware of how related bird species are likely to be found in slightly different habitats.

Mechanical isolation may result from an incompatibility in the structure of the genitalia; it is common in other animals but relatively rare in birds. However, mechanical isolation may be important in a few species of ducks (Chapter 6), in which males have extremely elongated organs (similar to the penis of mammals) for inserting sperm deep into a female's reproductive tract. A male duck that lacks such a long organ may have a hard time inseminating a female of such a species.

3.3.2 Speciation via geographic splitting

Every birder knows that the fastest way to add species to a life list is to travel to a new region of the world. No bird species exists everywhere, and closely related species often occur in different regions of a continent or on different but adjacent islands.

This physical separation of bird populations in space becomes a prime driver of bird speciation over thousands or millions of years. To understand why, consider what must happen for a single lineage of birds to evolve into two or more descendant species: something must divide the ancestral species, so that its descendants follow their own independent evolutionary paths, diverging in ways that cause them to evolve into distinct species. The easiest and simplest occurrence of evolutionary independence happens when some kind of barrier subdivides the original species into separated populations.

Although birds in general are relatively adept when it comes to **dispersal**—the way individuals spread away from one another, whether from parents or from an existing population—many kinds of barriers may limit their movements. For example, many landbirds cannot disperse easily over long stretches of open water, such as seas or even large rivers. Similarly, birds that occur in patchy habitats naturally form mosaic distributions. For example, if a particular bird species requires forest habitat, but that forest occurs in patches with regions of intervening grassland, populations of the same forest-dwelling bird species are separated; they may not interact if the grassland acts as a dispersal barrier. Likewise, major topographic features such as mountain ranges, deserts, or glaciers can impede the movements of birds, and island-dwelling birds may be isolated from nearby populations if they cannot easily cross the intervening water barrier (Box 3.05).

These and other types of dispersal barriers have the potential to create isolated populations that eventually may diverge and become separate species. This process is appropriately termed **allopatric** speciation ("allo" means "different," and "patric" means "place" or "fatherland"). Although ornithologists love to argue over the details, most agree that some form of allopatric speciation underlies nearly all situations in which one bird species has evolved into multiple descendant species (Fig. 3.17).

There are two ways that bird populations become separated in space, or allopatric. One is when a formerly widespread population becomes subdivided by changing habitat distributions or landscape features. For example, a changing climate may restrict formerly widespread habitats into isolated patches. This process has occurred commonly in the past over long timescales and sadly is occurring now at a much more rapid pace in response to human-caused alterations of habitats. These remnant fragments are often termed **refugia** because they can serve as habitat refuges, allowing populations of birds and other organisms to persist through times when their overall distributions are small or fragmented.

Geographic isolation: a barrier to interbreeding between two populations that arises from them being separated in space, often with some kind of geographic barrier to movement between them.

Habitat isolation: a barrier to interbreeding between two populations that arises from them being found in different habitats, even if otherwise they are in close proximity.

Mechanical isolation: a barrier to interbreeding between two populations that arises from an incompatibility between the male genitalia of one species and the female genitalia of the other species.

Dispersal: the movement of an individual bird from one breeding site to another.

Allopatric: populations that occur in separate regions with no geographic overlap.

Refugia: geographic regions that remained relatively unaltered by past changes in climate or other environmental shifts, and which therefore supported populations of organisms that were lost in the surrounding regions.

Box 3.05 Ring species

The complexities of speciation as a process are particularly apparent in unusual groups of populations termed ring species. Imagine populations of a species that are distributed across a wide area in a pattern that resembles an open ring. Ring species comprise a series of adjacently related populations in which birds can interbreed with birds from neighboring populations. In some cases, however, populations from the two ends of the open ring are so divergent that they no longer can interbreed, even though they are close together in space.

The Greenish Warbler (*Phylloscopus trochiloides*) of Asia is the most thoroughly studied avian ring species. This species occurs in forested habitats but is not found in higher elevations on the Himalayan plateau; instead, a series of Greenish Warbler populations encircle the Himalayas (Fig. 3.B5.01). Genetic reconstructions suggest that this ring formed recently, as birds from the south moved north on either side of the Himalayas, tracking the northward movement of forested habitats at the end of the Pleistocene ice ages (Irwin et al. 2005).

A series of careful song playback studies on populations all around this ring further shows that, nearly everywhere, warblers from adjacent populations respond aggressively to each other's songs. However, no such recognition exists in the northern zone where the two ends of the ring meet: in that area, the two populations overlap but treat one another as separate species.

This ring species represents a tantalizing intermediate stage in the process of speciation: moving the long way around the conceptual ring, the warbler populations are all recently connected, but they act as separate species at the ends of the ring. If this species' range moves even farther north, and the most southerly populations are lost, full speciation will occur as the southern connection is broken.

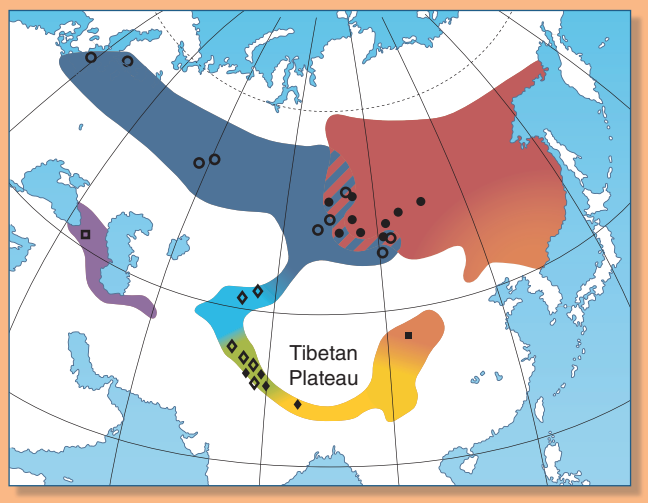


Fig. 3.B5.01 Ring species. Adjacent populations of Greenish Warblers (*Phylloscopus trochiloides*) around this ring can generally interbreed, but the overlapping populations in the north—the "ends of the ring" shown in hashed red and dark blue—occur in the same locations but do not interbreed. (From Irwin et al. 2005. Reproduced with permission from AAAS.)

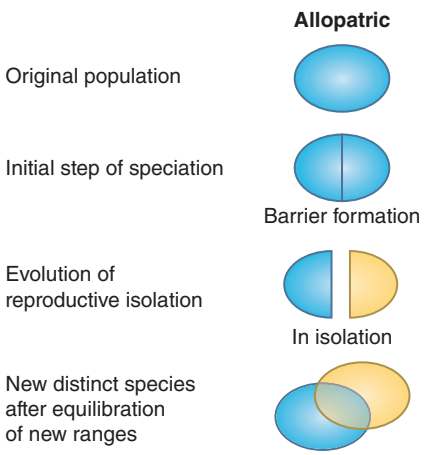


Fig. 3.17 Allopatric speciation. When a geographic barrier initially isolates two groups of an original population, the two diverge over time due to selective pressures or genetic drift. If members from both populations later come into contact again, reproductive isolation is maintained if the two groups do not interbreed. At this point, the two populations are considered two distinct species. (Adapted from Ilmari Karonen, https://commons.wikimedia.org/wiki/File%3ASpeciation_modes.svg. CC-BY-SA-3.0.)

The refugia concept has played a particularly prominent—and controversial—role in speculations regarding the origins of the bird species we see around us today. Once it was generally believed that most living bird species split from their closest relatives during the "ice age" climate cycles of the Pleistocene Epoch, the period spanning 2.5 million to 12,000 years ago when the global climate fluctuated many times between cold and warm periods. These climate oscillations had profound effects on habitat distributions around the world and therefore must have caused many changes in bird distributions. In the northern hemisphere, habitats shifted south when ice sheets expanded. Although not directly affected by glaciers, many tropical regions, including Amazonia and sub-Saharan Africa, experienced long periods of dry conditions. Sprawling rainforests were reduced to smaller refugia forest patches embedded in a surrounding matrix of savanna. Sea levels fell, because much of the seawater was trapped in massive ice sheets; as a result, many islands around the world became connected with other landmasses, only to separate again when the ice sheets melted and ocean levels rose.

Because these dramatic habitat shifts must have carried bird populations along with them, it was reasonable to suggest that the fragmentation of birds into refugia helped drive many of them towards speciation. However, the generality of this "Pleistocene refugia hypothesis" was questioned in the 1990s, when genetic studies suggested that most present-day species separated from their closest relatives before the advent of the Pleistocene. For example, John Klicka and Robert Zink (1997) used DNA data to date the splits between 35 pairs of closely related North American birds and discovered that nearly all of them split prior to the Pleistocene. This finding initiated a contentious debate among ornithologists regarding the ages of present-day bird species and the conditions that led to their speciation. After several decades of follow-up studies, it now seems that most birds classified as distinct species are indeed several million years old (or more) and therefore initially speciated before the Pleistocene ice ages. Nonetheless, some groups of birds did indeed diversify more recently; distribution changes caused by the Pleistocene climate cycles generated some of these particularly recently diverged bird species, and those climate oscillations certainly promoted many of the differences we now see among different populations of widespread bird species.

Many other processes may break up the distribution of a bird species. When a new physical barrier to movement causes the fragmentation of a species' geographic range, this process is termed **vicariance**. Diversification that results over time from this kind of allopatry is termed **vicariant speciation**. Many of the situations described above, including refugia caused by ice sheets or changing habitat mosaics, are examples of vicariance. A similar scenario occurs when landbird populations become trapped on **landbridge islands** by rising sea levels, which cut off their connection to a continent. As a result, landbridge islands often contain a subset of the bird species found on the nearby mainland. Given enough time and continued isolation, these island populations eventually may evolve into separate species.

In fact, how long a landbridge island has been isolated can be gauged roughly by the number of endemic bird species it contains. For example, based on its large size and high overall avian diversity, you might expect the neotropical island of Trinidad to harbor many species found only on that island, but it has only one endemic bird, the Trinidad Piping-Guan (*Pipile pipile*). All other landbird species on Trinidad are also found in northern South America, because Trinidad was connected to that continent during the most recent glacial period, when sea levels were lower. Similarly, but on a smaller scale, the hilltops on the tiny Islas de las Perlas in the Gulf of Panama were isolated by rising sea levels only recently; they contain remnant populations of birds such as the White-fringed Antwren (*Formicivora grisea*) that still occupy lowland habitats on the mainland.

3.3.3 Speciation via colonization of new areas

Allopatry also occurs when birds disperse and colonize a new area that is not connected to their original range. This process of range expansion via dispersal contrasts with the vicariance processes described in the previous section in which new barriers divide existing ranges. Birds everywhere undergo range expansions via dispersal, but these events are most conspicuous when birds immigrating from other islands or nearby continents colonize remote islands. For example, all landbird populations breeding on oceanic islands—islands that have never been connected to another landmass—originally must have arrived there via dispersal over the intervening seas.

In many regions of the world, islands harbor bird species that are closely related to different species found on nearby continents (Fig. 3.18). For example, seven landbird species are found only on the oceanic island of St. Lucia, a volcanic island in the Caribbean Sea. Unlike Trinidad just to the south, St. Lucia has never been connected to a continent or to nearby islands; therefore, the ancestors of all seven of its endemic bird species originally must have arrived on St. Lucia via overwater dispersal. Not surprisingly, these seven endemic species are all closely related to birds found elsewhere in the Lesser Antilles, although their subsequent movements among islands have been so rare that each island population has diverged to form a distinct species. Some of the world's most remote oceanic islands have bird faunas that resulted from long-distance dispersal over truly formidable expanses of open ocean. For example, the Hawaiian Archipelago has been colonized successfully by songbirds only six times (Box 3.06).

Bird surveys of other island groups show that some birds are particularly adept at dispersing across water barriers.

Vicariance: the subdivision of a species' originally large distribution into smaller and separated geographic fragments via some new geographic barrier or the fragmentation of the species' originally widespread habitat.

Vicariant speciation: speciation that results over time after populations that become divided by new barriers have diverged from one another.

Landbridge islands: islands that were formerly part of the nearby mainland, and which often retain some of the birds and other organisms from that earlier period, that were created by a rise in the level of the ocean. In contrast, oceanic islands rose directly out of the sea, and all land organisms on them had to have arrived by overwater colonization.

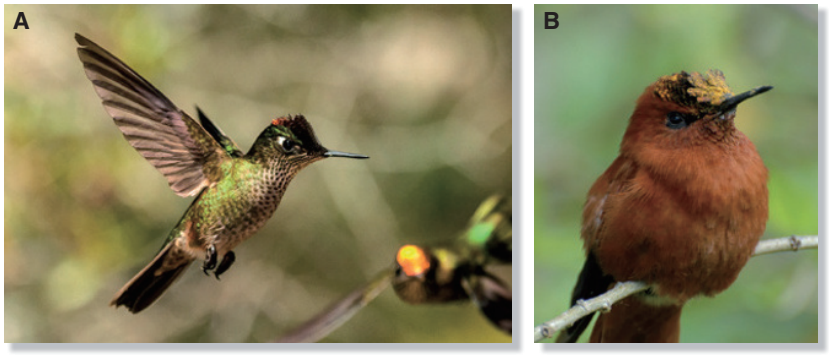


Fig. 3.18 Speciation via an oceanic barrier. Allopatric speciation probably caused the divergence of (A) the Green-backed Firecrown (*Sephanoides sephaniodes*), widespread within its range on mainland Chile and Argentina, and (B) the Juan Fernandez Firecrown (*Sephanoides fernandensis*), an endangered hummingbird endemic to a single island off the southwestern coast of South America. (Photographs by: A, Arturo Nahum; B, Peter Hodum, Oikonos.)

Box 3.06 Landbird colonization of the Hawaiian Archipelago

The Hawaiian Archipelago is the most remote island chain in the world, with 3900 km of ocean separating these islands from the nearest continent. This expanse of ocean has acted as a barrier to the dispersal and colonization of birds that cannot rest by landing on the surface of the sea. Nonetheless, landbirds have been able to colonize the Hawaiian Archipelago multiple times during the past several million years (Fig. 3.B6.01). Sadly, most of the archipelago's large-bodied birds went extinct about 1800 years ago, shortly after the first humans arrived. These extinct lineages of Hawaiian birds include various kinds of hawks, owls, waterfowl, rails, ibises, and crows, some of which evolved into flightless species restricted to single Hawaiian Islands.



Fig. 3.B6.01 Likely colonization routes for the landbirds of the Hawaiian Archipelago. These routes were reconstructed by identifying the most closely related species on the surrounding continents and islands. (© Cornell Lab of Ornithology.)

The Hawaiian songbirds that survived this initial wave of extinction derive from only six separate colonizations of the archipelago. Recent phylogenetic studies have clarified the likely routes of colonization for most of these lineages. The five recently extinct species of Oo (genera *Moho* and *Chaetoptila*) derive from an ancient colonization of the islands, probably from the north or east. These birds are so distinct that now they are placed in their own family, Mohoidae (Fleischer et al. 2008). The Hawaiian Crow (*Corvus hawaiiensis*) is likely the sole remnant of a larger group; it is most closely related to the Rook (*Corvus frugilegus*) of Eurasia (Jønsson et al. 2012). The three species of Elepaios (genus *Chasiempis*) result from a colonization from the southwest, part of a wave of colonization of many Pacific islands by these monarch flycatchers (Filardi and Moyle 2005). The two species of millerbirds (genus *Acrocephalus*) are most closely related to other reed-warblers found on South Pacific islands and hence colonized Hawaii from the southeast (Cibois et al. 2011). The five species of Hawaiian thrushes (genus *Myadestes*) are related to solitaires in the same genus from North and South America; this lineage likely colonized the archipelago from the east (Lovette et al. 2002). Finally, the spectacular radiation of Hawaiian honeycreepers resulted from a single colonization of the islands. Because this group is most closely related to the Asian rosefinches (Lerner et al. 2011), the ancestor of the honeycreepers probably dispersed from the northeast.

For example, one lineage of rails has successfully colonized nearly all the large oceanic islands in the western Pacific. This process of colonization sometimes has been witnessed as it plays out during short periods of time. For example, Jared Diamond (1974) surveyed the bird faunas of Krakatau and nearby islets in Indonesia on which all life was destroyed in 1888 by a massive volcanic eruption (Fig. 3.19). Diamond found that most of these islands had been recolonized by the same set of bird species, such as the Yellow-bibbed Fruit-Dove



Fig. 3.19 Colonization and dispersal. The infamous 1888 volcanic eruption of Krakatau Island, Indonesia remains one of the largest in recorded history. Nearly all life was destroyed on the island. Scientists are still documenting recolonization and biological succession stemming from this cataclysm. (From Symons 1888, public domain.)

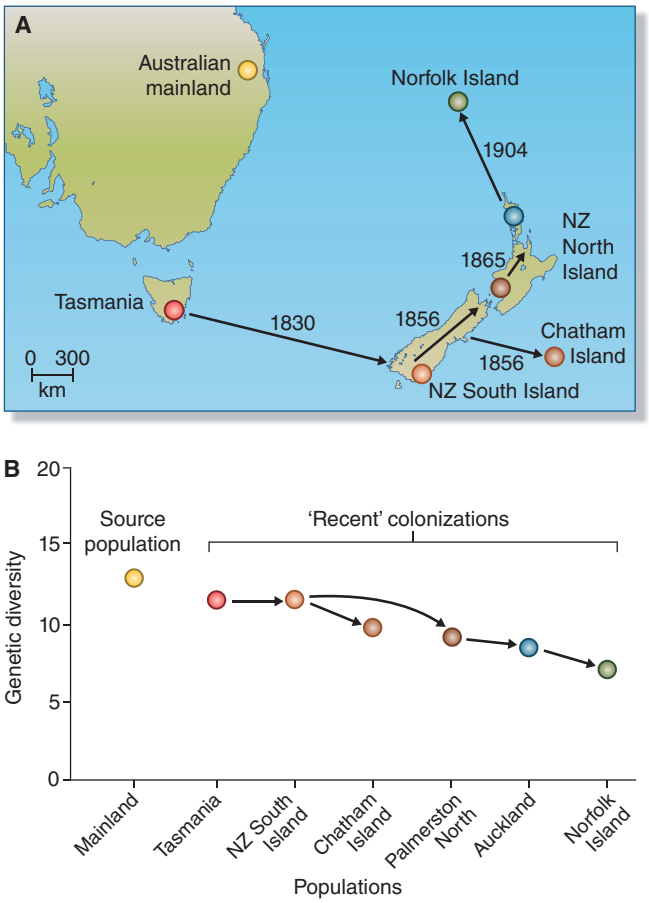


Fig. 3.20 Founder events reduce genetic diversity. (A) Beginning from Tasmania (and earlier from the Australian mainland), Silver-eyes (*Zosterops lateralis*) colonized New Zealand and then several remote islands in succession. Circles represent colonization events, and arrows denote ordering and dates of colonization. (B) Because these colonizations each involved only a few birds, each step in this chain resulted in a loss of genetic diversity compared with the larger population on the mainland where those colonists first originated. (From Clegg et al. 2002. Reproduced with permission from National Academy of Sciences, USA.)

(*Ptilinopus solomonensis*) and Louisiade White-eye (*Zosterops griseotinctus*). Diamond termed these early colonists **supertramp species**, in reference to their high dispersal and colonization success.

Colonization itself can launch a newly founded population toward speciation. If the environment of the newly colonized area is different from the original one, natural selection can cause the colonizing population to diverge in ways that reflect the pressures of its new setting. Furthermore, new populations almost always are very small during the initial stages of colonization and therefore may not contain the full genetic diversity found in their population of origin. Rare genetic variants—perhaps a gene encoding a distinct plumage color—can sweep much more easily through a population comprising just a few individuals.

These genetic changes via colonization are well documented in the Capricorn Silver-eye (*Zosterops lateralis chlorocephalus*), a small songbird originally found on Australia. Silver-eyes naturally colonized New Zealand in about 1830 and then subsequently dispersed from New Zealand to several even more remote islands. This kind of movement is termed **steppingstone dispersal**, because each newly colonized island provides a launching point for the next step in the chain of colonization. Genetic studies by Sonya Clegg and her colleagues (2002) showed that in each dispersal step, the colonizing population of Silver-eyes lost some of its genetic diversity (Fig. 3.20). This is the

Supertramp species: a term applied to bird species that are particularly good at dispersing long distances and at colonizing newly created habitats.

Steppingstone dispersal: the dispersal that proceeds by a series of colonizations, one after another, across a chain of islands or among habitat patches.

expected result of a **founder event**—a loss of genetic diversity that occurs when a new population is formed by a small subset of individuals drawn from a large original population. In the case of these Silver-eyes, however, the loss of diversity at each dispersal step was not detrimental, probably because the new populations were founded by a fairly large number of colonizing birds. In aggregate, however, the Silver-eye populations on the remote islands at the end of the dispersal chain had lost a substantial fraction of the genetic diversity found in the source population on the Australian mainland.

3.3.4 Speciation without geographic isolation

Although rare, it also is possible for two species to separate from one another without being geographically isolated in some way. This type of process is termed **sympatric speciation** ("sym" meaning "same" and "patric" meaning "place"). Sympatric speciation has long been controversial in ornithology and related sciences because even a small amount of interbreeding can stop the genetic divergence of two populations, keeping them homogenized. When the incipient species are not prevented from interbreeding by geography, they will set off on independent evolutionary paths only when some other strong force prevents them from intermixing.

Because sympatric speciation is inherently difficult, researchers set the bar high when considering possible evidence for its occurrence. In addition to breeding in the same places in the present day, bird species that arose sympatrically are expected to be each other's closest relatives. They must no longer interbreed and must have evolved some type of genetic difference. Furthermore, they should occur in settings where it would have been unlikely for them to diverge initially in separate locations and to have then come back together later on, after their speciation had taken place.

Isolated, single islands provide a useful test case when searching for instances of sympatric speciation. Birds frequently speciate—sometimes into spectacular diversity—on isolated groups of islands, but generally it is thought that this speciation gets started when populations are isolated on different islands within an archipelago. If sympatric speciation is readily possible, then birds that colonize single islands also should be able to diversify over time into multiple species while still confined to that one island. However, a worldwide survey of bird fauna on 46 highly isolated islands turned up only one potential example of sympatric speciation (Coyne and Price 2000). The two species of finch-like tanagers in the genus *Nesospiza* occur in the Tristan de Cunha islands in the South Atlantic, about 3400 km east of the South American continent, where their nearest relatives are found. These *Nesospiza* tanagers assume two forms: a large-billed species that specializes on woody fruits, and a smaller billed species that eats seeds and a variety of other foods. Although various lines of genetic evidence suggest that these birds diverged in sympatry on these islands, even this evidence for sympatric speciation is debatable: because the Tristan de Cunha group comprises three nearby islands, the original split between these two tanagers may have occurred at a time when they occupied different islands (Ryan et al. 2007).

A long history of sympatric speciation is very likely in another group of birds, the African indigobirds in the genus *Vidua* (Sorenson et al. 2003) (Fig. 3.21). All indigobirds are brood parasites (Chapter 13) that lay their eggs in the nests of other finches, with each indigobird species specializing on one species of host. As the young indigobirds grow up with their foster parents, they learn the songs of their hosts. As adults, male indigobirds mimic their host species' song, and female indigobirds choose mates based largely on the songs they likewise learned as nestlings. In this situation, where the nestling environment determines both the male's signal of "who am I" and the female's preference for mates, speciation can happen nearly instantaneously in the rare event that a female indigobird switches to laying eggs in the nests of a new host species. After such a host switch, the next generation of indigobirds will have learned a new set of host songs and are unlikely to mate with individuals of their parents' species; they might mate instead with siblings who learned their same song or with offspring of other females who made the same host switch. In this case, reproductive divergence would occur through these learned behaviors rather than through some form of separation in space. Although many indigobird species have gone on to evolve differences in other traits, such as the plumage color of the male and the mouth markings of the nestlings, studies that use song playbacks show that even males of the most similar species do not seem to recognize each other as potential competitors (Balakrishnan and Sorenson 2006).

Founder event: the loss of genetic variation that occurs when a new population is established by a very small number of individuals immigrating from a much larger source population.

Sympatric speciation: the speciation that occurs even when the two diverging populations breed in the same locations and therefore have the possibility of intermixing within each generation.

3.3.5 Speciation in time rather than space

A special case of sympatric speciation occurs when time, rather than space, separates two species via the time of year when their particular breeding seasons transpire. This type



Fig. 3.21 Sympatric speciation in brood parasites. Closely related species of African indigobirds such as (A) the Jambandu Indigobird (*Vidua raricola*) and (B) the Village Indigobird (*Vidua chalybeata*) learn aspects of their host species' song while in the nest, as in (C) this brood that includes two host Jameson's Firefinch (*Lagonosticta rhodopareia*) chicks and one Purple Indigobird (*Vidua purpurascens*) chick (at right). Adult indigobirds incorporate components of their host's song when mating themselves. Speciation can happen in a few generations if some indigobirds start to parasitize a new host species, since indigobird offspring raised by the same host species tend to mate with one another as adults. (A and B, from Sorenson et al. 2003. Reproduced with permission from Macmillan Publishers Ltd. C, photograph by Claire Spottiswoode.)

of speciation is variously referred to as **temporal** (time) or **allochronic speciation** ("allo" meaning different; "chron" meaning time). Ornithologists suspect that temporal speciation is at work on some islands that support two related seabird populations with non-overlapping breeding seasons (Friesen et al. 2007). The best-studied example comes from the widespread species (or some would say the group of related species) called the Band-rumped Storm-Petrel (*Oceanodroma castro*). These birds nest widely in the warmer regions of both the Pacific and Atlantic Oceans, but in some places throughout their range individual islands support two populations that breed at different times of the year. In some such cases, these populations with different times of breeding may be well on the way to becoming separate species.

In the Azores Islands of the eastern Atlantic, for example, one population of storm-petrels nests when the surrounding ocean waters are cold, and a second population breeds in the same location when the seas are warm (Fig. 3.22). On some such islands, these breeding seasons are so distinct that the cold- and warm-water breeders use the same burrows, but in different seasons. Detailed investigations into the origins of these populations show that in some places like the Galápagos Archipelago these two seasonal petrel populations are very closely related to one other, and individual birds may switch breeding seasons. In other places, such as the Azores, the local seasonal variants are each other's closest relatives but are so divergent genetically that they probably separated several hundreds of thousands of years ago. Because they no longer are exchanging genes, these populations may be well on their way to becoming separate species.

Temporal (or allochronic speciation): an unusual form of speciation in which the two diverging populations occur in the same location, but diverge because they reproduce at different times of the year.

Similar separation in time may lead to speciation in some other seabirds that have two distinct breeding periods within the same colonies. In general, however, most birds live in seasonal environments that do not allow two discrete, non-overlapping breeding periods within a single year. Nonetheless, subtle differences in the timing of breeding may help drive divergence more commonly than often recognized. For example, the Common Cuckoo (*Cuculus canorus*) of Eurasia is a brood parasite that lays its eggs in the nests of a range of host species, and most Common Cuckoo females are specialists in this regard. Many of these cuckoo "host races" (meaning that the brood parasite, even though it is the same species, is subcategorized by the species of bird that it parasitizes) have evolved patterns of egg spotting that mimic those of their particular host. Because several host races of cuckoos often are present in a single location, how they remain genetically distinct has long been a mystery. Analyses that examine their timing of egg laying suggest that the different host races tend to breed at different times within the spring season, as each tracks the breeding timing of its particular host species (Møller et al. 2011). These differences in the cuckoos' breeding periods eventually may keep the various host races from becoming genetically intermingled.

Timing of breeding may even isolate birds with more typical breeding behaviors. For example, McKay's Buntings (*Plectrophenax hyperboreus*) breed only on St. Matthew Island, a tiny and remote island located in the Bering Sea between Siberia and Alaska. McKay's Bunting is very closely related to a much more widespread bird, the Snow

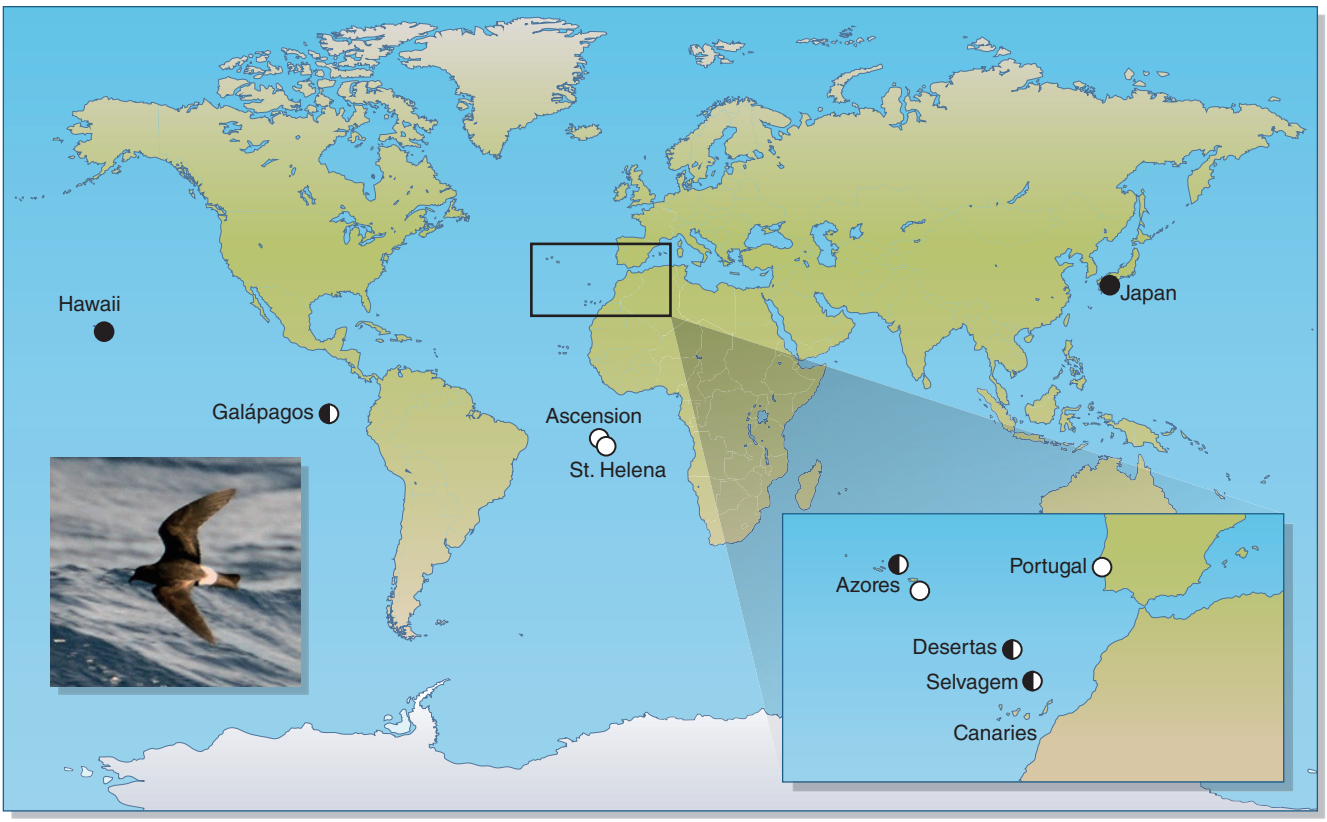


Fig. 3.22 Divergence via breeding season. Some islands harbor two distinct populations of Band-rumped Storm-Petrels (*Oceanodroma castro*) at different times of year. The cool season breeders (black circles) do not mix with the warm season breeders (open circles), even on the islands where both forms occur in different seasons (split circles). Because these populations no longer interbreed, they are likely in the process of becoming separate species. (From Friesen et al. 2007. Reproduced with permission from National Academy of Sciences, USA. Photograph by Jim Denny.)

Bunting (*Plectrophenax nivalis*). Although male Snow Buntings also occur on St. Matthew Island during the summer, these two species do not commonly hybridize there, perhaps because McKay's Buntings migrate only to the nearby mainland and therefore are able to return to the island very early in the spring. Snow Buntings migrate farther south, and by the time they return to St. Matthew's Island, McKay's Buntings have already started nesting (Maley and Winker 2010). This simple difference in the timing of spring arrival appears to keep the species from intermixing.

3.4 Hybridization

Hybridization is common in birds; more than 10% of the world's bird species have hybridized at least once (Fig. 3.23). Many such instances of hybridization are only rare occurrences, but some pairs of bird species hybridize routinely when they are in the same breeding location. In some cases, hybridizing pairs are genetically incompatible to the point that they can not produce any offspring: either the male's sperm cannot successfully fertilize the female's egg, or the developing young die before hatching. In these cases, the fitness consequences for the parents are extreme, because they will have no living offspring at all (unless one or both of them has also mated with a member of its own species).

This type of complete inviability is unusual among birds that hybridize naturally, because even species in different avian genera can often produce living offspring after hybrid matings. These offspring generally possess a mix of the plumage patterns and other morphological traits of both parent species. Some groups of birds seem more prone to hybridization than others; gulls and ducks, for example, seem particularly prone to cross-species pairings. Experienced birdwatchers know to consider the possibility that an odd-looking waterfowl or gull is a hybrid rather than a rarity visiting from another region.

Hybrid offspring may or may not suffer a fitness cost from their mixed ancestry. The offspring of some hybrid crosses are sterile. Others can reproduce but not as well as members of either pure parent species, whereas still other hybrids seem to suffer no detrimental effects at all. In general, the more evolutionarily distant the parent species, the more likely it is that their hybrid offspring will be sterile or have low fitness. Viable offspring usually are produced



Fig. 3.23 Hybridization. Compare the distinct physical characteristics of (A) the Hooded Merganser (*Lophodytes cucullatus*) and (B) Barrow's Goldeneye (*Bucephala islandica*); (C) is a hybrid of these two species. (Photographs by: A, Ken Lee; B, Dave Johnson; C, Jerry Ting.)

when the hybridizing species are in the same genus, but even a few species in different avian families have hybridized successfully (Price and Bouvier 2002) (Fig. 3.24).

Because related species so commonly can produce hybrid offspring, why are hybrids usually rare? One answer is that the most closely related bird species usually are found in different places, so they do not have an opportunity to interbreed. Another answer is that in most species the premating barriers to reproduction—songs, courtship behaviors, habitat preferences—are strong and effective.

In birds, female hybrids are more likely to be sterile or inviable than males. This pattern results from the fact that female birds have two different sex chromosomes (ZW), whereas male birds have two copies of the same sex chromosome (ZZ). Genetic incompatibilities often arise between the hybrid female's sole copy of the Z chromosome (which she inherited from her father) and the component of the rest of her genome that she inherited from her mother. The opposite pattern occurs in mammals, where the hybrid males have the different sex chromosomes (XY) and thus generally do worse than the hybrid females (XX). This pattern is named Haldane's Rule after J. B. S. Haldane, the geneticist who first discerned it in the 1920s.

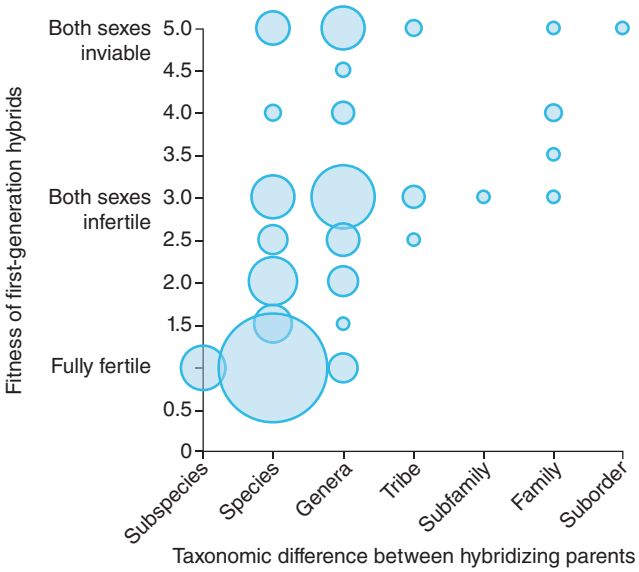


Fig. 3.24 Hybridization often has fitness consequences. This comparison of offspring fitness among 407 different combinations of hybridizing birds shows that closely related parents tend to produce fertile hybrids, whereas more distantly related pairs tend to produce hybrids that are either sterile or unable to survive. The sizes of the circles in each comparison correspond to the number of pairs with each level of fitness outcome in their offspring. (From Price and Bouvier 2002. Reproduced with permission from John Wiley and Sons.)

Several complications can create difficulties for researchers trying to determine whether hybrid offspring suffer from a loss of fitness. Hybrids in nature often are rare and difficult to come across, limiting the number that can be studied. Even if large numbers of hybrids are banded as chicks, it can be very difficult to follow them over the years until they attempt to breed on their own. Therefore, in wild birds the fitness of hybrids most often is assessed simply by comparing the fledging success of chicks from pure pairs of the parental species with that of chicks from mixed-species parents. These challenges were circumvented in a study of hybrids between Collared (*Ficedula albicollis*) and European (*Ficedula hypoleuca*) Pied Flycatchers in Sweden (Wiley et al. 2009). Using a variety of field and genetic techniques, the research team was able to measure both the immediate success of hybrid pairs in the form of fledged offspring and follow the fitness of the hybrid young and their offspring across several generations. The results were surprising: hybridizing pairs initially seemed to do fairly well, because they produced offspring at a rate close to that of pure pairs. Measured in this way, there was little fitness detriment of pairing with an individual of the opposite species. When the long-term fitness of the hybrid offspring was tracked across several generations, however, a very different pattern emerged: hybrids overall left far fewer descendants than non-hybrids. This result is sobering, because it suggests that researchers working on other hybridizing species may commonly underestimate the costs of hybridization if they can track the hybrid offspring only until they leave the nest where they were hatched.

If, as this study of flycatchers suggests, hybridization often is more costly than readily observed, this fitness cost would

help clarify why birds have evolved such effective ways of finding and choosing members of their own species as mates. In a situation where hybridization is particularly common (but still costly), mate selection may facilitate an additional element of natural selection, because the birds that pair with mates of other species will have fewer offspring than those that pair with mates of their own species. At least in theory, this process could select for evermore effective signals of species identity, such as divergent songs or plumages. This potential feedback loop between hybridization and divergence in reproductive traits is termed **reinforcement**, because natural selection directly reinforces the reproductive barriers between the two species. How often this reinforcement actually occurs in birds remains controversial, because it may require special conditions to be effective. For example, the selection imposed by hybridization is not likely to be strong in any situation where hybridization is rare as compared with normal pairing between members of the same species.

3.4.1 Avian hybrid zones

Although most hybrid crosses between bird species are rare and perhaps occur aberrantly, some pairs of species hybridize regularly. **Hybrid zones** form in areas where the distributions of two bird species meet and overlap. Hybrid zones play an important role in bird diversity research because they represent a kind of natural experiment, allowing researchers to study the interactions of species that still are able to mate with one another.

Hybrid zones are found on every continent, involving a very broad diversity of birds. In some places, hybrid zones are found in isolation, with only two hybridizing species. In other locations, multiple pairs of bird species may assume hybrid zones in the same general region. This overlapping pattern, sometimes termed a **suture zone**, arises when past changes to the topography or environment have brought together bird faunas that previously were separated in space. One of the best studied avian suture zones occurs in the Great Plains of central North America, where numerous pairs of species with western and eastern distributions come into contact, hybridizing within narrow, overlapping zones (Fig. 3.25).

Surprisingly, many hybrid zones are quite narrow, because the hybrids are found only in a small region where the two species meet and interbreed. All else being equal, hybrid zones should, in theory, widen quickly as every generation of hybrids disperses back into the respective distributions of the parent species. Without something to prevent this rapid blending, two species with an active hybrid zone would mix together quickly to become one combined species.

A narrow hybrid zone may simply be very new, especially if not enough time has passed for the two species to blend together fully. More interestingly, the two species might be meeting along an **ecotone**, a breakpoint in the underlying environment. If one bird species is better adapted to one side of the ecotone and the other species is better adapted to the habitat on the opposite side, the hybrid zone may naturally stay centered on the ecotone.

When the hybrid offspring themselves have low fitness, narrow hybrid zones can occur even without an underlying ecotone. If those hybrids cannot readily interbreed back into the parent populations, they cannot cause those species to blend together over time. Therefore, the hybrid zone does not expand and ultimately remains narrow.

Some of the most exciting recent research on avian hybrid zones takes advantage of new techniques for studying the pattern of genetic interchange between hybridizing species (Box 3.07). For example, the Lazuli (*Passerina amoena*) and Indigo (*Passerina cyanea*) Buntings are one of the hybrid pairs that meet in central North America. In one of the first intensive genetic surveys of an avian hybrid zone, Matt Carling and his collaborators (2010) teased apart which parts of these birds' genomes had been interchanged through interbreeding. The hybridization of these buntings has resulted in genes from each species moving into adjacent populations of the other species, but Carling discovered that this interchange primarily has involved the components of the birds' genomes that are inherited from both the mother and father. In contrast, there has been little such genetic interchange in parts of the genomes that are inherited solely from the mother. This pattern likely arises from the low fitness of hybrid female buntings that thus cannot carry genes between the species, whereas hybrid male buntings do sometimes backcross into one of the parent species.

3.4.2 Hybridization as a conservation issue

We live in a world where the distributions of many birds are increasingly affected by human activities, and consequently some species that previously were found in different places now coexist. When this new overlap results in

Reinforcement: a situation in which natural selection fosters the divergence of two hybridizing populations, either by selecting against hybrid offspring directly or by favoring individuals that choose members of their own population as mates.

Hybrid zone: a geographic area where two species (or distinct populations) come into contact and hybridize.

Suture zone: the somewhat controversial idea that broad-scale changes in past habitats have affected many species in similar ways and thereby created locations where multiple hybrid zones overlap.

Ecotone: a transition zone connecting two habitats and the communities of birds and other organisms that occur in them.



Fig. 3.25 A suture zone. Several pairs of western and eastern bird species meet and hybridize along the Great Pains Suture Zone (shown in red) in central North America. Examples include (top, left to right) Lazuli (*Passerina amoena*) and Indigo (*Passerina cyanea*) Buntings; (center, left to right) Bullock's (*Icterus bullockii*) and Baltimore (*Icterus galbula*) Orioles; and (bottom, left to right) Black-headed (*Pheucticus melanocephalus*) and Rose-breasted (*Pheucticus ludovicianus*) Grosbeaks. (Land image courtesy of Google Earth. Data SIO, NOAA, US Navy, NGA, GEBCO. Image Landsat. Image IBCAO. Photographs by: top left, Bill Bouton, https://commons.wikimedia.org/wiki/File%3ALazuli_Bunting%2C_Passerina_amoena_1.jpg. CC-BY-SA 2.0; top right, Henry Domke; center left, Shravans14, https://commons.wikimedia.org/wiki/File:Bullock%27s_Oriole_Feeding_on_Pride_of_Madeira_Flowers.JPG. CC-BY-SA 3.0; center right, Henry Domke; bottom left, Alan Vernon, https://en.wikipedia.org/wiki/File:Pheucticus_melanocephalus_-California,_USA-8.jpg. CC-BY-2.0; bottom right, John Harrison, http://en.wikipedia.org/wiki/File:RosebreastedGrosbeak08.jpg. CC-BY-3.0.)

hybridization, the formerly distinct species of birds may blend. This process is of particular conservation concern when a rare form is genetically swamped via hybridization with a much more widespread or common species. For example, Mallards (*Anas platyrhynchos*) have been introduced into many areas of the world where they do not naturally occur. Hybridization with invasive Mallards is contributing to the decline of related, native ducks, including the Hawaiian Duck (*Anas wyvilliana*) of the Hawaiian Islands, the Pacific Black Duck (*Anas superciliosa*) of New Zealand, and the American Black Duck (*Anas rubripes*) of eastern North America. A similar problem occurs in Europe, where Ruddy Ducks (*Oxyura jamaicensis*) introduced from North America hybridize readily with native White-headed Ducks (*Oxyura leucocephala*) (Fig. 3.26). Intensive efforts currently are underway to eradicate the introduced Ruddy Duck population in the UK and to hinder the spread of Ruddy Ducks into the rest of Europe.

3.4.3 Hybrids in the field

Identifying the parentage of hybrids can be a challenge for researchers and birders alike. First-generation hybrids often have a patchwork combination of the plumage traits found in the parent species, and their origin often can be deduced from these visible features. Identification becomes more complicated in hybrid zones where hybridization and backcrossing may have occurred across several generations. In these situations, researchers may score a **hybrid index**, which

Hybrid index: a number derived from measuring a series of traits or genes that describes the proportion of a hybrid individual's ancestors that belonged to each parental species.

Box 3.07 Manakin hybrids

Two closely related species of manakin come into contact and interbreed in the lowland rainforests of western Panama, near its border with Costa Rica (Fig. 3.B7.01). As their names suggest, the White-collared (*Manacus candei*) and Golden-collared (*Manacus vitellinus*) Manakins differ most conspicuously in the color of male plumage. Studies considering an array of plumage, morphological, and genetic traits show that these species occupy a narrow hybrid zone, but with one intriguing complexity: the location of the hybrid zone depends on which traits you are examining. In particular, the switch between male plumage color occurs farther to the west than the switch between other morphological or genetic traits (Brumfield et al. 2001).

Why do these hybrid zones, as measured in different sets of manakin traits, not overlap perfectly? One possibility is that the genes for the yellow plumage of the Golden-collared Manakin are being pulled into the range of the White-collared Manakin via sexual selection. Adam Stein and Al Uy (2006) tested this scenario by carefully tracking the behaviors and mating success of white and yellow manakins in the hybrid zone, where males of each color display in the same leks (Chapter 9). When both male colors were available, female manakins visited males of each color at similar rates, but they mated more often with yellow males. The mating advantage conferred by this yellow coloration may be causing it to spread south, slowly displacing the white coloration. This movement of the yellow coloration is slow, however, because females showed the strongest preference for yellow in leks where many males had that color; white-colored males do well in leks where yellow has not yet become common.

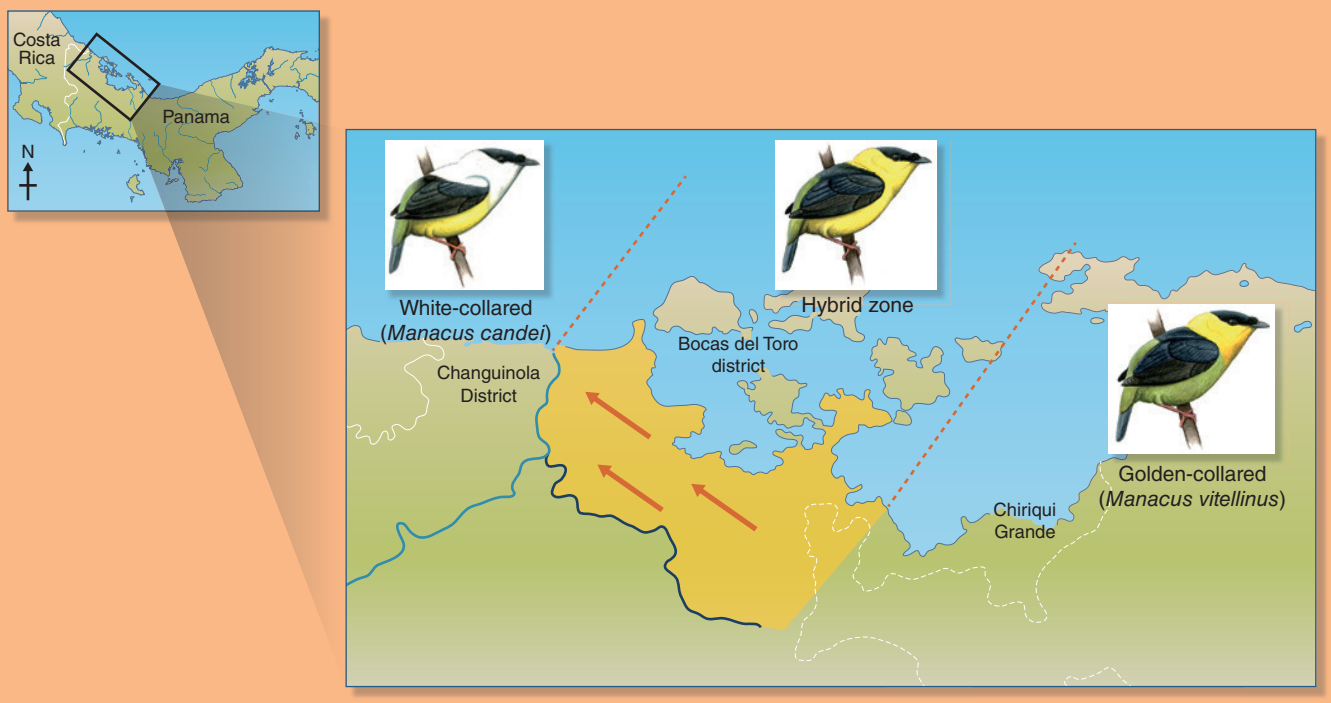


Fig. 3.B7.01 A manakin hybrid zone. The hybrid zone of White-collared (*Manacus candei*) and Golden-collared (*Manacus vitellinus*) Manakins in western Panama; the borders of the two species are shown by the dashed lines. Arrows indicate how the yellow-beard trait of the male Golden-collared Manakins is moving into the adjacent White-collared Manakins (golden arrows), as females of both species prefer yellow-bearded males. (From Brumfield et al. 2001. Reproduced with permission from John Wiley and Sons. Artwork by Luke Seitz © Cornell Lab of Ornithology.)

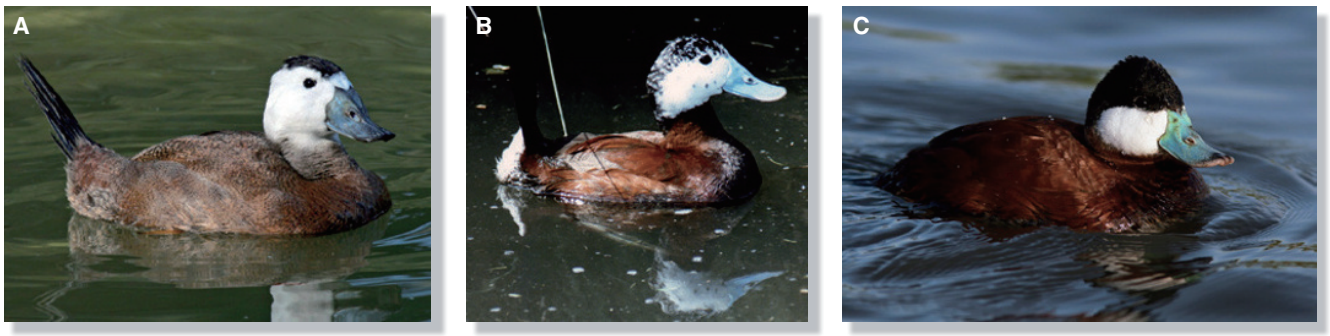


Fig. 3.26 Hybridization as a conservation issue. Sometimes an overabundance of hybrids can endanger one of their parent species. For example, European conservation biologists are concerned about the propensity for (A) native White-headed Ducks (*Oxyura leucocephala*) to mate with (C) introduced Ruddy Ducks (*Oxyura jamaicensis*) to produce (B) hybrids, a process that is contributing to the decline of the native species. (Photographs by: A, Dick Daniels, https://commons.wikimedia.org/wiki/File:White-headed_Duck_%28Oxyura_leucocephala%29_RWD1.jpg. CC-BY-SA 3.0; B, Mark Hulme, WWT; C, Brian Sullivan.)

sums many traits that distinguish one potential parent species from the other, with hybrids scored as intermediate. Traditionally, this kind of study was carried out by examining plumage or other morphological traits; today, researchers also commonly deduce the hybrid ancestry of birds using genetic markers.

Some birds routinely produce hybrid offspring with repeatable features. For example, in eastern North America, the Blue-winged (*Vermivora cyanoptera*) and Golden-winged (*Vermivora chrysoptera*) Warblers frequently hybridize, producing distinctive offspring, the so-called "Brewster's" and "Lawrence's" Warblers, which early ornithologists misclassified as separate species (Fig. 3.27). Similarly, many South American hummingbird "species" were described on the basis of single specimens collected in the 1800s. Although some of these appear to be true species that have never been seen again, a careful series of studies by ornithologist Gary Graves of the Smithsonian Institution has shown that many of these putative hummingbird species are actually just unusual hybrids.

3.5 What drives the divergence of bird populations?

When first learning about birds, nearly everyone initially fixates on identifying species. This process of mental categorization leads us—perhaps unconsciously—to a view of avian diversity that treats each species as a fixed, established entity. From an evolutionary perspective, however, it is important to remember that each existing group of bird species arose from a common ancestor and that some present-day species will be the founders of avian radiations in the future. Speciation therefore is most accurately viewed as an ongoing process, one that is slowly happening all around us.

What processes might cause bird populations to diverge over time? Traditionally, ornithologists interested in avian speciation focused on the various forms of geographic isolation that might keep populations separated. In recent



Fig. 3.27 Distinctive hybrid offspring. Two distinct hybrids of (A) Blue-winged Warblers (*Vermivora cyanoptera*) and (B) Golden-winged Warblers (*Vermivora chrysoptera*) are the so-called (C) "Brewster's" Warblers and (D) "Lawrence's" Warblers. These and other hybrid forms are becoming more common owing to increased hybridization between these parent species. (Photographs by: A, Henry Domke; B, Brian L. Zwiebel; C, Chris Davidson; D, Corey Hayes.)

years, however, their attention has turned more often to the underlying evolutionary forces that promote divergence in any setting. These include genetic mutations (which add new diversity to populations), natural selection (which causes one population to evolve adaptations specific to its particular environment), and sexual selection (which causes bird populations to diverge in traits important to mating).

A modern understanding of bird speciation links all these factors together. Complete isolation in space certainly helps promote the divergence of bird populations. However, populations linked by some level of intermating still can diverge if the forces promoting divergence are stronger than the tendency for homogenization via their exchange of genes. In the mountainous regions of northern Mexico, for example, Mexican Jays (*Aphelocoma wollweberi*) occur across a range of elevations that span lowland oak scrub to high-elevation pine forests. Although birds along this entire gradient breed with their neighbors, the jays at the lowland sites have evolved bill shapes that are better at opening acorns, whereas the high-elevation jays have bills better suited for extracting seeds from pine cones (McCormack and Smith 2008). Situations like this demonstrate how natural selection can cause divergence among these adjacent populations even in the face of gene flow among them. Under some circumstances, this type of divergence may cause populations to become distinct species over time. The term applied to this kind of diversification is **ecological speciation**, which occurs when divergent natural selection in different environments eventually leads to reproductive isolation. Ecological speciation can occur along environmental gradients, as in the case of the Mexican Jays that specialize on different foods along an elevation gradient, or more commonly in situations of allopatry, where populations separated in space experience different environmental conditions.

3.6 Adaptive radiations of birds

Some of the most spectacular examples of avian evolution have occurred in places where one ancestral bird lineage has diversified into many descendant species, each with distinctive morphologies and behaviors. These groups of species often are termed **adaptive radiations**, because natural selection presumably has driven each species to specialize on a different set of resources, such as food types.

The various species in nearly all groups of birds differ in some of their traits, and many of these differences likely stem from past episodes of natural selection, so in a very general sense adaptive radiation is pervasive in birds. In practice, however, the term adaptive radiation is applied most often to groups in which many species evolved rapidly from their common ancestor and in which the various descendant species have diverged notably from one another in ways that almost certainly are the result of natural selection.

All the best known examples of avian adaptive radiation involve groups of birds that have diversified on islands. This makes sense when you contrast the ecological pressures faced by a bird species that colonizes an island archipelago with the pressures experienced by a species that colonizes a new area of a continent. Because of their greater isolation and smaller size, islands nearly always have far fewer bird species than environmentally similar areas of continents. Therefore a bird species colonizing an island is faced with a smaller number of potential competitors. In fact, the island may offer open niches (Chapter 14); for example, a colonizing species may be able to take advantage of a food source that is inaccessible to other species, avian or otherwise, currently occupying the island. Furthermore, the different islands within an archipelago are somewhat isolated from one another, so if birds travel among them only rarely, a population on one island can diverge rapidly from populations on other islands.

Three such avian adaptive radiations are particularly famous, although for different reasons. The Darwin's finches are notable as a young adaptive radiation that is still in progress. They are found exclusively (with one exception, the Cocos Finch (*Pinaroloxias inornata*) of Cocos Island) in the Galápagos Archipelago, an isolated group of equatorial islands situated about 1000 km off the Pacific coast of South America. Evolutionary trees based on genetic surveys suggest that the Galápagos were colonized sometime in the past 2 million years by a finch-like bird that came from South America or the Caribbean (Burns et al. 2002). That single ancestral species has since diversified into 14 descendant species with a great variety of bill shapes, ranging from short, pointed bills in the insectivorous Green (*Certhidea olivacea*) and Grey (*Certhidea fusca*) Warbler Finches to the massive, seed-cracking bill of the Large Ground-Finch (*Geospiza magnirostris*). Some of these finch species are highly reproductively isolated from one another, but others hybridize frequently (Grant and Grant 2008). As described in Box 3.02, the evolutionary trajectory in many populations of Darwin's finches is highly

Ecological speciation: the evolution of reproductive isolation between populations as a result of divergent natural selection in their different locations or environments.

Adaptive radiation: evolutionary radiations that are exceptional in having quickly evolved many species from a common ancestor, in response to natural selection that causes these species to differ from one another in their use of their environment.

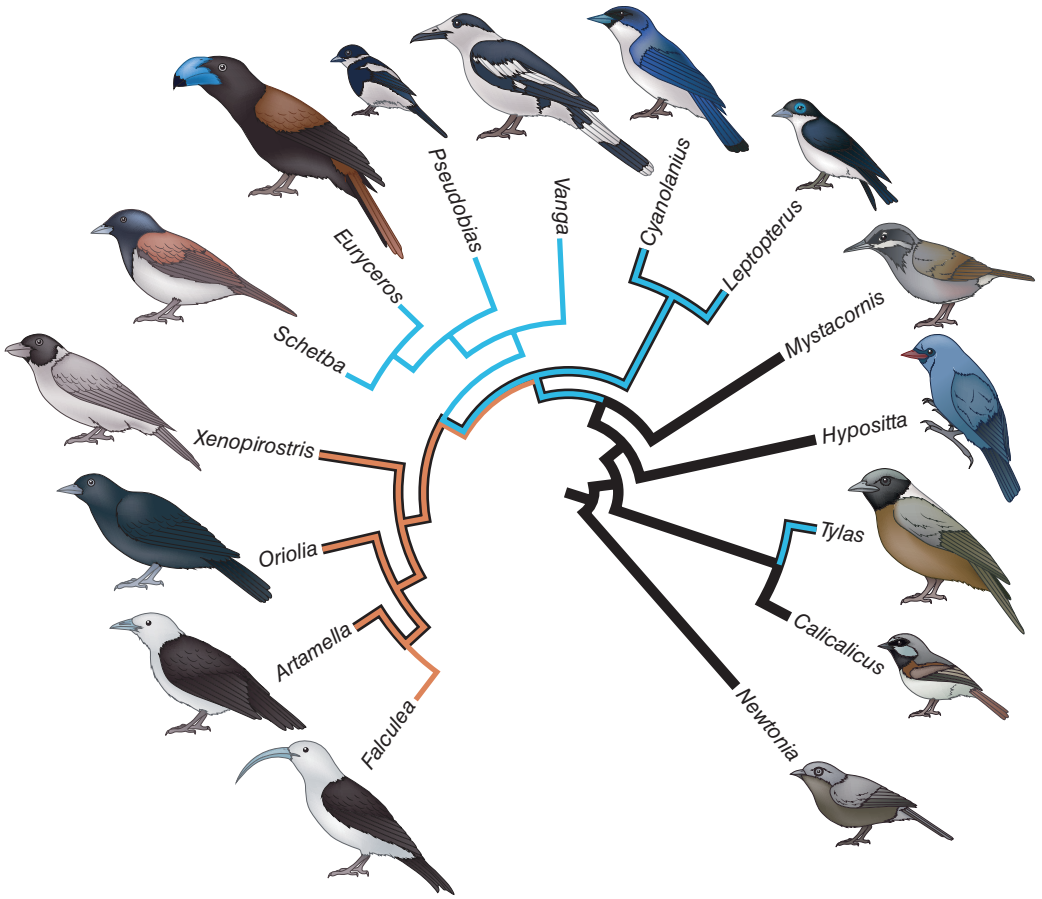


Fig. 3.28 Adaptive radiation of the Malagasy vangas. Phylogentic studies have revealed that these remarkably distinct birds are actually all part of the same family, having evolved from the same common ancestor. Various lineages have evolved many distinct traits; their different foraging behaviors are color-coded here: gleaning (black), probing (orange), and sallying (blue)—flying out suddenly from a perch to catch insects mid-air. (From Reddy et al. 2012. Reproduced with permission from the Royal Society.)

dynamic, because natural selection has caused short-term changes in their bill shapes and other traits. It is likely that if we could travel into the future and visit the Galápagos 100,000 years from now, we might find that natural and sexual selection have caused the present-day Darwin's finches to diversify into an even greater number of species.

A much older adaptive radiation on the island of Madagascar produced the remarkable morphological diversity of birds called vangas (Fig. 3.28). Many of the vangas are so different from one another that they were classified until very recently into various avian families, when a series of DNA-based studies showed that they actually are all part of a single, grand adaptive radiation restricted to Madagascar (Reddy et al. 2012). The common ancestor of the present-day vangas probably was an insectivore that gleaned insects off vegetation, but some of its descendants have evolved an aerial, flycatcher-like foraging style, and others probe into bark like woodpeckers. The common ancestor of the 21 living vanga species appears to have colonized Madagascar about 20 million years ago. The foraging-themed radiation occurred shortly after that colonization, as would be expected for a group that colonized a new setting with few competitors.

Hawaiian honeycreepers provide a final example of adaptive radiation. This group arguably represents the most spectacular example of adaptive radiation in birds, and perhaps in all vertebrates. Phylogenetic studies reveal that this radiation originated when an ancestral species similar to present-day rosefinches (genus *Carpodacus*) colonized the Hawaiian Archipelago (Lerner et al. 2011). In their native Asia, rosefinches often move nomadically in large flocks; perhaps the ancestor of the Hawaiian honeycreepers exhibited the same behavior. In any event, about 6–7 million years ago, an errant group of finches somehow traversed thousands of kilometers of ocean to the Hawaiian Archipelago, the world's most isolated group of islands. Over the following several million years, these finch-like colonists diversified into an incredible variety of forms,

resulting in a spectrum of more than 50 honeycreeper species that convergently mirror nearly all the bill shapes observed in the entire worldwide radiation of passerine songbirds, plus several bill shapes that are not found in any other birds. Sadly, this wonderful exemple of adaptive radiation has been much diminished by human-caused extinctions. The Hawaiian Islands have become a site for one of the world's greatest losses of avian diversity, a cautionary tale about how easy it can be to lose bird species and their adaptations that took millions of years to evolve.

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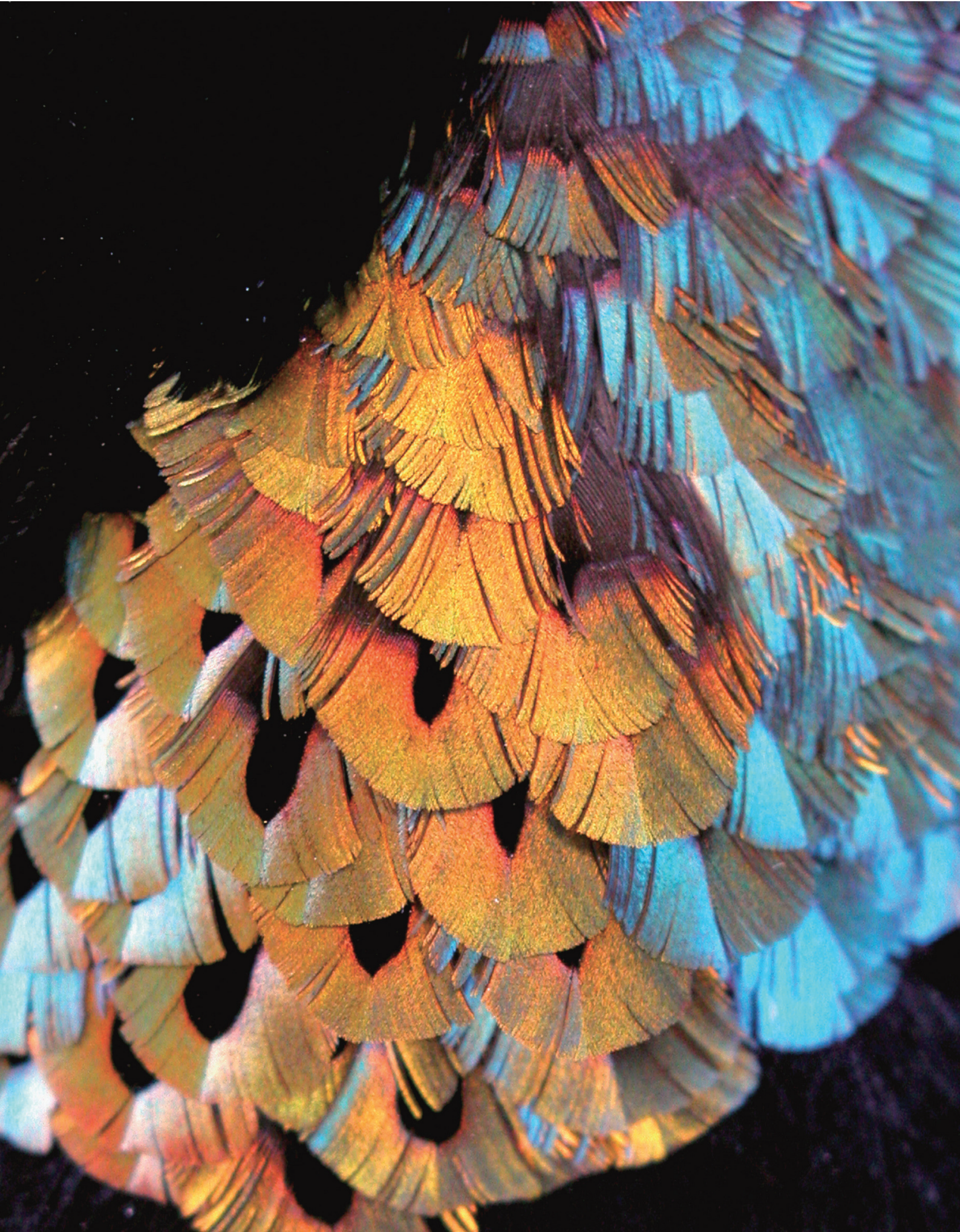
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Chapter 4 Feathers and Plumages

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From the radiant, glowing orange plumage of the Andean Cock-of-the-rock (*Rupicola peruvianus*) to the earth-toned and exquisitely filagreed patterns on the wing of a Great Argus (*Argusianus argus*), bird plumage is among the most striking and lovely of animal clothing. But even the simplest of feathers on the plainest bird have fascinating stories to tell: how individual feathers are made of intricately arranged structures; how feathers evolved from simple beginnings in pre-avian dinosaurs to their modern forms over millions of years; how variations on the basic feather theme led to hundreds of forms expressed among the world's nearly 10,000 bird species; how different feather types can serve many purposes simultaneously within a single bird; how birds are capable of producing feathers of every color we recognize, and many colors that we do not; how whole plumages are adapted to camouflage or sexually selected to advertise. Clearly, feathers are central to what it means to be a bird, and they represent a fascinating and captivating component of avian biology.

The first three sections of this chapter focus on "how to build" typical individual feathers from three different perspectives—purely anatomical, developmental, and evolutionary. In particular we examine the details of feather structure, how that structure is developed every time a new feather is grown, and how that structure likely evolved in a series of evolutionary steps in theropod dinosaurs. Taken together, these complementary sections provide an introduction to the finer structural details of feathers.

In the next three sections, we examine the practical aspects of wearing feathers at the level of plumages and individual birds. First we learn how ornithologists classify the diversity of different feathers found within and among bird species, and further, how these different feather types function for different purposes. Then, at the level of entire plumages, we investigate the pragmatic business of molting, looking at how birds replace their feather coats throughout their lifetimes. We end with a consideration of hygiene, exploring aspects of day-to-day feather care and maintenance.

Finally, in the last three sections we explore one of the most beguiling aspects of feathers: their visual properties, or appearance. We investigate how birds' feathers use the physics of light to produce all the colors of the rainbow, and a suite of visual textures no rainbow can produce. We close this discussion of feather appearances with a

Opposite: Iridescent reflectance. In the dense forests of Papua New Guinea, male Lawes's Parotias (*Parotia lawesii*) display in small light patches on the ground while females watch from above. Stereotyped movements reveal a dazzling breast shield, equipped with specialized feather barbules that reflect different colors at different angles—illuminating hues of either sparkling emerald-indigo or fiery yellow-orange. (Photograph by Justin Marshall.)

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whole-animal, plumage-level tour of how bird species customize their appearances using their feathers and plumages to serve their ecological and social needs.

4.1 Structural basics of feathers

Asked to draw a feather, even young children will illustrate three basic features. First, there is the **shaft**, the thin but stiff, central, rod-like portion. Second, the **vanes** extend in opposite directions from the shaft, forming two broad, flat, and more pliable regions of the feather. Third, on close inspection, the vanes—rather than being smooth and solid like a simple sheet of plastic—have a comb-like substructure. To round out this general description, a biologist would likely direct attention to a few more details of a typical feather (Fig. 4.01). The shaft can be subdivided into two regions, the more medial (or close to the body) portion of the shaft is vane-less and defines the area called the **calamus**. The calamus is relatively short and vane-free primarily because it is the portion of the feather that perforates the bird's skin, thereby anchoring the feather to the body. The rest of the shaft is distal (further from the body) relative to the calamus, and has the vanes extending from it. This region is called the **rachis**. Given that the rachis frequently comprises as much as 90–95% of the length of the shaft, the terms rachis and shaft are often used interchangeably.

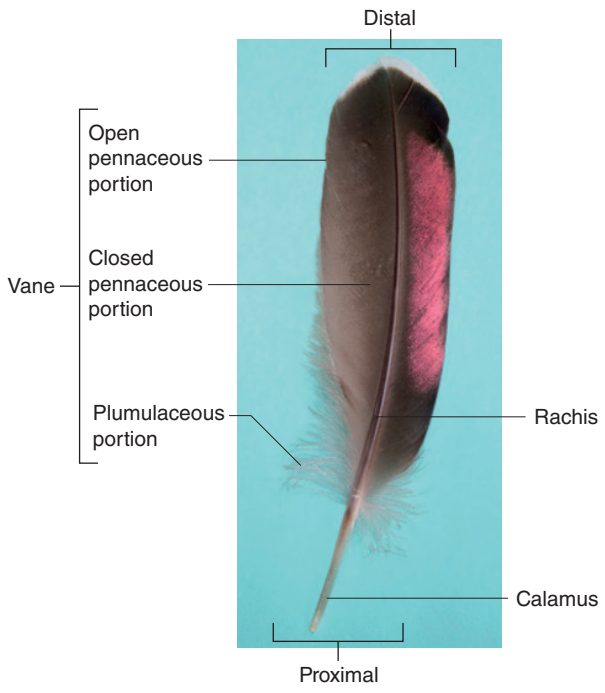


Fig. 4.01 Basic features of a feather. Anatomically speaking, a feather has a proximal (near) and distal (far) end relative to its attachment site on the wing and/or body. These terms also apply when describing a feather's component parts. (© Cornell Lab of Ornithology.)

When most people envision a typical feather, they tend to think of long wing or tail feathers rather than a small fluffy tuft of down—which is also a feather. This contrast draws attention to another fundamental structural feature of feathers, or, more specifically, of feather vanes. A typical wing or tail feather is **pennaceous**, a feather that has vanes with a relatively smooth, two-dimensional (flat) surface, and with a distinct shape or outline. A down feather is **plumulaceous**, a feather with barbs that are so fluffy as to be relatively formless. Plumulaceous feathers are incapable of holding any but the most delicate rounded form, and their overall shape changes drastically in response to the slightest breeze. In order to understand what underlies this difference in vane form (or lack thereof), one needs to understand in more detail the anatomical underpinnings of the firmer, pennaceous feather vane (Fig. 4.01).

Pennaceous vanes are a flexible, breathable, intricate mesh made of hundreds of tiny interlocking fibers. On close inspection, one can see that these vanes are comprised of a dense row of hundreds of long, slender, but stiff filaments, called **barbs**, branching off from the rachis one after the other, somewhat like teeth on a comb (Fig. 4.02A). At an even finer scale, the barbs themselves have a set of smaller structures, barely visible to the naked eye. That is, along the barbs the overall feather structure—the larger central shaft with many smaller fibers branching off on opposite sides—repeats itself at a smaller scale: each barb consists of a central shaft called the **ramus** that has its own

Shaft: the stiff, central spine of a feather from which the vanes, if present, extend.

Vanes: the broad, usually flat, surfaces that extend from the shaft of contour and flight feathers; the vanes are formed by interlocking barbs.

Calamus: the hollow lower portion of the feather shaft that lacks vanes.

Rachis: the portion of the feather shaft distal to the calamus; it is often relatively solid and supports the vanes, when present.

Pennaceous: describes that portion of the vane that is relatively flat and has a defined shape.

Plumulaceous: describes that portion of the vane for which the loose, fluffy barbs are not structured into flat vanes.

Barbs: the regular, parallel fibers that extend from each side of the rachis to form the feather vane.

Ramus: the central shaft of a feather barb (from which barbules extend).

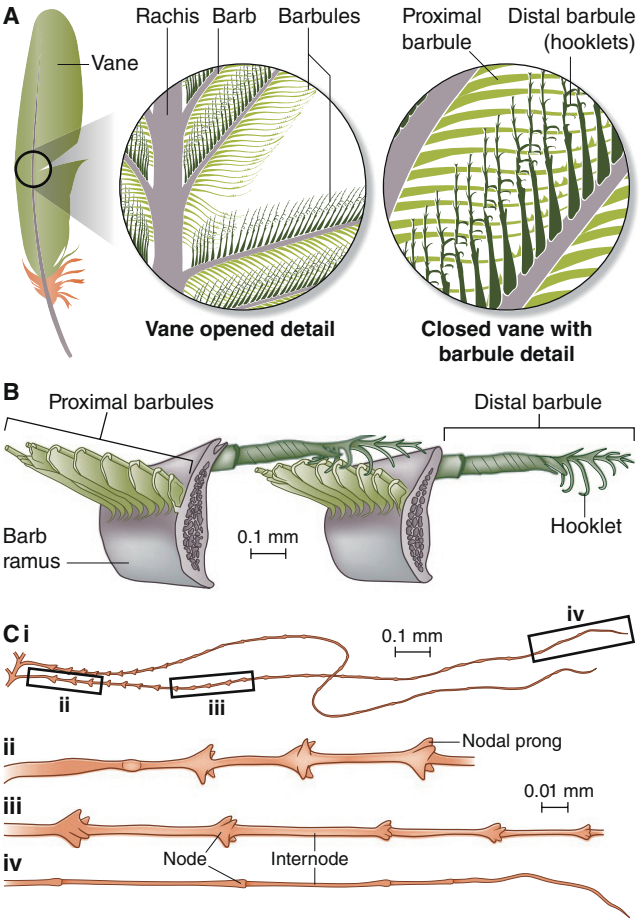


Fig. 4.02 Feather vane and barbule anatomy. (A) Detail of feather vanes with interacting proximal and distal barbules. (B) Detail showing hooklets interact with the barbules on the adjacent barb. (C) Two plumulaceous barbules (i) of a Rock Pigeon (*Columba livia*), with three regions from the proximal to distal tip (ii–iv) enlarged below. In (ii), the base and proximal nodes are relatively large compared with the central region of the barbule (iii). Distal barbule tips (iv) have substantially reduced nodes. (A, illustration by Andrew Leach © Cornell Lab of Ornithology. B and C, adapted from Lucas and Stettenheim 1972.)

rows of slender branches, called **barbules**, extending from either side. Barbules are generally not symmetrical off the two sides of the ramus, and we refer to the barbules that extend away from the bird's body (or away from the base of the feather) as the distal barbules, and those that extend toward the body as the proximal barbules. The two sides typically have complementary form and function; the distal barbules often have hook-shaped structures along their ventral (or under) surfaces, called **barbicels** or **hooklets** (Fig. 4.02B). The hooklets grab and hold the dorsal surface (or top) of the proximal barbules of the adjacent barb. Thus, although the barbs are long, thin, and can physically disconnect from one another, they are held parallel to neighboring barbs along their entire length by the hooklets on their distal barbules. In this way, barbules generate and maintain the continuous structure of the vanes—causing the feather to appear like one, smooth, continuous surface.

The fibers that create plumulaceous vanes are also barbs, but with a different structure. Barbs on plumulaceous feathers have proportionally longer and less stiff rami, and their barbules are typically reduced either to fewer, thinner, simple hairs (no hooklets), or even short nodules off the rami (Fig. 4.02C). In comparison to the densely packed, stiff, and hooked fibers of pennaceous vanes, the lack of barbule structure liberates the long thin rami to move independently from one another, and creates the loose, tufted form of a plumulaceous vane. The different functions of these contrasting vane forms are addressed later in this chapter.

All of these feather structures are made of the same material: **keratin**. Keratin is a proteinaceous connective tissue (the same basic material of human fingernails) produced inside specialized cells called keratinocytes. Among all the species in the animal kingdom, there are a diverse set of genes that produce keratin, and consequently diverse forms of keratin proteins exist. Within vertebrate animals, keratins belong to one of two fundamentally different structural forms (Fig. 4.03A). The alpha-keratins are found in all vertebrates (including ourselves), are relatively flexible, and make up much of mammalian skin, hair, and nails. Beta-keratins are unique to reptiles and birds, tend to be tougher, and are found in scales, claws, and feathers (Fig. 4.03B). The specific beta-keratin found in feathers is a form unique to living birds. The diversity of beta-keratins within birds is still largely unexplored and—given the importance of the material properties of keratin for feather function, and of feather function for birds in general—promises to tell some interesting stories about the evolution of feathers and birds (Glenn et al. 2008).

Barbules: Branchlets off the barbs of a feather that hook together with adjacent barbules.

Barbicels (or hooklets): tiny hooks on the barbules that allow them to attach to adjacent barbules, thereby forming the flat surface of a feather vane.

Keratin: a stiff protein that forms scales, claws, and feathers.

4.2 Feather development

One might imagine that the double-branched feather structure of a typical feather emerges as the feather grows, in a way analogous to how a tree grows branches: by small tips sending shoots off of a growing branch stock. Instead, feathers have their own surprising way of growing into their hallmark branched form.

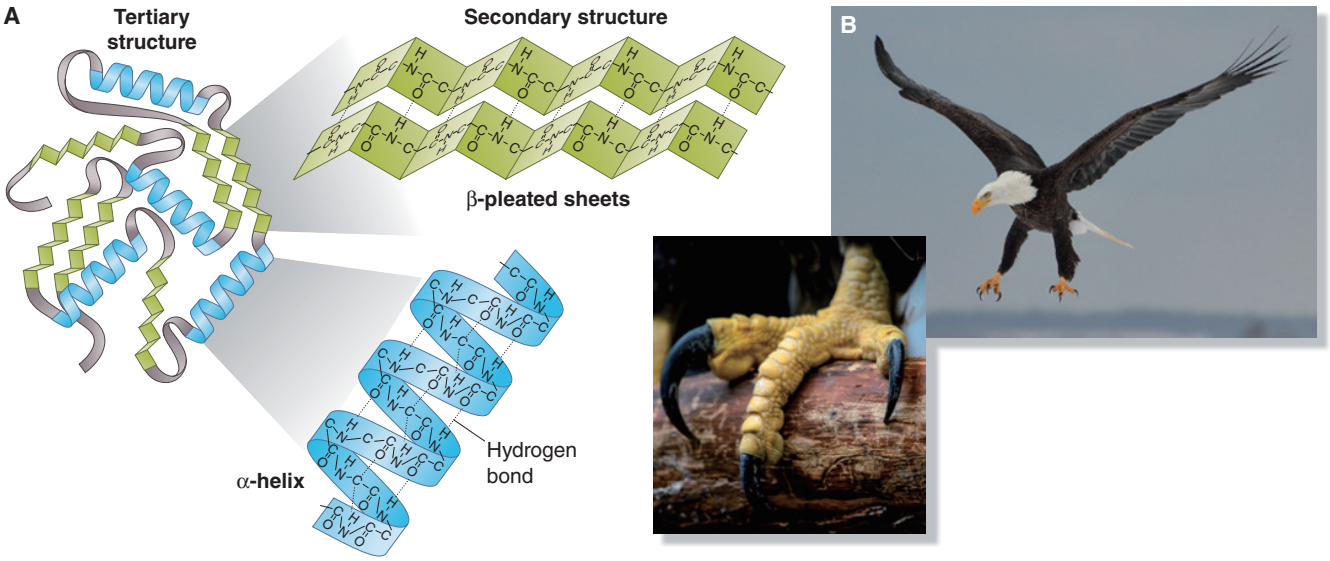


Fig. 4.03 Structure and use of keratin. (A) The different molecular structures of alpha- and beta-keratins create distinctive folding (tertiary) structures and properties. (B) Beta-keratins are unique to birds and reptiles and are the main structural component of feathers and claws, as in the talons of this Bald Eagle (*Haliaeetus leucocephalus*). (Photographs by: B (main), Peter Brannon; B (inset), David LaMason.)

4.2.1 Follicles

Feather development is a complex process that begins and ends with **feather follicles**, the specialized structures on the surface of the skin that generate feathers. If you have seen raw chicken, you have probably noticed feather follicles as the little bumps and/or pores on the skin surface (Fig. 4.04). The key to understanding how a follicle makes a feather is to understand its anatomy.

The skin of a bird (like our skin) consists of two major layers, the inner dermis and the outer epidermis. During development within the egg, the surface of the embryo's skin is visibly dotted with little bumps called feather buds or papillae. Each papilla is formed when a small swelling of dermis, the dermal core, pushes into its overlying thickened epidermal skin (called the epidermal placode) (Fig. 4.05A). As development progresses in the embryo, each papilla transforms into a feather follicle when the epidermal cells at the base of the papilla start growing back into the dermis. The growth of this layer of skin at the perimeter of the papilla is so rapid that the epidermis doubles back on itself, invaginating into the dermis and thereby forming a double wall inside the skin (the internal wall surrounds the dermal core, the outer wall connects to the surface of the skin) (Fig. 4.05B). Thus, a more formal definition of a feather follicle is a double-walled column of epidermis with a dermal core from which feathers are developed.

Once developed in the embryo, follicles remain in the skin for the rest of the bird's life. Complex cell growth occurs within the follicle each and every time a feather develops. The cells of the follicle's inner epidermal layer are the locus of this growth, and they are referred to as the



Fig. 4.04 Feather follicles. Each raised bump on the skin of this plucked chicken is a feather follicle. Occurring in distinct tracts called pterylae that follow the contours of the bird, they are separated by regions of bare skin without follicles. (Photograph by evp82/Shutterstock.com.)

epidermal collar (Fig. 4.05C). Within the epidermal collar, keratinocytes multiply rapidly and transform themselves into cells full of the keratin that becomes the feather. When the development of an individual feather is completed, the

Feather follicle: a small, epidermis-lined pit in the skin of a bird from which a feather grows and to which it remains attached.

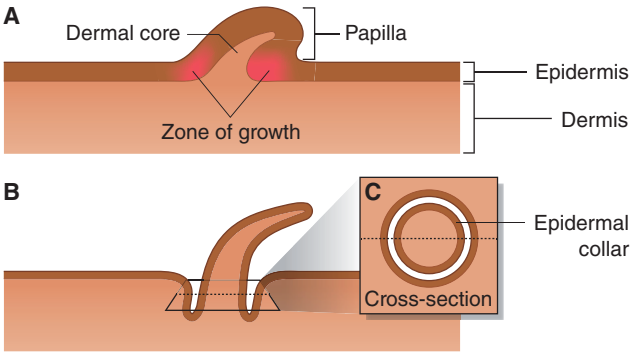


Fig. 4.05 Feather growth from dermal papilla. (A) The early bud of a new feather, rising from both the epidermal placode (thickened epidermal skin not shown) and dermal skin layers, forms the papilla. (B) Epidermal cells at the base of the papilla grow rapidly. These cells eventually double-back into the dermal layer, forming a double layer of invaginated epidermal skin—the feather follicle. (C) A cross-section of the growing feather within the follicle reveals the arrangement of epidermal skin, creating the epidermal collar and its dermal core. (Adapted from Prum 1999. Reproduced with permission from John Wiley and Sons.)

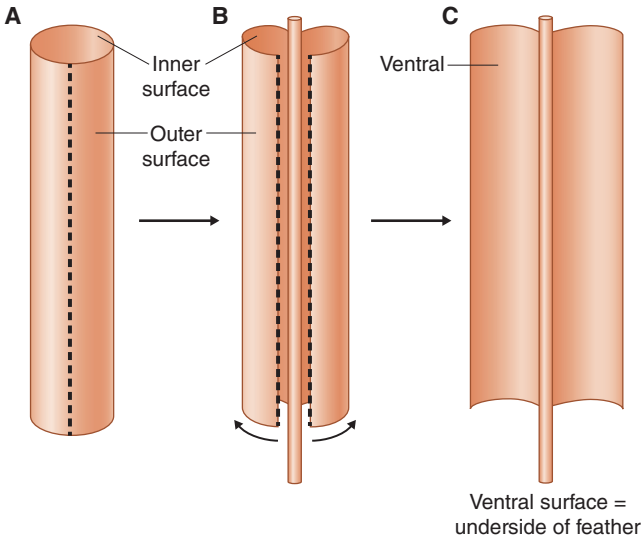


Fig. 4.06 Stages of an unfurling feather. (A) As it emerges from the dermal papilla, a feather resembles a straw with a slit in one side (black dashed line). The internal and external surfaces have different curvatures. (B) As it unfurls, the tube interior forms the ventral (underside) surface of the feather. (C) When a feather has unfurled completely, its ventral surface is concave and its dorsal surface is convex. (© Cornell Lab of Ornithology.)

cells cease to multiply within the follicle, and it goes dormant. However, the follicle, with its dermal core and epidermal collar, still exists, ready to restart the process when it is time to produce a new feather. New keratinocytes, through their rapid new growth, will then simply push their progenitors upward and outward from the collar, pushing out the old feather and replacing it with the next one. The same follicle can thereby produce several different feather types over a bird's lifetime.

Two aspects of follicle anatomy make the development of a feather a bit counterintuitive. The first is the fact that feather follicles are tubular structures. How does tissue extruded from a circular growing surface become a "flat" feather? This transformation is described in greater detail later in this section, but as a primer, imagine the growing feather within the follicle being pushed out from the skin as a hollow column of tissue shaped like a straw (Fig. 4.06A). Splitting open the straw along one side and uncurling it (Fig. 4.06B) then produces a long, flattened, but concave structure (Fig. 4.06C). Roughly speaking, feathers grow curled with the outside edges of their vanes touching. This sort of unfurling is the basis for how a flat feather emerges from its initial columnar shape.

The next challenge is to figure out how the follicle, which remains fixed on the surface of the skin, can grow an intricately branched structure backwards, from its outer tips to its base. That is, rather than sprouting out barbs from the growing rachis as the rachis grows out (and barbules from the barbs as barbs grow out), feathers develop and emerge from their distal tips first. The branching structure is produced when the finest growing fibers migrate or shift inside the cylindrical follicle with time, to fuse together into larger fibers (like small streams merging into larger rivers) as they grow. Thus, feathers are not so much intricately branched structures like trees, but instead are intricately fused networks of fibers in which the smallest fibers first originate, then merge together, and finally emerge from inside the feather follicle (Fig. 4.07).

With these two generalizations in mind—a feather is grown like a thin-walled straw that becomes unfurled along its long axis, and its branched structure is created by intricate fusing of fine fibers—let us examine the developmental biology of a typical pennaceous feather in more detail.

4.2.2 Generating the branched feather form

The epidermal collar is where everything happens to generate the branching structure of the feather. The geometric organization of the growing and fusing cells within the collar is what creates the classic feather shape of a central shaft (the rachis) with symmetrical side branches (the barbs). Because the position of the keratinocytes within the epidermal collar determines what part of the final feather the cells will become, it is important to understand the relationship between the position of cell growth within the follicle and the position of finished structures on the mature feather.

Just as the whole bird itself has a back, a belly, a head and a tail, the epidermal collar also has an orientation,

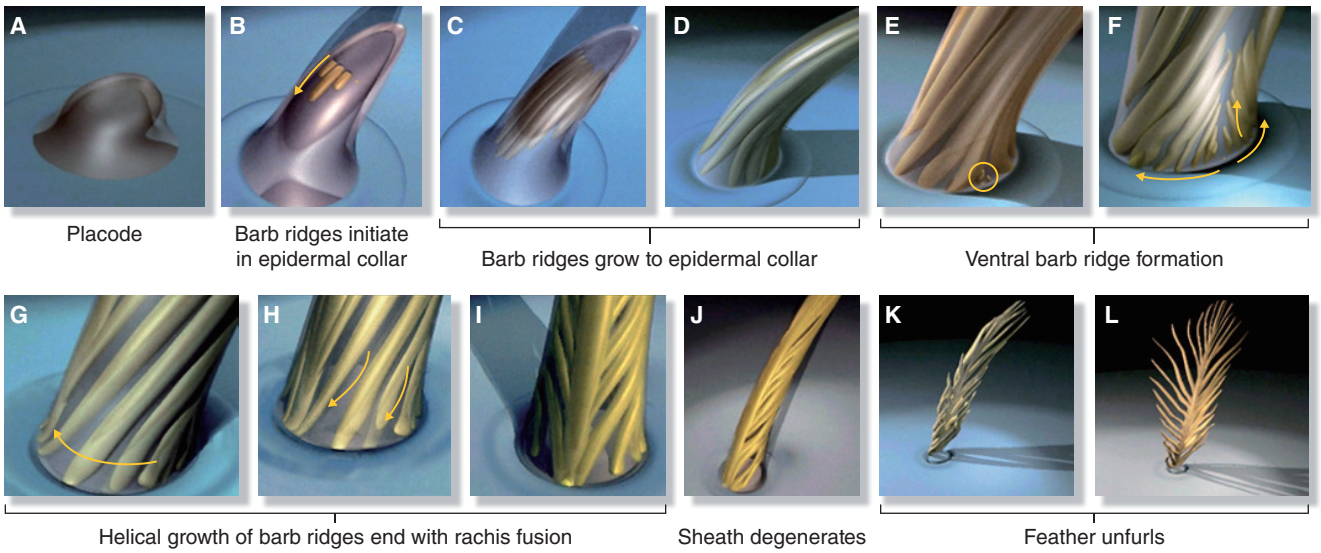


Fig. 4.07 Pennaceous feather growth. Growth begins inside the epidermal placode (A) with the initiation of feather barb ridges (B). Inside the feather sheath, the dorsal barb ridges continue to grow down (C, D), eventually meeting the epidermal collar around the placode base. The ventral base of the growing feather forms another barb ridge (E, F), with helical growth leading to the formation of a central rachis ridge of the still sheathed feather (G, H, I). The sheath then deteriorates (J), permitting the barbs of the pennaceous feather to fully unfurl (K, L). (Courtesy of Matthew Harris, John Fallon, and Richard Prum.)

or sides. Most simply, when unfurled, cells on the inside of the collar (the inside surface of the straw) become the feather's ventral (or bottom) surface, and those on the outside of the collar (the outside surface of the straw) become the feather's dorsal (or upper) surface (Fig. 4.08).

Another basic axis of a feather is proximal/distal (or close to the bird's body versus further away). As a feather grows, newer cells are generated under the older ones, such that the new growth forces the older growth outward, away from the body (much as our nails grow). Thus, the first cells grown correspond to the distal tip of the feather, and the last cells, the proximal base of the calamus (Fig. 4.01).

The epidermal collar has other visibly differentiated regions that correspond to regions of the mature feather. One area is a distinct swelling or ridge of keratinocytes called the rachis ridge (Fig. 4.09A). As you might expect, cells grown within the rachis ridge produce the rachis. The tissue forming the remainder of the collar is composed of barb ridges: strips of active keratinocytes, packed together in bundles (one bundle of keratinocytes per barb ridge) (Fig. 4.09B) and growing around in a semicircular route toward the rachis ridge. As the barb ridges grow they become the elongate, filamentous barbs that eventually converge upon and fuse with the continuously growing rachis (Fig. 4.10). New barb ridges continually form in the epidermal collar opposite the rachis ridge, and each barb ridge becomes exactly one barb.

When the epidermal collar is viewed in cross-section, it looks like a ring, with blocks of active tissue—the barb ridges—beading the perimeter, and with the rachis ridge



Fig. 4.08 Dorsal and ventral surfaces. These Scarlet Macaws (*Ara macao*) expose both sides of their primary feathers during flight. The dorsal side (top) of each primary is blue; the ventral side (bottom) is red. (Photograph by Stan Chapman.)

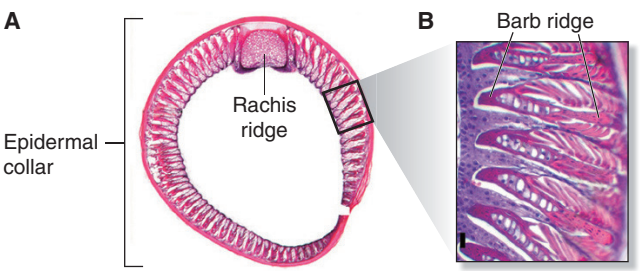


Fig. 4.09 Epidermal collar and barb ridge anatomy. (A) Cross-section of the epidermal collar and the rachis ridge, where the keratin generated by keratinocytes produce the rachis of a feather. (B) An enlargement of the barb ridges, which grow toward the rachis ridge. (Adapted from Yu et al. 2002. Reproduced with permission from Macmillan Publishers Ltd.)

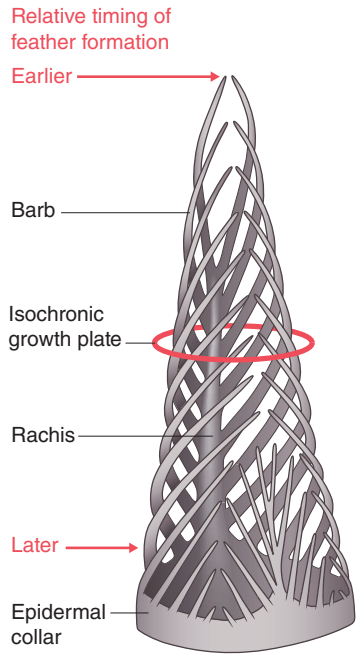


Fig. 4.10 Progression of feather growth from the epidermal collar. Counterintuitively, distal feather barbs (feather tip) grow out from the epidermal collar before they merge with the central rachis ridge later on during the growth process. (Adapted from Lucas and Stettenheim 1972.)

forming an enlarged portion on one side of the ring (Fig. 4.09A). On a finer scale, the individual barbs are formed by a process similar to that occurring within the epidermal collar as a whole, with cell migration during growth leading to slender barbules that ultimately fuse with the rami of the barb (Fig. 4.09B).

In summary, although the feather-growing structure, the follicle, is a hollow cylinder of tissue, the keratin-growing cells are distributed in strips within that cylinder. These cells migrate and fuse to one another in very specific ways, creating, when it unfurls, the feather's doubly branched, relatively two-dimensional structure. One result of this constantly extruded ring of growth is that all fibers at a particular point along the mature feather—whether those of the rachis, the barbs, or the barbules—originated at the same time (Fig. 4.10), and therefore represent a single moment of time during growth. For this reason, the different feather structures do not originate as a simple series. Instead, the distal tip of the rachis originates at the moment of initiation of each feather's development, while barbs originate over and over again, often in pairs, starting at their tips opposite the rachis, and growing back to merge with the rachis as the rachis ridge grows. Often dozens of barbs will be growing at the same time, each at different points along their length, and each sequentially joining to the rachis. Barbs continually originate as long as the vane is growing. In a process similar to barb growth, barbules originate at their tips in hundreds of pairs as each barb grows, and this process continues until the last barbule on a barb fuses with the rami near its attachment to the rachis.

As mentioned above, often the hardest part of this process is to visualize how the branching structure of the feather can emerge from a ring of tissue perpetually growing at its base. Yet consider the alternatives. If the feather follicle functioned like a simple pasta maker, squeezing out a hollow tube of keratin, the epidermal collar would simply produce keratinous macaroni or straws. Alternatively, if a feather was to branch into finer subdivisions as it grew from its base outward to its tips, like a plant, vessels and nutrients would be needed to support the tissues growing ever further out away from the body. Given the huge number of feathers on the bird, this would be a difficult undertaking. However, all the growth is in fact generated from one ring of multiplying tissue sitting near the surface of the skin. Thus, the only way for the branching shape to develop is for the many distal tips to grow inward and fuse into larger structures: barbules into barbs, and barbs into the rachi.

The dermal core—the structure that originally precipitated the development of the feather follicle—occupies the space inside the epidermal collar for the duration of feather development. While a feather is developing, blood vessels extend into the base of the growing feather, providing nourishment for the growing cells. As cells multiply, and they are pushed further and further from the epidermal collar, they stop receiving nourishment from the dermal core, and ultimately they dehydrate and die, while younger cells are still growing at the feather's base. When the feather is fully formed, the blood supply to the entire feather is cut off as the vessels are reabsorbed into the papilla through a hole at the very end of the calamus. On a large feather this hole often can be seen without magnification.

When viewing a living bird, growing feathers can be recognized by the presence of oddly thick, plastic-looking rods where feathers would otherwise be. These distinctive growing feathers are called **pin feathers**—newly grown feathers still enclosed within a bluish or grayish waxy covering called a **sheath** (Fig. 4.11). Developing independently from the rest of the feather, the sheath is produced by the outer layer of the epidermal collar as the feather grows. Functionally, the sheath protects the nascent feather as it grows and then dries and dies. It also holds the feather in its curled, cylindrical form while it continues growing at its base. As the feather matures, and its cells dehydrate and

Pin feathers: developing feathers that are still surrounded by a feather sheath.

Sheath: the temporary tube-like covering that surrounds a growing feather.



Fig. 4.11 Pin feathers. This Brown Thrasher (*Toxostoma rufum*) nestling has conspicuous pin feathers emerging from their waxy, bluish sheaths as it molts from its natal down to its juvenal plumage. Eventually, these pin feather sheaths will either break off or be removed by the bird during preening. (Photograph by Stephanie Sanchez.)



Fig. 4.12 Fault bars in feathers. When a bird experiences high levels of stress (such as severe food limitation) during early development or before an adult molt, fault bars—caused by a temporary reduction in fiber growth—may appear in its new feathers. Often these fault bars are most apparent in the rectrices (tail feathers). (Photograph by Nicholas Bayly.)

die, the sheath also dries, splits, and falls away or is preened away by the bird.

Although the general process of feather development described here proceeds by tightly programmed and regulated processes, external environmental factors can influence the development of feather structure. For example, brief nutritional deficiencies or short-term stresses can lead to a sudden reduction of the cross-sectional area of the barb and barbule fibers, creating visible lines on the mature feather known as a **fault bars** (Murphy et al. 1989) (Fig. 4.12).

4.3 Evolution of feathers

Among living organisms, only birds have feathers. As we have begun to see, feathers (and their development) are so intricate and complex, they raise questions about how they evolved in the ancestors of modern birds.

One modern hypothesis of the evolutionary steps that led to modern feather structure is summarized in Box 4.01. Feathers were long thought to be essentially a frizzy or frayed version of reptilian scales. However, evidence challenging this hypothesis comes from how feathers grow: rather than developing as plate-like structures like reptilian scales, feathers are produced by feather follicles, which, as we have seen, are miniature tubular developmental organs distributed over the skin. Although feathers have some features in common with the reptilian scale (like being distributed regularly across the skin, grown from the base, and made of beta-keratin), the columnar nature of the feather follicle itself is a unique feature. Thus, developmentally, from the creation of the follicle forward, all of the details of feather growth are also novel, with no direct parallels in other animals. In fact, the unique arrangement of the follicle means that a feather can be defined simply as any structure produced by a feather follicle.

This definition may seem trivial given that, at this point in history, all birds and only birds have feathers, but it becomes important when looking back through the fossil record to the origins of feathers in the ancestors of birds (Box 4.01). Over the past several decades, paleontologists working on exceptionally well-preserved fossils from Liaoning Province in China have filled in many of the details about how various anatomical features of birds, including feathers, evolved in the theropod dinosaurs (Chapter 2). Numerous non-avian theropod fossils have been found with clear imprints of so-called "integumentary appendages" surrounding the body—skin-covering structures like scales, feathers, and hair, presumably grown from the skin itself—forming pigmented halos around fossilized limbs, torsos, heads, necks, and tails (Fig. 4.13). When it was verified that these appendages were composed

Fault bars: transverse regions on a mature feather with slightly different coloring or texture that correspond to different stressful days of feather growth.

Box 4.01 One possible scenario regarding the evolution of feathers

Ornithologist Richard Prum (1999) has proposed a developmental model for the evolution of modern feathers (Fig. 4.B4.01). He suggested that feather evolution likely occurred via a series of six stages, each representing increasingly more complex versions of the avian feather follicle and its resultant feather. The last evolutionary stage is the modern feather follicle and modern feather; the earlier stages represent their potential evolutionary predecessors.

Stage I would have involved the origin of the simplest feather follicle, a hollow cylinder of undifferentiated, homogeneous tissue. No substructure within the collar, such as a rachis ridge or barb ridges, would be present—only a simple tube of keratin-growing cells. We can imagine that an epidermal collar of this structure would grow a hollow column of keratin, or a tubular feather.

The evolutionary novelty defining stage II would have been the creation of barb ridges. This would require differentiation of tissue within the epidermal collar into strips of keratinocytes growing cells separately from other strips within the collar. Such a follicle would create a tuft of unbranched barbs, much like the tuft of fluttering strips of paper on the end of a fringed party horn. With no rachis ridge formed, and thus with nothing for barb ridges to fuse with, no rachis would be formed, and the length of the feather would be limited to the length of its constituent barbs.

Stage III involves two steps that must be taken before the next stage could happen, here generating the two levels of branching structures found in modern feathers: barbs branching from (fusing with) the rachis, and barbules branching from (fusing with) the barb. Thus in stage III, a rachis ridge would have become differentiated such that a branching structure could have been formed by barb ridges fusing with the rachis ridge.

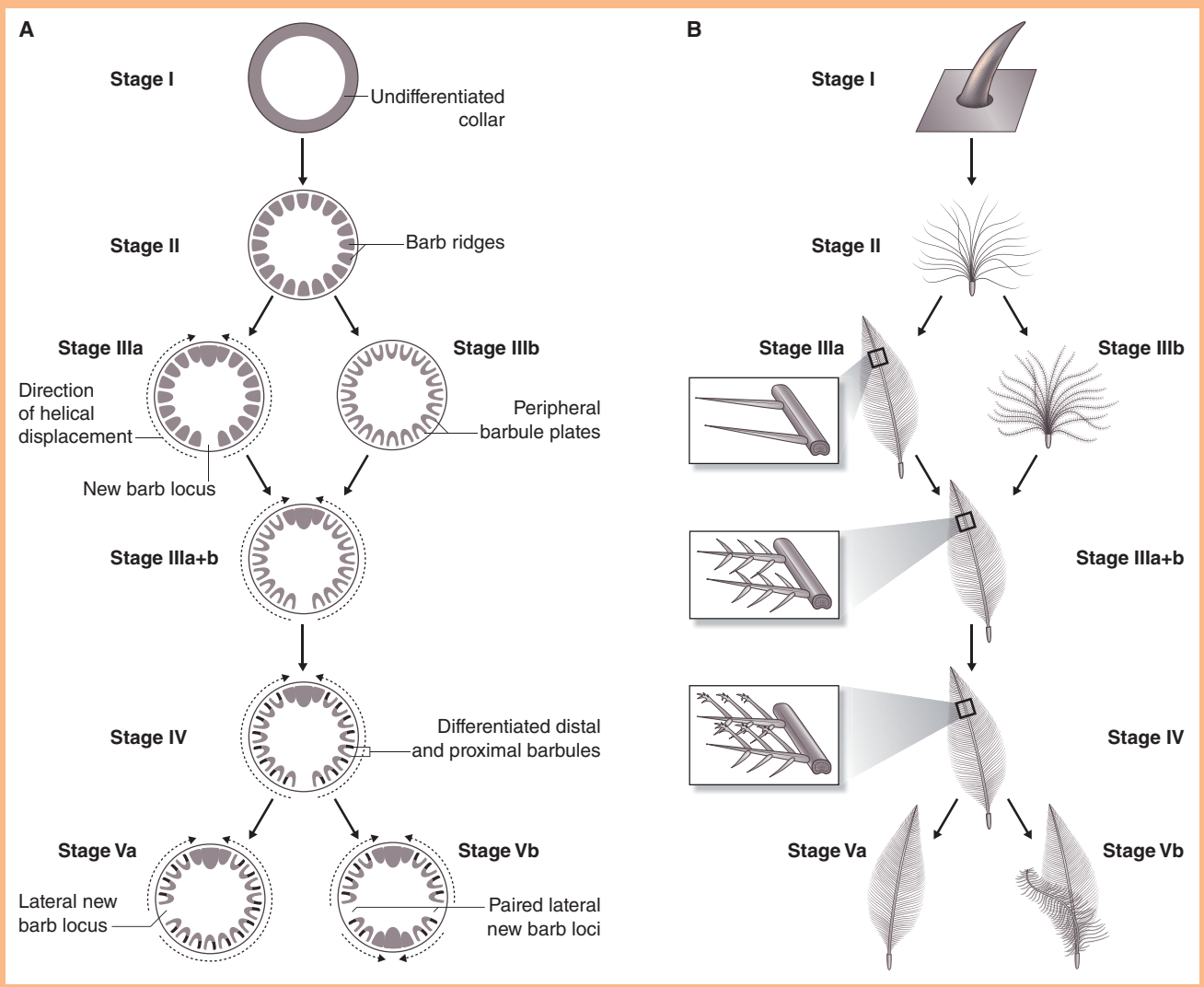


Fig. 4.B1.01 Hypothetical stages of feather evolution. (A) Developmental stages of feather growth from an anterior perspective of the epidermal collar. (B) One hypothesized transition of feather follicles. (Adapted from Prum 1999. Reproduced with permission from John Wiley and Sons.)

Continued

Additionally, the developmental substructure that produces the barbule must have formed within the barb ridges to create the branching structure of the barb. These two developmental advances result in two levels of branching hierarchy—barbs and barbules—on the feather itself.

Stage IV involved the advance from the mere presence of barbules to specialization of the barbule structure. In order to function the way they do in modern pennaceous feathers, the distal barbules must have the hooklets, or barbicles, that allow them to grab the proximal barbules of the neighboring barbs and create that special weave that closes the pennaceous vane. This is the hypothesized novelty of stage IV.

Finally, stage V is considered the "specialization stage," various modifications of the general developmental model generate the diversity in feather morphology we see within and among modern birds.

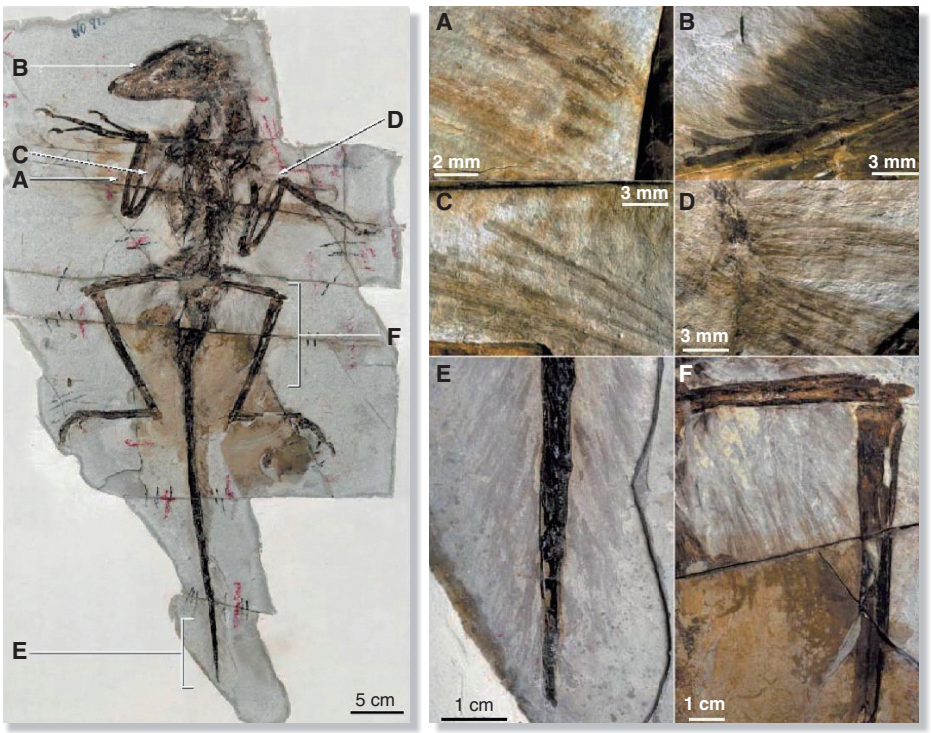


Fig. 4.13 Proto-feathers from dinosaur fossils. Integument structures surrounding the body of this small theropod dinosaur from Liaoning Province, China are feather-like in form and (likely) function. The close-ups of the six labeled regions on the fossil reveal the filamentous morphology at different areas of the body. (From Ji et al. 2001. Reproduced with permission from Macmillan Publishers Ltd.)

of beta-keratin, which is known to occur only in bird feathers and reptile scales, researchers became more comfortable referring to these thin, elongate structures as feathers (Schweitzer 2001).

Together, these fossils contribute to a coherent picture of feather evolution occurring in various steps through many millions of years. The greatest surprise has been how early the hypothesized evolutionary/developmental stages occurred relative to the origin of birds. Until recently, few researchers questioned the idea that feathers are, and have always been, limited to birds. In fact, feathers had long been considered a defining characteristic of birds, as hair is to mammals. But now, relatively simple filamentous feathers—those without the secondary and tertiary structure of barbs and barbules—have been found on some of the earliest fossil theropod dinosaurs that lived long before the first birds evolved. These fossils suggest that many theropod dinosaurs had primitive feathers covering their skin (Fig. 4.14). Similar structures have also been found in even more distantly related dinosaur groups, introducing the possibility that proto-feathers may have arisen very early in dinosaur evolution and been worn by many diverse dinosaur species.

In addition to the surprisingly ancient origin of primitive feathers, feathers that appear completely modern in form also pre-date the origin of birds. For example, Mark Norell et al. (2002) published evidence of a modern pennaceous feather from a group of theropod dinosaurs

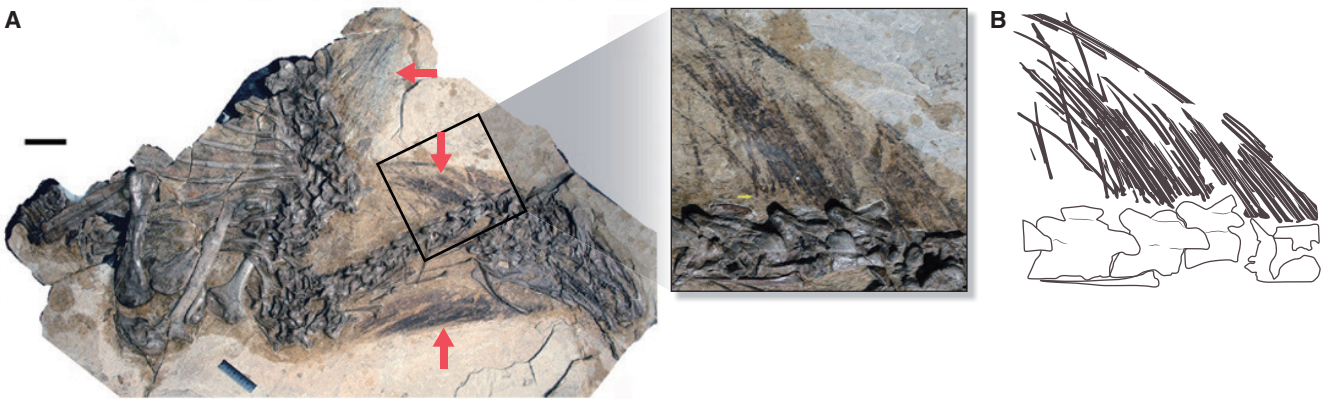


Fig. 4.14 Filamentous dinosaur feathers. (A) This early *Beipiaosaurus* species fossil provides evidence that filamentous feathers (red arrows) existed on dinosaurs long before the first birds evolved. (B) Close-up of the filamentous feathers near the spine of the specimen, drawn in monochrome on the right to clearly depict their slender, elongated form. (From Xu et al. 2009. Reproduced with permission from National Academy of Sciences, USA.)

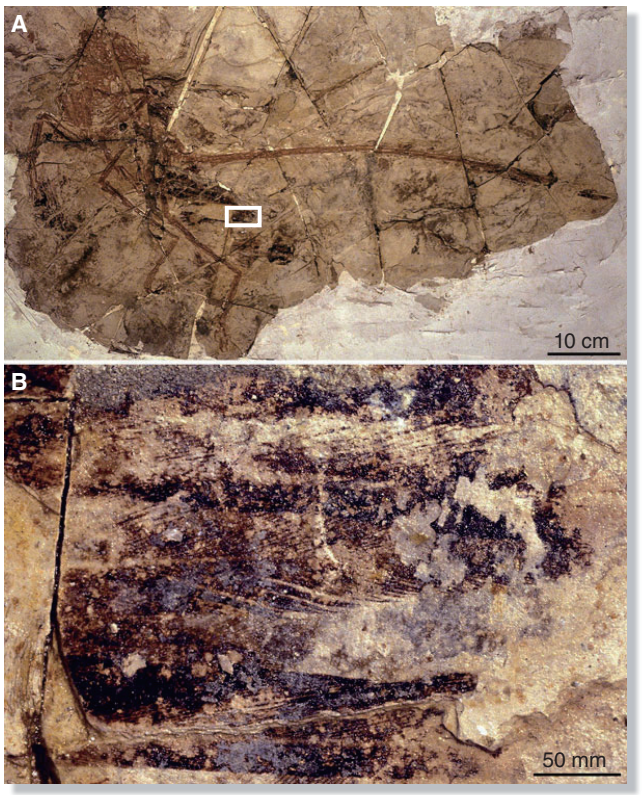


Fig. 4.15 Fossil with modern feather morphology. (A) The earliest known form of the modern, pennaceous feather comes from this small dromaeosaur skeleton. (B) A magnified view of the boxed area in A) reveals individual feather structures, including rachi and barbs. (From Norell et al. 2002. Reproduced with permission from Macmillan Publishers Ltd.)

(Fig. 4.15). Other dinosaurs have been found exhibiting a diversity of feather forms all over their bodies, resembling the diversity of feather forms found across the body of a single individual bird today, with distinctive down, body, and wing and/or tail feathers. One particularly exciting fossil discovery was that of a "four-winged" dinosaur, *Microraptor gui* (Xu et al. 2003), in which elongated feathers appearing just like modern flight feathers are visible along the hindleg (Chapter 2).

More evidence of modern-looking feathers in pre-avian dinosaurs includes a stunning set of publications relating the visual appearance of pre-birds and their feathers to those of modern birds. Researchers have found fossil evidence that, as in modern birds, ancient feathers had brown and black pigments inside them, including arrangements of these pigments that could indicate the presence of iridescent coloration (Vinther et al. 2008, 2010; Zhang et al. 2010). These discoveries have been used to reconstruct the plumage patterns of a handful of feathered dinosaurs. For example, one study reconstructed a striking coloration pattern that might have existed on the feathered dinosaur *Anchiornis huxleyi* (Li et al. 2010) (Fig. 4.16).

The original function of feathers, and their role in the origin of flight, has been a contentious issue for more than a century. These recent discoveries of feathers on non-avian dinosaurs have overturned many of the older arguments about why feathers evolved in the first place. The very ancient origin of feathers, in what appear to be very simple, unbranched forms, argues against feathers originating for aerodynamic functions, as a pennaceous vane is required for feathers to aid in flight. Instead, the variety of feather forms seen across many dinosaur lineages indicates that feathers did not originally evolve for flight at all; instead, they seem to have diversified rapidly from whatever their original function was to become adapted to many functions. That is, as in modern birds, feathers likely performed a variety of functions ranging from protective covering to social advertising or camouflage, with their aerodynamic or flight functions only evolving later, closer in time to the evolutionary radiation of birds themselves (Chapter 2).

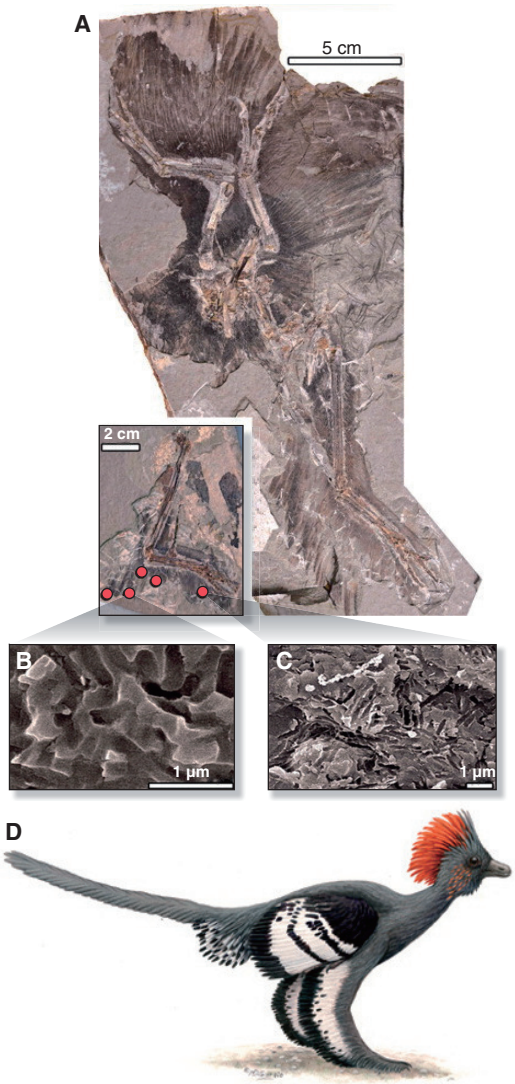


Fig. 4.16 Feathered dinosaur and its probable plumage coloration. (A) Jurassic troodontid (*Anchiornis huxleyi*) with the left forelimb in ventral view (inset) and the right in dorsal view. Selected samples (red dots on the fossil wing) show the location of melanosomes (B, C) used to determine the probable coloration of the dinosaur (D). (A–C, from Li et al. 2010. Reproduced with permission from AAAS and Jacob Vinther. D, illustration by Michael DiGiorgio.)

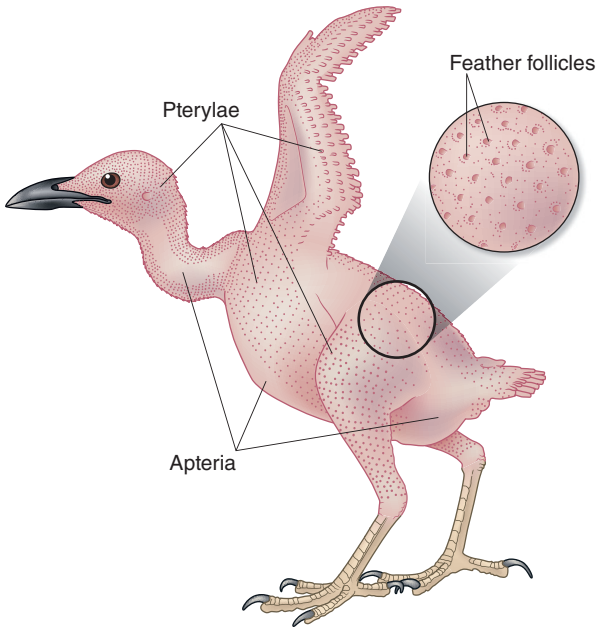


Fig. 4.17 Regions of feather growth. On young or plucked birds, the feather follicles are clearly arranged in feather tracts, or pterylae. Featherless areas are called apteria. (Adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology.)

4.4 Types of feathers: distribution, forms, and functions

Feather follicles are the sites of feather growth and development. Like hair follicles and their hairs, mature feathers remain attached to the body at the site of the follicle, but unlike hairs, feathers are distributed on the surface of a bird in more widely spaced but tightly regulated patterns. This can be seen on the skin of a whole fresh chicken (Fig. 4.04), turkey, or duck, where the follicles appear as small, distinct, and regularly—almost geometrically—spaced pores. In most birds, the feathers are not distributed uniformly over the body but are grouped into feather tracts, more formally called **pterylae**, which are defined groupings of feathers. Separating these tracts are regions of bare (unfeathered) skin called **apteria** (Fig. 4.17). Feathers from the pterylae easily extend over the spaces created by the apteria, and the downy bases of feathers tend to fluff out so that these bare patches are rarely visible on a living bird.

The detailed arrangement of feather tracts and bare patches across the body, collectively called the **pterylosis**, varies among groups of birds, and some birds have unique patterns of pterylosis. For instance, birds in the Corvidae family—which includes ravens, crows, and jays—have a characteristic apterium on their back, along the midline of their spine. On the other hand, a few kinds of birds,

Pterylae: feather tracts, the areas of a bird's skin to which feathers are attached.

Apteria: regions of bare or less-feathered skin between the feather tracts.

Pterylosis: the pattern and location of the feather tracts on a bird's skin.

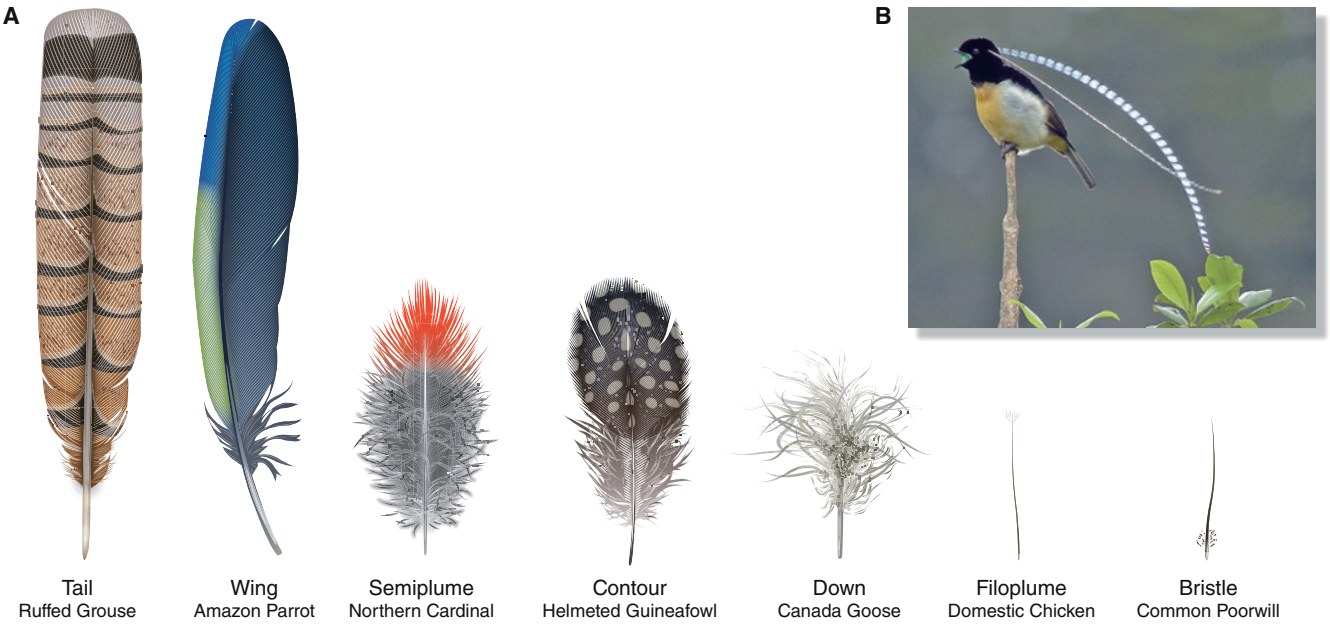


Fig. 4.18 Types of feathers. (A) Examples of six types of feathers: pennaceous feathers of the wing and tail, semiplume, contour, down, filoplume, and bristle. (B) Feathers used for display: during mate attraction displays, the male King-of-Saxony Bird-of-Paradise (*Pteridophora alberti*) thrusts its extraordinary head plumes forward while producing an otherworldly twittering sound. (A, illustration by Andrew Leach © Cornell Lab of Ornithology. B, photograph by Pete Morris.)

especially waterbirds such as penguins, have a continuous pterylosis with no apteria, presumably to help prevent water from penetrating to the birds' skin and chilling it. Historically, such distinctive patterns provided important clues for identifying some of the major evolutionary groupings of birds (Chapter 2).

Feathers often fulfill different roles on different parts of a bird's body, and thus the feathers populating the various pterylae come in a great variety of shapes and sizes (Fig. 14.18A). A typical bird might have a fluffy down undercoat for insulation; feathers covering the torso that act as sunscreen, a wind breaker, or a raincoat depending on the weather; vaneless bristles around the mouth for feeding functions; strong pennaceous wing and tail feathers used for flight; and ornamental plumes (that can be located in any number of places) for signaling to potential mates or rivals (Fig. 4.18B).

From an engineering standpoint, the various feather types interact beautifully with the two basic physical environments they encounter: fluid media (in the form of air and water) and electromagnetic radiation (in the form of heat and light). By varying the basic feather structures of the rachis, barb, and barbules, birds are able to vary the aerodynamic, hydrodynamic, insulative, repellant, acoustic, and visual properties of their feathers. The resulting diversity of forms underlies the wealth of feather functions. Feather diversity exists within an individual bird at a given time and in a given context, but also throughout an individual's life, and certainly among species.

Despite the great variety of feather forms and function, they tend to group naturally into six major feather types, each tending to be distributed in specific ways on the body, and each specializing somewhat for different functions. However, be aware that these groupings, despite helping to categorize many important biological properties of feather diversity, are just a useful way of organizing feather diversity, and that the world of feathers is rich with intermediates and exceptions to these general groupings.

4.4.1 Down: insulation

Down feathers are entirely plumulaceous, defined by having a rachis that is shorter than the longest barbs, or with the rachis missing entirely. Structurally, they are relatively simple: their barbs emerge more or less together as a tuft near the base of the feather, where they float free of one another with little or no rachis (Fig. 4.19). As a result, down feathers are fluffy and soft.

Down feathers: soft, fluffy feathers that typically lack a rachis.

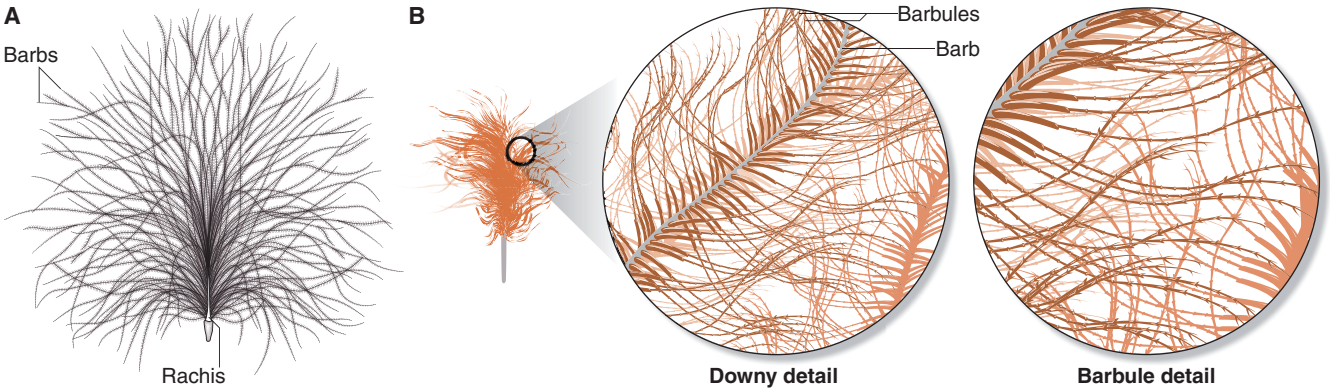


Fig. 4.19 Down feather anatomy. Down is an excellent insulator, as its free-floating barbs trap large quantities of air. (A) A typical down feather; note that the barbs extend substantially farther than the rachis. (B) Detail of down feather structure. (A, from Lucas and Stettenheim 1972. B, illustration by Andrew Leach © Cornell Lab of Ornithology.)



Fig. 4.20 Warm down provides insulation. Like many seabirds, this Chatham Albatross (*Thalassarche eremita*) chick is well insulated by down feathers. This species incubates its young on a cold, windy, oceanic island where effective thermoregulation is essential. (Photograph by Lorna Deppe.)

As warm-blooded creatures, birds must be able to manage their internal temperatures by thermoregulation: regulating heat loss and heat gain (Chapter 7). Down feathers are excellent insulators, in some ways superior to insulators used in human clothing such as wool and polyester. Down's role as a lightweight but high-quality insulator is especially important for small birds living in cold climates, as well as for birds that float on, dive into, or swim in water (Fig. 4.20).

Recent research has attributed the superior insulating abilities of down to its extremely fine fiber structure (Wan et al. 2009): the barbs and barbules form tiny, loose tangles that trap air and its heat. The relatively formless structure of downy feathers is one of the factors that make them great insulators. At the tiny scale of feather barbs and barbules, however, air behaves viscously, so air moving among the tangled barbs can be imagined as a thick substance, such as oil or honey, moving through a fine sieve. Down feathers, rather than relying on a closed barrier to reduce airflow, literally physically trap and tangle warm air in their fine fibers.

Birds have three distinct types of down feathers: natal downs, body downs, and powder downs. **Natal downs** generally cover the whole bird's body, are temporary (present only around the time of hatching), and arise from the same feather follicles that later produce contour feathers. In fact, the continuity of the feather follicle (and its epidermal collar) between the growth of subsequent feathers can be seen in some young birds whose natal downs remain attached to the tips of the subsequently growing contour feathers. This weak attachment between the natal down and subsequent contour feather results in the fluffy, unkempt appearance of some juvenile birds like thrushes, robins, and bluebirds (Fig. 4.11).

Precocial and altricial birds typically have distinct strategies of thermoregulation and therefore may have down for more (in the case of precocial birds) or less (in the case of altricial birds) time. Most precocial birds leave the nest shortly after hatching (Chapter 11) and must maintain

Natal down: the down feathers that cover the body of a hatchling bird.



Fig. 4.21 Downy plumage in precocial versus altricial nestlings. (A) Since precocial chicks must immediately maintain their own body temperature, they hatch with a thick layer of down and advanced motor skills. (B) Altricial young hatch completely helpless, with little insulating down (arrow). They rely on their parent(s) to provide warmth during the first stages of their lives. (C) Nestlings in an intermediate category—which includes many slow-growing species (such as hawks, eagles, and owls)—hatch with little mobility but substantial down, as they must sit exposed for hours awaiting their hard-to-capture meals. (Photographs by: A, Jennifer Hall; B, Lindell Dillon; C, Al Cecere © American Eagle Foundation. All rights reserved. Used by permission.)

their own body temperature in the form of insulating natal downs. For instance, newly hatched ducklings or chickens are known for their soft, fluffy look (Fig. 4.21A). In contrast, many altricial birds are much more helpless after they hatch and depend on warmth from a brooding parent bird. While down protects precocial nestlings by acting as an insulator between the nestling's body temperature and the environment, so too can down prevent desirable heat transfer between the nestling and its parent, and in these cases, too much natal down would prevent heat transfer from the parent's body to the young. Altricial nestlings therefore often have only sparse natal downs, allowing more efficient heat transfer to the nestling from the warm, naked skin on the belly of their brooding parent (Fig. 4.21B). In some cases, for more slowly developing young that cannot fly for weeks after hatching but who nonetheless spend hours alone in the nest, chicks may have an insulating cover of downy feathers that lasts for much of their flightless period. Young hawks and owls, for example, can have a prolonged downy cover (Fig. 4.21C).

Body downs are distinct from natal downs in that the body downs of adult birds arise from follicles that produce only down feathers. These adult down feathers are often distributed throughout the bird's plumage, and they are most abundant in waterbirds such as penguins, loons, petrels, auks, geese, and ducks (all of whom undoubtedly benefit from the extra thermal insulation). Many birds, such as female waterfowl, pluck body downs from their bellies to line their nests. Of these, the most famous is the Common Eider (*Somateria mollissima*) (Fig. 4.22). Clothing and bedding filled with eider down is notoriously expensive because the exceptionally soft down must be gathered by hand and each nest typically provides only about 15 grams of down.

Unlike the other two types of downs (and all other feather types, in fact), **powder downs** are distinctive in that they are never molted, but rather grow continually, disintegrating at their tips to produce a fine keratinous substance that resembles talcum powder in texture. The powder is abundant enough to permeate the bird's entire plumage, likely helping to make it waterproof. The appearance of



Fig. 4.22 Down as nest material. Many waterfowl line their nests with down—often plucked directly from the mother's breast—to insulate and protect their eggs, as a Common Eider (*Somateria mollissima*) has done here. (Photograph by Sergei Korsun.)

Body down: down feathers that lie under the contour feathers in many adult birds.

Powder down: specialized down feathers that grow continuously and disintegrate at their tips to produce a fine powder.



Fig. 4.23 Powder down patch. In a few groups of birds, the tips of powder down feathers, shown here on a Snowy Egret (*Egretta thula*), disintegrate to produce a keratinous water repellant that resembles talcum powder. (Photograph by Jennifer Miller.)

powder downs can vary; they look like fluffy contour feathers in some species, or like tiny body downs in others. Powder down occurs only in certain groups of birds, such as herons and pigeons, and these downs may be scattered throughout the plumage or clustered in patches (Fig. 4.23).

4.4.2 Contour feathers: feathers for all weather

Named **contour feathers** because they give a bird its characteristic shape or outline, these feathers cover most of the surface of an adult bird. Contour feathers are defined by having a rachis longer then the longest barb, and at least a portion of the rachis consisting of a pennaceous vane (Fig. 4.24). Frequently there is a plumulaceous portion of the vane at the base of contour feathers. Contour feathers have many roles, often serving a wide variety of functions simultaneously or in different contexts.

Positioned one atop another but offset like shingles on a roof, the pennaceous portions of contour feather vanes form a surprisingly effective barrier. The plumage can aid in thermoregulation by absorbing or reflecting heat-generating sunlight and in deflecting wind and/or trapping warm air. In terms of aerodynamics, contour feathers streamline the body during flight (Chapter 5). As demonstrated by the particularly smooth contours of swimming birds such as auks and penguins, the streamlining function is even more critical in water, where drag is much greater than in air.

Contour feathers: the feathers that make up the exterior surface of a bird, including the wings and tail.

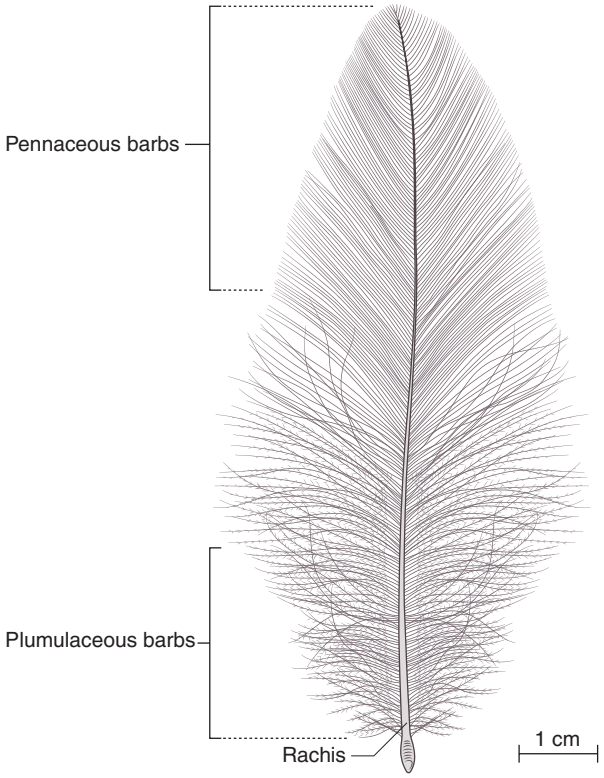


Fig. 4.24 Contour feathers. By definition, the rachis of a contour feather must be longer than the longest barb, and at least one portion must be pennaceous. Contour feathers create the characteristic silhouette of a bird. (Adapted from Lucas and Stettenheim 1972.)

The ability of feathers to repel water is another important property observed best in contour feathers, one that varies among bird species according to their feather morphology. The same contour feathers that perfect the contours of a diving duck also repel water beautifully, as illustrated by the idiomatic saying "like water off a duck's back." Oils from the uropygial gland at the base of the tail have been shown to improve water repellency, but the shape and spacing of the barbs and barbules of a feather are actually more important in conferring its water-repellent properties. This is because a fundamental physical property of water is that while it will tend to cling to most solid materials, like keratin, it cannot adhere to air spaces in materials (even very small spaces). So, when spanning air spaces in a material, water will form droplets (Fig. 4.25). Thus, if the barbs and barbules on a feather are spaced exactly right, water is forced to bead up and roll away. Alternatively, with barbs and barbules spaced differently (more closely together), water can be pulled in to the feather, saturating or permeating it. Some downs (but not all) therefore tend to be vulnerable to saturation. A few diving birds such as cormorants and anhingas have feathers that are relatively easy to wet (Fig. 4.26). The more water-absorbent nature of cormorant feathers allows them to dive



Fig. 4.25 Water-repellent feathers. (A) Water beads on the surface of most feathers due to air spaces between the barbs and barbules. (B) When waterfowl such as this Wood Duck (*Aix sponsa*) resurface from a dive, water pools and slides off their feathers with ease. (C) The uropygial gland (the small yellowish bump at the base of the tail) excretes oils that birds use to maintain and waterproof their feathers. Here a White-winged Crossbill (*Loxia leucoptera*) accesses its uropygial oils with its beak, which it will then use to spread the oils over its plumage. (Photographs by: A, Christine Hall; B, David Nelson; C, Darroch Whitaker, https://en.wikipedia.org/wiki/File:White-winged_Crossbill_Uropygial.JPG. CC-BY-SA 3.0.)

underwater without carrying along bubbles of air trapped in the feathers, whose buoyancy would work against the diving efforts of the birds (Grémillet et al. 2005).

The plumulaceous portion of the vane at the base of many contour feathers is usually protected from the elements by the pennaceous portion, and tends to contribute an insulating function to contour feathers. Some contour feathers have an **afterfeather** (also sometimes called an aftershaft), a minor feather that sprouts from the same follicle, but is (usually) smaller than the main feather, and (usually) completely plumulaceous (Fig. 4.27A). Developmentally, afterfeathers are formed inside a feather follicle by sectioning off a portion of the epidermal collar, and creating a second rachis ridge, toward which a subset of the barb ridges then grow. Afterfeathers provide extra insulation, and are especially well developed in grouse (most of which live in seasonally cold or arctic regions). The flightless Emu (*Dromaius novaehollandiae*) of Australia is unique in having afterfeathers that are as large as the main contour feathers (Fig. 4.27B).

Contour feathers, although relatively long, flat, and broad, are attached to the body at a single small point. It would seem that, like leaves in the wind, such feathers



Fig. 4.26 Water-absorbent feathers. Some diving birds have tighter barb and barbule configurations that facilitate water absorption. Birds with absorbent feathers are faster swimmers, but must dry off before flight. Species such as the Anhinga (*Anhinga anhinga*) do so by spreading their wings while sunning. (Photograph by Nathan Corry.)

Afterfeather: a second, smaller feather that grows from the shaft of a larger contour feather.

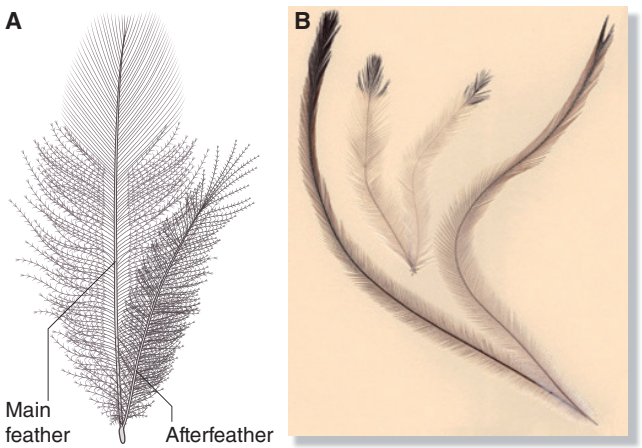


Fig. 4.27 Plumulaceous afterfeathers. (A) A typical contour feather with a plumulaceous afterfeather connected on the right. Afterfeathers, which develop from the same follicle, may serve to protect the main feather. (B) Two double-shafted plumulaceous feathers of an Emu (*Dromaius novaehollandiae*), the only species that develops an afterfeather as long as the main contour. (A, adapted from Lucas and Stettenheim 1972; B, photograph by Lois Hellemond, Mt. Sicker Family Farm.)

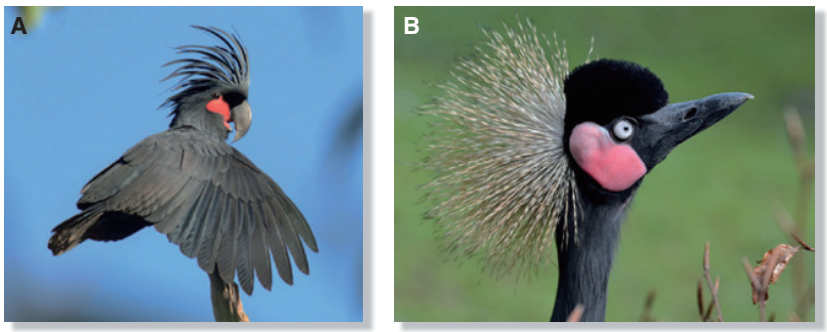


Fig. 4.28 Modified contour feathers. In some species, special contour feathers serve as signaling ornaments, such as (A) the crest feathers of a Palm Cockatoo (*Probosciger aterrimus*), or (B) the stiffened, golden crown feathers of a Black Crowned-Crane (*Balearica pavonina*). (Photographs by: A, Christina N. Zdenek; B, Olaf Oliviero Riemer, https://commons.wikimedia.org/wiki/File:Balearica_pavonina_(Schwarzer_Kronenkranich_-_Black_Crowned_Crane)_-_Weltvogelpark_Walsrode_2012-0-120426_0206.jpg. CC-BY-SA 3.0.)

would be prone to becoming disheveled or disorganized relative to one another. In order to maintain their neat organization, each contour feather is attached to a set of tiny, specialized muscles. Located beneath the surface of the skin in a perimeter around the follicle, tension in these muscles keeps the feather positioned correctly. These muscles also allow a bird to move its feathers voluntarily. In some cases, muscle sheets immediately beneath the skin act together with the individual feather muscles to coordinate movement of the feathers along an entire feather tract. Most feathers are incapable of being moved individually, and the movement of most feathers is limited to raising and lowering the feathers, alternately fluffing and sleeking them.

The ability to move contour feathers is especially important for signaling in social contexts. The signaling that birds do with their feather movements can be conspicuous and extreme, as in crest movements of Australian cockatoos, or relatively subtle as can be witnessed during interactions among songbirds at birdfeeders worldwide.

The length, coloration, and/or barb and barbule morphology of contour feathers of some bird species are modified to alter their appearance. In such cases, these feathers often act as ornaments, morphological structures whose appearance is modified for the purpose of social signaling and/or display. The curly body feathers of the Curl-crested Manucode (*Manucodia comrii*) of New Guinea, the erectile crest feathers of the Palm Cockatoo (*Probosciger aterrimus*) of Australia (Fig. 4.28A), the stiff, straw-like crown feathers of the Black Crowned-Crane (*Balearica pavonina*) of Africa (Fig. 4.28B), and the long elegant plumes of many herons and egrets worldwide are just a few examples. Male birds-of-paradise have made the most of their contour feathers, using them for display as head wires, breast shields, and silhouette-hiding capes.

4.4.3 Flight feathers: lift and control in air

The **flight feathers** are an easily defined and identified group, with their own specific locations, structural modifications, and functions. Flight feathers form the majority of the wing and tail surfaces of birds; typically they are the stiffest, largest feathers on a bird, and they are almost completely pennaceous. The width of the two sides of the vanes—lateral and medial, or anterior and posterior, respectively—are often asymmetrical, as the leading edge (or anterior edge, the edge that cuts into air) is typically thinner than the trailing edge (or posterior edge) (Fig. 4.29). This is an adaptation that stabilizes the feather under the pressures of air currents during flight.

There are two sets of flight feathers, those that originate from the wing, called **remiges** (singular: remige), and those that form the tail, called **rectrices** (singular: rectrix). Unlike most other feathers, which attach only to the skin, remiges are attached firmly to the bones of the wing, either directly or indirectly via ligaments, and to each other by ligaments connecting their calami. The rectrices form the fan of the tail, and also are connected to one another near their bases by ligaments. The most central pair of retrices attaches directly to the tail bone (pygostyle).

Flight feathers: the feathers that form the wings (remiges) and tail (rectrices).

Remiges: flight feathers that originate from the wing bones and form the wing surfaces/airfoil.

Rectrices: flight feathers that originate from the tail bones and form the tail surfaces/airfoil.

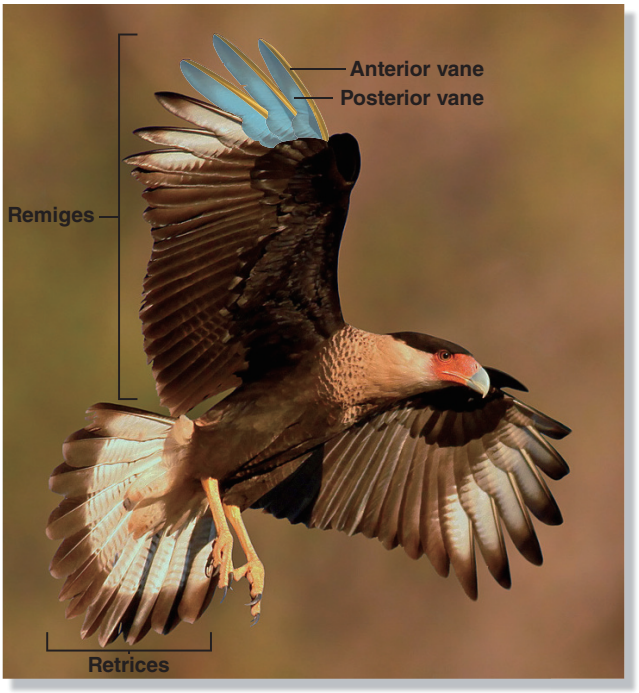


Fig. 4.29 Flight feather terminology. As this Crested Caracara (*Caracara cheriway*) glides down to land, the flight feathers on its wings (remiges) and tail (retrices) are fully extended. Notice that anterior (leading) edges (shaded yellow) face the direction of flight, while the broader posterior edges follow behind (shaded blue). (Photograph by Alfred Yan.)

The number of rectrices ranges from 6 to 32 among flying birds, with the higher numbers occurring in larger birds (Box 4.02). The outermost (distal) remiges of the wing are termed the **primaries**, defined by their attachment to the skeleton of the "hand" or manus (Chapter 6). Depending on the species, birds most commonly have between 9 and 12 primaries. The remainder of the remiges—known as the **secondaries**—extend from the forearm (more specifically the ulna; Chapter 6) of the bird wing (Fig. 4.30A). Bony bumps on the ulna, called quill knobs, indicate the points of attachment for the secondaries and often are visible on the skeletons of larger flying birds (Fig. 4.30B). Across groups of birds, the number of secondaries varies more than does the number of primaries, ranging from 8 to 32. Birds with long wings, such as albatrosses, have higher numbers of secondaries, giving them a larger wing surface. To identify and discuss the biology of important flight feathers, ornithologists have developed a standardized numbering system for individual feathers (Fig. 4.31).

Primaries: the flight feathers of the outer wing that are attached to the manus.

Secondaries: the flight feathers of the inner wing that are attached to the ulna.

Box 4.02 Feather facts

Number of feathers

How many feathers does a bird have? As you might expect, larger birds tend to have more feathers than smaller birds. The record low count (contour feathers only) is 940—from a Ruby-throated Hummingbird (*Archilochus colubris*) (Wetmore 1936). The highest number was reported by Ammann (1937), who patiently counted 25,216 contour feathers on a Tundra Swan (*Cygnus columbianus*). Of these, 80% (20,177) were on the swan's head and neck.

Feather number also varies with a bird's need for insulation. For example, birds living in cold climates have more feathers in winter than in summer. Wetmore (1936) found that in winter White-throated Sparrows (*Zonotrichia albicollis*) have about 2500 contour feathers, but in summer they have only 1500—a 40% decrease. In addition, aquatic birds tend to have more feathers than terrestrial species of a similar size—undoubtedly due to the rapid loss of heat experienced by birds in water.

Size of feathers

Bigger birds not only have more feathers, they have bigger feathers. Not surprisingly, the smallest contour feathers known are from the world's smallest bird: the feathers from the eyelids of the Bee Hummingbird (*Mellisuga helenae*) are a mere 0.4 millimeters long. At the other end of the size range, the feathers forming the peacock's train may be up to 1.5 meters in length.

Weight of feathers

Feathers are, indeed, "light as a feather." Although the feathers of some birds, such as owls, seem to make up half their volume, the feather coat commonly accounts for only 5–10% of a bird's total weight. And yet, as light as they are, a bird's feathers are still usually two to three times heavier than its skeleton.

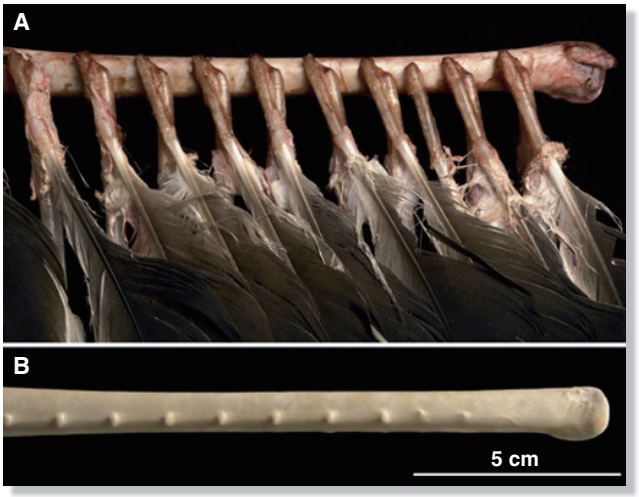


Fig. 4.30 Quill knobs. A Turkey Vulture's (*Cathartes aura*) secondary flight feathers attach directly to the ulna (A) via bony protrusions called quill knobs (B), shown here without the attached feathers. (From Turner et al. 2007. Reproduced with permission from AAAS.)

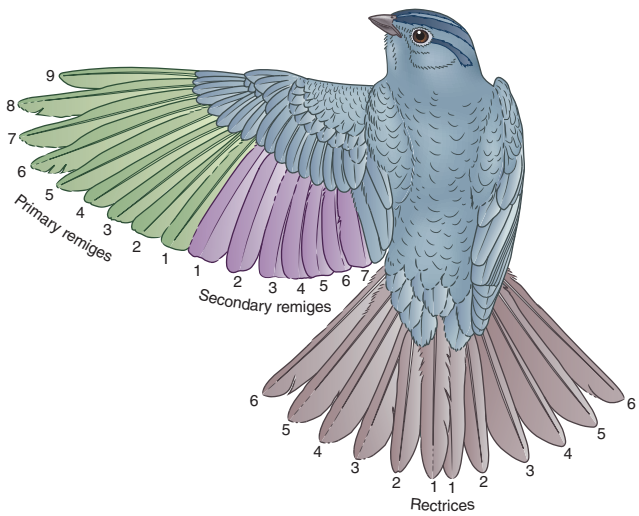


Fig. 4.31 Numbering system for remiges and rectices. Ornithologists subcategorize remiges based on their attachment site: primary feathers extend from the metacarpal bone, while secondary feathers attach to the ulna. Each remige is assigned a number, starting at the meeting point of the two wing bones; therefore, primaries are numbered from right to left, secondaries from left to right. Numbering of rectices begins at the center of the tail and extends outward in both directions. Note that flight feather counts vary widely among species. (Adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology.)

Bordering and overlying the remiges and rectrices on both the dorsal and ventral sides of the wing and tail are rows of contour feathers called **coverts**. Coverts are particularly important in contributing to the streamlined shape of the wing and tail; the aerodynamics of the wing are extremely sensitive to the details of wing shape (Chapter 5).

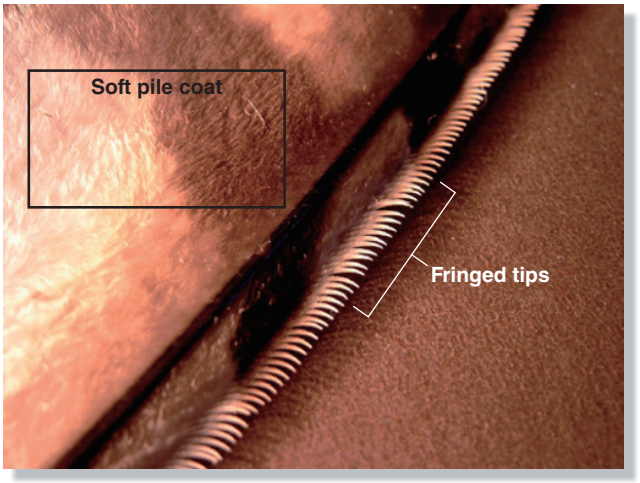


Fig. 4.32 Owls have specialized flight feathers. Owls are extremely quiet fliers, thanks to two main differences in their flight feather microstructure. The inner vanes develop a soft pile of elongated distal barbules (boxed area) that reduces the noise of feathers moving over one another. The leading edges of their primaries have a comb-like fringe that reduces air turbulance and its associated noise. (Photograph by Kersti, https://commons.wikimedia.org/wiki/File:EulenfederTeil3.jpg. CC-BY-SA 3.0.)

The crucial importance of flight feathers for generating lift and establishing control in the air is discussed in greater detail in Chapter 5. Suffice it to say here that remiges are the primary sources of lift generation, and while rectrices also generate lift, they are particularly important for stability and control in flight. Beyond their roles in the aerodynamics of flight, it is worth noting the specific material properties of flight feathers that make them so excellent at manipulating and managing the fluid media of both air and water. Most obviously, in order to generate lift in the very thin medium of air, the feathers of the wing and tail need to form long and broad surfaces that are at once firm, flexible, and lightweight. Feather keratin, as a material, is both firm and flexible, and the woven structure of the pennaceous vane augments these properties by creating a very specific shape while reducing weight and contributing even greater flexibility than could be provided by a solid sheet of keratin.

One incidental effect of the wing feathers moving through air is that their movements tend to generate sounds. Microstructural modifications that intensify or minimize sound production during flight are widespread. In most owls, for instance, the leading edge of the first several primary feathers has a loose fringe; the dorsal surface of the inner vanes of most flight feathers has a soft pile composed of elongated distal barbules (Fig. 4.32). These modifications

Coverts: the smaller, overlapping feathers that overlie the bases of the flight feathers of the wing and tail.

allow owls to fly very quietly, creating little noise even within the high-frequency range that their rodent prey can hear quite well. In contrast, many species of New World flycatchers, as well as pigeons and doves worldwide, have specializations of the primary feathers that exaggerate the sounds produced by incidental wing movements into sounds that function as signals (Hingee and Magrath 2009). As Charles Darwin himself noted, males of many bird species have feather modifications that have evolved for sound production associated with display behaviors and sexual selection (Darwin 1871) (Box 4.03).

4.4.4 Semiplumes: insulation around the edges

Semiplumes represent an intermediate form between down and contour feathers (Fig. 4.33). Unlike contour feathers, the barbules of semiplumes often lack hooks, and thus the barbs do not cling together to form a pennaceous vane. This results in a vane that is not completely formless like down, but that nonetheless is not connected tightly together like the pennaceous portions of contour feathers. Unlike down feathers, the rachi of semiplumes are longer than the longest barb. Semiplumes often occur at the edge of contour feather tracts, sometimes visible and sometimes hidden beneath the contour feathers, and at the inside of the wings (essentially in the bird's armpit) or similarly at the inside of the thigh. Semiplumes are probably contour feathers that have lost the pennaceous portion of their vanes, as they are located in areas relatively protected from the elements by the contours of the bird's body. They likely complement the insulating function of down.

4.4.5 Bristles: detection and protection

Bristles are a highly specialized feather type in which the rachis is relatively stiffened, more strongly tapered, and lacking barbs along most of its length. Bristles are essentially contour feathers that have been simplified for functional purposes, and they are found almost exclusively in the region of the avian head (Fig. 4.34). The best-known bristles are **rictal bristles**, which project from the base of the beak. Many birds, especially those that catch insects in the air such as flycatchers and nightjars, have rictal bristles (Chapter 8). Other regions of the head may also sport bristles, and bristles themselves are categorized by their location, for example as facial bristles (from the sides of the head), narial bristles (on the cere or behind the nares), and loral bristles (from the lores).

Some ornithologists have suggested that bristles might help birds funnel insects into the mouth, but few studies have been conducted to test this supposition. In a study of Willow Flycatchers (*Empidonax traillii*), Michael Conover and Don Miller (1980) found that experimentally taping down or removing the rictal bristles did not affect the birds' success in capturing insects. By using a wind tunnel, however, these researchers demonstrated that the bristles do protect the birds' eyes, as more particles struck the eyes of birds whose rictal bristles had been removed. Rictal bristles are particularly prominent in certain groups (such as the neotropical puffbirds) that regularly capture scaly moths, butterflies, and other large, noxious insects; these bristles may protect the face and eyes of these birds. Similarly, "eyelashes" in birds are often bristles, and these are particularly well developed in birds such as the Ostrich (*Struthio camelus*) and Emu (*Dromaius novaehollandiae*), and in various species of rheas, hawks, turkeys, hornbills, and cuckoos (Fig. 4.35). Another possible but basically unstudied potential function of rictal bristles is detecting the motion of prey held in the beak, providing a sensory function akin to the sensitive whiskers of some mammals (Cunningham et al. 2011).

Bristles: specialized contour feathers in which the rachis is stiffened and lacks barbs.

Rictal bristles: stiff, hair-like feathers projecting from the base of the beak in some birds.

Filoplumes: hair-like feathers having a rachis but few or no barbs.

4.4.6 Filoplumes: feather kinesthetics

Scattered among and usually hidden by the contour feathers of most birds is a distinctive but rarely visible type of feather. These **filoplumes** are the smallest feathers, with an extremely slender, bare rachis and a tiny tuft of barbs (if any) only on the tip (Fig. 4.36). Otherwise reminiscent of the much larger bristles, filoplumes are distinct in lacking feather muscles, instead having distinctive sensory receptors in the skin next to their follicles. These miniscule feathers are thought to monitor movement within the feather coat (Necker 1985). Birds presumably use this information to monitor and detect changes in feather positions that might be caused by wind or body movements (Brown and Fedde 1993).

4.5 Molts and plumages

Although feathers are strong and flexible for their size, the fine structures of which feathers are composed deteriorate with use. Like a hair, a mature feather is a dead structure; it cannot be repaired if it becomes worn or broken. Unlike hair, however, feathers do not grow continuously, but instead develop to maturity fairly rapidly and then remain on the bird's body. Use, sun, and the elements ensure that

Box 4.03 Sounds produced by feathers

Many birds use their beaks, feathers, and other parts of their external anatomy to make sonations, non-vocal sounds that they use for display or other forms of communication. Beak rattling by courting storks and frigatebirds, tail winnowing by courting snipes, and beak splashing by courting Ruddy Ducks (*Oxyura jamaicensis*) are just a few examples of these sonations. Charles Darwin was fascinated with this phenomenon, and he noticed two things about them: first, they tend to be used in courtship displays, and therefore Darwin believed that sonations often arise via sexual selection. Second, in some birds these sonations involve a modification of the bodies of the males, often to the feathers of the wings and/or tail.

Sonations in manakins

In more than half of the 40 species of neotropical manakins, males make prominent wing sounds during courtship displays. Manakins appear to have evolved the capacity to make wing sounds several different times, and even within a single species a male can use as many as five distinctive mechanisms to produce his wing sonations (Prum 1998; Bostwick and Prum 2003).

The Club-winged Manakin (*Machaeropterus deliciosus*) of the northern Andes is the superlative example of how sexual selection can generate adaptations for sonation. Although they look like relatively normal birds, with one flick of his wings above his back, a male can do something no other bird can do: make a short but sustained, harmonically rich, violin-like "ting" sound with his wings. To make this sonation, male manakins flip their wings above their back into a unique posture (Fig. 4.B3.01), and then vibrate them in that position at a rate of 107 Hertz—faster even than hummingbirds beat their wings. Studies using high-speed video have shown that the manakin's wings are not just vibrating, but knocking along their inner edges (Bostwick and Prum 2005).

Club-winged Manakins are named for their set of unique secondary feathers, found on the inside of the wing, in which the rachi are enlarged. One pair of these enlarged feathers (the sixth secondaries) has a series of ridges, and the neighboring feathers (the fifth secondaries) have kinked ends that causes the tip of its rachis to lie on top of the ridges of the sixth secondary (Fig. 4.B3.02). During sound production, when the male knocks these modified feathers together above his back, the knocking causes the fifth feather's "pick" rachis to slide over the sixth feather's "washboard" rachis, and this vibrates the club-shaped feathers. The club-shaped feathers are "tuned" to vibrate at exactly the frequency at which they are being stimulated,



Fig. 4.B3.01 Sonation in Club-winged Manakin (*Machaeropterus deliciosus*) mating displays. Males assume this posture while knocking the inner edges of their secondary wing feathers together at about 100 times per second. (Photograph by Tim Laman.)



Fig. 4.B3.02 Club-winged Manakin (*Machaeropterus deliciosus*) wing feather adaptations for sonation. The secondary wing feather rachi of this species are rigid and substantially enlarged, unlike any other bird. During mating displays, male manakins rub and knock their secondary feather vanes to produce a violin-like tone that is unique among birds. (Photograph by Kimberly Bostwick.)

which is also the frequency of the "ting" sound produced during courtship. In other words, the secondary feathers of male Club-winged Manakins are modified to act as a carefully tuned instrument.

Yet the story of the Club-winged Manakin's sonations does not end here. The resonating feathers stimulate the whole wing to vibrate as a unit, like a membrane (Bostwick et al. 2010). Further, this species is unique among birds in having massive, solid wing bones that are adaptations to

this species' unique form of sonation (Bostwick et al. 2012). These birds also have specialized muscles that allow them to vibrate their wings at such extremely fast rates. Although some of these adaptations are unique to the Club-winged Manakin, other closely related manakin species also produce wing sounds in similar but less extreme ways.

Sonations in hummingbirds

Through studies combining high-speed video and feather manipulation experiments, it has become clear that some North American hummingbirds use their wings and tails to produce a diversity of sonations (Clark and Feo 2008). Courting males of these species engage in display flights in which the male dives towards a perched female; depending on the species, this diving flight is accompanied by sonations generated by the male's tail or wing feathers. These sonations occur during flight dives that are as fast as 385 hummingbird body lengths per second—the highest known length-specific velocity attained by any vertebrate—with centripetal accelerations nearly nine times greater than gravitational acceleration (Clark 2009), an aerobatic feat rivaled among vertebrates only by human jet-fighter pilots.



Fig. 4.33 Semiplumes are intermediate feather forms. Semiplumes lack barbule hooks like down but have barbs shorter than the rachis, as in contour feathers. (Photograph by Jennifer Layton.)

over time feathers become brittle, faded, and frayed. To restore their feather coats, birds must replace them regularly, usually annually or semiannually, with new feathers. This regular practice of replacing all or part of the feather coat, usually over a relatively short period of time, is called molt or **molting**.

In a complete molt, all feathers of the body are replaced; in a partial molt, only some subsets of feathers are replaced

Molting: the process of shedding some or all of the feather coat and replacing it with newly grown feathers.

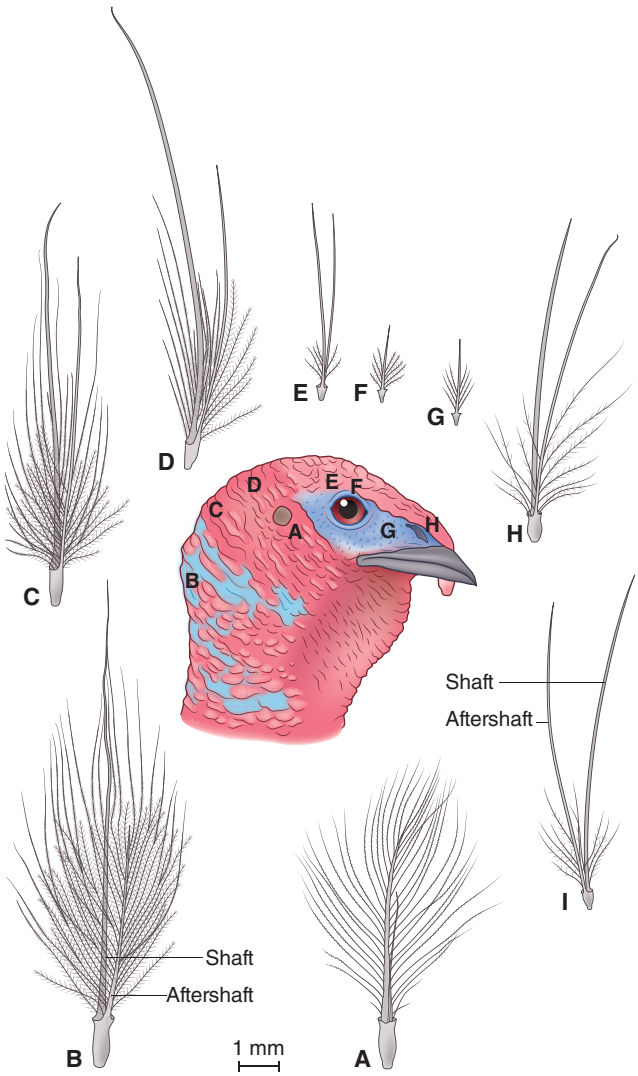


Fig. 4.34 Bristle feather variations. Bristle points of origin are shown here on a Wild Turkey (*Meleagris gallopavo*). Bristles often have a shaft and an aftershaft, both used to collect sensory information. (Adapted from Lucan and Stettenheim 1972.)

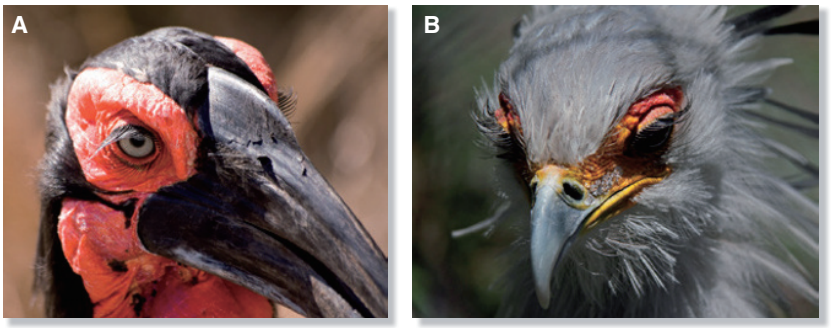


Fig. 4.35 Bristle feathers ("eyelash"). Presumably these bristle feathers provide the eyes with extra protection, which may be particularly important for open country birds such as (A) the Southern Ground-Hornbill (*Bucorvus leadbeateri*) and (B) the Secretary-bird (*Sagittarius serpentarius*). (Photographs by: A, Debbie Aird Photography; B, Cynthia Mammoser.)



Fig. 4.36 Filoplumes: the smallest feather type. Subtle changes in filoplume position—caused by a bird's motions or surroundings rather than muscles near the follicle—may provide important sensory information relevant to processes such as thermoregulation. (Illustration by Charles L. Ripper © Cornell Lab of Ornithology.)

during that particular molt. Not all feather replacement constitutes a molt; for example, if a whole feather is entirely lost between molts, it usually grows back right away. However, partially damaged, broken, or worn feathers do not necessarily stimulate the feather follicle, and therefore these feathers are replaced only during the regular molt cycle.

An individual bird generally experiences two series of molts: those that occur as the bird matures from chick to adulthood, and those that occur in annual cycles throughout the bird's adult life. The molts that accompany the maturing of an individual from a hatchling to an adult are fairly variable across species, but because the appearances of the resulting plumages vary predictably within a species, they can often be used by researchers to determine an individual bird's age. The molts that occur once an individual achieves adulthood are annual changeovers of major parts of the plumage, and in some bird species they provide a semiannual opportunity to change appearance. Accordingly, some birds' plumages appear the same molt after molt, whereas others alternate between different plumage patterns in different seasons.

4.5.1 Subadult versus definitive plumages

During all molts, growth of the new feathers pushes the old feathers from their follicles. As mentioned above, in juvenile birds, each natal down feather may be physically attached to the tip of its successor, the juvenal feather, which is the first true contour feather grown by a young bird (Fig. 4.11). Note that the term "juvenal" is applied to feathers and plumages, whereas "juvenile" designates a young bird itself; these two similar words often are confused.

For a variety of reasons, young birds usually pass through one or more subadult (immature) plumages, eventually reaching the definitive plumages of a mature bird. Subadult plumages are defined as those plumages that come before the definitive plumage, and usually only differ from definitive plumages in the coloration or patterning of the feathers. The age at which birds reach definitive plumage varies greatly among bird species. Many songbirds take less than a year, although in many species there may be subtle differences in the definitive plumages of younger and older birds. In general, long-lived species such as large raptors, gulls, and ocean-going seabirds retain their subadult plumages for a longer period of time. For example, the Bald Eagle (*Haliaeetus leucocephalus*) of North America does not attain its definitive plumage until its fourth or fifth year. Before acquiring a clean white head and tail, young birds go through several subadult plumages that are much less tidy, with a blotchy or mottled brown-and-white appearance. Many gulls also take several years to reach definitive plumage. In so-called "three-year gulls" such as the Ring-billed Gull (*Larus delawarensis*) and Mew Gull (*Larus canus*), birders can distinguish first-winter, second-winter, and adult birds. Four-year gulls, such as the Herring Gull (*Larus argentatus*), Great Black-backed Gull (*Larus marinus*), and Lesser Black-backed Gull (*Larus fuscus*), sport at least four different plumages on their way to maturity (Fig. 4.37). Male Steller's Eiders (*Polysticta stelleri*) acquire definitive plumage in their third fall; the males of the larger Common (*Somateria mollissima*) and King (*Somateria spectabilis*) Eiders do so in their fourth fall. Slowly maturing birds such as albatrosses may take as long as 7 or 8 years to reach their definitive plumage.

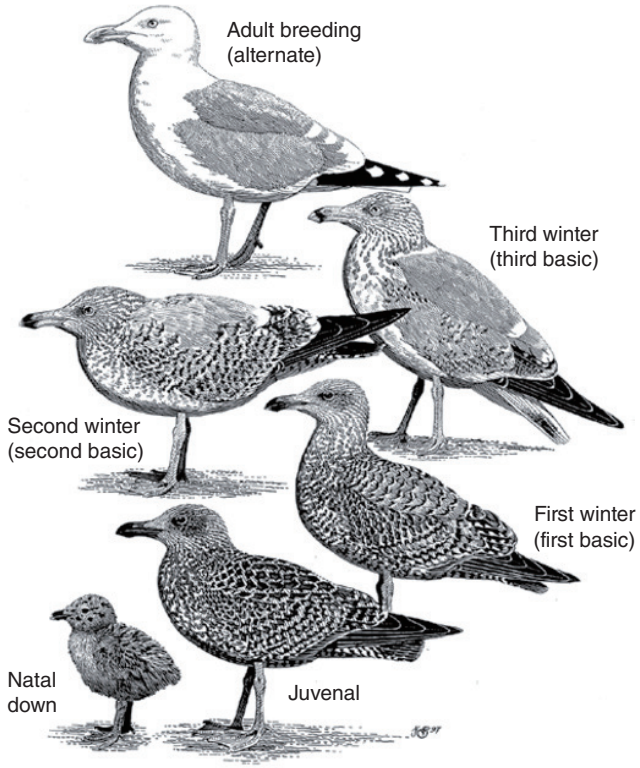


Fig. 4.37 Complete plumage cycle of the Herring Gull (*Larus argentatus*). Many gull species follow a similar plumage trajectory, involving 3 years of subadult plumage—each year slightly different from the last—before reaching a definitive (adult) plumage. Plumages here are labeled using the Humphrey–Parkes system. (Illustration by N. John Schmitt.)

In some species, one sex remains in subadult plumage longer than the other, a situation termed delayed plumage maturation. The male American Redstart (*Setophaga ruticilla*) of North America, for instance, does not wear his orange-and-black definitive breeding plumage until his second breeding season. His first breeding plumage is nearly identical to that of the adult female, who has yellowish patches and who acquires her definitive plumage by her first breeding season.

4.5.2 Annual cycles: molt and wear

Once birds obtain their definitive plumages as adults, they continue molting in annually driven cycles, which vary in frequency, type, and timing across species. Some birds undergo only one complete molt each year. Many songbirds that breed in temperate regions undergo a complete molt after the breeding season and then a partial molt in winter or spring. This partial molt may include all of the contour feathers, but not the wings and tail, and provides brighter colors for the breeding season. Only a few species are known to have two complete molts per year; most of these live in harsh habitats in which feathers wear out quickly. Examples include Marsh Wrens (*Cistothorus palustris*) and Bobolinks (*Dolichonyx oryzivorus*) of North America, which move within abrasive vegetation, and several species of African larks that dwell in windy, sandy deserts.

Some songbird species that have only one complete molt per year may nevertheless be able change their appearance seasonally by taking advantage of the natural process of feather wear. For example, European Starlings (*Sturnus vulgaris*) have prominent buff-colored tips on their belly and breast feathers after they molt in mid- to late summer. By the time they are ready to breed in the following spring, these buff-colored tips have worn off, and the birds' underparts are dark and glossy. Similarly, adult male Purple Finches (*Haemorhous purpureus*) in North America have dull red heads after their annual molt in late summer (Fig. 4.38A), but feather wear slowly removes the outer barbules, revealing the bright, cherry-red color below (Fig. 4.38B). The plumages of male Northern Cardinals (*Cardinalis cardinalis*) in North America and Common Chaffinches (*Fringilla coelebs*) in Eurasia have a grayish or buffy cast in fresh fall plumage, but these drab-toned feather edges wear away; by late spring both species sport their brightest colors, although neither has undergone an intervening molt.

4.5.3 Plumage naming systems

In the most general sense, **plumage** is a bird's entire feather coat at a given point in time. A molt produces new plumage, and molts are named for the type of plumage they

Plumage: refers either to a bird's entire feather coat, or to the set of feathers produced by a particular partial or complete molt.

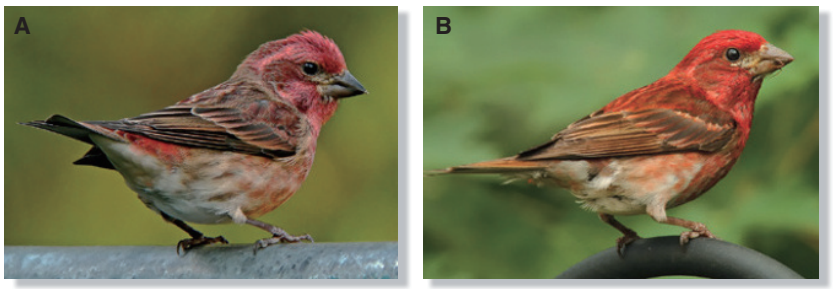


Fig. 4.38 Feather wear affects seasonal plumage. Male Purple Finches (*Haemorhous purpureus*) have (A) a dull plumage in the fall, but as the gray barbules wear away over winter they reveal (B) the bright cherry-red breeding plumage of the underlying barbs. (Photographs by: A, Kevin Bolton; B, Christian Dionne.)

Table 4.01 The Humphrey–Parkes nomenclature for plumages and molts. Note that molts are named for the feathers they produce, not for the feathers they shed. Subadult plumages are numbered as first, second, third, and so forth. After a bird molts into its definitive plumage, this numbering is no longer used.

Traditional system	Humphrey–Parkes system
Natal down (if any)	**Natal down (if any)**
Postnatal molt	Prejuvenal molt
Juvenal plumage	**Juvenal plumage**
Postjuvenal molt	1st prebasic molt
1st winter plumage	**1st basic plumage**
1st prenuptial molt	1st prealternate molt
1st nuptial plumage	**1st alternate plumage**
1st postnuptial molt	2nd prebasic molt
2nd winter plumage	**2nd basic plumage**
2nd prenuptial molt	2nd prealternate molt
2nd nuptial molt	**2nd alternate plumage**
2nd postnuptial molt	3rd prebasic molt
3rd winter plumage	**3rd basic plumage**
When a bird reaches its definitive plumage, the numerical designations are dropped. For this example, we assume definitive plumage is reached after the 3rd winter or 3rd basic plumage:	
Prenuptial molt	Prealternate molt
Nuptial plumage	**Alternate plumage**
Postnuptial molt	Prebasic molt
Winter plumage	**Basic plumage**
etc.	**etc.**

produce (rather than for the plumage they are changing from). To study how and why molts and plumages evolved, ornithologists require a system for naming and comparing them among species.

Historically, one common practice was to name plumages for the presumed presence or absence of breeding activity at the time the bird wore that particular plumage. Thus, birds were said to be in nuptial (breeding) plumage in the spring and summer, and in postnuptial or winter plumage in the fall and winter. This system is inherently problematic, however, because many birds do not fit into this simple breeding/non-breeding plumage dichotomy. First, many birds never change into anything that could be called a distinct breeding plumage; they appear the same year-round. Second, different plumages are not necessarily linked with reproductive activities or seasons of the year. In many tropical regions, for instance, there often is no annual season analogous to winter.

As part of a larger effort to identify similarities among the plumages of different bird species, Phil Humphrey and Kenneth Parkes (1959) developed a system for classifying plumages that still bears their names: the Humphrey–Parkes or H-P plumage nomenclature (Table 4.01). Under this system, an adult bird's main plumage each year—the one it wears the longest and the one usually produced by a complete molt—is termed the **basic plumage**. This term can be confusing for bird enthusiasts in the temperate zone, who generally think of a bird's nuptial or breeding plumage as the "main" plumage because it usually is the most noticeable and colorful. However, the breeding plumage is rarely worn for as long as the non-breeding plumage, and it often follows only a partial molt. Instead, the basic plumage of many long-distance migrant birds is a duller non-breeding or winter plumage, and the molt producing it occurs in the late summer or fall.



Fig. 4.39 Breeding plumage in a seasonal temperate migrant. The alternate plumage of a male Scarlet Tanager (*Piranga olivacea*) is a combination of its basic molt and a partial molt before breeding. (Photograph by Larry Gridley.)

How might we explain the beautiful breeding plumages of many birds? Humphrey and Parkes reasoned that other plumages are likely inserted as needed between basic plumages depending on a species' social system and ecology. Thus, when a partial molt occurs before breeding, it produces an additional plumage, the **alternate plumage**. This is the plumage that temperate zone bird enthusiasts usually think of as the breeding plumage. It is this molt, for example, that produces the brilliant red of the male Scarlet Tanager (*Piranga olivacea*) of North America (Fig. 4.39), the rosy breast and crown of the Eurasian Linnet (*Carduelis cannabina*) of Eurasia, and the contrasting rust, black, and white patches on dozens of species of migrating shorebirds worldwide. If, in addition to the basic and alternate plumages, the bird produces another plumage within an annual cycle, as do ptarmigans and certain New World buntings, that plumage is termed supplemental. Supplemental plumages are relatively uncommon.

Basic plumage: the plumage that a bird wears for the longest period within the year, between molts to another plumage.

Alternate plumage: the plumage that results from a partial molt of the basic plumage before breeding.

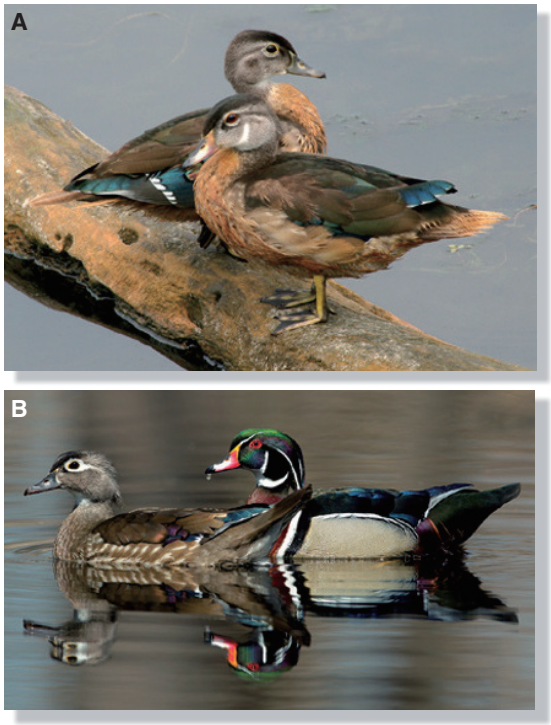


Fig. 4.40 Eclipse versus alternate molts in adult waterfowl. (A) Shortly after breeding, both male and female Wood Ducks (*Aix sponsa*) complete their similarly drab prebasic eclipse molt. (B) As courtship begins weeks later, the male completes a partial prealternate molt into flashy mate-attracting plumage. In both photos, the male can be distinguished by his bright red iris. (Photographs by: A, Walter P. Szymanski; B, Steve Patterson.)

The H-P system is simple but flexible, and it works well even for molt and plumage sequences that are highly specialized, such as those of ducks. In early summer after mating, many ducks, such as the Wood Duck (*Aix sponsa*) of North America, have a complete prebasic molt, producing a dull-colored basic plumage termed **eclipse plumage**. Most male ducks in eclipse plumage resemble females (Fig. 4.40A). Female Wood Ducks also undergo a prebasic molt a bit later in summer, after their young are independent—although their appearance does not change much. The basic plumage of both sexes is soon lost in a molt of the body feathers—a partial prealternate molt—which produces the brightly colored head and other distinctive features of the male (Fig. 4.40B). The occurrence of the prealternate molt immediately after the prebasic molt (much sooner than in most species) is related to the timing of courtship in these ducks, which begins in the fall. Thus, like the colorful Wood Duck, many male ducks are in basic plumage for only a few weeks of the year.

Eclipse plumage: the set of dull-colored feathers worn briefly after the breeding season in adult birds such as ducks.

4.5.4 The four molting strategies

The H-P system has long provided the standard ornithological terminology for describing avian plumages, with some useful later variants that incorporate new findings. For example, the original H-P nomenclature defined the first molt after the juvenal plumage (which follows the natal down) as the first prebasic molt that generated the first basic plumage. However, this first post-juvenal molt occurs at different times in various species and results in plumages with different functions, so this assignment effectively threw off the alignment of the subsequent definitive basic molts. More recently, some researchers (Howell and Corben 2000; Howell et al. 2003) have suggested that the juvenal plumage itself be considered the first basic plumage, as it is a complete molt that tends to be timed in a way that establishes the annual basic molt cycle most accurately. Under this modification to the terminology, any plumages intervening between this initial juvenal/first basic plumage and the second basic plumage are recognized as alternate, supplemental, or formative plumages.

With this modification in place, four basic strategies of plumage development become evident. These four strategies result from different combinations of two patterns. The first dichotomy is whether the species has only one molt each year, and thus employs a "basic" molt strategy, or has two molts each year, and thus uses an "alternate" molt strategy. The second dichotomy is whether any plumages (such as alternate, supplemental, or formative plumages) are inserted between the juvenal plumage and the next, or second, basic molt. If so, the species has a "complex" molt strategy; if not, it has a "simple" one. Thus, the four molt strategies are simple basic, complex basic, simple alternate, and complex alternate.

4.5.5 Progression and timing of molt

In most birds, especially landbirds, a molt occurs through an orderly, sequential replacement of feathers along a feather tract, so that in any particular tract only a subset of the feathers are being replaced at any one time (Fig. 4.41). This strategy is particularly important for the flight feathers; rarely does a landbird molt more than a few wing or tail feathers at a time. In many woodpeckers, for example, the stiffened rectrices act as a prop to support the bird while it searches up and down tree trunks. Molting of these feathers starts with the second innermost rectrices and progresses to the outside. The long central pair of rectrices is replaced only after the other tail feathers have grown in, so the tail can continue to serve as a sturdy brace throughout the molt cycle.

On the other hand, many waterbirds—including loons, grebes, anhingas, swans, geese, and ducks—drop all their

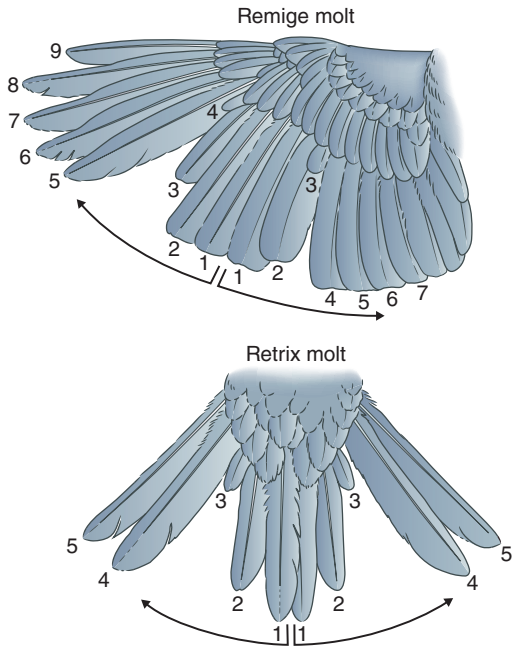


Fig. 4.41 Molt progression in flight feathers. Most birds molt a few feathers at a time over several weeks. Each feather is lost and subsequently regrown in the order of the arrows. Wing molt often starts at the boundary between the primaries and secondaries, while tail molt proceeds outward from the center. In the illustration above, the first retrix pair has regrown to its fullest extent; pair number three has re-emerged most recently and must develop almost completely (like the second pair) before the fourth pair drops. (Adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology.)

remiges simultaneously, leaving the birds unable to fly for as long as a month during their prebasic molt. Similarly, some of the smaller owls, such as the Northern Pygmy-Owl (*Glaucidium gnoma*), the Little Owl (*Athene noctua*), and the Burrowing Owl (*Athene cunicularia*), molt all their rectrices at once, as do some other short-tailed birds that use their tails very little in flying, such as alcids and rails.

Females of a number of hornbill species also molt abruptly. In these Old World cavity nesters, females are sealed inside the nest cavity by a mixture of mud and saliva that nearly closes the cavity entrance, likely an adaptation to exclude predators such as climbing snakes and monkeys from the nest (Chapter 11). Females remain cavity-bound throughout incubation and the early part of their nestlings' life; during this time, female hornbills undergo a full molt, which creates an extended flightless period.

Occasionally, a bird will shed many feathers all at once in response to some external stress. This shock molt or fright molt has been reported for dozens of species in numerous avian families but occurs only in unusual circumstances. For instance, in a clearly adaptive strategy, a bird may shed its tail feathers when its tail is grabbed by a predator. Fright molt occasionally occurs when a bird is handled by people. The mechanism of shock molt has not been determined, but clearly some relaxation of the muscles holding each feather shaft must be involved, because under normal circumstances substantial force is required to pull out even a single feather.

The rate of a molt varies with latitude and the extent of seasonal change in the climate. Molt often is more rapid, for example, in arctic-nesting gulls than in closely related gulls of the temperate zone. Birds breeding at polar latitudes in the arctic simply do not have time for a multi-week molt after breeding, because soon they must head south for the winter. The abundance of food and continual daylight for foraging in the arctic undoubtedly help these birds in gathering the resources they need to molt rapidly. In some tropical species, on the other hand, molts may be prolonged. For example, Rufous-collared Sparrows (*Zonotrichia capensis*) in northern South America take 2 months to molt. Breeding seasons in the tropics also may last a long time, and the energy demands of some species are low enough that they are able to overlap molt and breeding activity.

Birds generally molt when they are not engaged in other energetically demanding activities, such as feeding young or migrating. Long-distance migrants may molt before they migrate, after they migrate, or partly before and partly after—but rarely, if ever, during migration. In the north temperate zone, adults of many species of songbird molt during late summer, when they no longer are caring for young and before the rigors of fall migration.

4.6 Feather care

Feathers are essential but delicate structures, so birds spend a good deal of time caring for them. Because the mature feather is a dead structure, it has no circulatory system for internal maintenance. Therefore, a bird provides all feather care from the outside.

In **preening**, a bird grasps a feather near its base and then slides its bill along the shaft toward the tip of each feather (Fig. 4.42), smoothing the barbs to re-establish any broken connections and remove stale oil and dirt. The bird fluffs the feathers in the section of the body it is preening and turns and twists its head and body as needed to reach the desired area. Preening keeps the feathers neat and clean, preserving their streamlining and insulating effects. Preening also helps remove external parasites, or **ectoparasites**, such as flies, ticks, and lice.

Preening: feather maintenance behavior in which a bird tends to its feathers with its bill.

Ectoparasites: parasites such as flies, ticks, lice, and mites that inhabit the exterior of a host's body.



Fig. 4.42 Feather preening. A Swallow-tailed Kite (*Elanoides forficatus*) preens its rectrices. Birds spend a great deal of time maintaining their feathers to remove dirt and ecotoparasites, spread protective oils, and re-zip barbs and barbules. (Photograph by JimGrayImages.com.)

When preening, many species use the beak to spread oily secretions from their **uropygial gland** (also called the oil gland or preen gland) over their feathers. The uropygial gland, one of the few glands in a bird's skin, is located on the rump at the base of the rectrices. A preening bird frequently nibbles on a specialized tuft of feathers on the uropygial gland, which transfers the gland's oils onto the bill. The oil becomes distributed throughout the plumage as the bird preens its feathers. Oil gland secretions help keep feathers water repellent but are not essential; when the oil glands of ducks were removed, their feathers did not lose their waterproofing ability immediately. Instead, the secretion acts like a conditioner that prevents feather barbs and barbules from becoming brittle and breaking prematurely (such breakage changes the surface characteristics of the feather vane, and thus wetability of the feather) (Jacob and Ziswiler 1982). As described earlier, the actual waterproofing of feathers seems to result primarily from the microstructural arrangement of the barbs and barbules, which provide an evenly spaced surface of ridges with narrow gaps between them that sheds water very effectively. Thus, spreading oil gland secretions seems to facilitate waterproofing only indirectly; feathers provide the waterproofing, but oil gland secretions make feathers last longer.

To condition the feathers on the head (which cannot be preened with the beak), a bird can rub its head directly on the gland, or wipe oil on its feet with its beak and then scratch its head. Birds use one of two scratching techniques, either a direct method where they bring their foot forward under the wing (Fig. 4.43A), or through an indirect method by stretching their leg and foot over the wing (Fig. 4.43B). Virtually all species use only one of these two techniques. Of course, birds can also scratch their heads when not applying secretions, and do so as a general means of preening feathers they cannot reach. Birds that cannot scratch their heads with their feet, either because of accidental injuries or the experimental use of neck collars, tend to have more ectoparasites living on their heads (Clayton 1991).

Bathing is another feather-maintaining behavior that complements preening. Birds may bathe in water, snow, or even dust. The manner of bathing tends to be quite consistent within various avian families, with most species

Uropygial gland: a gland near the upper base of the tail that secretes oils that a bird distributes across its feathers via preening.



Fig. 4.43 Scratching techniques. To maintain out-of-reach feathers (such as those at the top of the head), many birds apply preening oils with their feet, either by (A) raising the leg and foot under the wing while bending down, as demonstrated by this Yellow-crowned Night-Heron (*Nyctanassa violacea*), or (B) bringing the leg and foot over and above the wing, as demonstrated by this Rufous Hummingbird (*Selasphorus rufus*). (Photographs by: A, Andrew McCullough; B, Robert T. Moore.)



Fig. 4.44 Dust bathing. A male Gambel's Quail (*Callipepla gambelii*) fluffs its feathers in powdery desert soil, a practice that may remove excess oils that attract ectoparasites. Alternatively, dust bathing may desiccate or clump ectoparasites already in the oils, making it easier to preen them off. (Photograph by Eric Gofreed.)

prefering water baths. Swallows and swifts drop down repeatedly and skim the surface of a lake, pond, or stream to wet their feathers. Terns plunge into the water from the air, and kingfishers do so from an overhanging branch. Many forest birds bathe in rainwater or dew that has collected on leaves. Most songbirds stand or squat in shallow puddles, vigorously ruffling their feathers and shaking both wings, creating a veritable shower. Hummingbirds may dart in and out of the spray from a garden hose on a hot day. Common Nighthawks (*Chordeiles minor*) may bathe on the wing during intense downpours, alternately flapping rapidly and ruffling the body feathers amid the deluge. However, wetting the body, even for bathing, must occur within limits; a thoroughly wet bird can be quite helpless, and many are unable to fly efficiently when soaked, making them particularly vulnerable to predators. Because birds must dry as soon as possible, certain drying behaviors are commonplace: after bathing, a bird typically shakes its body to throw off extra water, whirs its wings, fluffs its feathers to promote evaporation, and preens vigorously. In favorable circumstances, a soaked bird can dry itself in a matter of minutes.

Dust bathing is reported most often for species that spend a lot of time on the ground, such as House Sparrows (*Passer domesticus*) and Wild Turkeys (*Meleagris gallopavo*). This behavior is not a substitute for water bathing, and many species of birds do both. In dust bathing, a bird usually squats or lies down in a dusty area, often a dirt road, and drives fine particles through its plumage by beating its wings in the dust, rolling its body, fluffing its feathers, and wiping with its head and beak (Fig. 4.44). The Greater Rhea (*Rhea americana*) of South America goes as far as picking up dust and throwing it over its body. The bird removes some of the dust by violent shaking, but often much dust remains, staining the bird's plumage the color of the soil. Presumably dust bathing can help reduce ectoparasites, but this possibility has not been studied experimentally. Many ectoparasites are arthropods, which breathe through small holes in their outer skeletons that are vulnerable to clogging and/or desiccating from dust exposure. Comparisons of birds with and without opportunities for dust bathing have shown that dust bathing also helps to remove substances coating the feathers, such as old oil gland secretions.

Sunning also is thought to maintain feathers (Simmons 1986), but exactly how it does so is not well understood. Sunning birds adopt varied and sometimes comical postures: commonly the bird's feathers are fluffed, the tail is spread against the ground, and a wing is extended on at least one side, sometimes on both. Sunning birds frequently lie on the ground in a warm place, with the head lowered and tipped to the side, remaining nearly motionless for many seconds or minutes. Although sunning has been described for numerous species of birds, few experimental studies have tested its functions. Suggested purposes include conditioning the feathers by keeping them supple through limited heating, harming or repositioning ectoparasites, and saving energy by taking up solar heat through the feather coat.

Many large birds, including cormorants, anhingas, herons, pelicans, storks, and New World vultures, stand for extended periods with their wings extended to the side in a pose known as the spread-wing posture (Fig. 4.26). Cormorants (also known as shags) and anhingas (also known as snakebirds) are closely related. Both types of bird prey on fish and use the spread-wing posture to dry their feathers after swimming. However, the feathers of anhingas are more permeable to water. This permeability reduces buoyancy and allows them to swim for long periods with only their necks and heads above the surface. Because their permeable feathers take up extra water, anhingas take longer to dry. Furthermore, anhingas generate less heat internally than do cormorants, and in cooler areas anhingas may use the spread-wing posture to absorb sunlight. The difference in anhinga and cormorant energy production is reflected in their geographic distributions: cormorants can live in much cooler regions than can anhingas.

Like bathing and sunning, anting is believed to help control ectoparasites. In passive anting, a bird simply stations itself among a swarm of ants, permitting them to run all over its body and move in and out among the feathers (Fig. 4.45). In active anting, a bird picks up an ant or other chemically potent object, such as a millipede, and deliberately rubs it on its feathers. Objects rubbed in the feathers during anting (in its broad sense) include insects, plant material, and even cigarette butts. Ornithologists assume that the rubbed materials contain chemicals that are noxious to ectoparasites. Because birds sometimes eat the arthropods used in anting, it is possible that the process also helps rid a potential food item of its most noxious chemical protection.



Fig. 4.45 Passive anting. Similar to sunning and dusting, some birds remove ectoparasites by allowing ants to crawl through their feathers. This American Crow (*Corvus brachyrhynchos*) sits among a group of ants (look closely on the back and neck), wings slightly outstretched to enable access. (Photograph by Sean McCann.)

4.7 Coloration: form and function at the scale of light

Birds exhibit a spectacular range of colors and patterns with their feathers—consider the sparkling, metallic iridescence of a hummingbird's throat, or the earthy brown, leaf-like patterning that renders a frogmouth virtually indistinguishable from its surroundings. More than just decoration, coloration is another level of feather form and function. That is, just as feathers are able to use basic properties of air and water to generate lift, trap air or shed water, they can also—at an even finer scale—manipulate light to produce a magnificent array of colors and patterns. These colors and patterns in turn play important roles in the ecology and behavior of birds, through things like predator avoidance and social signaling. However, no matter what level of biological function you are interested in, the key to unlocking the many fascinating secrets of color in feathers is to have a basic understanding of light.

4.7.1 Light, perception, and color

Light is one form of electromagnetic radiation: a complex but basic physical force that can be thought of as an energy-carrying wave. One general property of waves is that they maintain a specific measurable distance between successive peaks of the wave—the wavelength. Electromagnetic radiation can manifest itself in a broad continuum of wavelengths in what is called the electromagnetic spectrum (Fig. 4.46). The wavelengths of the electromagnetic radiation in the electromagnetic spectrum range from very long radio waves (many kilometers in length) to very short gamma rays (with wavelengths on the scale of atomic nuclei).

Our sun emits electromagnetic radiation across a wide range of wavelengths from all over the electromagnetic

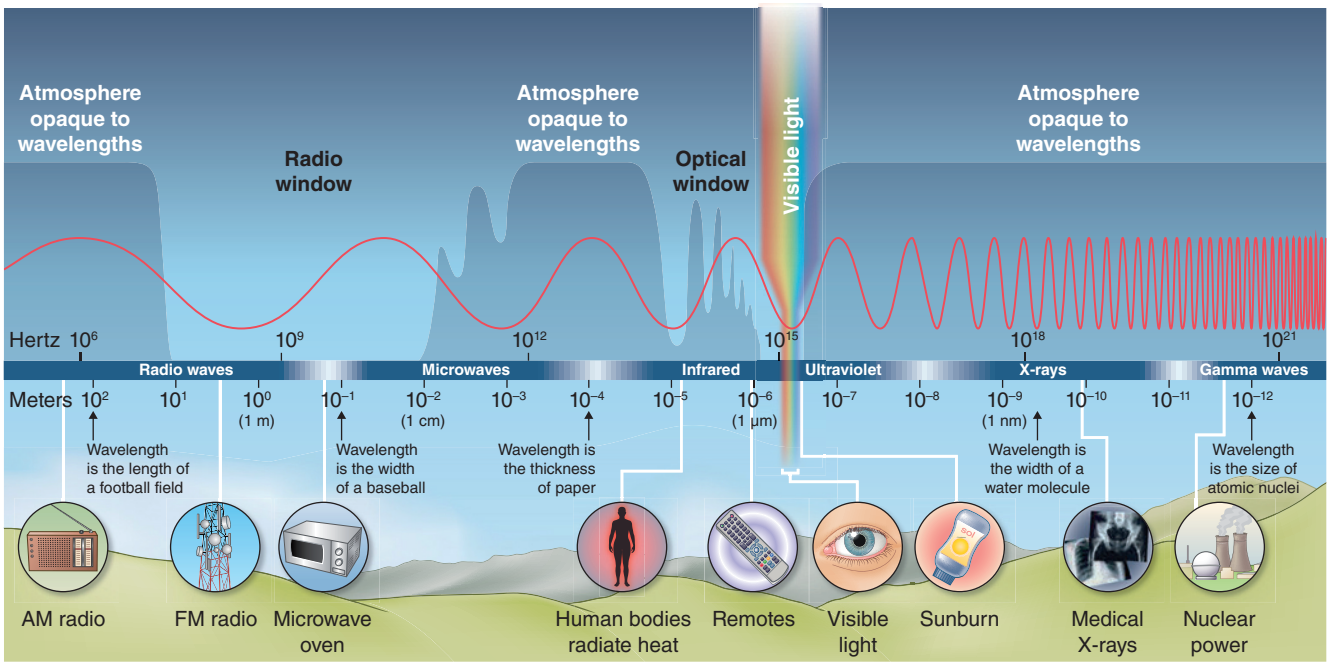


Fig. 4.46 The electromagnetic spectrum. Visible light is one of the many types of electromagnetic energy we use, and is only a small portion of the full spectrum. The full spectra of other energy forms and their relative wavelengths are shown in Hertz (Hz). (Courtesy of NASA.)

spectrum. Some of this radiation we feel (heat), some of it we see (light), some of it we are affected by but do not directly perceive with our senses (ultraviolet or UV), and some of it we are mostly oblivious to (X-rays and gamma rays, which are powerful and destructive but which we are largely protected from by our atmosphere). Most of the energy from the sun is emitted in the portion of the electromagnetic spectrum that our eyes sense directly; this portion of the electromagnetic spectrum is called the visible spectrum.

While visible light is defined as the portion of the electromagnetic spectrum that human eyes are sensitive to, other animals can perceive a lesser or greater portion of the overall electromagnetic spectrum. Birds' eyes are sensitive to a greater portion of the spectrum than humans—birds can see both slightly longer and shorter wavelengths. In other words, birds literally see some of the energy that we can only feel as heat, and they can also see color that is invisible to us in the UV portion of the spectrum.

The property that we recognize as "color" represents the ability of our human eyes to distinguish among the different wavelengths of light across the visible spectrum. Whereas the spectrum is continuous, our eyes have three types of cone cells—color-sensitive receptors—each of which is sensitive to a different part of the visible spectrum, corresponding to what we perceive as red, blue, and green wavelengths. By interpolating between these receptors, we are able to break the continuous spectrum up into about six basic colors (red, orange, yellow, green, blue, and violet) plus their various shades and combinations.

The eyes of birds have more types of color receptors than ours do (Chapter 7), and additionally birds have the anatomical equivalents of color filters that can further fine-tune how light is received by their color receptors. This means that a bird's ability to resolve different parts of the visible spectrum is much better than ours. Thus birds not only see a greater portion of the overall electromagnetic spectrum than we do, but they also see more colors within the spectrum than we can discern (Box 4.04). For this reason, it is important to remember that the color of any object, including a feather, is determined by a combination of two things: (1) what happens to light when it interacts with the object; and (2) how this information is interpreted in the visual system of the observer. For now, we will ignore the differences between bird and human visual systems, and instead focus on how light interacts with objects like feathers.

In order to "see" the independent spectral colors present in sunlight (cumulatively defined as white light) we can use a prism to spread the individual wavelengths out to form the discreet bands of color as seen in any rainbow. In a rainbow, you are witnessing a sequence of light wavelengths from long (red) to short (indigo). Feathers, skin, and other objects appear the color that they do according to the subset of wavelengths that emerge from their surfaces after interacting with light. For example, white feathers reflect the full spectrum of long to short wavelengths visible in sunlight, and therefore appear to be white in color. Alternatively, when only a subset of wavelengths (e.g. red) return to the viewer after hitting a bird's feathers, those wavelengths stimulate specific receptors that correspond to our recognition of red. Feathers will appear black when little or no light escapes from them, and thus few visual receptors are triggered in our eyes. In addition to the colors we perceive, birds see a wider rainbow, with more colors in between; what we see as the "blue" part of the rainbow would be several distinct colors to a bird.

Light is often affected by the specific properties of the object with which it interacts, being reflected, transmitted, absorbed, and/or emitted (Box 4.05). Ornithologists have categorized two basic mechanisms by which light produces colors in skin and feathers. The first mechanism is influenced by pigments (molecules, or assemblages of atoms) that absorb and interact with light at the atomic level, and result in subtractive coloration. Subtractive coloration occurs when pigments change or remove light. In contrast, additive coloration involves mechanisms that are influenced by structural arrangements of materials (e.g. keratin) that can reflect and transmit light in specific ways. Birds may use both of these mechanisms separately or in concert to produce the various colors that humans see on them, and to produce the additional colors that birds can perceive but humans cannot.

4.7.2 Producing color in feathers

At first the distinction between pigment colors and structural colors may seem too subtle to matter for an ornithologist, but actually this dichotomy is fundamental to understanding avian coloration. Certain categories of avian colors tend to be produced entirely by pigments, others by structures, and many shades of colors can be produced only by combining the two methods. Further, how and where different colors are deposited within a growing feather can be limited depending on how the colors are generated. These differences add up to broad evolutionary and ecological patterns of where, how, and why birds create color in their feathers. (The same is true for other areas of their bodies; note that although this chapter is focused on feathers, similar coloration mechanisms apply to avian skin and irises.)

For example, the lovely plumages of New World orioles are heavily pigmented (Fig. 4.47A). Most generally, pigments can be thought of as colored substances—often large and complex molecules—that can absorb white light, interact with its energy at an atomic level, and then emit only certain wavelengths, or colors. The specific wavelengths emitted depend on the light's effect on the pigment molecule's molecular bonds. Roughly speaking, light can shake

Box 4.04 Color and perception

As the saying goes, "beauty is in the eye of the beholder." With human vision we cannot fully appreciate the beauty of the Budgerigar (*Melopsittacus undulatus*), one of the many birds with UV markings that we do not perceive. But how well do we really understand why we see what we see? Here we briefly explore color-related terminology by considering the relationship between the physical characteristics of light, how we perceive it, and how we characterize it.

Color in terms of hue, saturation, and intensity

What do you mean by a "dull mustardy yellow"? When you look at an object you might describe its "color," but in fact, hue, saturation, and intensity are the three basic axes of variation that influence our perception of an object's color (Fig. 4.B4.01). Hue, also called chroma, is the most intuitive aspect of coloration. When we ask ourselves what color something is, we are usually thinking about its hue. What we are identifying is the wavelength of light at which an object's reflection is most intense. Although the distribution of wavelengths from most objects is usually a very complex mix of many wavelengths, often one is a bit more intense than the others, and that is what we perceive as the object's color. Saturation is the complementary term to hue. Given that hue only indicates the peak wavelength of light, saturation indicates how many other wavelengths are mixed in with the peak color. Another way of putting it would be that saturation is a measure of the purity of the hue. As one might guess, intensity is essentially the brightness of a light or color—how much light there is. Together hue, saturation, and intensity combine to give us a sense of an object's color. A dull mustardy yellow would be a color with peak reflectance in the yellow wavelengths, but with a specific mix of other wavelengths (the mustardy part), and also the peak frequency would not be very intense (and hence our adjective "dull"). In contrast, a bright lemon-yellow could have its peak reflectance at the same wavelength as the mustardy yellow, but without the mix of other wavelengths, and probably more intense overall.

Color perception and color spaces

It is impossible to separate the visual effect of the optical properties of an object from those of the receiver of the reflected images: if you wear rose-colored glasses you will see a rose-colored world. At the same time, it is very difficult to imagine color in any other way than we perceive it. This creates a bit of a conundrum for the ornithologist who wants to understand the significance of bird coloration to birds.

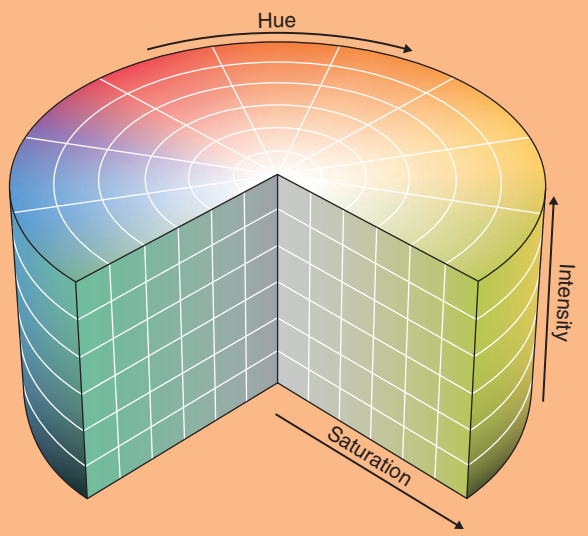


Fig. 4.B4.01 Perception of color. This schematic shows the relationship between hue, saturation, and intensity. (Illustration by SharkD, https://commons.wikimedia.org/wiki/File:HSV_color_solid_cylinder.png. CC-BY-SA 3.0.)

Colorblind people and people with normal vision can not imagine what each other sees. It turns out that human beings in general could equally be considered "colorblind" relative to birds. Most colorblind people do not simply lack the ability to perceive different wavelengths of light, or colors. Instead, they have only two of the three normal visual pigments functioning compared to people with normal human vision. The effect is that many colorblind people have difficulty distinguishing between what most of us see as the distinct colors green and red. Birds on the other hand, have four color cones: three similar to ours, and one that is sensitive in the shorter UV wavelengths. Therefore, birds join many other animals in a whole additional dimension of color definition than we enjoy. For instance, there are feather patches on some birds that appear evenly yellow to us, but whose color spectrum indicates that part of the patch reflects only yellow wavelengths, while another area reflects both yellow wavelengths (which we see) and UV wavelengths (which we do not). This patch would therefore appear as two totally distinct colors to a bird, much as red mixed with blue wavelengths appears as a third color, purple, to us.

Box 4.05 Encountering an object? Light has four options …

Four things can happen to light when it encounters the feathers or skin of a bird. First, it can be reflected; we are most familiar with reflection because of our experience with mirrors, which are somewhat perfect reflectors. But beyond an idealized mirror, reflection as a general phenomenon is responsible for so much of what we see. Many objects we look at are passively reflecting light into our eyes, but unlike a perfect reflector like a mirror, (1) they often differentially reflect different wavelengths of light, giving objects their characteristic colors (Fig. 4.B5.01A); and (2) often their surfaces are not glassy smooth, so that they do not appear shiny per se (shininess being our favorite hallmark of reflection). Rough surfaces can reflect also, but just in a less organized way. So light coming off a white wall can be shiny, glossy, or, more formally, specular, indicating a relatively smooth surface. Alternatively, the same white wall can appear matte, or more diffuse, if the surface is rough and the light is reflected with less perfect geometry, introducing more random scatter, and often "blurring" reflected light beyond recognition. Nonetheless, these are all different manifestations of reflection.

Alternatively to reflection, light can be transmitted or go right through an object, as happens with the majority of light hitting clear glass or water. Even with transparent objects we still can often perceive that some of the light is reflected, as when see our own reflections in store windows. In transparent objects or materials, however, the vast majority of light goes right through as if the object did not exist, and reciprocally comes through from the other side so we can see objects on the far side. Transmitted light is often bent, or refracted, as it passes from one material to the other, a property that is important for creating iridescent colors in bird feathers (Fig. 4.B5.01B).

In special cases, such as with some pigment molecules, the light energy can be absorbed by a molecule, converted to specific wavelengths of light, and then emitted (Fig. 4.B5.01C). In these cases the pigment molecule actually converts white light into light of specific wavelengths, usually producing relatively "pure" colors (those of very specific and limited wavelengths of light).

If light does not simply bounce off, or pass through objects, the only other alternative is for it to interact with the substance. If the light becomes trapped so that its energy is lost or dissipated, we say it is simply absorbed. Black objects absorb all wavelengths of light equally and relatively completely, which is why black objects in sun often feel warm. In many cases objects absorb only some subsets of wavelengths and reflect others.

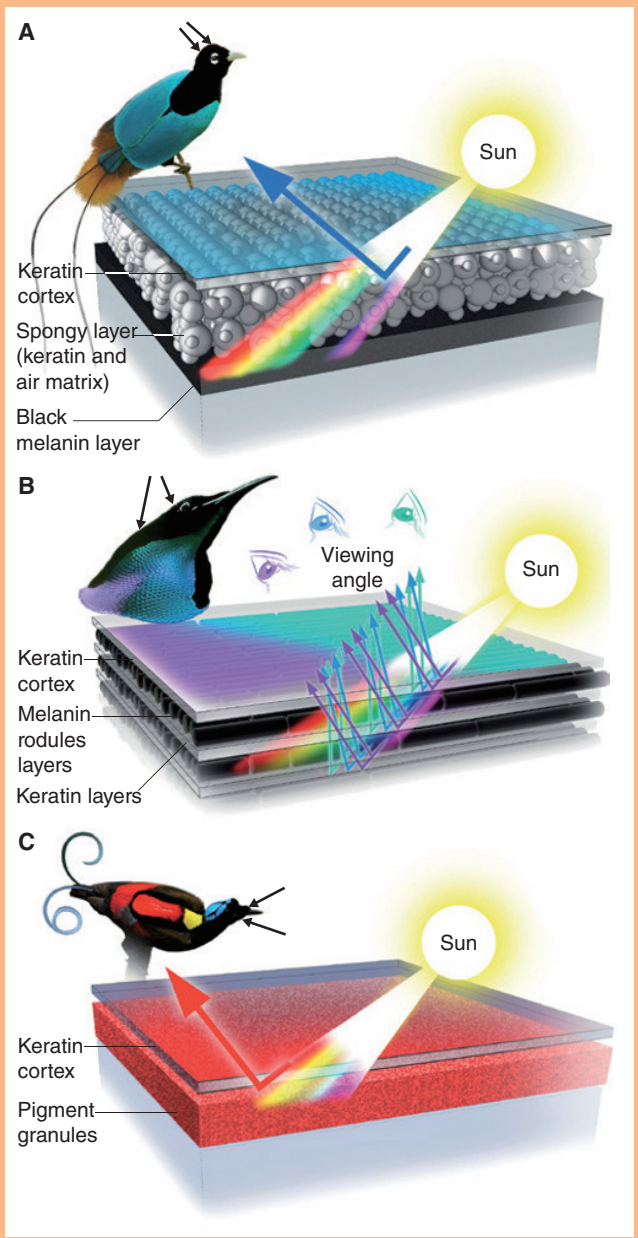


Fig. 4.B5.01 Light interacts with feathers in four ways. (A) *Reflection*. When light hits a feather and bounces off completely, we see pure white. Many feathers, however, differentially reflect light. The blue feathers on this Blue Bird-of-Paradise (*Paradisaea rudolphi*) have structural properties that reflect only the lowest (blue) wavelengths of light. (B) *Transmission*. When light travels through a feather it bends (refracts) as it exits through the other side. Iridescent feathers on the throat of this Magnificent Riflebird (*Ptiloris magnificus*) change hue as the angle of incoming light and/or observation shifts, due to specific layering configurations of melanin and keratin. (C) *Emission*. In rare cases, a pigment molecule absorbs light particles and converts them into a certain wavelength of light. Here, the red pigment in this Wilson's Bird-of-Paradise (*Cicinnurus respublica*) emits pure red light. *Absorption*. When feathers absorb all wavelengths of light, they appear black (arrows on each bird). (Illustrations by Andrew Leach © Cornell Lab of Ornithology.)

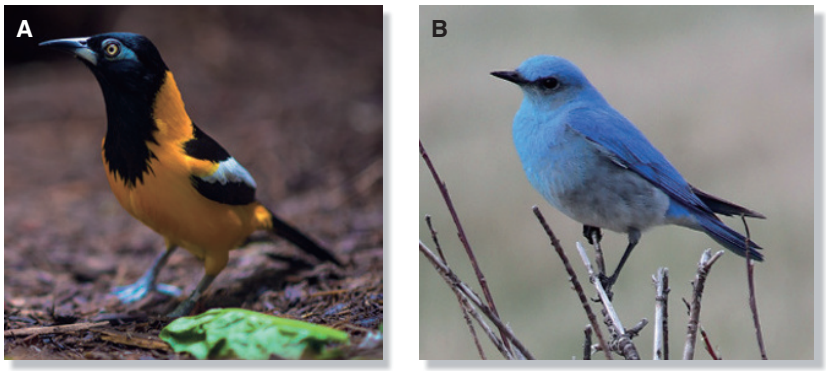


Fig. 4.47 Pigmented versus structural colors. (A) The hues of this Venezuelan Troupial (*Icterus icterus*) are mostly an effect of feather pigments, which absorb certain wavelengths and reflect others. These pigments are independent of feather structure. (B) In contrast, the sky-blue hues of this Mountain Bluebird (*Sialia currucoides*) are almost entirely structural, created by scattering only the blue wavelengths of incoming light with bubbles of keratin and air. (Photographs by: A, Sébastien Clermont-Petit; B, Brenda Sand.)

or twist atoms within a molecule, or promote electrons to higher orbital levels.

In contrast, the Mountain Bluebird (*Sialia currucoides*) has an almost entirely unpigmented plumage (Fig. 4.47B). Its structural colors are created instead by very specific physical arrangements of keratin and air. For structural colors, usually very few (two or three) different substances (such as melanin, keratin, and air) cause light to behave in such a way that only certain wavelengths of light are reflected and reinforced, while others are just transmitted or are lost. Thus, just as the water droplets that create a rainbow are not themselves colored, structural colors in feathers often are produced by the arrangement of uncolored objects (such as keratin and air) that interact with light but have no inherent color themselves.

4.7.3 Pigmentary colors: absorbing and transforming light

Pigments are given their characteristic colors by atomic-level processes that occur when light hits and excites a molecule that has specific light-responsive properties. Without going into the details of the chemistry, energy in the form of white light can be differentially absorbed and/or re-emitted by these specialized pigment molecules in a specific subset of wavelengths. The two main classes of pigments found in birds are melanins and carotenoids.

Melanins are complex molecules found in all vertebrates and give mammals their hair and skin colors. Melanins are the most abundant pigments in birds and primarily occur in melanosomes, melanin-containing bodies embedded within skin cells and feathers (Fig. 4.48). Birds synthesize their own melanins from amino acids, which they obtain from the proteins in their diet. In general, the melanins are excellent light absorbers and are mainly used to produce the earth tones in bird plumages. Depending on the concentration and distribution of specific melanins in skin and feather tissues, their colors can vary from the darkest blacks through subtle grays, and from muddy browns, to red-browns, yellow-browns, and pale yellows. There are two classes of melanins: the eumelanins and the phaeomelanins. Eumelanins tend to be blacks and grays; for example, they color the all-black members of the genus *Corvus* (crows and ravens) found worldwide. Pheaomelanins create browner hues, such as the reddish browns of many owls, shorebirds, and pheasants. The antbirds of the neotropics create beautiful patterns by combining various earth-toned melanin pigments. Because melanins are synthesized within cells, their deposition can be very tightly controlled and used to create extremely intricate patterns (Fig. 4.49).

Carotenoids are the other major class of avian pigments. Generally made of long carbon chains, carotenoids re-emit light from very specific parts of the visible spectrum, often producing bright reds, oranges, and yellows. Unlike melanins, carotenoids are synthesized only by plants, algae, and fungi; therefore birds must acquire them in their diet, either directly by eating plants or indirectly by eating something that has eaten plants. Many bird species consume a diversity of plant-generated carotenoid molecules (or carotenoid precursor molecules that are not fully formed) and change them into a specific form that they then embed in their plumage (Fig. 4.50A). In some species, differences in the specific types of carotenoids in the diets of individuals can cause color variations in their plumage. For example, some Cedar Waxwings (*Bombycilla cedrorum*) in North America have tail-feather tips that are more peachy red than the typical yellow (Fig. 4.50B)—these individuals have eaten berries of the japanese honeysuckle (an invasive plant species) that contain an unusual reddish carotenoid pigment that the waxwings are unable

Melanins: pigments, manufactured within cells, that generally produce a range of earthy colors in various shades of black, brown, gray, reddish brown, and pale yellow.

Carotenoids: pigments obtained by birds through their diet that often produce bright yellow, orange, or red colors.

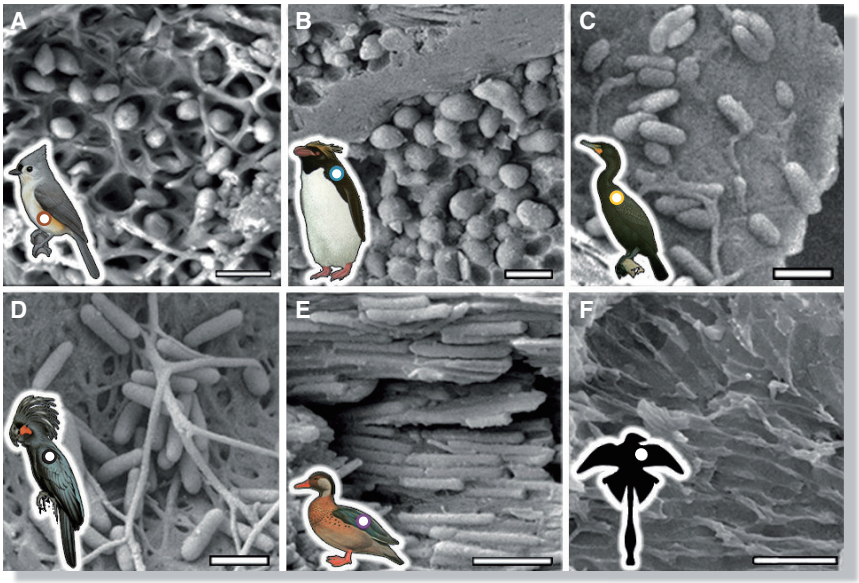


Fig. 4.48 Melanosome variations. Micrographs (photographs taken by a microscope) reveal a diversity of melanosome structures across species. The different melanin molecules within such melanosomes create different feather hues: (A) brown in a Tufted Titmouse (*Baeolophus bicolor*), (B) brown-black in a Macaroni Penguin (*Eudyptes chrysolophus*), (C) gray in a Double-crested Cormorant (*Phalacrocorax auritus*), (D) black in a Palm Cockatoo (*Probosciger aterrimus*), and (E) iridescence in a Brazilian Teal (*Amazonetta brasiliensis*). (F) Melanosome structure in a fossil microraptor. The dot on each bird indicates the approximate sampling location. (From Li et al. 2012. Reproduced with permission from AAAS. Insets A–E from del Hoyo et al. 2016. Reproduced with permission from Lynx Edicions.)

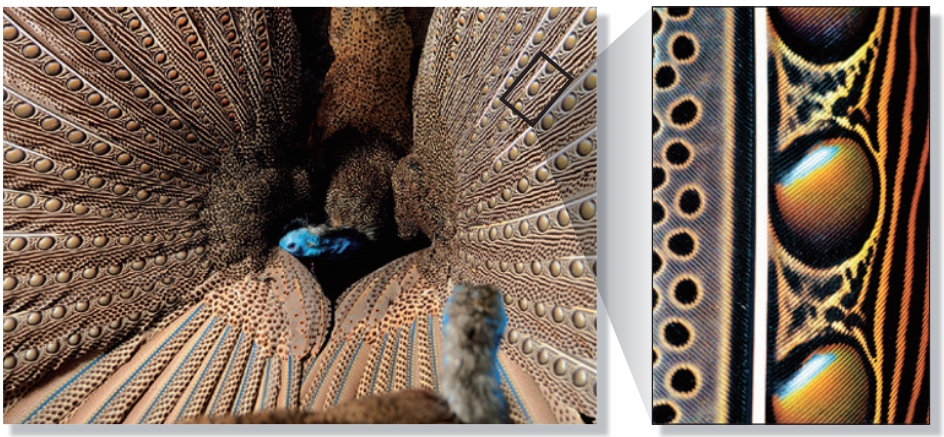


Fig. 4.49 Melanins can create elaborate feather patterning. Melanin pigments form stripes and eyespots in the feathers of a Great Argus (*Argusianus argus*); here a male is displaying for an observant female. Cell-by-cell level control allows extremely intricate patterning within a tail feather. (Photographs by Jeremy Johnson, Meddling with Nature: left, CC-BY-SA 4.0, retrieved March 15, 2015, www.meddlingwithnature.com; right, CC-BY-SA 3.0, retrieved November 5, 2014, Wikimedia Commons.)

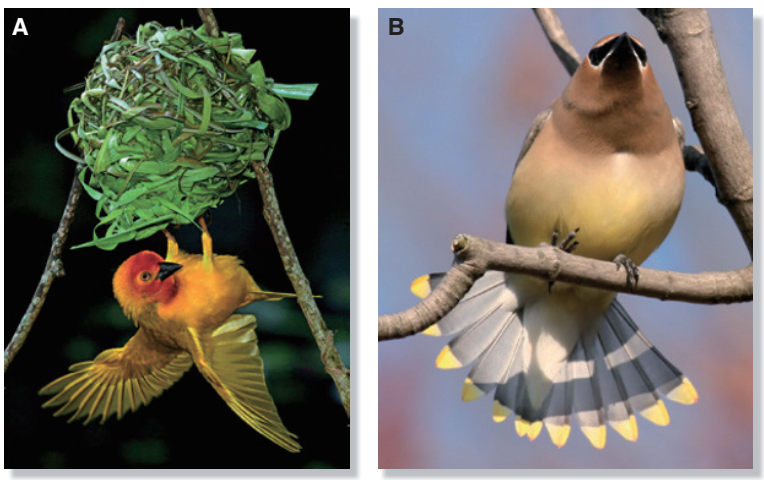


Fig. 4.50 Carotenoid pigments. Obtained from the diet, carotenoids create warm red, orange, and yellow hues, as featured in (A) the facial feathers of this Golden Palm Weaver (*Ploceus bojeri*). (B) Cedar Waxwings (*Bombycilla cedrorum*) typically have yellow-tipped tail feathers. (Photographs by: A, Peter S. A. Baker, DPAGB, LRPS; B, Dave Spier.)

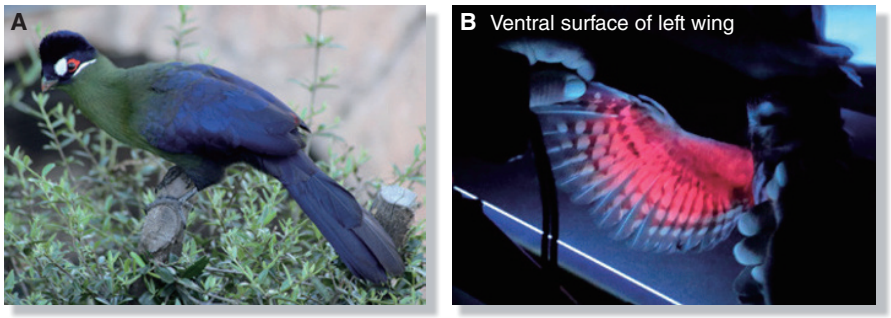


Fig. 4.51 Porphyrin pigments. (A) Most of the green and violet-blue feathers on this Hartlaub's Turaco (*Tauraco hartlaubi*) are a product of porphyrin pigments, which are rare in birds. (B) Easily degraded by UV sunlight, porphyrins are useful markers of feather age in the nocturnal migrant species in which they occur. Recently molted feathers of Northern Saw-whet Owls (*Aegolius acadicus*) fluoresce bright pink under UV light. (Photographs by: A, derekkeats, https://commons.wikimedia.org/wiki/File:Hartlaub%27s_Turaco.jpg. CC-BY-SA 2.0; B, Joe Subolefsky.)

to metabolize fully to their preferred yellow pigment type (Mulvihill et al. 1992).

Currently, although hundreds of carotenoids have been found in nature, only a few dozen have been identified in bird diets, blood serum, and/or feathers. In general, most terrestrial birds seem to have diets relatively rich in the carotenoid pigments lutein and zeaxanthin, whereas aquatic birds have greater access to gazaniaxanthin and rubixanthin pigments. The roles of rarer carotenoids in avian coloration are still largely unknown.

In addition to the very common, widespread pigment groups of melanins and carotenoids, some birds use other types of more exotic pigments. For example, porphyrins are complex, nitrogen-containing molecules related to hemoglobin, which birds (and other living things) make by modifying amino acids. Porphyrins are most striking in the purplish reds and greens of the turacos, a family of colorful African birds (Fig. 4.51A). The porphyrin pigment turacoverdin, which produces the spectacular green in the plumage of many turacos, is one of the few green pigments known in birds. Most greens in other birds are thought to be produced by yellow carotenoid pigments overlying blue structural colors. Porphyrins produce interesting shades of red, browns, greens, or pinks in a number of different avian orders. They also can interact with melanins to produce the browns of many owls, and they are found in various pigeons and gallinaceous birds. In eggshells, porphyrins may appear pink or red, or they may be masked by melanins. Although the exact chemical structure varies from pigment to pigment, all porphyrins fluoresce bright pink under UV light (Fig. 4.51B).

Another unusual group of pigments are the psittacofulvoids, which, as their name suggests, are found only in parrots. These pigments, which are fundamentally different from the carotenoids, produce many of the vivid hues found in parrots (Fig. 4.08).

Pigment molecules are used extensively in avian visual signaling; because pigments are obtained in different manners (some are manufactured within the body whereas birds obtain others from their diet) they have the potential to carry information about the health and vigor of an individual bird. This information can help birds advertise their overall desirability as healthy mates, or undesirability as strong competitors.

4.7.4 Structural colors: bending light

To understand structural colors, it is necessary to understand a few more aspects of the physics of light. First, light refracts, or bends from its straight path, when it passes between one kind of material and another; for example, when it passes from air to glass, water, or keratin (Fig. 4.52A). However, all the wavelengths of light do not bend at the same angle as they move between materials. Different wavelengths refract at different angles, with longer wavelengths bending less and shorter wavelengths bending more. Therefore, if white light hits a material boundary, the different wavelengths separate. Light moving through the flat, parallel surfaces of window glass is bent and separated when it enters the glass; however, it is bent back exactly in reverse when it moves from the glass to the air again, so the original structure of the light is restored, and no separation of color is visible to us. In contrast, the glass surfaces of a classic prism are not parallel; light traveling through is bent both at the entering and exiting surfaces, but the non-parallel surfaces cause the light to become separated into its complete spectrum of colors. Using a rainbow as a real-life illustrative example once more, refraction is how white light can become separated by the structure of materials. Under certain lighting conditions, the curved surfaces of water droplets falling in rain act like a prism, separating the white light passing through and creating the rainbow (Fig. 4.52B).

Refraction in feathers

Birds have the materials necessary to use this property of light to make color in their feathers. The degree to which light refracts when moving between materials depends on

the difference in the refractive index (a quantification of the light-bending property) of the materials. Feathers are made of keratin, which has a refractive index sufficiently different from air to cause substantial refraction. Other common materials in feathers include pigments, especially melanins, which have a refractive index distinctive from both air and keratin. Thus, the ability to refract light is one of the material properties of feathers. With the necessary properties of their constituent materials in place, two fundamentally different forms of light scattering potentially could occur in feathers, incoherent and coherent scattering.

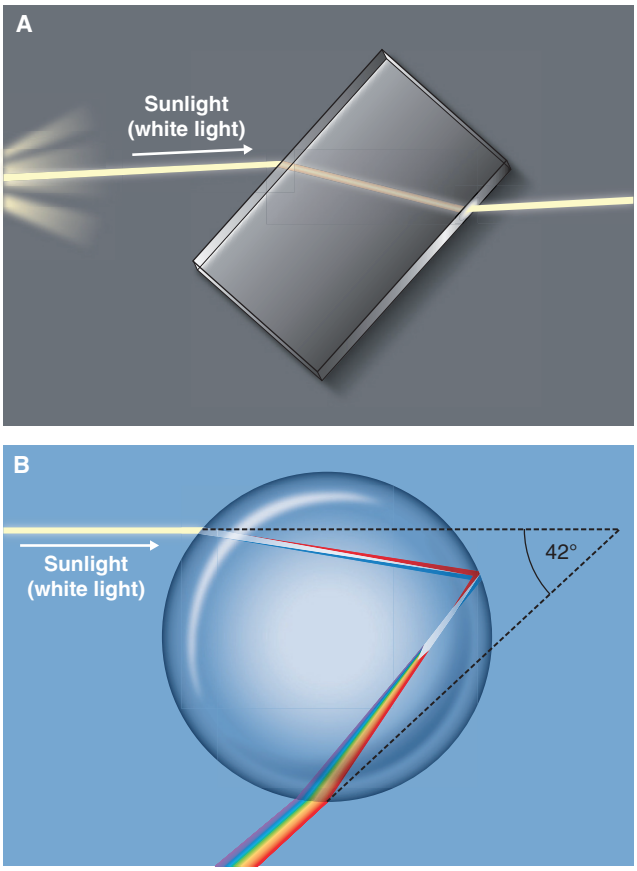


Fig. 4.52 Light properties that can produce color. (A) Light bends as it passes through distinct materials. Here, wavelengths separate inside the glass but bend in reverse as they contact air again, reuniting once more as white light. (B) When white light passes through a falling raindrop at a 42-degree angle, it refracts and separates into independent wavelengths (forming a spectral rainbow, as in a prism). (Illustrations by: A, ajizai. http://wikimedia foundation.org/wiki/File:Refraction_photo.png; B, KES47. https://commons.wikimedia.org/wiki/File%3ARainbow1.svg.)

Incoherent scattering

For many years, blue colors in birds were erroneously attributed to a group of related physical mechanisms termed Raleigh, Tyndall, or Mie scattering. To achieve Raleigh scattering, air bubbles inside the keratin matrix of the feather were modeled as being small enough to allow the passage of larger wavelengths of light around them (the reds, oranges, yellows, and greens) but large enough to scatter all wavelengths of a certain size and smaller in random directions (blues and purples). The defining property of such incoherent scattering is the true randomness of the air bubbles within the keratin, and thus the randomness of the scattering of larger wavelengths of light. Although incoherent scattering does produce some of the subtle blues and bright whites found in nature, such as the sky and blue ice (Fig. 4.53A), there is no evidence of this process producing a blue color in birds or other living animals. Instead, the only "color" produced using incoherent scattering in bird feathers is white (Fig. 4.53B).

Coherent scattering

Research during the past several decades has shown that all known structural colors beyond white in birds are produced through coherent scattering. Coherent scattering occurs in feathers when the air bubbles, melanin, and keratin are arranged in very specific patterns relative to one another in ways that separate and reinforce only certain wavelengths of light. Two fundamentally different kinds of structural colors are produced from coherent scattering: structural blues and iridescent colors. In order to understand how these two forms of structural colors differ from

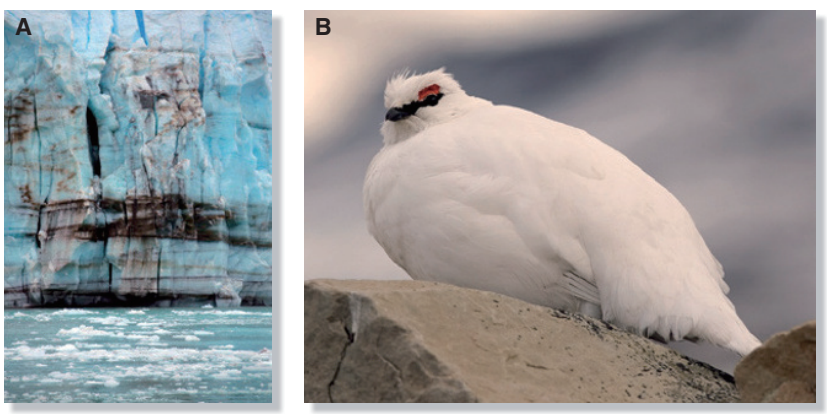


Fig. 4.53 Incoherent scattering of light. (A) Icebergs appear to have a blue hue due to the random arrangement of trapped air bubbles, which scatter shorter wavelengths of light. (B) In feathers, incoherent scattering within the keratin matrix can only produce white (reflectance of all hues cumulatively), as on this Rock Ptarmigan (*Lagopus muta*). (Photographs by: A, Christopher Michel, http://wikimediafoundation.org/wiki/File:Alaska_(3733278715).jpg. CC-BY-2.0; B, Perhols, https://commons.wikimedia.org/wiki/File%3ASvalbard_rock_ptarmigan_svalbardrype_pho_w_5266.jpg. CC-BY-SA-3.0.)

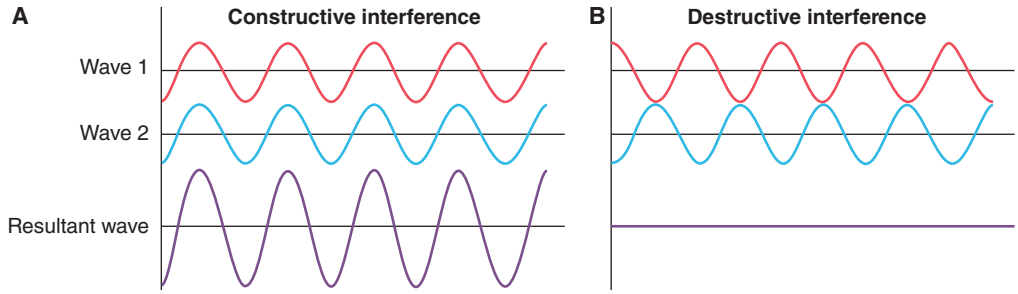


Fig. 4.54 Two extremes of wave interaction. (A) Constructive interference occurs when two waves of equal frequency rise and fall at the same time (occuring "in phase"); their energy combines and the amplitude doubles. (B) Conversely, when two waves of equal magnitude occur in exact opposition (one wave hits its peak while the other hits its valley), they cancel each other out. This is called destructive interference. (Adapted from Haade, http://wikimediafoundation.org/wiki/File:Interference_of_two_waves.svg. CC-BY-SA 3.0.)

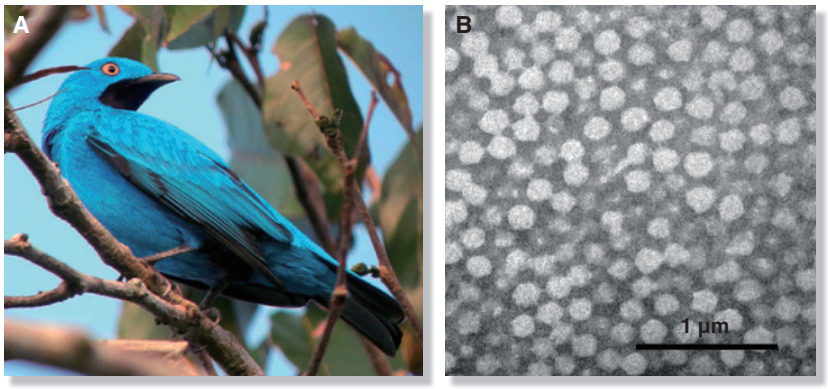


Fig. 4.55 Quasi-ordered keratin and visible light. (A) The electric-blue color of this Plum-throated Cotinga (*Cotinga maynana*) is purely structural. (B) In this species, the quasi-ordered arrangement of keratin and air spaces—shown here at a microscopic level—is isotropic (uniform in all directions), scattering light in a way that produces these particular blue wavelengths. (A, photograph by Félix Uribe. B, from Noh et al. 2010. Reproduced with permission from John Wiley and Sons.)

one another, it is necessary to consider one more physical property of light—interference—that contributes to the behavior of light inside a feather.

Interference

Interference is what occurs when waves interact with one another. If two light waves of the same wavelength are added together, they will continue to oscillate at that same wavelength, but their amplitudes—perceived by us as their intensities—will add together differently depending on how the individual waves are lined up. If waves are timed to be exactly in phase (oscillating together so that their peaks and troughs coincide), their amplitude will double; this is called constructive interference (Fig. 4.54A). If they are timed exactly so that one wave peaks as the other bottoms out, their intensity sums to zero, and they cancel each other out—a phenomenon called destructive interference (Fig. 4.54B). In these ways, light of the same wavelength may interact with itself in predictable ways so that its waves can either strengthen or weaken each other.

Sunlight provides a constant stream of light containing manifold wavelengths. Some subset of all this light shares the same wavelength, and this light has the opportunity to interact constructively to increase the intensity of the light at that specific wavelength. Coherent scattering occurs when a feather's keratin (and embedded materials such as air or melanin) are arranged in such a way that a large proportion of the incoming light of one specific frequency, determined by the spacing of the keratin itself, is scattered outward from the surface of the feather in phase and thus is reinforced and intensified. All other wavelengths are absorbed or transmitted backward towards the bird's body, thus minimizing or canceling out their effects.

Structural blues

Structural blues are produced when the air bubbles within the feather's keratin matrix are found in a specific spatial distribution, termed quasi-ordered (Fig. 4.55). When the air bubbles within the keratin are distributed this way, they scatter only the shortest wavelengths of light back out, and they scatter specific wavelengths back out in phase, thus reinforcing and intensifying them. Colors produced in this way are limited to those at the short end of the spectrum, and thus are primarily blues and frequencies in the UV end of the spectrum that humans cannot see.

It is worth noting that pigments are often used in conjunction with structural colors in bird plumage. For

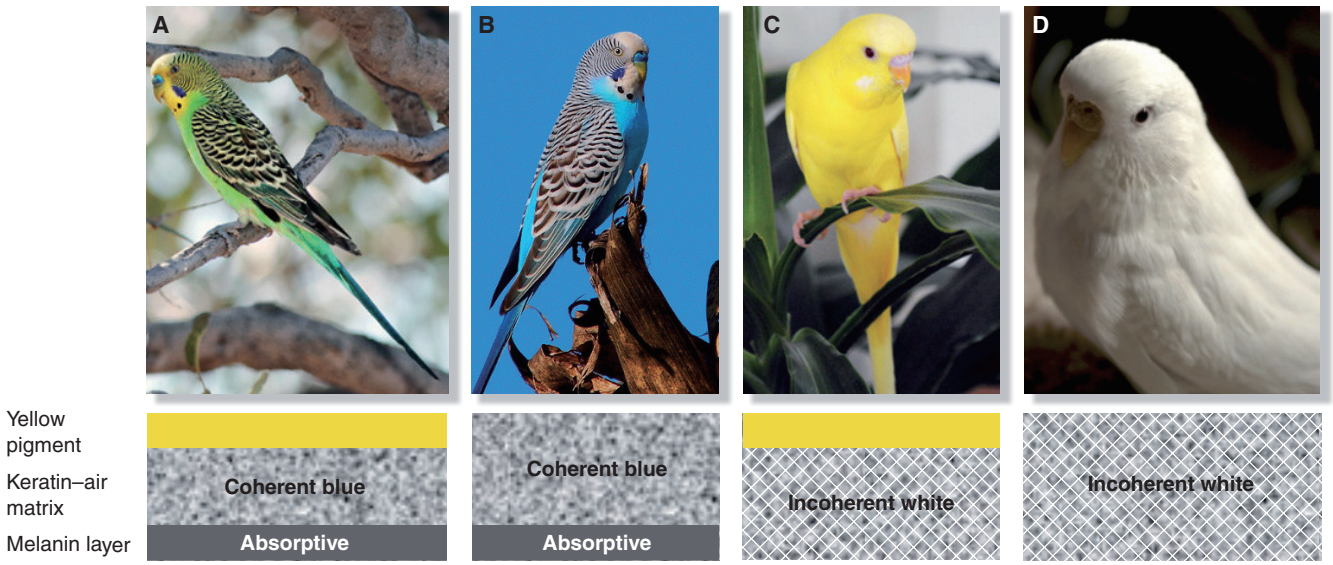


Fig. 4.56 Budgerigar (*Melopsittacus undulatus*) color morphs. (A) Three elements create the green color in the barbs of wild-type Budgerigar feathers: coherent scattering of blue-green frequencies via the keratin–air matrix, yellow pigment embedded in the keratin (above), and a layer of melanin on the underside of the barb. A change in any of these properties results in a different color morph. (B) Blue Budgerigar feathers maintain the structural components of the wild-type, but lack the yellow pigment. (C) Pure yellow morphs maintain the top layer of yellow carotenoids, but lack the coherently structured blue layer and melanin layer below. (D) White Budgerigar feathers lack the yellow pigment, the coherent blue, and bottom melanin layers. (Photographs by: A, Benjamint444, https://commons.wikimedia.org/wiki/File:Budgerigar-male-strzelecki-qld.jpg. GFDL 1.2; B, Isidro Vila Verde; C, Kelsey Lee; D, Brandi Brussel.)

example, black and dark brown melanins are often used as background layers under structural blue feather surfaces. As such, these pigments absorb unwanted colors of light that otherwise would wash out the purer structural colors that are being isolated and reinforced. Alternatively, colorful carotenoid pigments are often combined with structural colors to create hues of color that neither carotenoids nor structure can make by themselves. For instance, in a pet store you might see Budgerigars (*Melopsittacus undulatus*) of different colors. Wild-type (green) Budgerigars have a matrix of keratin and air that scatters blue wavelengths, sandwiched between a top layer of yellow pigment and a bottom layer of melanin (Fig. 4.56A). To produce a saturated green, the yellow pigment reflects and emits yellow wavelengths while the blue wavelengths are reflected by the scattering matrix, and the melanin absorbs whatever other wavelengths make it through the first two layers. The other Budgerigar color morphs occur when one or more of these elements is missing. Blue Budgerigars lack the yellow pigment layer, allowing the reflection of the blue wavelengths (Fig. 4.56B); yellow Budgerigar feathers lack both the coherently scattering blue layer and the bottom melanin layer (Fig. 4.56C). The absence of both pigments, which leaves only the incoherent scattering layer, results in white feathers (Fig. 4.56D).

Structural blues in feathers have some distinctive observable properties. With a microscope you can see that the keratin–air arrays that make the blue are found only in the rami of feathers (not the rachis or barbules). When lit from underneath (the ventral surface), a blue feather will look brownish because the melanin layer underlying it filters out much of the light before it can reach the "blue" structures. This direction-dependent effect is not seen in a pure pigment-produced color: if a pigment-produced yellow feather is held up to light, it still looks yellow, because the color is produced by pigments, which are not directionally sensitive.

Iridescence

Informally, observers of birds recognize iridescence as a certain set of optical properties—usually, bright and intense colors, often with a metallic shininess, and often more intense if viewed from a certain direction. Formally, however, the most defining property of iridescence is that the exact hue (Box 4.04) of color observed shifts depending on the angle at which it is viewed. Thus, the colors of the "eyes" of a peacock's plumes, the shine of a sunbird gorget, and the sheen on the back of many black birds shift hue with the angle of view. As often seen in hummingbird gorgets, hues can switch abruptly by going from a bright, saturated color to the complete absence of color, or black. In optical physics, iridescence is defined as a phenomenon created by specific micro- or nanostructures. In birds, the nanostructures necessary to create iridescent colors are produced only inside barbules by various combinations of keratin, air, and melanin.

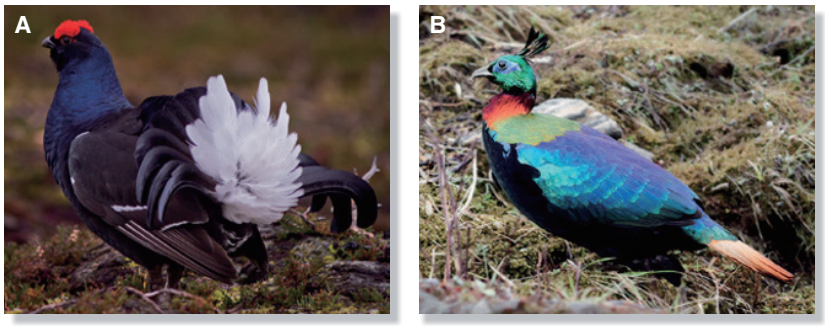


Fig. 4.57 Nanostructural varieties of iridescence. (A) Light refracts through a thick matrix of keratin, situated above a layer of melanin, to generate the midnight-blue sheen in the neck and breast feathers of this Black Grouse (*Tetrao tetrix*). (B) Layers of melanin organized in "quarter wave stacks" reflect light at different angles, creating the spectacular rainbow iridescence of this Himalayan Monal (*Lophophorus impejanus*). (Photographs by: A, Conrad Mackinnon; B, Dibyendu Ash, https://commons.wikimedia.org/wiki/File%3AHimalayan_Monal_Adult_Male_East_Sikkim_Sikkim_India_11.05.2014.png. CC-BY-SA 3.0.)

Iridescence is typically produced when the melanin inside the feather barbules is arranged in more highly ordered configurations than the quasi-ordered air-in-keratin matrix used to produce structural blues. In principle, any wavelength of light (not just blue) can be reflected and reinforced simply by varying the spacing of these melanin structures. This allows for the diversity of iridescent colors observed among and within species of birds. While the arrangement of melanosomes can vary greatly, all conform in some way to a geometric system of layers, and they always occur in the barbules of the feather. The layered or stacked structures of melanin near the surface of the barbules force the incoming light not only to interfere constructively to intensify certain colors (as with the isotropic blues discussed above) but also to do so in such a way that, as an observer's angle changes relative to the barbule surface and light source, the distance the light travels between the reflecting layers effectively changes, and therefore the hue of the color that is reinforced changes accordingly.

Because iridescence has evolved numerous times among different groups of birds, there is quite a bit of nanoscale morphological diversity underlying the phenomenon. Consequently, variation in the hue and intensity of iridescence can produce a subtle purple-blue or green sheen via a thick film of keratin over a layer of melanin (Fig. 4.57A) or a display of intense and saturated colors created by many layers of melanin organized in "quarter wave stacks" (Fig. 4.57B). However, the basic principle is always the same: to use the internal nanostructural geometry to generate refraction and interference that separates and reinforces only a subset of wavelengths of light. An added condition is that the subset of wavelengths that is reinforced changes with the relative angle between the surface of the object, the light source, and the viewer. The glistening and shimmering metallic effect typically associated with iridescence is an almost incidental by-product of the very smooth surface and subsurface structures generally needed to generate iridescence.

4.8 Feather and plumage texture: light at the scale of barbules, barbs, and whole feathers

The appearance of the plumage involves more than just the color of the feathers. Sun glinting off the wing of a jet-black raven can appear almost like white patches. Sun reflecting off a European Starling's (*Sturnus vulgaris*) "black" breast might have a purple, blue, or green iridescent hue. In contrast, no sunlight at all seems to reflect off from the velvety black breast feathers of a Carola's Parotia (*Parotia carolae*) of New Guinea, no matter the angle from which they are examined. These variations in black birds can be seen at relatively far viewing distances. Closer at hand—at the distances at which birds often interact with one another—there is often even more to see, and these effects can be quite spectacular. Brilliant reds can be very different, from the plastic-looking, opaque reds of the Cut-throat (*Amadina fasciata*) of Africa to the glassy, transparent reds of the Black-necked Red-Cotinga (*Phoenicircus nigricollis*) of Amazonian South America. Some feathers, even when uniformly colored or patterned, form a plumage that looks distinctly scaled or plated, as in the African Emerald Cuckoo (*Chrysococcyx cupreus*), whereas in other birds individual feathers appear to merge together and create a continuous silky surface over the entire bird, as in the Purple Glossy-Starling (*Lamprotornis purpureus*) of Africa (Harvey et al. 2013).

What causes these differences in feather textures? To answer this question, we need to consider the effect of the surfaces of the rachis, barbs, and barbules of feathers—structures that are large relative to the nanostructures of pigments and structural colors.

Plumulaceous feathers invariably create an overall soft, fluffy appearance, like that of a downy chick. Their

relatively fine barbs and barbules are long, loose, and therefore are not aligned or organized so that light can reflect from them in any structured way. Light scatters equally in all directions, and thus there is no shininess or directionality to it.

One variation of a soft, downy, look can be caused by a different mechanism: a velvety feather surface in adult birds can be created by exceptionally long, upright, distal barbules sticking out from the otherwise flat surface of a pennaceous feather vane. One great example of this is evident in the velvety-appearing feather surfaces of owl feathers (Fig. 4.32). If you examine them very closely with a magnifying glass, you can actually see these barbule hairs coating the feather surface like a sea of grass. Although evolved to silence the owl's flight, the visual effect is to reduce the glossiness of the feather. Many of the black birds-of-paradise, on the other hand, have broad areas of velvety black feathers with similarly protruding barbules capturing any and all light sent in their direction. This light-absorbing background is used to set the stage for their showy iridescent ornaments.

A hairy appearance can be created in various ways. For example, the New Zealand kiwis have feathers with relatively long, thin rachi and very narrow vanes created by short barbs. Alternatively, the seemingly hair-like neck feathers of many herons have relatively stiff, open pennaceous vanes in which the barbules are so reduced as to leave the barbs running parallel but free from one another. In these cases, the barbs of the vane are stiff enough that they lie relatively parallel to one another even without barbules to hold them together. The parallel-lying fibers then create a hair-like appearance.

At the other end of the continuum, birds can use barb and barbule orientations and surface shape to create almost mirror-like reflections of light. An overall glossy or shiny effect can be generated in various ways, including by a smooth planar rachis and/or barb surfaces in a firm pennaceous feather. Rachi in general usually have a very smooth surface; thus, when they are viewed at a particular angle, light often reflects off the surface of the rachi in a shiny manner—the wider the rachis, the stronger this effect. Likewise, broader, flatter barb surfaces can generate a feather that is more likely to reflect light in a shiny way. For that reason, the wings and tails of birds tend to appear shinier than other parts of their bodies, where the larger feathers have broader rachi and barbs.

A suite of other feather textures and appearances exists: transparent versus opaque, glassy versus plastic-like, scaled versus silky. All are caused by variations in the rachi, barb, and barbule surfaces and internal structures, but many of these are only beginning to be studied. Finally, although individual feathers contribute enormously to the apparent surface texture of birds, all the feathers constituting a plumage ultimately overlap and thus can interact with one another to create a great diversity of visual effects.

4.9 Visual functions of plumage

Coloration and patterning play important roles in the behavioral ecology of birds. All animals must strike an evolutionary balance between hiding from predators and being conspicuous for social signaling. For many animals, concealment is prioritized over advertising. Thus, just as the earthy, cryptic colors of many mammals, reptiles, and amphibians make them relatively inconspicuous, so too, many birds sport brown, gray, and olive-green tones that render them harder to see. On the other hand, many birds are brightly colored, perhaps because flight makes them less vulnerable to predators, perhaps because bright colors are concealing in some habitats (in sunlit, fruit- and flower-laden forest canopies, for instance), or perhaps because colors are so crucial for birds' social interactions. Birds' plumages declare the identity of their species, their age and status as individuals, advertise their health, and are the centerpieces of a lot of sexual selection (Chapter 3). The inherent ability of feathers to form complex colors and patterns, when coupled with the social and communicative nature of birds themselves, has made birds some of the most ornate animals on earth.

4.9.1 Predator avoidance

Predation is a significant threat for most birds, and avoiding predation appears to be the main reason so many birds have evolved cryptic coloration. There are numerous ways for a bird to create **crypsis**, or patterning that generally causes an animal to blend in with its background.

Many birds use background matching: their plumages include colors and patterns that mimic the substrates on which they are most often found. The mottled patterns on birds of the scrub or forest floor are excellent examples; the woodcocks of the northern hemisphere, button-quails of Australia, and many other birds worldwide resemble the leafy litter in which they are frequently found. Nearly all shorebirds, from sandpipers to curlews, have mottled brownish backs that conceal these ground nesters during incubation as well as during foraging on beaches, mud flats, or in grasses (Chapter 11). Worldwide, birds of grasses and reeds—the bitterns, many Old World warblers and Old World buntings, most New World sparrows, and the cisticolas of Africa—often have patterns with many shades of

Crypsis: patterning or coloration that allows a bird to remain concealed by blending into its environment.

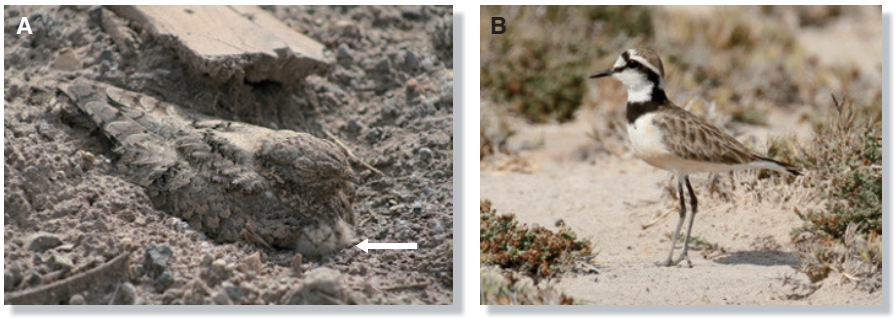


Fig. 4.58 Two types of disruptive coloration. (A) This Egyptian Nightjar's (*Caprimulgus aegyptius*) plumage—with its irregular steaks, mottled blotches, and general hue—almost perfectly matches its surroundings (arrow denotes the virtually indistinguishable nestling beneath the adult). Camouflage is essential for this species, which nests in exposed rocky areas. (B) The neckbands of this Madagascar Plover (*Charadrius thoracicus*) break up the outline of its body, disrupting the focus of an onlooker. Different areas of its body also blend in with the landscape: its belly and face match the sand, while its back and head match the vegetation. (Photographs by: A, "K K," https://commons.wikimedia.org/wiki/File%3ACaprimulgus_aegyptius.jpg. CC-BY-SA 3.0; B, © bryanjsmith.)

brown arranged in long streaks to help them blend into the stripy vegetation they live within. The northern-dwelling ptarmigans molt from their mottled-brown summer plumage to a coat of pure white that blends with heavy snow cover in winter; similarly, the Snowy Owl (*Bubo scandiacus*), Snow Goose (*Chen caerulescens*), and Snow Bunting (*Plectrophenax nivalis*) of the arctic tundra all wear snow-matching white plumages. Even birds that look gaudily colored in pictures may blend perfectly into their natural surroundings; many birders visiting the tropics have had the humbling experience of scrutinizing a well-lit, bright green, and visually "birdless" tree that is nonetheless squawking with birds, before finally glimpsing one well-camouflaged leaf-green parrot just as the flock of a hundred takes off!

Some birds use **disruptive coloration**. Like the camouflage of military and hunting gear, disruptive plumage coloration uses larger patches, streaks, or other bold color patterns to break up the outline of the bird—distracting an observer from noticing the whole bird as one form (Fig. 4.58A). For example, the bold, black neckbands of many plovers make it more difficult to distinguish the whole bird as one form (Fig. 4.58B). Similarly, the eyelines—lines of feathers above or through the eye that contrast with the base head color—found in so many birds are thought to help distract from their otherwise conspicuous dark, round eyes, by either drawing out the round eye with a dark lengthening line extending back from it, or with a brighter, usually white, line above the eye. Disruptive coloration provides the added advantage of camouflage on a variety of backgrounds.

Employing another strategy to minimize detectability, many birds are hard to see because they are darker on top than below, a pattern known as **countershading**. Many bird species, including smaller plovers, sandpipers, and songbirds, exhibit this pattern. With the darker back lit by the bright sun overhead and the lighter underparts in the shade of the bird's own body, the bird appears to be nearly one color, and until it moves, predators have difficulty seeing it as a three-dimensional object. In addition, white underparts may reflect the color of the ground, producing even more effective camouflage. Countershading is especially widespread in open-country birds that are vulnerable to distant predators hunting by sight. It also is common in birds that spend much time on or flying above water, such as loons, grebes, ducks, auks, gulls, terns, and many pelagic birds (Fig. 4.59).



Fig. 4.59 Adaptive function of countershading. A Great Black-backed Gull (*Larus marinus*) attacks a Ring-necked Duck (*Aythya collaris*), thanks in part to countershading: from below, the gull's plumage (dorsally dark, ventrally light) blends into the white sky, camouflaging its presence and movements. (Photograph by Ajay Sequeira.)

Disruptive coloration: a type of camouflaging coloration in which patches, streaks, or other bold patterns help break up and distract from the overall shape of the bird.

Countershading: a pattern of coloration in which a bird is darker on top than below.

Birds may further increase the benefits of cryptic plumage by using behaviors that add to their crypsis. Simply holding still is a good way to avoid attracting the attention of predators. By freezing and flattening against the beach, young terns and gulls eliminate their shadows and look just like bumps on the sand. The nocturnal potoos of the neotropics complement their mottled brown-and-gray plumage with behavior; they spend most of the day just sitting, often perched on the limb of a dead tree, with neck stretched up and large eyes closed, looking like an extension of the limb. Many small owls adopt similar stick postures. The strategy of remaining relatively still also works for many predators, such as herons prospecting for fish or frogs along a shoreline. In some contrasting cases, subtle movement can actually enhance concealment. For example, bitterns—which accentuate their streaked pattern by standing in a marsh with their beaks pointed skyward—will sway slightly from side to side with the surrounding reeds as the wind blows.

In a creative twist regarding the use of behavior to enhance concealing plumage, many birds have conspicuous tail or wing markings that draw attention only once the bird flies off. The barred black-and-tan upperparts of New World flickers and the black-and-white upperparts of the Eurasian Hoopoe (*Upupa epops*) are easily overlooked against the ground on which they forage. Yet in flight, the bright yellow wings and white rump of the flicker and the bold, black-and-white wing pattern of the Eurasian Hoopoe are visually striking (Chapter 14). When such attention-grabbing plumage patterns are revealed suddenly, they may startle an approaching predator. Similarly, many passerines have distracting contrasting (usually white) outer tail feathers or feather tips that may cause a predator to hesitate or to strike the bird's tail and miss the primary target of its body. Because these conspicuous markings can be made to disappear when the bird lands, suddenly concealing the bird's position, they may further confuse predators that had focused primarily on the bold markings during pursuit.

Predation avoidance via feathers is not restricted to their appearance: at least one group of birds sequesters toxins in its feathers that make them distasteful—and potentially even poisonous—to predators (Box 4.06).

One final note on predation and avian coloration: bear in mind that different predators have different visual capabilities, so one cannot assume that all prey appear as conspicuous or as cryptic to predators as they do to humans. For instance, most mammalian predators and nocturnal avian predators (such as owls) lack color vision. Many bright yellow or red birds thus may be relatively inconspicuous to these predators, which see the colors as shades of gray. On the other hand, hawks, eagles, and other avian predators that are active by day generally have full color vision including some UV wavelengths. Thus, markings on a bird may be cryptic for one kind of predator but not for another.

4.9.2 Social recognition and signaling

Birds use external appearance in the form of color and pattern to distinguish species, age classes, sexes, and/or individuals. These forms of recognition are outlined below.

Many of the most important interactions in the life of a bird occur between an individual and its conspecifics, the other members of its own species, including its parents, offspring, potential mates, and competitors. At a basic level, birds must recognize conspecifics to choose an appropriate mate and/or exclude appropriate competitors. Plumage, along with other signals and cues such as song and behavior, plays an obvious role in distinguishing the relevant parties.

It generally is true that individuals who mate solely with their own species likely will be more successful at producing young, and this tendency will be favored strongly by natural selection (Chapter 3). As a result, the appearance of an individual can play a role in species recognition, literally the ability of members of a species to recognize other members of their own species. However, whether species recognition has been a driving force of plumage evolution per se is a harder question to answer. That is, although researchers have long assumed that both color and pattern function in species recognition, devising experiments that clearly demonstrate a selective role in species recognition is difficult, and few supporting data exist for this idea (Mendelson and Shaw 2012). For instance, when conspicuous species-specific markings, such as the red epaulettes of the male Red-winged Blackbird (*Agelaius phoeniceus*) of North America (Chapter 9), are experimentally covered, the sexes nevertheless continue to establish pairs (Searcy and Yasukawa 1983), and these experimentally altered males are recognized as conspecifics by other males. Clearly, species recognition involves a variety of cues acting together; songs and behavior play key roles, and species-specific color patterns also influence how conspecifics treat one another.

Likewise, patterns exhibited in different plumages may be used for age recognition, the ability of individuals to distinguish between age classes. Many birds have distinctive subadult plumages before they become sexually mature. Further, in many species the males continue to wear these subadult plumages for one or more years after they are capable of reproducing. Territorial adult males are often more tolerant of males in subadult plumages on their territories than they would be of definitive males. Additionally, given a choice, females usually select mates in their adult, definitive plumages. Yet it can be difficult to assess whether these interactions are mediated solely on the basis of the age-indicating plumage itself, rather than some other indicators of age.

Perhaps more critically, plumage coloration likely plays a role in sex recognition: ascertaining the gender

Box 4.06 Yuck! Rubbish-bird! *Pit-oou-i!*

Bold and colorful markings in some animals, such as insects (especially butterflies), and frogs, are thought to be aposematic: visually striking in order to warn off would-be predators. That is, these species wear a memorable signal that predators come to associate with an unpleasant dining experience, usually due to bad flavors or toxins in the consumed tissues. A fascinating additional phenomenon sometimes arises among aposematic species—occasionally unrelated but distasteful species converge upon each other's appearance, presumably enhancing their cumulative "advertising" effectiveness, a phenomenon called Müllerian mimicry. The primary role of birds in the phenomenon of aposemetism is as the predator "audience" that the moths and frogs are advertising their distastefulness to.

There is one notable exception. While working in New Guinea, ornithologists Jack Dumbacher and Bruce Beehler learned of birds that the native people of New Guinea knew as distasteful "rubbish-birds," not to be eaten unless specially prepared. They also noticed burning and numbing sensations in their own noses, lips, and tongues after handling these same birds. As it turns out, several members of the genus *Pitohui* from New Guinea carry potent neurotoxic alkaloids in their feathers (Fig. 4.B6.01). These species are also black, reddish brown, and orange, coloration very typical of other aposematic animals. Members of this genus vary in their toxicity, and also in their orange to reddish brown and black coloration. However, there is evidence that both the toxicity and the contrasting orange-and-black plumage have evolved numerous times independently, indicating that Müllerian mimicry could be working to select shared coloration, flocking behavior, and morphology despite what appear to be parallel but separate evolutionary originations of poison sequestration (Dumbacher et al. 1992, 2008).



Fig. 4.B6.01 Aposematic coloration. This Hooded Pitohui (*Pitohui dichrous*) is one of three known poisonous bird species, containing a neurotoxin in their feathers (homobatrachotoxin). This same toxin, which is derived from their diet, is also found in New World poison dart frogs (family *Dendrobatidae*). (Photograph by Alexandra Class Freeman.)

of a conspecific. Many species of birds show **sexual dimorphism** (Chapter 3); males and females are distinctive from one another in some aspect of their morphology. Sexual dichromatism, in which one sex is colored differently from the other, is a particularly common form of sexual dimorphism in birds. To a bird looking for a mate, knowing the sex of another individual is key, but sex recognition also is critical in numerous other social interactions, including defending resources, territories, or mates. In species in which the sexes differ dramatically in appearance, sex recognition is likely straightforward. However, plumage differences between sexes can be very subtle. In many woodpeckers, for example, the amount of red on the head reveals the sex (Fig. 4.60). In one classic experiment, a researcher painted malar stripes onto female woodpeckers that made them look more like males, and their mates then chased them away (Noble 1936).

Note that birds do not necessarily require different plumages to recognize the opposite sex. Even when UV reflectance is taken into account, many songbirds are **monomorphic**, or have the same plumages in both sexes. In these species, males and females likely recognize each other by some other cue, such as song or behavior. Therefore sexual differences in plumage may arise for a variety of reasons other than sex recognition, including the different roles played by each sex in courtship, nest attendance, and territorial defense, for example. Sexual selection—the differential fitness that arises from competition within and between the sexes—also plays an important role in creating sexual dimorphism. Along with predation, sexual selection has been a predominant force driving the evolution of the incredible diversity of avian plumage (Chapter 3).

Sexual dimorphism: a situation in which males and females of the same species differ in aspects of their size, color, or form.

Monomorphic: describes species in which males and females are similar in outward appearance.



Fig. 4.60 Sexual dichromatism. Male and female White-backed Woodpeckers (*Dendrocopos leucotos*) can be distinguished by their head color; males have red crowns, while female crowns are black. (Photograph by Koichi Saito.)

Lastly, birds use plumage differences for individual recognition, because many birds clearly recognize other individual birds, especially their mates. How do they do so? Birds probably identify familiar individuals the same way humans recognize other people, by subtle differences in color, head and body shape, posture, and voice. Several studies have demonstrated that birds use color and pattern to recognize individuals. When Ruddy Turnstones (*Arenaria interpres*)—arctic-breeding shorebirds with highly variable plumage—were shown models that mimicked their neighbors or strangers, they reacted aggressively only toward the strangers (Whitfield 1986), strong evidence that they could distinguish their neighbors by appearance alone. In addition, several colonially nesting species, including Ring-billed Gulls (*Larus delawarensis*) in North America, can pick their own young from a crowd of young by their facial markings.

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Chapter 5 Avian Flight

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Flying is a spectacular and captivating accomplishment of birds, one that captures the imagination of everyone who watches a swirling flock of shorebirds, the seemingly effortless soaring of a vulture, the plummeting descent of a diving falcon, or a darting hummingbird moving among flowers. Not all birds fly, but those that do have a host of physiological and anatomical adaptations that allow them to take great advantage of the air as a medium for rapid movement and access to otherwise inaccessible resources.

Although the flight of birds seems almost magical, many of the underlying physical properties of flight are reasonably well understood. Some of this knowledge comes from studies of birds themselves, but much of the underlying theory derives from the field of fluid dynamics, and from discoveries made by human engineers as they designed airfoils for the wings of aircraft and the propeller blades of helicopters. Contemporary research into the biomechanics of bird flight involves the development of new techniques for measuring the flight performance of birds, making it ever more feasible to study birds' evolutionary solutions to the many physical challenges of flight.

The evolution of powered, flapping flight in birds has influenced nearly all aspects of avian biology, including internal and external anatomy (Chapters 4 and 6), physiology (Chapter 7), foraging behavior (Chapter 8), and the ecology of avian movements (Chapter 12). In this chapter, we focus on the biomechanics of flight itself. First, we explore the aerodynamics of flight, beginning with the forces of lift and drag. We then turn to how birds power their flight: how the flight muscles generate power and how power demands vary with flight speed. Finally, we investigate interactions between flight styles and avian behavior.

5.1 Aerodynamics

How does a bird counteract the force of gravity, lift off from the ground, and stay aloft while flying? Understanding this phenomenon requires a consideration of the basic physics of the forces produced by air flowing over the surface of a bird's wing.

5.1.1 Airflow over a wing produces lift

Birds are able to fly because their wings have evolved into a particular shape that produces **lift** when air flows around them. Understanding lift requires a consideration of the various factors that act as a bird moves through the air. When air hits the leading edge of a wing, the air is deflected from its original path (Fig. 5.01). This incoming air has velocity relative to the surface of the wing created by a combination of the movement of the air itself—in other words, by wind—and by the movement of the bird through

Lift: the force acting on a moving airfoil (such as a bird's wing) perpendicular to the direction of airflow.

Opposite: Hummingbirds are among the most agile flyers. This Lazuline Sabrewing (*Campylopterus falcatus*) and all other hummingbird species can hover thanks to various skeletal and morphological adaptations. (Photograph by Murray Cooper.)

Handbook of Bird Biology, Third Edition. Edited by Irby J. Lovette and John W. Fitzpatrick.
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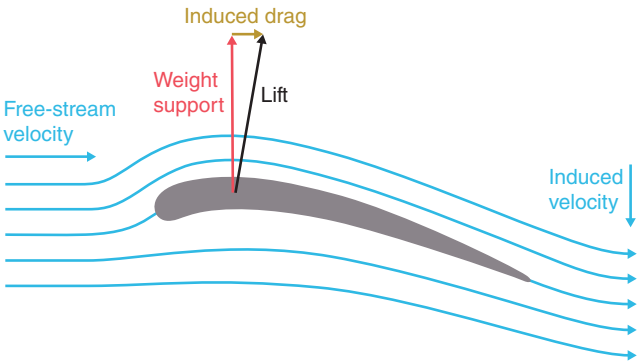


Fig. 5.01 Origin of wing lift. When free-stream velocity is horizontal, the wing induces a downward vertical velocity onto the oncoming air. Lift is perpendicular to the net velocity (free-stream + induced); induced drag tilts the net lift slightly backward. (© Cornell Lab of Ornithology.)

Box 5.01 The physics of pressure

The static and dynamic pressures exerted on a bird's body and wings are related to one another and to the velocity that the bird is moving through the air. The Bernoulli equation can be written as:

$$p + \frac{pv^2}{2} = \text{constant}$$

The first term p is static pressure and the second term $(pv^2)/2$ is dynamic pressure. The sum of these two terms is always the same at a given altitude (air pressure); they trade off with one another depending on the velocity by which air moves over the surface of the bird. Thus, as air velocity (v) increases, dynamic pressure increases and static pressure decreases.

the air. You can feel some of these same forces yourself when you put your hand (carefully) out of the window of a moving vehicle.

In physics courses, students learn that velocity can be represented as a "vector quantity," a value that has both a magnitude and a direction. By directing incoming air onto a new path, bird wings change the air's direction and velocity. Newton's Second Law of Motion describes how force equals mass multiplied by acceleration (a change in velocity over time). In the case of a flying bird, the mass of air that is accelerated by the wings is equal to a force. We next need to consider how that force is directed to keep the bird in the air. Newton's Third Law of Motion dictates that the magnitude of this force is equal and opposite to the force that the air exerts upon the wings of the bird. Thus as the bird's wings accelerate the air, the air accelerates the entire bird upwards, and we identify the force involved as lift.

This is the most basic theoretical level by which air moving over a bird's wing can create lift. However, the real world is far more complex than this simple model, so a more comprehensive description of the factors involved in producing the lift must also consider the many aspects of the air surrounding the wing. We begin with a description of the pressure distribution about the wing as air flows past it, in part so that we can explore how lift is only one component of the total force acting on a wing.

We do not often think of air as a fluid, but as far as the physics of bird flight are concerned, air acts as one—just a fluid that is far less dense and less viscous than more familiar fluids like water. Whenever a fluid and a solid object come into contact, force generated by the bombardment of the fluid's molecules against the object's surface is distributed as pressure. The still air all around us exerts pressure on every surface that is exposed to the atmosphere, and this force is what meteorologists measure with a barometer. The atmospheric air pressure decreases with elevation above sea level, and it also varies with weather conditions.

In contrast, **dynamic pressure** arises when the air (or fluid) is in motion. We can feel the dynamic pressure of air when we put our hand out a car window or stand outside on a windy day. The faster the airflow, the more dynamic pressure it will exert on an object. In fact, the dynamic pressure increases rapidly with increasing airflow: it is proportional to the square of the velocity of the air. The Bernoulli equation (Box 5.01) describes how static and dynamic pressures are related: as air velocity over a solid object increases, the dynamic pressure increases and the static pressure on the surface of the object decreases.

Any suitably shaped object, even a flat plate, can produce lift if held at an appropriate angle relative to the flow of passing air. Wings are especially good at generating lift because they have an **airfoil** shape, which causes differences in pressure between their upper and lower surfaces. When air flows over a wing, the shape of the wing deflects the air and causes changes in its velocity. Because pressure below the wing is higher than pressure above it, the wing is pushed upwards and lifts into the air.

Another way to visualize the flow of air over a wing producing lift is to consider the circulation of air around a

Dynamic pressure: the pressure of a flowing fluid, or of movement through a fluid such as air or water. You feel dynamic pressure when wind blows against your face.

Airfoil: a suitably shaped object—such as an airplane wing or bird wing—that creates lift when placed in a current of flowing air.

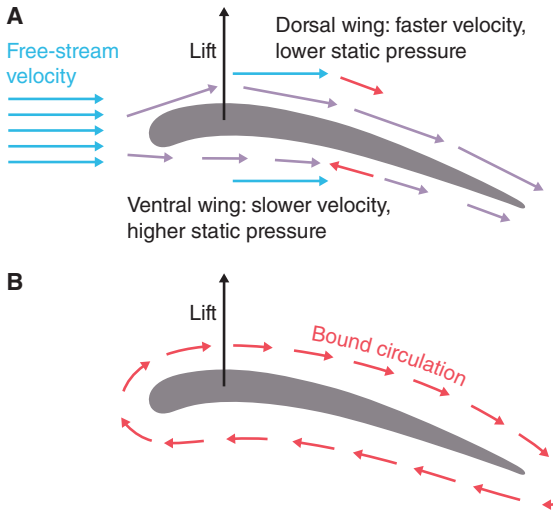


Fig. 5.02 Bound circulation on a wing. (A) Velocity distribution in the upper and lower wing flow-field, with free-stream velocity shown in blue and local velocity in purple. Red arrows represent the component left over when free-stream (translational) velocity is subtracted from local flow. (B) This pattern of flow around the surface of the wing is called the bound circulation. (© Cornell Lab of Ornithology.)

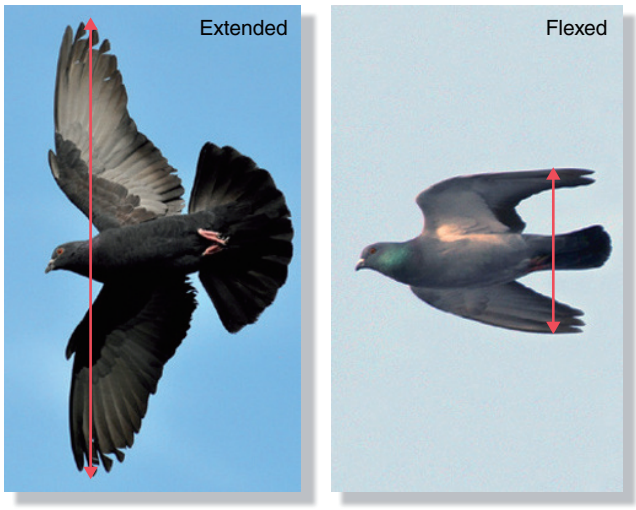


Fig. 5.03 Wingspan and lift. During flight, birds adjust their wingspans (the distance between the wingtips) to alter the degree of lift. These Rock Pigeons (*Columba livia*) extend their wings to generate a high degree of lift, and flex their wings to reduce it. (Photographs by: left, Miriam Wohlgemuth; right, David Wheeler.)

cross-section of the wing (Fig. 5.02). The shape of an airfoil causes the local flow of air to have a higher velocity over the upper surface of the wing than below the wing. This difference in velocity generates lift.

5.1.2 Modulating lift

Birds have many ways to vary the lift that they produce with their wings. Lift is a direct function of the overall length of the wings, so perhaps the simplest factor to consider is overall **wingspan**, or distance between wingtips. Individual birds can control their wingspans by extending or flexing their wings (Fig. 5.03). The images shown in Figure 5.03 are views of a pigeon in **gliding flight**; for a given glide speed, lift is greater when the bird has its wings maximally extended than when the bird flexes its wings. Wingspan varies even more among different species and groups of birds. Birds well adapted to soaring—like vultures, condors, frigatebirds, and albatrosses—have particularly long wingspans, since soaring requires the particularly efficient generation of lift.

Wingspan: the distance between the tips of the fully extended wings of a living bird.

Gliding flight: unpowered flight, as in birds that are flying without flapping their wings.

The next two mechanisms to consider affect the circulation of air around the wing. The first is **camber**, which is a measure of the curvature of the wing (Fig. 5.04). A wing with greater camber produces more circulation than a wing with lower (or no) camber. For example, the wings of many pheasants and their relatives are highly arched (cambered), and these birds usually must flap their wings very quickly while flying. This action is consistent with their need to produce

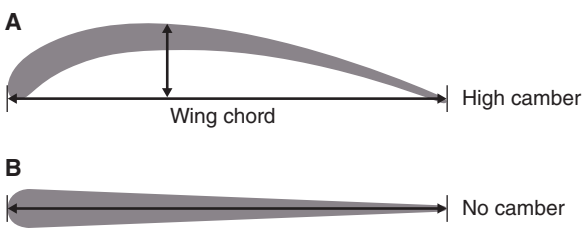


Fig. 5.04 Camber and lift. (A) Grouse and similar birds have wings with high camber, or curvature (vertical arrows). Curved wings generate considerable lift, but at a high cost in terms of drag. (B) In contrast, birds like swifts have flatter wings; although not well suited for self-powered takeoff, wings with low camber offer impressive lift-to-drag ratios during gliding and forward-cruising flight. In both schematics the wing chord—the distance between the leading and trailing edge of an airfoil—is depicted with horizontal arrows. (© Cornell Lab of Ornithology.)

Camber: the curvature of the wing as seen through a cross-section; highly cambered wings are more arched and therefore the upper and lower surfaces are less symmetrical.

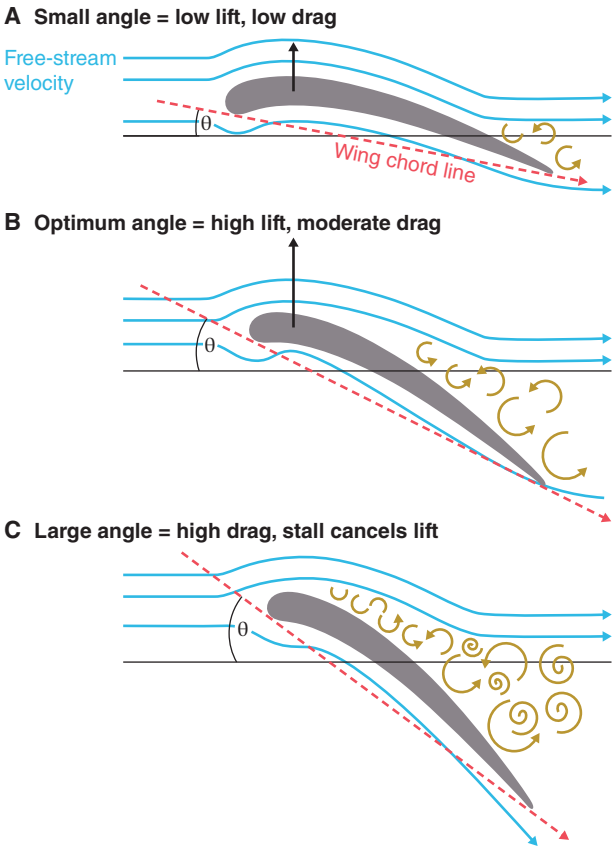


Fig. 5.05 Angle of attack in relation to flight. The angle of attack (Θ) describes the position of the wing chord (red dotted line) relative to incoming, free-stream air (blue lines). (A) When this angle is small, minimal lift is generated with almost no drag on the wings. (B) As the angle increases, air separates from the dorsal wing in a higher location, creating more drag (yellow arrows). However, an optimal wing angle generates considerably more lift, canceling out the drag and enabling efficient production of upward force. (C) When angles of attack are too large, drag overcomes the wing's lift-generating force and hinders flight. (© Cornell Lab of Ornithology.)

high lift, because these birds use their wings almost exclusively for burst takeoff and short duration flights to escape from predators. Within limits imposed by the overall shapes of their wings, all birds can control camber using their wing muscles.

Also, using their forelimb muscles, birds can adjust an important variable termed the **angle of attack**. In essence, the angle of attack has to do with the way the chord of the wing (the imaginary line running from the leading edge of a wing to its trailing edge, Fig. 5.04) is rotated relative to the incoming flow of air (Fig. 5.05). As the front edge of a bird's wing rotates upward against the incoming air, the angle of attack increases. Lift increases along with angle of attack up to a point, but decreases at very high angles of attack. When high angles of attack result in the loss of lift, we call this a "stall."

Angle of attack: in a flying bird, the angle between the main surface of the wing and the oncoming airstream.



Fig. 5.06 Wing loading. With the largest wing area relative to its body mass, the Magnificent Frigatebird (*Fregata magnificens*) holds the record for lowest wing load. Able to generate high lift over a broad range of conditions, this species is effective at taking off and landing, carrying heavy food items, and maneuvering to steal food from other flying birds. (Photograph by Brendan Ryan.)

Remarkably, birds have evolved a mechanism to deal with high angles of attack at low speeds through the **alula**, which helps to regulate airflow over the upper wing surface. In general, however, optimal lift is generated at an intermediate angle of attack, with the exact angle of greatest lift depending somewhat on the shape and orientation of each bird's wing.

Finally, for a given amount of circulation and wingspan, lift varies with the velocity of the air as it passes over and around the wing. The relationship between lift and velocity is exponential: lift is proportional to translational velocity squared. Later in this chapter we will learn that birds can exploit this relationship in at least two ways: they can fly into a headwind to increase the air velocity over their wings and thereby increase lift, or they can flap their wings—in a sense, creating their own wind—to increase the velocity of the air passing over them. Furthermore, for a given body mass, a bird with a greater area of wing surface will produce more lift. The Magnificent Frigatebird (*Fregata magnificens*) holds the record among living birds for having the greatest wing area relative to its body weight; therefore, this species has the greatest ratio of lift generation (Fig. 5.06).

5.1.3 Forms of drag

Another consequence of the fluid behavior of air is that a flying bird experiences **drag** from the surrounding air. Three forms of drag act on a bird: induced drag decreases

Alula: the small "thumb" of a bird's wing that bears three to five small, asymmetrical flight feathers.

Drag: a force on a moving object that opposes the direction of travel of the object through a fluid (such as air). Induced drag comes from accelerating air to produce lift; pressure and friction drag are due to air colliding with and moving past the object.

as flight speed increases, whereas pressure drag and friction drag increase with the square of velocity in the same manner as lift.

Induced drag can be thought of as a direct cost of producing lift. Induced drag results from the pressure differences between the upper and lower surfaces of the bird's wing as it is passing through the air. In situations where the wing is producing lift, the air pressure near its upper surface tends to be lower than the air pressure near its lower surface. Accordingly, some air leaks around the edges of the wing, following this pressure gradient. This air movement breaks up the smooth airflow around the wing's surface, generating small and unstable swirls of air (vortices), especially at the trailing edge of the wing and near the wingtips. Induced drag is a result of the pressure that these vortices exert on the wing. Induced drag can be reduced by adaptions in the shape of a bird's wing; for example, the wide spaces between the outer primaries of a Bald Eagle (*Haliaeetus leucocephalus*) and other large soaring birds, help reduce the formation of the vortices that cause induced drag (Fig. 5.07).

Another way to think of induced drag is the cost of accelerating air downward as lift is produced. The downward airflow is called induced velocity. This downward flow alters the overall pattern of airflow around the wing, creating some airflow that opposes the direction of travel. Thus, the resulting force is drag (Fig. 5.01). Induced drag is very high during hovering and slow flight because a bird's wings only intercept the air swept by the wings, providing a relatively large acceleration to a small mass of air. As a bird flies faster, the wings intercept more air, and only a moderate acceleration of a greater mass of air is necessary for the bird to remain aloft. Therefore, induced drag is less.

The other two forms of drag are caused by the interaction of body surfaces with moving air. Pressure drag arises when solid objects—in this case the wings and body of the bird—displace the air, creating a higher pressure on the front of the moving surface than on its rear. One way of thinking about pressure drag is to imagine air molecules slamming into the front of the flying bird. Friction drag is caused by the adhesion of air molecules to the surface of the bird and the cohesion (viscosity or "stickiness") that air molecules have for each other. At the microscopic surface of the moving bird, the velocity of the air is zero. This is called the "no-slip" condition. The air in adjacent layers of the airflow near this no-slip layer is slowed owing to its viscosity. Because this deceleration right at the surface of the bird robs the air of momentum, friction drag also opposes forward motion of the bird.

5.1.4 Effects of wing and tail shape

Both lift and drag vary with total wing area, but it is the shape of the wing that determines the ratio of these two forces. **Aspect ratio** is defined as the wingspan divided by the average wing chord, or as the square of the wingspan divided by wing area. It can be thought of as a measure of overall wing pointiness. Aspect ratio is a useful way of summarizing how the variation in wing shape contributes to the variation in flight styles of many birds. For example, birds like albatrosses and frigatebirds, which use dynamic soaring, typically have long wings with high aspect ratios that maximize lift while minimizing drag (Fig. 5.08A). In contrast, many songbirds have shorter wings with lower aspect ratios, helpful when maneuvering through tight environments and for quick takeoffs (Fig. 5.08B). Because the calculation of aspect ratio involves one linear measurement (usually wingspan squared, in centimeters) that is divided by another with the same units (usually wing area, in centimeters), the units cancel out, resulting in a so-called "dimensionless number." This quality of aspect ratio measurements is useful because it describes wing shape independently of a



Fig. 5.07 Induced drag. Bald Eagles (*Haliaeetus leucocephalus*) and other large soaring birds spread their flight feathers to create slots between the feather tips. These slots increase the effective lift-producing part of the wing surface by horizontally and dispersing wingtip vortices, which could otherwise create induced drag. (Photograph by William Jobes.)

Aspect ratio: the ratio of an object's length to its width. In birds, it refers to the shape of the wing: birds with higher aspect ratios generally have more pointed wings.

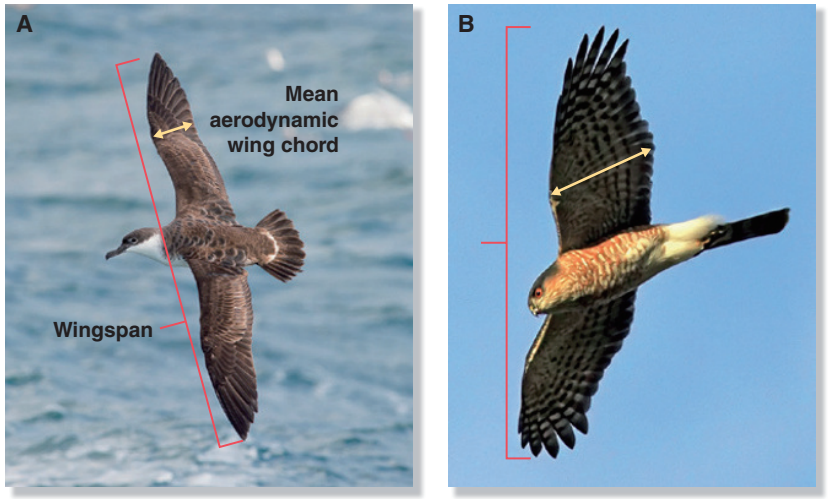


Fig. 5.08 Wing aspect ratio. Aspect ratio is the wingspan (red brackets) divided by average width (yellow arrows) (shown here by the mean wing chord). (A) Birds with long, slender wings—like this Great Shearwater (*Ardenna gravis*)—have a high aspect ratio, providing greater efficiency via a high lift-to-drag ratio—thus requiring less energy for flight. (B) For Sharp-shinned Hawks (*Accipiter striatus*) and other species with shorter, wider wings (and therefore a low aspect ratio), flight efficiency is traded for maneuverability and rapid takeoff. Note that aspect ratio is important to consider in tandem with wing loading, as the mass of the bird will also influence flight performance. (Photographs by: A, Ray Hennessy; B, Beth Hamel.)

bird's body size, making aspect ratios a useful way to compare the aerodynamic abilities of different kinds of birds.

In fast flight, for a given surface area, a wing with a higher aspect ratio will exhibit a higher lift-to-drag ratio than a wing of lower aspect ratio. The primary reason for this difference is that longer wings experience lower induced drag, since swirling air vortices that form at the ends of the wings affect proportionally less of the total wing surface when a bird has long, thin wings, and since the longer wings interact with a greater mass of air and give it a proportionally smaller acceleration compared with wings of lower aspect ratio.

We commonly think of the wings as the sole generators of lift for a flying bird. The body and tail regions generate some drag that resists a bird's forward motion, but it turns out that these parts of the bird may also provide some lift on their own. Studies of small birds that fly in undulating paths have been used to explore the aerodynamics of the tail and body acting in isolation, without the lift added by the wings. This is possible because these birds typically hold their wings close to their bodies during the non-flapping parts of this cycle. These studies reveal that the body and tail alone can have a lift-to-drag ratio of up to 1.2 and can support up to 15% of bird's body weight (Tobalske et al. 2009).

After the wings, the tails of many birds are the most important generators of aerodynamic forces. Modeling studies have suggested that the highest lift-to-drag ratio is generated by tails that are slightly forked when folded, and triangular when fanned (Thomas 1993) (Fig. 5.09A). Departures from this optimum shape are often due to sexual selection pressures (Chapter 3), as seen in the highly elongated tails of species like the Streamertail (*Trochilus polytmus*) hummingbird of Jamaica, the Streamer-tailed Tyrant (*Gubernetes yetapa*) of southern South America, or Reeve's Pheasant (*Syrmaticus reevesii*) of China (Fig. 5.09B).

The tail may reduce pressure drag on the body by functioning as a structure termed a splitter plate (Fig. 5.10), a rearward-facing projection that directs airflow around the back of the bird's body in such a way that the air velocity

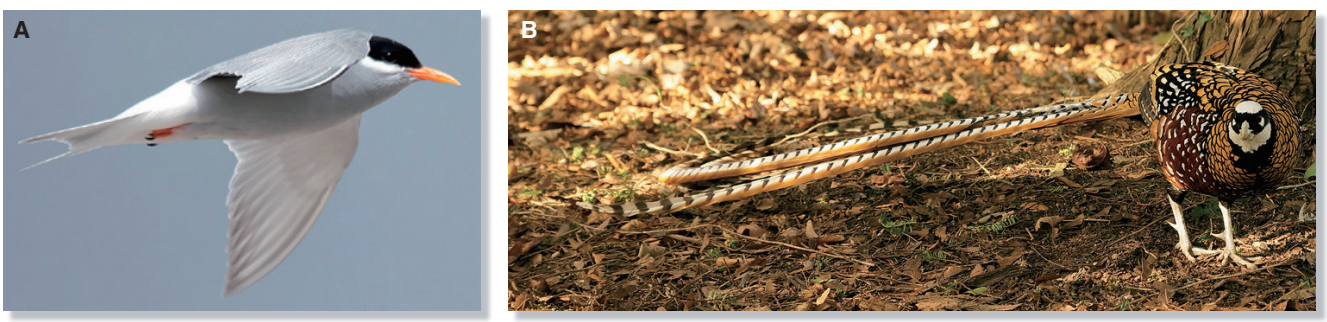


Fig. 5.09 Ideal lift-generating tails and departures from the optimum. (A) This Black-fronted Tern (*Chlidonias albostriatus*) has an aerodynamic, lift-generating tail that helps it float on ocean winds with minimal energetic cost. (B) In contrast, the elaborate, exaggerated tail of Reeve's Pheasant (*Syrmaticus reevesii*) has evolved as a mate-attracting ornament via sexual selection. Flight with this tail is suboptimal at best. (Photographs by: A, Glenda Rees, www.flickr.com/photos/nzsamphotofanatic; B, Peter Carr.)

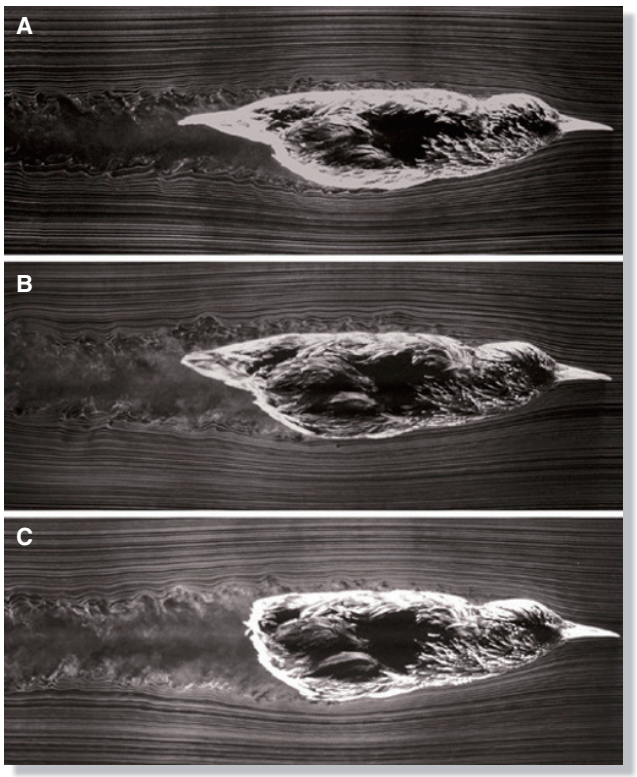


Fig. 5.10 Evidence that tails reduce pressure drag. These images depict the drag vortices around and behind European Starling (*Sturnus vulgaris*) specimens in a wind tunnel. (A) An intact tail, functioning as a splitter plate, creates a narrow diameter, turbulent wake. (B) Removing the tail feathers results in a larger diameter wake, creating significantly more drag. (C) Tailless birds create even greater wakes and associated drag. (From Maybury and Rayner 2001. Reproduced with permission from the Royal Society.)

changes more gradually as it moves caudally, dynamic pressure remains lower, and static pressure is relatively higher (Maybury and Rayner 2001). All of these factors help reduce the width of the wake behind the bird, which thereby reduces drag.

5.2 Power for flight

Only three groups of vertebrates have ever evolved self-powered flight using flapping wings: birds, bats, and the extinct pterosaurs. Active flying requires both lift to keep the animal aloft and thrust to allow it to move forward through the air. Birds often take advantage of wind to move air across their wings while flying, but more often they power their own forward movement by flapping their wings. Although there are some commonalities in flapping styles shared by all flying birds, birds with different shapes have modified their flying styles in various ways to match their ecological requirements.

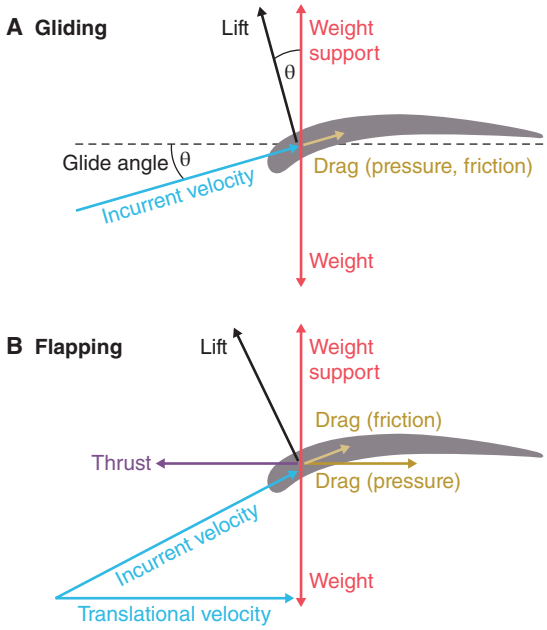


Fig. 5.11 Force balance during flight. (A) During gliding, the wings produce enough lift to provide weight support. However, a gliding bird will descend at a specific angle determined by its total lift-to-drag ratio. (B) While flapping, the generated velocity adds to the horizontal translational velocity so that lift inclines forward. Lift thereby contributes to weight support and thrust, helping overcome pressure and friction drag on the wings and body. Induced velocity is not shown. (© Cornell Lab of Ornithology.)

5.2.1 Flapping and thrust

During steady gliding, a bird produces lift mostly with its wings and experiences drag on its whole body. This lift is sufficient to support the bird's weight; however, when there is no force present to counterbalance the drag, a gliding bird gradually descends. In doing so, it trades a loss in altitude to maintain its forward motion, which in turn is necessary to generate lift. The **glide angle**—the angle at which the bird descends—is inversely related to its lift-to-drag ratio (Fig. 5.11A). This makes intuitive sense: all else being equal, a bird experiencing less lift or more drag will descend more rapidly.

Active flapping contributes **thrust** to overcome drag so that a bird can increase in altitude or maintain a level flight path. A bird flapping its wings experiences two kinds of velocity relative to the air through which it is flying (Fig. 5.11B). First, the entire bird is moving forward; this

Glide angle: the angle at which a gliding bird descends through the air.

Thrust: in a bird, the portion of the force generated by the flapping wings that propels the bird forward.

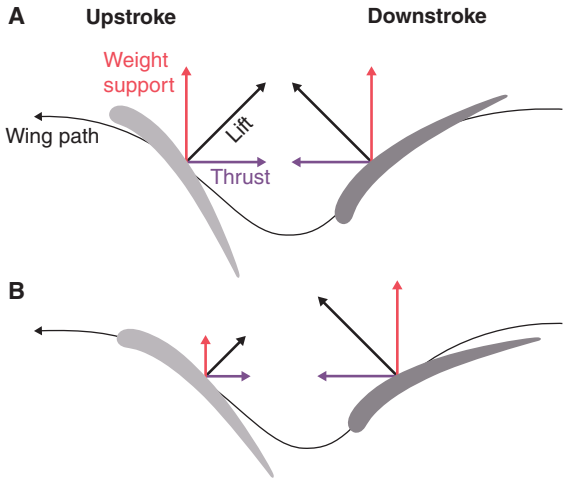


Fig. 5.12 Producing net positive thrust during forward flapping flight. (A) Hypothetically, in symmetrical wing flapping, the forward thrust of the upstroke would cancel out the rearward thrust of the downstroke. (B) Birds use asymmetrical flapping to overcome the upstroke problem, rendering weight support continuous with a net positive thrust. (© Cornell Lab of Ornithology.)

velocity of the bird relative to the surrounding air is termed translational velocity. Second, wing flapping also generates an additional force termed flapping velocity. These velocities add together to give an incurrent velocity of the air relative to the wing. The lift experienced by the bird acts perpendicularly to this incurrent velocity; the vertical component of lift provides weight support for the flying bird, and the horizontal component provides its forward movement (or thrust). When thrust matches the horizontal component of drag, the bird is able to maintain a steady horizontal flight speed.

This description works well for the downstroke of the wing during a single flap, but a potential problem emerges when one considers the upstroke. If the upstroke was executed in a manner that exactly mirrored the downstroke—with the same velocity, angle of attack, and, hence, circulation—the bird could support its weight throughout the wingbeat, but it would produce a forward thrust during the upstroke that would cancel the rearward thrust produced during the downstroke (Fig. 5.12A). Thus, there would be no means of producing an overall positive forward thrust to overcome drag.

Birds usually solve this problem by changing the shape, speed, and orientation of their wings to produce less force during the upstroke than during the downstroke (Fig. 5.12B). To reduce lift production, birds may flex their wings, decrease their angle of attack, reduce wing camber, or reduce flapping velocity. Although downstroke wing motions are relatively invariant among many birds, these patterns of upstroke movements differ among species. In birds that have pointed wings with a relatively high aspect ratio, such as pigeons, the mid-upstroke posture changes as a function of flight speed. During slow flight, these birds rotate their wings and hold them extended in what is known as a "tip-reversal" upstroke, which may represent a simple recovery stroke or may provide some lift. As flight speed increases, they shift gradually to a flatter wing posture during upstroke, with wing flexion increasing as flight speed increases. The flight posture at intermediate speed is called "feathered," and in fast flight it is called "flexed." In contrast, birds with relatively rounded wings with a low aspect ratio tend to adopt a flexed wing posture during upstroke, regardless of their flight speed.

These alternative strategies give rise to wing-flapping patterns that differ among birds with high aspect ratio wings and birds with low aspect ratio wings. In birds with high aspect ratio wings, flight speed determines flapping pattern. In slow flight, wingtips trace a figure-of-eight pattern when viewed from the side (lateral view) (Fig. 5.13A). The arc of their flapping wings—the distance they move up and down—is greatest during slow flight. In faster flight, the wingtips and wrists track an elliptical path. These features are typical of birds with high aspect ratio wings. In contrast, in birds with lower aspect ratio wings, the wingtip path is elliptical regardless of flight speed, and the wings are drawn close to the body during the upstroke (Fig. 5.13B).

Birds like swifts—which do not flex their wings during the upstroke—have a different solution for generating forward thrust while flapping (Fig. 5.14). With an overall lift-to-drag ratio of 13:1, swifts in gliding flight are among the most aerodynamically efficient birds known (Henningsson and Hedenström 2011). In these rapidly flying species, small and continuous changes in circulation during downstroke and upstroke give rise to their overall weight support and forward thrust. As they flap, these birds make subtle changes that vary the angle of attack, velocity, or camber of the wings in order to vary the pattern of airflow over their surfaces.

5.2.2 Hovering

Hovering is a special case in which flapping wings direct thrust downward to provide lift. Many kinds of small birds may hover briefly, but hummingbirds are unique in their ability to sustain a hover in otherwise still air. The primary aerodynamic challenge in hovering is that there is no forward movement to generate airflow over the wing. Instead, while hovering, a bird's pectoralis and supracoracoideus muscles (Chapter 6) must supply most of the power necessary to move air across its wings. In contrast, during forward flight, or when larger species hover against a headwind, a portion of the air velocity necessary for producing lift is provided by the movement of the surrounding air relative to the bird.

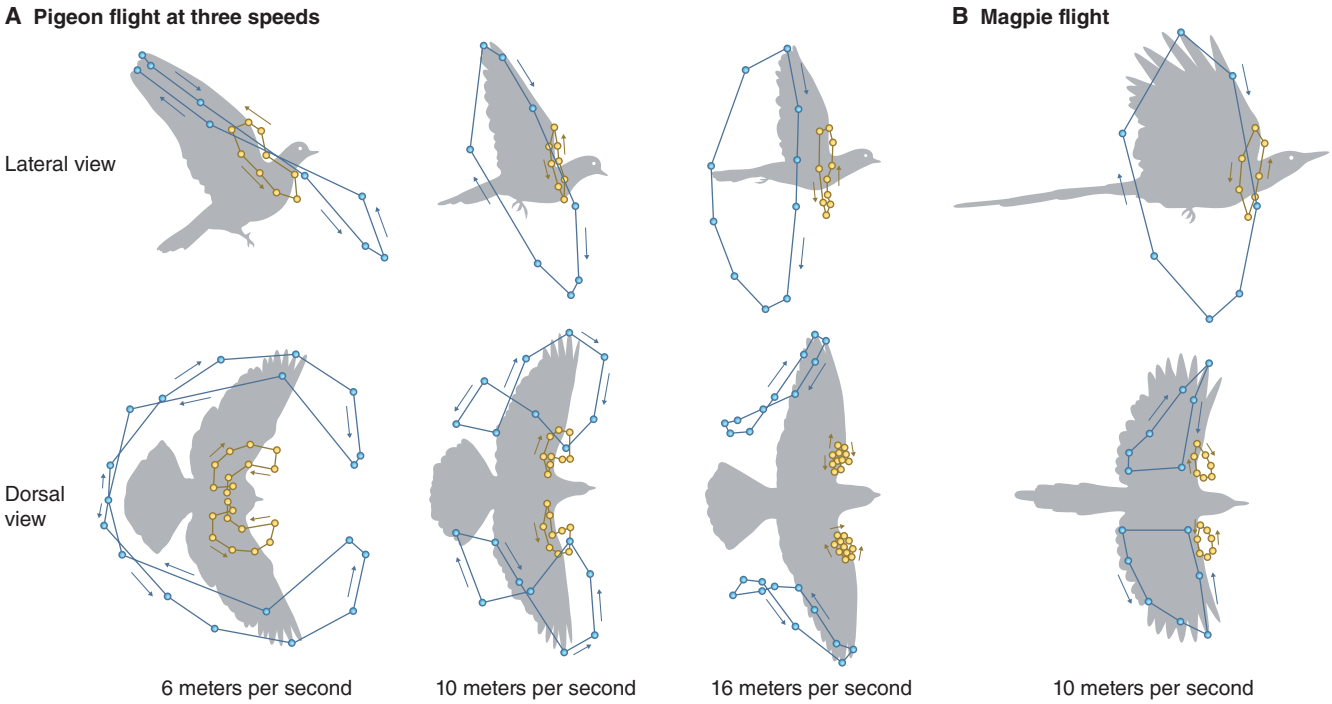


Fig. 5.13 Wingbeat motions. Wingbeat trajectories of the wingtips (blue dots) and wrists (yellow dots) depend on the aspect ratio of the wings. (A) Rock Pigeons (*Columba livia*) have relatively pointed wings with high aspect ratios; paths differ depending on flight speed. (B) Since Black-billed Magpies (*Pica pica*) have more rounded wings with lower aspect ratios, their wingtip paths are nearly identical regardless of flight velocity. (Courtesy of Bret Tobalske.)



Fig. 5.14 Agile and efficient flight. Swifts, such as this Alpine Swift (*Apus melba*), make subtle modifications to wing camber and angle of attack as they fly rapidly and efficiently through the air. (Photograph by Isolino Peréz Tuya.)

A hummingbird's hovering is remarkably similar to the flight style of some insects, but hovering flight also has some of the features of slow flight in larger bird species that have pointed, high aspect ratio wings. Hummingbirds do not flex their wings during the upstroke; tracing the path of their stroke cycle reveals that the upstroke reverses the downstroke trajectory (Fig. 5.15). From a side view, their wingtips and wrists trace a figure-of-eight pattern that resembles the path used by other pointed-wing bird species during slow flight (Fig. 5.13A). During the upstroke, hummingbirds rotate the outer part of their wing in a manner akin to the tip-reversal upstroke of other bird species with pointed wings, but in hummingbirds almost the entire wing turns over.

Another commonality between hovering in hummingbirds and slow flight in other birds is that the large induced velocity and high angle of attack, required in both of these modes, leads to high induced and pressure drag. As a result, the best lift-to-drag ratios during these kinds of flight are only in the 2:1 range, considerably lower than the ratios generated by birds in faster gliding flight. In this context of low lift-to-drag wing performance, the hovering ability of hummingbirds is particularly remarkable; this difference also helps underline the wonderful aerodynamic efficiency of forward flight by larger flapping birds. In contrast, the goal of a bird during hovering or slow flight may be better thought of as efficacy: pushing the envelope of these demanding flight styles to gain control in takeoffs and landings, escape from predators, access to hard to reach yet energetically rich food, or display to potential mates.

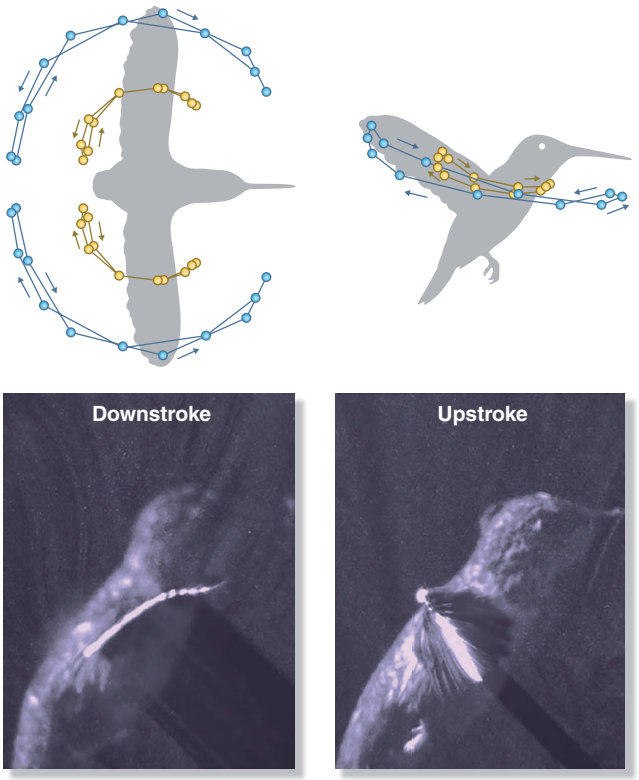


Fig. 5.15 Hovering kinematics in hummingbirds. Wingtip (blue dots) and wrist (yellow dots) paths track a figure-of-eight pattern when viewed laterally and a large circular area in dorsal view. In hummingbirds, wing posture is cambered in the downstroke and twisted so that the ventral (underside) faces up in the upstroke. (Courtesy of Bret Tobalske.)

5.2.3 Power requirements for flying birds

Of all the various forms of animal locomotion, self-powered flight is the most demanding in terms of its energy cost per unit of time, or **aerodynamic power**. However, the total cost of transport through the air—that is, the energy required per unit of distance traveled—is often quite low. During flapping, a bird produces power to provide lift and forward thrust. We can estimate the total aerodynamic power required for steady flight by determining the total amount of drag acting on the bird when it is flying at that velocity.

Mathematical models that estimate the aerodynamic power of birds were initially developed using approaches borrowed from studies of fixed-wing aircraft, and then later expanded to incorporate some of the ways birds have evolved to flex their wings and bodies during flapping flight. The characteristic feature of the relationship that emerges from all of these models is that aerodynamic power varies with flight speed as an upwardly parabolic curve (Pennycuick 1975; Rayner 1999) (Fig. 5.16). Two points on this curve are of particular interest because they lead to predictions about how birds might optimize their flight behavior. The lowest aerodynamic power is obtained at an intermediate speed, referred to as **minimum power speed**. Birds should fly at this speed if their goal is to stay in the air for as long as possible for a given energy expenditure. An example might be a raptor slowly coursing over a field while it searches for small mammals. The greatest efficiency per unit of distance traveled is obtained at the **maximum range speed**. Birds should fly at this speed when they are trying to maximize flight distance. An example might be a long-distance migrant that must fly for several days between locations that are thousands of kilometers apart.

Scientific studies regarding the mechanical power output of the pectoralis, or main avian flight muscles (Chapter 6), support the prediction that the aerodynamic power curve is U-shaped. The shape of the curve and estimates of minimum-power speed and maximum-range speed differ among bird species (Fig. 5.17), due to differences in morphology (such as

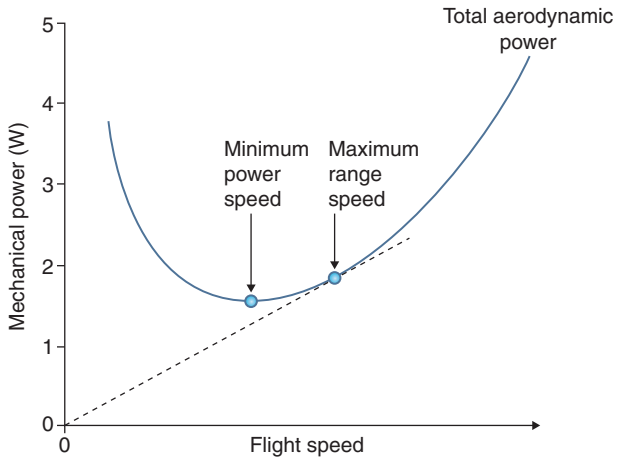


Fig. 5.16 Mechanical power requirements as a function of flight velocity. Minimum power speed occurs at the bottom of this curve, at an intermediate flight speed. Maximum range speed is the point on the curve that provides the most efficient flight distance for the amount of energy expended. (Adapted from Rayner 1995. Reproduced with permission from Elsevier and Jeremy Rayner.)

Aerodynamic power: for birds, the total power required to match the various forms of drag and thereby maintain flight.

Minimum power speed: the flight speed that maximizes time in the air for a given amount of energy.

Maximum range speed: the flight speed that maximizes the distance traveled for a given amount of energy.

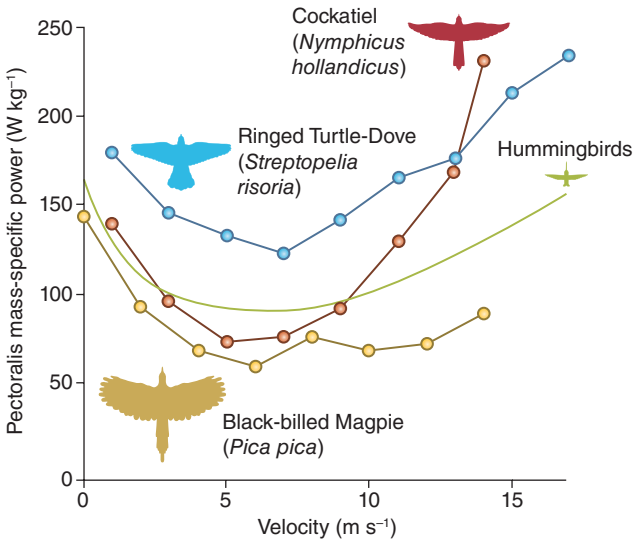


Fig. 5.17 Mechanical power varies among species. Power curves, which measure the mechanical output of the flight muscles, vary across bird groups, owing to differences in morphology, flight style, and kinematics. Virtually all birds lack the mass-specific power to hover at low velocities for long periods. However, hummingbirds have an exceptional aerobic capacity to sustain high mass-specific power. (From Warwick et al. 2012. Data from Clark and Dudley 2010, Tobalske et al. 2003, and Dial et al. 1997. Reproduced with permission from Elsevier.)

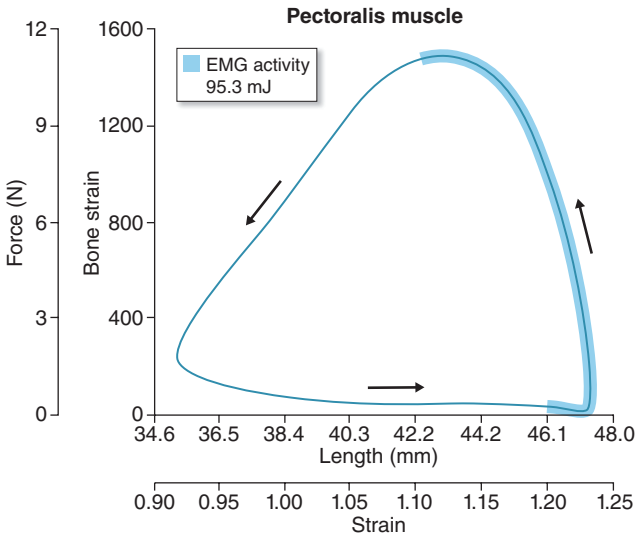


Fig. 5.18 Direct measure of mechanical work and power in pectoral flight muscle. Muscle force as a function of muscle length during one wingbeat. The area inside the loop is the net positive pectoral muscle work output. Arrows show the direction of one cycle with the shaded region showing when the pectoral muscle is active. (Adapted from Tobalske et al. 2003. Reproduced with permission from Macmillan Publishers Ltd.)

the aspect ratio of their wings) and flight style. Such studies have measured the contractile velocity and force production of the muscle itself in live birds with surgically implanted sensors. These sensors are placed into the muscle so that they move closer together when the muscle shortens and farther apart when the muscle lengthens. The time required for sound transmission between the sensors can then give a measure of the muscle's changing length as it contracts and relaxes. Similarly, a strain gauge attached to the humerus bone can measure the deformation of its shape in response to the contractions of the pectoral muscles during flight; the surface of the bone changes in length (strains) when the muscle contracts, and the strain gauge measures this bending. Finally, researchers use electrodes implanted in pectoral muscles to measure when the muscle is activated by the nervous system.

The results of these various measurements of flight muscle activity can be plotted as a work loop, where the area inside the loop represents the work done by the muscle during a single contraction (Fig. 5.18). Dividing this work by the duration of the wingbeat provides power output. Such studies have demonstrated that the pectoralis muscle of flying birds undergoes a proportionally large change in length (strain) during contraction—up to 30–40% of the resting length of the muscle in birds such as a pigeon—to meet the work and power requirements for flight (Jackson et al. 2011).

Although this pattern of mechanical power output is relevant to understanding the aerodynamics of avian flight, what matters more to a bird is its use of chemical energy, or metabolic power input to the muscles. The shape of power curves and predictions about optimal flight speeds like minimum-power speed and maximum-range speed can be altered substantially by the efficiency at which metabolic energy input to the muscles is converted into mechanical power output from the muscles. As described in Chapter 7, the overall metabolic rates of birds over days or weeks are often easy to measure. It is methodologically more challenging to determine the amount of energy used over short periods by birds flying at different speeds. One approach scientists have utilized is to fly live birds in wind tunnels while measuring the amount of oxygen they metabolize as a proxy for their energy consumption (Fig. 5.19A).

Early measurements of the metabolic demands of flying birds were somewhat surprising, with most species demonstrating relatively flat curves that suggested their muscles were least efficient at converting energy into mechanical power at the birds' intermediate (and preferred) flight speeds. However, obtaining these same measurements at the extremes of the range of speeds at which a bird can fly is particularly challenging in wind tunnel experiments. Further studies over a wider range of speeds generally support this trend—that power varies as a U-shaped curve with flight speed (Fig. 5.19B).

Flapping flight has an additional efficiency advantage, as it facilitates some energy storage and recovery between successive flaps. Like a bouncing rubber ball that returns some potential energy (height) after being dropped, the recovery of energy represents a cost savings that otherwise would be lost to the environment. In European Starlings (*Sturnus vulgaris*), for example, the furcula (wishbone) is

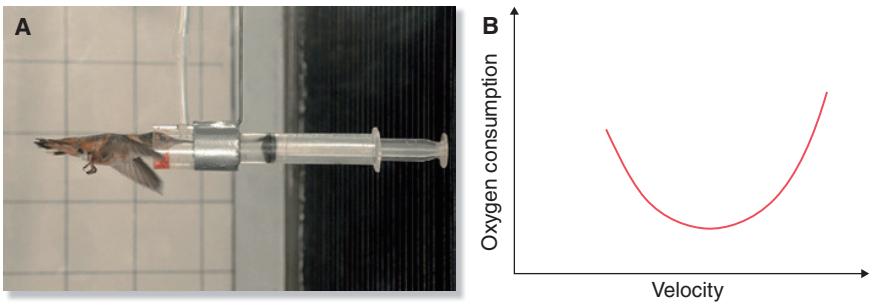


Fig. 5.19 Metabolic power requirements determined by gas respirometry. (A) Hummingbirds and other bird species can be trained to visit feeders equipped with sensors that determine oxygen consumption, a measure of aerobic metabolism. (B) Oxygen consumption is assumed to be directly proportional to power, and varies as a U-shaped curve with velocity. The graph here depicts the change in oxygen consumption of a medium-sized bird flying at different velocities. (A, photograph by Donald R. Powers. B, © Cornell Lab of Ornithology.)

stretched—loaded with strain energy—by the pectoralis muscle during downstroke, and the recoil of the furcula transfers energy that helps power the next upstroke as well as breathing (Jenkins et al. 1988). Additionally, the primary upstroke muscle, the supracoracoideus, is connected to a long, thin tendon. In Rock Pigeons (*Columba livia*), the storage and release of the strain energy in this tendon equals up to 60% of the net work of the supracoracoideus, thus substantially reducing the work and power required for upstroke (Tobalske and Biewener 2008).

5.2.4 Power available from the flight muscles

On average across all birds, as body size increases, flight performance declines dramatically. For example, large waterfowl, such as swans, find it harder to take off and ascend rapidly during escape flight than small ducks. As described above, the tiny size of hummingbirds has allowed them to develop a unique capacity for sustained hovering. Likewise, small songbirds can literally fly circles around larger species like hawks, a useful ability when mobbing predators.

A principal reason for this scaling pattern is that larger birds have longer wings, and their wingbeat frequencies are therefore slower. No swan could hope to beat its wings as rapidly as a hummingbird. All else being equal, muscle mass and work output from the muscle scale roughly proportionately with body mass, so larger birds have the general ability to add more work into each wingbeat. As size increases, however, wings get longer and the cycle time for a muscle contraction takes longer; wingbeat frequency therefore goes down. Dividing a constant amount of mass-specific work (from the muscles) by progressively longer time intervals (from having longer wings that beat less rapidly) means that the relative power for flight declines as body size increases (Fig. 5.20). In other words, the absolute power available for each wingbeat increases as body mass increases, but since the pace of wingbeats is slower for larger birds, their total flight power does not increase as fast as mass does. Accordingly, the flight performance of birds during maximal effort—such as takeoff and escape flight—scales approximately with wingbeat frequency.

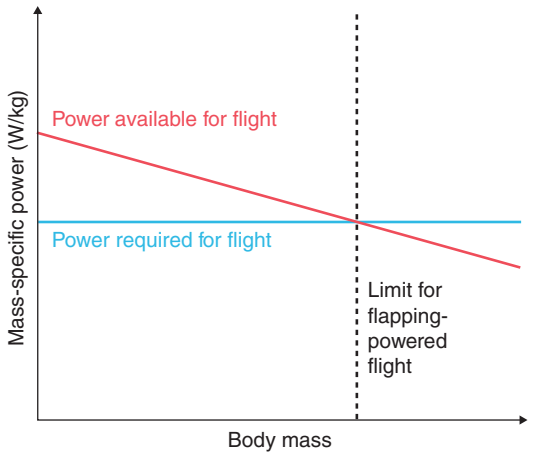


Fig. 5.20 Scaling of self-powered flight capability. Mass-specific power generated in the flight muscles declines as body mass increases; birds above a critical size threshold cannot generate enough power to fly. (© Cornell Lab of Ornithology.)

Taken together, the U-shaped power curve and the fact that the power available for flight diminishes relative to mass help explain why the overall range of flight performance is greater in small birds than in larger birds. A hummingbird has sufficient burst and sustainable power for activities ranging from hovering to fast forward flight. As species get larger, the decrease in marginal power available results in limitations on flight styles (Fig. 5.21). Birds larger than a hummingbird cannot hover efficiently. Still larger birds like loons require a running start to take off from water, and birds like the Waved Albatross (*Phoebastria irrorata*) of the Galápagos must take off into the wind to become airborne. Finally, the largest flight-capable birds, like condors, have only enough burst power to take off at their minimum power speed and then need to extract energy from the environment, using thermals in order to stay aloft.

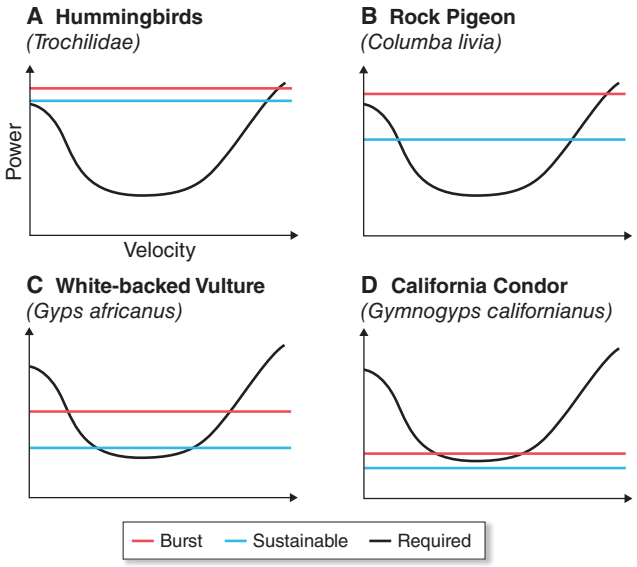


Fig. 5.21 Body size affects marginal power and flight style. (A) With such a small body size, hummingbirds typically generate more power than is required for hovering flight. (B) Larger birds like Rock Pigeons (*Columba livia*) can sustain enough power to hover briefly during takeoff, but must maintain forward speed to stay aloft. (C) White-backed Vultures (*Gyps africanus*) and other Old World vultures must first accelerate (by running on the ground) to gain the power necessary for flight. (D) The California Condor (*Gymnogyps californianus*), one of the heaviest flying birds, needs virtually continuous incoming wind velocity or thermal currents to maintain the power necessary to fly. This species rarely flaps its wings. (From Pennycuick 1968. Reproduced with permission from Company of Biologists Ltd.)

The negative scaling of mass-specific power available from the flight muscles is an inevitable consequence of increasing body size and wingspan, but there are some ways in which this trend can be partially offset, at least over limited ranges of body size. As noted above, wing shape has substantial effects on flight performance. Similarly, there are physiological differences in the flight muscles of different birds that are adapted to the power requirements of their flight styles.

5.2.5 Energy-saving flight strategies: intermittent flight and soaring

Flapping flight requires high work and power output from the muscles. Birds employ at least two strategies to reduce the power required during flight. Many species use forms of **intermittent flight**, when phases of flapping are interrupted by non-flapping, fixed-wing pauses. Birds can also extract the potential energy available in the air—thermals and wind—for soaring.

Intermittent flight: a common flight style among small and medium-sized birds that consists of flapping phases interspersed with flexed-wing bounds or extended-wing glides.

If you carefully watch a small or medium-sized bird as it moves through the air, you are likely to witness intermittent flight, where the flight path undulates in altitude. These birds flap their wings to accelerate and gain height; deceleration and altitude loss occur during intermittent pauses in flapping. The non-flapping phases of intermittent flight may consist of a flexed-wing "bound" during which the wings are held tightly against the body, a "glide" during which the wings are fully extended (Fig. 5.22A), or some intermediate posture. During intermittent glides, the pectoralis muscle contracts and the supracoracoideus muscle is inactive, whereas both muscles are inactive during bounds (Chapter 6).

Mathematical models of power requirements generally suggest that flap-bounding offers savings in power during fast flight at maximum range speed or faster (Fig. 5.22B), particularly when lift from the body and tail contributes to

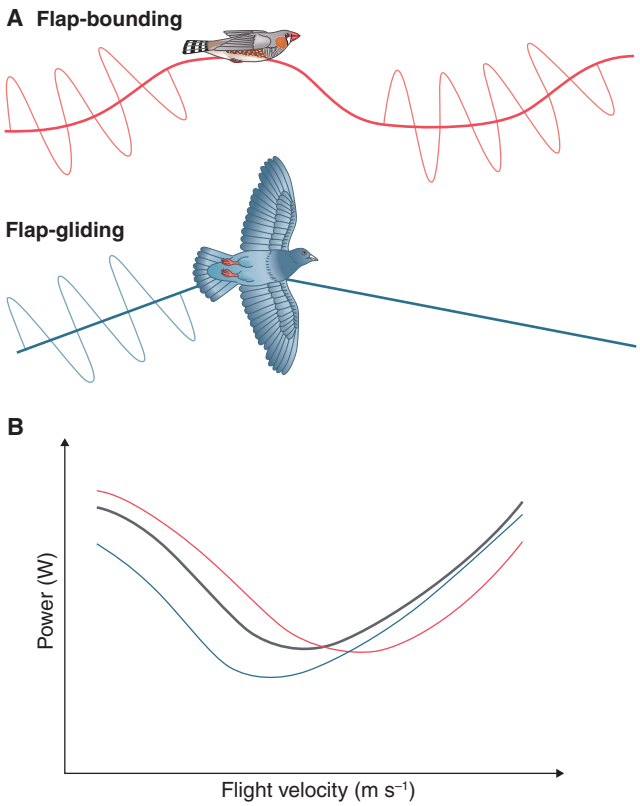


Fig. 5.22 Intermittent flight. (A) Pauses in wing flapping during intermittent flight may consist of a flexed-wing bound (top) or an extended-wing glide (bottom), depending on the mass–velocity efficiency, body mass, and flight style of a given species. (B) Flap-bounding (red line), compared with continuous flapping (black line), may save power at faster flight speeds. Flap-gliding (blue line), on the other hand, is most energetically beneficial at slow and moderate flight speeds. (A, from Dyke and Kaiser 2011. Reproduced with permission from John Wiley and Sons. B, adapted from Rayner 1995. Reproduced with permission from Elsevier and Jeremy Rayner.)

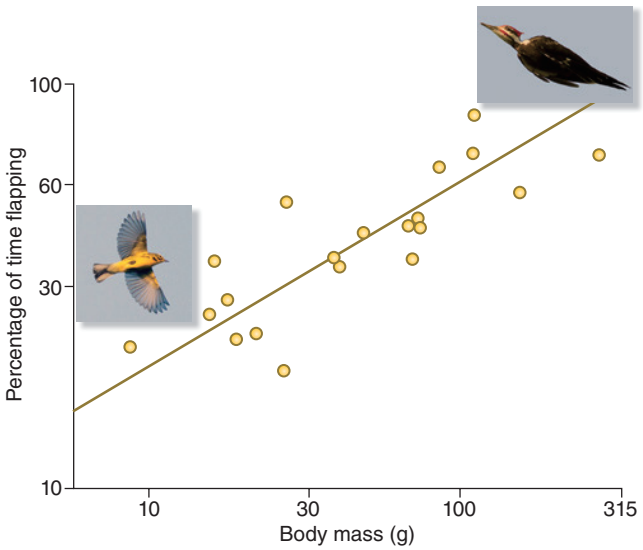


Fig. 5.23 Flapping and body size. Data from birds of different sizes, including Prairie Warblers (*Setophaga discolor*) and Pileated Woodpeckers (*Dryocopus pileatus*), show that the proportion of flapping time increases with body size. Bounding is not energy efficient for birds with high body mass. (Courtesy of Bret Tobalske. Photographs by: left, Sam Galick; right, James Tarolli.)

weight support during the bound. In contrast, flap-gliding is estimated to be less costly at most flight speeds, particularly slow and intermediate. An ideal strategy for saving energy while flap-gliding is to gain altitude rapidly using high-power wingbeats and then to descend slowly during the glide phase.

Some birds are known to vary their non-flapping posture, shifting from intermittent glides when flying slowly to intermittent bounds when flying fast. Budgerigars (*Melopsittacus undulatus*), Barn Swallows (*Hirundo rustica*), Common House Martins (*Delichon urbicum*), European Starlings (*Sturnus vulgaris*), and Black-billed Magpies (*Pica hudsonia*) all exhibit this behavior during wind tunnel experiments, and Lewis's Woodpeckers (*Melanerpes lewis*) exhibit similar behavior in the field (Tobalske 2001). There appears to be a relationship between body mass and wing design that affects the use of intermittent flight. Small birds with rounded, low aspect ratio wings such as the Zebra Finch (*Taeniopygia guttata*) (13 grams; aspect ratio=4.2) appear to use only intermittent bounds. In contrast, species of about the same body mass but with more pointed, high aspect ratio wings such as the Barn Swallow (20 grams; aspect ratio=6.2) and Northern House Martin (17 grams, aspect ratio=6.5) use both bounds (or partial bounds) and glides. Regardless of aspect ratio, species of intermediate mass, from 34-gram Budgerigars (aspect ratio=7.1) to 150-gram Black-billed Magpies (aspect ratio=4.1), use both forms of intermittent flight. Birds heavier than about 300 grams do not appear to be able to use intermittent bounds; for example, pigeons only glide during pauses in wing flapping (Tobalske 2001).

The largest species observed to bound regularly is the Pileated Woodpecker (*Dryocopus pileatus*) (270 grams) of North America (Tobalske 1996). What creates this upper size limit on the ability to fly using bounds? As in the general decline of overall flight performance with increasing mass among bird species, there is a decline in the performance of bounds as body size increases. Among passerines engaged in migratory flight and woodpeckers engaged in foraging flight, the percentage of time spent flapping increases with increasing body mass (Fig. 5.23).

Soaring is distinguished from gliding in the way energy is extracted from the environment. A soaring bird may use the energy it harvests to maintain or gain altitude. During **slope soaring**, an upwash of air is created by wind flowing over an inclined surface such as a hill or cliff (Fig. 5.24A). The upward direction of airflow permits the bird to maintain a glide while holding its place relative to the ground. The vertical and horizontal components of the wind velocity create the relative velocity that would be necessary for the bird to glide forward and downward if it were in still air. During **thermal soaring**, birds such as large raptors take advantage of rising currents of warm air (Fig. 5.24B). Thermals are generated when the sun warms the ground unevenly, and the air over the hotter parts of the surface gains heat from the ground and therefore expands and rises. As in slope soaring, it is the velocity of the air relative to the bird that permits this flight behavior: from the bird's perspective, it is descending relative to the air inside the thermal. However, if the air in the thermal is rising at a faster rate relative to the ground than the bird is descending, the bird will rise relative to the ground.

Dynamic soaring is used by seabirds such as albatrosses and petrels to gain energy from the wind as it passes over the ocean (Fig. 5.24C). In the boundary layer of air adjacent to the surface of the ocean, there is a gradient from zero velocity

Slope soaring: a type of soaring in which a bird derives lift from the air currents that are deflected upward when wind strikes a hill or ridge, or from rising eddies created when wind spills over a cliff.

Thermal soaring: a type of soaring in which birds use rising air thermals—rising columns of warm air—to gain height.

Dynamic soaring: a type of flight in which birds use the gradient in wind speed that exists over the surface of the ocean to travel long distances without expending much of their own energy: the bird glides down the gradient at an angle, then turns and rises abruptly into the wind, using its momentum to gain height quickly. It then turns and glides down again, crossing the waves in large zig-zags. Dynamic soaring is used most by albatrosses and other large pelagic birds.

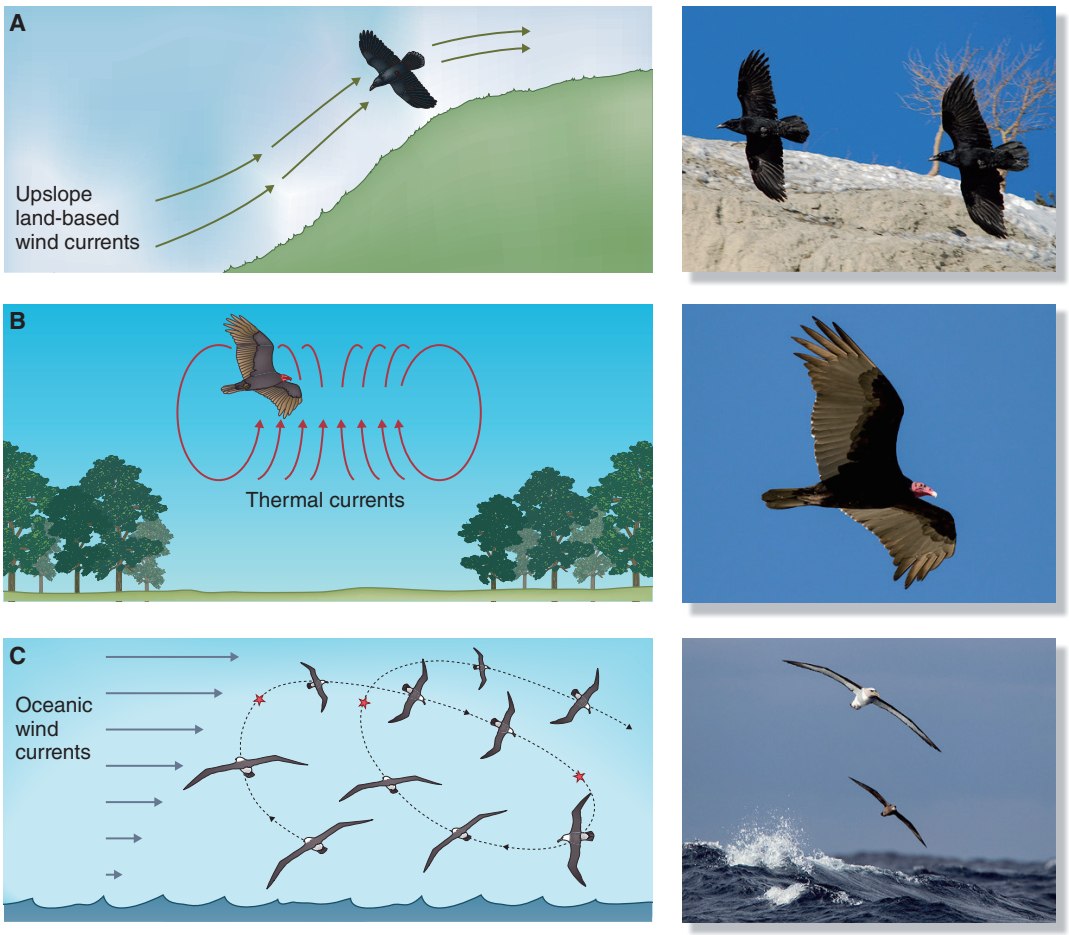


Fig. 5.24 Soaring. While soaring, birds harness kinetic energy from the environment to maintain altitude with little energetic cost. (A) During slope soaring, birds like Common Ravens (*Corvus corax*) fly into land-based currents rising up and over slopes. (B) Many raptors, including this Turkey Vulture (*Cathartes aura*), rely on thermals, rising currents of warm air, to cover large distances. (C) Seabirds like the Buller's Albatross (*Thalassarche bulleri*) (top) and Great-winged Petrel (*Pterodroma macroptera*) (bottom) dynamically soar by taking advantage of the velocity gradient caused by wind as it passes over the ocean. (From Vogel 2013. Reproduced with permission from Princeton University Press. Photographs by: A, Keith Williams; B, Ned Harris; C, Tobias Hayashi.)

right at the surface to the full wind velocity a bit above it. By facing into the wind and initiating a gain in altitude, the bird encounters progressively faster velocity as it rises in altitude, especially if it rises from a wave trough to fly over the crest of a wave in this process. The bird can then use this gain in altitude and turn to fly downwards into the next wave trough. By repeatedly rising, turning, and descending, the seabird can continue to trade the kinetic energy of the air for its own gain in potential energy. This method of harvesting energy from the wind gradient at the ocean's surface means that the bird will move gradually downwind as it soars.

5.3 Maneuvering and stability

Thus far in this chapter, as we have considered the mechanisms that birds use to counteract gravity, we have assumed they are moving through the air in a more-or-less straight line. Watching a real bird for even a moment shows that this simple, linear path is rare: a bird's life in the air features constant maneuvers, and even when it is trying to fly steadily in one direction, it must maintain its flight path despite variable gusts of wind. Here we explore their ability to maneuver and, conversely, to control their position and be stable in the air.

As terrestrial animals, humans have a tendency to interpret our perceptions in the context of the two-dimensional plane on which we spend most of our time. In can therefore be counterintuitive for us to contemplate the three-dimensional world of a flying bird. When we maneuver on the ground, we can turn one of two ways, left or right, relative to our vertical axis (our z-axis). For a bird in the air, there are two other axes about which it can rotate to alter its flight path. Organizing the world in "bird-centered" coordinates, a bird can roll about its x-axis, pitch about its y-axis, and yaw about its vertical or z-axis (Fig. 5.25).

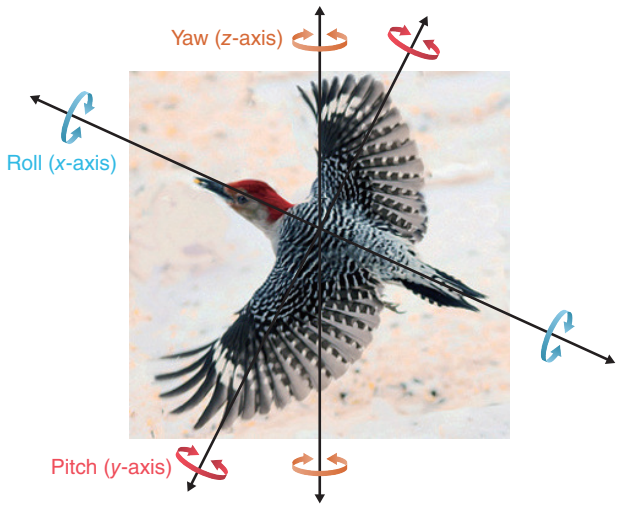


Fig. 5.25 Maneuvering and stability. Birds maneuver and stabilize in a three-dimensional environment. Changes in body orientation are expressed relative to three axes: rolling (*x*-axis), pitch angle (*y*-axis), and yaw (*z*-axis). (Photograph by Amber Elmore.)

To produce a maneuver, a bird must create force asymmetry using its wings or tail so that a rotational force (torque) is produced about its center of mass. Any torque will result in rotation about a given axis, and most flight maneuvers include rotation about all three axes. To self-stabilize, a bird must generate a force asymmetry to correct for any perturbations—like a sudden gust of wind coming from one side—that would cause a rotation about one or more of these axes. Highly maneuverable birds like hummingbirds are able to respond to perturbations quickly, so they are able to maintain their path during flight in turbulent conditions better than intrinsically more stable birds that, faced with buffeting winds, exhibit a jittering flight path.

Maneuvering during flight is related to a measurement called **wing loading**, which is the weight of the bird divided by the projected surface area of its wings and, by convention, the area of the body between the wings. Birds with relatively large wings and relatively low weights have low wing loading; conversely, birds with smaller relative wing areas and higher mass have high wing loading. As a general pattern, as wing loading increases, the intrinsic or preferred flight speed increases, as higher velocities of air passing the wing are required to generate the lift to keep these relatively heavy birds aloft. This relationship has an important implication for maneuvering with fixed (gliding) wings: birds with lower wing loading can turn with a tighter radius than birds that have higher wing loading. For example, among two relatively large birds, a Golden Eagle (*Aquila chrysaetos*) can accomplish a tighter circle than a Greylag Goose (*Anser anser*) (Fig. 5.26).

In a simple gliding turn, the turn is effected by creating roll about the long axis of the bird's body to establish a bank angle, thus redirecting the lift force to provide a turning force. To produce this roll, a bird can manipulate one or more of the things that produce lift: wing surface area, angle of attack, or wing speed. In fast gliding flight, a turning bird simply can increase the angle of attack of one wing by rotating it upwards, while simultaneously flattening the other to decrease its angle of attack. The wings can be used to create rotation around the other two body axes as well. By moving the wings' center of lift forward or backwards relative to the bird's center of mass, birds can create pitching rotation to direct themselves upwards or downwards. Likewise, any left–right asymmetry will produce both differences in lift and in drag, causing yawing rotations.

Wing loading: the ratio of body weight to wing area; wing loading is a measure of how much load each unit area of wing must carry when a bird is in flight.

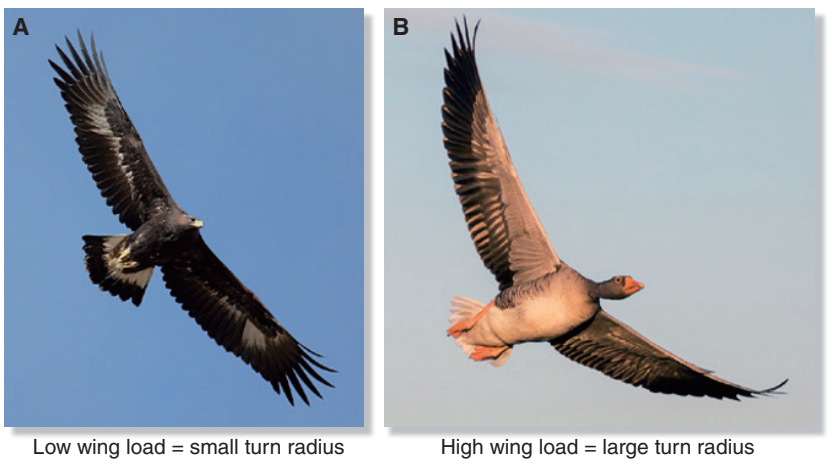


Fig. 5.26 Wing loading influences gliding maneuverability. Although they are both relatively large species, (A) Golden Eagles (*Aquila chrysaetos*) have lower wing loading and can therefore accomplish smaller turns than (B) Greylag Geese (*Anser anser*), which have a higher mass to wing area. (Photographs by: A, Beth Hamel; B, Benedikt Halfdanarson.)

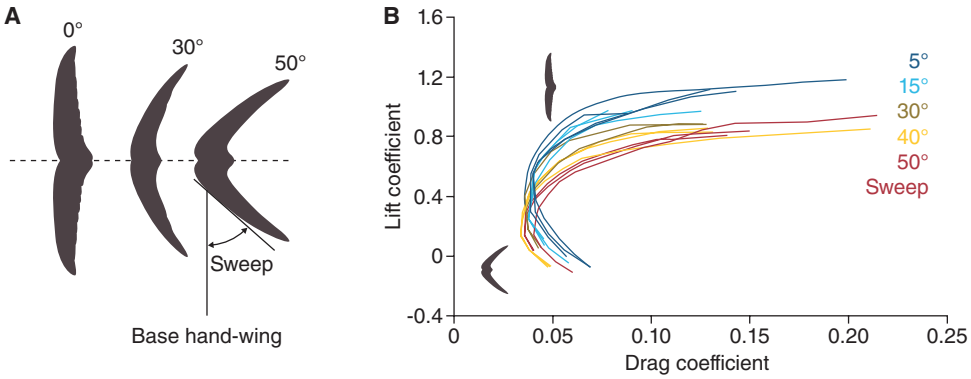


Fig. 5.27 Controling wing shape. (A) Swifts can change the sweep angle of their wings to (B) generate lift and decrease drag more efficiently in various contexts. This graph shows the relationship between lift and drag for wings across a range of sweep angles, from shallow (blue) to acute (red). (From Lentink et al. 2007. Reproduced with permission from Macmillan Publishers Ltd.)

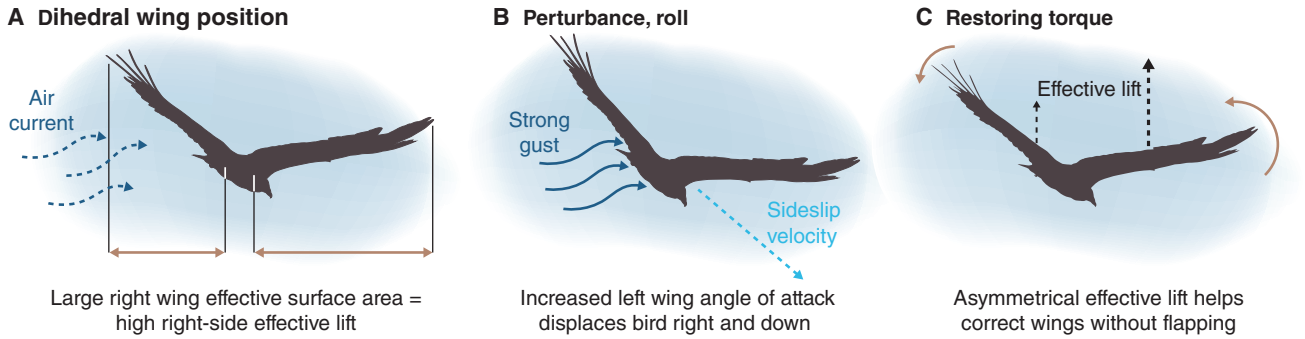


Fig. 5.28 Restoring stability during passive gliding. (A) Passive roll stability can be accomplished via a dihedral (upturned "V") wing posture, often assumed by Turkey Vultures (*Cathartes aura*). (B) If a sudden gust of wind causes the bird to roll, it will sideslip down and to the right. (C) As this occurs, the angle of incidence relative to the wind velocity increases on the right wing and effective lift is greater on the left wing, together causing a restorative roll to the left. (© Cornell Lab of Ornithology.)

Maneuverability influences many aspects of the ways birds use flight. For example, variations in wing loading and maneuverability help account for differences in foraging behavior and prey selection in swallows, birds that often use gliding when foraging (Warrick 1998). Moreover, gliding wings are not absolutely fixed in terms of posture. For example, swifts can change the sweep of their wings, holding them straight out or angling them back towards their tail (Fig. 5.27). These subtle changes in their wing orientation allow swifts to use glides to maneuver through a wide array of flight velocities and changes in altitude (Lentink et al. 2007).

Passive stability: when applied to flying birds, components of the bird's aerodynamic structures that cause the bird to return to an original flight posture when it is disrupted by an outside force (such as wind) without flapping or other active movements.

Passive stability is the ability to return to an original flight posture when it is perturbed by a gust of wind or other disturbance, without flapping or other active movements. Passive stability stems from avian bilateral morphology and relative air velocity. During gliding, many birds adopt a dihedral wing posture, in which the wings form a V-shape when the bird is seen from the front or rear. For example, Turkey Vultures (*Cathartes aura*) of the Americas often soar with such a posture (Fig. 5.28A), which confers roll stability. If, for example, the gliding bird is perturbed by a gust of air such that it rolls to the right about its *x*-axis, it will sideslip to the right and down (Fig. 5.28B). The lift asymmetry between the two wings will create a restoring torque that rolls the bird to the left, back to its initial orientation (Fig. 5.28C).

Another example of passive stability, yaw stability, is offered by the tail and, in some species with long legs, by the feet trailing behind the body of the bird (Fig. 5.29). Consider a bird moving level and forward that suddenly experiences a yaw rotation to the left. Its tail area will be

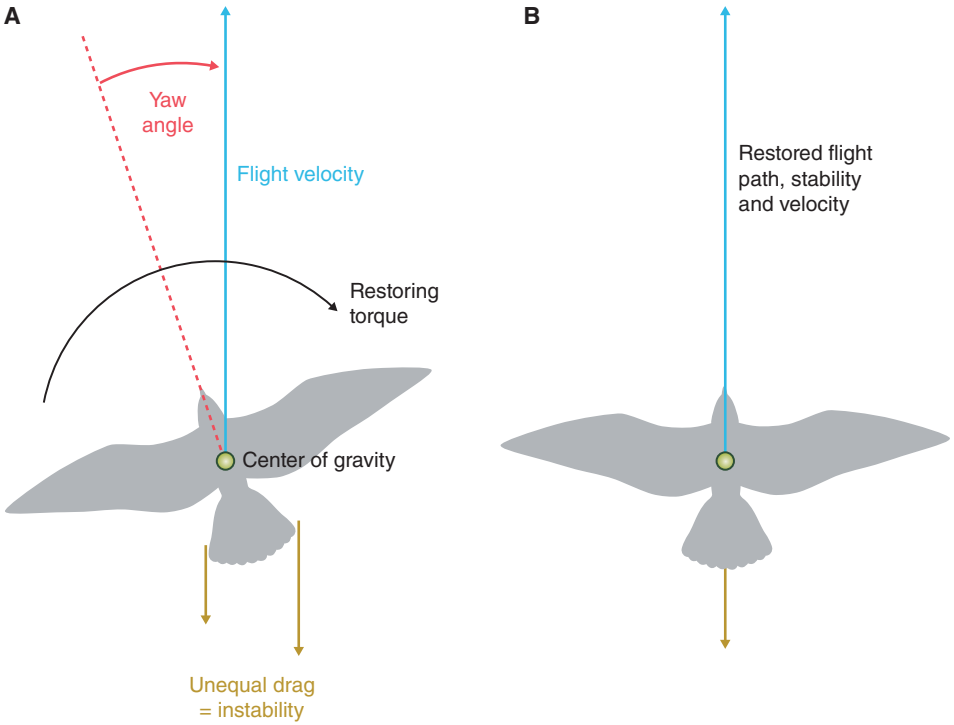


Fig. 5.29 Tails help restore stability during yaw. Just as the roll or pitch of a flying bird can shift, yaw may shift during a sideslip motion. (A) Hypothetically, a bird may be displaced from its forward flight path at a lateral left angle around its center of gravity. It will then experience an uneven profile drag on its tail, with the side opposite the yaw-shift having more drag. A restoring torque results from this drag, (B) returning the bird to a stable, symmetrical orientation in its preferred flight direction. (Adapted from Sachs 2007. Reproduced with permission from Elsevier.)

more exposed to oncoming air on the right side compared with the left. Drag on the tail, multiplied by the distance of the tail from the bird's center of mass, creates a torque that restores the bird to its symmetrical body position relative to forward flight. This is similar to the process by which the large tail of a weathervane keeps it orientated into the wind on a gusty day.

Flapping motions may affect both maneuverability and stability. The contributions of flapping make it very challenging to study the act of maneuvering because the velocity of flapping wings changes in relation to the air during the procedure. Studies on avian maneuverability during flapping flight are a subject of ongoing experimentation. More generally, the wonderful complexity of avian flight biomechanics likely still holds many new discoveries about how birds are adapted to their aerial lifestyles.

Visit birdbiology.org for many online resources on the topics covered in this chapter.

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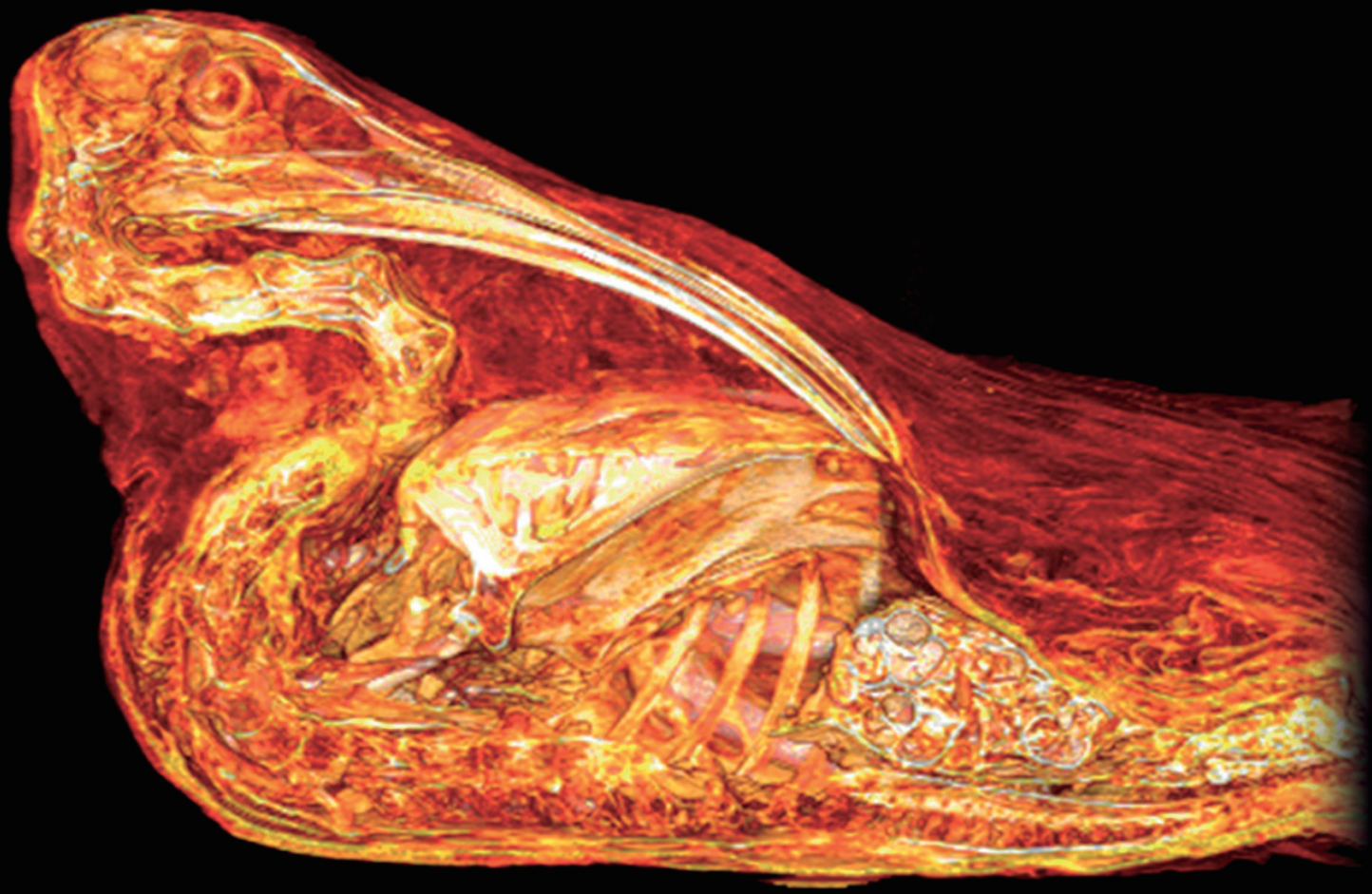
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Chapter 6 Avian Anatomy

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Much of the thrill we experience when watching and learning about birds centers around their collective ability to sing, to fly and dive, to attract mates, to build nests, to forage, and to produce and care for young. Yet rarely do we consider just how the bird's body actually accomplishes these wonders. Exactly what are the various parts and pieces that work together to make a bird?

Birds come in a variety of shapes and sizes. Yet compared to other classes of vertebrates, birds are all rather similar to one another—built on the same basic plan, with the same basic parts. Even birds as distinctive as ostriches, hummingbirds, ducks, and penguins have the same anatomical foundation: a rigid beak, a relatively long neck, two wings, at least partially fused vertebrae, strong hindlegs, and a short tail. No living bird varies from this basic design.

Similarly, just about everything relating to a bird's anatomy has been shaped by the demands of flight—all birds come from flying ancestors, even the species that do not fly today. Flight is extremely demanding and creates strong anatomical and physiological constraints. Therefore, birds have lightweight, rigid bodies with extremely efficient internal systems, particularly those that facilitate motion and respiration.

In this chapter we discuss the important features that are mostly "inside" a bird, considering the internal organ systems one by one to understand the component parts. Keep in mind that these systems rarely function independently, and that their interaction and integration are of vital importance. Much of the pleasure in understanding avian anatomy lies in discovering how these systems work together to allow birds to live such varied lifestyles.

The anatomical terms used in this chapter were agreed upon by an international committee of avian anatomists, who deliberated for several years at meetings of the World Association of Veterinary Anatomists. The resulting illustrated list was published as the *Handbook of Avian Anatomy: Nomina Anatomica Avium* (Baumel et al. 1993), and it remains the standard reference for avian anatomical terminology.

6.1 Skeletal system

The skeletal system is composed of bone and cartilage, which support and protect the soft structures of the body (Box 6.01). Birds have lightweight skeletons, an adaptation that allows them to minimize the energetic costs of flight, carry heavy eggs, and later incubate those eggs without

Opposite: A 2500-year-old mummified Sacred Ibis (*Threskiornis aethiopicus*). The ancient Egyptians mummified many bird species, such as the one here wrapped in linen. Through CT scanning of a different ibis mummy, researchers discovered that the Egyptian preparators had removed the internal organs, but then returned the gizzard after stuffing it with seeds and snails—presumably to feed the bird during its mythical journey through the afterlife, where it was expected to serve as a messenger. CT scanning is an important tool for research on avian anatomy. (Top, RM2727.01 © Redpath Museum, McGill University. Bottom, image by Nicholas Morin, from Wade et al. 2012. Reproduced with permission from Elsevier and Andrew Wade.)

Handbook of Bird Biology, Third Edition. Edited by Irby J. Lovette and John W. Fitzpatrick.
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Box 6.01 Preparing skeleton specimens

Bones provide essential scaffolding in vertebrates, defining how muscles attach, where organs sit, and the overall shape of the animal. Museums collect skeletons so that researchers have access to different species, and multiple specimens within a single species, to answer scientific questions.

Bird skeletons are delicate and require careful extraction methods to ensure that all the bones remain intact and undamaged. Specimens selected for skeletonization are often those that are unsuitable for round skins (Chapter 2)—usually due to decay or damage to feathers and soft tissue—or those that have been specifically requested, either by a researcher or for a collection. Sometimes specimens are rare enough that preparators try to preserve both the skin and skeleton. To do this, special care is taken when removing as many bones as possible from the skin. Although most skin specimens include feet and beaks in addition to the skin and feathers, in these cases, the leg and skull bones remain with the rest of the skeleton.

Most institutions use dermestid beetles (in the family Dermestidae) to remove the flesh from a skeleton. Colonies of these flesh-eating beetles are easy to keep and pose the least amount of risk to even the smallest bones. Other methods suitable for preparing mammal skeletons—such as simmering bones in hot water—have a greater potential to damage fragile bird bones.

First, a preparator manually removes the skin, organs, and as much soft tissue from the skeleton as possible; the eyes are left in place because birds have bones, called sclerotic rings, within their eyes. Next, the bird is placed in a tucked position, with its legs and wings folded close to its body, and bound in thick thread to stabilize its position (Fig. 6.B1.01). Aluminum tags (as opposed to paper, which the beetles would eat) are marked with the species and preparator's number and attached to the leg of the bird. Next, the body is placed in an open plastic container under a ventilated hood to dry, after which it is moved into the container with the beetles. The beetles meticulously eat all the remaining flesh (Fig. 6.B1.02). After they have completely cleaned the skeleton, it is removed from the beetle colony, frozen (to be sure that no beetles travel into the museum itself), and placed in a new box. Finally, the box and specimen are labeled with all associated data, catalogued, and placed into the museum collection (Fig. 6.B1.03).

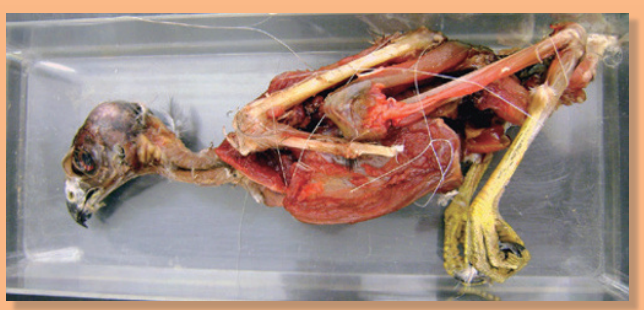


Fig. 6.B1.01 Cooper's Hawk (*Accipiter cooperii*) skeleton ready to dry. A skeleton is first prepared by removing most of a bird's feathers, skin, organs, and muscle. It is then tightly bound with string and set to dry before being cleaned in a dermestid beetle colony. (Photograph by Jennifer Campbell-Smith.)



Fig. 6.B1.02 An egret skeleton in dermestid beetles. This skeleton was recently added (the eye is still intact) to a dermestid beetle colony. When it is finished, the museum curator will carefully remove the bound skeleton from the colony and clear away any remaining debris. (Photograph by Jennifer Campbell-Smith.)



Fig. 6.B1.03 Finished museum-ready raptor skeleton. Clean, dry, and tagged skeletons are typically stored in neatly labeled boxes in pest-free museum drawers. (Photograph by Jennifer Campbell-Smith.)

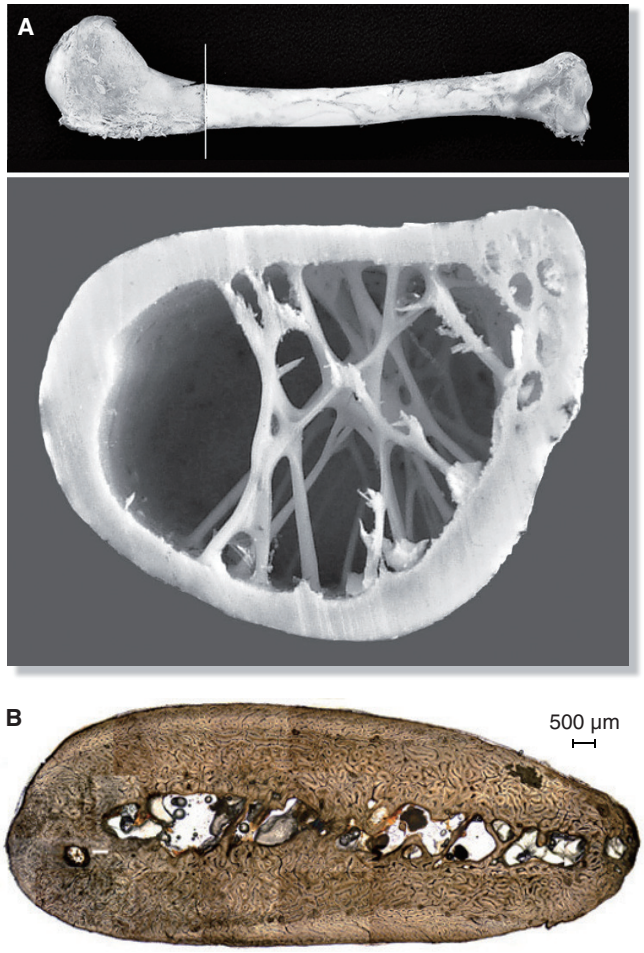


Fig. 6.01 Internal bone structure in flying versus flightless birds. (A) Flying birds typically have lightweight, pneumatic bones for weight efficiency in flight. Despite being mostly hollow, internal struts—as seen here in this cross-section of a Whooper Swan (*Cygnus cygnus*) humerus—provide structure and strength. (B) In contrast, flightless birds often have heavy, less pneumatic bones, as seen in this cross-section of a Chinstrap Penguin (*Pygoscelis antarcticus*) humerus. (A, from Pennycuick 2008. Reproduced with permission from Elsevier. B, photograph by Laura E. Wilson.)

breaking the shell. Species that do not engage in flight often or at all, typically have thicker, heavier bones. However, contrary to popular belief, bird skeletons contribute proportionately as much to their total body and soft-tissue mass as do the skeletons of terrestrial mammals (Prange et al. 1979). Yet bird bones are indeed lightweight with respect to their strength and stiffness per unit of bone mass when compared with mammals (Dumont 2010).

Like the bones of other vertebrates, bird bones contain marrow, which consists of blood-forming cells and fatty tissue. However, most bones in a bird's skeleton are **pneumatic**, meaning they also include spaces filled with air that keep the weight of their bones minimal for efficient flight (Fig. 6.01). Air spaces in a bird's skull bones usually connect with nasal passageways; the air spaces in the humerus, vertebrae, sternum, ribs, pelvis, and femur are connected either directly to the lungs or to **air sacs** (which connect bone cavities with the lungs). Although some other vertebrates have air cavities in their bones, birds are the only ones in which bone cavities are connected to the air sacs and lungs. The largest and most efficient flying birds, such as albatrosses and frigatebirds, even have interconnected air spaces passing through their joints (such as from the humerus of the wing into the digits), further reducing their weight. The connection between the respiratory system and air cavities within bones comes at a price, however: injury to a pneumatic bone—such as a gunshot—allows blood from broken vessels to enter air passageways and the lungs, often resulting in death.

Bones provide sites for the attachment of muscles, which move the skeleton. Bones act mechanically like levers for the action of muscles, and continued use results in the formation of a bump—or process—where the muscle attaches. These features are so characteristic that they often serve as landmarks in fossil bones, helping researchers precisely identify a particular bone type, discern the presence of a muscle long since decayed, or even identify the species of the bird.

One might assume that once fully formed, adult bones are dead structures that remain the same throughout life—similar to coral or seashells—but this is not the case. Bone is a tissue composed of living cells in a matrix called osteoid, a gelatinous substance made of fibrous protein. It has a blood supply that constantly deposits or moves mineral components from one place to another. Bones are therefore very much alive, constantly changing shape and composition in response to fluctuations in diet and physical stress caused by movement. When a muscle contracts and pulls on a bone, it activates resorption (breaking down/taking away) or deposition (provision) of calcium. The calcium residing in one bone in the morning may move to another bone by the afternoon, or to an eggshell if the bird is in the process of completing a clutch (Chapter 11). The transfer of calcium occurs constantly, but it is especially important during the healing process and can serve as a buffer of sorts when abnormal pressure is placed on a bone.

Cartilage is also composed of living tissue with cells and a blood supply; it is capable of growth and resorption

Pneumatic: describes bones that are filled with air spaces and may contain air sacs; nearly all the bones of most birds are pneumatic.

Air sacs: found only in birds, thin-walled, transparent sacs extending from the mesobronchi or the lungs to different regions of the body; they act as bellows to bring air into the body and store it until expiration.

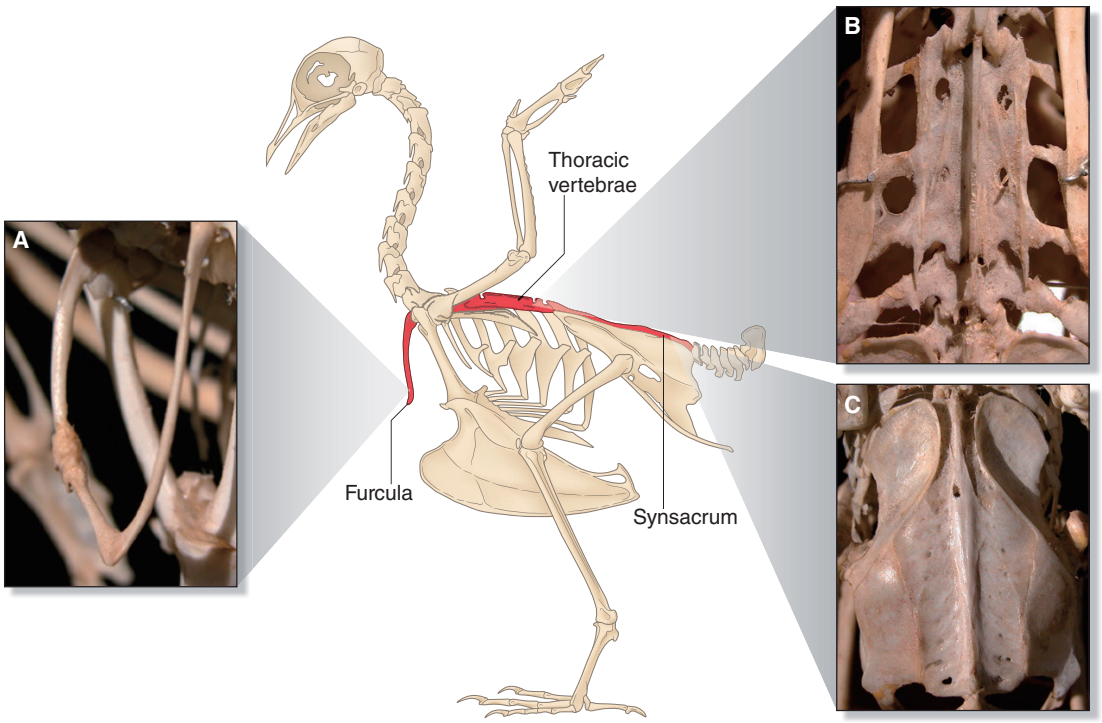


Fig. 6.02 Avian skeletal fusion. Fused bones support several large muscle-bearing regions, allowing birds to maintain lightness without sacrificing the strength necessary to make powerful movements (like wingstrokes). The three main regions of fusion occur in: (A) the clavicle bones, fused into the singular furcula (where the major flight muscles attach), (B) the thoracic vertebrae that support the ribs and air sacs, and (C) the synsacrum, formed by the fusion of the sacral and pelvic bones, which aids in shock absorption during landing and jumping. (Illustration adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press. Photographs by Renn Tumlison, Henderson State University.)

as well as **ossification** (transformation into bone). During development, cartilage becomes bone very rapidly. As a bird grows older, this process slows down. Bone also can be formed directly without going through a cartilage stage. Such direct ossification occurs in skull bones in most birds, and tendons of the leg muscles in some species.

Birds are unlike most other vertebrates in having several fused vertebrae as well as regions of fusion in their collarbones and in the pelvis (Fig. 6.02). This fusion makes these structures more rigid, thereby strengthening the avian skeleton so it can handle the stressful actions of landing, jumping, and flying. The skull bones of a bird are fused to one another as well, which helps prevent damage that might occur from the impact of using the beak like a chisel and hammer, as exemplified by woodpeckers. Although this fused skeleton does not allow for as much overall body mobility in birds compared with many other vertebrates, birds partially compensate by having unusually long, flexible necks.

By convention, the avian skeleton is divided into an axial skeleton (the head, neck, trunk, and tail) and an appendicular skeleton (the pectoral and pelvic girdles, wings, and legs).

Ossification: the hardening or calcification of soft tissue (such as cartilage or tendon) into bone or a bone-like material.

Mandible: in birds, usually refers to the lower half of the beak; the lower jaw.

6.1.1 Axial skeleton

The skull is composed of a cranium (braincase) that incorporates the ear opening on the lower rim of each side (Fig. 6.03). In adult birds, most of the cranial bones are fused so completely that any sutures (seam-like junctions between two bones) or boundary lines are virtually undetectable. Therefore, the presence of skull sutures indicates that a bird is still young.

The large orbits—or eye sockets—of the avian skull are so deep that the eyes almost meet on the midline of the skull. Only a thin, sometimes incomplete, interorbital septum separates them. Aside from the bill, the orbits are the most prominent feature of the bird skull. Attached to each side of the skull, the lower jaw, or **mandible**, consists of two

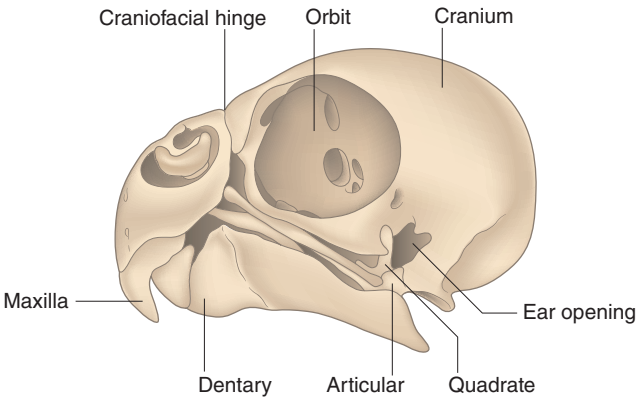


Fig. 6.03 Avian skull. The cranium of an adult Budgerigar (*Melopsittacus undulatus*) does not have notable sutures, the joints found in the skulls of most non-avian vertebrates and in young birds. The large eye orbit, smaller ear opening, and jaw bones (maxilla, dentary, quadrate, articular) are all evident in this side (lateral) view. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

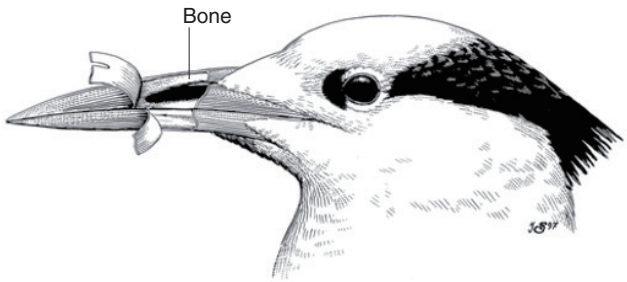


Fig. 6.04 Rostrum of the bill. Vascularized, nerve-rich tissue covers the bones forming the bill (and talons). It is coated with rhamphotheca, a protective, keratinized integument that can be soft or stiff, depending on bill function. (Illustration by N. John Schmitt.)

bones on each side, the dentary and the articular. The dentary bones almost meet at the tip of the bill, though there is a V- or U-shaped (depending on the species) space between the two bones. The upper jaw is often referred to as the **maxilla** and is embedded into the forehead and the sides of the skull via the three-pronged intermaxillary bone. Both jaws are attached to a movable, rectangular, quadrate bone on each side of the skull (Fig. 6.03).

The terms **bill** and **beak** are often used synonymously in referring to bird anatomy; both refer to the rostrum, or external part of the mouth. Bird's beaks (and talons) are composed of a bony core, followed by a thin vascular layer of tissue with nerve endings and blood vessels, and covered with a sheath of keratinized integument called the **rhamphotheca** (Fig. 6.04). In many birds, such as passerines, the rhamphotheca is dry, hard, and horn-like; in others, such as waterfowl, it is soft and supple.

A bird's cranium joins the bones of the jaw at a semi-flexible craniofacial hinge, which is apparent in any skull (Fig. 6.05A). This hinge articulates with numerous other bones in the jaw, as well as both mandibles, when birds open and close their bills. The bill opens (Fig. 6.05B) when the quadrate bone pivots forward, pushing on the jugal arch and palatine, which lifts the frontal portion of the maxilla, called the premaxilla. This, in turn, rotates the maxilla up at its junction, the craniofacial hinge. When the bill begins to close again (Fig. 6.05C), the actions are reversed: the craniofacial hinge rotates down, the premaxilla and maxilla drop, and the quadrate rotates back. This ability to move both jaws (as opposed to one of the jaws remaining stationary, as in most mammals) is called cranial kinesis. Such movement or kinesis allows the bill to grasp food with forceps-like precision. Cranial kinesis also allows a bird to manipulate food within its mouth to aid in swallowing. In some bird species, the upper and lower bills are also flexible, due to bony units called elastic zones. Movement of the bill in this region is known as **rhynchokinesis** (Fig. 6.06); diverse species of shorebirds, snipes, and woodcocks demonstrate this ability (Chapter 8).

Positioned between the lower jaws, a series of articulated bones called the hyoid apparatus supports the tongue. (More generally, the term "apparatus" refers to a collection of the bones and cartilages that forms a particular structure.) The muscles that attach to the hyoid bones extend and retract the tongue. Each cornu or horn of the hyoid is composed of two bones that curve around the back of the skull. These cornua are particularly long in woodpeckers (Fig. 6.07A) and other birds that are able to protrude their tongues (Chapter 8). Many birds, especially granivores and

Maxilla: in birds, refers to the upper half of the beak; the upper jaw.

Bill: a bird's upper and lower jaws, including the external covering. In current ornithological usage, synonymous with beak.

Beak: a bird's upper and lower jaws, including the external covering. In current ornithological usage, synonymous with bill.

Rhamphotheca: the outer covering (sheath) of the beak.

Rhynchokinesis: the ability of some birds to independently move or open the upper tip of a long bill, most often seen in birds that feed by probing in soil or mud.

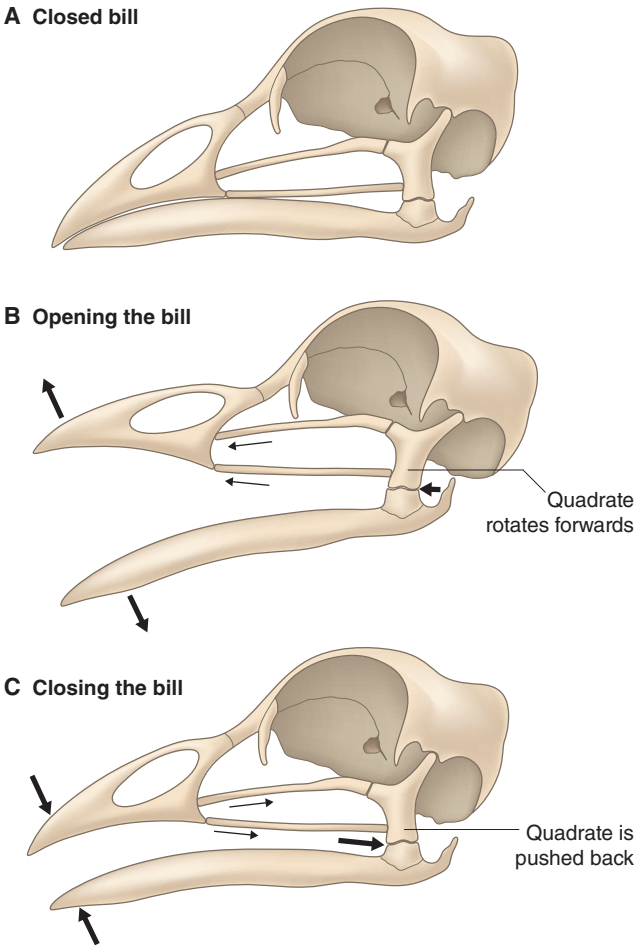


Fig. 6.05 Cranial kinesis. (A) The closed, resting position of a bird's jaw shows that the maxilla and dentary are in contact. The cranium sits on the craniofacial hinge in a neutral position. The articular and the quadrate are also in neutral positions, held in place by the slight pressure of the jugal arch and palatine bones. (B) When the quadrate bone pivots forward, it begins to push on the jugal arch and palatine, lifting the premaxilla and opening the jaw from the craniofacial hinge. (C) When the bill begins to close again, the actions are reversed: the craniofacial hinge rotates down, the premaxilla and maxilla drop, and the quadrate rotates back. (Adapted from King and McLelland 1975. Reproduced with permission from Elsevier.)

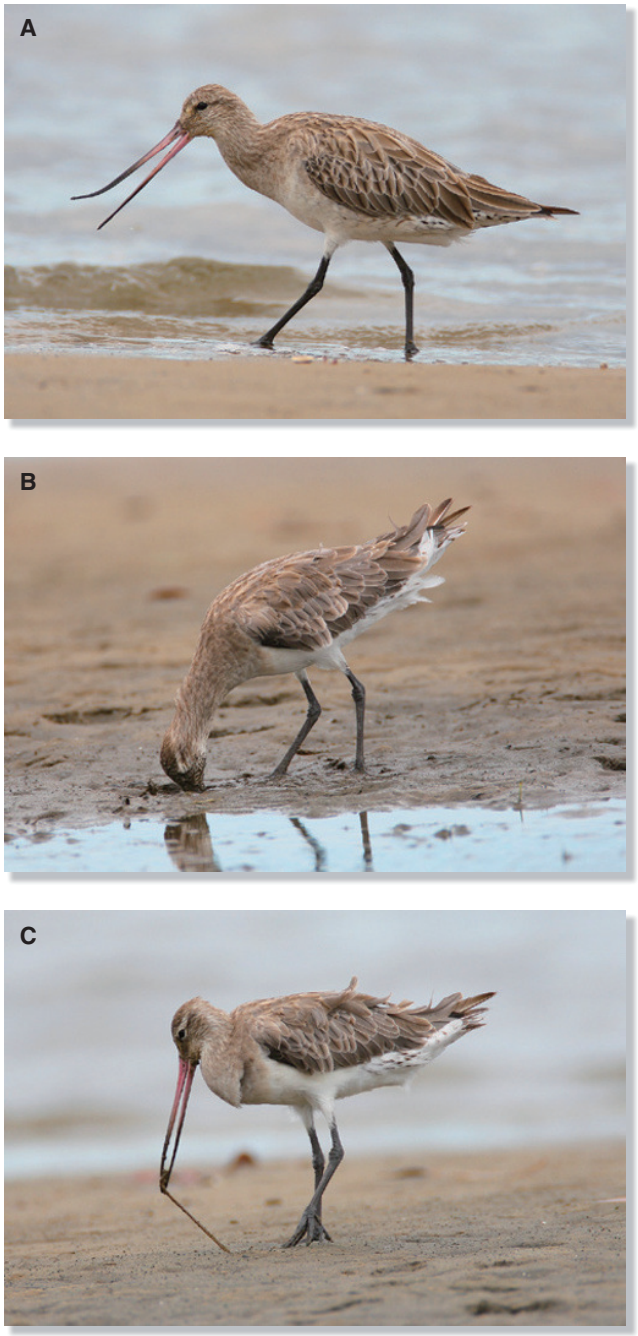


Fig. 6.06 Rhynchokinesis. Elastic zones of both the upper and lower bill permit some species, like this Bar-tailed Godwit (*Limosa lapponica*), to flex the tips of their bills, as in the top image. When the bird is probing in the mud, this ability allows such species to grip slippery prey. (Photographs by Jon Irvine.)

carnivores, cannot protrude their tongues; these birds have shorter hyoid horns and use their tongues to manipulate food within their oral cavity instead (Fig. 6.07B).

No living bird has teeth, although several birds, particularly fish-eaters like mergansers, have serrated bills to grip fish. Ancient Jurassic birds, such as *Archaeopteryx* (Chapter 2), had teeth, as did most birds throughout the Cretaceous—although various lineages lost their teeth independently of Neornithines, the line leading to modern birds.

6.1.2 Vertebral column

The avian vertebral column, or backbone, consists of a series of articulating or fused vertebrae that vary in number depending on the species. As in other vertebrates, the vertebrae are named and numbered for each region: *cervical* in

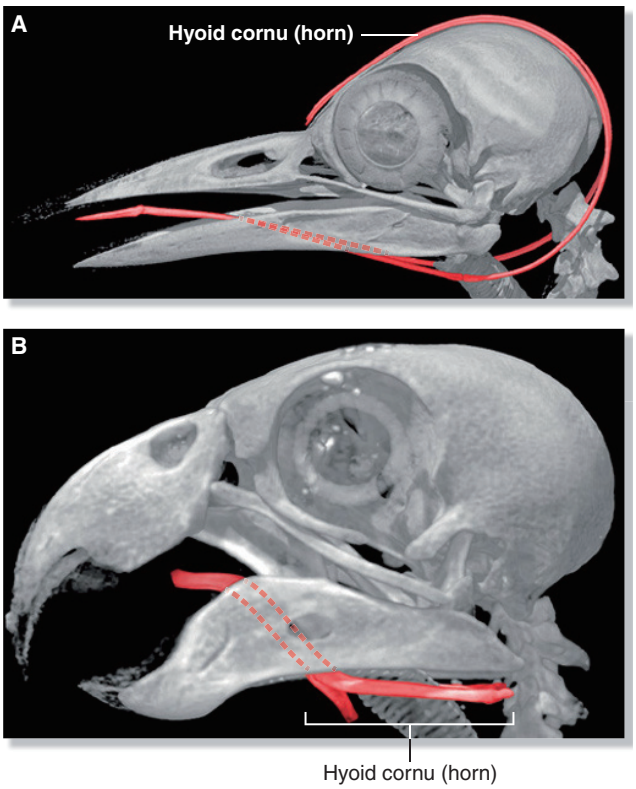


Fig. 6.07 Hyoid apparatus. The bones that support the tongue and aid in manipulating food are anatomically distinct in different groups of birds, reflecting their dietary needs. (A) The hyoid apparatus of the Eurasian Green Woodpecker (*Picus viridis*) is exceptional, with cornua bones wrapping around the back of the skull to house the long, protruding tongue. (B) Many granivorous and frugivorous birds like the Golden-winged Parakeet (*Brotogeris chrysoptera*) have non-protruding tongues and small hyoids, as food is processed in their mouth. (Courtsey of DigiMorph.org.)

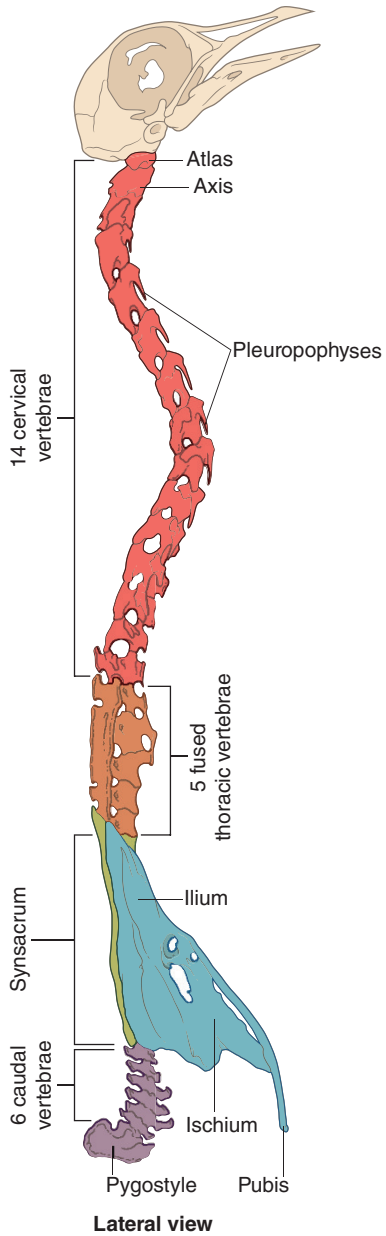


Fig. 6.08 Avian vertebral column. Fused in various areas but articulated in others, avian vertebrae are distinguished by their location and vary in number depending on the species. The cervical vertebrae begin at the skull attachment site, followed by the thoracic vertebrae supporting the ribcage, the lumbar vertebrae extending through the lower back, the sacral vertebrae—fused bones of the pelvis—and finally the caudal vertebrae, including the fused pygostyle tail-supporting vertebrae. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

the neck, *thoracic* in the ribcage, *lumbar* in the lower back, *sacral* in the pelvic region, and *caudal* in the tail (Fig. 6.08). In birds, however, various fusions of bones blur some of these distinctions.

Most birds have 14 or 15 cervical vertebrae, but this number varies: cuckoos and most passerines have 12, while swans have 25. Surprisingly, however, the number of cervical vertebrae in a given bird species does not generally correlate with neck length, and several kinds of long-necked birds have fewer cervical vertebrae than some short-necked species. Overall, the relatively large number of cervical vertebrae in birds allows for a marked suppleness of the neck and easy turning of the head; birds have no trouble looking behind themselves. Some species with unusually short necks (such as woodcocks) compensate by having a large field of vision, facilitated by the special position and size of their eyes, which eliminates the need to turn their head.

The atlas, or first cervical vertebra, is small and articulates with the single occipital condyle on the base of the skull (Fig. 6.09). The second cervical vertebra, or axis, has a peg-like process that extends through the atlas and attaches to the skull via a ligament. The remaining cervical vertebrae have fused rib remnants called pleuropophyses,

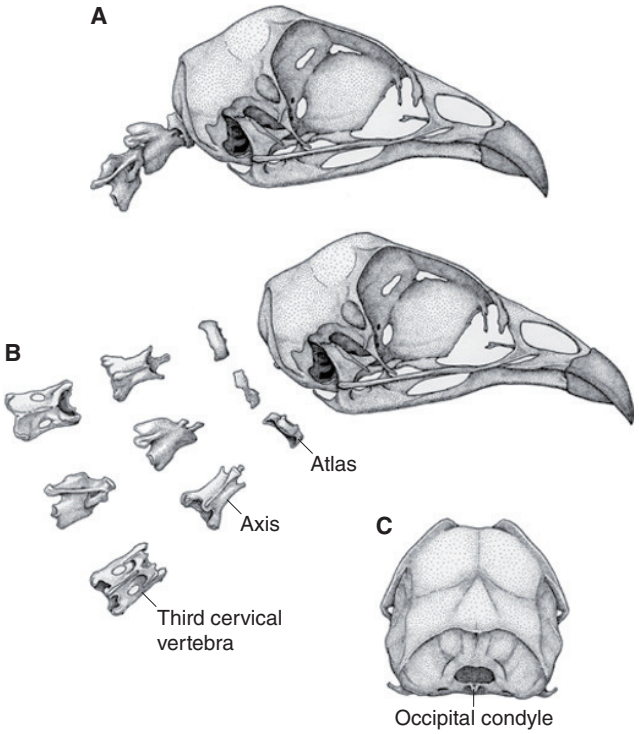


Fig. 6.09 Attachment sites and movement of the skull. These views of the skull and first three cervical vertebrae of a Ruffed Grouse (*Bonasa umbellus*) show how these bones fit together to allow almost full rotation of the head. The occipital condyle is a small bulge extending from the posterior base of the skull. The first cervical vertebra—the atlas—fits into the occipital condyle via peg-like processes, which permit spinal movement while maintaining head and neck support. The second cervical vertebra, the axis, similarly connects with the atlas. (A) The bones articulated in their natural orientation; (B) the first three cervical vertebrae from above (dorsal), side (lateral), and below (ventral) views; and (C) the back of the skull. (Illustration by Misaki Ouchida © Cornell Lab of Ornithology.)

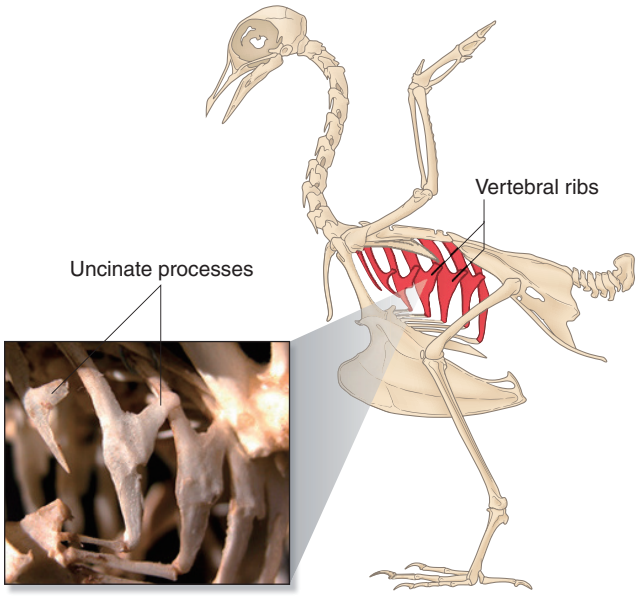


Fig. 6.10 Uncinate processes of vertebral ribs. These structures provide an increased surface area for muscle attachment, strengthening the ribs. They exist only in birds and some reptiles. (Illustration adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press. Photograph by Renn Tumlison, Henderson State University.)

residual from the period when every tetrapod vertebra had associated ribs. When cervical vertebrae support ribs, which may not reach the **sternum** (breastbone), it is difficult to distinguish them from thoracic vertebrae; therefore, the term cervicodorsal vertebrae is sometimes used for this entire region.

When a rib articulates with the sternum, either directly or by a ligament, the associated vertebra is considered a thoracic vertebra. Most birds have four to six thoracic vertebrae. In chickens, pigeons, herons, flamingos, and many other birds, some of the thoracic vertebrae fuse with one another to form a notarium, which provides even more rigidity to the backbone.

The ribs, together with the thoracic vertebrae above and the sternum below, form a bony **thoracic cage** enclosing the heart, liver, and lungs as well as the thoracic air sacs. Each thoracic rib has a dorsal and a ventral part connected by a cartilaginous hinge. The upper or vertebral rib articulates with a thoracic vertebra; the lower segment or sternal rib articulates with the sternum. Because a bird has no diaphragm to produce negative pressure for drawing in air, this hinged arrangement allows the thorax to act as a bellows. The sternum moves downward and forward to expand the thorax during inhalation, then upward and backward for compression during exhalation. The inhaled air enters the air sacs, which expand. The lungs remain the same size during inhalation and exhalation because they are fixed between the ribs and vertebrae within the thoracic cavity.

Unique to birds and some reptiles, flat extensions of bone called uncinate processes project caudally from the vertebral ribs. Each process overlaps with the rib behind it, providing more secure attachment sites for the muscles, which in turn strengthen the rib cage (Fig. 6.10).

Sternum: the breastbone; it provides an attachment site for the ribs and pectoral muscles. In all flying birds except tinamous, the sternum has a keel (carina).

Thoracic cage: the rib cage; in birds it consists of the ribs connected to the thoracic vertebrae above and to the sternum below.

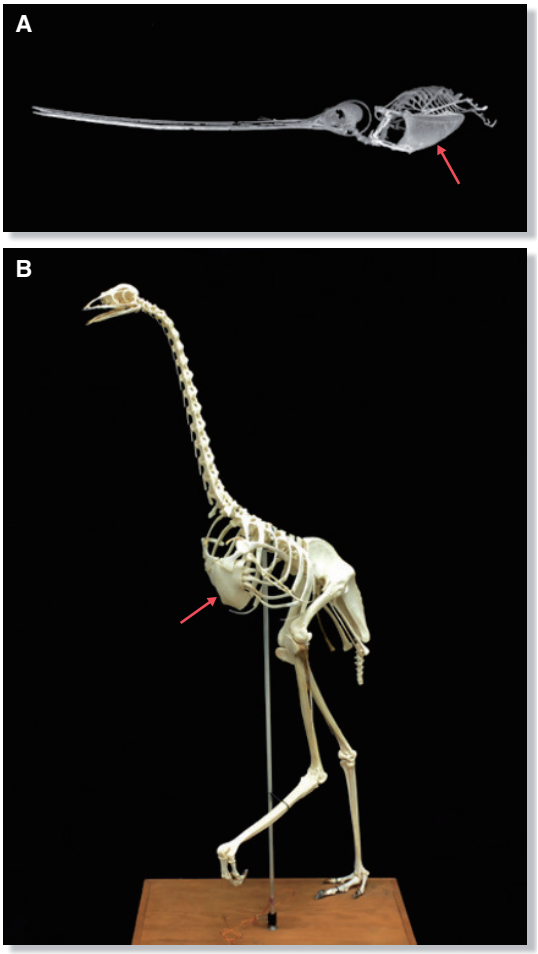


Fig. 6.11 Carinates and ratites. (A) Flying birds have a keel or carina (arrow), a broad and sturdy attachment site for robust flight muscles, protruding from their sternum. The Sword-billed Hummingbird (*Ensifera ensifera*) has one of the largest carina-to-body-size ratios, an indication of its powerful flying ability. (B) Large, flightless birds like this Emu (*Dromaius novaehollandiae*) have no need for a carina; ratite sternums are therefore flat (arrow). (A, photograph courtesy of Slater Museum of Natural History, University of Puget Sound. B, photograph by Barry K. Rhoades, Wesleyan College.)

Some birds, called carinates, have a ridge along their sternum called the mid-ventral **keel**, or **carina**. The pectoralis and supracoracoideus muscles, which provide power for each wing stroke during flight or swimming, attach to the carina and constitute about one-fifth of the muscle weight of most birds. By looking at a bird's sternum, one can judge the relative size of its pectoral muscles and consequently its flying ability. Hummingbirds, which are agile fliers, have the largest keel of any bird relative to body size (Fig. 6.11A). Large, flightless birds such as the Ostrich (*Struthio camelus*) of Africa, Emu (*Dromaius novaehollandiae*) of Australia, rheas (*Rhea* species) of South America, and cassowaries (*Casuarius* species) of New Guinea have flat, raft-like sternums with no carina (Fig. 6.11B).

Although a solid sternum is more functional for breast muscle attachment, notches and openings exist on the sternum of some bird species. In birds like chickens and turkeys, long processes called xiphisternal horns protrude from each side of the sternum. Covered by a sheath of fibrous tissue called fascia, they serve as attachments for breast muscle. In other birds, such as pigeons, the sternum may have only a notch. If the notch closes as the bird ages, as it does in parrots, only an opening, or sternal foramen, may be left.

A unique feature of the avian vertebral column is the **synsacrum** (Fig. 6.02C). It consists of a fusion of a few lower thoracic vertebrae with all of the lumbar, all of the sacral, and the first few caudal vertebrae. This rigid segment is fused in turn with the ilium, the upper part of the pelvis. The number of vertebrae involved in the bird's synsacrum varies from 10 to 23, depending on the species.

A bird's tail consists of four to nine non-fused caudal vertebrae and a terminal triangular bone called the **pygostyle**, which is formed by several fused vertebrae (Fig. 6.08). The rectrices, or tail feathers, attach to the pygostyle. In woodpeckers, a shield-like disk on the caudal margin of the pygostyle serves as a special attachment for the muscles that depress their rectrices for balance while climbing a tree.

6.1.3 Appendicular skeleton

The avian appendicular skeleton consists of the wing and leg bones, along with their supporting pectoral (shoulder) and pelvic (hip) girdles (Fig. 6.12).

Three bones on each side of the body—the clavicle, the coracoid, and the scapula—form the shoulder or pectoral girdle (Fig. 6.13), which provides anchorage for the wing to pivot upon. In nearly all birds, an interclavicle fuses

Keel: a mid-ventral ridge of bone that projects outward from the sternum and provides an attachment site for the pectoral flight muscles. Synonymous with carina.

Carina: a mid-ventral ridge of bone that projects outward from the sternum and provides an attachment site for the flight muscles. Synonymous with keel.

Synsacrum: the segment of the vertebral column of birds that is formed by the fusion of some thoracic vertebrae with all of the lumbar and sacral vertebrae and the first several caudal vertebrae.

Pygostyle: the tail bone of birds, formed by the fusion of the final several caudal vertebrae; it provides an attachment site for the flight feathers of the tail.

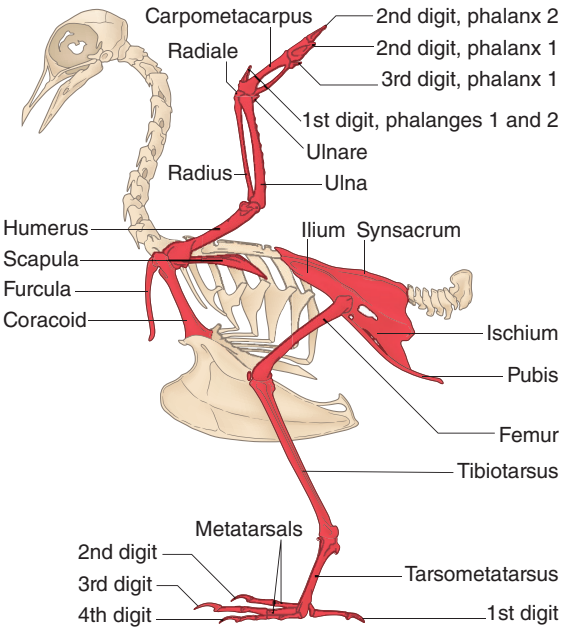


Fig. 6.12 Appendicular skeleton. Consisting of the bones that protrude laterally from the axial skeleton, the appendicular skeleton (shaded) supports movements associated with flying, running, swimming, and jumping. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

the right and left clavicles to form the **furcula**, a single V-shaped bone popularly known as the "wishbone." In most birds, the ventral end of the furcula is attached to the sternum by a ligament, but in a few birds, such as pelicans, the two bones are actually fused together. In frigatebirds, the coracoids fit tightly to the sternum, but the actual bone-to-bone fusion occurs between the coracoid and the furcula. The Budgerigar (*Melopsittacus undulatus*) and most other parrots have only small remnants of the clavicle on each side; some parrot species have lost the clavicle completely.

Coracoids, the stoutest and strongest bones of the pectoral girdle, hold each shoulder away from the body. The coracoid and scapula meet to form a shallow depression, the glenoid fossa or shoulder joint, in which the head of the humerus wing bone articulates (Fig. 6.13). The broad base of each coracoid bone fits into a groove on the anterior end of the sternum, while each upper end articulates with the scapula and clavicle. This forms an opening called the canalis triosseus, or supracoracoid foramen. In penguins, this foramen (a general term for opening) is very wide, allowing

Furcula: a V-shaped bone of the pectoral girdle in birds, formed by the fusion of the right and left clavicles with a small interclavical bone. Commonly called the "wishbone."

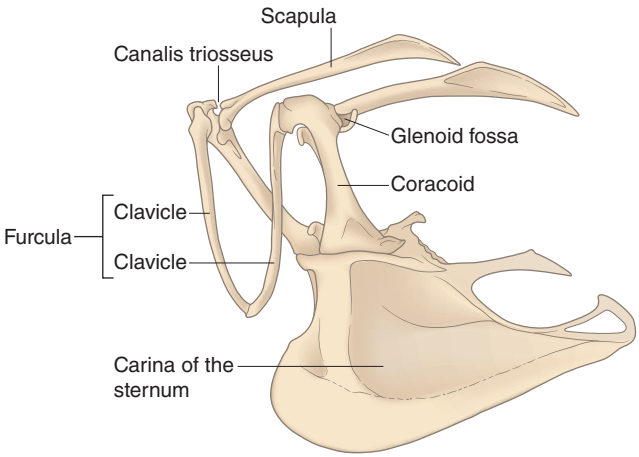


Fig. 6.13 Pectoral girdle. The upper part of the appendicular skeleton is the pivot point for powered flight. Major bones in the pectoral girdle include the clavicles (typically fused into a single furcula, or "wishbone"), coracoids (strong bones that hold the shoulder away from the body), and scapula (which meets the coracoid via the glenoid fossa and forms the canalis triosseus with the clavicle). (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

the correspondingly large supracoracoideus muscle to pull the wing forward and upward—a difficult task in swimming, as the upstroke occurs against the force of the water. Similar to a bowsprit, which projects from the front of a sailboat to provide support for the mast's ropes, the coracoid projects from the sternum to provide the wing with a fixed pivot point away from the body.

Modern flightless birds show the same basic arrangement of the wing skeleton as flying birds. Wing bones in penguins are simply shortened, flattened, and generally strengthened in a collectively blade-like manner, forming a flipper to suit the requirements of swimming underwater. Ratite wing bones are also substantially reduced in size and strength. This is especially true for the kiwis of New Zealand, whose tiny wings are hidden beneath their hair-like feathers (Fig. 6.14).

The metacarpals (hand bones) and digits of birds' forelimbs (wings) are short and small in number. Several carpal and metacarpal bones have been fused together to form the carpometacarpus, leaving only two carpals in the wrist. All birds have three short fingers, which consist of one phalanx or two phalanges (finger bones) (Fig. 6.15).

In a variety of birds—swans, ducks, cranes, rails, owls, some passerines, and others—claws may extend from the terminal phalanges. Young Hoatzins (*Opisthocomus hoazin*), pheasant-like birds of the Amazon Basin, have temporary claws on their wing digits. When threatened by a predator, Hoatzin nestlings leap from their nests—usually built above water—and use their wing claws to climb back up after the danger has passed (Fig. 6.16A). However, the wing claws on embryos or the young of most living species

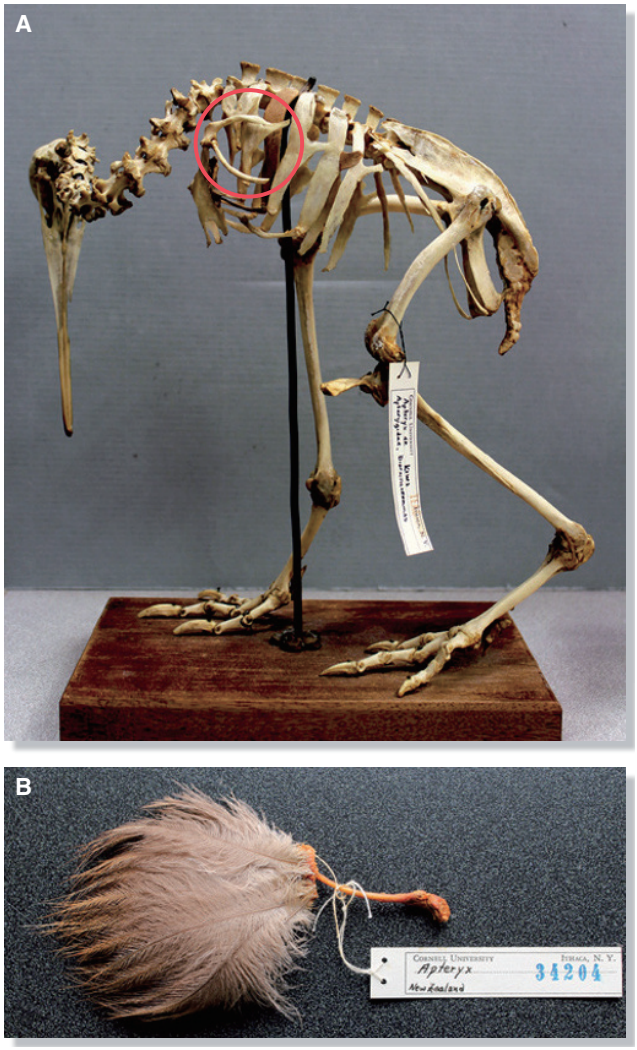


Fig. 6.14 Reduced wing bones of the flightless kiwis. (A) Fully grown kiwis (genus *Apteryx*) have proportionally small wing bones (circled). (B) This is an entire kiwi wing; hair-like feathers attach to the primary wing bones. (Photographs by Alexandra Class Freeman, courtesy of Cornell University Museum of Vertebrates.)

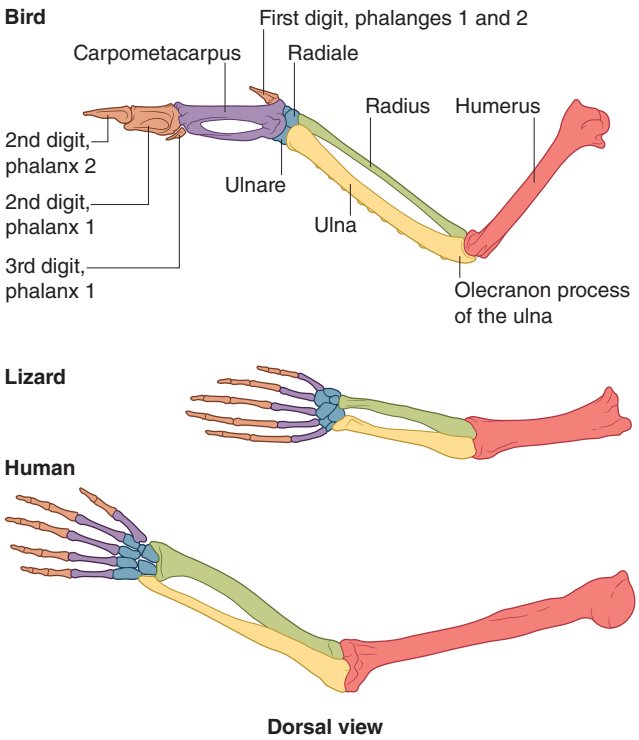


Fig. 6.15 Homologies in forelimb bones of three tetrapod vertebrates. Birds are unique in that they have reduced wrist and digit bones compared with other tetrapods. (Top, adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press. Bottom, © Cornell Lab of Ornithology.)

are likely **vestigial**, holdover structures from ancestral species that have lost their function. Many ancient groups of birds had claws, including the Enantiornithes (Chapter 2). Claws are associated with digits and are not synonymous with spurs (although some birds have both).

Spurs are bony outgrowths that can occur anywhere on the appendicular skeleton. Birds with wing spurs include cassowaries, screamers, some plovers, sheathbills, and jacanas (Fig. 6.16B). In male fowl and pheasants, bone growth is stimulated around a spur papilla on the skin of the tarsometatarsus (Fig. 6.16C). Wing and leg spurs are often employed in aggressive disputes. Indian Peafowl (*Pavo cristatus*) use their spurs to fight for territories and mates; domestic chicken (*Gallus gallus*) cocks sometimes fight to the death, causing much bloodshed with their leg spurs.

Transitioning to the hip and leg region, the pelvic girdle has three bones on each side: the ilium, ischium, and pubis (Fig. 6.17). The right and left ilia are fused to the synsacrum, forming a rigid support for each half of the pelvis. In all birds except rheas (whose pubic bones connect ventrally), the pelvis is open below, which facilitates the laying of large eggs (Fig. 6.18).

The femur is relatively short in all birds. The easily visible, usually unfeathered part of the leg is called the tarsus by most ornithologists, but this designation is a bit of a misnomer. That area is composed mostly of fused metatarsal bones, homologous with the human foot between the ankle and the base of the toes. The distal portion of the tibia fuses with the proximal tarsal (ankle) bones to form the tibiotarsus. The tibiotarsus is generally the longest leg

Vestigial: describes a structure with little current apparent function that is thought to be present solely because it derives from a structure that was functional in an ancestor.

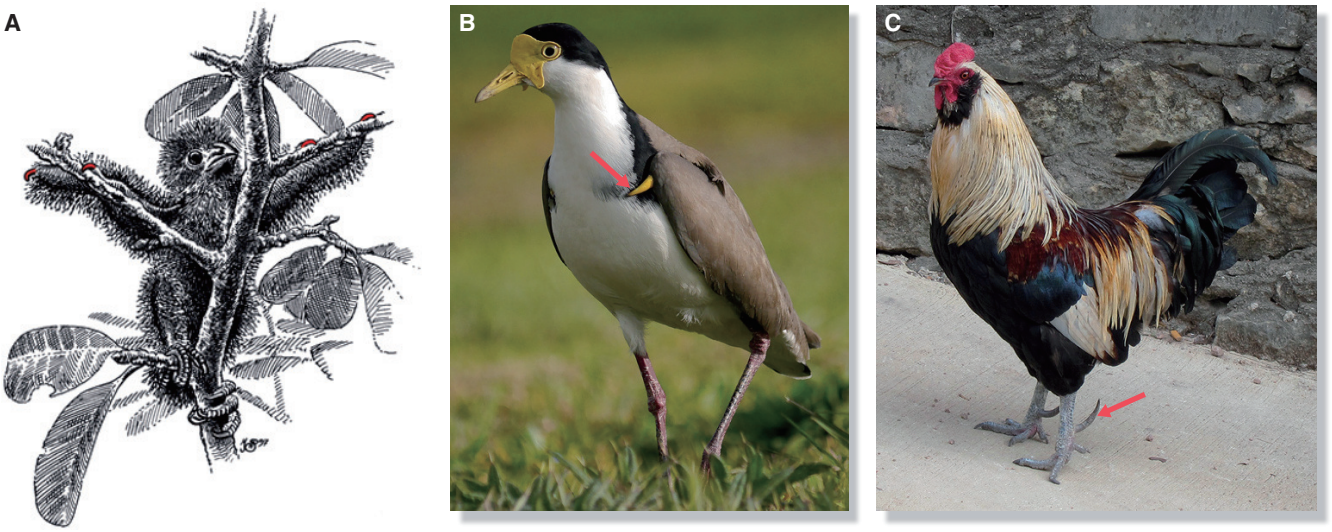


Fig. 6.16 Wing claws versus spurs. (A) Fledgling Hoatzins (*Opisthocomus hoazin*) leap from their nests to escape predators and subsequently use their wing claws (colored, two per wing)—which grow out like nails from their digits— to climb back into their nests. (B) Wing spurs (arrow) grow from bone that is surrounded by a keratinized sheath, as demonstrated in this Masked Lapwing (*Vanellus miles*). (C) Leg spurs (arrow) develop in a similar way to wing spurs, and are prominent in roosters and other territorial birds that employ them as weapons. (A, illustration by N. John Schmitt. Photographs by: B, Kaylene Helliwell; C, Wayne D. Roth.)

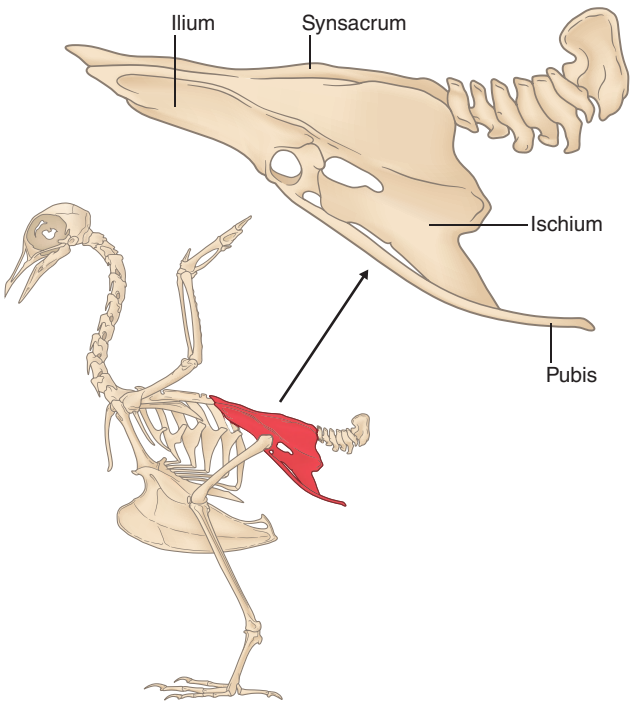


Fig. 6.17 Bones of the pelvic girdle. Three bones—the ilium, ischium, and pubis—are fused to the synsacrum and provide stability to the hips. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

bone in birds, double the length of the femur in large wading birds. The fibula is a splint-like bone that articulates with the lateral condyle (a round bump on a bone that forms a joint) of the femur. The distal end of the fibula has been reduced over evolutionary time. The second, third, and fourth metatarsals fuse with the distal tarsal bones to form the tarsometatarsus, where the toes attach (Fig. 6.19).

The small head of the femur fits deeply into the hip joint or acetabulum. At the lower end of the femur, a patella or kneecap glides in a deep trochlear groove, adding stability to the knee joint. The patella is a bone embedded within the tendon of the quadriceps muscle, a major extensor of the knee joint. In several birds, the patella fuses with the cnemial crest, a ridge at the head of the tibiotarsus for muscle attachment that serves as a projecting lever arm for more rapid extension of the leg. The area that appears to be the knee of a bird is actually the intratarsal joint, which is homologous with the ankle in humans (Fig. 6.19). Thus, birds are digitigrade, walking only on their toes.

Most birds have four toes on each foot, although some have three. The Ostrich (*Struthio camelus*) is unique among living birds in having only two toes. Groups with only three toes include most of the other ratites (Fig. 6.20A), some shorebirds such as most plovers and the Sanderling (*Calidris alba*), some tree-climbing insectivorous birds including several woodpeckers (Fig. 6.20B), and some birds known for their ability to swim underwater, such as diving-petrels, auks, murres, and puffins. Several different configurations of toes exist among birds, with whole orders and families often exhibiting a particular configuration (Box 6.02).

The claws extending from each terminal foot phalanx often reflect a bird's habits. Species that climb tree trunks, such as nuthatches and creepers, usually have strongly curved claws that help them grasp irregularities on bark



Fig. 6.18 An open pelvis facilitates egg laying. As shown in this X-ray, kiwis lay exceptionally large eggs relative to their body size, a feat made possible by their open pelvic bones. (Photograph courtesy of Otorohanga Kiwi House, New Zealand.)

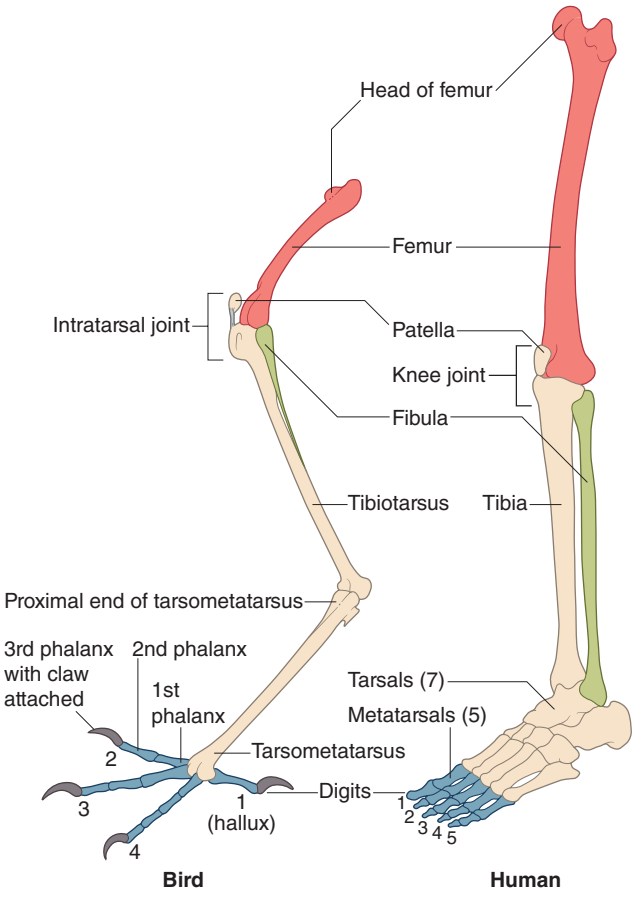


Fig. 6.19 Leg bone homology in birds versus humans. Colored bones are homologous in birds (left) and humans (right). Birds have several fused bones that are composites of separate bones in humans. For example, the tibiotarsus in birds is essentially a combination of the knee joint, tibia, and upper tarsus bones in humans. Similarly, the tarsometatarsus in birds is a fusion of the lower tarsus and metatarsal bones in humans. (Adapted from Brooke and Birkhead 1991. Reproduced with permission from Cambridge University Press.)

without impairing their ability to perch. Many ground-dwelling songbirds such as larks and pipits are noted for their long hind claws (Fig. 6.21A), which may help them avoid sinking into mud, sand, or other soft surfaces. In a few birds, including Barn Owls (*Tyto alba*), nightjars, and herons, the claw of the third digit has a comb-like, serrated edge (Fig. 6.21B). This **pectinate claw** (sometimes called a "feather comb") likely functions as a preening or parasite-removal tool.

6.2 Muscular system

The major role of any skeleton is to facilitate locomotion, but bones cannot move themselves or maintain posture without muscles. Muscle is a tissue composed of contractile fibers that shorten when stimulated by a nerve impulse. When muscles contract, they produce both movement and heat. Tendons attach muscles to bones, transmitting the force of muscles as they contract. Due to the centralization of muscles, the route between a muscle and its eventual insertion into a bone can be long and complex. For example, muscles in the upper leg of birds flex the toes after passing over the intervening ankle and digit joints.

Skeletal muscles—which often have names that indicate their function, location, shape, or derivation—move the skeleton, while smooth muscles are associated with the digestive tract and blood vessels. The heart is made of a special kind of involuntary muscle called cardiac muscle.

Pectinate claw: a modification of the side of the middle toe claw into a comb-like, serrated edge used for preening.

Box 6.02 Avian toe configurations

Toe configurations vary among groups of birds, and they often provide clues about a bird's lifestyle. As a standardized reference, the toes are numbered from inside (medially) to the outside (laterally), so that the rear-facing hallux is the first toe (Fig. 6.B2.01A). The "classic" bird foot form, termed anisodactyl, has four toes in total, with the hallux orientated rearward and the remaining three toes pointing forward. This form is typical of passerines, doves, hawks, and many other birds. Another fairly common foot form is termed zygodactyl, in which the fourth toe is oriented posteriorly, or rearward, along with the hallux. This foot form is found in cuckoos, woodpeckers, parrots, and others. Owls are flexible, but typically sit in a zygodactyl arrangement. Other relatively rare toe configurations include heterodactyl (toes one and two back, as in trogons), syndactyl (middle toes connected, as in some kingfishers), and pamprodactyl (four toes forward, as in swifts). Birds that routinely perch on branches usually are anisodactyl, with a strong hallux, or zygodactyl. Ground-dwelling and aquatic birds may have the anisodactyl arrangement with a reduced or nearly vestigial hallux.

The degree of webbing between toes also varies (Fig. 6.B2.01B). Ducks and gulls provide good examples of palmate feet, in which the front three toes are completely webbed together. The hallux is additionally webbed to the second toe in totipalmate feet (as in pelicans). Many shorebirds sport semipalmate feet, in which the front three toes are partially webbed together at their bases. Finally, some semiaquatic birds such as coots and grebes have lobate feet, in which each toe is bordered by its own webbing to assist with foot-propelled swimming.

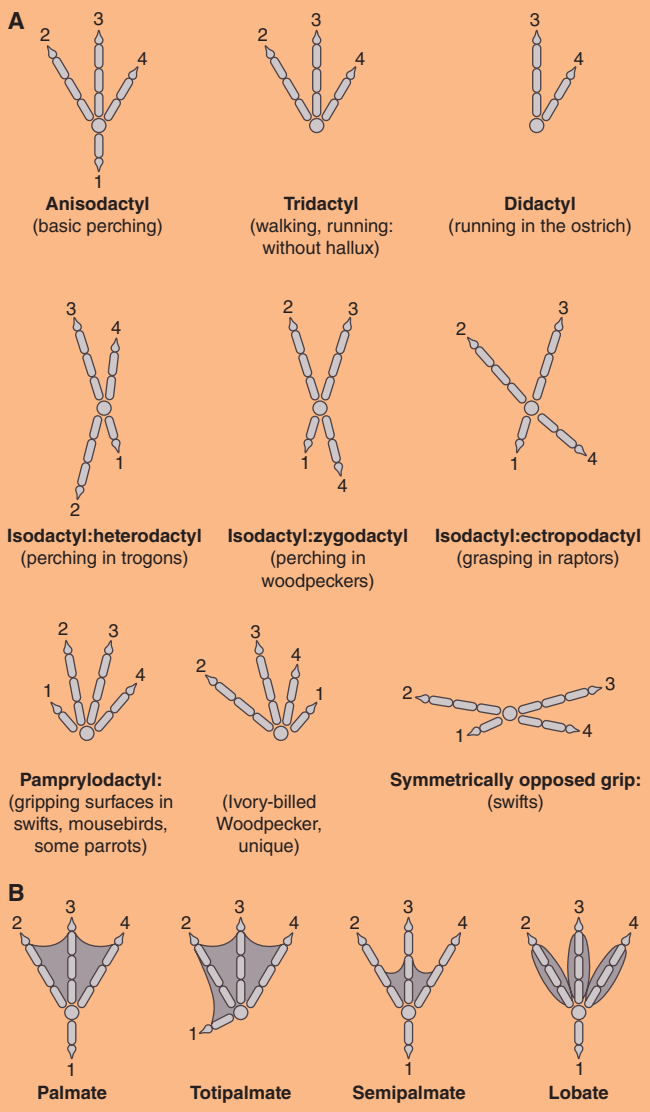


Fig. 6.B2.01 Avian toe arrangements and webbing. (A) Bird toes come in many distinct arrangements. The hallux (big toe) is always numbered first. (B) Birds that swim or forage on wet, muddy, or uneven substrates often have webbing between their toes, which increases weight distribution and/or force during swimming. (A, adapted from Kaiser 2007. Reproduced with permission from University of British Columbia Press. B, adapted from Darekk2, https://commons.wikimedia.org/wiki/File:Bird_feet_-_webbing_and_lobation_EN.gif. CC-BY-SA 3.0.)

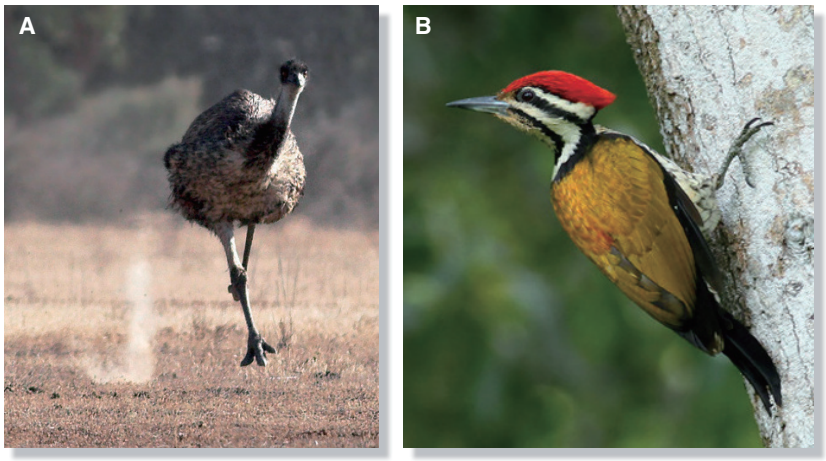


Fig. 6.20 Birds can have different numbers of toes. Although most birds have four toes, some species only have three, including (A) the Emu (*Dromaius novaehollandiae*) and (B) the Olive-backed Woodpecker (*Dinopium rafflesii*). (Photographs by: A, Julian Robinson; B, Eddy Lee Kam Pang.)

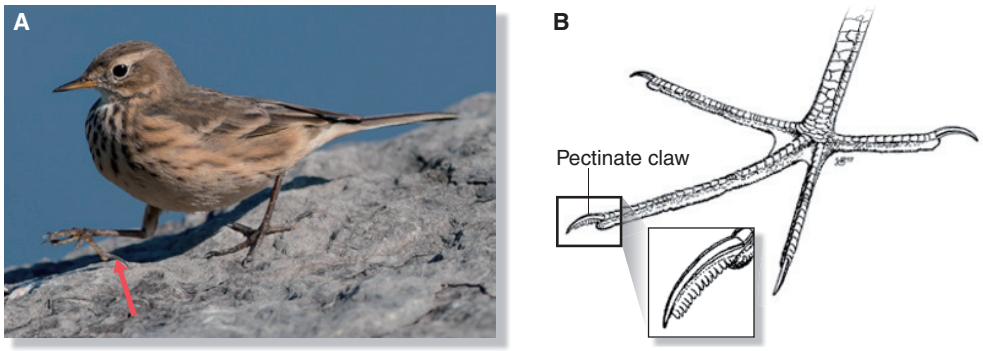


Fig. 6.21 Functions of the avian claw. Different groups of birds use the claw on their terminal digit in various ways. (A) American Pipits (*Anthus rubescens*) are thought to use their elongated hind claw (arrow) to balance on soft substrates as they walk along the ground. (B) A few birds, including herons and some owls, have a pectinate claw on their third digit, a serrated edge that may preen or remove parasites when combed through the feathers. (A, photograph by Bill Reid; B, illustration by N. John Schmitt.)

6.2.1 Skeletal muscles

Skeletal muscles move the bones and constitute what we generally term the "meat" of an animal (Fig. 6.22). The actions of skeletal muscles are under conscious control and they are therefore often referred to as voluntary muscles. Each muscle consists of several hundred to several thousand muscle fibers bound together by a thin and shiny connective tissue called a fascia. Bridging one or more joints, these bundles of fibers attach to the bone in order to produce movement at the joint when the muscles contract. Connecting fasciae may form a tendon (which in bird limbs may ossify, especially in the legs). Shiny, broad sheets of fasciae that do not form tendons are called aponeuroses.

Skeletal muscles that move the wings and legs act antagonistically: when one contracts, the other relaxes in a continuous fashion, producing smooth movements. An example of this muscular antagonism occurs during powered flight or wing-propelled swimming. The pectoralis muscle is responsible for powering the downstroke and the supracoracoideus powers the upstroke. The muscles are positioned on top of one another on the sternum. On the downstroke, the pectoralis muscles contract, pulling the wing bones down (Fig. 6.23A). Simultaneously, the supracoracoideus tendon—which passes through the supracoracoid foramen like a pulley—relaxes, allowing the muscles to extend and release the humerus downward. On the upstroke, the pectoralis muscles stretch, allowing the supracoracoideus to contract and pull the humerus upward via a foramen (passage through the bone) called the canalis triosseus (Fig. 6.23B). The tips of the furcular then return to their relaxed position. More force is required to produce lift from the downbeat of the wing; the pectoralis muscle is therefore the largest muscle in flying birds. Among birds

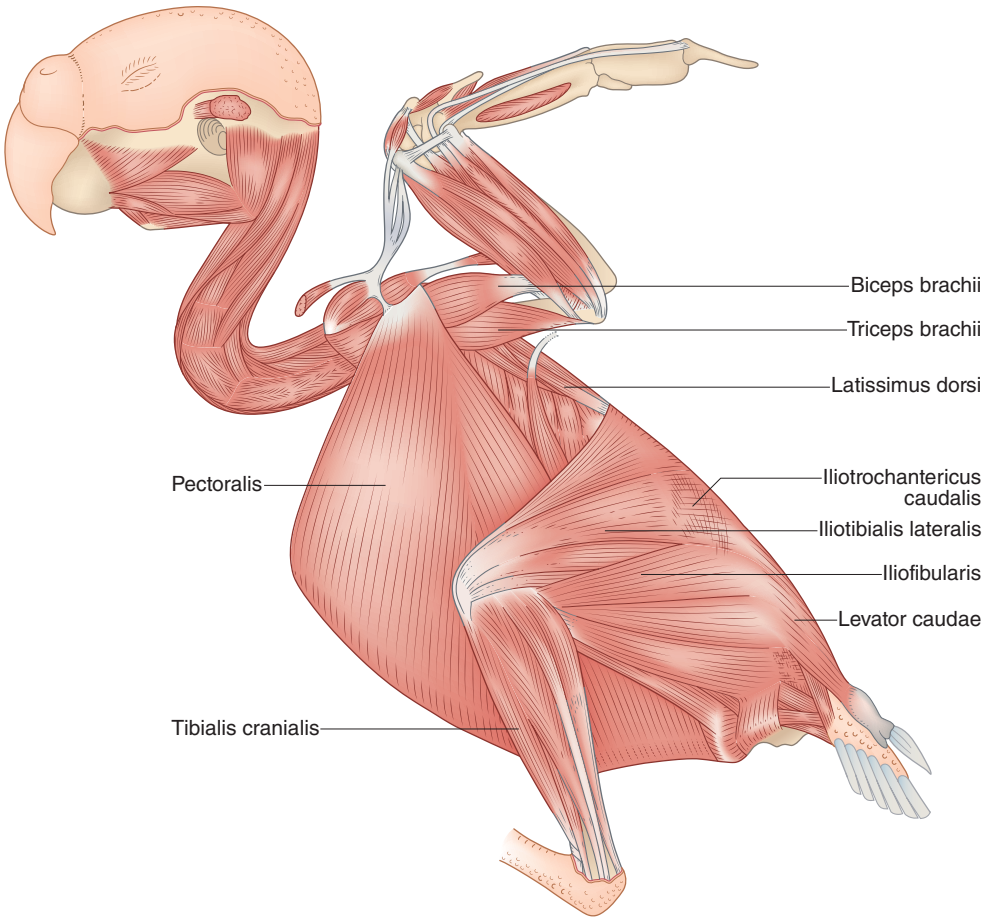


Fig. 6.22 Skeletal muscles. The major voluntary skeletal muscles of a bird are labeled. Each skeletal muscle consists of several hundred to several thousand individual muscle fibers, bound together by thin connective tissue. Bundles of skeletal muscle fibers attach to bones, producing movement at the joints when the muscles contract. Layers of thin connective tissue form fascia, which in turn form tendons connecting to bone. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

that can fly, relative flight muscle weight often correlates with flying ability: for example, the weight of the pectoralis and supracoracoideus muscles in hummingbirds—swift and maneuverable fliers—may equal 21–34% of their total weight, while these same muscles account for only about 8% of total weight in reluctant fliers like rails.

6.2.2 Smooth muscle

Smooth muscle, also known as involuntary (visceral) muscle, is composed of spindle-shaped cells with a central nucleus. Smooth muscles are normally not under voluntary control. These muscles are found in the walls of hollow organs, such as the stomach, as well as in the walls of smaller blood vessels—arterioles and arteries that distribute the heat produced by muscle contraction.

Cardiac muscle is a special category of smooth muscle that forms the bulk of the heart. The muscle fibers are arranged in a network or syncytium of nerve fibers with central nuclei. Cardiac muscle is capable of rhythmic contractions under involuntary control.

6.3 Respiratory system

The avian respiratory system is unique among vertebrates: birds have relatively small, non-inflatable lungs and nine air sacs that play an important role in ventilation but are not directly involved in the exchange of gases. The air sacs are thin walled and opaque, extending throughout the body cavity and into the hollow bones of birds. Air flows in through the nostrils and mouth of a bird and then travels through its trachea and a series of smaller and smaller tubes (the bronchial system) into the lungs and air sacs.

In large part due to an extremely efficient respiratory system—which, for example, delivers oxygenated air during

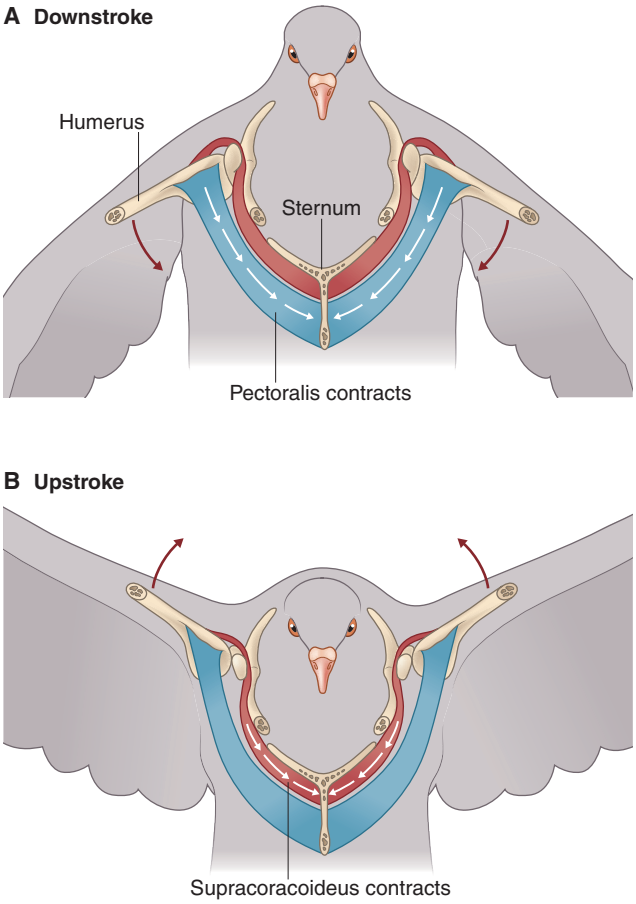


Fig. 6.23 Skeletal muscle opposition powers flight. (A) The downstroke is powered by the contraction of the large pectoralis muscles (red), which work to pull the humerus down as the supracoracoideus stretches (blue). (B) During the upstroke, the supracoracoideus contracts, enabling its tendon to pull the humerus up while the pectoralis muscles stretch. (© Cornell Lab of Ornithology.)

both inhalation and exhalation—many birds can seamlessly move between normal atmospheric pressures and areas of low oxygen. A Swainson's Thrush (*Catharus ustulatus*) might depart from sea level in Florida (USA) on its fall migration, and fly at altitudes of over 2000 meters on the way to its South American wintering grounds; a King Penguin (*Aptenodytes patagonicus*) might routinely reach depths of 200 meters during a series of 4-minute dives. These species and many others accomplish such feats via adaptations in their respiratory and circulatory systems.

6.3.1 Nostrils and nasal cavities

In birds, the nostrils—or **nares**—usually occur at the base of the bill and open into the nasal cavities. Nares occur in different shapes and sizes, depending on the species. Many ground-feeding birds, such as starlings, pigeons, and domestic chickens, have independently evolved a protective flap called an operculum. This structure partially covers the nares, presumably to keep out debris (Fig. 6.24A). Some diving species also have opercula, which keep water from entering the nostrils. The nares of raptors, curassows, and some parrots are located in a leathery band of skin known as the **cere**, a structure that extends across the base of the maxilla (Fig. 6.24B). Ceres often serve as sexual signals, indicating a bird's sex and/or condition. Kiwis, which have an unusually keen sense of smell and extremely large

Nares: the two openings of the nasal cavity located in the upper beak, usually near its base. Singular: naris.

Cere: a leathery band of skin covering the base of the bill in some birds, into which the nostrils open.

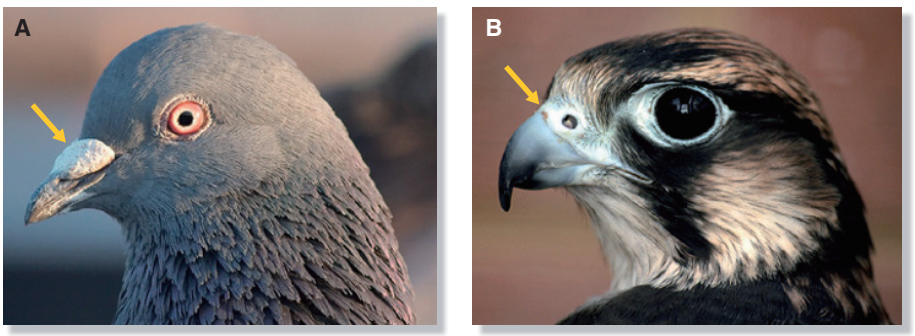


Fig. 6.24 Variation in naris anatomy. Some species have evolved nasal coverings to keep out debris, food, and water (depending on their ecology). (A) Ground-feeding birds like this Rock Pigeon (*Columba livia*) have a protective skin flap called an operculum that extends partially over their nares, potentially to keep out debris. (B) Like most birds of prey, Saker Falcons (*Falco cherrug*) have ceres, protective skin over the maxilla, to protect the nares. (Photographs by: A, Dori, https://commons.wikimedia.org/wiki/File:Pigeon_portrait_4861.jpg. CC-BY-SA 3.0; B, Keven Law, Los Angeles, USA, https://commons.wikimedia.org/wiki/File:Saker_Falcon_profile_shot.jpg. CC-BY-SA 2.0.)

olfactory bulbs in the brain, are the only birds with nostrils near the tip of the bill—presumably to smell invertebrates while rummaging through leaf litter on the forest floor. The nares are completely closed in adult gannets, frigatebirds, cormorants, and anhingas; a functional secondary nare is formed by a gap at the base of the bill, allowing these birds to breathe through their mouths with a closed bill (MacDonald 1960). Albatrosses, petrels, and other ocean-living members of the Procellariiformes have nares encased in extended tubes. The function of the tubes is still under debate, but they may help in detecting the direction of odors; this order has the most developed sense of smell known in birds, and they use olfaction for finding food and for navigation to nesting islands (Chapter 7).

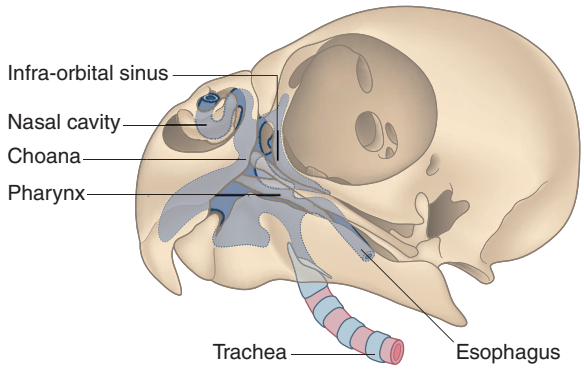


Fig. 6.25 The choana. The choana is a single slit on the roof of the mouth that, when open, allows air to enter through the nares, and when closed, seals the oral cavity. This schematic depicts the choana in a Budgerigar (*Melopsittacus undulatus*), with the infraorbital sinus situated posterior to the choana, and the pharynx (where digestive and respiratory functions meet) below. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

Internally, a medium septum usually divides the nasal cavity in half, although in many bird species the nares are completely open and daylight can be seen through the bill. The two nasal cavities lead back, opening into the roof of the mouth through a single slit, the choana (Fig. 6.25). A large infraorbital sinus, in communication with the nasal cavity and an air sac behind the skull, is usually present on each side beneath the eye. Each cavity filters inhaled air via mucus and small hair-like structures called cilia. Vascularized, scroll-like projections called conchae (Fig. 6.26) occur within each nasal cavity as well and are covered by a mucous membrane. Embedded with olfactory neurons, this membrane allows the bird to smell when air passes over the conchae.

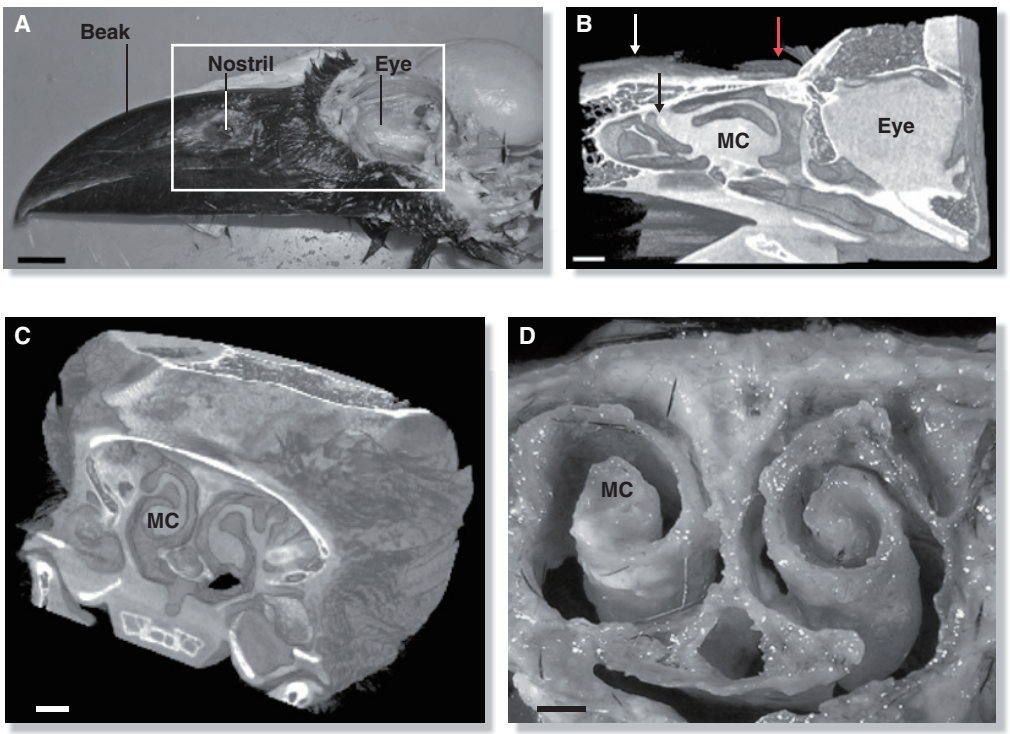


Fig. 6.26 Nasal conchae. (A) The boxed area on this head of a Large-billed Crow (*Corvus macrorhynchos*) is depicted in (B) a CT scan of the nasal region, including the large maxillary conchae (MC) inside the nares. (C) A CT scan of the skull also reveals these scroll-like MC pairs. (D) A cross-section shows the conchae structure; the nasal septum (st) bisects highly vascularized tissue that enables a bird to smell. Scale bars A–C = 10 mm, D = 1 mm. (From Yokosuka et al. 2009. Reproduced with permission from Oxford University Press.)

A duct from the salt gland, located in a shallow depression (fossa) above or within the eye socket, extends onto the sides of both nasal cavities. This gland, which is largest in marine birds, helps expel excess salt from the body. Albatrosses and other "**tubenoses**" excrete large amounts of excess salt in a fluid that travels into the nasal cavities, out the nostrils, and into grooves that extend to the bill tip. Salty fluid then drips away or evaporates far from the nostrils, reducing the possibility of residual salt clogging the entrances, perhaps because these birds rely so heavily on their sense of smell (Chapter 7).

6.3.2 Pharynx

The pharynx begins at the back of the tongue. Here, the pathways for food and air cross (Fig. 6.27A). Folds on the roof of the pharynx surround the openings to the nasal cavities and auditory tubes. From the middle ear cavity, the auditory tube enters the pharynx on the midline of the palate and allows air pressure to be balanced on both sides of the tympanic membrane. In the floor of the pharynx, laryngeal folds border the glottis, the entrance to the trachea. The entrance to the esophagus is behind the glottis.

6.3.3 Larynx

Situated above the trachea, a bird's larynx (Fig. 6.27B) does not contain vocal chords as it does in mammals. Rather than producing sound, its primary function is to serve as a valve, regulating the flow of air into the trachea. The slit-like glottis, or opening to the larynx, is behind the tongue, formed by two pieces of cartilage covered with a mucous membrane.

6.3.4 Trachea and syrinx

The trachea, or windpipe, is a tube that conducts air from the glottis of the larynx into the lungs and air sacs. A series of cartilaginous rings holds the trachea open for the passage of air. These rings telescope into or away from one another when a bird bends, extends, or shortens its neck. In most birds, the trachea follows a straight course from the glottis to the forking of the bronchi.

Some birds have unusually long trachea, an enhancement that may improve the resonance of their calls. In North America, the tracheas of the Trumpeter Swan

Tubenoses: birds in the order Procellariiformes—including albatrosses, shearwaters, fulmars, petrels, and storm-petrels—all of which have tube-shaped nares.

Syrinx: the primary sound-producing organ of birds, located at the point where the trachea divides to form the two bronchi.

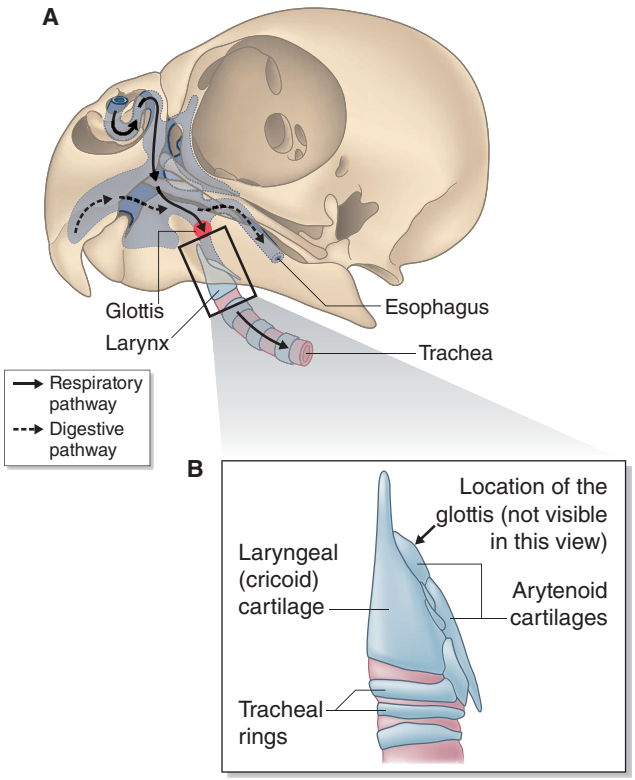


Fig. 6.27 Passageways into the throat. The avian pharynx is a dual passage for air and sustenance. (A) Nasal passageways bring air into the oral cavity (solid arrows), while food enters through the mouth and proceeds back to the esophagus (dashed arrows). In the floor of the pharynx, the slit-like glottis (shaded area) serves as the entrance to the larynx and trachea. (B) The larynx, a valve that allows air into the trachea, is composed of cartilaginous rings. (A, adapted from Evans 1996. Reproduced with permission from Howard E. Evans. B, adapted from Bock 1978. Reproduced with permission from Wilson Ornithological Society.)

(*Cygnus buccinator*), Tundra Swan (*Cygnus columbianus*), and Whooping Crane (*Grus americana*) enter the carina of the sternum and pass caudally within it before looping back to their point of entry, where they make another bend to enter the thoracic inlet. A few passerines, such as the Trumpet Manucode (*Phonygammus keraudrenii*) of Australia and New Guinea, have coiled tracheas (Fig. 6.28). Emus (*Dromaius novaehollandiae*) have several open tracheal rings that allow air to exit into a sac beneath the skin on the lower portion of the neck. Many ducks have a trachea expansion (bulb or bulla) on one side at the lower end just before the syrinx. These specializations modify the sounds produced.

The **syrinx** is the vocal sound-producing organ in birds (Chapter 10). A cartilaginous expansion covered by muscles, the syrinx lies at the lower end of the trachea where it branches into two bronchi before entering the lungs. The syrinx is formed by modifications of tracheal rings, bronchial half-rings, or a combination of both. Thus birds



Fig. 6.28 Coiled trachea. The Trumpet Manucode (*Phonygammus keraudrenii*) has an exceedingly long and coiled trachea, an adaptation that enhances the resonance of its call. (From van Grouw 2013. Reproduced with permission from Princeton University Press.)

can have a tracheal syrinx (Fig. 6.29A), separate bronchial syrinxes as in the cave-dwelling Oilbird (*Steatornis caripensis*) of northern South America (Fig. 6.29B), or, most commonly, a tracheobronchial syrinx (Fig. 6.29C).

In the avian syrinx, highly elastic tympanic membranes stretched between specialized syringeal cartilages and muscles vibrate to produce sound waves when air is forced past them. The syringeal muscles produce the different sounds within a bird's song or call by changing the tension of the membranes and the diameter of the constricted passage in the syrinx. An increase in the frequency of vibrations raises the pitch; an increase in the diameter of the passageway increases the volume.

Some species can control the two sides of the syrinx independently, allowing them to produce two different sounds at once (Chapter 12). Songbirds have an extremely complicated syrinx. In addition to complex muscle arrangements, songbirds have additional syringeal structures: a median cartilage called the pessulus at the bifurcation of the bronchi and a semilunar membrane extending from the pessulus into the cavity of the syrinx.

6.3.5 Lungs

In simple terms, bird lungs are masses of interconnecting air tubes (Fig. 6.30). Two small, non-inflatable lungs lie in contact with the vertebral column and ribs. The trachea

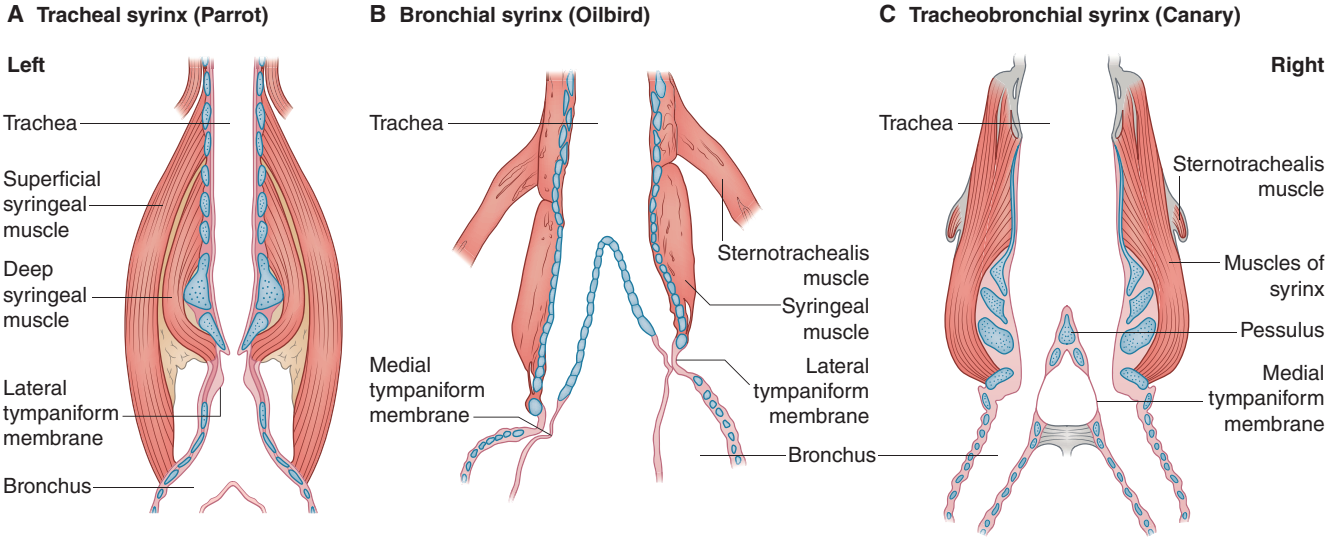


Fig. 6.29 Anatomy of the syrinx in three different birds. The syrinx is located at the lower end of the trachea, above the bronchial entrances. (A) Birds can have a tracheal syrinx, as in parrots; (B) separate bronchial syrinxes, as in the Oilbird (*Steatornis caripensis*); or (C) a tracheobronchial syrinx, as in the domesticated Island Canary (*Serinus canaria*) and many other birds. (Adapted from Suthers 2004. Based on illustrations in King and McLelland 1989, Suthers and Hector 1985, and Nottebohm and Nottebohm 1976. Reproduced with permission from Elsevier.)

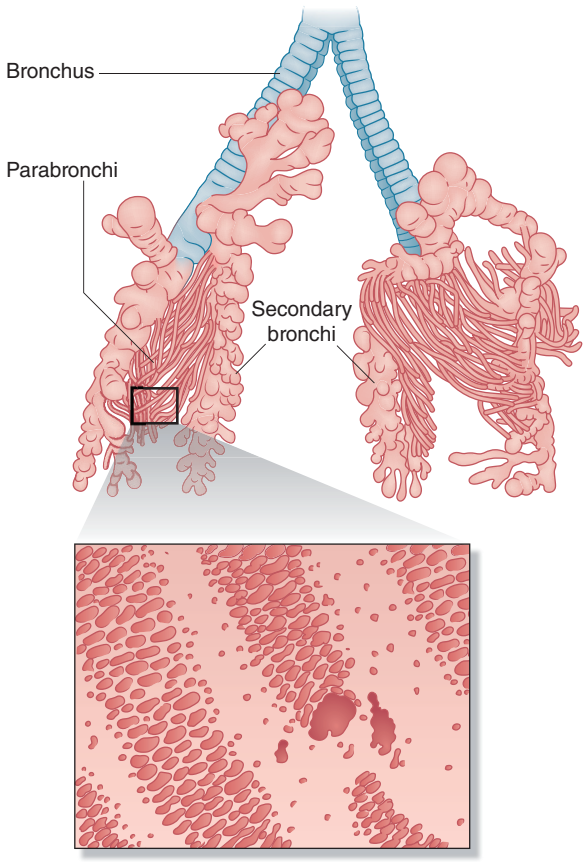


Fig. 6.30 Anatomy of the avian lung. Bird lungs are non-inflatable and relatively stiff. The trachea splits into dual bronchi on opposite sides of the bird. Primary bronchi shrink in diameter as secondary bronchi branch off in numerous locations before passing into the lung. Small and abundant, secondary bronchi branch further into parabronchi, the main respiratory unit of the lungs. (Top, illustration of a cast of these air spaces, courtesy of Howard E. Evans. Bottom, adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

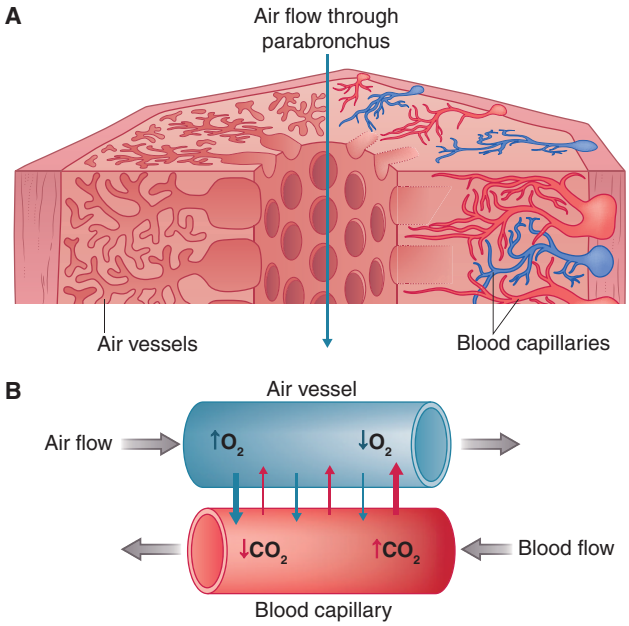


Fig. 6.31 Function of parabronchi. (A) Parabronchi supply fresh oxygen via air vesicles (capillaries) for the air exchange that occurs in capillary networks that run through the lungs. (B) After carbon dioxide is exchanged for oxygen within the air capillaries, it is transported into the arterioles. Deoxygenated blood flows back out through the pulmonary venules. (A, adapted from Brooke and Birkhead 1991. Reproduced with permission from Cambridge University Press. B, © Cornell Lab of Ornithology.)

splits into two bronchi; as each bronchus enters its respective lung, the half-rings of cartilage disappear. Each continues as the primary bronchus or mesobronchus through the lung, gradually decreases in diameter, and ends at the entrance to the abdominal air sac. Many secondary bronchi branch off the mesobronchus and pass into the lung. Most of these secondary bronchi branch again to form parabronchi, which are the major respiratory units of the lung. Air moves to the ventrobronchi after passing through the parabronchi.

The parabronchi are tightly packed, thick-walled tubes; parabronchial walls contain hundreds of air vesicles within the tissue, sometimes called air capillaries, which intertwine with a network of blood capillaries (Fig. 6.31). These stem from the numerous pulmonary arteries and veins that are also embedded in the parabronchial walls. As blood flows through the capillaries—supplied by the pulmonary artery and drained by the pulmonary vein—oxygen and carbon dioxide are exchanged via the surrounding air vesicles. In mammals, this respiratory exchange takes place in dead-end alveoli at the termination of bronchioles, which do not exist in birds.

Rather than a diaphragm, birds use their hinged thoracic cage and extensive system of air sacs (Fig. 6.32)—with flexible walls as thin as soap bubbles—to force air in and out of their stiff lungs. These air sacs do not contain blood vessels and play no part in the exchange of oxygen and carbon dioxide. Instead, they expand and contract to facilitate airflow and serve as holding chambers for air before it passes through the bronchi and into the parabronchi of the lung.

Most birds have nine air sacs. At the thoracic inlet, the clavicular air sac surrounds the branching point of the trachea. In addition to a large central sac, the clavicular air sac also consists of smaller extensions that connect to the air spaces within the coracoid, cervical vertebrae, humerus,

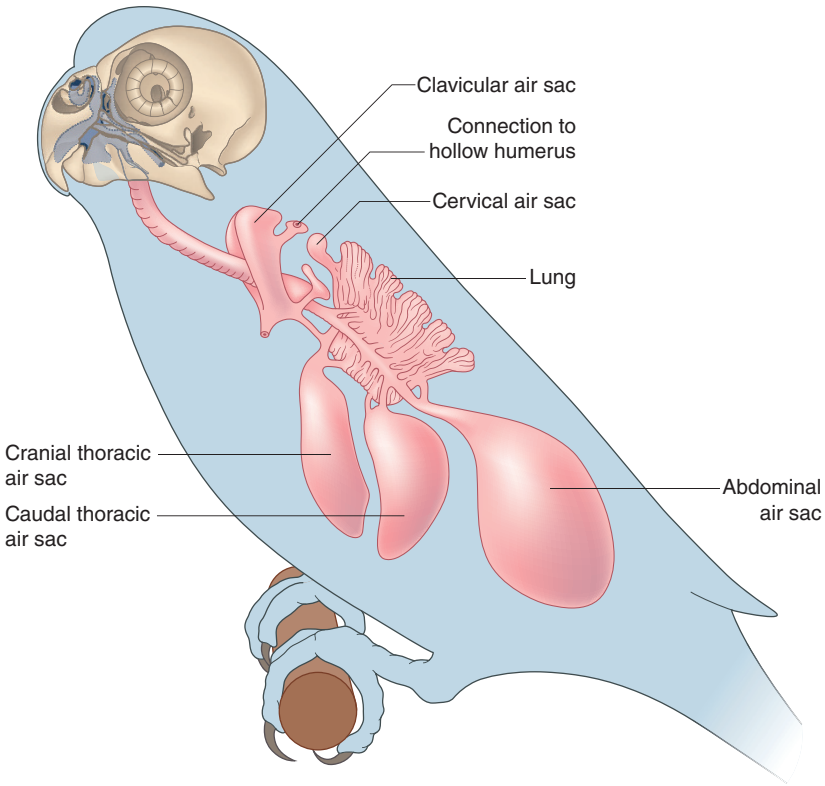


Fig. 6.32 Anatomy of air sacs. This diagram of a Budgerigar (*Melopsittacus undulatus*) depicts the arrangement of the lungs and major air sacs in relation to the air passageways that connect them. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

and sternum. Cervical air sacs connect to the cervical vertebrae as well. Two thoracic air sacs surround the lung in a fixed position; two abdominal air sacs sit adjacent to the posterior thoracic air sacs and can shift their position within the abdominal cavity. Although the pairing is difficult to illustrate, each of these air sacs (with the exception of the clavicular and sometimes the cervical air sac) occur on both sides of a bird's body.

As a bird inhales, air passes through the trachea and down through the mesobronchus (Fig. 6.33). Half of the incoming air moves to the lungs while the other half is stored directly in the caudal air sacs. At the same time, deoxygenated air moves from the lungs into the cranial sacs. Upon exhalation, air from the lungs and the cranial air sacs moves out via the trachea while fresh air stored in the caudal air sacs moves into the lungs. This system allows birds to receive fresh, oxygenated air during inhalation *and* exhalation—which means that oxygen and carbon dioxide are exchanged continuously via the blood and air capillaries. Air flows through the lungs in one direction only; air is not "mixed" with higher and lower levels of oxygen, as in mammals. This mechanism allows more oxygen to reach the blood, which in turn facilitates a higher metabolic rate, as well as the ability to fly at higher altitudes with less oxygen (Chapter 7). The practice leading to the expression "canary in a coalmine" is a tribute to the efficiency of the avian respiratory system. Well into the 20th century, workers would bring caged canaries into coalmines to test for carbon monoxide; since the birds breathed in the poison while exhaling as well as inhaling, they would react faster than the human miners, allowing the workers to escape before it was too late (Chapter 15).

6.4 Digestive system

Digestion involves the ingestion of food, the uptake of nutrients, and the elimination of wastes. Birds do not chew their food. The act of swallowing involves grasping (and sometimes crushing) food with the bill, manipulating it with the tongue, and passing it into the alimentary canal (Fig. 6.34).

6.4.1 Tongue

Although most of a bird's taste buds do not occur on the tongue, the tongue does facilitate taste, and some birds also use their tongue to detect texture and temperature. However, birds mainly use their tongues to secure, manipulate, and swallow food.

Bird tongues assume many forms. Rectangular, cylindrical, lance-like, flat, cupped, grooved, spoon-shaped, or forked tongues—often enhanced with specialized spines or hair-like structures—function as probes, brushes, sieves,

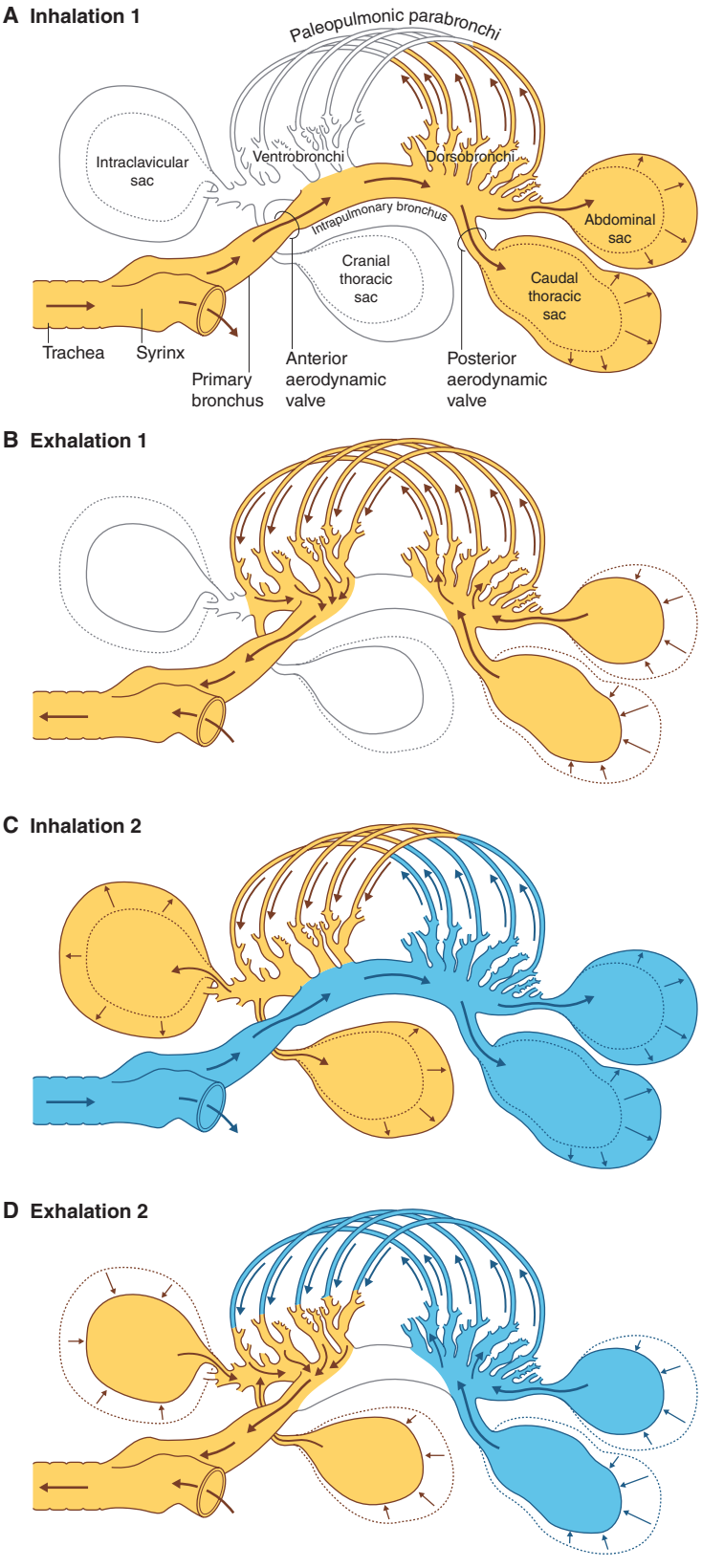


Fig. 6.33 Airflow through the air sacs. Air sacs connect the primary bronchial passages to each lung and hold air as it flows through the air passageways and out again. From start to finish, a single packet of air would take two cycles of breath to leave the body. (A) In the first inhalation, air (yellow) enters the passageways. Expanding air sacs pull the air in, which opens passageways into the posterior thoracic and abdominal air sacs. (B) As the bird exhales, the air sacs contract, pushing the same air (yellow) into open parabronchial spaces not closed off by valves (circles around air passageways). (C) In the second inhalation, new air (blue) is pulled into the expanding thoracic and abdominal air sacs while air from the first inspiration (yellow)—still in the parabronchi—travels into the intraclavicular and cranial thoracic sacs. (D) The second exhalation pushes the old air (yellow) out of the mouth of the bird as new air (blue) is simultaneously drawn back into the posterior thoracic sacs and the process repeats. (Courtesy of John Ludders and Michael Simmons, Cornell University.)

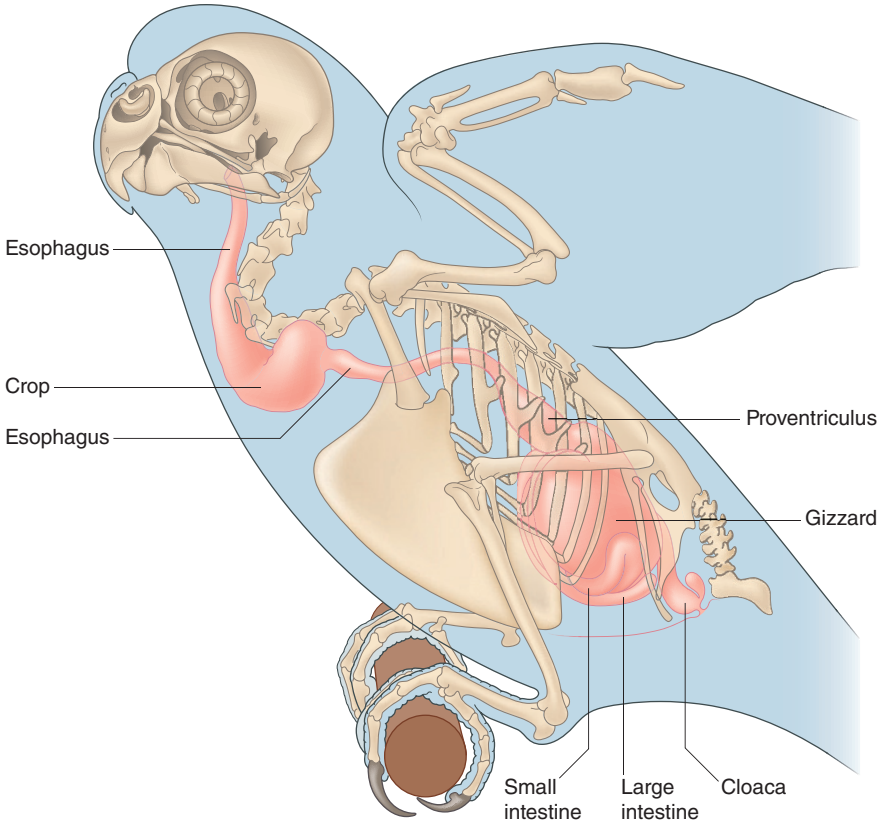


Fig. 6.34 Avian alimentary canal. This diagram shows the alimentary canal of a Budgerigar (*Melopsittacus undulatus*) in relation to its skeleton. As food enters the esophagus, it is pushed by muscular action to the crop, a pouch-like extension of the esophagus where food is stored and softened. From there, food travels to the proventriculus and gizzard—the two parts of the avian stomach—then though the small and large intestine, and finally exits through the cloaca via the vent. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

or coarse files. Like the bill, the structure of the tongue corresponds to feeding specialty (Chapter 8). For example, penguin tongues have sturdy spines to force fish, which often vigorously wiggle to escape capture, into the esophagus (Fig. 6.35). Hummingbirds tend to have forked tongues with folded edges—this configuration creates small troughs that channel nectar from flowers into the mouth. Many bird tongues also have horny, spiny, fleshy, or brush-like tips. When woodpeckers project their tongues into a bark crevice or an excavation, the backward-projecting barbs

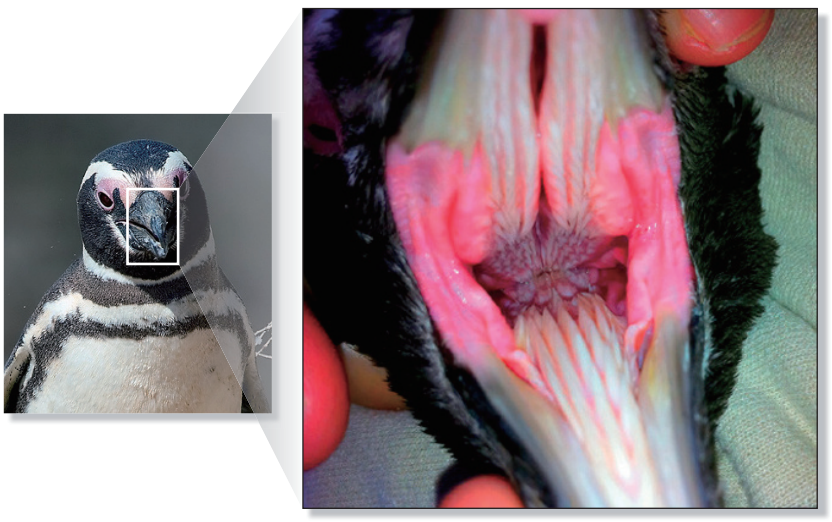


Fig. 6.35 Tongue and mouth of a penguin. Magellanic Penguins (*Spheniscus magellanicus*) have evolved a specialized posterior-facing mouth and tongue barbs, which aid in the capture of slippery prey. (Photographs by: left, David, https://commons.wikimedia.org/wiki/File:Magellanic_penguin,_Valdes_Peninsula,_e.jpg. CC-BY-2.0; right, Anthony Brown.)

at the tips help snag insects and insect larvae. The tongues and hyoid bones of woodpeckers and hummingbirds are so long that they curve around the skull, in some cases reaching the nostrils. The shorter tongues of sapsuckers are equipped with forward-projecting, hair-like structures to collect sap. Since pelicans, gannets, ibises, spoonbills, storks, and some kingfishers swallow their food whole, their tongues are very small.

Salivary glands secrete saliva to moisten food in the mouth. The presence of salivary glands in a bird is generally correlated with the kinds of food it eats. Species that eat seeds, plants, and insects have well-developed salivary glands. Birds that obtain their food from the water have little need to moisten it; thus, birds such as the Anhinga (*Anhinga anhinga*) do not have salivary glands.

Some groups of birds have specialized saliva. The Chimney Swift (*Chaetura pelagica*) of eastern North America, the Common Swift (*Apus apus*) of Europe and southern Africa, and the Glossy Swiftlet (*Collocalia esculenta*) of the western Pacific and Asia use their saliva as an adhesive, firmly securing their nests to walls (Chapter 11). The salivary glands of woodpeckers secrete a special sticky fluid onto the tongue, which allows them to extract insects—which stick to the tongue—from deep burrows.



Fig. 6.36 Esophageal air sacs as sexual signals. This male Greater Sage-Grouse (*Centrocercus urophasianus*) inflates its bizarre skin sacs—outpockets of the esophagus—to produce auditory and visual displays for females, which assess male quality based on his performance in the lek. (Photograph by Gerrit Vyn.)

6.4.2 Alimentary canal

The alimentary canal begins with the esophagus, a relatively straight and thin muscular tube. Most birds can temporarily expand their esophagus to hold large quantities of food. Some gulls, for example, are capable of holding one end of a large fish in the esophagus while digesting the other end in the stomach. Avian esophageal walls contain mucus-secreting glands that moisten incoming food.

Muscular pouches called diverticula serve various roles within the esophagus of most birds. Redpolls and other finches use them to store seeds. Other outpockets serve as resonance chambers for sound signals in courtship displays, as in pigeons. Grouse and prairie-chickens have esophageal air sacs that externally inflate to produce both auditory and visual signals as part of a display for females. These sacs, generally covered with brightly colored skin, emit loud sounds when air vibrates within them (Fig. 6.36). Pigeons, doves, gallinaceous birds, and some passerines have a permanent dilatation of the lower esophagus called the **crop** (Fig. 6.34). This special area allows a bird to consume food quickly and then move to safety, as it serves as a holding chamber until the bird is ready to pass it to the stomach or regurgitate the food to its young. In some birds—such as pigeons, flamingos, and some penguins—a sloughing of cells from the crop lining produces "crop milk," a lipid-rich material that the parent regurgitates to feed its young. A thin muscle over the surface of the crop aids in the swallowing of food.

Crop: an enlargement of the lower esophagus that stores food in some groups of birds.

The Hoatzin (*Opisthocomus hoazin*), a pheasant-sized bird from the Amazon, has an exceptionally large, thick-walled crop (Fig. 6.37). It is the only bird that digests food within its crop and lower esophagus instead of its stomach. The Hoatzin eats food that is uncharacteristically fibrous for a bird, as 85% of its diet is thick leaves. Like many other foregut-fermenting herbivores (such as cows), the Hoatzin retains food in its foregut where it is digested by microbes. Microbial digestion enhances the detoxification of plant defenses, production of amino acids, and extraction of nutrients. While most birds only require 1 or 2 hours for digestion in the stomach, microbial digestion in the crop requires about 20 hours. Since plant tissue breaks down within the Hoatzin's specialized crop, its stomach is much smaller.

All birds have a two-part stomach. The elongated first portion is called the proventriculus; its gastric glands secrete digestive enzymes, including pepsin and hydrochloric acid, which break down the proteins in food. A few types of birds (including petrels, cormorants, herons, gulls, terns, some hawks, and some woodpeckers) can expand the proventriculus to hold food temporarily for later feeding, either for themselves or their young. The ventriculus, or



Fig. 6.37 Anatomy of the Hoatzin (*Opisthocomus hoazin*) digestive system. This strictly herbivorous bird digests food in its exceptionally large, thick-walled crop rather than its stomach, which is greatly reduced. Its diet of thick leaves can require 20 hours of microbial digestion. (Adapted from Grajal 1995. Reproduced with permission from American Orthithologists' Union. Photograph by Morten Ross.)

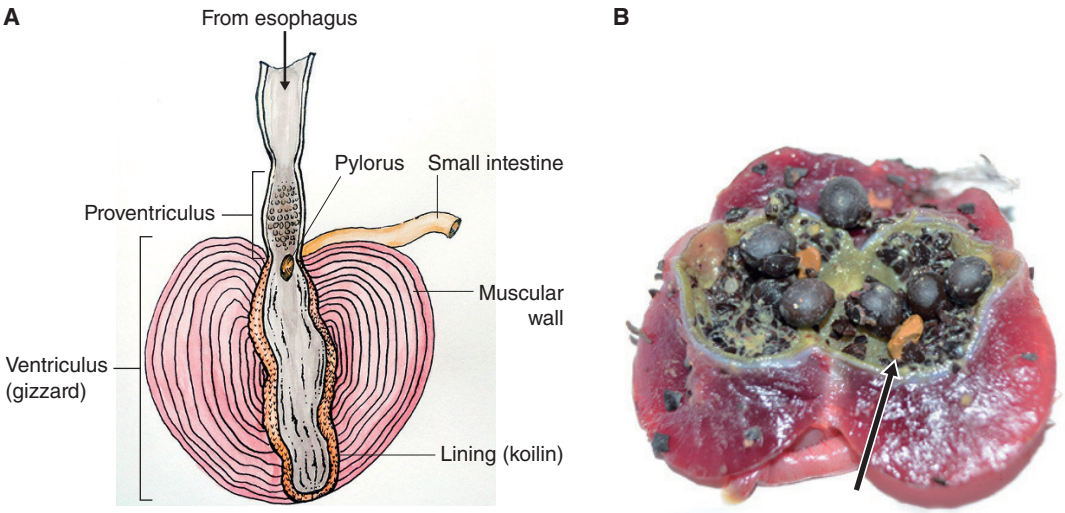


Fig. 6.38 Granivore gizzards. (A) The alimentary canal of a domestic turkey has well-developed muscular walls around the ventriculus (gizzard), which is lined with koilin. The pylorus leads into the small intestine. (B) This cross-section of a White-winged Dove (*Zenaida asiatica*) gizzard reveals the contents of its last meal: hard, waxy seeds and some bright yellow rocks (arrow) that were ingested to help crush the seeds. The white lining is the koilin and the lime green is the muscle wall interior. (A, © Cornell Lab of Ornithology. B, photograph by Jace G. Stansbury.)

gizzard, is the second part of the avian stomach. The gizzard grinds food by contracting its thick muscular walls. Seed-eating birds with well-developed gizzards, such as grouse and turkeys, ingest pebbles and gravel to augment this grinding process (Fig. 6.38). Glands within the gizzard secrete a protective, leathery lining called gastric cuticle or koilin, a mixture of carbohydrates and proteins. Since koilin is constantly worn away by the grinding action of the walls, its secretion is continuous.

Gizzard: the muscular lower part of the avian two-part stomach that grinds and softens food, often with the aid of stones held within the gizzard.

After a carnivorous bird swallows a prey item, the indigestible parts (such as bones, teeth, feathers, fur, and exoskeletons of some insects) form a pellet within the gizzard. The bird may regurgitate the pellet hours later, after digesting the flesh. Pellet formation is characteristic of owls, hawks, grouse, nightjars, swifts, and many

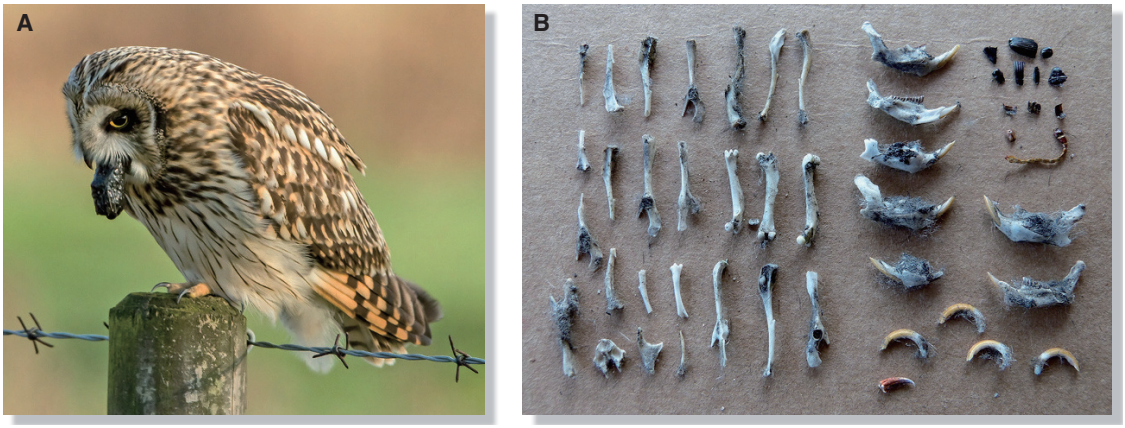


Fig. 6.39 Indigestible remains. Many carnivorous and insectivorous birds cannot digest the hard parts of their prey since their proventriculus is small and lacks muscular walls. (A) Thus, they must regurgitate pellets, as demonstrated by this Short-eared Owl (*Asio flammeus*). (B) Skeletal remains of small mammals within these pellets reveal the identity of the owl's principal prey species. (Photographs by: A, David Newby; B, Adam Tilt.)

passerines (Fig. 6.39). Grebes are thought to swallow their own feathers to slow the rate of digestion and protect the stomach from sharp fish bones. After the stomach acid dissolves the bones, grebes regurgitate pellets that consist mainly of feathers and indigestible plants.

The final processes of digestion take place in the small intestine—named for its small diameter, not length. The inner surface of the small intestine has longitudinal folds and minute finger-like projections in carnivores, and flattened leaf-like structures in many birds that eat seeds and other parts of plants. It consists of three externally indistinguishable parts: the duodenum, the jejunum, and the ileum (Fig. 6.40). Most nutrients absorb through the intestinal wall lining and into the blood stream, while metabolized fat passes into the lymphatic system—the network of vessels through which white blood cells drain from tissues into the blood (Box 6.03).

The small intestine is the longest part of the digestive tract in every bird except the Ostrich (*Struthio camelus*). Typically, birds that eat foods that are difficult to digest or that are low in nutritional value have longer digestive tracts. For example, the Dusky Grouse (*Dendragapus obscurus*) and the Spruce Grouse (*Falcipennis canadensis*) of western North America mainly feed on low-nutrient conifer needles; their small intestines are therefore about 28% longer than similarly sized birds with a more nutrient-rich diet. This phenomenon can even occur within the same species, as in the California Quail (*Callipepla californica*). The small intestines of quail that live along the humid coast of northern California are about 11% longer than those of quail inhabiting the arid interior, since the former eat considerably more green food (Leopold 1953).

Within the intestinal walls, small glands secrete fluids to aid in digestion. Bile, an alkaline fluid secreted by the liver, splits fats into tiny particles and neutralizes the acid passing into the intestine from the stomach. Several bile ducts from the liver and gall bladder drain into the duodenum, the first U-shaped loop of the small intestine (Fig. 6.40). The duodenum is very similar in all birds, beginning at a circular band of muscle called the pylorus. The pancreas, which secretes insulin, glucagon, and various digestive enzymes to break down proteins and fat, is situated within the duodenal loop. The remainder of the small intestine continues to loop and coil as the jejunum and later the ileum. A remnant of the yolk sac—a small pouch called the vitelline diverticulum—occurs at the junction of the two.

Long pouches called colic cecae (singular, cecum) mark the end of the ileum and the beginning of the large intestine (Fig. 6.40). Often paired, they hold material for bacterial digestion, eventually refluxing the contents into the large intestine. Herons and bitterns have a single cecum, while the Secretary-bird (*Sagittarius serpentarius*) has two pairs; cecae are absent or barely present in anhingas, parrots, pigeons, kingfishers, swifts, woodpeckers, and some hummingbirds. Diet plays a large role in this variation: herbivorous birds tend to have longer cecae than their seed-eating relatives, probably to enhance breakdown of the cellulose in tough plant fibers.

In most birds, the large intestine is a short, straight tube extending from the colic cecae to the cloaca. After reabsorbing the remaining water, the large intestine passes waste contents to the cloaca, which also receives semi-solid uric acid from the kidneys and eggs from the ovary (Chapter 7).

The liver processes digestive products into useful substances for the body, neutralizes harmful substances in the blood, and produces bile to aid in digestion. The largest internal organ of the avian body, the liver, has two lobes;

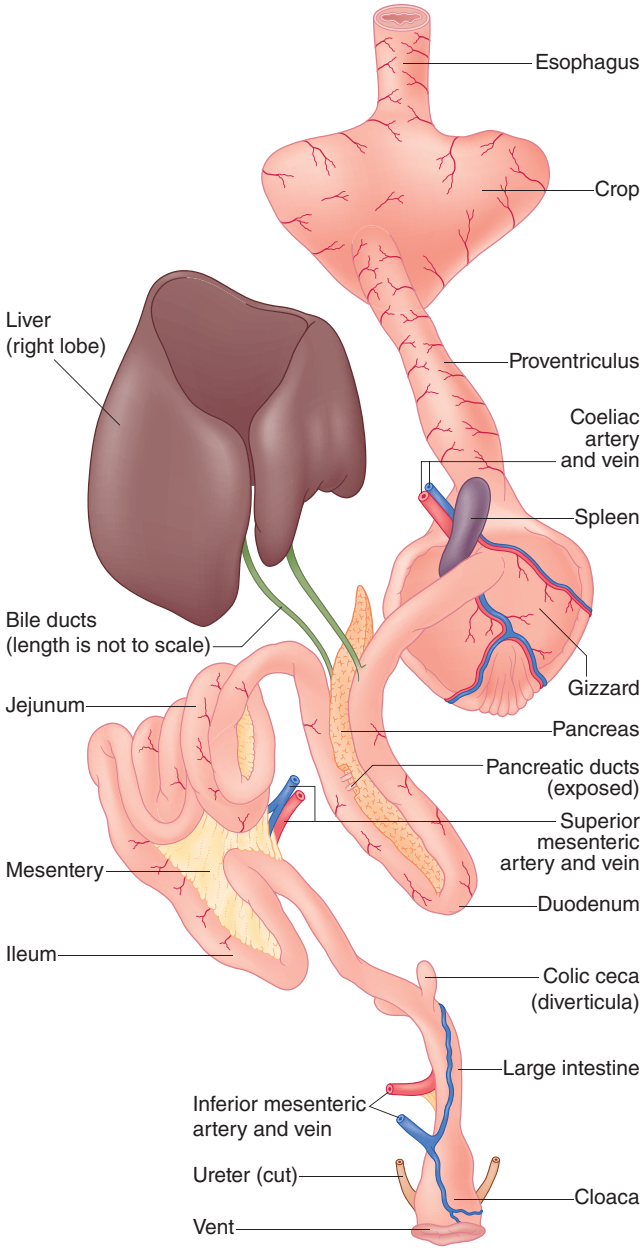


Fig. 6.40 Posterior digestive anatomy. The primary parts of the digestive system include the major arteries and veins, liver and associated ducts, small intestine (duodenum, jejunum, ileum), pancreas (and ducts), cecae, large intestine (relatively small in most birds), cloaca, ureters, and vent. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

usually the right lobe is larger than the left (Fig. 6.40). Several bile ducts lead directly into the duodenum from each lobe. Many birds have a gall bladder, which serves as a reservoir for the storage and concentration of bile; depending on the species, the gall bladder may be oval, sac-like, or long and tubular. Other birds—such as parrots, cuckoos, hummingbirds, pigeons, and some woodpeckers, falcons, and passerines—lack a gall bladder altogether.

6.5 Urogenital system

The urinary and reproductive systems function together as the avian urogenital system (Fig. 6.41). The urinary system, which removes toxic nitrogenous wastes from circulation, develops first. In young birds, the cloacal bursa opens into the roof of the cloaca and produces B cells that populate lymphatic tissues (Chapter 7).

Unlike other systems in the bird's body, the reproductive system is active only part of the year in many bird species. The gonads of seasonally breeding birds shrink after breeding; for example, the testes of the European Starling (*Sturnus vulgaris*) decrease in length from 19 millimeters during breeding to 2.5 millimeters in winter (a change in volume of over 1000×) (Bissonnette and Chapnick 1930). Gonads enlarge in resident seasonal breeders as well; testes in Spotted Antbirds (*Hylophylax naevioides*) grew to a maximum of 3×5 millimeters while breeding, compared to a minimum of 0.8×0.8 millimeters during other times (Wikelski et al. 2000).

Ovary size and condition vary during the breeding season even more dramatically than do testes. The ability to lay eggs facilitates efficient flight, eliminating the need for females to carry young while they develop. Female birds develop and lay eggs one at a time, and most develop only a left ovary, possibly another weight-saving adaptation.

6.5.1 Excretory organs and ducts

The avian urinary system, sometimes called the excretory system, includes a pair of kidneys and their excretory ducts (Chapter 7). The kidneys control fluid and ion levels while removing nitrogenous waste products from the blood.

With the exception of the South American rheas, birds do not have urinary bladders. The liver produces uric acid rather than urea. Uric acid is more concentrated and is not as water soluble; the kidneys reabsorb most of the water before the toxic waste is excreted. The excretory ducts, called ureters, conduct a thick white slurry of uric acid to the cloaca, where it either mixes with or surrounds the feces. Reflux of urine into the lower part of the digestive tract allows reabsorption of water.

6.5.2 Male and female gonads

Male gonads are termed testes. Oval or elliptical in shape, avian testes are paired and lie within the body cavity at the anterior end of each kidney (Fig. 6.41A). Generally, testes produce one of two sperm cell types, depending on the

Box 6.03 Lymphatic system

The avian lymphatic system returns tissue fluid to the blood, supports antibodies, and filters out degenerate cells and foreign substances. Extensive but inconspicuous, its vessel walls are extremely thin and its fluid is clear.

When blood leaks out of capillaries as cell-free tissue fluid and enters the lymphatic capillaries, it becomes lymph. The lymphatic capillaries lead to progressively larger lymphatic vessels that eventually enter the venous system. Lymphatic channels in the intestinal wall carry most of the products of fat digestion to the venous system by way of the intestinal lymph trunk and thoracic duct, whereas the hepatic portal vein carries digested proteins and carbohydrates directly to the liver (Fig. 6.B3.01).

The cloacal bursa is the primary lymphatic organ in birds and forms as a dorsal pouch close to the vent. Usually located near the caudal vertebrae, contracting lymph vessels (called lymph hearts) pump lymph into the main veins. In young birds, the cloacal bursa produces B lymphocytes, which are distributed throughout the body for immunological competence. Lymph moves through its vessels via pressure created by body movement and contracting muscles.

After hatching, lymph organs disappear in most birds—although they persist in ostriches, ducks, and some passerines. Lymph organs remain functional in species that rely on lymphatic engorgement to erect a phallus.

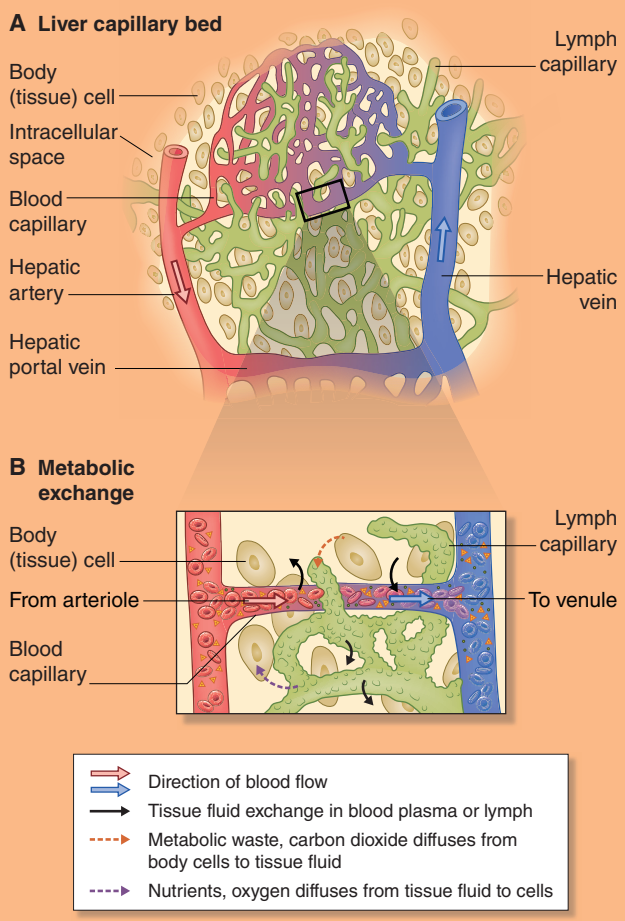


Fig. 6.B3.01 Metabolic exchange in hepatic lymph tissue. (A) Lymph tissue (green) occurs around the capillary beds. Blood flows from the hepatic arteries through the capillaries and into the hepatic veins. (B) This detailed view depicts the metabolic exchange occurring among the capillaries, body cells, lymph tissue, and veins. Fluid leaking from the capillaries is cell-free and enters the lymphatic capillaries, becoming lymph. Lymph in the liver carries digested proteins and carbohydrates; other lymph systems, like those of the intestine, carry mostly fats. (© Cornell Lab of Ornithology.)

species: a short, simple type in non-passerine orders, and a longer, spiral-shaped type in passerines (Fig. 6.42A). With the approach of the breeding season, avian testes increase greatly in size. Deferent ducts carry sperm from the testes to the cloaca. The configuration of each duct creates the illusion of striations. In most birds, a spindle-shaped terminal swelling at the end of each duct, called the ampulla, opens as a papilla into the cloaca. When the male everts its cloaca during copulation, this papilla enters the female cloaca and may even contact the opening of the oviduct. During the breeding season, the cloacal region of male passerines swells so much that the protuberance serves as an indicator of a bird's breeding condition (and by proxy, its sex) (Fig. 6.42B).

The female gonad, or ovary (Fig. 6.41B), contains many ova. In this context, the term "egg" is confusing, as it may refer to the female reproductive cell in general or the shelled version of the same cell after it has passed through the

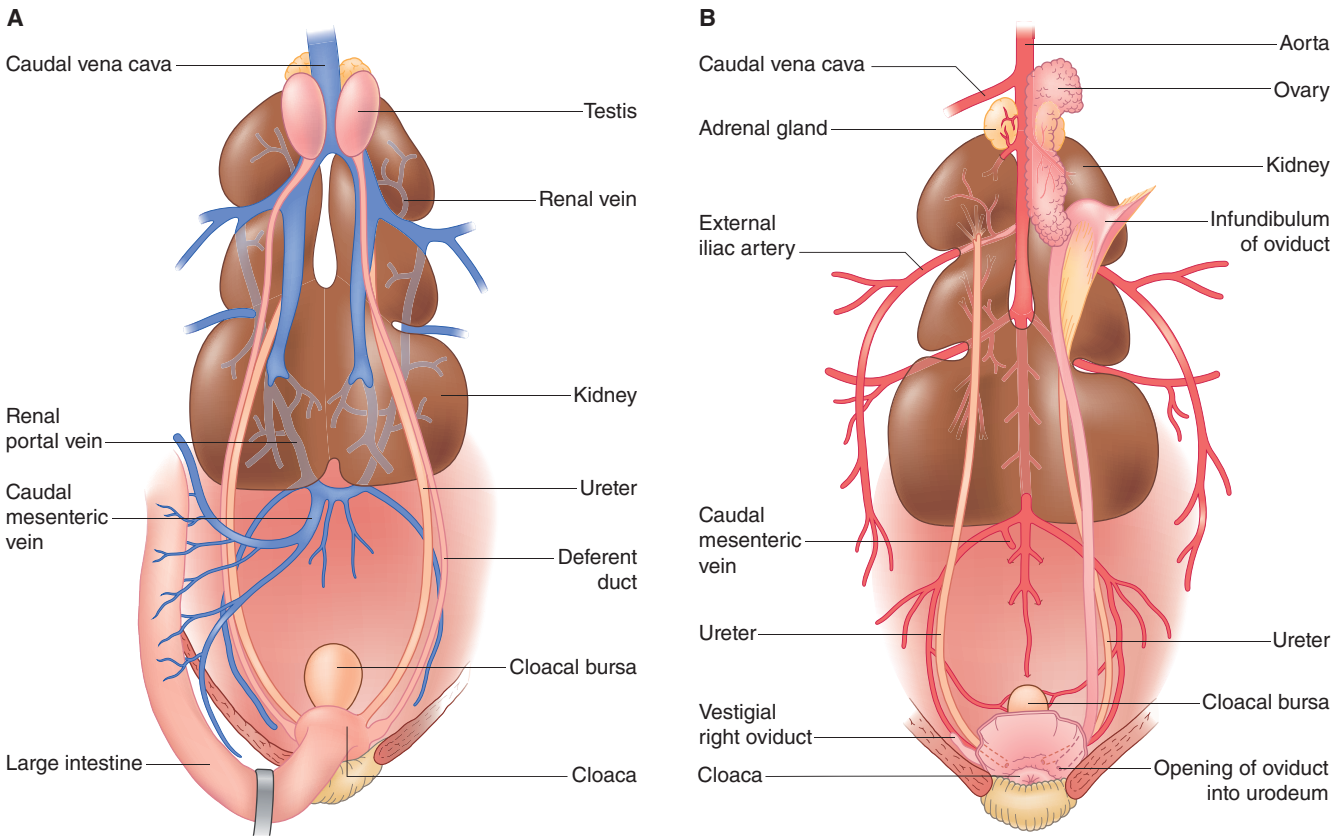


Fig. 6.41 Avian urogenital system. Since the urinary and reproductive systems function together in birds, the major components include the gonads, kidneys, ureters, and cloaca. Although their urogenital anatomies are similar, (A) males have testes and an ejaculatory duct, and (B) females have an ovary and oviduct. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

reproductive tract. To avoid confusion, in this chapter we use the term "ovum" (plural ova) while these cells are still within the female ovary, versus "egg" after it has been laid. Most female birds only have one functional ovary, the left. During ovulation, an ovum breaks out of the ovary and into the abdominal cavity (Fig. 6.43).

Suspended from the dorsal body wall by a ligament, the oviduct begins as a flattened, funnel-shaped opening called the infundibulum. The infundibulum then "swallows" the ovum. After entering the infundibulum, a long glandular region called the magnum secretes albumen (protein-rich egg white), which protects the ovum and eventually serves as the embryo's water supply. The shell membranes form as the ovum passes through a short isthmus. The ovum then travels to the well-vascularized uterus, or shell gland. Here, secretory papillae deposit mineral calcium, which forms the shell. Depending on the bird, this gland may secrete pigments as well. An ovum typically spends most of its time (18–20 hours) in the shell gland. In the last portion of the oviduct, most birds rotate the ovum 180 degrees before passing it blunt-end-first into the cloaca.

6.5.3 Copulation and fertilization

Insemination occurs when male sperm enter a female's cloaca. In this process, the male bird usually stands on the female's back while both birds evert their cloacas and press them together. Sperm is transferred when the papilla of the male deferent duct contacts the lining of the female cloaca or, in some cases, enters the opening of her oviduct. Often referred to as a "cloacal kiss," this contact between a mating pair is brief.

Ostriches, rheas, tinamous, ducks, and geese have a more advanced copulatory organ, the **cloacal phallus** (Fig. 6.44). Although often called a "penis," this structure

Cloacal phallus: the copulatory organ of male ratites and waterfowl, an elongated, spiral, ridged structure that erects during copulation. Sperm travel along its surface to reach the cloaca of the female.

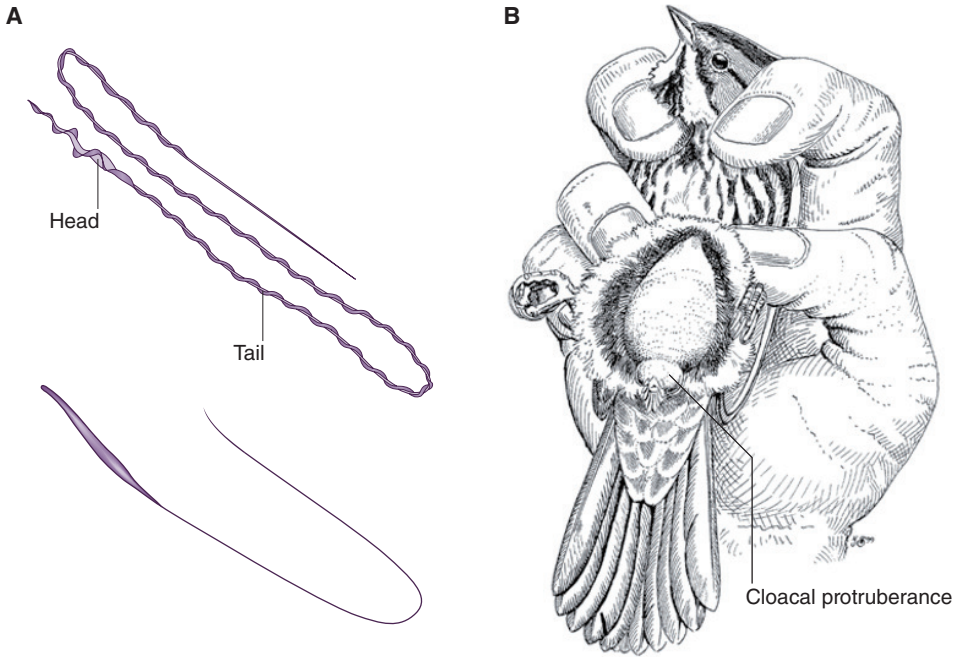


Fig. 6.42 Sperm and male cloacal swelling. (A) Passerines and non-passerines generally have different sperm types. Compare the spiral-shaped sperm of the European Greenfinch (*Chloris chloris*) (above) with the shorter, simpler domestic chicken (*Gallus gallus*) sperm (below). (B) Checking the cloacal protuberance size in a male passerine involves lightly blowing away the lower abdominal feathers and measuring the girth and length of the swelling with calipers. Reproductively receptive males have much larger cloacal protuberances during the breeding season. (Illustrations by: A, Christi Sobel © Cornell Lab of Ornithology; B, N. John Schmitt.)

differs from the mammalian equivalent: since it lacks an internal urethra, sperm must travel along the external surface of the phallus.

Since many female birds store sperm in tubules located within the oviduct, sperm generally survive longer within birds than in mammals (Chapter 7). Sperm are likely released from these tubules following the passage of an ovum. A female turkey may lay as many as 15 fertile eggs following a single insemination; even after 30 days, 83% of her eggs may be fertile. In contrast, species that lay a single egg each season, such as the Eurasian Griffon (*Gyps fulvus*) of Europe and Africa, may copulate frequently for a month before laying (Margalida and Bertran 2010). An extended copulation period may provide more opportunities for sperm competition (Chapter 3), pair bonding, and/or paternity assurance (Chapter 9).

Sperm deposited into the female cloaca enter the oviduct and swim to the infundibulum, where fertilization takes place before albumen covers the ovum. The nuclei of the sperm cell and the ovum unite to form the zygote. Cell division proceeds as the fertilized ovum travels down the oviduct. After the female lays an egg, zygote growth ceases until incubation begins.

6.6 Circulatory system

A vast network of organs and vessels, the circulatory system distributes oxygen and nutrients to cells throughout the body, removes waste products such as carbon dioxide, and distributes heat produced by muscles. It also circulates antibodies to prevent and fight infection as well as hormones produced by the endocrine glands. Blood facilitates this transport via the heart to pump it, arteries to distribute it, and veins to return it to the heart.

Bone marrow, which produces red blood cells, is thick and heavy in mammals, but many avian bones lack marrow. Only the radius, ulna, femur, tibiotarsus, scapula, furcula (clavicles), pubis, and caudal vertebrae produce red blood cells. Bird blood contains erythrocytes (red blood cells), leucocytes (white blood cells), and thrombocytes (platelets).

6.6.1 Heart

Made of cardiac muscle, the avian heart has four chambers: two thick-walled pumping chambers called ventricles, and two thin-walled receiving chambers or atria (Fig. 6.45).

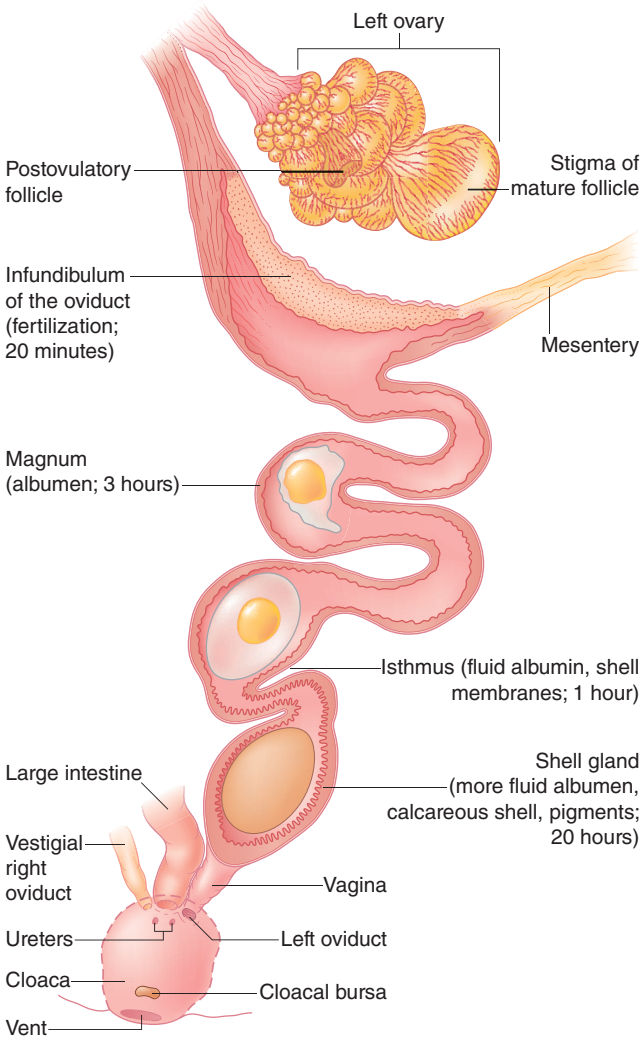


Fig. 6.43 Ovulation and the passage of an ovum through the reproductive tract. Most female birds only have one functional ovary. To initiate ovulation, the infundibulum temporarily opens to permit the entry of an ovum. From there, it travels to the magnum, where albumen (egg white) is secreted around the yolky ovum. In the isthmus, more watery albumen and shell membranes are deposited. The shell forms as the ovum passes through a short isthmus and into the uterus, where the shell and pigments are added. The ovum then typically rotates 180 degrees in the vagina to be laid with the blunt end first, via the cloaca. (© Cornell Lab of Ornithology.)



Fig. 6.44 Cloacal phallus. A few bird species have a cloacal phallus, an adaptation that mitigates morphological or ecological situations that make mounting and copulation difficult (such as mating in water). Some ducks have unusually long cloacal phalluses; this Lake Duck (*Oxyura vittata*) holds the record for the longest avian phallus at 42.5 cm. (From McCracken et al. 2001. Reproduced with permission from Macmillan Publishers Ltd.)

To ensure that oxygenated and deoxygenated blood does not mix, partitions in the heart separate the pulmonary (lung) circulation from the systemic (body) circulation. The right atrium receives deoxygenated blood (rich in carbon dioxide) from the head and body via the caval veins; the right ventricle pumps that blood into the pulmonary arteries to be oxygenated in the lungs. The left atrium receives oxygenated blood from the lungs via the pulmonary veins; the left ventricle then contracts to pump that blood into the aorta for distribution throughout the body. Pumping blood into the body requires much more power, and the muscular wall of the left ventricle is much thicker than that of the right ventricle.

With each dilatation and contraction, the heart receives and propels blood to and from the lungs, the body, and the heart itself. Veins carry blood to the heart, while arteries carry it away. Offshoots are called branches in arteries and tributaries in veins.

6.6.2 Arterial system

Arteries conduct blood away from the heart. Elastic fibers within the artery walls, which are thicker than veins, stretch as blood pumps into them and contract between heartbeats, helping keep blood pressure relatively constant. Large arteries branch into distributing arteries; these pathways become smaller as they continue to branch. Small branches called arterioles, made of smooth muscle rather

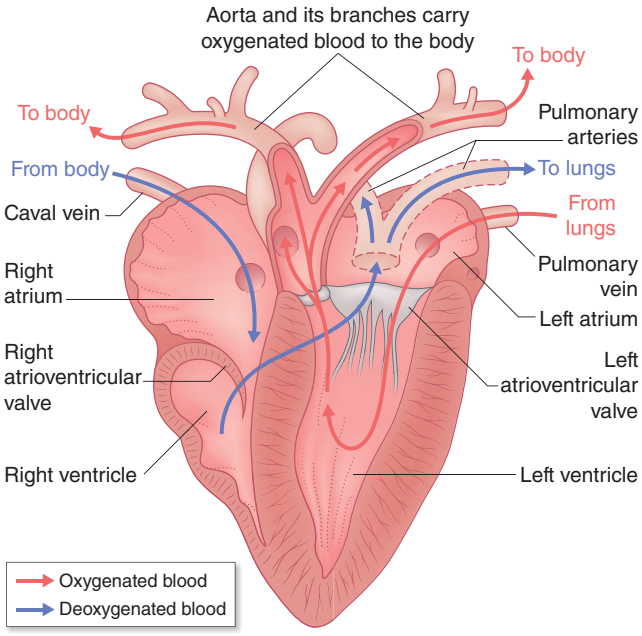


Fig. 6.45 Avian heart anatomy. The avian heart is composed of four muscular chambers—two pumping chambers called ventricles and two thin-walled receiving chambers called atria—which are segregated by valves and partitions to prevent oxygenated (red) and deoxygenated blood (blue) from mixing. (Adapted from Brooke and Birkhead 1991. Reproduced with permission from Cambridge University Press.)

than elastic tissue, lead to capillaries. The smallest vessels of the circulatory system, capillaries lack a muscular coat and remain relatively constant in diameter. Blood drains from capillaries into venules to connect the arterial and venous systems as a network.

The aorta is the largest artery in a bird's body. Originating in the left ventricle as the aortic arch, the aorta curves to the right as it passes upward toward the back. As it approaches the vertebral column, the aorta curves again and passes toward the tail (eventually becoming the descending aorta). Birds are unique in having only a right aortic arch. Reptiles have both a right and left aortic arch; mammals only have a left.

The aortic arch gives rise to the two large innominate arteries on the left and right, which branch further into the subclavian arteries (leading into each wing) and the carotid arteries (leading to the neck and head). Presumably because neck length varies greatly among birds—for example, compare a woodcock or snipe to any of the large herons—avian carotid arteries assume many different forms. Instead of two equal carotids on each side of the neck, some birds have a single carotid artery, or a large carotid artery on one side and a small one on the other. Other birds lack carotid arteries altogether; in these birds, other arteries carry blood to the neck and head.

Branches of the descending aorta carry blood to the rest of the body. A series of paired arteries passes around the body wall between the ribs; three large, singular arteries supply blood to the liver, pancreas, spleen, stomach, intestine, and cloaca. As the aorta continues toward the tail, other paired arteries branch off to the kidneys, legs, and organs of the pelvic region. Eventually, the aorta becomes the lone artery supplying blood to the tail.

6.6.3 Venous system

Veins are larger and have thinner walls than arteries; their size depends on the amount of blood they carry. Veins return both oxygen-poor and oxygen-rich blood to the heart; valves within each vein prevent blood from flowing backwards. Throughout most of the body, veins carry oxygen-poor blood. However, the reverse is true for lung circulation: pulmonary veins carry oxygen-rich blood to the heart.

Tiny venules receive blood from the capillaries. The blood then travels through a series of increasingly larger veins until it reaches the right atrium of the heart. Although each heartbeat creates pressure to power blood flow, muscle contraction is also important to maintain flow in the leg and wing veins.

Generally, veins follow the same routes and share the same names as arteries. One exception is the jugular vein, which returns blood from the head and neck to the heart. Venous blood from the wings, head, and neck drains into the subclavian, jugular, and pectoral trunk veins, which converge on each side to form the right and left cranial vena cava. Venous blood from the legs, tail, kidneys, and posterior part of the body wall drains into a single, short caudal vena cava. Each vena cava empties into the right atrium.

Venous blood from the digestive tract flows through vessels that terminate in the hepatic portal vein, located between the small intestine and the liver. Entering the blood via capillaries within the small intestine, simple products of digestion are borne directly to the liver, where the blood passes through a capillary network. When capillary networks pool into one another without circulating to the heart, it is called a portal venous system; all capillary and blood vessel (vein or venule) networks in the system are interconnected. This is an uncommon phenomenon in animals, because most capillary beds drain into the heart, not another capillary bed. In birds, portal venous systems occur inside the kidney (renal portal system), the small intestine, the hypothalamus and adrenals (hypophyseal portal sytem), and the liver (hepatic portal system).

Deoxygenated blood from the organs typically exits the liver in large hepatic veins, which empty into the caudal vena cava just before entering the right atrium of the heart. Venous blood from the lower portion of the digestive tract drains into the kidney via the caudal mesenteric vein.

Some of the blood passes through a capillary bed in the kidney before renal efferent veins recollect it and join the caudal vena cava.

6.7 Nervous system

The nervous system is responsible for all a bird sees, hears, smells, tastes, feels, thinks, and does. In other words, the nervous system transmits sensory stimuli, evokes appropriate motor responses, and regulates all internal body functions. The structural components of the nervous system are similar in all vertebrates, although they differ in their degree of complexity, and birds are on the higher end of this spectrum.

The central nervous system consists of the brain and spinal cord; cranial and spinal nerves serve various parts of the body as the peripheral nervous system. The autonomic nervous system is composed of sympathetic and parasympathetic nerves, which originate in the brain and spinal cord. These nerves regulate smooth muscle of the viscera, glands, and blood vessels. These systems consist of nerve bundles, which transmit information via specialized cells called neurons.

6.7.1 Sensory and motor neurons

There are two main types of neurons, distinguished by the direction and function of their impulses (Fig. 6.46). Sensory neurons convey impulses from all over the body *to* the central nervous system (spinal cord and brain). These sensations may be triggered by conscious stimuli, such as visual food items, sounds of a predator, or pain from an injured wing. However, impulses may also be subconscious: muscles, tendons, and joints inform control centers of limb and muscle position via **proprioceptive** impulses. These proprioceptive neurons allow humans to know the exact position of their arms and legs, even with closed eyes. These subconscious "senses" are very important for the proper functioning of skeletal muscle. Imagine how important proprioceptive impulses must be to a flying bird, especially in the dark.

Motor neurons convey impulses *from* the brain and spinal cord to stimulate muscle contraction or gland secretion. Food stimulates olfactory or visual nerves, which send an action potential to stimulate the brain, which then sends a command via motor neurons to the salivary glands in the mouth. Motor nerves are of vital importance to muscle health. For example, if a motor nerve leading to a skeletal muscle is cut or dies, the muscle will become paralyzed. Unless the nerve is able to regrow, this muscle will waste away over time.

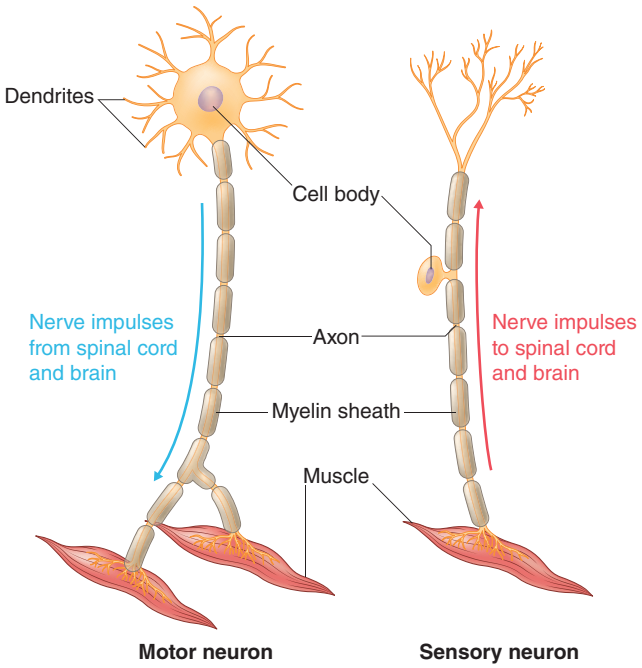


Fig. 6.46 Two types of neurons in birds. Sensory neurons bring information (both conscious and unconscious impulses) from the body to the spinal cord and brain. To activate the muscles, motor neurons send impulses from the brain via the spinal cord out to the body. (© Cornell Lab of Ornithology.)

Sensory and motor neurons provide a basis for automatic or learned **reflexes**, the simplest kind of actions. When the central nervous system receives an emergency sensory impulse, it stimulates quick action via motor nerves that govern a specific muscle or gland. We withdraw our hand almost instantaneously after touching a hot stove, well before our brains even register the danger. The same process applies to birds: upon encountering many kinds of danger, a bird's sensory and motor neurons trigger a flight response before its brain has a chance to process the incident.

Proprioceptive: nerve stimuli that give information on the position and movement of the body or parts of the body.

Reflex: a relatively simple, rapid, and stereotyped response to a stimulus; it may be either automatic or learned.

6.7.2 Central nervous system

The central nervous system consists of the brain and the spinal cord (Fig. 6.47), where millions of neurons receive sensory information, relay messages to many other centers, and send out motor impulses. Vascularized membranes called meninges protect the brain and spinal cord. A tough

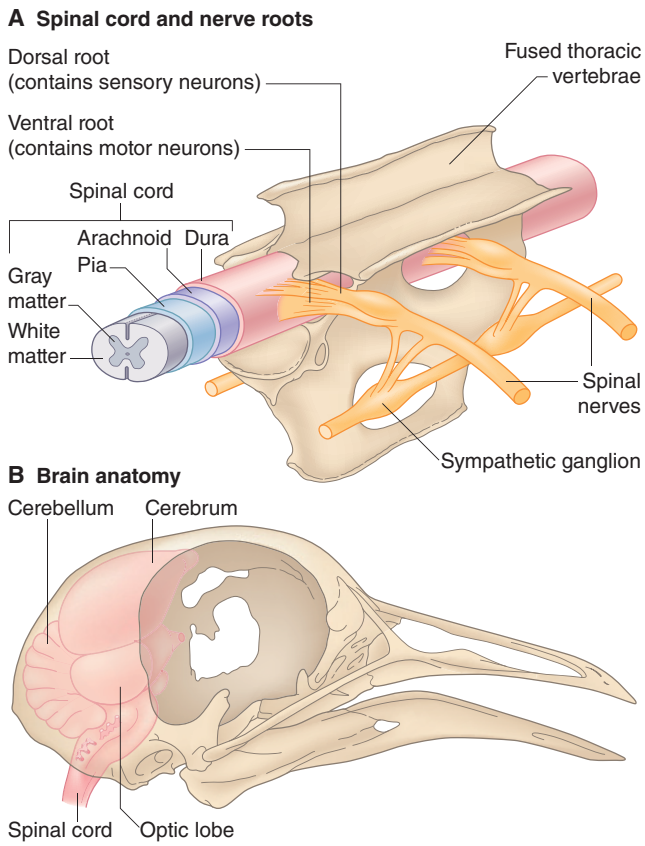


Fig. 6.47 Avian central nervous system and brain. (A) The spinal cord houses the roots of all motor and sensory neurons. Protective meninges cover the delicate neuronal bodies (gray matter) and axons (white matter). Together these components are responsible for transmitting signals to and from the brain. (B) This diagram of a Rock Pigeon (*Columba livia*) demonstrates the relative proportion and placement of the main avian brain regions. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

connective tissue called the dura forms the outer membrane, a thinner protective arachnoid membrane is found inside of the dura, and the delicate pia membrane envelopes the surface of the brain and spinal cord. Inside the meninges are the axons and neurons that transmit information to and from the brain. These are divided into the gray matter (neuronal cell bodies and unmyelinated axons) and white matter (long-range myelinated axons) (Fig. 6.47A). The gray matter processes and directs sensory (motor) stimuli generated in sensory neurons and other areas of the gray matter, to nerve cell synapses that stimulate a motor response. Millions of non-neural cells called glia transmit nutrients to the neurons, and capillaries provide constant blood flow, making this nerve tissue a grayish-pink color. The white matter mainly transmits signals to the gray matter via myelinated (fatty protective covering that increases neuronal signal transmission ability) axons that are white in color. Note that the gray matter is found inside the spinal cord, whereas the white is on the outside, an arrangement that is reversed in the brain.

The avian brain is rather bulbous, and very large compared with the size of the skull relative to most other vertebrates (Fig. 6.47B). Since the avian skull is thin, the brains of birds are quite susceptible to injury. Most of a bird's brain lies posterior to the orbits, filling the cranial cavity almost completely. The characteristic ridges (sulci) of a mammal brain do not occur on the brain of a bird; the two cerebral hemispheres of the avian forebrain are smooth. Two layers of nerve cells cover the cerebral hemisphere, providing meager protection compared with the five or six layers of a mammalian cortex. A bird's brain lacks a neocortex (or highly developed gray matter in general). This is a noticeable difference between the avian and mammal brain, but other parts of the avian brain perform the same functions as the mammalian neocortex. Beneath the cerebral hemispheres, two large optic lobes lie within the avian midbrain and a large, transversely folded median cerebellum lies in the hindbrain.

The avian forebrain or telencephalon is narrow anteriorly and wide posteriorly; it overlaps and partially hides the optic lobes. The forebrain consists of two smooth cerebral hemispheres pointed at their anterior ends, where the olfactory nerves from the nasal cavity enter. The avian midbrain or mesencephalon consists primarily of two greatly enlarged optic lobes that receive crossed inputs. (Information from the right eye transfers to the left side of the brain, and vice versa.) The mesencephalon is caudally joined to the cerebellum—which serves as the bird's automatic pilot—and which attaches to the dorsal aspect of the brainstem, or medulla oblongata. The cerebellum controls posture and movements of the legs and wings. It thus regulates the highly complex muscular actions necessary for flight.

Hidden dorsally by the cerebellum, the medulla extends back through the foramen magnum, the hole in the base of the skull through which the spinal cord passes. The nuclei of cranial nerves V–XII (Box 6.04) occur within the medulla and are instrumental in controlling vocalization and breathing reflexes.

The spinal cord passes through the neck and trunk within a protective canal formed by the arches of successive vertebrae. Essentially a cable of neurons, the spinal cord conducts impulses to and from the brain. However, many muscular functions—particularly flying and walking—can be accomplished independently of the brain via reflex action within the spinal cord. These reflexes explain why a bird's legs and wings continue to function for a brief period after a bird is decapitated.

Along the course of the spinal cord, spinal nerves branch off between vertebrae (Fig. 6.48). Each spinal nerve has sensory and motor roots that combine as one spinal nerve outside the vertebral canal. Spinal nerves in the wings and

Box 6.04 Peripheral nervous system

The peripheral nervous system consists of cranial nerves, which leave the brain and exit from the skull, and spinal nerves, which leave the spinal cord and exit from the vertebral canal. There are 12 pairs of cranial nerves in birds, conventionally identified by Roman numerals as listed below (Fig. 6.B4.01). These nerves vary in function: some are sensory, others are motor, and some are mixed.

- The olfactory nerve (I) is entirely sensory. The cell bodies lie within the olfactory epithelium of the nasal cavity.
- The optic nerve (II) is sensory. It enters the optic foramen of the skull from the retina, crosses to the opposite side in the optic chiasma, and enters the optic nucleus of the thalamus and the optic lobe of the mesencephalon. It is larger than any other cranial nerve.
- The oculomotor nerve (III) leaves the midbrain and innervates the eye muscles. It conveys motor impulses to the rectus and to the ventral oblique muscles. It also supplies the eyelid muscles and the gland of the third eyelid.
- The trochlear nerve (IV) is a small nerve that conveys motor impulses to the dorsal oblique eye muscle. It originates on the dorsal surface of the brainstem between the midbrain and cerebellum.
- The trigeminal nerve (V), the second largest cranial nerve, has both sensory and motor components. It divides into the ophthalmic, maxillary, and mandibular nerves. The ophthalmic nerve is sensory from the nasal cavity, eyeball, upper eyelid, forehead, and upper bill. It is very important in ducks and geese, as this nerve innervates the bill tip organ. The maxillary nerve is sensory from the skin of the face, upper jaw, upper eyelid, and conjunctiva. The mandibular nerve is sensory to the lower beak and rictus, and conveys motor impulses to the muscles used in mastication.
- The abducent nerve (VI) supplies motor impulses to the lateral rectus muscle of the eyeball and to the quadratus and pyramidalis, the two skeletal muscles that pull the third eyelid across the eyeball to clean its surface.
- The facial nerve (VII) supplies motor impulses to the hyoid muscles for tongue protrusion, to the depressor muscle that lowers the mandible, to constrictors of the neck, and to the muscle that tenses the columella ear ossicle.
- The vestibulocochlear nerve (VIII), formerly called the auditory, acoustic, or statoacoustic nerve, is the sensory nerve for hearing and balance. It is composed of two parts. The vestibular part for balance comes from ampullary cristae of the semicircular ducts and the maculae of the utricle and saccule. The cochlear part for hearing comes from the basilar papilla of the cochlear and the lagena macula. No part of this nerve ever leaves the skull.
- The glossopharyngeal nerve (IX) supplies sensory and motor impulses to the tongue, pharynx, esophagus, and throat both directly and through anastomoses with the vagus, spinal accessory, and hypoglossal nerves

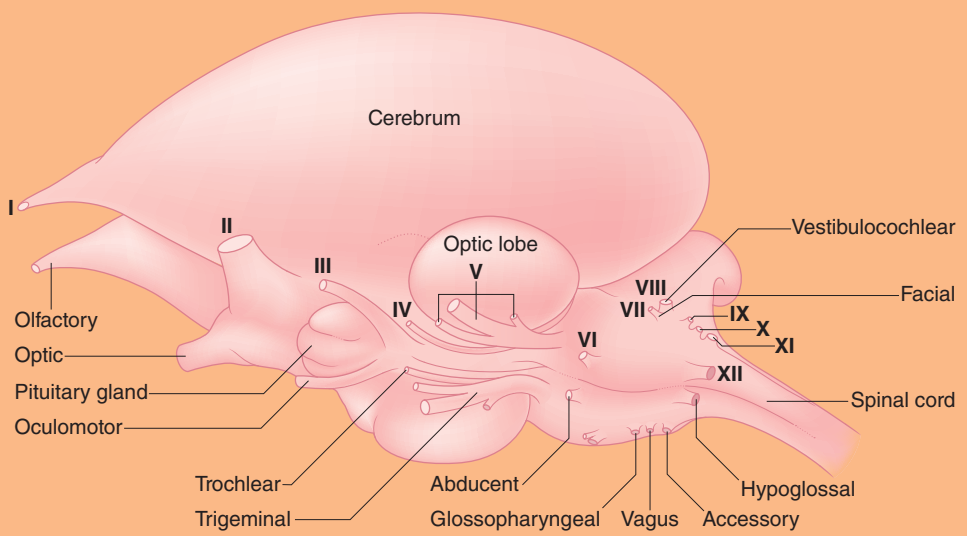


Fig. 6.B4.01 Brain and cranial nerves. This illustration of a Budgerigar (*Melopsittacus undulatus*) brain shows the location of nerves I–XII within the brain. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

(all described below). The glossopharyngeal nerve also receives sympathetic fibers from the cranial cervical ganglion on their way to blood vessels and parasympathetic motor fibers on their way to the lingual salivary glands.

- The vagus nerve (X) is the major visceral sensory and visceral motor nerve to the abdominal organs. It arises from the medulla by a series of rootlets in close association with the glossopharyngeal and accessory nerves with which it exchanges fibers. After leaving the skull, it sends fibers to the pharynx and larynx before passing down the neck on the jugular vein. Within the thorax, it branches to the heart and lungs before sending branches to the proventriculus, liver, and intestine.
- The accessory nerve (XI) arises from the first two cervical segments of the spinal cord, ascends through the foramen magnum, and exits from the skull with the vagus. It is distributed in the head region with the vagus.
- The hypoglossal nerve (XII) is formed by a series of rootlets on the ventral surface of the medulla, it then leaves the skull and unites with the first cervical nerve. The combined trunk supplies the tongue, larynx, tracheal muscles, and syringeal muscles.

Spinal nerves from the spinal cord are paired. The amount varies with the number of vertebrae in the vertebral column. For example, the Rock Pigeon (*Columba livia*) has 39 pairs of spinal nerves; the Ostrich (*Struthio camelus*) has 51.

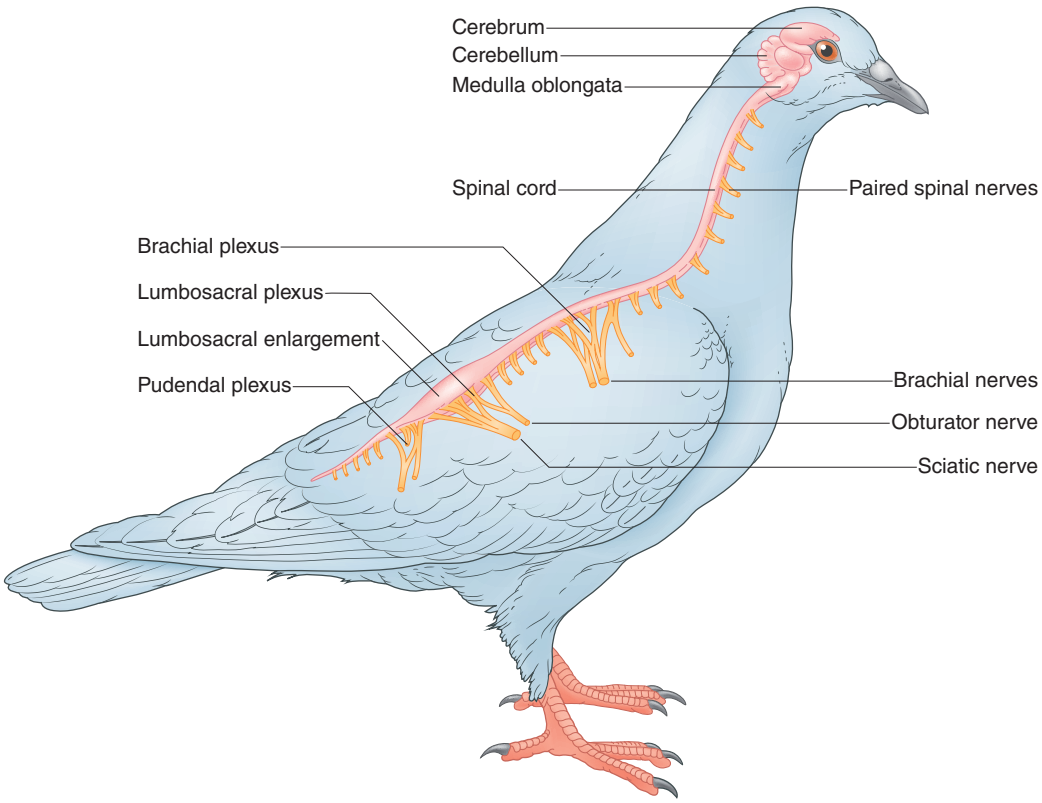


Fig. 6.48 Avian peripheral nervous system. In this diagram of a Rock Pigeon (*Columba livia*), branching plexi and some major nerves extend from the spinal cord as it exits the brain and travels down the vertebral column. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

hindlimbs are large and join one other to form plexi outside the vertebral canal. The brachial plexus of the wing forms an enlargement of the spinal cord within the vertebral canal, and the lumbosacral plexus of the hindlimb forms a similar enlargement. The size of each swelling depends on the locomotive abilities of the species: the nerves to and from the wings are comparatively larger and more abundant in birds that are highly aerial; the opposite pattern holds for birds that spend most of their time walking or swimming.

6.7.3 Autonomic nervous system

The autonomic nervous system involuntarily controls the body's internal organs. As in mammals, the avian autonomic nervous system consists of a sympathetic and parasympathetic division. Both systems innervate the same organs, but with opposite effects.

The **parasympathetic system** acts on smooth muscle to promote actions such as digestion and egg laying. Parasympathetic nerves calm the bird; some carry impulses that reduce heart rate, while others promote gastric secretion and digestion. The parasympathetic system originates in cranial nerves III, VII, IX, and X (Box 6.04), as well as in three spinal nerves. After leaving the brain, the vagus nerve (X) connects to the head, neck, thorax, and abdomen. To cause a contraction of smooth muscle within an organ's walls, the first neuron within a parasympathetic nerve chain must pass from the brain or spinal cord into the organ itself. When neurons originate in the brain, their axons must be very long in order to reach organs such as the stomach. Parasympathetic nerve impulses originating within the spinal cord do not have to travel as far. For example, to send an impulse to induce egg laying via the contraction of uterine smooth muscle, a nerve beginning in the sacral region of the spinal cord sends a message through its axon to the nearby uterus.

Under conditions of stress, the **sympathetic system** initiates an instinctive physiological response—sometimes called "fight or flight"—that either prepares a bird to resist or escape. Sympathetic nerves quicken the heart rate and increase blood pressure, allowing for deeper breathing and greater muscular contraction; they also dilate pupils and slow or stop digestion. Sometimes birds vomit, defecate, or urinate when frightened; numerous seabirds often defecate or disgorge the contents of their stomachs in the direction of an intruder. The sympathetic system originates in the thoracic and lumbar levels of the spinal cord. The cell bodies of the first neurons occur outside the spinal cord, forming visible nodules on the surface of the vertebrae. The nodules appear as a chain because the axons of these neurons may travel up or down the vertebral column before passing to organs as sympathetic ganglia (Fig. 6.49).

Parasympathetic system: the part of the autonomic nervous system that acts on smooth muscle to reduce the heart rate and regulate physiology under non-stressful conditions.

Sympathetic system: the part of the autonomic nervous system that functions under conditions of stress, preparing the body for "flight or fight."

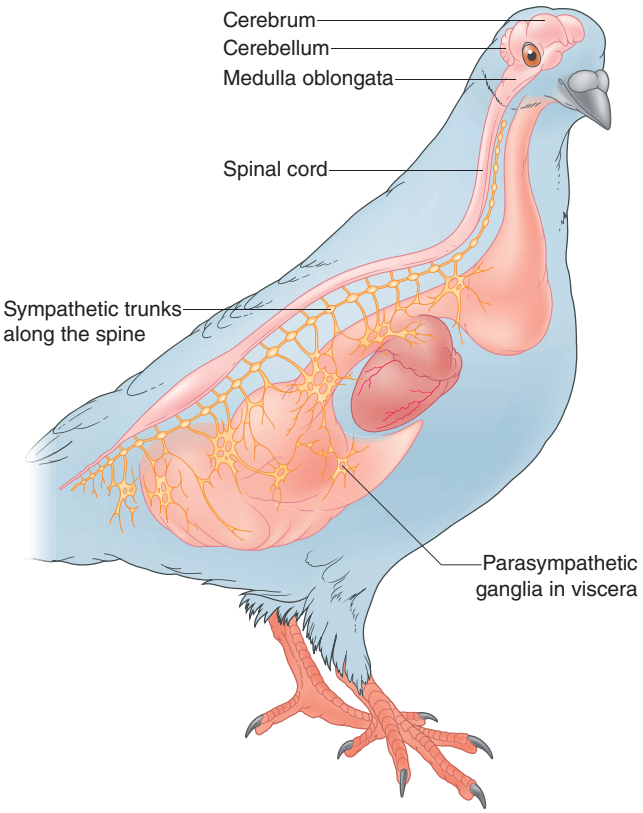


Fig. 6.49 Avian sympathetic nervous system. This diagram of a Rock Pigeon (*Columba livia*) depicts the overlap between the parasympathetic and sympathetic ganglia. Communicated via the parasympathetic ganglia, the sympathetic ganglia transmit sudden signals of stress or state changes from the organs, up the spinal cord, and to the brain. (Adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

6.8 Sense organs and the sensory system

To appreciate how a bird perceives the outside world, we must consider its sense organs as they constantly gather and transmit information. Although birds and mammals both experience the world via sight, hearing, smell, taste, and touch, avian sensory organs often differ in structure and function from those of mammals. Birds also have remarkable sensory capabilities for orientation in migration and homing.

6.8.1 Eye and vision

As a class, birds have the best vision in the animal kingdom. Birds are generally equipped with very large eyes to allow for wide views and sharp images; some species have eyes that together weigh more than their brain. Most of the

complex variation among avian eyes pertains to their relative size, placement in the skull, and color of the iris (Box 6.05).

The structure of the eyeball begins with a tough outer layer of connective tissue called the sclera, which contains a ring of very small bones (ossicles) (Fig. 6.50). The exposed, transparent surface of the sclera is called the cornea. The middle layer, or choroid, contains the eye's blood vessels. It also forms the ciliary muscle and the iris—a flat, ring-shaped membrane behind the cornea that controls the diameter of the pupil, which in turn regulates the amount of light entering the lens. Situated behind the iris and suspended by ciliary bodies, the transparent lens focuses light onto the innermost layer of the eyeball, the pigmented retina.

The avian eye consists of three main chambers. The vitreous chamber claims the majority of the inner eye, which contains a clear, jelly-like material called the vitreous body. A non-sensory, comb-like vascular structure of the choroid called the pecten nourishes the retina and controls the pH of the vitreous. The pecten projects into the vitreous body from the same site where the optic nerve exits. The shape of the pecten varies across different groups of birds. The remaining two chambers occur between the lens and the iris (posterior chamber) and between the iris and the cornea (anterior chamber). Aqueous fluid—constantly produced from the blood and secreted into the posterior chamber—passes through the pupil, into the anterior chamber, and finally into the sinus spaces and veins at the base of the iris where it re-enters the blood.

Lacrimal glands occur on each side of the eye, moistening the exterior and nourishing the cornea. The gland of the third eyelid, which secretes into the conjunctival space between the third eyelid and the cornea, is quite large. The smaller lacrimal gland has many ducts that enter the conjunctival space beneath the lower lid. Tears from both glands drain into canals in the medial corner of the eye to enter the nasal cavity.

Birds have a third eyelid called a **nictitating membrane**, which passes laterally across the cornea (Fig. 6.51). In addition to protecting the eye, this membrane cleans the surface of the cornea and keeps it moist. Some aquatic birds, such as loons, cormorants, diving ducks, and alcids, have nictitating membranes with a central, window-like area that acts like a contact lens over the cornea. These birds can see through their membrane even when it is closed and protecting the cornea. The American Crow (*Corvus brachyrhynchos*) has an opaque, white nictitating membrane that it flashes in certain calling displays.

Nictitating membrane: the "third eyelid" of birds, a thin, translucent fold of skin that sweeps across the eye.

When light reflects off an object and enters a bird's eye, it passes through the cornea and the lens before focusing on the retina, where light-sensitive rods and cone cells transmit signals to the brain. Rods facilitate monochromatic vision in conditions of poor light, while cones require bright light to process sharp, colorful images. The former are clearly more important for owls and other nocturnal birds. Birds have four different types of color-detecting cones in their retinas, one more than people have. The presence of a near-ultraviolet-sensitive cone allows birds to see more colors than humans do (Chapter 7). Axons of the rods and cones pass over the surface of the retina and converge to form the optic nerve, which leaves the eyeball to enter the optic lobe of the brain. The positioning of the nerve layer on top of the sensory cell layer actually interferes with vision in vertebrates, creating a blind spot. Vision is best where the nerve layer is thinnest: for all birds and most mammals, this occurs at the retina's central fovea, where the cones are highly concentrated.

The process of accommodation allows the eye to focus on images at varying distances by adjusting the curvature of the lens and the amount of light entering the pupil. To focus on distant objects, the lens flattens and the pupil widens (allowing more light to reach the retina). In contrast, when the eye focuses on a closer object, the lens becomes rounder and the pupil constricts. The ciliary muscle adjusts pressure on the lens to change its curvature, and the muscles in the iris open and close the pupil just as the diaphragm in a camera controls the size of the aperture.

Many birds show a remarkable range and speed of accommodation—able to keep objects in focus at rapidly changing distances. Hawks are able to keep their prey in focus during the entire duration of an approach: from high up in the sky to just centimeters above the ground. Songbirds flying swiftly through a forest see well enough ahead to avoid the tree trunks and branches in their path. Some birds, on the other hand, are nearsighted; penguins are notably myopic on land as their vision has evolved to facilitate navigation and hunting underwater.

Most birds have monocular vision: that is, when the eyes are set on each side of the head, a given object is only visible with one of the two eyes. This eye placement generates an extensive field of vision, sometimes as wide as 340 degrees. Many birds with this arrangement can see ahead and behind at the same time. Owls and raptors often have both monocular and binocular vision because their eyes are set in the front of their skulls; their vision permits a 70-degree visual field at most. However, binocular vision enhances depth perception and judgment of object solidity against different backgrounds—creating a strong three-dimensional effect.

In addition to the central fovea, which provides excellent acuity for birds with monocular vision, hawks and other fast-flying diurnal fliers (such as hummingbirds, terns, and kingfishers) have another area with concentrated

Box 6.05 Iris color in birds

The underlying mechanisms that determine eye coloration follow the same general principles as feather coloration (Chapter 4). Although most birds have a dark (often brown) iris around a black pupil, many species have more conspicuously colored irises: white, yellow, orange, blue, red, or even, as in some grebes and parrots, concentric circles of two or more colors. The goldeneye ducks of the Holarctic, the Red-eyed Vireo (*Vireo olivaceus*) of North America, and the White-backed Fire-eye (*Pyriglena leuconota*) of the neotropics are all named for their irises (Fig. 6.B5.01). In Malaysia, mixed flocks of bulbuls may include several species that are almost identical in size and plumage color but are quite different in eye color; the differences may help birds, as well as birdwatchers, distinguish among the species.

Sometimes iris color differs among individuals within the same species, either between sexes or among the same species at different ages. For example, mature male Brewer's Blackbirds (*Euphagus cyanocephalus*) in western North America have a yellow iris, while females have a brown iris (Fig. 6.B5.02). In East Africa, Superb Starlings (*Lamprotornis superbus*) have brown irises until they reach adulthood, at which point their irises turn bright yellow. Commonly, if the adult has a bright iris color, the juvenile's is duller; this difference helps to indicate the age of a bird, especially when plumage does not differ obbviously between adults and juveniles. In some species, eye color continues to change as the bird ages. For example, young accipiter hawks begin life with a bright yellow iris, but as the bird grows older, its eye color transitions to light orange, then medium orange, then dark orange, and finally to a deep, dark red. This pattern of change is so predictable that scientists can determine a bird's age by eye color alone (Rosenfield et al. 1992). Although the role of iris color within avian social behavior has not been studied extensively, it presumably can affect social interactions and reflect positions within a group—comparable to the role of plumage differences between and within species.



Fig. 6.B5.01 White-backed Fire-eye (*Pyriglena leuconota*). This species is named for its bright red iris. (Photograph by Daniel Lane.)



Fig. 6.B5.02 Iris color dimorphism. Brewer's Blackbirds (*Euphagus cyanocephalus*), among many other species, are sexually dimorphic. Females (left) are chocolate brown, including the iris, while males (right) are iridescent blue-black with a golden iris. (Photographs by: left, Jim Cummins; right, Kris Petersen.)

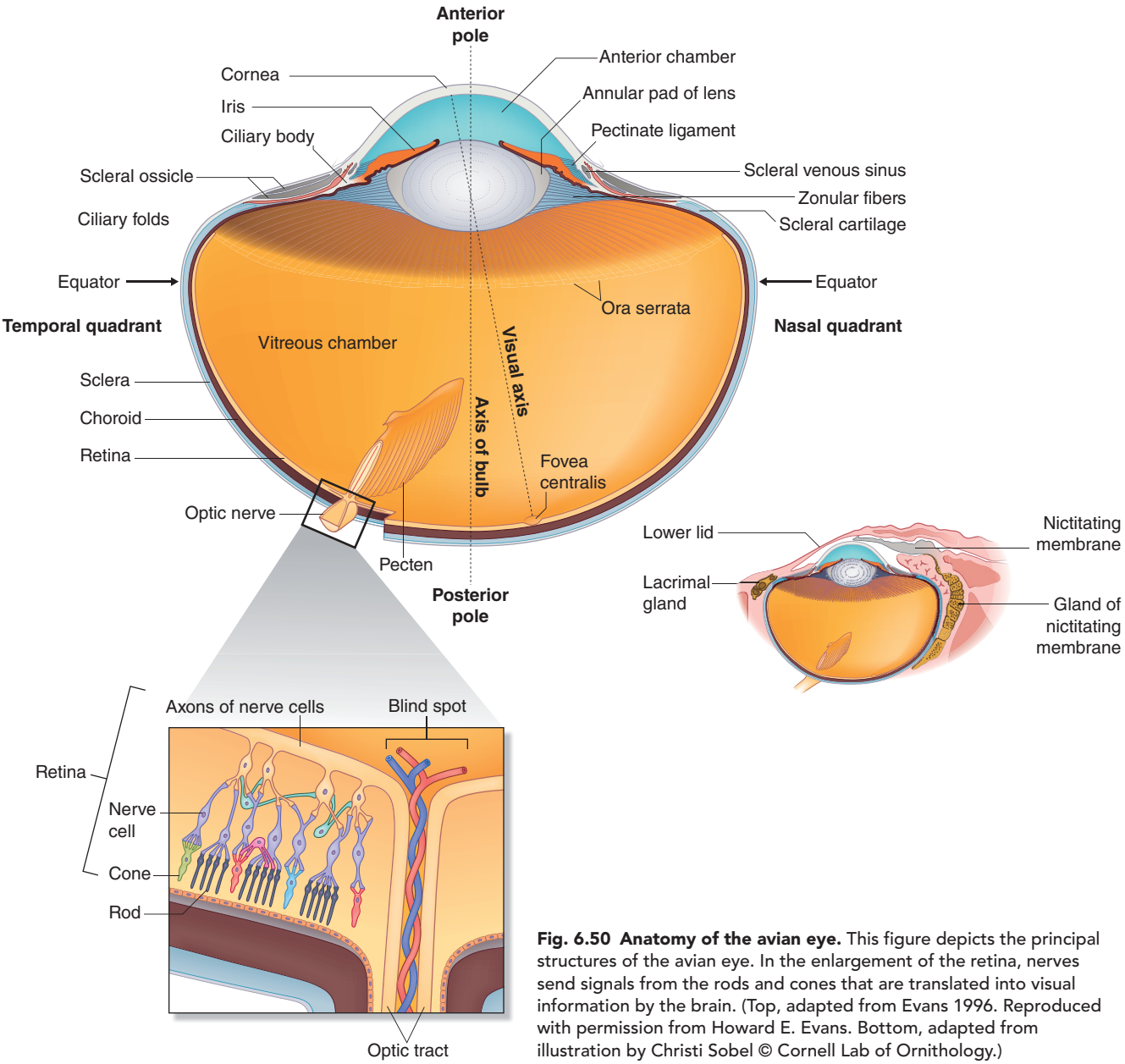


Fig. 6.50 Anatomy of the avian eye. This figure depicts the principal structures of the avian eye. In the enlargement of the retina, nerves send signals from the rods and cones that are translated into visual information by the brain. (Top, adapted from Evans 1996. Reproduced with permission from Howard E. Evans. Bottom, adapted from illustration by Christi Sobel © Cornell Lab of Ornithology.)



Fig. 6.51 Nictitating membrane. Birds (as well as reptiles, sharks, and a few mammals) have an extra membrane to protect the eye. In birds, this membrane can cover the entire eye and moves horizontally—as demonstrated in this series of photos of a Masked Lapwing (*Vanellus miles*). (Toby Hudson, https://commons.wikimedia.org/wiki/File:Bird_blink-edit.jpg. CC-BY-SA 3.0.)

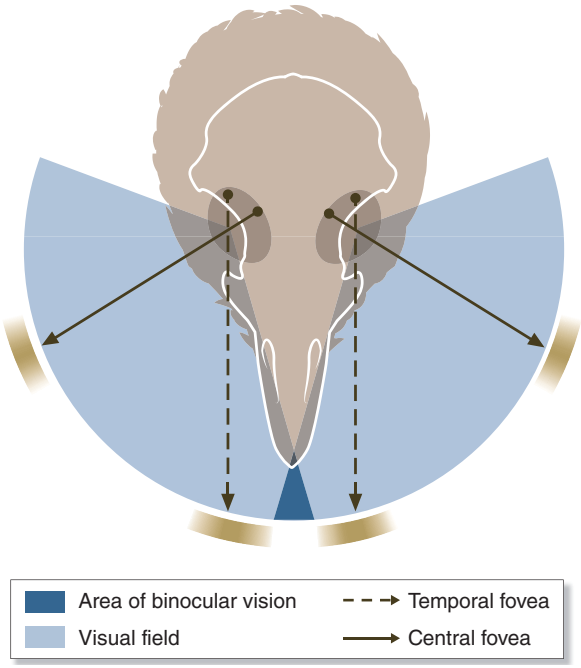


Fig. 6.52 Fovea and fields of vision. Many raptors have more than one fovea (the area where cones in the retina are concentrated). The temporal fovea facilitates visual acuity in the frontal plane (solid arrows), necessary for hunting. The central fovea provides focus to objects viewed from either side of the head (dashed arrows). The field of view for each eye is shown in lilac, occurring from behind the eye to an area of overlap (dark blue) in front of the bill—where the bird can use binocular vision, an ability common among species requiring sharp vision for aerial hunting. (Illustration by Andrew Leach © Cornell Lab of Ornithology.)

cones called the temporal fovea, located in the posterior quadrant of the retina. This area facilitates clear frontward vision (Fig. 6.52). Owls, which have fixed forward-facing eyes, have only temporal foveas. Birds with both a central and a temporal fovea have clear monocular views of the visual fields they are passing, and a clear binocular view of the visual field they are entering—an obvious advantage when pursuing prey or for accurately probing small, tubular flowers. In addition to the foveas, some birds have an extended "visual stripe" of concentrated cones running horizontally across the retina. This structure appears to provide discrimination in peripheral vision along the horizon, a useful ability for detecting predators while foraging in open environments.

The eyes of most birds move very little in their sockets. All vertebrates have four rectus and two oblique muscles that move the eyeball; although present in birds, these muscles are quite reduced. Birds compensate for this lack of eye movement by having relatively long and very mobile necks. For example, owls only have forward binocular vision; for binocular views of the sides, they turn their heads, sometimes halfway around, sweeping a much wider field than other birds.

All birds with wide monocularity can obtain stereoptical effects through head movements. In fact, nearly all animals—including insects and humans—employ this technique, known as **motion parallax**. As the head moves, close objects appear to move faster, while more distant objects move more slowly, or do not appear to move at all. Side-to-side motions of a bird's head are often an attempt to get a better impression of distance, either of prey or predators. Similarly, birds cock their heads at different angles before eating to assess a food item's form and edibility.

Head-bobbing, the forward–backward movement of the head during locomotion in some birds, is also vision-related. Although birds such as pigeons and domestic chickens appear to move their heads more than other birds while walking, they actually keep their heads still for longer—allowing extended views from a fixed spot while moving. During the hold phase, the head stays still as the body travels forward; this creates the illusion that the head is moving backwards. The length and flexibility of a bird's neck allows the head to remain still as the body moves forward—this facilitates image stabilization on the retina, as well as detection of movement in the environment (Davies and Green 1988). When the speed of the head becomes greater than the speed of the body, it thrusts forward, where it stays still in the next hold phase. Although the rate and timing of head-bobbing does vary with locomotion style, visual needs constrain locomotion, not the other way around (Hancock et al. 2014). If these birds are tested on a treadmill, a situation in which the surrounding visual stimuli remain constant, they do not bob their heads as they walk (Frost 1978).

6.8.2 Ear and hearing

Although birds essentially lack an external ear, they can hear quite well (Chapter 7). Small feathers—which buffer sound and prevent direct exposure to the elements—effectively conceal the ear holes of birds. Lacking an external ear structure also allows birds to be more aerodynamic in air or water.

The ear canal, which is very short, leads to the tympanic membrane or eardrum. The middle ear—a small air-filled cavity—lies beyond it, bounded by bone and open to the pharynx via the auditory tube. In birds, the auditory tubes join and enter the roof of the pharynx through a common opening (Fig. 6.53A). Attached to the inner surface of the tympanic membrane, the extracolumellar cartilage

Motion parallax: a depth cue that results from the motion of the observer, as objects that are closer move farther across the visual field than do objects that are more distant.

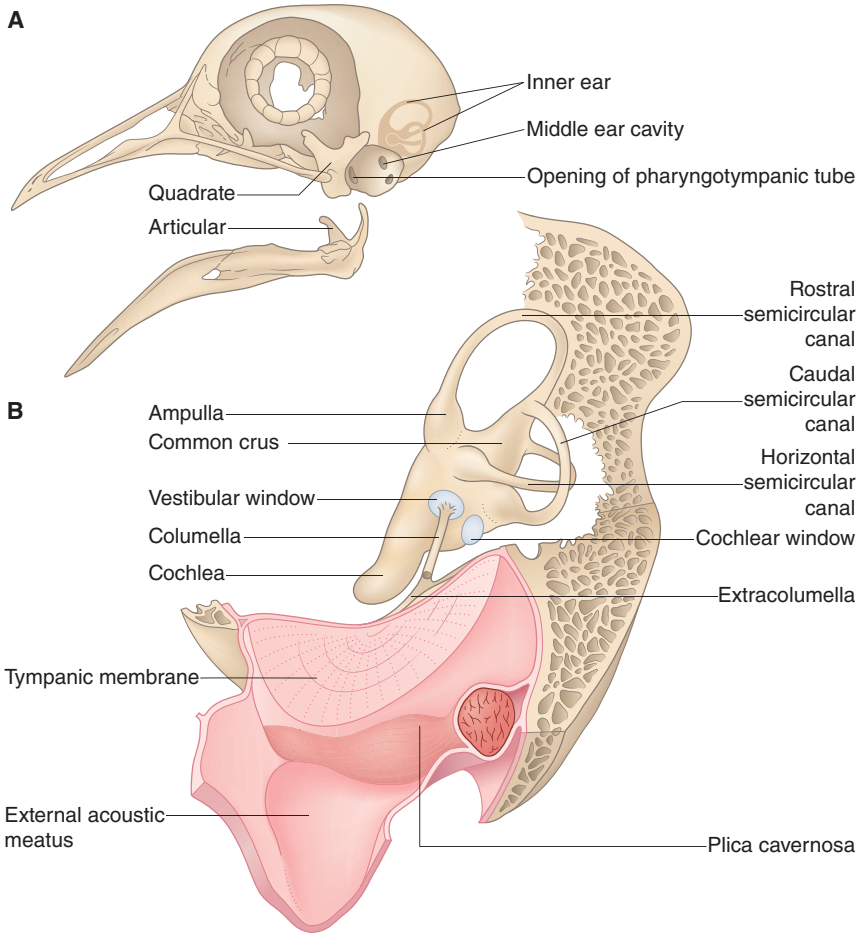


Fig. 6.53 Anatomy of the avian ear. (A) The avian ear is surrounded by the articular and quadrate bones of the jaw. The pharyngotympanic tube connects the ear to the pharynx. (B) The detailed anatomy of the outer, middle, and inner ear. (Adapted from Evans 1996. Reproduced with permission from Howard E. Evans.)

transmits sound to the inner ear via a rod-like bone called the columella (Fig. 6.53B). A small columella muscle from the surface of the skull enters the middle ear cavity, passes under the edge of the tympanum, and attaches to the extracolumella. This muscle functions to limit the movement of the columella. When a loud noise is received, the muscle contracts instantaneously to restrict transmission of the full force. The columella extends across the middle ear cavity to contact the vestibular window of the inner ear.

The inner ear consists of two fluid-filled systems, called labyrinths, one within the other. The membranous labyrinth (Fig. 6.54) is the first to develop in the embryo. Patches of sensory hairs in macula sensory structures are innervated by the vestibulocochlear (VIII) cranial nerve and help with balance (Box 6.04). A bony labyrinth of semicircular canals and the cochlea surround the membranous labyrinth. Within this bony labyrinth, the vestibular window occurs where the columella abuts. Sound waves transmitted by the eardrum to the columella send pressure waves through the fluid in the cochlea; the cochlear window serves as a damper for the system. In birds, the cochlea is short and straight (unlike mammalian ears, in which the cochlea is shaped like a spiral). Within the cochlear duct, the basilar membrane interprets the wave impulses through the vestibulocochlear nerve to the brain.

Although each bird species can hear within a slightly different range, most birds can detect sounds within a range similar to humans. The Budgerigar (*Melopsittacus undulatus*) can hear sounds as low as 40 cycles per second (cps), similar to our lower hearing range. At the other extreme, the Common Chaffinch (*Fringilla coelebs*) can detect high-frequency sounds in the 29,000 cps range, well above the 20,000 cps upper limit of human hearing. Differences in hearing ability also exist within species, depending on age. For example, young domestic fowl primarily respond to the low-pitched clucks produced by hens, whereas hens are especially sensitive to the high-pitched peeps of chicks.

Some birds can detect infrasound—sounds below 20 cps (Chapter 12). Homing pigeons (a domesticated breed of the Rock Pigeon, *Columba livia*) are able to detect sound down to 0.05 cps (Kreithen and Quine 1979). Evidence suggests that these pigeons use infrasound to navigate to their home

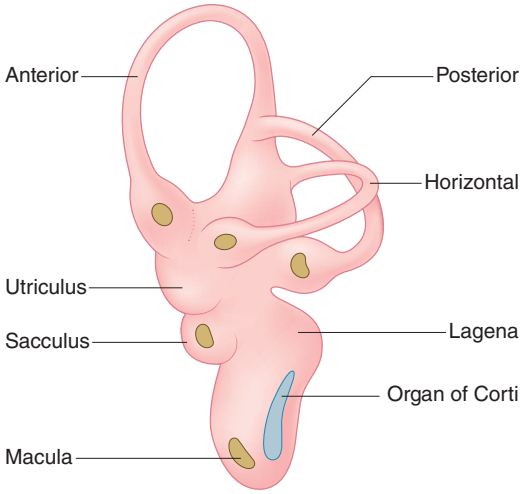


Fig. 6.54 Membranous labyrinth of the avian ear. The semicircular ducts (anterior, posterior, horizontal) end in ampullae (terminal swellings of the ducts) outfitted with macula organs (tan areas). Inside the macula, sensory hairs in endolymphatic fluid send balance and orientation signals to the brain. The utriculous, sacculus, and chochlear ducts of the inner ear aid in sound signal transmission, along with the organ of Corti—an organ unique to birds—in the lagena. (© Cornell Lab of Ornithology.)

loft (Hagstrum 2013). A number of species of grouse and other birds in the order Galliformes produce infrasound in their mating displays, mostly by mechanical—rather than vocal—means. A recent study demonstrated that both male and female Indian Peafowl (*Pavo cristatus*) respond to infrasound elements of a male's display (Freeman 2012).

Certain birds use echolocation to avoid obstacles while flying in the dark. Oilbirds (*Steatornis caripensis*), which nest in caves in South America and the southern islands of the Caribbean (Chapter 11), utter a continuous series of very short sounds that bounce back from the cave walls, informing the bird of its position while flying. The response of a flying bird to these sounds is much more rapid than the response of humans to sounds. The Cave Swiftlet (*Collocalia linchi*) of Indonesia and Malaysia also uses echolocation.

6.8.3 Taste and smell

Taste and smell are related, in that they are both types of chemical reception. All vertebrates taste via receptors within taste buds. Most birds have about 300 taste buds, the majority of which occur on the roof of the mouth or deep within the oral cavity. Compared with mammals, birds have few or no taste buds on the tongue (Fig. 6.55). Birds are often thought to have a poor sense of taste. Some birds, especially those that do not chew their food before consuming it, may not have much need for taste. However, others, such as parrots, do seem to taste their food before swallowing.

It has long been known that the "tubenose" seabirds, the Turkey Vulture (*Cathartes aura*), and the kiwis (genus

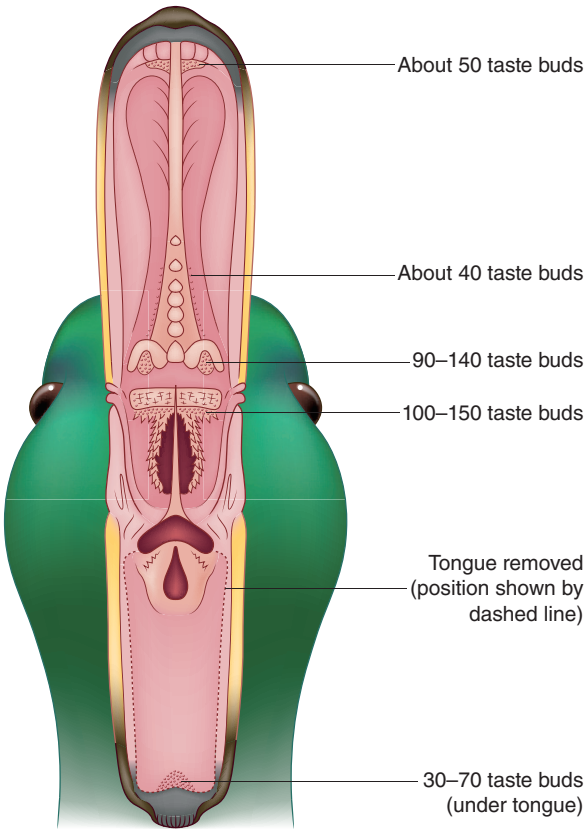


Fig. 6.55 Tastebuds in birds. This illustration shows the distribution of tastebuds in the mouth of a Mallard (*Anas platyrhynchos*); note that this duck has been drawn without a tongue, as its tastebuds exist elsewhere. (Adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology.)

Apteryx) all have a good sense of smell. Kiwis are the only birds with nostrils near the tip of the bill, and their olfactory lobes of the brain are about 10 times larger than in other birds. Yet even these specialized traits do not necessarily imply that their sense of smell is superior—kiwis primarily use chemoreception to find their food and smell to localize it (Chapter 7). Recent research suggests that other birds might use smell more than previously thought. Birds have many olfaction-related genes, and a larger proportion of them are active in birds than in people (Steiger et al. 2008). Other studies have shown that individual birds produce their own odor profile, which birds may use to identify one another. This ability has been documented in passerine songbirds (Whittaker et al. 2010) in addition to tubenose petrels (Bonadonna et al. 2007).

6.8.4 Tactile specialties

Birds have a large number of different types of tactile nerve endings in the skin, tongue, palate, muscles, joints, feather follicles, and viscera. Some sensory organs respond to touch and vibration, others to heat or chemical

sensations. The bill tip organ of ducks, geese, and shorebirds (such as snipe and sandpipers) is really an aggregation of sensory structures that can detect changes in pressure, which is helpful when foraging blindly in water or mud. The dexterity of parrots when shelling and manipulating seeds is often attributed to a collection of tactile corpuscles within their beaks. Some species of megapodes in Australia and New Guinea incubate their eggs within decaying vegetation or mounds heated by volcanic steam (Chapter 11); they use their tongues to sense the temperature within their nest mounds and then add or remove nesting material accordingly.

Visit birdbiology.org for many online resources on the topics covered in this chapter.

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Chapter 7 Bird Physiology

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Consider a small songbird on a cold winter day. How does it stay warm despite the low temperatures? If the bird gets fat during winter to help it survive the cold, how does the bird use environmental cues to time this seasonal change? How does it avoid becoming obese, or running out of fat on an especially cold winter night? How much food must the bird eat each day, and are the seeds from a bird feeder all that it needs to stay healthy? How does the bird obtain the water that all organisms require, if all drinkable water is frozen? And what inspires songbirds to sing as winter wanes and spring beckons? Answers to such questions fall within the purview of avian physiological ecology.

One of the most important concepts in any discussion of avian physiology is that of **homeostasis**—the maintenance of relative constancy of the conditions inside a bird's body. If a feature of the bird's internal environment drifts too far, then there is usually some physiological feedback pathway that will move that feature back toward its appropriate set point. What is this internal environment (as opposed to the external environment, which is outside the bird proper), why must it be kept fairly constant, and what aspects are regulated for constancy?

Complex organisms like birds are made up of highly integrated systems of cells, with different cell types comprising different tissues and organs, and organized into systems such as the cardiovascular system, neuromuscular system, and reproductive system. Each cell within such a system has a job to do, whether it is to help pressurize blood so it moves from the heart to the rest of the body, to help the wings beat so the bird can fly, or to secrete a hormone that brings the bird into reproductive condition. The internal environment is the milieu that surrounds these cells: the plasma around the blood cells, the interstitial fluid around most cells, and the cerebral spinal fluid surrounding cells in the central nervous system. The premise of homeostasis is that the internal environment around the cells must be kept within particular bounds so that the cells can perform their functions. Any one cell cannot control its own environment, just as any one person in a large city cannot maintain the entire urban infrastructure. However, the

Homeostasis: the ability to maintain relatively constant physiological conditions within the body.

Opposite: Emperor Penguins (*Aptenodytes forsteri*) have exceptional physiological adaptations. These birds can make extended (up to 18 min) deep dives in subfreezing water—individual penguins have been tracked at depths of up to 535 m. To conserve energy during these long foraging dives, Emperor Penguins lower their metabolism and shut down unnecessary organs. (Photograph by Norbert Wu, Minden Pictures.)

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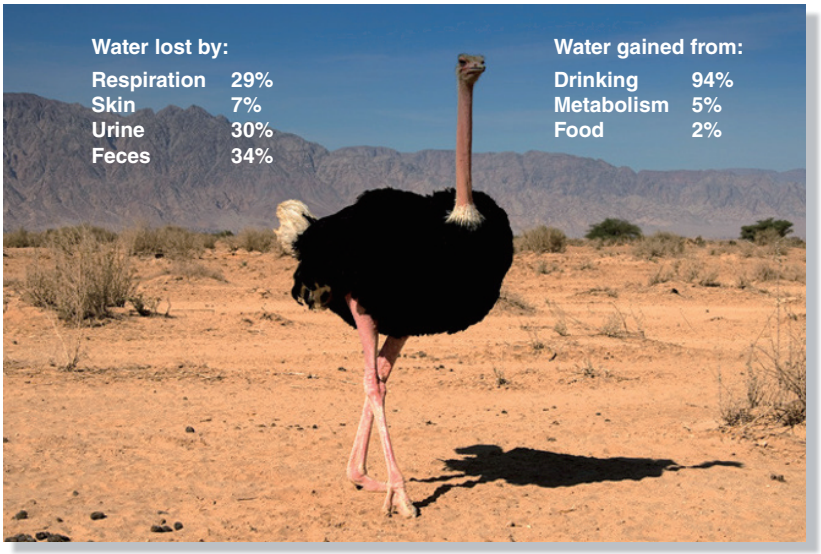


Fig. 7.01 Daily water budget for an Ostrich (*Struthio camelus*). Water turnover for a 90 kg Ostrich when water is available is about 8 liters per day. Relative percentages of water gained and lost were measured in Ostriches during experimental conditions where water was freely available in the environment. When water is freely available, water input equals output and the water budget is balanced. When drinking water is unavailable, Ostriches begin losing mass and their water budget is not balanced. (Photograph by Judith Anenberg. Data from Withers 1983.)

integrated systems of cells within every living bird must regulate water content, salt content, temperature, pH, nutrient and oxygen levels, and waste and carbon dioxide levels.

Regulating and balancing a bird's internal environment would be easier if nothing in the external environment ever changed—if food and water were supplied at a constant rate, ambient temperature never varied, and the bird never had to exert any extra effort to avoid a predator or find a mate. Yet life for birds is fraught with changing conditions. Food and water may be plentiful at times, but the next day there may be none at all. Some days are hot and humid, and other days are cold and dry. Some days a bird may merely have to sit on its eggs and be fed by a mate; other days she may have to migrate hundreds of kilometers. Despite these challenges, birds have evolved the ability to live in nearly every habitat on earth. It is their ability to regulate their internal environment and maintain homeostasis across vastly different external environments that enables them to be so widespread.

7.1 Maintaining an internal balance

Most birds live in terrestrial or saline environments where oxygen is easy to come by, but dehydration is a constant danger. Birds require an integrated means of using their kidneys, salt glands, and guts to achieve water and salt balance.

7.1.1 Water and salt budgets

Life as we know it requires water, which is sometimes termed the "universal solvent." The bulk of a bird's body is water, usually 60–70%, although a bit less in very fat birds because fat contains less water than other tissues. Most chemical reactions for life take place in an aqueous environment. Water is a component of many such reactions, and water bound to many macromolecules like proteins is necessary for their function. If the water content of a cell decreases or increases such that the cell shrinks or swells, its function may be jeopardized. If the water content of a bird's blood decreases or increases such that its blood pressure falls or rises, the bird may lose the ability to supply adequate blood to vital tissues. Yet despite the importance of keeping water content within a particular range, as much as 25% of total body water in a small bird can "turn over" every day, as it is lost to the environment or consumed in chemical reactions. These losses must be regained through water consumption and through the breakdown of other molecules to release water (Fig. 7.01).

It is impossible to consider the importance of water for birds without simultaneously considering the inorganic salts dissolved in the water. These salts are sometimes called **electrolytes**, because in their dissolved state they carry

Electrolytes: dissolved inorganic salts that carry either positive or negative charges.

either positive or negative charges and make the solution electrically conductive. The most abundant and important electrolytes in birds are sodium (Na^+), chloride (Cl^-), potassium (K^+), and calcium (Ca^+). An unequal distribution of these ions between the inside and outside of cells is absolutely necessary for allowing muscle and nerve cells to function, for controlling secretions of molecules like hormones from cells, and, most importantly for our discussion here, for controlling the movement of water.

Of all the elaborate and complicated processes that organisms exhibit, none has ever evolved the ability to move water across cell barriers by active transport: cells have no internal machinery that can grab water molecules and use energy to move them directly. Water can, however, move across cell membranes by the process of **osmosis**. Osmosis occurs when water moves across semipermeable membranes (such as the membranes that surround the cells within a bird's body) from areas of lower to higher solute concentration. Water is moved between compartments in the bird's body by this solute-linked transport mechanism. For example, if cells use energy to pump Na^+ into the lumen of the gut, water will follow by osmosis.

Water movement across cell membranes generally keeps the total concentration of dissolved solutes equal throughout the body, even though the concentrations of the individual solutes differ between the inside and outside of cells. There is far more K^+ inside cells than outside and the opposite for Na^+ and Ca^+. If the total amount of these abundant electrolytes increases, then water is retained; if the solutes are lost or are in low abundance, then water is lost. People with high blood pressure are often put on low salt diets because decreasing Na^+ means that they lose water, decreasing their blood volume and thus its pressure. Likewise with birds, defending water balance, blood pressure, and cellular water content also requires defending electrolyte concentrations. Interestingly, many birds have greater tolerance than mammals for variable concentrations of body fluids. Dehydrated or salt-stressed birds such as desert quail that have a limited ability to fly to water sources, or incubating penguins that cannot eat or drink for weeks or months, often have osmotic concentrations up to 10% higher than when they are well hydrated.

It is useful to think of water and salt in terms of budgets, for which the input and output must be balanced in the long run. For birds, feeding and drinking provide the inputs of salts and water, and additional water is produced through the breakdown and **metabolism** of food. Water and salt are lost via excretion from the bird's kidneys and gut, and by evaporation across its skin and respiratory surfaces. Some birds have salt glands that provide another important conduit for salt loss. Body size affects these factors because smaller birds have a higher metabolism relative to their body mass, which affects both the rate of metabolic water production (proportional to **metabolic rate**) and the rate of evaporative water loss. This relationship explains why the water turnover as a proportion of body mass is higher in smaller birds than in larger ones, and why the timescale over which the water and salt budgets must be balanced is shorter for small birds (Fig. 7.02).

The input and output sides of a physiological balance equation can vary dramatically both within and among bird species. Consider an albatross that may spend years at sea without access to any fresh water, compared with a lake-dwelling duck that can freely drink fresh water at any time. Alternatively, in birds inhabiting deserts, where free water may be extremely rare, the loss of body water may be essential in order to achieve evaporative cooling (discussed in more detail later in this chapter). In species that migrate, the increase in oxygen consumption to support flight will necessarily be accompanied by an increase in water loss across the permeable respiratory membranes, perhaps at just the time when that bird is least likely to have access to water. For seed-eating birds, the water content of the food can be as low as 10%, necessitating access to free water in all but the best-adapted desert bird species. For carnivorous and insectivorous birds, on the other hand, the water content of their food is probably just about the same as that of their own body, so they may have no need to drink free water. Birds that obtain their food or water from the ocean or saline lakes take on a large salt burden at the same time. On the other hand, some birds—like hummingbirds that forage on dilute nectar—obtain far more water in the process of gaining energy than they need, and consequently produce copious amounts of very dilute urine (Fig. 7.03).

The balance of water and salts can be accomplished in part by regulating intake and minimizing losses of water across the skin and permeable respiratory surfaces. But the day-to-day variation in the intake of salt and water means that the fine-tuning of salt and water balance falls to the bird's kidneys, gut, and salt glands. Smaller birds with higher rates of energy expenditure can in general produce more concentrated urine than larger birds. There is no urinary bladder in birds, and the kidney ureters empty directly into the cloaca (Chapter 6). The cloaca and lower gut can then further modify urine before it is excreted, a feat that is not possible in mammals. Salt glands are found in essentially all marine birds and in some desert birds, and

Osmosis: the movement of water or another solvent through a semipermeable membrane into a region of higher solute concentration, tending thereby to equalize the concentrations of solutes between the two sides of the membrane.

Metabolism: all chemical processes that take place in the cells and tissues of the body, including those involved in energy use and heat production.

Metabolic rate: the rate of energy production (often measured as heat production) in an organism.

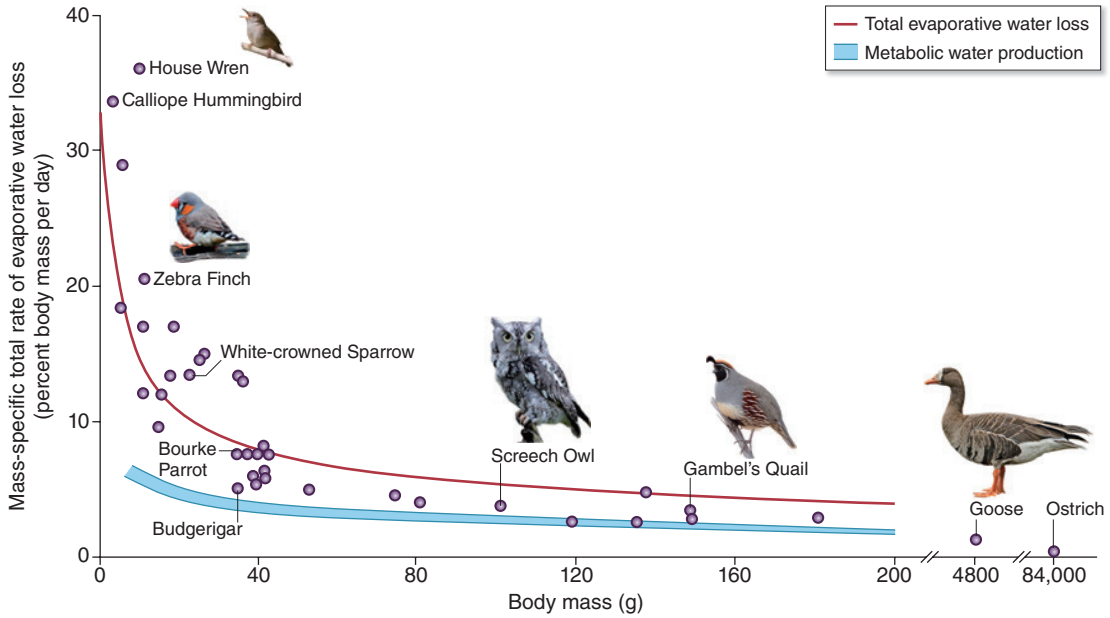


Fig. 7.02 Body mass and water balance. Smaller birds have higher metabolism per unit mass than larger birds. One product of metabolism is water production. In small birds with high mass-specific rates of metabolism, such as House Wrens (*Troglodytes aedon*) and Zebra Finches (*Taeniopygia guttata*), more mass-specific metabolic water is produced. Furthermore, small birds have a high surface area to mass ratio, increasing their evaporative water loss across the skin and lung membranes. In comparison, large birds—such as Eastern Screech-Owls (*Megascops asio*), Gambel's Quail (*Callipepla gambelii*), and Greater White-fronted Geese (*Anser albifrons*)—have relatively low metabolic rates, low metabolic water production, and low rates of evaporative water loss. (From Hill and Wyse 1989. Reproduced with permission from Richard Hill. Adapted from Bartholomew and Cade 1963. Reproduced with permission from American Ornithologists' Union. Photographs by, left to right: Susan Schalbe; Paul Le Roy; Jen St. Louis; Pat Gaines; Ryan Schain.)

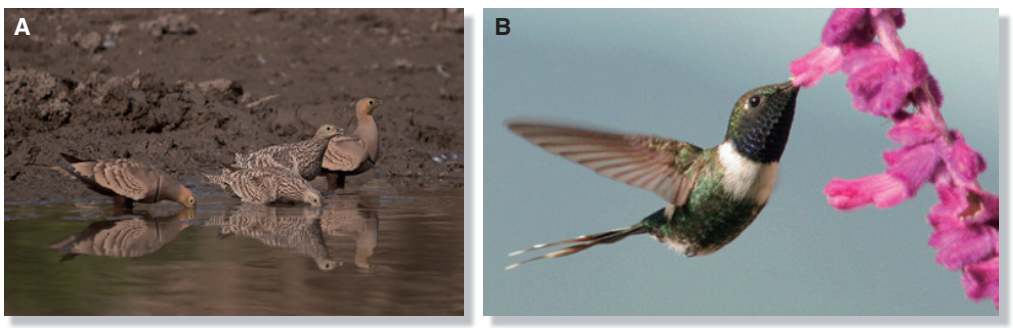


Fig. 7.03 Differences in daily water intake. (A) The Desert-dwelling Chestnut-bellied Sandgrouse (*Pterocles exustus*) must frequently fly long distances to find water sources. Many desert-adapted birds obtain water from their food or produce water via metabolism of dietary fats. It is common for such species to conserve water by producing hyperconcentrated uric acid in place of dilute urine. (B) In contrast, species that consume a dilute nectar diet, like this Sparkling-tailed Hummingbird (*Tilmatura dupontii*), must constantly excrete excess water to balance their physiological water budget. (Photographs by: A, Arpit Deomurari; B, Karen Ness, Guatemala.)

it is their ability to rid the body of excess salt that allows these birds to drink salty ocean water or consume very little free water.

7.1.2 Avian kidneys

Birds, like other vertebrates, have a pair of **kidneys** that are well supplied by blood. Bird kidneys possess some features in common with those of both mammals and reptiles. The major function of the kidneys is to excrete salts and nitrogenous waste, while minimizing water loss in urine. Each kidney is divided into numerous lobes containing

Kidneys: organs that maintain water and electrolyte balance and filter the blood of metabolic wastes, thereby producing urine.

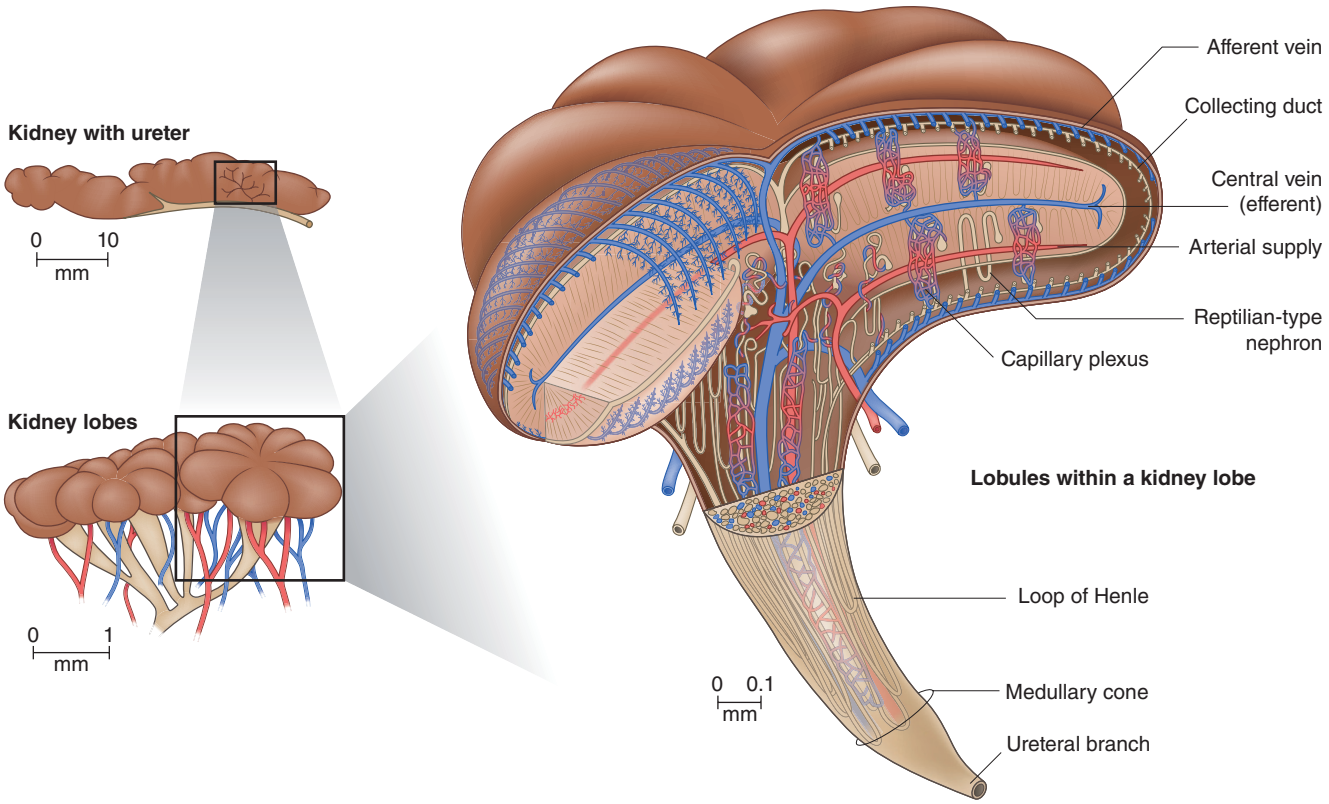


Fig. 7.04 Lobule of an avian kidney. Within the avian kidney, some nephrons, the structures that produce urine, have loops of Henle—necessary for concentrating urine—much like mammalian kidneys. These are found deep within the kidney, with very long loops that extend into the medullary cone. Most avian nephrons, like reptilian nephrons, lack loops of Henle. Note that the avian kidney connects directly to the ureter, the vessel that carries urine to exit the body (orientation shown in the lower diagram). (From Braun and Dantzler 1972. Reproduced with permission from American Physiological Society.)

functional units called **nephrons**, tiny tubular structures that produce the urine (Fig. 7.04). Each lobe empties into a central medullary cone that drains the nephrons into common collecting ducts and then into the ureters, from which the urine is voided via the cloaca.

In general, kidneys do not regulate the constituency of the blood by removing unwanted materials and simply excreting them. Rather, a large fraction (often about 20%) of the plasma and dissolved ions that flow to the kidney is filtered at the entrance to the nephron tubule, leaving behind the blood cells and large molecules like proteins. Then the walls of the nephrons selectively reabsorb the molecules that need to be reclaimed. Some molecules such as uric acid are also secreted into the nephron and added to the urine. Because the blood flow to the kidney is quite large, the entire blood volume of the bird can be filtered several times a day in this fashion. The filtration rate can be highly variable and this is one major way that osmotic balance is achieved. In House Sparrows (*Passer domesticus*), the filtration rate can fall by up to half with dehydration, thus conserving water. In some cases, such as heavily salt-loaded European Starlings (*Sturnus vulgaris*), the filtration rate is increased and Na^+ reabsorption is decreased in order to lose salt (Goldstein and Skadhauge 2000). In general, how different species of birds handle excess NaCl depends in part on whether or not they possess salt glands.

Nephrons in birds come in two recognizable types: those that are structurally similar to reptilian nephrons and those that are akin to mammalian nephrons (Braun and Dantzler 1972). The reptilian-like nephrons of birds are small, structurally simple, and located around the periphery of their kidneys. Larger mammalian-like nephrons are located deeper in the kidney lobule and are recognizable by the characteristic loop of Henle that dips into the heart of the medullary cone (Fig. 7.04). The loop of Henle is important because it creates an osmotic gradient that can then be used

Nephrons: structures within the kidney that filter wastes from the blood to produce urine.

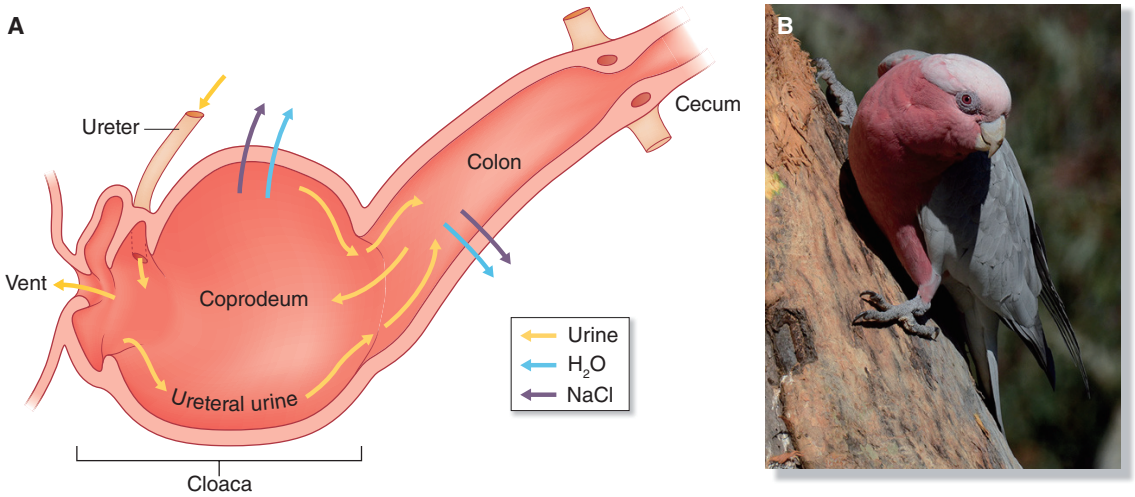


Fig. 7.05 The avian cloaca. (A) The cloaca is the common chamber where the colon and ureters from the kidney converge. This configuration allows urine to move backwards into the gut, where water and salt can be absorbed before the waste products are expelled through the vent. (B) This ability is especially important for birds that do not obtain much water from their diet, such as this seed-eating Galah (*Eolophus roseicapilla*). (A, from Goldstein and Skadhauge 2000. Reproduced with permission from Elsevier. Adapted from Choshniak et al. 1977. Reproduced with permission from John Wiley and Sons. B, photograph by Mary Bomford.)

to pull water out of the nephron and back into the blood, producing urine with a higher salt concentration than that of the other fluids within the bird's body. Different species of birds have nephrons that may be more or less similar to reptilian-type or mammalian-type nephrons. The greater the proportion of mammalian-like nephrons with long loops of Henle, the greater the osmotic gradient that can be set up and the greater the potential to concentrate the urine. Desert-dwelling birds that must conserve water therefore tend to have more mammalian-like nephrons.

The nephron structures that concentrate urine are always present in a bird's kidneys, but how much the urine is actually concentrated is highly variable and is under hormonal control. For example, water permeability in the collecting duct of the nephron is controlled by antidiuretic hormone (ADH); in birds, the ADH hormone is arginine vasotocin. The urine that leaves the avian kidney can be much more dilute than body fluids if ADH levels are low, or, in some species, 2–3 times greater than body fluid concentrations (nearly as salty as seawater) if ADH levels are maximal.

Another role of the kidneys in all vertebrates is the excretion of nitrogen waste products generated by protein metabolism, yet the chemical nature of this nitrogen varies across vertebrate groups. In fish and aquatic amphibians for which water is plentiful, the major excretory product is ammonia, which is highly toxic and is dealt with by dilution. Mammals excrete primarily urea, which is less toxic and requires less water for its excretion. Birds and reptiles excrete mainly **uric acid**, which is relatively non-toxic, but is not very soluble in water. Consequently it is excreted as a semisolid paste. A benefit of producing uric acid is that little water is lost in the process. The energy cost of producing uric acid as the nitrogenous waste product, however, is relatively high compared with producing either ammonia or urea. For birds, this evolutionary balance between water conservation and energy conservation appears to have fallen toward water conservation.

Birds can tolerate uric acid concentrations in their blood at levels that would cause gout (crystals of uric acid in the joints) in humans. Although you would not know it when looking at the pasty nature of a bird dropping, the physical structure of uric acid is actually quite complex and wonderfully adapted to avoid water loss by binding with other molecules. This helps birds excrete excess salt, and it keeps the uric acid from precipitating as crystals that could otherwise form kidney stones.

7.1.3 Cloaca and lower intestine

In birds, the urine that leaves the kidneys is not the final end-product for excretion as it is in mammals. This is because the avian ureters empty into the bird's **cloaca**, which allows further modification of the urine as ions are actively taken up from the fluid, followed by water (Fig. 7.05A). If the urine was as highly concentrated as in some mammals, at this point the salts it contains would

Uric acid: the less toxic molecule to which the liver of birds coverts the highly toxic nitrogenous waste products of protein metabolism.

Cloaca: the common opening of the digestive, excretory, and reproductive systems at the lower end of the avian digestive tract.

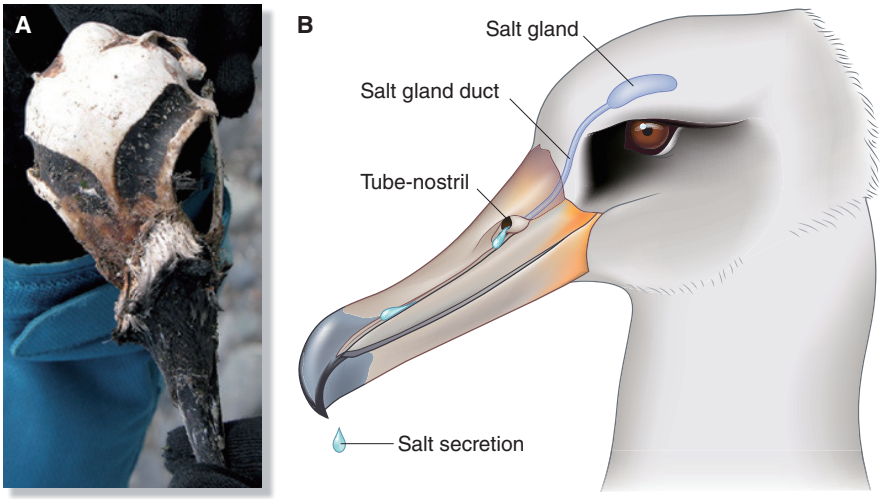


Fig. 7.06 Salt glands. (A) Salt glands sit within large grooves above the eye sockets, prominent on this Gentoo Penguin (*Pygoscelis papua*) skull. (B) Pathway of salt secretion from the ducts to the nostrils in the Laysan Albatross (*Phoebastria immutabilis*). (A, photograph by C. M. Vleck. B, © Cornell Lab of Ornithology.)

easily re-enter the body by diffusion, and conversely water could be pulled from the bird's body into the cloaca, and thereby be lost. Instead, birds have evolved alternate methods of water conservation. The excretory system of the bird can actually run backwards: the contents of the cloaca can reflux back into the colon and lower intestine of the bird. This has complicated putting together a complete picture of osmoregulation in birds because it is difficult to know exactly how much the voided urine has been modified before excretion from the cloaca, or how much has been mixed with fecal material from the gut. In a hummingbird that has recently consumed a large amount of watery nectar, the dilute urine is voided every few minutes and cloacal modification is unlikely to play any role. On the other hand, in some species, especially seed-eating birds like Galahs (*Eolophus roseicapilla*) (Fig. 7.05B), House Sparrows (*Passer domesticus*), and domestic chickens (*Gallus gallus domesticus*), substantial NaCl (up to 70% of that arriving from the kidneys) and 10–20% of the water can be retrieved in the cloaca and colon. The kidneys of Emus (*Dromaius novaehollandiae*) make urine that is only slightly higher in osmotic concentration than their plasma, but they can still retrieve water from the urine in the cloaca and colon (Dawson et al. 1985). This is not a means to rid the body of excess NaCl, but it does retrieve water that would otherwise be lost.

7.1.4 Salt glands

Although birds cannot achieve the phenomenally concentrated urine of some small desert-dwelling rodents, many can secrete a clear fluid that is several times more concentrated with salts than their urine. All birds apparently have paired **salt glands** in their heads, usually located just above the orbit of the eye, but only birds that have an evolutionary history of living in marine or desiccating habitats have evolved the ability to secrete salt solutions (Fig. 7.06A). These salt glands rid the body of excess salts, primarily NaCl, allowing these birds to drink seawater or to eat prey—such as squid and crabs—that are as salty as seawater. Highly developed salt glands are found in all marine birds, including penguins, gulls, auks, ducks, albatrosses, pelicans, and herons. Salt glands are also found in the Greater Roadrunner (*Geococcyx californianus*), a member of the cuckoo family found in the southwestern deserts of North America, and in several raptors. The salt gland solution exits through the bird's nostrils on top of the beak and runs or is shaken off the tip. In the procellariiform group of seabirds, the nostrils are located in the conspicuous "tubenose" located high on the beak (Fig. 7.06B). In a few diving birds the external nostrils are closed, probably to protect against water entry when the birds dive from great heights. In these birds, the salt gland secretion flows along the roof of the mouth and drips from the tip of the beak.

The concentration of the salt solution secreted from the salt glands varies with the habitat and diet of the bird. Coastal cormorants eating fish secrete a fluid relatively low in salt content compared with plankton-feeding, oceanic petrels in which the concentration of NaCl is more than twice that of seawater. The activity of the salt gland depends on a bird's recent exposure to salt, as the

Salt glands: paired glands that extract and excrete excess salt from the blood; most conspicuous in marine birds, especially the "tubenosed" seabirds.

Box 7.01 Salt gland experiments

The influential comparative physiologist Knut Schmidt-Nielsen studied the functional significance of the salt glands in Great Black-backed Gulls (*Larus marinus*) more than 50 years ago. In one experiment, he gave a bird by stomach tube an amount of seawater equal to one-tenth its body mass. After 3 hours, the bird had totally eliminated the salt load using secretions from its cloaca and bill, but the salt elimination from the salt gland was about 10 times higher than that from the kidney (Schmidt-Nielsen 1960). This amount of salt intake is equivalent to a 70-kilogram human ingesting about 7 liters of seawater, which of course is fatal. In contrast, birds with active salt glands can obtain pure water from drinking seawater because they can extract and excrete the salts while retaining the water.

gland will grow with use and shrink with disuse. The mechanism of salt excretion involves the active transport of NaCl across cell membranes from the body into ducts in the gland, requiring considerable energy. Thus it is probably significant that the gland remains small and inactive except when the bird faces an osmotic stress. This flexibility is in contrast to kidneys that must continually produce urine. The strength of the correlation between having enlarged salt glands and a marine existence is such that fossil birds such as *Ichthyornis* and *Hesperornis* (Chapter 2) that have clear impressions on the skull where a large gland was located are assumed to have lived in marine environments (Box 7.01).

The bottom line is that birds are just as effective as mammals at osmoregulation because they use a combination of drinking and eating, letting body fluid concentrations rise slightly, adjusting water conservation in the kidney and lower gut, or excreting excess NaCl from the salt glands. One of the ways that this ability to conserve water can be crucial is in avian thermoregulation in hot climates, as we will see in the next section.

7.2 Not too hot or cold

Thermoregulation is the ability of an organism to keep its body temperature within a temperate range, one that is usually different from that of the surrounding environment. Birds and mammals are the only groups of animals that produce heat to keep their internal environment at a fairly constant temperature—making them **endothermic homeotherms**. Endothermy means that the metabolic rate, and thus the capacity for heat generation, is high enough to maintain a core body temperature different from that of the ambient temperature. In fact, by adjusting metabolic rates in accordance with ambient temperatures, birds and mammals can maintain a fairly constant core body temperature (homeothermy). Bird body temperatures tend to be slightly higher than those of mammals, and also quite high relative to average air temperatures over most of the globe. Daytime core body temperature in birds is usually 39–43 °C. These high body temperatures may be adaptive in birds because warm muscles are better able to achieve instantaneous takeoff in flight. Core body temperatures in birds are actually dangerously close to lethal temperatures at which macromolecules like proteins start to change their structure and thus lose their function. The brain temperature of many birds in hot climates is often lower than their core temperatures. This is accomplished through heat exchange between warmer blood flowing to the head and cooler blood returning from the bird's nasal passages.

Maintaining a high core body temperature means that birds spend a large proportion of their total energy consumption to achieve homeothermy. This energy is then not available for body growth or reproductive output. In fact, the average metabolic rate of a bird is often 10 or more times higher than that of a similar-sized reptile. Why do birds spend such a large amount of energy to maintain their high body temperatures? The reason seems to be that the evolution of endothermic homeothermy opened up niches as the activity of birds became relatively independent of ambient temperatures. Cold reptiles, for example, are usually quite inactive, whereas homeothermic birds living in the same chilly ambient temperatures can continue to forage, fly, and defend territories. Homeothermy also allows all the biochemical reactions occurring within a bird's body to be tailored for just one temperature. Regulating body temperatures on the high side means that only occasionally will outside temperatures be higher than a bird's body temperature. This is important because when birds must cool down in the face of hot ambient temperatures, the only way to do this is to use evaporative cooling that expends precious body water.

Thermoregulation: the active ability of an organism to modulate its internal body temperature.

Endothermic homeotherm: an organism able to use metabolic heat production to keep its internal body temperature within a restricted temperature range despite conditions in the surrounding environment.

Box 7.02 Calculating a bird's heat balance

For birds and other endothermic animals, the general heat balance equation is:

$$HM = \pm Hcond \pm Hconv \pm Hr + He$$

Where:
HM = rate of metabolic heat production
*H*cond = rate of conductive heat loss or gain
*H*conv = rate of convective heat loss or gain
*H*r = rate of radiation heat loss or gain
*H*e = rate of evaporative heat loss

Conductive heat loss or gain is proportional to the difference in temperature between the bird and any object with which it is in contact (like the ground). Insulation will decrease heat flow between objects in contact. An important function of feathers, in addition to providing an aerodynamic surface, is to provide insulation against heat loss or gain from the environment. A naked bird is a cold bird. Some birds also insulate their core by employing a layer of subcutaneous fat that has a low conductance. In swimming penguins, for example, the air caught in the feathers plus the fat layer under the skin allow the birds to be perfectly comfortable in water at temperatures near 0°C, whereas on land this same insulation means that birds can quickly become too hot when exposed to direct sun, even in Antarctica.

Convective heat transfer occurs because of temperature gradients between the bird and any moving fluid (air or water) with which it is in contact. Convection accelerates heat loss by conduction because of the continuous replacement of fluid in contact with the bird, analogous to the wind chill experienced by humans. Flying birds easily lose any excess heat created through metabolism by convection, except under the hottest air temperatures.

Radiation heat transfer takes place between all objects, even when they are not in contact. Birds radiate heat to their environment and vice versa. Color affects radiation, as a dark body radiates and absorbs radiation more strongly than a more reflective body. So in theory, a black bird would absorb more radiant energy from the sun or its surroundings than a white bird. Many dark-colored birds such as vultures and cormorants take advantage of radiant heat transfer when they sunbathe, thus absorbing electromagnetic radiation.

Evaporative heat loss occurs when water evaporates from the surface of a bird, just as the evaporation of sweat can cool a human. Evaporation itself draws energy in the form of heat. It is extremely fortunate that evaporation requires a lot of energy (over 2000 joules are required to evaporate 1 gram of water at physiological temperatures), because this means that relatively little water is lost to achieve quite a large heat loss for a bird using evaporative cooling.

7.2.1 Physics of heat transfer

For a bird's body temperature to remain constant, heat loss must equal heat gain. Alternatively, heat can be lost or stored—thereby decreasing or increasing body temperature—but we will discuss this process later in this chapter. In thinking about the behavioral and energy costs of thermoregulation, it is useful to consider a heat balance equation that allows us to examine the various factors involved in heat exchange (Box 7.02).

It can be quite difficult to solve a complete heat balance equation because the routes of heat exchange are so complicated, and heat exchange also varies with the bird's posture and orientation toward the sun. Thermophysiologists have avoided some of these problems by measuring heat gain and loss directly, using life-like models of birds that are covered in real bird skins. The researchers can then determine the equilibrium temperatures of bird models placed in particular postures and in certain places. This procedure integrates all sources of heat exchange plus the bird's resistance to heat loss (insulation). To make these models even more like living birds, researchers sometimes place electric heaters inside the taxidermy mounts. By adjusting the heater, they can determine how much heat the model bird must "produce" to maintain a constant internal temperature under various environmental conditions (Fig. 7.07). Such mounts have been used, for example, to estimate that during the winter, American Goldfinches (*Spinus tristis*) can reduce their energy consumption by about 20% if they roost in sheltered locations rather than in the open (Buttemer 1985).

7.2.2 Costs of thermoregulation

In order for a bird to maintain a constant body temperature, its heat production must increase as outside temperatures decrease, because there is a greater temperature gradient for heat loss. However, this is only true below what is known as the bird's **thermal neutral zone**, which is

Thermal neutral zone: the range of ambient temperatures over which a bird does not require additional metabolic energy for the heating or cooling of its body.

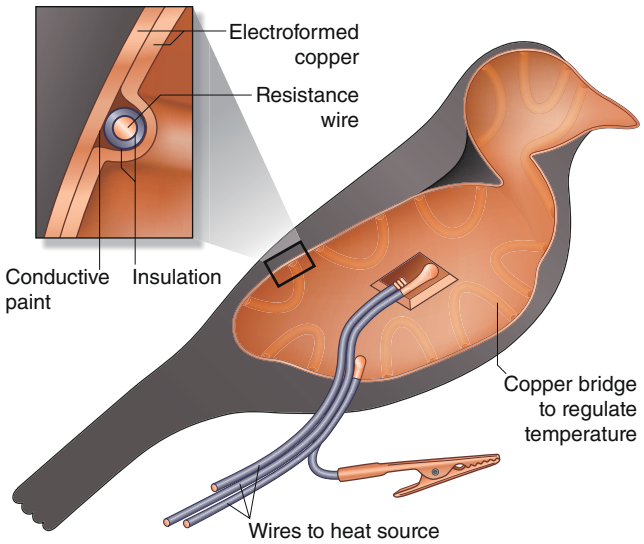


Fig. 7.07 Using taxidermy mounts to measure heat balance in birds. To estimate heat gain and loss in a particular environment, researchers insert electric wires beneath the feathers and skin of a mounted bird that contains a molded wax interior to simulate its original mass. By heating these wires, the amount of heat necessary to maintain a constant core body temperature can be measured and compared among birds. (Adapted from Bakken et al. 1983. Reproduced with permission from Ecological Society of America.)

defined as the range of ambient temperatures over which the bird's rate of metabolic heat production does not change (Fig. 7.08A). Metabolism can be constant in the thermal neutral zone because the bird can change its own rate of thermal conductance (insulative value) to keep heat loss constant at essentially no energy cost. For example, a bird can affect heat exchange simply by changing posture—by facing into the sun (Fig. 7.08B), pulling down its neck and head, tucking its beak under a wing, or sitting or standing—and it can also fluff up its feathers or open/close "thermal windows" in the feathers by raising/lowering its wings or feather patches to expose/hide unfeathered areas of its skin. Birds can also influence their heat loss with little cost in overall energy by changing the blood supply to their skin: increased blood flow to the skin will increase heat loss at the surface of the bird and vice versa.

Below the lower end of the thermal neutral zone, these low-cost and heat-saving adaptations are no longer sufficient, and the only option left to a homeothermic bird is to increase heat production by raising its metabolic rate. The rate at which heat production must increase to maintain body temperature is again a function of how well the bird is insulated. In general, smaller birds have higher and narrower thermal neutral zones, but this is not invariable because birds of the same size can still differ in the thermal conductance of their body due to differences in the insulative value of their feathers. Metabolic rates of birds also increase with activity and with the digestion of food. Heat generated from these activities can substitute for heat generated solely to maintain body temperature, but it is technically difficult to measure the extent of this substitution.

Although it might be counterintuitive, at the high end of the thermal neutral zone, a bird's metabolic rate also increases (Fig. 7.08A). Why would an overheating bird expend even more energy? In this temperature range, birds must pant or use **gular fluttering** (Fig. 7.09), a vibration of the hyoid bone and floor of the mouth. These movements require energy, but they increase airflow across moist

Gular fluttering: a behavior of opening the bill wide and vibrating the thin gular membranes of the throat in order to dissipate heat via evaporative cooling.

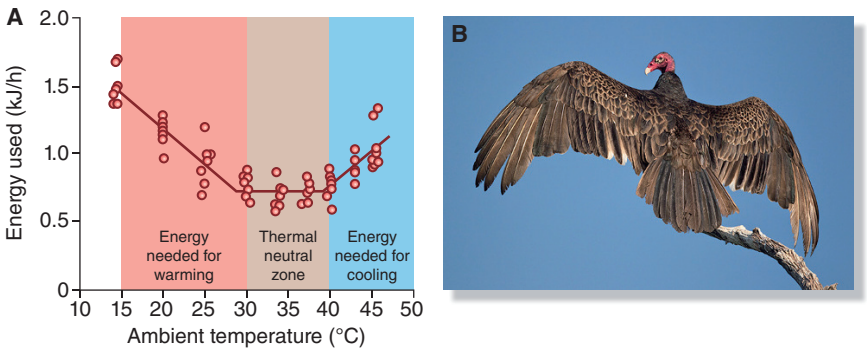


Fig. 7.08 Metabolic heat production. (A) The thermal neutral zone, where metabolic rate is relatively independent of ambient temperature, occurs between about 30 and 40°C for Variable Seedeaters (*Sporophila corvina*). However, metabolic rate increases with temperatures above and below this range due to the costs of thermoregulation. (B) Postures that facilitate heat absorption from the sun allow birds like this Turkey Vulture (*Cathartes aura*) to maintain body temperature at a lower metabolic cost. (A, from Weathers 1997. Reproduced with permission from American Ornithologists' Union. B, photograph by Jeff Dyck.)



Fig. 7.09 Gular fluttering. Here, a young Tricolored Heron (*Egretta tricolor*) vibrates the base of its white upper throat skin to facilitate evaporative cooling, a behavior termed gular fluttering. Water in the throat evaporates through the open mouth, dissipating heat in the process. Birds without this ability often rely on panting to cool off, since birds do not sweat. (Photograph by Kelly M. Riccetti.)

surfaces and thereby increase the effectiveness of **evaporative cooling**. Panting or gular fluttering are especially important ways to facilitate evaporative heat loss because birds do not possess sweat glands.

7.2.3 Birds in cold places

The extent to which heat loss can be minimized and heat production increased determines whether or not a particular bird can survive in cold climates. Of course one strategy for avoiding cold is for birds to migrate seasonally to more benign latitudes or altitudes (Chapter 12). Birds that live in cold environments must adapt physiologically, yet most birds do not show the major seasonal adjustments in insulation that are common in mammals, which often add both hair and fat as winter approaches. Birds that must face temperatures below their thermal neutral zone have two other options: either increase heat production—usually through shivering of the large flight and leg muscle groups—or abandon homeothermy, either for a period of time or in parts of their body.

Small birds with relatively large surface areas for heat loss—like finches, chickadees and tits, and kinglets—must be able to increase their metabolic rate in the winter in response to cold. This is quite an amazing feat given that at the same time they also face shortened day lengths that limit their foraging time, long nights of low temperatures, and often less access to food due to snow cover or inclement weather. **Acclimatization** may be necessary, particularly for species in high latitudes. For example, many studies of birds such as European Goldfinches (*Carduelis carduelis*), Common Redpolls (*Acanthis flammea*), Dark-eyed Juncos (*Junco hyemalis*), and Black-capped Chickadees (*Poecile atricapillus*) have shown that they have a greater capacity to increase heat production in response to cold temperatures in the winter than they do in the summer. In House Finches (*Haemorhous mexicanus*) and House Sparrows (*Passer domesticus*), individuals in northern populations tend to have higher metabolic rates than those in southern populations (Hudson and Kimzey 1966; Root et al. 1991). We also know that some small high-latitude residents like Great Tits (*Parus major*) and Common Redpolls will allow their core body temperature to drop slightly, but only when food is in short supply, thereby achieving significant energy savings. In contrast, Willow Tits (*Poecile montanus*) in the same habitat lower their body temperature on cold nights even when food is abundant (Reinertsen and Haftorn 1986).

Another way birds decrease heat loss in the winter is to choose protected roosting sites such as dense foliage or tree cavities. Grouse and ptarmigan that roost in snow burrows may actually be within their thermal neutral zone under the snow. In North America, Verdins (*Auriparus flaviceps*) build winter nests, which provide more insulation than summer nests (Buttemer et al. 1987), and there are reports of up to 16 Black-tailed Gnatcatchers (*Polioptila melanura*) roosting together in winter Verdin nests (Walsberg 1990). Presumably most birds do not roost in winter nests even in cold climates because of the inherent danger of predation when they return each evening to a predictable and conspicuous location.

Birds like ducks and gulls that must spend long periods standing in icy water use **regional heterothermy**, maintaining the temperature of their core body while allowing the temperature of their extremities to fall to near ambient temperatures (Fig. 7.10). Because of their large surface area, low heat production, and poor insulation, appendages like webbed feet are very hard to keep warm; for a duck or gull standing on ice, keeping the entire leg and foot warm would entail a tremendous energy cost. Instead, these

Evaporative cooling: the loss of heat via the energy required to evaporate water.

Acclimatization: changes in a bird's physiology after it has been in a new environment for several days or weeks that allow it to function better in the new conditions.

Regional heterothermy: the ability to maintain core body temperature while allowing the temperature of the extremities to deviate from the core temperature.

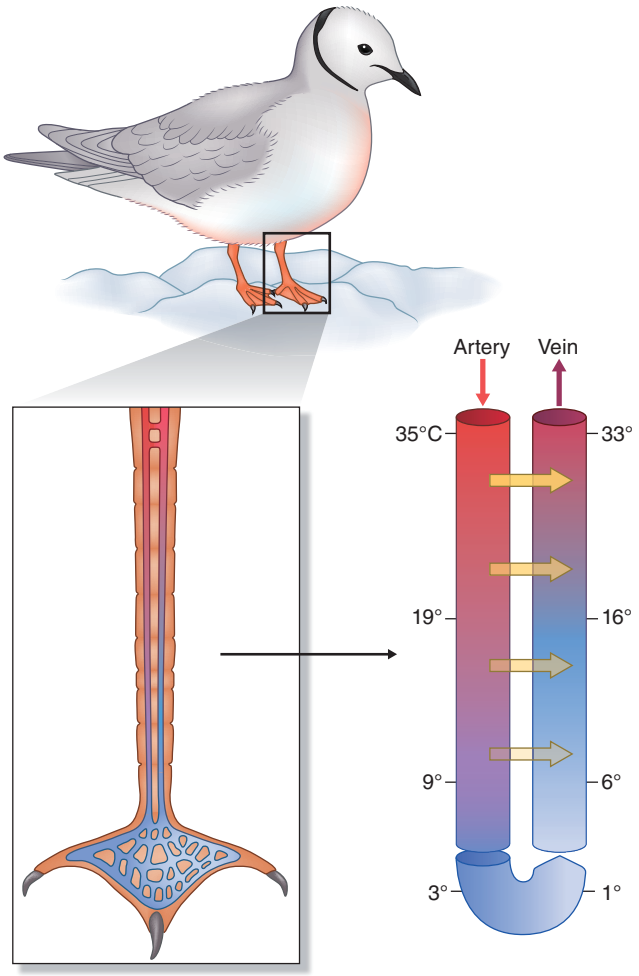


Fig. 7.10 Regional heterothermy. Birds that swim in cold water or stand on ice minimize heat loss by allowing temperatures inside their feet to drop, nearly to ambient levels. Intricate networks of blood vessels—in close proximity to one another—act as countercurrent heat exchangers, cooling blood flowing to the feet (artery) and heating blood as it returns to the body (vein). This steep temperature gradient (yellow arrows) reduces heat loss and saves a tremendous amount of energy. (© Cornell Lab of Ornithology. Adapted from Randall et al. 2002.)

birds allow the foot to approach freezing temperatures, thus decreasing the temperature gradient for heat loss to the environment. Blood must still be supplied to the foot, however, and the birds use a **countercurrent heat exchange** system to reduce heat loss. Heat from the warm blood in arteries supplying the foot and leg is transferred to the adjacent veins grouped around the artery that are returning cool blood back from the foot. This countercurrent heat exchange system can be very efficient at maintaining heat in the core and minimizing heat loss from the foot because a gradient for exchange is maintained all along the length of the leg, so long as the vessels are in close proximity and flow is in opposite directions. Periodic increases in blood flow allow a little heat to reach the foot and prevent it from freezing. Bird feet can also withstand low temperatures without damage because they do not consist of much muscle or nerve tissue. Since this is not the case for human feet, our own countercurrent exchange systems do not prevent frostbite.

Emperor Penguins (*Aptenodytes forsteri*) are famously known for surviving cold exposure. Male Emperor Penguins must incubate their single egg in the midst of the antarctic winter at temperatures as low as –30 to –40 °C. During an extended incubation bout of over 2 months, the male does not eat while he waits for his mate's return at about the time the egg hatches. Despite their large size and thick insulation, the energy male penguins would need to maintain homeothermy under these conditions, plus the energy needed to walk back to the ocean where food can be obtained, is greater than could be generated even if they used up their entire fat stores. It appears that the only way these males can survive this ordeal is to huddle closely together in large groups. Birds in the center of the huddle are protected from heat loss by their closely packed neighbors, thereby conserving energy, until they are forced to take their turn on the perimeter of the huddle where heat loss and metabolic expenditures are much greater.

Some birds regularly abandon homeothermy altogether, allowing their core body temperature to drop while they undergo bouts of **torpor**, a strategy known technically as temporal heterothermy. Shallow torpor, sometimes called nocturnal hypothermia, is a relatively modest decline in body temperature, usually to no lower than 30 °C. Shallow torpor has been observed in numerous birds, including vultures, anis, doves and quail, and several passerines including some sunbirds and manakins. Deep torpor (decreases in body temperature to levels at which the bird cannot respond to external stimuli) has been observed in hummingbirds, some poorwills and nightjars, mousebirds, and some swifts. In most cases, these birds appear to be reluctant heterotherms, only resorting to torpor when facing an energy crisis in the face of inclement weather. This is understandable because a torpid bird has very poor escape reflexes and is therefore highly vulnerable to predators.

Countercurrent heat exchange: in birds, the direct exchange of heat between warm outgoing blood (such as that traveling to the feet in arteries) to adjacent returning cold blood (such as that returning from the feet in veins) that helps retain heat within the body.

Torpor: a resting state in which the body temperature drops, metabolic processes slow, and reactions to external stimuli are slow or lacking.

On the other hand, some hummingbirds in cold regions of the high Andes appear to use bouts of torpor essentially every night (Carpenter 1974), and this may be true of other small nectar-feeding species as well (Fig 7.11A). Deep torpor is a strategy that is most easily employed by small birds because it simply takes too long for a large bird to cool down and rewarm on a daily basis. One species, the Common Poorwill (*Phalaenoptilus nuttallii*) of North America, is the only bird known to use multi-day bouts of torpor, interrupted by brief bouts at normal body temperature, much like hibernation in mammals (Fig. 7.11B). Torpor is not a complete abandonment of thermoregulation, but is still a physiologically controlled state, since birds can spontaneously arouse (rewarm) to the normal body temperature. In addition, during torpor, a bird's heat production often varies with changes in ambient temperature, just at a lower set point than normal (Fig. 7.11C).

The energy savings to be gained from abandoning homeothermy at cold temperatures is obvious. It might seem less obvious why several tropical species also employ temporal heterothermy. Any drop in body temperature, however, will produce an energy savings. Golden-collared (*Manacus vitellinus*) and Red-capped (*Ceratopipra mentalis*) Manakins in Panama, for example, will let their body temperatures drop to as low as 26 °C (close to the ambient temperature) on nights following rainy afternoons that preclude the last foraging bout of the day. By doing so they can save nearly 60% of the energy it would have cost them to remain homeothermic (Bartholomew et al. 1983). These savings could be quite important for small birds like manakins that eat low-energy fruits. Likewise the shallow torpor that desert roadrunners use is probably important in the winter when reptiles and insects—their typical prey—decrease dramatically in abundance. Given the common occurrence of some level of hypothermia in so many species of birds, it is probably an important strategy that contributes to the ability of birds to occupy a wide array of habitats and climates.

7.2.4 Birds in hot places

We are not surprised to see a rich bird life in productive, hot deserts. What is more surprising is to find birds living and breeding in the world's hottest, driest, and least productive deserts, such as those found in the Arabian Peninsula (Box 7.03). Not only are birds present even in these extremely challenging environments, but they are often visible (albeit less active and often in the shade) at the hottest times of the days, unlike most desert rodents that avoid the heat of the day by retiring to cooler underground burrows. Birds have been said to be preadapted to desert life because of the high temperatures (often over 40 °C) at which they regulate their body temperature. High body temperatures mean that most of the time a gradient still exists for birds to lose heat to a cooler environment. Increases in air temperatures associated with global climate change, however, are likely to increase the incidence of catastrophic mortality events in desert birds, as air temperatures exceed the upper critical temperature at which birds can survive (McKechnie and Wolf 2010). Flight activity will further generate heat as a by-product of metabolism, but during flight, convective heat loss increases, as does respiratory evaporative cooling. Excess body heat must be dumped when the bird lands, at which point the bird is forced to pant or gular flutter.

Most birds can deal with slight **hyperthermia**, storing excess heat with a rise in body temperature. Pigeons, quail, and domestic fowl are more likely to show hyperthermia when they are dehydrated. Such a strategy could work well for a large bird, such as a desert-dwelling Ostrich (*Struthio camelus*) that can then lose excess body heat during the cooler night. On the other hand, hyperthermia is a dangerous strategy for a small bird that could quickly reach lethal body temperatures. The only physiological way that heat can be lost when ambient temperatures are greater than body temperature is through evaporative cooling, from water loss across the skin or respiratory surfaces. Birds can increase the efficiency of respiratory evaporative water loss by panting or through gular flutter (Fig. 7.09). Even though birds do not possess sweat glands, they still lose significant water across their skin, which can contribute to evaporative cooling. Cutaneous evaporation often accounts for half or more of total evaporative heat loss when birds are not active and in warm, non-humid air. Well-hydrated, heat-acclimated Rock Pigeons (*Columba livia*) can maintain core body temperatures at ambient temperatures up to 60 °C even without panting if humidity is low, with evaporative cooling accounting for about 75% of the heat dissipation under these circumstances. When dehydrated, however, these birds pant at temperatures over 45 °C and respiratory evaporative cooling plays the larger role (Arad et al. 1987).

A few birds such as Wood Storks (*Mycteria americana*) and New World vultures augment evaporative cooling by urinating on their bare legs, thus obtaining even more benefit from the water lost in their urine. External water sources can also be used for cooling. Black-necked Stilts (*Himantopus mexicanus*), Egyptian Plovers (*Pluvianus aegyptius*), and various species of sandgrouse bring water back to their nests by wetting their abdominal feathers at external water sources. The water is then used to cool the eggs or chicks (Chapter 11).

Birds that live in hot places have evolved adaptations to reduce the cost of thermoregulation, including decreasing their metabolic rate to limit heat production, having efficient kidneys or salt glands to limit unnecessary water loss, and decreasing water loss across the skin and respiratory

Hyperthermia: internal body temperatures higher than typical.

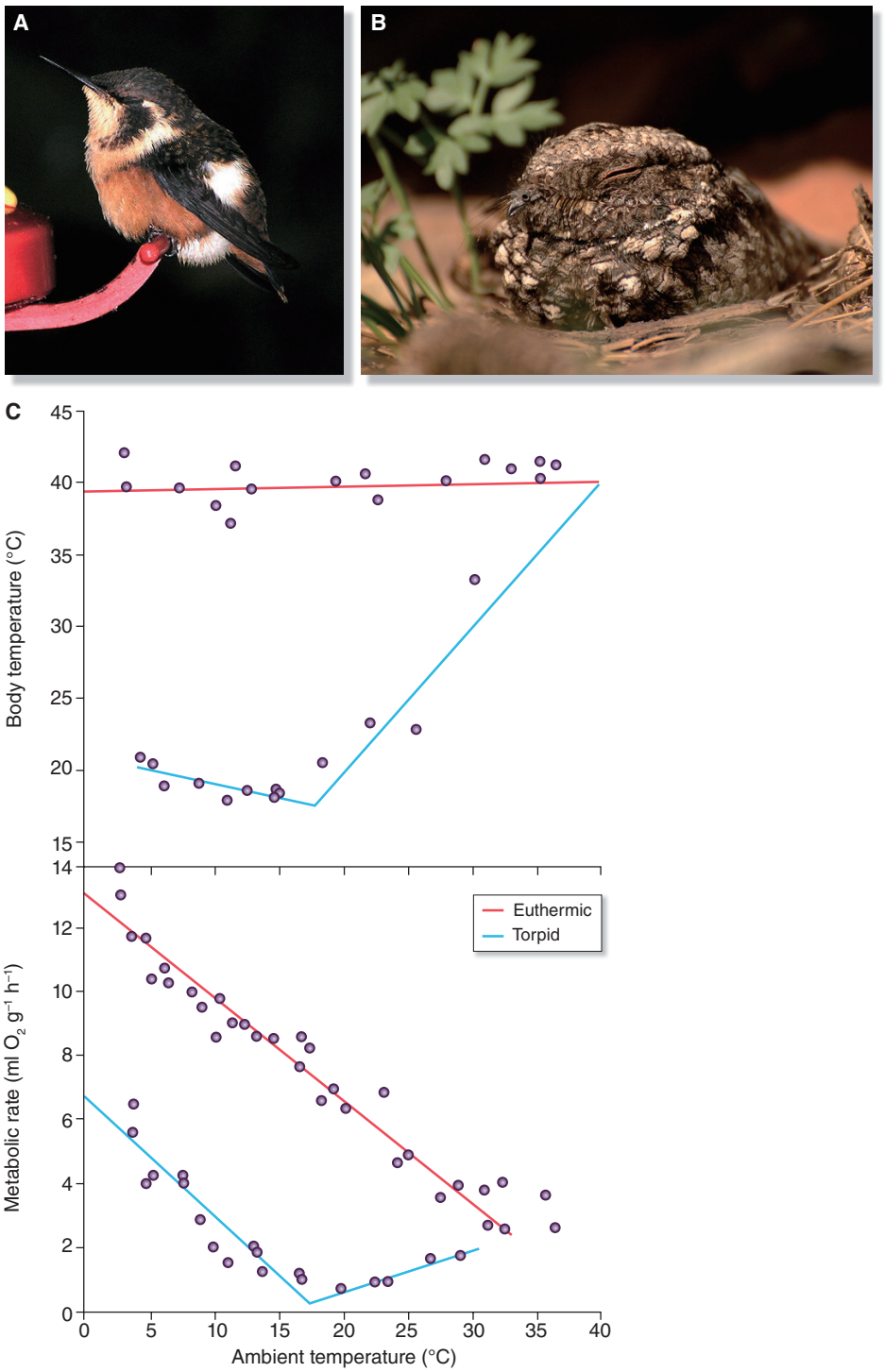


Fig. 7.11 Torpor. (A) Small nectar-feeding species such as this female Purple-throated Woodstar (*Calliphlox mitchellii*) decrease body temperature and metabolic rate, a strategy called torpor, to conserve energy in harsh conditions. (B) The Common Poorwill (*Phalaenoptilus nuttallii*) is the only bird species known to employ torpor over multi-day periods, similar to hibernation in mammals. (C) To maintain a high and nearly constant (euthermic) body temperature, metabolic rate must increase as temperature falls (red line in each panel). As a bird enters torpor, body temperature falls to ambient levels (blue line in each panel). However, torpor is still a regulated state, as evidenced by the rise in metabolic rate and body temperature when ambient falls below 17°C. (Photographs by: A, Mary Beth Stowe; B, Christian Nunes. C, from Hainsworth and Wolf 1970. Reproduced with permission from AAAS.)

Box 7.03 Desert larks subsist on little water or food

The Greater Hoopoe-Lark (*Alaemon alaudipes*) is a common resident of the Arabian Peninsula's Rub 'al Khali, the largest sand desert in the world (Fig. 7.B3.01). In their comparative work on Old World larks ranging from the wetter areas of the Netherlands and South Africa to the arid Arabian Peninsula, Joe Williams and Irene Tieleman (2005) have laid out the physiological, behavioral, and life history traits that allow larks to exist in such hot, dry deserts with low primary production. Physiological differences between lark species of desert versus wetter habitats include low rates of energy metabolism in the desert larks and low total evaporative water loss due to changes in the lipid structure of the skin. The skin lipids in the desert birds have a higher proportion of ceramides (an ingredient of expensive face creams) and a lower proportion of free fatty acids, which reduces their permeability to water. The desert birds also have relatively small clutch sizes and slow nestling development, further reducing the necessity for high rates of energy consumption. These desert species have achieved maximum economy with the two resources in greatest demand in deserts—energy and water—allowing them to exploit some of the most formidable habitats on earth.



Fig. 7.B3.01 Heat-tolerant Greater Hoopoe-lark (*Alaemon alaudipes*). This desert ground-foraging bird can tolerate soil-surface temperature as high as 69°C. (Photograph by Omar Alshaheen.)

surfaces whenever possible. Comparisons of the rates of metabolism and water flux of desert-dwelling species with those of species from wet habitats suggest that desert birds do, indeed, have lower metabolic rates and lower rates of evaporative water loss (Tieleman and Williams 2000) (Fig. 7.12). Metabolic energy use is about 40% lower in desert species compared with their counterparts from wet habitats, which allows the desert species to substantially reduce their heat load and their use of evaporative cooling (Box 7.03).

The extent to which birds can use their behavior, morphology, and physiology to thermoregulate under a variety of environmental conditions has shaped much of their biology. Thermoregulatory capacity affects species' ranges and influences when and where birds breed. It impacts whether or not migration evolved in a particular species. It also affects the energy and water requirements of birds, and we now turn to the acquisition of food and water in a discussion of nutrition.

7.3 Nutrition (digestion and metabolism)

Birds must find and eat enough food each day to satisfy their nutritional requirements. In this section we describe how energy and nutrient requirements are estimated, the differences between species in these requirements, and how energy and nutrient requirements in birds change between seasons and in response to environmental change.

The energy and nutrient requirements of birds have been estimated during controlled studies of captive birds that are fed diets that differ only in levels of the nutrient of interest. Nutrient requirements are defined as the minimum amount of the nutrient in the diet required for the bird to maintain body mass or, more directly, when nutrient intake equals nutrient output (Fig. 7.13). These estimates of the energy and nutrient requirements of captive birds in different physiological states (such as steady state maintenance, during growth, while thermoregulating at cold or hot temperatures, or actively flying or running) are helpful in establishing general patterns that vary with factors such as bird body size, and for comparing bird species with different lifestyles and ecology. These estimates can be extrapolated to free-living birds as long as additional information about their time–activity budgets (the time spent active and resting) and environmental conditions (such as temperature) in the wild are well documented (Fig. 7.14).

Birds require certain amounts of energy, protein, vitamins, and minerals. Birds are able to obtain energy from a variety of different food components (such as carbohydrates, proteins, and fats) but they must build their proteins from amino acids, some of which they can synthesize. Some nutrients are classified as "essential" because they are required, yet birds cannot synthesize them in sufficient

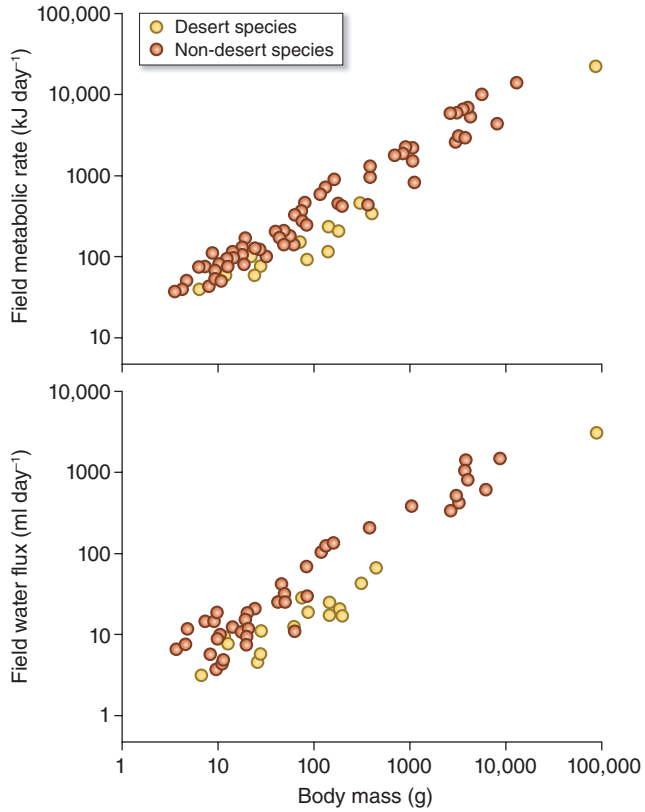


Fig. 7.12 Rates of metabolism and water flux in desert and non-desert species. Desert species have lower metabolic rates (top) and water flux rates (bottom) compared with non-desert birds of the same body mass. Note that the logarithmic scales decrease the apparent difference; metabolic rates are actually about 40% lower in desert species than non-desert species. (From Tieleman and Williams 2000. Reproduced with permission from University of Chicago Press.)

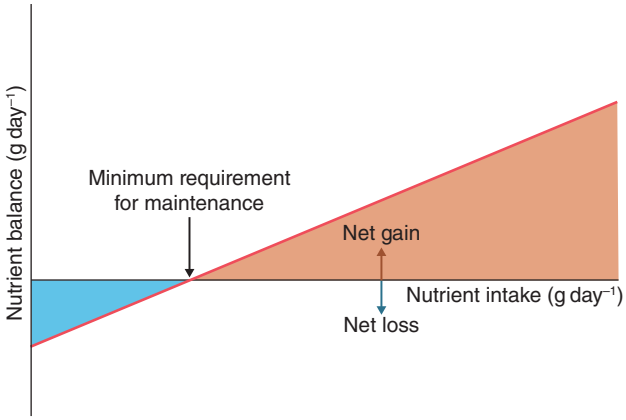


Fig. 7.13 Determining nutrient requirements for physiological maintenance. By incrementally limiting a certain nutrient (protein, amino acid, vitamin, etc.) in a bird's diet, researchers can assess the specific optimal nutritional requirements for physiological maintenance. The minimum amount required to maintain energetic balance occurs when nutrient intake equals output. Levels below this point are considered a net loss (blue area), levels above a net gain (orange area). (From Barboza et al. 2009. Reproduced with permission from Springer Science + Business Media.)

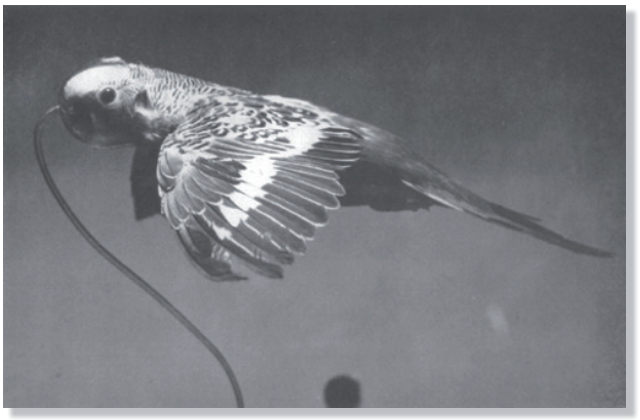


Fig. 7.14 Measuring metabolic rates in a flying bird. Oxygen consumption (an accurate measure of metabolic rate) can be continuously measured during flight by training birds like this Budgerigar (*Melopsittacus undulates*) to fly with a facial mask. This bird is flying in an experimental wind tunnel where the air speed is actively manipulated to determine the metabolic cost of flying at different speeds. (From Tucker 1968. Reproduced with permission from Company of Biologists Ltd.)

amounts to satisfy their requirements. Thus, essential nutrients must come from the bird's diet. For most birds and mammals, about 38 nutrients are required in the diet, including 10 essential amino acids, 1–3 essential fatty acids, 13 vitamins, and at least 14 essential minerals.

7.3.1 Energy requirements

The daily energy requirements of a bird and the energy value of its food largely determine the amount of food a bird must eat each day. This means that daily energy requirements can be estimated during controlled feeding studies if one knows the energy density and amount of food eaten and the composition of the excreta produced by the bird. As birds and all other animals obtain energy from food or body stores by chemically oxidizing the food, daily energy requirements can also be estimated by measuring heat production, oxygen consumption, and/or carbon dioxide production.

The energy requirements of a bird change to some extent with environmental temperature as described in the earlier sections on thermoregulation. Energy requirements also increase with activity and during periods of production (during a bird's growth, fat storage, and reproduction). However, metabolism and energy use continue even when

Box 7.04 Metabolic rate and body mass in birds

The metabolic rate of birds and mammals generally increases with body mass (Fig. 7.B4.01), according to the following allometric (metabolism as related to body mass) equations (where resting metabolic rate is measured in kJ/day):

Passerine birds:

$$\text{Resting metabolic rate} = 114.8(\text{body weight in kg})^{0.726}$$

Non-passerine birds:

$$\text{Resting metabolic rate} = 73.5(\text{body weight in kg})^{0.734}$$

Eutherian (placental) mammals:

$$\text{Resting metabolic rate} = 57.2(\text{body weight in kg})^{0.716}$$

Marsupial mammals:

$$\text{Resting metabolic rate} = 46.6(\text{body weight in kg})^{0.737}$$

The similar exponents close to 0.72 among these classes of animals suggest a common allometric relationship between metabolic rate and body size. This relationship between metabolic rate and body size is crucial because we can use it to predict metabolic rate and food intake of any bird, and because such allometric relationships underlie the evolution of many aspects of a bird's life history and ecology. The nutritional implication of this allometric relationship is that smaller animals have higher energy requirements per unit body weight than do larger animals. In addition, the higher value of the multiplication constant in birds compared with mammals demonstrates that birds have higher energy costs for a given body size than do mammals. For example, using the equations above, a 2-kilogram non-passerine bird such as a goose would require 122 kilocalories per day to satisfy the energy costs of its resting metabolic rate, compared to only 94 kilocalories per day (or about 25% less) for a similar-sized placental mammal such as a hare.

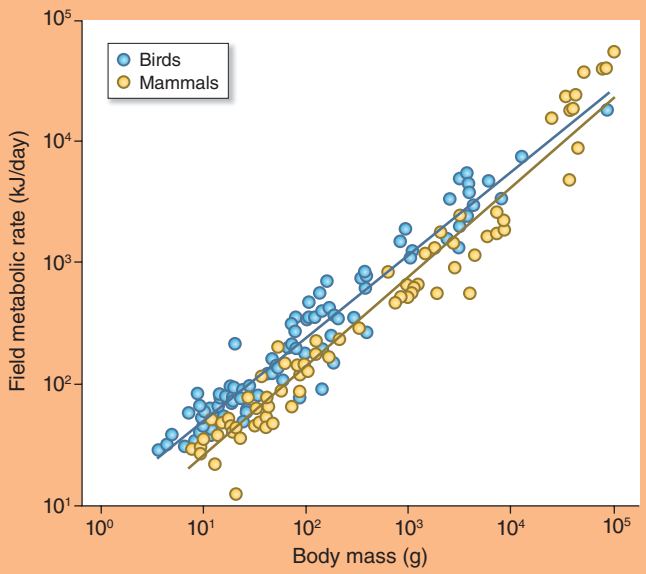


Fig. 7.B4.01 Allometry of field metabolic rate for birds and mammals. Although the relationship between metabolic rate and body mass is similar in birds and mammals (smaller animals need more energy per unit mass), birds have higher energetic needs than mammals overall. (Adapted from Nagy et al. 1999. Reproduced with permission of Annual Review of Nutrition.)

a bird is at rest. **Basal metabolic rates** of birds (and all other animals) increase with body mass in a very predictable way (Box 7.04). Andrew McKechnie and David Swanson (2010) presented a refined estimate of the allometric scaling of basal metabolic rate (and other important measures of energy expenditure) in birds that ranged in size from the 2.9-gram Blue-tailed Emerald (*Chlorostilbon mellisugus*) to the 100-kilogram Ostrich (*Struthio camelus*). For mammals this is usually shown as a "mouse-to-elephant" relationship, whereas for birds it is more appropriately called a "hummingbird-to-ostrich" relationship (Fig. 7.15).

The additional energy required to fuel the costs of thermoregulation, activity, and production are also important in determining the total energy requirements of a bird. Each of these costs can be estimated separately and then added together to estimate total energy requirements for the bird, although most such estimates use captive birds in various degrees of restraint. Nutritional ecologists also use particular isotopes of hydrogen and oxygen to label the metabolic water of free-living animals (Box 7.05).

Basal metabolic rate: the rate of heat production by a bird that is in a non-active state of rest, not digesting, and within thermoneutral environmental temperatures; a measure of the energy required for basic physiological processes alone.

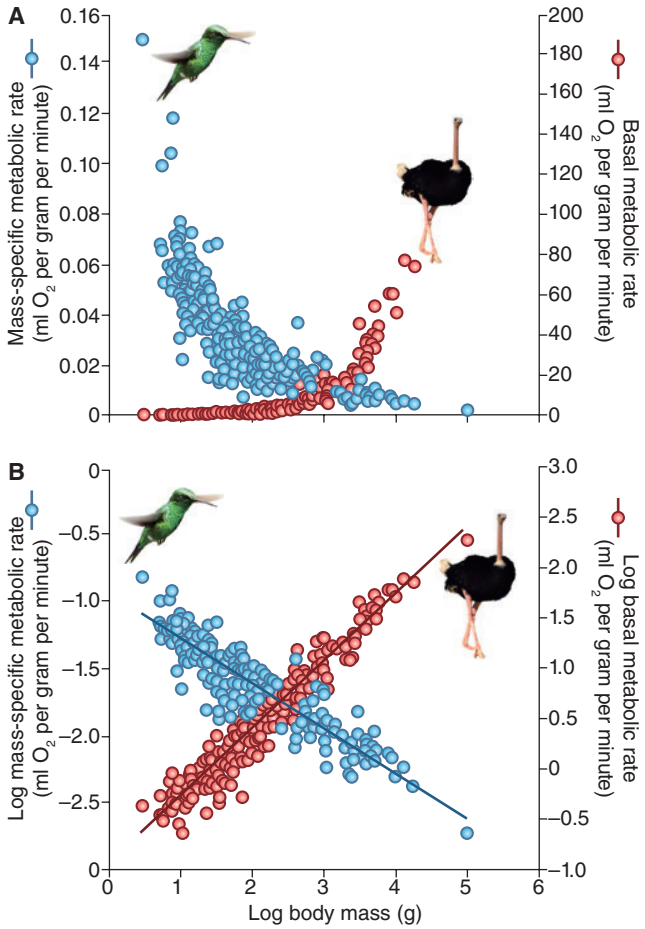


Fig. 7.15 Basal and mass-specific metabolic rates. Basal metabolic rate (BMR) measures an animal's resting oxygen (energy) consumption. This measure is fundamentally different from the mass-specific metabolic rate, which depends on the amount of oxygen consumed per gram of mass within a specific time period. (A) Data from a variety of bird species demonstrate that as body mass (depicted on a logarithmic scale) increases, the basal metabolic rate (red points) also increases. In contrast, the blue points shows that as a bird gains body mass, its mass-specific metabolic rate decreases. (B) Logarithmic scales are often used to observe whether exponential relationships are predictable across broad data ranges. In this case, there is an extremely predictable 0.65–0.75 exponent to overall avian metabolic rate in relation to body mass. (Data adapted from McKechnie and Swanson 2010. Photographs: hummingbird by Carlos E. Otoya Rojas; ostrich by Judith Anenberg.)

This doubly-labeled water method provides an estimate of the total energy use of the free-living animal as it goes about its daily routine. This total energy consumption by a free-living bird is termed its **field metabolic rate**.

The field metabolic rates of free-living birds (and other animals) conform to many of the patterns seen in the energy requirements of resting birds. First, field metabolic rates are usually about three times higher than maintenance energy requirements. Remember that the field metabolic rate includes a 24-hour daily routine, so it includes some periods of inactivity or sleeping when the bird's metabolic rate is minimal, as well as active periods when its metabolic rate is much higher. Second, the field metabolic rates of birds are on average about two times higher than in equivalent-sized mammals, and 12–20 times higher than equivalent-sized reptiles. Third, after taking into account body size, most of the variation in field metabolic rates of birds (and other vertebrates) is related to their ecology and life history. For example, the daily energy expenditure of sedentary tropical songbirds is lower than their more active migratory songbird counterparts.

7.3.2 Protein and amino acid requirements

Proteins are **amino acids** chemically bound together by peptide bonds. Birds can use protein from the foods they eat to build body protein, fat, or carbohydrate, whereas birds cannot use fats or carbohydrates from their diet to make body protein. Hence, insufficient dietary protein has serious consequences for birds. Of the 20 or so common amino acids, most birds are unable to synthesize nine (arginine, isoleucine, leucine, threonine, lysine, methionine, phenylalanine, tryptophan, and valine) and so they must obtain these essential amino acids entirely from their diet. We say "most birds" here because the amino acid requirements of the vast majority of wild birds are unknown, and therefore what we assume about the amino acid requirements of birds in general is based almost entirely on studies of domestic chickens. As long as birds eat enough protein, they can synthesize all the other non-essential amino acids.

Protein requirements are related to a bird's body size, ecology, and foraging strategy. Just as with energy, these protein requirements increase with body mass, although diet also plays an important role. For example, birds that eat other animals, seeds, or a combination of both are

Field metabolic rate: the rate of heat production by a bird that is engaging in a natural daily routine of activities; a measure of the total energy required for physiological maintenance, movement, digestion, heating and cooling, etc.

Proteins: complex molecules composed of strings of amino acids; proteins are the main building blocks of birds and other organisms and also act as enzymes in the chemical reactions within a bird's cells and tissues.

Amino acids: a class of organic compounds that are the chief components of proteins.

Box 7.05 Measuring the field metabolic rate of free-living birds using the doubly-labeled water method

The energy expenditure of free-living birds can be measured, rather ingeniously, using an injected (or consumed) amount of water that is enriched in stable isotopes of hydrogen (deuterium, ^{2}H) and oxygen (^{18}O). This so-called "doubly-labeled water" technique (Fig. 7.B5.01) usually involves taking an initial blood sample to establish baseline levels of the hydrogen and oxygen stable isotopes (measured using mass spectrometry) in the bird, then injecting it with a known amount of water with a certain concentration of ^{2}H and ^{18}O, allowing the isotopes to equilibrate with normal body water (about 30 minutes for small songbirds, up to 2 hours for the largest birds), and then taking a second blood sample to establish initial isotope concentrations. The bird is then released and recaptured a day or two later, and a third blood sample is drawn at a known time since injection.

This method is useful for measuring carbon dioxide production by the bird—and thereby its overall metabolic rate—because of the differing metabolic fates of the hydrogen versus oxygen in the water within its body. Hydrogen isotopes remain associated with water and so their concentration declines over time as water is lost through evaporation or excretion. Oxygen isotope concentration declines more rapidly than hydrogen because oxygen is lost both with water (H_2O) as well as via the CO_2 lost during respiration. The difference between the rates of oxygen isotope loss and hydrogen isotope loss allows us to estimate the bird's rate of CO_2 production, and thus more or less its metabolic rate. Energy expenditure estimated using the doubly-labeled water method in free-ranging animals is called "field metabolic rate," which incorporates all metabolic costs incurred by the animal over the measurement period—including basal metabolism, thermoregulation, activity, growth, etc.

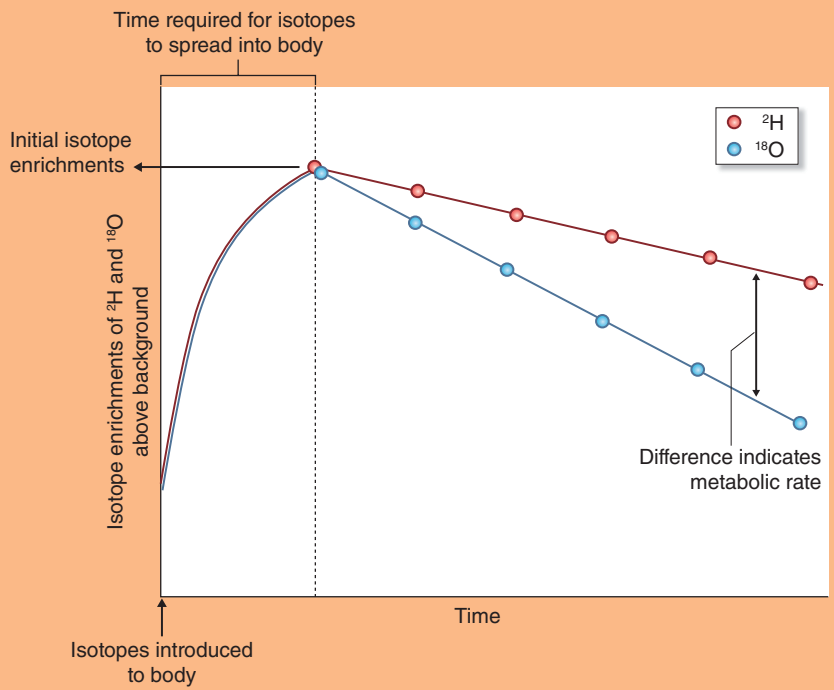


Fig. 7.B5.01 Using doubly-labeled water to measure metabolic rate. By injecting a bird with rare isotopes of oxygen and hydrogen, researchers can measure metabolic rates in free-living birds by measuring the difference in the loss of ^{2}H and ^{18}O over time. (From Speakman 1997. Reproduced with permission from John R. Speakman.)

usually consuming relatively high-protein diets with an appropriate balance of amino acids. Conversely, diets of fruits or leaves are usually low in protein as well as imbalanced in their amino acid composition. The overall protein needs of frugivorous birds are on average much lower than would be predicted for their body size alone, a pattern that may be an evolved adaptation to eating fruits with low protein.

Protein requirements also depend on the physiological state of the bird. For example, protein requirements are highest in growing birds, generally decline with age, and

increase during productive periods such as egg laying. The quantity of protein required by a bird also depends on the energy content of its diet and the amino acid composition of dietary protein. If there is a shortage of dietary fat or carbohydrate, then some protein must be used to satisfy energy requirements, so not all the dietary protein is available to satisfy the bird's protein requirements.

Importantly, the amino acid composition of dietary protein must be a balanced mixture of essential amino acids. If a bird's diet provides an insufficient amount of even one essential amino acid, then its rate of protein synthesis will decline and other unused amino acids will quickly be lost. The same holds true for other vertebrates, including humans. This is why satisfying protein demands requires eating a well-balanced set of essential amino acids—in short, body protein is constantly replenished and recycled, and animals cannot stockpile enough amino acids to overcome any short-term imbalances.

7.3.3 Carbohydrate and fat requirements

Carbohydrates and fats are the primary energy sources in the diets of most birds, except for some raptors and other pure carnivores. Dietary requirements for specific carbohydrates and fats are less exacting than for proteins (Box 7.06). Carbohydrates are a diverse group of compounds that vary widely in how completely they can be digested by birds. For example, the most abundant forms of carbohydrate in plants are cellulose and starch. Birds and other vertebrates lack cellulase, the digestive enzyme that digests cellulose, and so cellulose is either not utilized at all by birds or it is digested by microbes in the bird's digestive tract. The high metabolic rate of birds combined with their relatively small body size and lack of cellulase may explain why so few birds eat diets exclusively of leaves.

Birds can grow normally on a diet without carbohydrates, provided sufficient fats are available for satisfying energy requirements. In contrast, birds do require a few specific fats; three fatty acids (linoleic, linolenic, and arachidonic acid) are usually said to be essential for vertebrates, although current evidence suggests that for birds only linoleic acid is essential (Klasing 1998).

7.3.4 Vitamin and mineral requirements

Vitamins and minerals are often referred to as micronutrients because they are required in small quantities compared with macronutrients such as protein, carbohydrates, and fats. Birds require 14 minerals, including some (such as calcium, phosphorus, sodium, potassium, magnesium, chlorine, and sulfur) that are needed in relatively large amounts, plus trace elements that are needed in much lower amounts (iron, zinc, manganese, copper, molybdenum, iodine, selenium, cobalt, fluoride, and chromium).

Most vertebrates require 13 vitamins: fat-soluble vitamins include vitamins A, D, E, and K; water-soluble vitamins include thiamin (B_1), riboflavin (B_2), pyridoxal (B_6), nicotinamide (B_7), pantothenic acid, biotin, folic acid, cyanocobalamin (B_{12}), and choline. Fat-soluble vitamins can usually be stored by the animal so that deficiencies are extremely rare in free-living birds. Excesses of fat-soluble vitamins, especially vitamins A and D, can be extremely toxic. In contrast, most water-soluble vitamins cannot be stored and excesses are excreted, although some vitamin B_{12} and riboflavin can be stored in the bird's liver. Thus, a regular dietary supply of water-soluble vitamins is needed to satisfy a bird's vitamin requirements. Problems resulting from a diet deficient in vitamins can include growth retardation, dermatitis, poor feathering, and reduced reproductive output. In addition to these 13 vitamins required by most vertebrates, vitamin C is required in the diet of some passerine birds, whereas other birds are able to synthesize vitamin C in their kidney or liver, and so do not need to consume it in their diet. In mammals, bacteria and other microbes living in the digestive system may synthesize other vitamins, but the importance of microbial production of vitamins is not well studied in wild birds.

7.3.5 Digestive physiology and metabolism

The gross morphology of the digestive system of birds is relatively simple (Chapter 6). The general route of food through the digestive system of birds is from the mouth to the esophagus (some birds such as grouse, chickens, and pigeons store food in an enlarged pouch—the crop) to the stomach (divided into the proventriculus and gizzard) and then through the small intestine and large intestine before exiting through the cloaca. At the transition from the small to large intestine, birds have paired caeca that can be quite large in those few species that use microbial fermentation in the hindgut to digest higher fiber foods such as leaves.

Most food consists of proteins, fats, and carbohydrates, which are large molecules that must be broken down into simpler units to be absorbed and utilized. In birds this breakdown takes place primarily in the stomach and midgut using both mechanical and chemical processes. These mechanical processes involve contractions of the stomach that mix the food, saliva, and stomach secretions. The stomach initiates chemical breakdown of protein by secreting digestive enzymes and hydrochloric acid. The stomach of most birds is divided into a proventriculus, where chemical digestion is initiated, and a gizzard, where ingested food is mechanically mixed and ground (replacing the function

Box 7.06 Frugivory is harder than you think

Most fruits are "made to be eaten" in the sense that they are often widely available, easily consumed, and the plant–frugivore relationship is usually mutualistic, meaning fruit consumption benefits both the bird (nutrients) and the plant (seeds dispersed). But the relationship is not quite that simple. Common wild fruits offer birds mostly simple carbohydrates or fats, with relatively little protein (Fig. 7.B6.01), much seed bulk and water content, and a mixture of other compounds that can reduce the nutritional value of the fruit (Smith et al. 2007; Alan et al. 2013). Thus, fruits may be easy for birds to acquire, but their nutritional composition presents some physiological challenges (Levey and Martínez del Rio 2001). Nonetheless, some birds eat mostly fruits throughout the year, and many songbirds switch from eating mostly insects during spring and summer to eating mostly fruit during the fall migration.

Birds are picky when it comes to the fruits they select. For example, particular birds tend to eat either mostly high-fat fruits (as do most thrushes) or mostly high-carbohydrate fruits (as do waxwings), in part because these types of fruits require different and conflicting digestive strategies—fats are more slowly digested and so require longer retention time in the bird's gut, whereas carbohydrates are more rapidly digested so birds can eat and process more of these fruits per unit time (Karasov 1990; Witmer and Van Soest 1998).

Carbohydrates in fruits include glucose, fructose, and sucrose as well as structural carbohydrates such as the fiber in fruit pulp, and not all birds can digest all these various carbohydrates. Given that entire lineages of birds (such as the starlings, thrushes, and their relatives) cannot digest sucrose, these birds must behaviorally avoid eating fruits that contain much sucrose (Martínez del Rio 1990).

The nutrient composition shown in Fig. 7.B6.01 does not include seeds and water in the fruits because these do not provide nutrients to the birds (seeds are either regurgitated or passed undigested by most frugivorous birds). However, seed bulk and high water content do take up

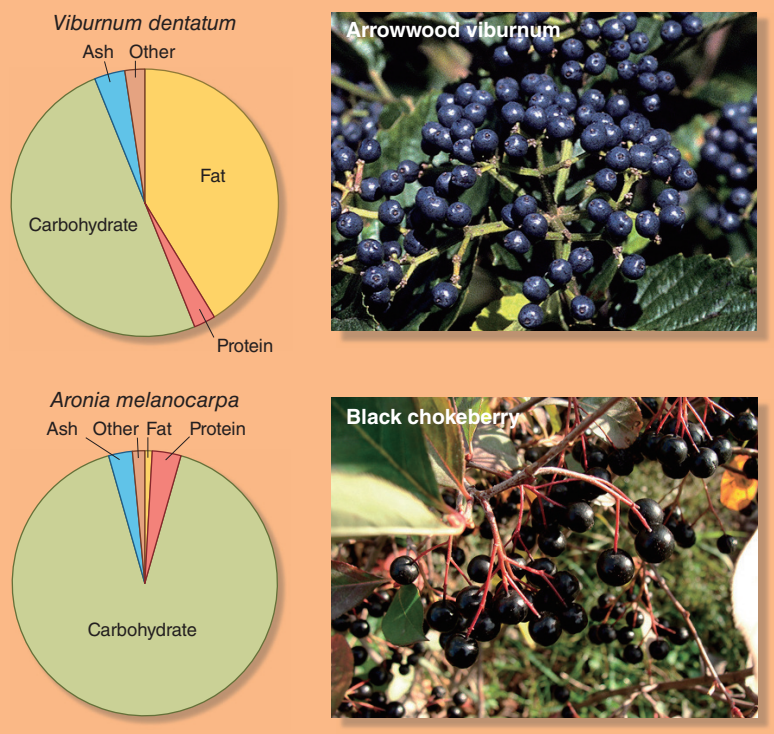


Fig. 7.B6.01 Dietary compositions of wild fruit. The pie charts illustrate the relative ratios of nutrients in two fruits (not including their seeds) commonly eaten by North American birds. Note the low protein content in both kinds of fruits despite their large difference in fat and carbohydrate content. (Data adapted from Smith et al. 2007. Photographs by: top, Jim Ault; bottom, Damon Taylor.)

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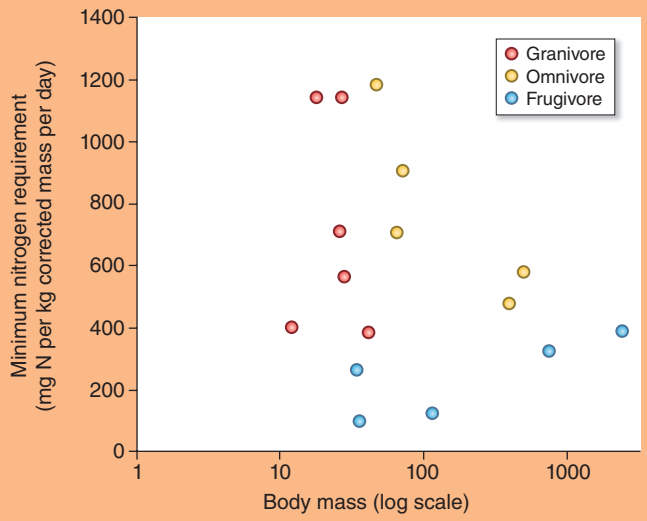


Fig. 7.B6.02 Minimum protein requirements for bird species with distinct foraging preferences. Across this diverse set of 16 bird species, frugivorous species require the least daily protein (measured here as nitrogen on the *y*-axis). (Data adapted from Langlois and McWilliams 2010.)

space in birds' digestive systems, limiting the rate at which their guts can process and digest the fruit (McWhorter and Martínez del Rio 2000).

Fruits may contain a diverse array of compounds that can reduce the nutritional value of the fruit. For example, some are directly toxic to birds and so limit the amount of that fruit the bird can eat, whereas others interfere with protein digestion and hence affect protein nutrition of birds (Cipollini and Levey 1997; Witmer 2001).

Birds that eat only fruit (Fig. 7.B6.02) have evolved lower protein requirements than other birds that may eat lots of fruit when in season but are otherwise primarily granivores or omnivores. Protein requirements of birds also change during molt, reproduction, and growth. Recent studies of songbirds reveal that protein requirements are lower during migration compared with non-migratory periods and this may facilitate a songbird's seasonal switch to eating mostly fruit during migration (Klasing 1998; Tsahar et al. 2006; Langlois and McWilliams 2010).

of teeth). Often small, hard objects such as pebbles are swallowed to aid in the grinding of food in the gizzard.

Digestive enzymes are proteins produced by cells of the stomach, intestine, and pancreas that regulate the rate of chemical breakdown of food compounds. Like all enzymes, digestive enzymes are to some degree specific for a certain substrate or reactant molecule, and the activity of digestive enzymes is sensitive especially to temperature and pH. Each of the three major types of foodstuffs has a corresponding group of enzymes associated with its digestion (Fig. 7.16).

The activity of digestive enzymes generally varies in response to different diets; thus a bird eating a high-protein diet will have a higher proportion of protein-digesting enzymes. Although this generalization holds for domestic poultry, the few wild birds studied to date exhibit somewhat different patterns. Specifically, wild birds fed diets with higher carbohydrate concentrations did not increase the relevant digestive enzymes, whereas birds fed diets with higher protein concentrations increased their protein-digesting enzymes (Karasov and Martínez del Rio 2007).

The chemical digestion of proteins, fats, and carbohydrates along with absorption of the end-products of digestion primarily occurs in the bird's small intestine. Digestive enzymes secreted from the liver and pancreas are delivered into the first portion of the small intestine. In the latter portion of the small intestine, digestion is completed and absorption takes precedence. The products of digestion are absorbed across the intestinal wall (Fig. 7.17) and then move via blood circulation into the bird's tissues and cells.

7.3.6 Microbial symbiosis and digestion

Cellulose—the primary structural material in plants—is one of the most abundant biological compounds. However, no vertebrate produces cellulose-digesting enzymes (called cellulases). Instead, some have microbes (primarily bacteria and some protozoa) inside their digestive system that break down cellulose and other complex plant carbohydrates. The evolution of enlarged portions of the foregut and/or hindgut to house symbiotic microbes was crucial in the radiation of herbivorous mammals, because it provided the appropriate conditions for microbial fermentation. However, few birds have evolved such homes in their guts for symbiotic microbes, in part because birds are relatively small and have high metabolic rates, and fermentation proceeds relatively slowly. Since metabolic rate determines an animal's energy needs, and gut size determines an animal's capacity to process food into nutrients, smaller herbivores generally—and avian herbivores especially—must process food rapidly in order to satisfy their higher metabolic rates. Avian herbivores are particularly intriguing in light of these constraints, because they have relatively high metabolic rates and are generally smaller in size compared with mammalian herbivores.

Fermentation in an animal's foregut is efficient, because the fermentation occurs before the material passes into the intestine, where absorption occurs. The Hoatzin (*Opisthocomus hoazin*) of South America is the only living

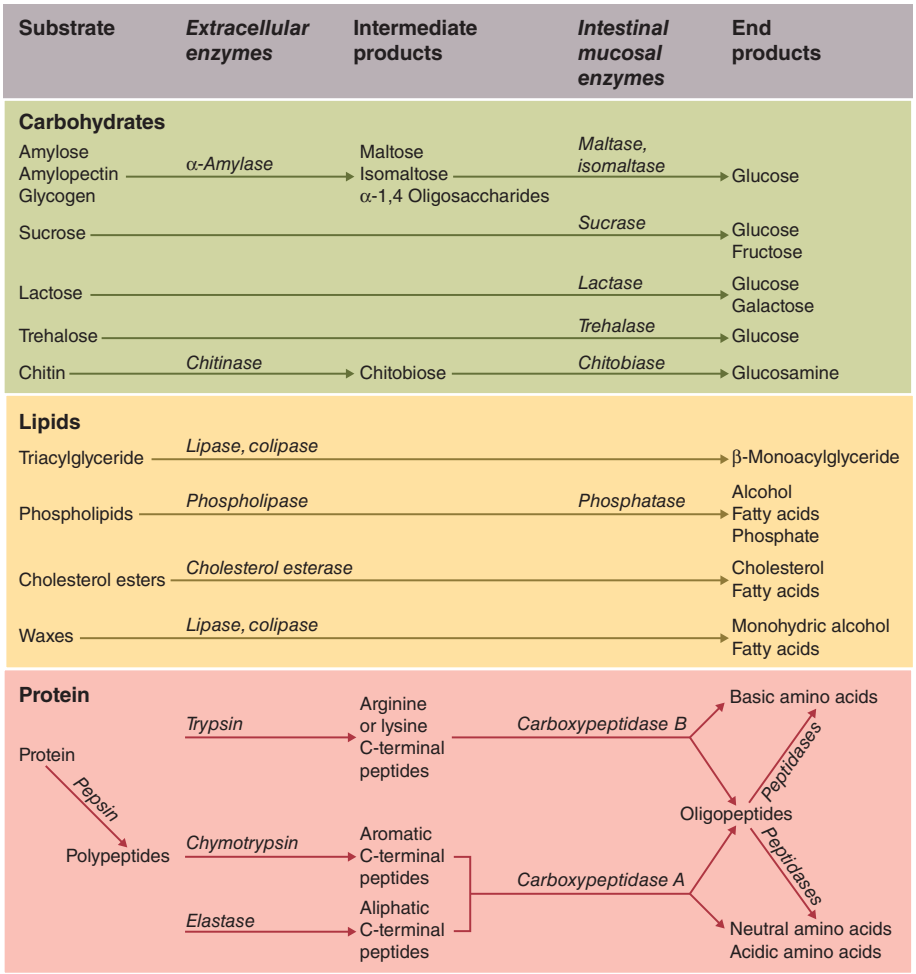


Fig. 7.16 Digestive enzymes. The three major food types for birds and other vertebrates—carbohydrates, lipids, and protein—are depicted with the corresponding enzymes responsible for their chemical breakdown. Complex carbohydrate and protein digestion require two steps. (From Stevens and Hume 1995. Reproduced with permission from Cambridge University Press.)

example of a foregut-fermenting bird (Chapter 6). Instead, most herbivorous birds (and reptiles) typically have enlarged **caeca**—side pouches that open into the large intestine or rectum—where plant material is microbially digested. Because fermentation in the hindgut occurs after the primary site of absorption (the intestine), digestion is less efficient in hindgut compared with foregut fermenters.

With the exception of the Hoatzin, all avian herbivores harbor microbes in the hindgut (in their intestines, caeca, or colon). Large and fibrous particles move through the hindgut relatively rapidly while smaller, more soluble particles are routed through the caeca. This allows these avian herbivores to maintain high rates of food intake, to quickly excrete the hard-to-digest material (careful inspection of goose feces makes this obvious), and to focus on the more digestible fractions of the diet. This selective retention of the more digestible fibers helps these birds avoid some of the constraints of a vegetarian diet, as they can maintain relatively fast passage rates to satisfy their energy and nutrient requirements.

However, the rarity of avian herbivores suggests that the nutritional challenges associated with eating leaves are formidable and not often compatible with a lifestyle that involves lots of flying. A leaf-exclusive diet is challenging for birds because leaves contain lots of indigestible fiber, and only gut microbes can digest this fiber. Yet this takes a long time, and most birds cannot really afford the wait. Only 3% of existing bird species eat leaves, and most birds that do so—such as grouse, quail, ptarmigan (all in the order Galliformes), and the Hoatzin—do not fly much or

Caeca: in the digestive tract of birds, side pouches that open into the large intestine or rectum.

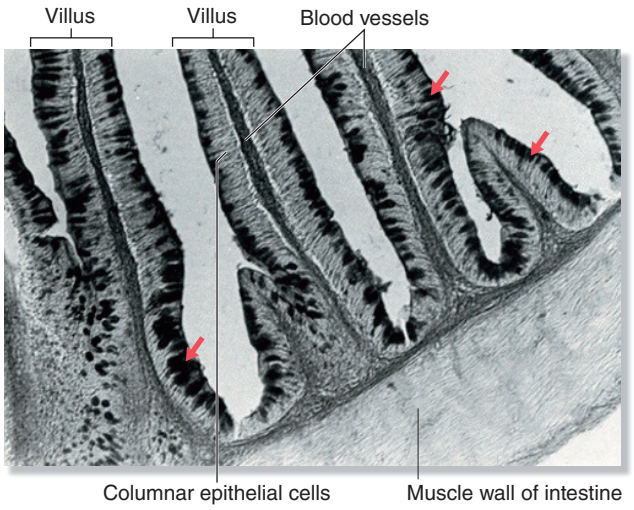


Fig. 7.17 Intestinal structure. A cross-section of a Spotted Nothura's (*Nothura maculosa*) small intestine shows the major structures necessary for nutrient absorption in the gut. Columnar epithelial cells secrete digestive enzymes and absorb nutrients with the help of protective mucous, secreted by the goblet cells (red arrowheads). Absorbed nutrients enter into the bloodstream via vessels inside the villi that project into the interior of the small intestine from the peripheral muscular wall. (From Chikilian and de Speroni 1996. Reproduced with permission from John Wiley and Sons.)

far. Geese are exceptional among herbivorous birds in that they are strong flyers that range in adult body size from the diminutive Ross' Goose (*Chen rossii*) and Red-breasted Goose (*Branta ruficollis*) (ca. 1000 grams) to the 'giant' subspecies of Canada Goose (*Branta canadensis maxima*) (ca. 7000 grams).

When high-fiber forage is available, then hindgut-fermenting herbivores like geese are favored over foregut-fermenting herbivores like the Hoatzin, because they can increase their intake and passage rate and so obtain adequate nutrients despite the fast passage rates and large amounts of undigested residue. Foregut-fermenting herbivores have difficulty eating high-fiber forage because they must retain the large fiber particles in the foregut for longer.

7.4 Dealing with pathogens

Survival always depends on an organism's ability to combat the omnipresent pathogens in its environment, including bacteria, viruses, and both internal and external parasites. A complex **immune system** to combat disease organisms has evolved in birds and other vertebrates. The basic elements of the avian immune system are well known and similar to those of mammals, yet the ecological importance of the immune system in free-living birds, and how the costs of immune challenge trade-off against other aspects of a bird's existence, represent an exciting area of research within ornithology. Here, as in many other branches of biology, birds have played a key role in advancing the general field of ecoimmunology because of their accessibility and their wide range of ecological adaptations. The emergence of pathogens that can infect both birds and humans—such as West Nile virus and avian influenza—has also spurred research on avian immune systems.

7.4.1 Elements of the immune system and how they interact

The role of the avian immune system is to recognize foreign microbes as distinct from the bird itself, and to react to them in order to fight disease and maintain homeostasis. The immune system has historically been classified into two components: the **innate immunity** arm that confers immediate but non-specific defense, and the **adaptive** (or **acquired**) **immunity** arm that confers specific defense to a particular pathogen. The division between these two components is somewhat artificial because they share many elements and often work together to fight pathogens. The innate system includes chemical and physical barriers—such as skin and mucosal membranes, acid secretions in the gut, and tears that can kill some bacteria. Cellular components on the innate side include specialized **phagocytic cells** that can envelop pathogens, along with cells that produce natural **antibodies**. Chemical (or humoral) components of the innate immune system include the proteins

Immune system: the organs, tissues, cells, and antibodies that differentiate self from non-self and which act in concert to neutralize potentially pathogenic organisms or substances.

Innate immunity: components of the immune system that are standard responses to a potential pathogen, not arising from or requiring previous exposure to that pathogen.

Adaptive (or acquired) immunity: components of the immune system that become tailored to respond to previously encountered pathogens, usually involving antibodies that recognize and attack specific antigens on those pathogens.

Phagocytic cell: a cell that engulfs and absorbs potential pathogens, waste compounds, or other foreign bodies.

Antibody: a blood protein able to attach to an infectious pathogen, thereby guiding other components of the adaptive immune system to attack that pathogen.

that initiate inflammatory responses or that rupture the cells of harmful microbes.

The innate immunity arm recognizes general structures shared by different classes of microbes and reacts accordingly, whereas the adaptive arm relies on receptors that recognize specific microbes. Components of the adaptive arm include two cell types—T lymphocytes (of many types) and B lymphocytes—that produce specific circulating antibodies. Antibodies act to neutralize and eliminate microbes or the toxins they produce and to facilitate their uptake and digestion by phagocytic cells. The innate components are the first line of defense against pathogens because they are present before an infection occurs. The adaptive components are the second line of defense because they are not activated until an infection occurs, and are therefore slower to respond. An initial exposure to a pathogen results in "immunological memory," so that the adaptive immunity system can often mount a more rapid and intense response if a bird is exposed to that same pathogen later in its life.

Birds are historically important in the field of **immunology**. B lymphocytes are so named because in the 1950s they were originally found to mature in the avian bursa of Fabricius, a pouch off the lower gut near the cloaca in birds (Chapter 6). The bursa of Fabricius regresses before sexual maturity in birds, but is active during earlier periods of growth and development. Stem cells from the liver travel to the bursa during embryonic development and there mature into B cells.

Other tissues like spleen, lymph, and bone marrow are also important contributors to the avian immune system. A female bird can even transfer antibodies to her offspring through the egg yolk. These maternal antibodies are an important source of immune protection for chicks early in life, disappearing from their circulation at about the same time the young birds can first manufacture their own antibodies.

7.4.2 Ecoimmunology

Even though we know much about how the avian immune system works, how that function relates to the survival and fitness of birds in the real world is often less clear. The importance of the immune system for survival might seem obvious, but how might individual variation in its strength—termed **immunocompetence**—affect avian life history traits (Chapter 13) like reproductive success or senescence? In turn, how might other aspects of a bird's biology—such as stress or nutrient limitations—influence its immune function?

There are demonstrable energy costs to mounting an immune response, and if energy is limiting there are trade-offs in allocating energy to immune defense versus other demands such as egg production. Investing in the greatest possible immune response is not necessarily the best strategy for an individual bird when such trade-offs ultimately lower its fitness for other reasons. For example, chickens artificially selected to have strong immune responses have smaller combs and lower testosterone levels that probably affect their reproductive success (Verhulst et al. 1999).

Given the complexity of the immune system, it is little wonder that it is challenging to study in free-living birds. The cellular and humoral components of the immune system can be dissected and studied in captive birds, but identifying the most critical components in an ecological setting is rarely straightforward. In these cases it is tempting to extrapolate from measurements of only one component of the immune system, yet it is risky to make broader assumptions from knowledge about only one part of such a complicated system.

One way to assess a wild bird's immune strength is to test the ability of the bird's plasma to kill different bacteria strains under controlled lab conditions. These methods help provide assessments of how the avian immune system works under natural conditions. Better yet would be a way to determine how immune functionality directly affects a bird's lifetime reproductive success and survival. These types of studies are difficult in field situations; however, scientists have been able to study survival and selection in response to diphtheria injections in Blue Tits (*Cyanistes caeruleus*) (Fig. 7.18). Birds with an intermediate innate immune response to diphtheria had the highest survival (Råberg and Stjernman 2003).

For a bird, being in good enough condition to mount a strong immune response—or conversely, being in such bad condition that investment in immune function is too costly—can have far-reaching implications. For example, avian biologists have long speculated that elevated testosterone decreases a bird's immune function, providing a mechanism for the "immunocompetence handicap hypothesis" in which only the males in the best overall condition should be able to display costly sexual ornamentation (Chapter 3). Although these ideas remain controversial, they spurred many studies of immunology, parasitology, disease, and fitness in wild birds. Under this hypothesis, if overall energy is limiting for a bird, then the trade-offs of mounting an immune response should be most evident at times when it must engage in other energy-intensive activities as well. This idea has been supported in studies of North American Tree Swallows (*Tachycineta bicolor*) that were forced to

Immunology: the study of the immune system.

Immunocompetence: an individual bird's ability to mount a functioning immune response after exposure to a pathogen or antigen.

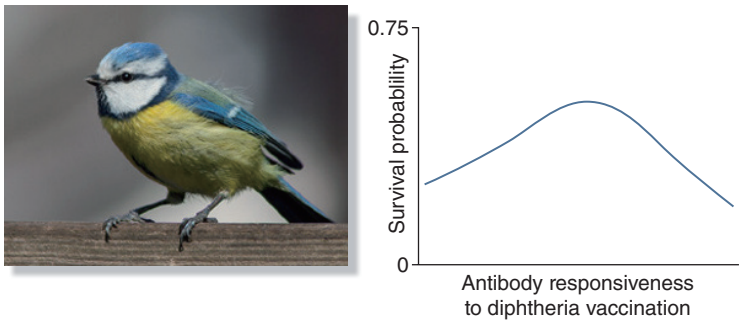


Fig. 7.18 Survival probability as a function of antibody responsiveness. Researchers measured antibody responsiveness to diphtheria vaccines in Blue Tits (*Cyanistes caeruleus*) to test the relationship between survival and immune response. Lower survival was observed at the low and high ends of the immune responsiveness curve for diphtheria, suggesting that birds mounting immune defenses incurs fitness costs. (From Råberg and Stjernman 2003. Reproduced with permission from John Wiley and Sons. Photograph by Johan van Beilen.)

increase their workloads when additional chicks were added to their nests or when some of their flight feathers were trimmed. These birds subsequently had lower immune function, suggesting that these increased demands lowered their energy investment in their immune systems (Ardia 2005). Similarly, Common Eider (*Somateria mollissima*) females fast during egg laying and incubation, losing up to 40% of their body weight; females in the worst condition showed the greatest suppression of their immune system and frequently abandoned their brood. This presumably occurred because they could no longer manage the trade-off of a suppressed immune function in order to breed without risking their own survival (Hanssen et al. 2003).

Immune challenges can limit birds in many ways. For example, even when they are infected with a relatively benign strain of avian influenza, Tundra Swans (*Cygnus columbianus*) show poor migratory ability, with delayed departure and longer stopover periods en route (van Gils et al. 2007) (Fig. 7.19). When House Sparrows (*Passer domesticus*) are injected with a component of bacterial cell walls that mimics an actual infection, they have lower reproductive success, particularly when their brood size is large (Bonneaud et al. 2003). Deterioration of the immune system in older birds has been demonstrated in several species, particularly in the adaptive response component of the avian immune system (just as in older humans). Older Tree Swallows that are forced to mount an immune response are more likely to decrease the rate at which they are feeding chicks compared with younger birds (Palacios et al. 2011). This pattern is not universal, however: the oldest males in a Blue-footed Booby (*Sula nebouxii*) population respond to an immune challenge by investing more heavily in reproduction than younger birds so treated, suggesting these old boobies were making an elevated investment in reproduction near the ends of their lives (Velando et al. 2006).



Fig. 7.19 Tracking infection effects. This Tundra Swan (*Cygnus columbianus*) is infected with avian influenza. By tracking such individuals, researchers have discovered that infected birds delay migration, travel shorter distances, and feed at reduced rates compared with uninfected birds. (From van Gils et al. 2007. Photograph by W. Tijsen. CC-BY-3.0.)

7.5 Exercise physiology of flying birds

Birds burn at least twice the energy each day as similar-sized mammals, and for many the primary mode of locomotion (flying) is very costly. How do birds sustain this energetically expensive way of living? Birds have special features to ensure rapid and efficient energy distribution within their bodies, including efficient lungs, a large, fast-beating heart, and a simple yet highly efficient digestive system. In this section we describe the circulatory and

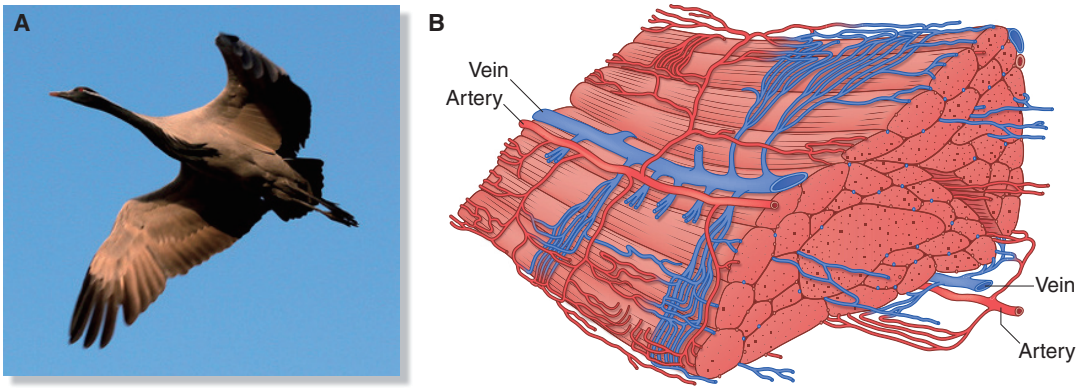


Fig. 7.20 Adaptations for flight. (A) Demoiselle Cranes (*Anthropoides virgo*) attempt an arduous migration across the Himalayan Mountains every year. In the process, their pectoral muscles power flight over mountain passes—some almost 8000 meters high—against strong winds, and while avoiding predators like Golden Eagles (*Aquila chrysaetos*). (B) Schematic of the pectoralis flight muscle. Specialized circulatory innervations facilitate enhanced blood flow necessary for high-powered flight. (A, photograph by Bhisham Pratap Padha. B, from Mathieu-Costello et al. 1994. Reproduced with permission from Elsevier.)

respiratory system of birds with special emphasis on those aspects that allow birds to live such active lifestyles.

7.5.1 Integrated physiological systems

The high metabolic rate and extensive daily activity of birds requires extraordinary capacity to deliver oxygen and energy to their muscles and organs, as well as rapid removal of the waste products (like carbon dioxide) that are generated through metabolism. The circulatory and respiratory systems of birds accomplish these integrated tasks. For example, the respiratory system transports oxygen from the atmosphere to the circulatory system, and the circulatory system transports carbon dioxide from the bird's body back to the atmosphere. Of course, the circulatory system also transports other important compounds (such as digested and absorbed dietary nutrients) and waste products (such as uric acid).

The unidirectional routing of air through a bird's respiratory system (Chapter 6) is important, because it means that air moving through a bird's lungs is constantly refreshed and has high oxygen content. In contrast, airflow in the mammal lung is bidirectional (in and out of the blind-ending air capillaries with every inhalation and exhalation), which mixes the new air coming in with oxygen-depleted air that has already been in the lungs. This difference results in birds having a more efficient rate of gas exchange than mammals.

The avian and mammalian circulatory systems are similar in basic design: both are closed systems with a four-chambered heart that separately pumps oxygenated blood to the body (systemic circulation) and deoxygenated blood to the lungs (pulmonary circulation). However, a bird's heart weighs up to twice as much and pumps much more blood than that of a mammal of equal body size. The energy-hungry muscles of birds need a bigger, faster beating heart to send them plenty of oxygen and nutrients and thereby meet the high metabolic demands of flight (Fig. 7.20A). Smaller birds such as hummingbirds have relatively larger hearts than larger birds such as geese. Since the avian heart produces the highest blood pressures among vertebrates, birds in turn have particularly strong tubes and valves in their circulatory system (Fig. 7.20B). As in mammals, birds acclimated to high altitudes have an increased density of capillaries in their muscles to facilitate their heightened demand for respiratory gas exchange.

Hemoglobins are the proteins within blood cells that bind and transport oxygen. In general, avian hemoglobins have higher oxygen-binding affinities than those of mammals. This heightened oxygen affinity means that they can better supply oxygen under challenging conditions, such as the low-oxygen environment birds experience during high-altitude flights (Box 7.07).

7.5.2 Fat is the primary fuel

Birds fuel their high-intensity endurance exercise—such as migratory flights—primarily by metabolizing fat along with a small amount of protein. Long-distance migratory birds must rely on stored fat to fuel each flight, and then must rapidly restore the necessary energy and nutrients at stopover sites along their migration route. Migratory birds primarily use fat to fuel their long-duration flights because fat provides substantially more energy than an equal mass of either carbohydrate or protein. Birds are able to enhance their use of stored fats during migratory flights in several important ways (McWilliams et al. 2004). First, they may change the fatty acid composition of their fat stores to enhance the rate of mobilization and oxidation. Fatty acid composition of stored fat changes in birds during

Box 7.07 Bar-headed Geese fly at high altitudes

Bar-headed Geese (*Anser indicus*) are the highest altitude migrants on the planet (Fig. 7.B7.01). Every year, some individuals fly from the lowlands of India through the Himalayan Mountains, commuting between their nesting grounds in Tibet and their wintering grounds in India (Bishop et al. 2015). At times, these birds fly at altitudes above the peak of Mount Everest (8848 meters). Other bird species that may also fly at extreme altitudes include Whooper Swans (*Cygnus cygnus*), which have been observed by a pilot at 8230 meters over the Atlantic Ocean, and Rueppell's Griffon Vulture (*Gyps rueppelli*)—an individual of the latter was sucked into a jet engine at 11,552 meters above Ivory Coast in Africa. However, most migratory birds fly at much lower altitudes.

How do Bar-headed Geese fly at such high altitudes, where atmospheric oxygen levels are very low? Birds are preadapted to low-oxygen conditions since the design of their respiratory and circulatory systems makes their oxygen uptake highly efficient. Like other birds, Bar-headed Geese produce more hemoglobin, more red blood cells, and more myoglobin (the hemoglobin equivalent in muscle cells) as they prepare for migration. These changes enhance their blood's capacity to bind and transport oxygen (Scott and Milsom 2006).

However, Bar-headed Geese are exceptional in several ways that allow them to perform unusually well at high altitudes. They have relatively larger lungs and a special type of hemoglobin that allows them to extract more oxygen from each breath. Bar-headed Geese also have more blood capillaries in their heart and flight muscles than do other geese, and these capillaries penetrate deep within the muscle. They also have a special form of an enzyme (nicknamed COX) involved in energy production within their muscle cells. Thus, Bar-headed Geese provide an impressive example of the multiple ways that animals can adapt to high altitude and perform remarkable feats under low-oxygen conditions (Scott et al. 2011).



Fig. 7.B7.01 Bar-headed Geese (*Anser indicus*) can fly long distances at very high altitudes. Mount Everest, the highest mountain in the world, represents an incredible physiological test for human climbers, but this species migrates over its passes every year with ease. (Photograph by Jim Almond.)

migration primarily in response to diet and to preferential metabolism of certain fatty acids. Second, birds may increase the membrane proteins involved in transporting lipids into cells from the carriers in the blood plasma. Lastly, birds may increase the activity of cellular enzymes and so increase the oxidative capacity to use fatty acids.

7.6 Avian endocrine system

The endocrine system of birds, like that of other vertebrates, consists of a number of different organs or tissues that produce hormones. These organs include the gonads (testes and ovaries) (Chapter 6), the adrenal and pituitary glands, which will be emphasized here, and also the thyroid and several other organs. **Hormones** have traditionally been defined as chemicals produced by organs or tissues that are conveyed through the circulatory system to act on target tissues located at a distance from their source. A classic example is testosterone: over 150 years ago, the German physiologist Arnold Berthold showed that a secretion—later shown to be testosterone—from a rooster's testes acts on its comb to increase its size and redness.

7.6.1 The HPG and HPA axes

Hormones and their effects involve complex feedback loops. In birds, hormone production elsewhere in the body is often regulated by hormones produced by the anterior

Hormones: chemicals produced by organs or tissues that are conveyed through the circulatory system to act on target tissues located at a distance from their source.

pituitary gland. These anterior pituitary hormones are in turn regulated by hormones produced by the hypothalamus of the brain, from which the pituitary "hangs." These regulatory relationships form three-tiered endocrine axes. The two three-tiered endocrine axes regulate hormone production by the gonads and by the cortex of the adrenal gland (Fig. 7.21). These two axes are referred to as the hypothalamic–pituitary–gonadal axis (HPG) and the hypothalamic–pituitary–adrenal (HPA) axis, respectively. The top tier of the HPG consists of neurons that produce the releasing hormones gonadotropin-releasing hormone (GnRH) and gonadotropin-inhibiting hormone (GnIH). These are conveyed to the anterior pituitary by a special portal circulatory system to increase (GnRH) or decrease (GnIH) the production of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) by the anterior pituitary. In turn, FSH and LH are conveyed by the general circulation to the ovaries and testes to regulate the production of sex steroid hormones such as estradiol and testosterone. In a similar vein, the HPA begins with hypothalamic neurons that produce the releasing hormones corticotropin-releasing hormone (CRH) and arginine vasotocin (AVT), which act on the anterior pituitary to increase production of adrenocorticotropic hormone (ACTH), which in turn acts on the cortex of the adrenal gland to increase production of corticosterone (the avian version of human cortisol).

Two features of these axes are especially important for understanding the adaptive functions of the avian endocrine system. First, the hypothalamus and anterior pituitary have receptors (proteins that bind hormones) that inform them of the levels of the hormones that reach them through the circulation, so that the levels can be adjusted downward if they are too high, and upward if they are too low. That is, the circulating hormones exert negative feedback at the higher levels of the axis. This serves to maintain circulating hormone levels within a desirable range, and to return them to these levels when they start to deviate. These feedback loops are analogous to a household furnace and thermostat: if the room temperature falls below the thermostat setting, the thermostat tells the furnace to turn on, and if the room temperature rises above the setting, the thermostat shuts off the furnace. Accordingly, if you were to administer testosterone to an adult rooster, his testes would shrink—not grow—because the feedback loops of his HPG axis would conclude that his testes were overproducing testosterone and then signal them to reduce their hormonal production.

The fact that a region of the forebrain called the hypothalamus ultimately regulates these hormones is the second important feature. The brain constantly receives information about the external world. Is the breeding season coming soon? Is there a predator nearby? Has a rival entered the territory? All these stimuli are capable of causing a change in a bird's hormone levels. The secret of how these external stimuli are able to alter the bird's internal physiology lies in the brain's position at the top of the endocrine axes, acting through the hormones produced by the hypothalamus that regulate the pituitary. Control by the brain, the most complex organ in the body, means that the endocrine axes are regulated in a biologically intelligent manner.

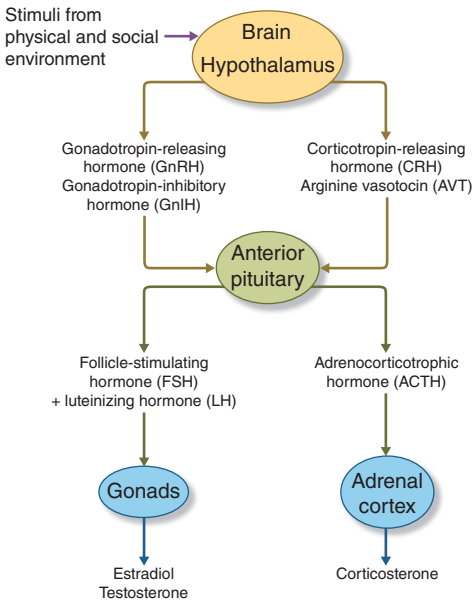


Fig. 7.21 The HPA and HPG endocrine axes. Environmental stimuli trigger internal hormonal regulation via the hypothalamic–pituitary–adrenal (HPA) and hypothalamic–pituitary–gonadal (HPG) endocrine axes. Hormonal regulation is imperative for adaptive responses including reproductive and territorial behaviors, fight-or-flight responses to threats, and migratory restlessness. (Courtesy of Elizabeth Adkins-Regan.)

The production of hormones by the hypothalamus is just one of several examples of hormone production by tissues containing neurons, the communicating cells of the nervous system. Other examples include the posterior pituitary gland, which is neural tissue and which produces hormones that circulate throughout the body. Thus it is difficult to draw a sharp distinction between the avian endocrine and nervous systems. Hormones can be produced by either system, and sometimes the same hormone is produced by both.

7.6.2 Types of hormones

The endocrine systems of vertebrates have been relatively conserved over long periods of evolutionary time, and birds share all of their known hormones with other vertebrates. These hormones fall into several different chemical categories, each with different properties that help account for where they go and how they work.

Most of the hormones produced by the gonads and the adrenal cortex are steroids. In the popular media, "steroid"

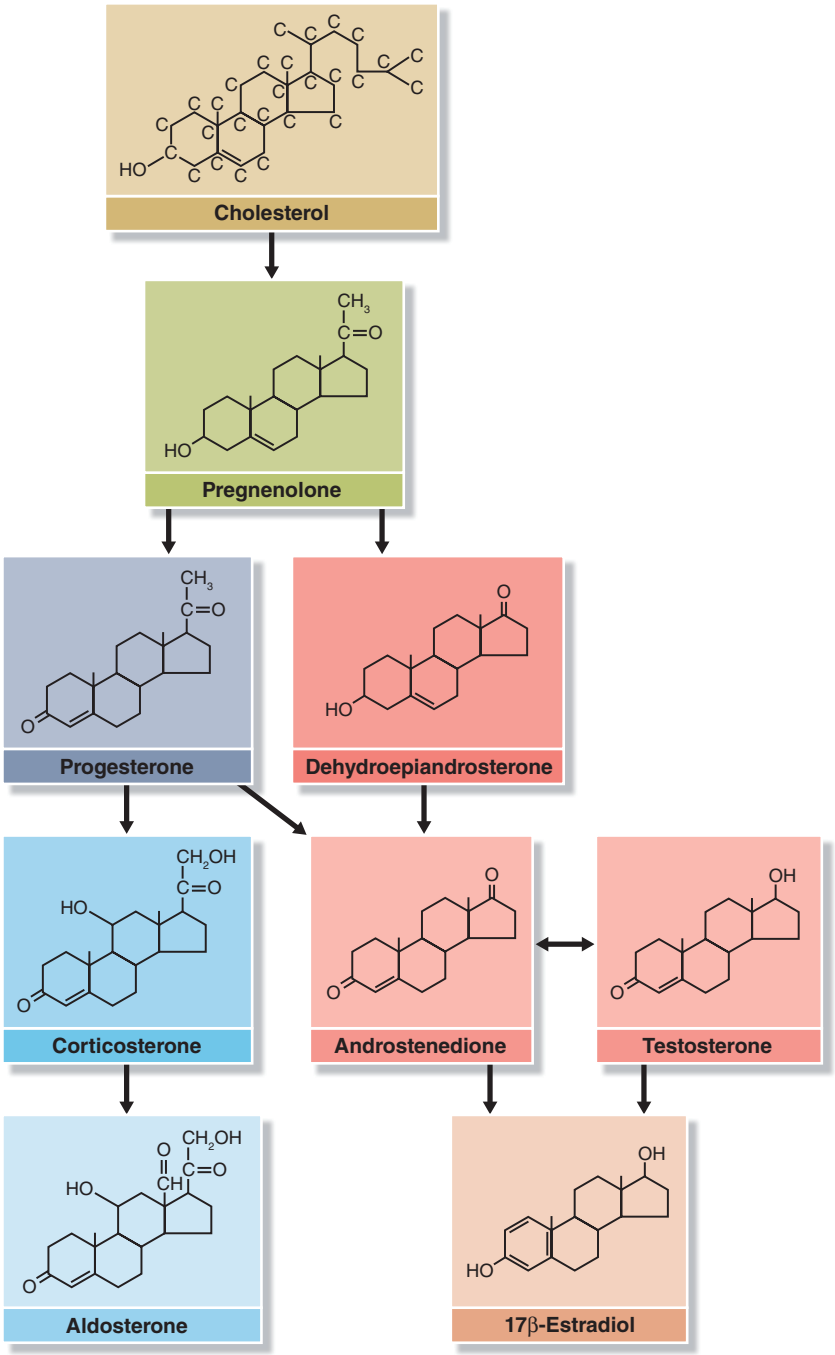


Fig. 7.22 Predominant steroid hormones. All steroid hormones have a basic four-ring structure derived from a cholesterol precursor. Note that some intermediate steps have been omitted from the biosynthetic pathways for simplicity. (Adapted from Nelson 2011. Reproduced with permission from Sinauer Associates.)

has come to mean the anabolic steroids taken by athletes to build muscles. The term actually refers to any chemical having the basic four-ring structure derived from an initial cholesterol molecule (Fig. 7.22). The sex steroids (those that the gonads produce) and corticosteroids (those produced by the adrenal cortex) are closely related; animals make them from cholesterol, which has the same ring structure. The corticosteroids include aldosterone, a hormone that acts on the avian kidney to regulate sodium concentrations, and corticosterone, a glucocorticoid steroid that will be discussed later in this chapter in connection with responses to stressors. The sex steroids produced by a bird's

gonads include androgens, which are "masculinizing" sex steroids (testosterone is a specific example of an androgen, but there are others), estrogens ("feminizing" sex steroids, of which estradiol is a specific example), and progestogens (progesterone is a specific example). The words "masculinizing" and "feminizing" appear in quotes because those categories oversimplify where these hormones are produced and what they do. Both sexes produce androgens and estrogens, and androgens and estrogens function in both sexes.

Sex steroid hormones can also be produced in the brain and in other tissues outside of the gonads, indeed anywhere in a bird that the right enzymes for their synthesis are produced. Bird brains can synthesize sex steroids directly from cholesterol. They can also take testosterone that has arrived from the gonads via the circulation and make estrogens such as estradiol from it. This happens in male birds as well as females. The steroids that are synthesized in the brain are increasingly being recognized as important components of how hormones influence avian behavior and brain function.

Other hormones are not steroids and fall into several different chemical categories. For example, the hormones of the adrenal medulla, such as adrenaline, are chemically different from thyroid hormones. Hormones such as insulin (from the pancreas) and prolactin (from the anterior pituitary) are polypeptides (large, protein-like molecules). The hypothalamic hormones that regulate the pituitary, such as GnRH and CRH (Fig. 7.21), are peptides.

7.6.3 Measuring hormones in wild birds

Hormones are most often measured by taking blood samples, yet hormones occur in very small concentrations in blood plasma (the part of the blood after red blood cells have been removed). For example, testosterone concentrations in bird blood plasma might be only 5 nanograms (10^{-9} grams) per milliliter, and estradiol concentrations are usually much lower still, in the order of picograms (10^{-12} gram) per milliliter of plasma. Several different kinds of assays have been developed that are capable of measuring such small quantities of hormones. Nonetheless, the measurement of hormone levels in birds, especially wild birds, presents special challenges. Peptide or polypeptide hormones that are produced in the brain cannot be measured at all in blood samples. Capture and handling may cause a bird stress, which then alters its hormone levels, making it essential to obtain a blood sample within just a few minutes of capture. Even obtaining sufficient blood can be a problem, as many birds are so small that it is difficult to draw sufficient blood without causing the bird harm.

For these practical reasons there has been great recent interest in the possibility of measuring hormones in samples that can be collected from birds non-invasively, such as in droppings or shed feathers. These methods have their own special challenges. Matching a dropping to a particular individual is feasible for birds like geese on a golf course, but is very difficult in small, fast-flying, or flocking species. Digestive system enzymes also degrade hormones. Hormone concentrations in droppings often reflect what the bird ate recently and the transmission time of food through the gut as much as they do the bird's circulating hormone levels.

7.6.4 Hormones and avian sex differences

A bird begins life as a fertilized egg that already has a sex. Female birds have ZW sex chromosomes, whereas male birds have ZZ sex chromosomes. Females produce ova that contain a Z or W chromosome, which are then fertilized by Z-bearing sperm, and so females are the sex-determining parent. Because some birds lay eggs with sex ratios that deviate from 1:1, there is considerable interest in understanding what determines which sex chromosome goes into an ovum, how a female's system might be able to bias that process, and whether sex hormones from the mother are a part of this process. The hormones from the mother include those in her circulation but also those that pass into the yolks of the eggs, which have been shown to exert long-lasting effects on other aspects of the offspring. At this time it is not yet clear how sex ratio biases are produced or to what extent hormones are involved in the process.

Gonadal hormones and the HPG axis that regulates them are involved in most aspects of avian reproduction, including the production of eggs and sperm, courtship and mating behavior, nest building, and incubation. They also serve to promote other types of behavior related to reproductive success, such as territorial defense. In addition, these hormones are responsible for some of the ways in which males and females look different and differ in internal reproductive anatomy.

During development in the egg, the avian embryo forms testes or ovaries and then male or female internal organs, a process called sexual differentiation. These organs include the male and female gonaducts, which will eventually become the vasa deferentia in males and the oviduct of females (Chapter 6). The embryonic gonads begin resembling ovarian or testicular tissue and producing hormones early in development, after just a few days of incubation. In the best studied bird species—domestic chickens, quail, and ducks—the gonads of both sexes produce androgens and estrogens, but the embryonic ovaries produce much more estrogen, so that the ratio of estrogens to androgens is higher in female embryos. These embryonic gonads also produce a non-steroidal hormone that causes regression of the female embryonic gonaducts in male embryos and regression of the right gonaduct in females. This all takes place before hatching. Later in their lives as the birds enter

reproductive maturity, increases in their gonadal sex steroids cause growth of the organs that were organized during embryonic life. In females ovarian estrogens enlarge the left oviduct, and in males testicular androgens enlarge the vasa deferentia. This second stage of hormone action on the reproductive organs is referred to as activation.

Some species of birds have additional anatomical characters that differ by sex, such as the phallus of male (but not female) waterfowl, the combs of chickens (larger and redder in males), and the more colorful and ornamented plumages of males of many species (Chapter 4). Experiments in the 1950s by the pioneering French endocrinologist Etienne Wolff showed that duck embryos develop a phallus if ovarian hormones are not present, and do not develop a phallus if they are present. In this case, the absence of hormones gives the male phenotype, and their presence gives the female phenotype. Other sex differences arise from more subtle differences in hormone levels. For example, both sexes of chickens (and their wild ancestor, Red Junglefowl, *Gallus gallus*) have combs, and the sex difference in comb size and color is primarily a response to the higher testosterone levels of adult males.

There is notable variation among groups of birds in whether and how hormones are involved in generating sex differences in plumage. In waterfowl and galliform birds (sister groups in the phylogenetic tree of living birds, Chapter 2), adult birds have male plumage so long as they do not have the high estrogen levels associated with ovaries. If the gonads are removed from both sexes, males retain a masculine appearance and females acquire male plumage. Androgens like testosterone are not involved in the production of the male's fancy feathers. In some songbirds, males have features because of higher testosterone levels, like a black bib that females lack (as in House Sparrows, *Passer domesticus*), or males that have redder color than females (as in House Finches, *Haemorhous mexicanus*). A third pattern occurs in other passeriform species such as Zebra Finches (*Taeniopygia guttata*), in which gonadal hormones appear to have nothing to do with sex differences in plumage ornaments. Genetic females with functioning testes grow female plumage, and genetic males with functioning ovaries retain male plumage. So it is not possible to make general statements about all birds on the relationship between hormones and sexual dimorphism, such as "testosterone makes males look like males."

7.6.5 Hormones and behavior

Males and females behave noticeably differently in most bird species, especially during the reproductive season. Sometimes only males sing. Sometimes females have a special copulation solicitation posture. Sometimes females care for the young by themselves, but occasionally males raise the chicks. The mating act differs between the sexes, with the males usually the mounters (on top). It is easy to assume that hormones have something to do with these sex differences, but very seldom is the role of hormones actually understood. Most of what has been established comes from a small number of domesticated birds. In some cases, the sex difference is primarily a hormonal activation phenomenon. For example, if adult female Canaries (*Serinus canaria*) are given testosterone, they begin to sing like males. If adult male Japanese Quail (*Coturnix japonica*) are given estradiol, they adopt the female receptive posture and allow other males to mate with them. Thus these sex differences seem to be a consequence of sexual dimorphism in the hormone levels within adult individuals. The reason females show the receptive posture during mating and males do not is because females have more estrogen (the receptivity hormone) than males. However, the fact that males mount and females do not arises earlier in development; just as embryonic hormones organize the internal sexual anatomy, they also have a permanent effect on whether the birds will show mounting during mating (Fig. 7.23). In chickens and quail, the high estrogen-to-androgen ratio naturally produced by the embryonic ovaries permanently removes the female's tendency to mount, whereas male embryos retain the mounting tendency.

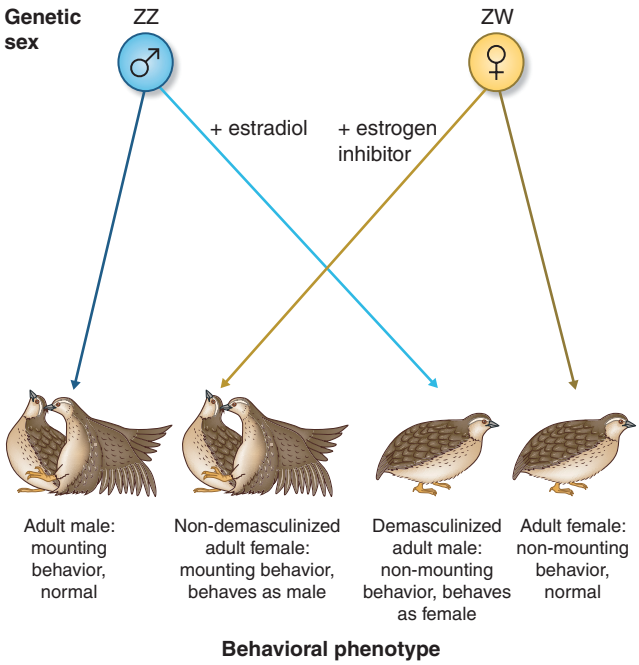


Fig. 7.23 Hormonal manipulation alters mounting behavior. Normally, only males mount to initiate copulation. However, when male Japanese Quail (*Coturnix japonica*) embryos are treated with estradiol, they fail to mount as adults. Treated males are effectively "demasculinized"—genetically male, but behaviorally female. Female embryos treated with an estrogen inhibitor do not undergo the normal demasculinization process and therefore exhibit mounting male behavior as adults. (Adapted from Balthazart and Adkins-Regan 2002 and Balthazart 1983. Reproduced with permission from Elsevier.)

7.6.6 Hormones, sex, and reproduction

The gonads of birds have dual functions—producing hormones but also gametes (eggs and sperm). Gonadal hormones both travel elsewhere in the body to act on distant target organs and are involved in regulating the production of eggs and sperm.

Avian sperm, like those of other vertebrate groups, are produced in vast numbers, and many thousands or even millions are contained in a single ejaculate. Sperm production is correlated with overall testis size, which in turn is associated with the mating system of the species (Chapters 3 and 9) and the degree of **sperm competition** between the ejaculates of different males. Testes are relatively small in bird species that are strictly monogamous and larger in those where females mate with multiple males. Unlike female mammals, female birds can store viable sperm for days or even weeks, depending on the species. A portion of the oviduct contains special sperm storage tubules (Fig. 7.24), and the stored sperm are released from there to travel up to the site of fertilization near the top of the oviduct. How these tubules function, and what their role is in sperm competition or female fertilization strategies is poorly understood. What is clear, however, is that although the egg is only fertilizable for a brief period as it passes through the upper oviduct, females would not necessarily have to mate at any particular time of the day or even day of the week in order for an entire clutch of eggs to be fertilized. Sperm that have already been stored can be released to do that job.

Avian eggs are large, and several days are required for the production of an egg that is ready to be laid. The egg formation, ovulation, and laying sequence is best understood in domestic chickens, but many features of the process are likely to be similar in other birds that lay a series of eggs on a roughly daily basis until their clutch is complete. Prior to clutch onset, the ovary contains primordial follicles. One at a time, and roughly a day apart, a follicle begins to mature, and to sequester yolk. A laying bird's ovary contains a set (sequence) of yolked follicles, each one day different in yolk amount, with the largest (the one about to be laid) having a yolk the same size as in a freshly laid egg. At ovulation, the yolk breaks free of the ovary and enters the top of the oviduct. As it travels down the oviduct, first it is fertilized near the top of the oviduct, if the female has mated. Next it acquires a layer of albumin ("egg white"). Closer to the bottom of the oviduct, the shell membranes and shell layers are added, then (if the egg is pigmented) the colors are added to the shell, and finally the egg is laid. The whole process from ovulation (when mature eggs leave the ovary) to oviposition (when an egg is laid) takes about 24 hours, and in most species that have been studied ovulation of the next egg commences within an hour after oviposition of the previous one (Chapter 6).

Sperm competition: in birds, a form of intrasexual selection that arises after more than one male has copulated with the same female, and therefore the sperm of multiple males are in competition to fertilize an egg within the female's reproductive tract.

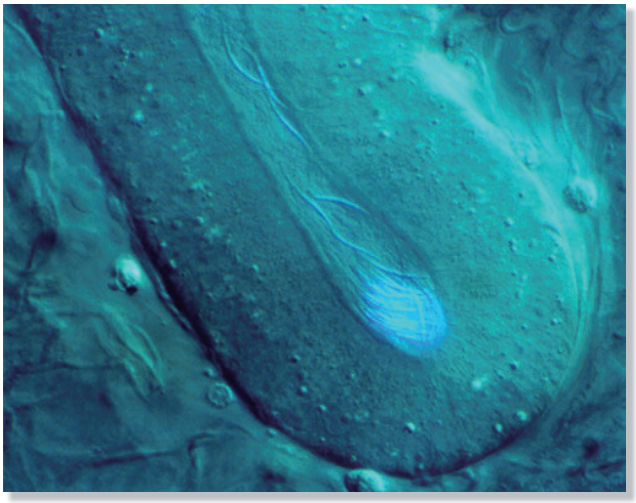


Fig. 7.24 Sperm storage tubule. This micrograph shows the end of a chicken (*Gallus gallus*) sperm storage tubule containing many sperm, which appear like long filaments that are lined up in parallel within the interior of the tubule. (From Bakst 2011.)

The hormones of the HPG axis are involved in all aspects of the egg production process and the ovulation and oviposition cycle. As each ovarian follicle matures, the cells around it produce increasing amounts of estrogen and androgen. The estrogens stimulate the production of major yolk constituents by the liver, which are transported to the developing yolks. As ovulation approaches, the sex hormone environment of the follicle consists mainly of progesterone (Fig. 7.25). A surge of LH from the pituitary then triggers ovulation, but only of the follicle that is next in line to ovulate.

What gets a female bird to start laying eggs in the first place? Does there have to be a male around for the female to start a clutch? Does she have to mate? The answers to these questions depend on the bird species, for interesting reasons. As anyone who raises chickens knows, there does not have to be a rooster in the flock for hens to start laying eggs. They just have to be old enough for the ovaries to mature—that is, for the HPG axis to ramp up to a sufficient level; once that happens, hens ovulate and lay eggs spontaneously. Yet it has been known for centuries that female pigeons and doves usually do not lay any eggs unless there is a courting male present. Female Ringed Turtle-doves (domesticated African Collared-Doves, *Streptopelia roseogrisea*) respond to a courting male by entering into a mutual nest-soliciting display with him, and the sound of

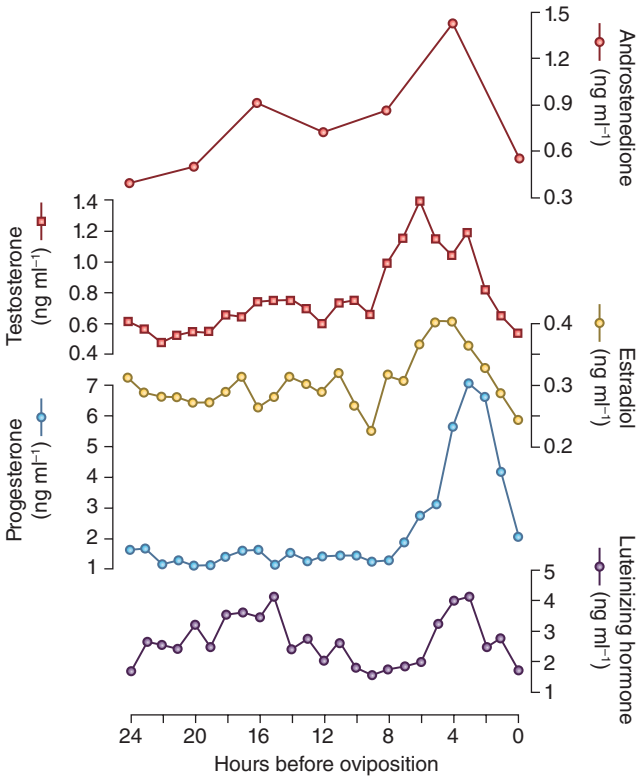


Fig. 7.25 Hormonal changes before oviposition. Circulating levels of progesterone and other steroids surge a few hours before a female lays an egg. (From Etches 1990. Reproduced with permission from Science Reviews 2000.)

the female's own coos in response to the male stimulates increased LH production from her pituitary gland, which then stimulates growth of the ovarian follicles and yolk deposition. As you might expect, different mating and parental care systems help determine which species of birds ovulate spontaneously or in response to an interaction with a male. Birds such as chickens have parental care by the females only, and the birds do not form exclusive male–female pairs. In this type of situation, the female bird should produce a clutch at a time that is opportune for her; there is nearly always a male nearby to fertilize the eggs. Birds such as pigeons and doves, however, have biparental care, and form male–female pairs that need to be well synchronized in order to share incubation and to raise the chicks together (Chapters 9 and 11). The female needs to have a partner willing to share those duties before proceeding to produce a clutch, otherwise the eggs will be wasted.

7.6.7 Annual cycles of hormones and seasonal breeding

Birds living almost everywhere have pronounced breeding and non-breeding seasons. Seasonal breeding cycles are associated with a corresponding annual cycle of hormones. Figure 7.26 shows the annual hormonal and gonadal cycles of male and female White-crowned Sparrows (*Zonotrichia leucophrys*), the first free-living bird species to have its hormones measured throughout the course of the seasons. The particular population in the figure (of the *gambelii* subspecies) is migratory, spending the winter in Washington or California and breeding in Alaska (USA), where they produce only a single brood each year. The males arrive first on the breeding grounds, and establish territories by singing and (if necessary) fighting. They arrive with their testes already fully developed and producing sperm, and with relatively high levels of testosterone (Fig. 7.26A). Then females arrive, mates are chosen, pairs form, and mating occurs. Female estradiol levels are high at this time (Fig. 7.26B). Nests are built and eggs are laid while sex steroid levels are high. At the onset of incubation, sex steroid levels fall, and by the time the chicks hatch their levels are low and the birds' gonads have greatly decreased in size. Hormone levels remain low in both sexes for the remainder of the year, after which they begin to rise again the following late winter/early spring to repeat the cycle (if the birds have survived).

There are many variants of this basic pattern, but also important questions to ask about the cycles themselves. What causes these annual cycles of hormones? Do the hormonal cycles cause the annual cycles in breeding behavior and the transitions from one breeding cycle stage to another?

This first question has inspired decades of discoveries about the role of day length in the timing of birds' annual reproductive cycles. The length of daylight in each day—sunrise to sunset—is the daily **photoperiod**. Photoperiod varies systematically and predictably throughout the year. The fact that the days start to get longer after the winter solstice invariably predicts that spring temperatures will arrive in a few months. Birds often time their reproduction such that their young are growing during the period when food is most abundant, but considerable time is required to get to that stage—for the White-crowned Sparrows in the previous example, this preparation includes migration to the breeding grounds, setting up of territories, nest building, laying of the clutch, and incubation. Thus a cue that predicts the right time well in advance is extremely useful. Day length is such a cue, so it is not surprising that most birds breeding at latitudes where day lengths vary by several hours across the year have annual hormonal cycles that are turned on and off by day length. Other cues may

Photoperiod: the amount of a 24-hour day in which birds are exposed to light; or the relative lengths of light and dark periods of the day.

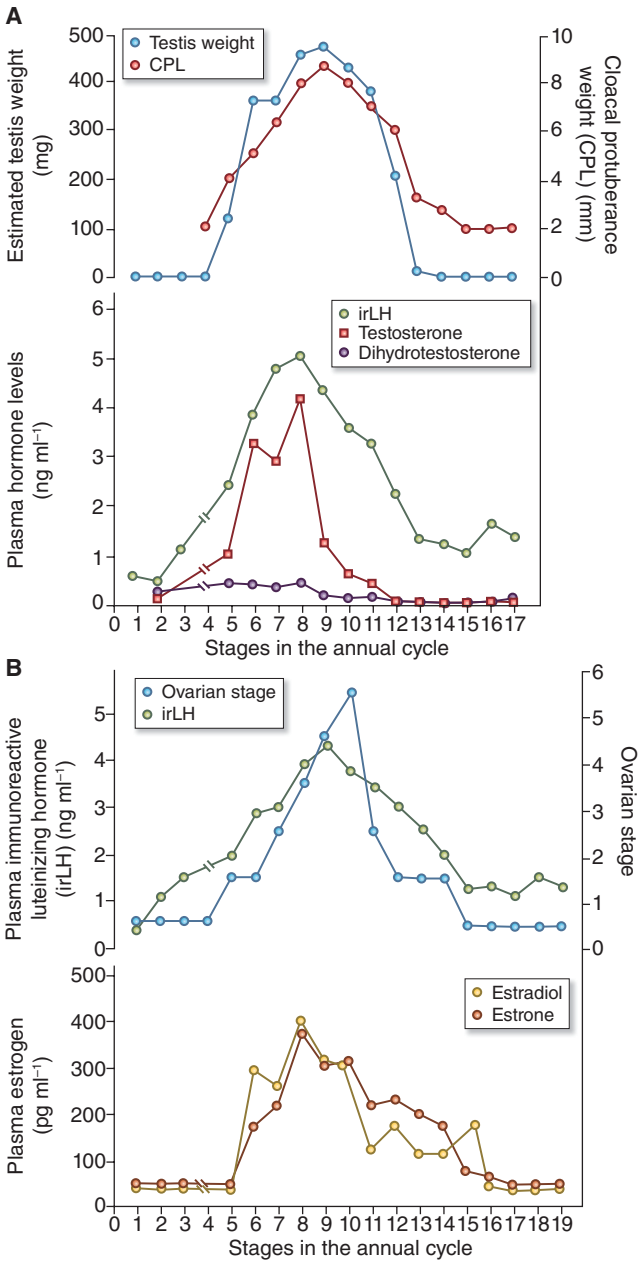


Fig. 7.26 Hormone cycles throughout the year. Annual hormonal and gonadal cycles in (A) male and (B) female White-crowned Sparrows (*Zonotrichia leucophrys*). In males, testes and cloacal protuberances begin to enlarge prior to arrival at the breeding grounds, once reproductive hormones begin to increase seasonally. In females, seasonal ovarian growth correlates with increasing estrogens and lutenizing hormone. Ovarian stages (right *y*-axis, B): 0, inactive; 1–3, seasonal growth begins; 4, yolking; 5, approaching ovulation; 6, ovulated, egg in follicle. Annual stages (*x*-axis, A and B): 1–4, birds on wintering grounds; 5, 6, spring migration; 7, birds just arrived on breeding grounds; 8–10, mating and egg laying; 11, 12, incubation; 13, 14, chick rearing; 15–17, postnuptial molt; 18, 19, fall migration. (From Wingfield and Farner 1978. Reproduced with permission from Society for the Study of Reproduction.)

Box 7.08 Day length and avian annual cycles

How can the length of the days regulate hormones to make the gonads of birds grow and shrink? It has been known for many decades that the light detectors for the gonadal response to day length in birds are not the eyes, but instead are cells located in the hypothalamus. Light, especially long (red) wavelengths, passes through the skin, skull, and brain regions above the hypothalamus to reach these deep brain photoreceptors. Recent research suggests that these photoreceptor cells contain the same photosensitive chemical—vertebrate ancient opsin—found in fish, frogs, and lizards, a type of opsin that is different from the opsins found in the rods and cones of the bird's eyes. These opsin-containing neurons connect to the site of releasing hormone regulation of the HPG, influencing the cascade of hormones that regulate the bird's annual cycle.

supplement the information from day length, especially as the time for breeding gets closer and more precise regulation becomes necessary. These include cues from the physical environment such as temperature, biological cues such as food supply, and social cues such as the courtship activity of the mate.

How does the bird's HPG axis "know" how long the days are? This is a different question, one that has also inspired some amazing discoveries (Box 7.08). Increasing or long day lengths turn on the HPG and thereby stimulate the gonads to produce hormones and gametes. Yet in birds like European Starlings (*Sturnus vulgaris*), the HPG shuts down and gonads regress in June, after the bird's primary breeding season, but at a time when day lengths are still increasing (Fig. 7.27). This phenomenon is called photorefractoriness, and seems to be common in birds of the temperate zones. Although the precise hormonal pathway is unclear, the ultimate cause of this phenomenon is the strong selection pressure against starting a clutch that will produce hungry chicks when the insect supply is diminishing, and when the parents need time after breeding to molt and increase body fat reserves prior to fall migration.

The annual cycle in which breeding occurs in the spring is not characteristic of all birds. Exceptions include opportunistic breeders, those that do not breed at a predictable time of the calendar year but instead in response to an unpredictable food supply. Two of the best studied examples are Zebra Finches (*Taeniopygia guttata*) and White-winged Crossbills (*Loxia leucoptera*). Zebra Finches start breeding in response to the unpredictable rainfall in the Australian interior that leads to the ripening seeds that they

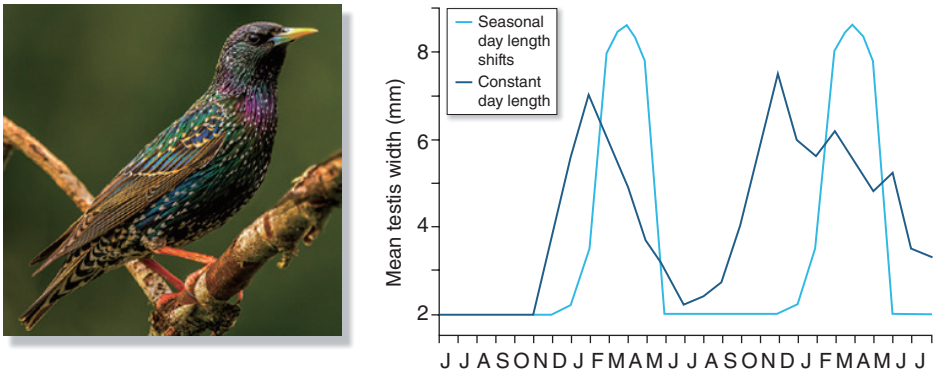


Fig. 7.27 Gonads change with seasonal photoperiod. Testis size in male European Starlings (*Sturnus vulgaris*) naturally fluctuates in response to seasonal day length shifts (pale line). When experimentally exposed to a constant day length of 12 hours of light and 12 hours of darkness, this response changes (dark line) to running freely on a circannual internal clock. The annual cycle is depicted in calendar months, beginning with June. (From Dawson 1997; adapted from Schwab 1971. Reproduced with permission from Bioscientifica Ltd. Photograph by Sandy Stewart.)

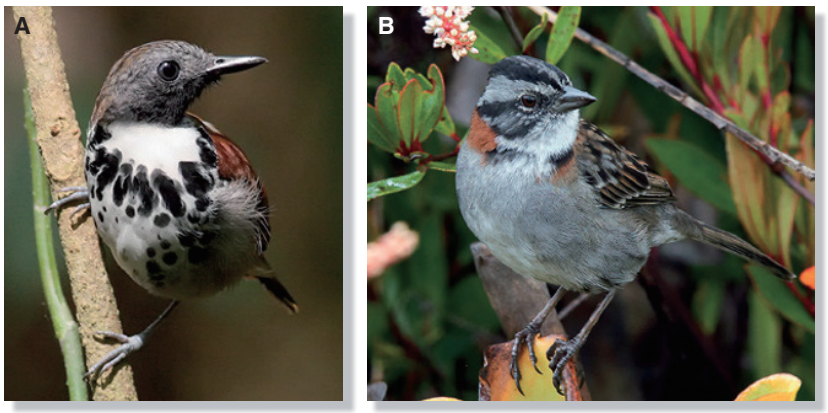


Fig. 7.28 Timing of breeding by reliable cues in less seasonal, tropical environments. (A) Although the Spotted Antbird (*Hylophylax naevioides*) is a tropical species, it primarily relies on changes in photoperiod to trigger its annual breeding cycle. (B) Rufous-collared Sparrow (*Zonotrichia capensis*) populations in the tropics may use photoperiod cues in seasonal environments away from the equator, while populations near the equator likely use local cues (like rainfall, changes in food abundance, or social cues) to determine when to breed. (Photographs by: A, Charles R. Smith, MD; B, Brad Wilson.)

will feed their chicks. Zebra Finches maintain a partially activated HPG axis year-round that can ramp up quickly to produce eggs when good breeding conditions occur. White-winged Crossbills live in conifer forests across Eurasia and North America, and in many areas they wander nomadically in search of a good seed crop, stopping to breed when they find one. The hormone cycles of these opportunistically breeding birds differ from those of spring breeding birds in not being strongly influenced by day length.

Birds living at tropical latitudes are often seasonal breeders, especially where there are pronounced annual cycles of rainfall, yet there is much less variation in day length near the equator. It used to be assumed that these small differences in tropical day length could not possibly be a useful predictive cue for birds in timing annual breeding cycles. Instead, experiments conducted in Panama have shown that the gonads of male Spotted Antbirds (*Hylophylax naevioides*) grow when the photoperiod changes from 12 hours of light per day to 13 hours (Hau et al. 2008) (Fig. 7.28A). This does not mean that photoperiod is necessarily the most important cue for most tropical species, however. For example, two populations of Rufous-collared Sparrows (*Zonotrichia capensis*) breeding at the equator less than 30 kilometers apart, but in very different habitats, breed at different times of the year (Moore et al. 2006) (Fig. 7.28B).

This brings us back to the question of whether annual cycles of hormones are in fact the cause of annual cycles of breeding behavior. Although the two are strongly correlated (Fig. 7.26), we need to know much more to conclude a causal connection between them. Based on experiments with both wild and domestic birds, it seems very likely that

HPG activity is responsible for the annual cycle of reproductive behavior in most birds. The sex steroid hormones in particular are an important facilitator of increased courtship activity, territory establishment and defense (for those species that defend territories), and nest building as breeding begins, when levels of these hormones are at their maximum. Amidst this generalized picture, species differ in hormone levels, as well as in how long male testosterone remains elevated before declining, that may be related to the different mating systems of the birds (Fig. 7.29). For example, socially monogamous species (those in which the sexes form pairs) tend to have the shortest periods of elevated male testosterone and the smallest sex differences in maximum testosterone.

7.6.8 Stressors and the HPA axis

Birds respond hormonally to both short- and long-term stress. Many of the stimuli that elicit an HPA axis response (Fig. 7.21) are potential threats to survival. In birds, the hormone corticosterone rises within a few minutes when individuals suffer blood loss, are exposed to pathogens or cold temperatures, experience a painful stimulus, are deprived of food, are caught by a predator, are defeated in a fight—or even when they anticipate that any of these stressors are about to happen (Fig. 7.30). The dynamics of the response to these kinds of stressors include a rapid rise from the bird's baseline level of corticosterone, followed by (if the problem goes away or the animal escapes from it) an eventual return to that baseline. This up-and-down cycle represents the classic acute **stress response**. If the problem does not go away, the bird may have elevated corticosterone levels for a long period (the chronic stress response).

Stressors also cause the release of epinephrine (adrenaline) within seconds. The acute endocrine response to stressors is thought to be adaptive. The elevated corticosterone and epinephrine have a wide array of physiological and behavioral effects that all serve to help the bird deal with the emergency. Fuel (glycogen) is mobilized from the liver. The digestive system shuts down (whatever food it contains can be digested later). Blood flow to the limb muscles and brain increases, and locomotor activity and strength increase. The hormonal responses also aid the formation of a long-lasting memory, helping the bird to avoid that place or situation in the future. This physiological state of emergency cannot be sustained for very long, however, and if it continues unabated it can cause illness or death.

Stress response: in avian endocrinology, the rise and fall in hormone levels (particularly corticosterone) during and after a bird is exposed to some kind of stressor.

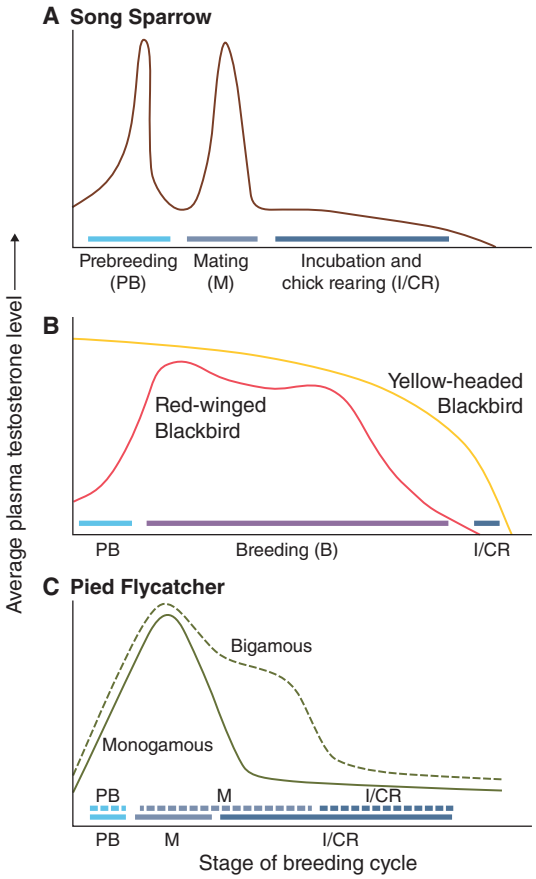


Fig. 7.29 Male testosterone levels vary by breeding stage and mating system. (A) Song Sparrows (*Melospiza melodia*) are monogamous and have two peaks of testosterone around prebreeding and mating periods each year. (B) In contrast, Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Red-winged Blackbirds (*Agelaius phoeniceus*) are polygynous, and have high testosterone from prebreeding until the incubation and chick-rearing stage without any dip in high hormone levels. (C) The seasonal hormone profile of a European Pied Flycatcher (*Ficedula hypoleuca*) depends on its mating system, which can be monogamous or bigamous. Stages of the breeding cycle: PB, prebreeding; M, mating (when copulation occurs); B, breeding (social pairs form, reproduction can occur); I/CR, incubation and chick rearing. (From Beletsky et al. 1995. Reproduced with permission from Springer Science + Business Media. B, adapted from Beletsky et al. 1989 and 1990. Reproduced with permission from American Ornithologists' Union.)

7.6.9 Hormones, life stages, and life history trade-offs

Hormones are thought to be responsible for the transitions between one life stage and the next as animals go from fertilized egg to senescent adult. Most of the major transitions in avian life, such as hatching, fledging, dispersal from the natal area, and the onset of reproductive maturity, have not yet been well explored hormonally in wild species, but

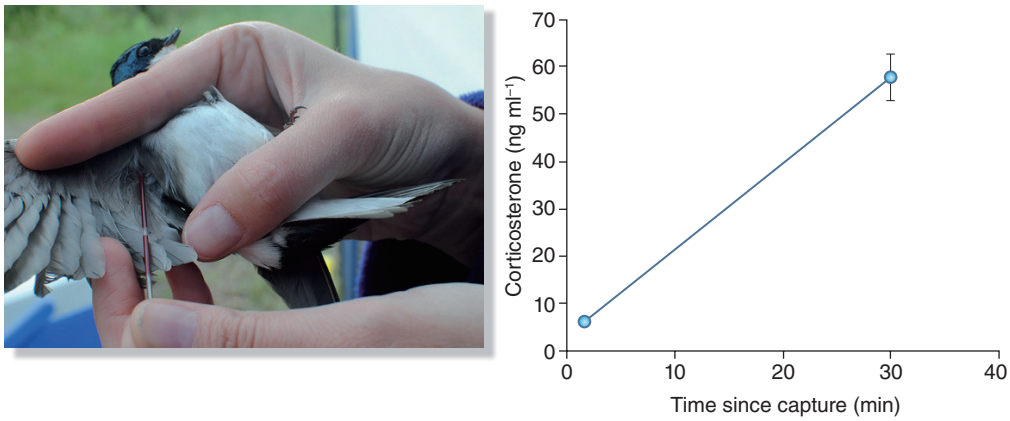


Fig. 7.30 Holding a bird elicits stress hormone release. In Tree Swallows (*Tachycineta bicolor*) and most other species, standardized handling (such as capture and blood sampling, as shown here) causes a physiological stress response that results in elevated corticosterone levels. (Courtesy of Maren N. Vitousek.)

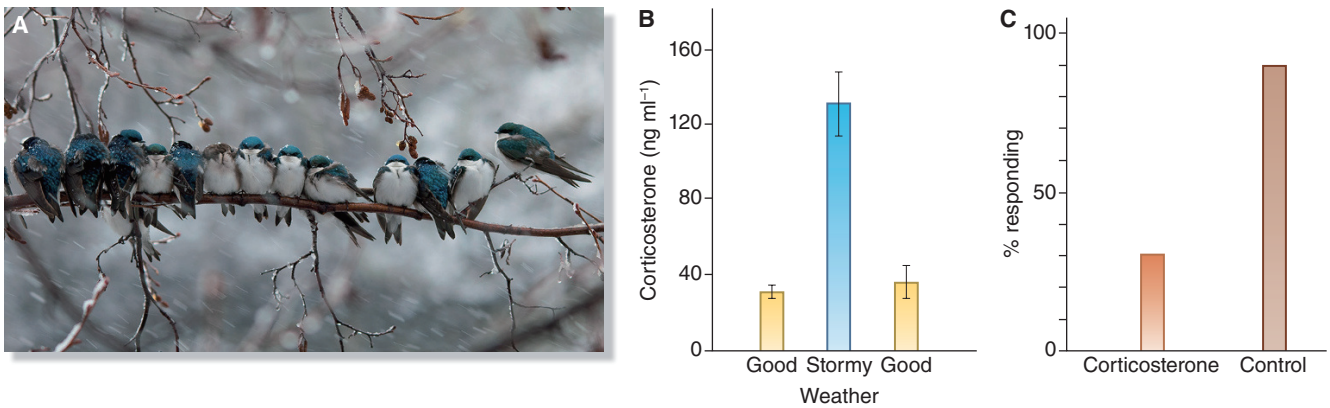


Fig. 7.31 Corticosterone levels and behavior. (A) Tree Swallows (*Tachycineta bicolor*) that have arrived early to the breeding grounds huddle in a late winter snow flurry to conserve heat and avoid heightened corticosterone levels (stress), which can impact physiological condition. (B) Male White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) experience higher corticosterone levels during winter storms than during fair-weather periods before or afterwards. (C) Male White-crowned Sparrows injected with corticosterone are less aggressive than non-injected (control) birds, supporting the idea that stress hormones decrease aggressive behaviors in favor of survival. (A, photograph by Keith Williams. B, from Wingfield 1988; adapted from Wingfield et al. 1983. Reproduced with permission from Springer Science + Business Media and American Ornithologists' Union. C, from Wingfield 1988; adapted from Wingfield and Silverin 1986. Reproduced with permission from Springer Science + Business Media and Elsevier.)

the few studies that do exist suggest fertile ground for new discoveries. For example, studies in Idaho (USA) have shown that corticosterone increases prior to the dispersal of juvenile Western Screech-Owls (*Megascops kennicottii*) (Belthoff and Dufty 1998).

As birds and other animals go through life, they face life history trade-offs with respect to energy allocation (Chapter 13) (Fig. 7.31A). Because of their connection to surviving emergencies and meeting energetic challenges, hormones are thought to be important in mediating between survival and reproduction. For example, glucocorticoids may benefit immediate survival at a cost to current (acute response) or future (chronic elevation) reproduction. The best evidence so far concerns trade-offs occurring over relatively short timescales. In White-crowned Sparrows, some populations breed in mountains where blizzards occur in the spring after males have arrived and established territories (Fig. 7.31B). Corticosterone is elevated during blizzard conditions, and the males' behavioral repertoires shift from singing and other forms of territorial defense to staying close to the ground (in more sheltered places) and foraging, or even abandoning their territory temporarily and moving to a lower altitude (Wingfield 1988). Experiments have shown that elevated corticosterone levels cause a shift away from behavior serving a defensive, reproductive goal towards behavior aiding immediate survival (Fig. 7.31C).

7.7 Bird brains

The term "bird brain" in everyday language is a mild insult, implying a tiny brain with little intelligence. One of the more exciting developments in avian physiology has been the discovery of just how poorly this description applies to avian brains. Let us begin with overall brain size. Obviously a hummingbird could not possibly be expected to have a brain as large as an Ostrich, so overall body size needs to be taken into account in comparing brains of different types of birds. In the same way that metabolic rate was related to body weight earlier in this chapter, the standard way biologists account for body size is to plot the brain sizes of an array of species on a graph with body weight on the *x*-axis and brain weight on the *y*-axis (Fig. 7.32). When both axes are on logarithmic scales, the data points can fit a straight line. Bigger birds have bigger brains, but brain size does not increase proportionally to body size. A bird that is 10 times heavier than another does not have a brain 10 times as large; instead, the larger bird will have a brain somewhat less than 10 times as large.

In Fig. 7.32B, the individual data points are not shown, and instead lines have been drawn that form the smallest polygon that just barely contains all the values for all bird species. The figure also outlines the equivalent polygons for mammals and a few other kinds of vertebrates. Now we can pose the question: Are bird brains smaller than those of mammals? The answer is both no and yes. The polygons for birds and mammals overlap extensively. Yet for any given body size, there is always some mammal that has a larger brain than any bird. That does not mean those mammals are more intelligent, however. It is likely that birds have been under stronger evolutionary selection for keeping body organs compact and light to reduce flight load. Smaller bird brains might be more densely packed with cells, instead of having lower total numbers of cells.

Another look at Fig. 7.32A reveals a lot of scatter in the relationship between bird body size and brain size. For a given body size (say, 500 grams), there are some bird species with much larger brains than others—for example, compare the woodpecker with the partridge. Macaws, ravens, tits, and other species with noticeably larger brains

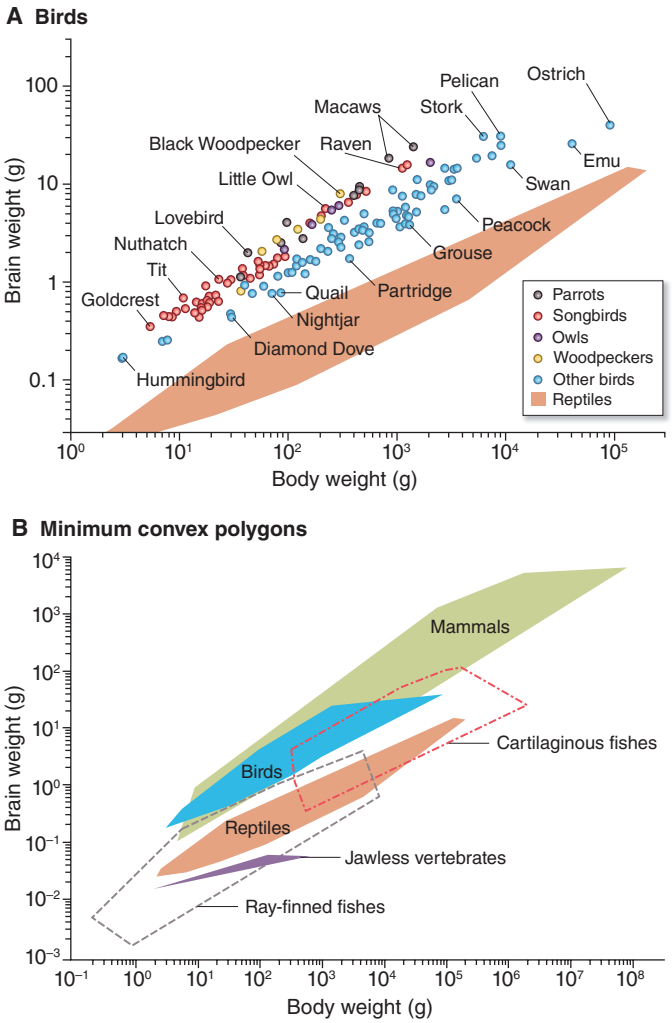


Fig. 7.32 Brain weight differs across species and taxa. Here, brain weight is plotted against body weight on a logarithmic scale. (A) Although all birds have larger brains than other reptiles, avian species with similar body weights can vary extensively in brain size. (B) To make visual comparison easier, data points for each vertebrate group have been enclosed into a separate polygon. Avian brain sizes overlap extensively with mammals. (A, from Striedter 2005. Reproduced with permission from Sinauer Associates. B, from Striedter 2005; adapted from Jerison 1970. Reproduced with permission from Sinauer Associates.)



Fig. 7.33 Navigation and the hippocampus. If specific regions of its hippocampus are disabled, this homing pigeon (*Columba livia domestica*) would lose its ability to navigate. Studies of this domestic pigeon breed have provided many insights into avian navigation and its underlying neurobiology. (Photograph by Aaron McBride.)

for their body sizes are thought to be unusually adept at learning new ways to obtain food and/or remembering the locations of stored food; many live in complicated societies.

Many of the structures of the mammalian brain are also present in birds. One, the hippocampus, has many ecologically relevant functions related to animals' perception and memory of space. Some of the best studied examples in birds come from scatter hoarding species such as Black-capped Chickadees (*Poecile atricapillus*) and Clark's Nutcrackers (*Nucifraga columbiana*). These species appear to have powerful memories that are able to recall the locations of stored food months after caching. Comparative studies suggest that scatter hoarding birds have a larger hippocampus (relative to the rest of the brain) than related species that do not scatter hoard, suggesting that the ecological pressure of needing to find stored food over the winter has led to the evolution of a larger hippocampus.

The navigational ability of migrating birds or birds that forage at distant locations and return to the nest also suggests excellent "brain power" with respect to use of space. Again, the hippocampus has been proposed to be critical for such abilities, and research with homing pigeons (domestic *Columba livia*) supports this idea, as pigeons with a disabled hippocampus can no longer find their way home (Bingman et al. 2006) (Fig. 7.33).

7.7.1 Song system in the avian brain

Most birds, and some other vertebrates as well, vocalize as one way of communicating with other members of their species, producing a repertoire of calls and (in some cases) songs. Oscine passerine birds are famous for learning some of the features of their songs. One of the most exciting discoveries in the modern study of avian brains is that the telencephalon of oscine passerine brains contains a set of interconnected brain regions (nuclei) that are dedicated to a remarkable extent to the learning, production, and perception of song (Chapter 10). In species of oscine passerines where only the males sing, such as Zebra Finches (*Taeniopygia guttata*), the song system nuclei are larger in males than in females. In species where both sexes sing, such as some tropical wrens, the song system nuclei are more similar in size in males and females.

In birds of the temperate zone, singing often varies on a seasonal basis, with more singing during the breeding season. The sizes of the song system nuclei also change seasonally in concert with song production. Experiments have shown that seasonal changes in the size of the singing and song system nuclei are regulated by hormones, especially testosterone, acting both directly and through conversion to estrogen.

7.7.2 Sleep in birds

Birds, like many other animals, sleep. Diurnal (day active) birds sleep at night and nocturnal (night active) birds sleep during the day. The function of sleep—that is, why it is adaptive—has long been a mystery. The need for bodily rest seems straightforward, but why is the period of rest spent in a non-awake (unconscious) state of unresponsiveness to the outside world? In mammals, sleep is a brain-driven phenomenon: falling asleep and waking up are products of brain activity, and the brain itself sleeps. The sleeping brain produces very different patterns of neuronal activity than are seen during resting wakefulness, and enters into multiple sleep states, with different patterns of neuronal activity in each. In mammalian sleep, there are two broad categories: (1) REM (rapid eye movement) sleep, with recognizable low-amplitude, fast-changing brain waves, and (2) non-REM sleep, with high-amplitude, slow-changing brain waves. Recent research demonstrates that birds probably use these same brain sleep phenomena (Fig. 7.34A, B). However, unlike most mammals, active sleep periods are short in birds, and in some species sleep is interrupted frequently to permit vigilance against potential predators.

A remarkable discovery from avian sleep research is that birds have the ability to sleep only one half of their brain at a time, as has been observed in chickens, gulls, ducks, and Zebra Finches (Fig. 7.34C). The visual systems of birds are crossed in relation to the brain halves; that is, neurons from each eye go to the opposite side of the brain. By alternating the sleeping half of the brain throughout the night, these birds can still be watching out for predators with one eye always open, while still getting their required brain rest and perhaps dreaming (Box 7.09).

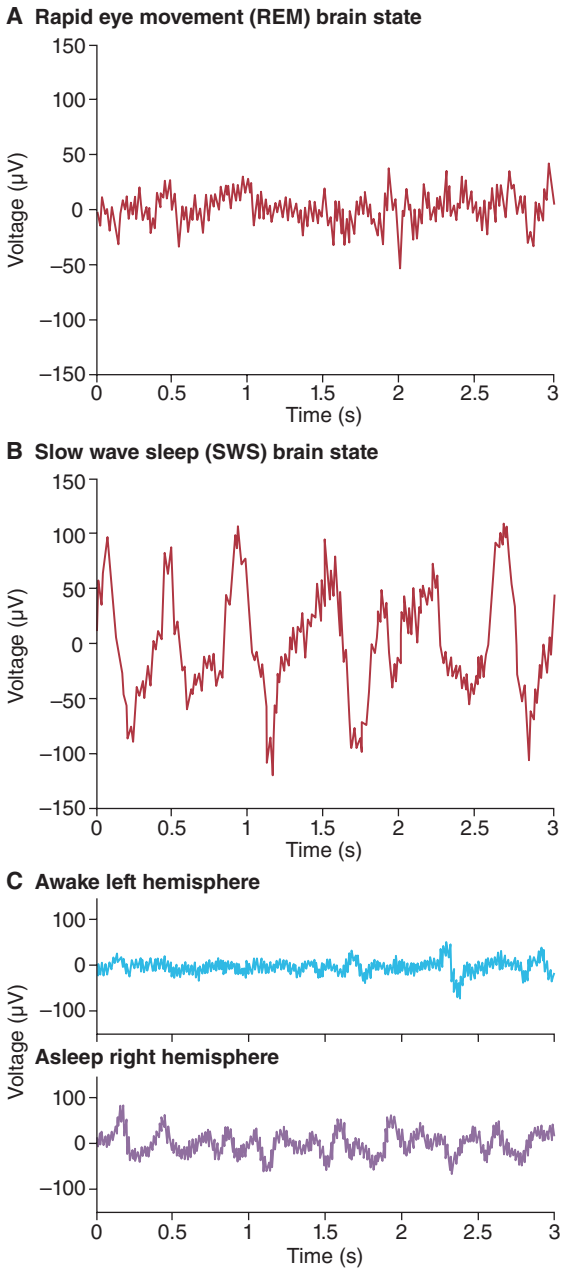


Fig. 7.34 Brain activity and sleep in birds. Brain activity in Zebra Finches (*Taeniopygia guttata*) shows similar sleep states as in mammals: during two states of sleep, birds were shown to have periods of (A) REM, low-amplitude, fast-wave sleep and (B) non-REM, high-amplitude, slow-wave sleep. (C) Birds are also known to sleep with one hemisphere of their brain active while the other half sleeps. (From Low et al. 2008. Reproduced with permission from National Academy of Sciences, USA.)

Can birds also sleep while flying? It has long been speculated that nocturnal migrants or birds like albatrosses that are over open ocean for days at a time can sleep while they are aloft. Studies have shown that Alpine Swifts (*Apus melba*) can remain airborne for months, suggesting that all vital physiological processes, including sleep, can be achieved in flight (Liechti et al. 2013). But how does a bird fly while sleeping? The phenomenon of unihemispheric sleep has led to a revival of interest in this question, and an answer is likely to be forthcoming soon thanks to the development of miniaturized wireless technology for recording the brain activity of flying birds.

Box 7.09 Do birds dream?

If humans are awakened when an electroencephalogram indicates that they are in active (rapid eye movement or REM) sleep, they are very likely to report that they had been dreaming. Birds and other mammals also show REM sleep. Are they dreaming? What are they dreaming about? These are fascinating questions, but unfortunately they cannot be answered scientifically at the present time. In humans, researchers can study in great detail patterns of activity in different brain regions during REM sleep, and then study the verbally reported content of the dream in relation to those patterns. In birds, the patterns of neuronal activity in different brain regions during REM sleep can also be determined, but we cannot get reports of dream content from them. Yet in male Zebra Finches (*Taeniopygia guttata*), neurons in the song system show spontaneous bursting patterns during sleep that resemble those seen when the birds are awake and singing. It is thought that this kind of dream-like "replay" during sleep might aid song learning and memory.

7.8 Sensory physiology

Birds, like humans and other vertebrates, have more than five senses. As fast-moving flyers with rich vocal communication systems, their vision and hearing impress human observers and have been well studied by scientists. The avian smell and magnetic senses used in navigation have also received substantial attention from researchers.

7.8.1 Hearing

Birds do not have external ears, but most species have keen hearing. By training birds to respond to acoustic stimuli, it is possible to measure their sensitivity to different sound frequencies. Birds can hear over a wide range of frequencies, but are most sensitive in the middle of their range, between about 1 and 5 kilohertz (depending on the species), with a moderate or steep drop-off in sensitivity beyond that range (Fig. 7.35). Their peak sensitivity is in a similar range to

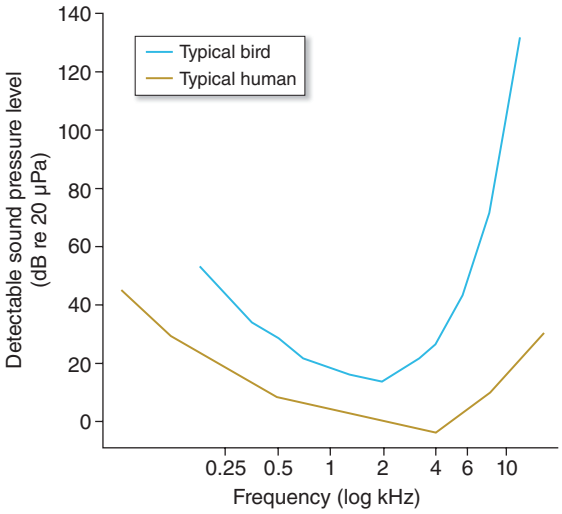


Fig. 7.35 Average hearing thresholds for birds and humans. Similar to humans, birds can hear over a wide range of frequencies. Many birds surpass humans in their ability to discern finer temporal sound structures. (From Dooling 2004. Reproduced with permission from Elsevier.)

ours, and their upper and lower limits of hearing are roughly similar as well. Where their hearing is superior to ours is in their ability to discern the fine temporal structure of complex sounds. This may be why many bird songs sound more musical to our ears if they are played at a slower than natural speed (Chapter 10).

These are generalizations about avian hearing. There are, however, many kinds of birds that produce very different calls and songs. There may be a match between the frequencies that predominate in each species' vocalizations and the peak sensitivities of its range of hearing. On the other hand, birds use their auditory systems for many functions in addition to hearing songs and calls of their own species, including for predator detection and hearing the mobbing calls of other species. Larger bird species generally have their peak hearing sensitivity at lower frequencies, and have a lower upper frequency limit of hearing. Larger species also tend to produce lower frequency sounds due to the physics of sound production. So there is a relationship between body size, sound production, and hearing sensitivity.

Birds need to be able to not only hear acoustic stimuli, but to also determine where the sounds are coming from (their location). This is especially important for species such as owls that hunt in the dark and use acoustic cues to locate and capture prey. Two features help them do this with accuracy and speed. One is having two ears, one on each side of the head. Two ears means that a sound coming from the left side of the bird will strike the left ear slightly before the right ear and also will be more intense at the left ear than the right, because the head casts a sound "shadow." Bird heads are not very large, so these cues work best for higher frequency (high pitched) sounds. The second feature, neurons in the auditory system of their brains, allows owls to compare and analyze these very small differences and then feed those computations to the brain regions responsible for decisions about how to attack the prey.

Barn Owls (*Tyto alba*), which can catch rodents in complete darkness using acoustic cues alone, have been a favorite avian subject for studying sound localization. These birds have additional features that aid sound localization. One is a facial ruff of feathers that reflects sounds into the ears. Another is that their two ears are markedly asymmetrical, with one being higher on the head than the other, and one ear canal aimed upward and the other downward. This arrangement enables these owls to localize sounds in the vertical dimension as well as from side to side, resulting in a very sophisticated auditory map (Fig. 7.36).

7.8.2 Magnetic senses

Birds are famous for being able to find their way around over long distances. They are capable of using a variety of cues to orient toward home or migrate between winter and summer ranges, including using the earth's magnetic field (Chapter 12). When we want to know which direction is magnetic north, we use a compass with a needle containing iron. Birds and many other animals have particles of magnetite, a type of iron oxide, in their bodies. In birds, some of this magnetite is found in the skin at the edge of the upper beak and in the nasal cavity, areas that are served by one of the major cranial nerves. In an experiment with Silvereyes (*Zosterops lateralis*), a passerine native to Australia and New Zealand, birds whose upper beak skin was anesthetized no longer shifted their migratory orientation in response to a strong magnetic pulse (produced by the researchers) in the way they normally would (Wiltschko et al. 2009). This finding lends support to the still controversial hypothesis that there is a magnetic sense with receptors located in the area around the beak. It is also possible that birds have two or more magnetic senses. Another proposed magnetic sense is based on photopigments, chemicals in the eyes that are affected by both light and magnetic fields. There is some evidence (Zapka et al. 2009) that this sense is used by European Robins (*Erithacus rubecula*), but again this hypothesis is still being investigated.

7.8.3 Vision

Birds have excellent vision. The range of their feather colors (Chapter 4) suggests well-developed color discrimination, and their foraging techniques and predator avoidance suggest great capabilities to detect movement. In fact, the vision capabilities of birds generally exceed those of

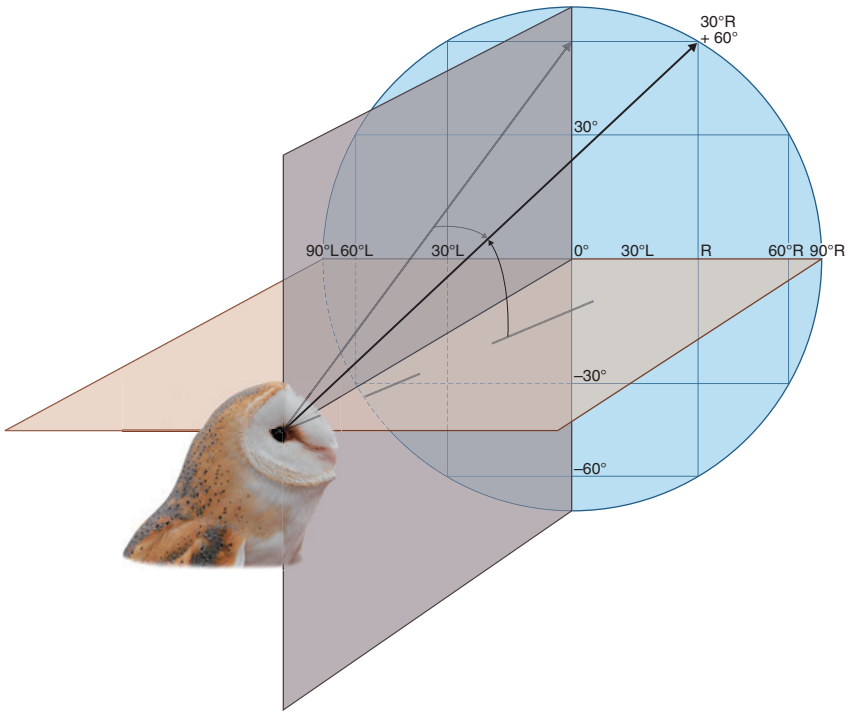


Fig. 7.36 Sound localization. To localize sounds in the dark, Barn Owls (*Tyto alba*) employ a two-coordinate system that detects both the elevation of the sound (the vertical dimension, how high or low it is) and its azimuth (the horizontal dimension, how far to the left or right). The ability to create such a sophisticated auditory map is related to the asymmetrical ear location in this and many other owl species. (Adapted from Knudsen 1981. Reproduced with permission from Scientific American, Inc. Photograph by Michael Cummings, Owl-Images.com.)

humans, even extending into the ultraviolet (UV) range, which has made it difficult for us to fully appreciate, until relatively recently, just how birds' use of vision differs from our own.

The avian eye, like other vertebrate eyes, provides a pathway (including the cornea and lens) by which light is gathered and focused onto the photoreceptor cells in the retina. Light energy is converted into electrical impulses, which are then conducted via a network of neurons, converging in the optic nerve, and the information is conveyed to processing centers in the brain.

In most birds, the eye has limited ability to rotate in the socket, and the bird must move its head to shift its field of vision. A few kinds of birds including herons, hornbills, and cormorants can rotate each eye independently between 14 and 18 degrees, thereby altering the overlap of the visual fields. The eyes of woodpeckers are particularly firmly seated, which helps explain why these birds do not suffer eye damage from their violent head movements. In only a few birds such as Ostriches, eagles, albatrosses, and hornbills does an eyelash or eyebrow shade the eye. The top eyelid is usually stationary and the bottom one closes the eye. A transparent nictitating (third) membrane can be brought horizontally across the eye to moisten it and may function as a "goggle" during flight to protect the eye. The nictitating membrane of some diving birds such as ducks and loons has a clear lens-like window to help focus the eye while underwater.

Eyes can be forward-facing to achieve binocular vision with overlapping visual fields, as in hawks and eagles (Fig. 7.37), but this placement results in large blind areas to the rear. If eye placement is more to the sides, then birds achieve a wider, monocular view of the world with less binocular vision. Eye placement and the shape of visual field appear to be affected by how a bird forages, and how it feeds its chicks (Martin 2007). Birds that feed by pecking or lunging require overlap in the frontal binocular fields. Filter feeders or birds that find food by tactile means, like many ducks and shorebirds, and that do not provision their chicks, have visual fields that only overlap about 5 degrees. This seems sufficient for flight, and their greater ability to see behind helps them detect approaching predators. Flamingos feed by filtering but need binocular vision to feed their chicks and have eyes facing forward. Likewise, skimmers forage by "blind trawling" (Chapter 8), but need forward-facing eyes to see what they have caught in the beak before swallowing it. Many birds such as pigeons look at distant objects preferentially with their lateral, monocular vision, orienting themselves sideways to inspect distant objects. This probably maximizes visual acuity because it projects the image onto the central part of the retina where visual cells reach peak densities.

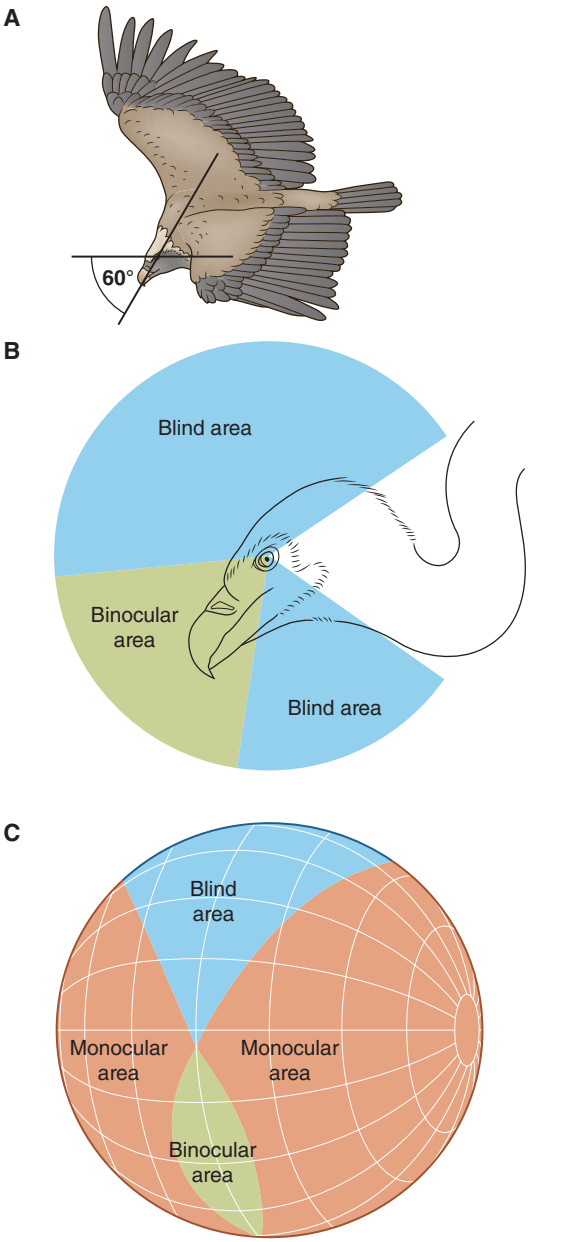


Fig. 7.37 Visual fields during flight. (A) While foraging, this Griffon Vulture (*Gyps fulvus*) holds its head at about 60 degrees below horizontal. (B) A vertical schematic of this vulture's visual field. While aiming its binocular vision toward the ground, its blind spots occur straight ahead as it flies, as well as above, below, and behind its head. (C) An orthographic projection of the same visual field (imagine the vulture's head at the center of the sphere with the bill pointed at the center of the binocular area). As the vulture searches for prey, its relatively small binocular field focuses on the ground. Relatively large monocular fields (seen with just one eye) occur on each side, possibly to track other raptors. A blind area persists in the forward direction, possibly shielding the vulture's eyes from direct sunlight. However, this blind area may also explain why flying raptors regularly collide with wind turbines and power lines. (From Martin et al. 2012. Reproduced with permission from John Wiley and Sons. A, drawn from a photograph by Todd Katzner.)

Avian eyes are usually large on both absolute and relative scales and in relation to the brain. An Ostrich eye is twice as large as the human eye, but in a smaller head. In contrast, nocturnal kiwis have very small eyes with very little binocular overlap, and instead rely heavily on olfaction. The visual acuity of Wedge-tailed Eagles (*Aquila audax*) (Fig. 7.38A) is more than twice as high as that of humans. American Kestrels (*Falco sparverius*) have a visual acuity that enables them to discriminate a 2-millimeter insect from the top of an 18-meter tree (Fox et al. 1976).

Most mammals have only three types of visual cells: rods that are excited in low light, plus two classes of cones used in daytime vision (humans and other primates usually have three classes of cones). Birds have four cone types, giving them tetrachromatic color vision. By comparing the relative stimulation of the four different cone types, birds achieve an even greater capacity to distinguish colors than humans (Fig. 7.38B). It is the fourth cone type in birds that allows them to distinguish light in the near UV as a distinct color, a part of the electromagnetic spectrum that we cannot see. In addition, each cone in the avian retina contains colored oil droplets, a feature that was lost during mammalian evolution. Light must pass through these oil droplets before reaching the photopigment portion of the cell. The oil droplets function as cut-off filters to remove short wavelengths and narrow the absorption spectra of the visual pigments. These features allow birds to distinguish even more colors when the brain combines the neural input from all the cone types.

Birds can use their UV sensitivity to view objects such as the waxy coats of many fruits and berries reflecting UV light, and Eurasian Kestrels (*Falco tinnunculus*) can locate the trails of voles using their UV-reflecting urine and feces. Perhaps more importantly, birds can see UV light reflecting from other birds' feathers, and UV-reflecting plumages are widespread in birds (Chapter 4). In 108 species of Australian birds from a broad array of taxa, the feathers reflecting in the UV spectrum (or those that are fluorescent, as is common in parrots) are more likely to be used in courtship displays than feathers found elsewhere in the body (Hausmann et al. 2003). In Budgerigars (*Melopsittacus undulatus*), the juxtaposition of the UV/blue-reflective cheek patch and fluorescent yellow plumage on the crown and the rest of the cheek leads to high visual contrast to the bird's eye, suggesting areas of special importance for sexual signaling.

7.8.4 Smell

Birds are usually considered to have a poor sense of smell compared with mammals, in part because most birds have relatively small olfactory bulbs in their brain. The physiology behind the sense of smell of birds is similar to that in other vertebrates. Although most birds rely more on vision than olfaction, smell can be quite important for birds when they use it to forage, navigate, or recognize each other. Studies

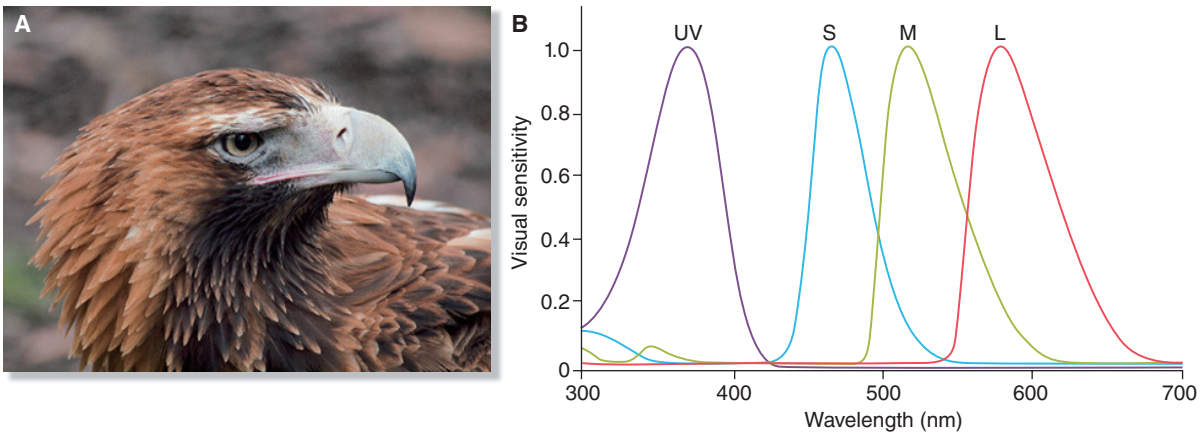


Fig. 7.38 Visual acuity in birds. (A) One of the world's largest birds of prey, the Wedge-tailed Eagle (*Aquila audax*) is an extremely specialized aerial predator with remarkable visual acuity. (B) Normalized spectral sensitivities of a typical bird, showing the four peaks of color sensitivity that correspond to the four cone types in bird retinas: ultraviolet (UV), blue (S, short), green (M, medium), and red (L, long) wavelengths. Most mammals, including humans, lack the cones necessary to see UV light. (A, photograph by Jeremiah Blatz. B, from Goldsmith 2006. Reproduced with permission from Scientific American, Inc.)

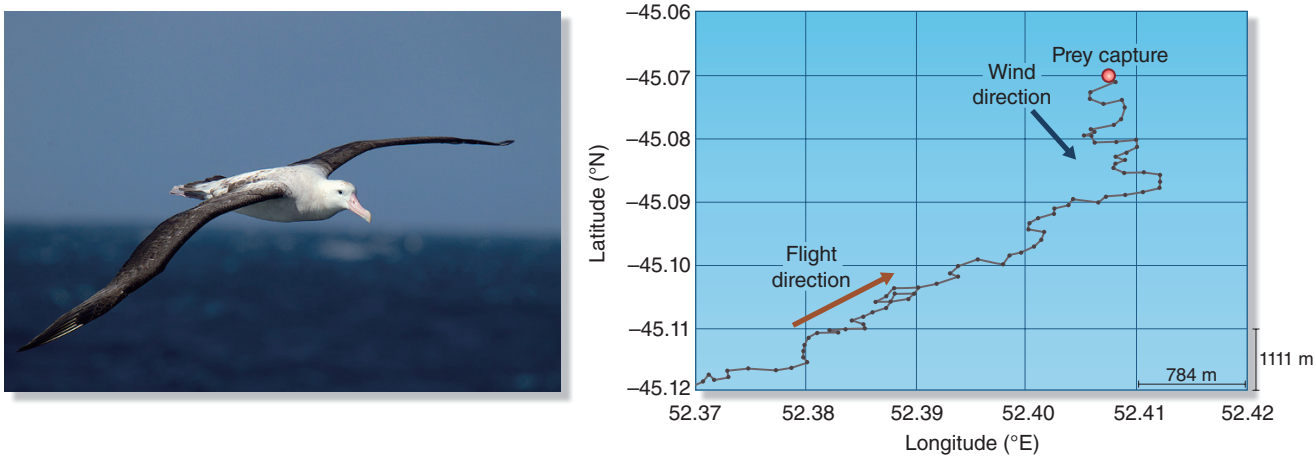


Fig. 7.39 Navigation by odor. Wandering Albatrosses (*Diomedea exulans*) and other seabirds tend to fly crosswind, optimizing the likelihood of encountering an odor plume of prey. Once detected, these birds use a zigzag flight pattern to approach their prey, beginning their decent about 2.5 kilometers downwind of the capture site. (From DeBose and Nevitt 2008. Reproduced with permission from Springer Science + Business Media. Photograph by Graham Ekins.)

by Gabrielle Nevitt and her colleagues have demonstrated that petrels, albatrosses, and shearwaters use odors to locate prey over vast distances across the ocean (Nevitt 2008) (Fig. 7.39). These odors include those released from crushed krill and fish prey as well as dimethyl sulfide, a metabolite produced by phytoplankton when they are eaten by krill, fish, and squid. Some of these same species also use their sense of smell to locate their individual nesting burrows.

Olfaction is also important for nocturnal kiwis, homing pigeons that use odor gradients to locate their home loft, and vultures foraging on carrion that emits ethyl mercaptan. In fact, in the 1930s, the Union Oil Company of California introduced this chemical into their gas lines so that they could use the presence of turkey vultures to locate leaks in remote areas. A good sense of smell is also evident in various other birds, including Kakapo parrots (*Strigops habroptila*) where it is used in foraging (Hagelin 2004), Crested Auklets (*Aethia cristatella*) that emit a tangerine-scented odor thought to be used in chemical communication (Douglas 2008), and in Blue Tits (*Parus caeruleus*) that can be trained to detect lavender odor (Mennerat et al. 2005). Other studies have shown that individual birds produce their own odor profile and that other birds can tell who they are just by smell. This ability was found, perhaps unsurprisingly, in the tubenose petrels (Bonadonna et al. 2007), but also in passerine songbirds (Whittaker et al. 2010).

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Chapter 8 Avian Food and Foraging

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Chapter contents

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Watching even common birds feed, as naturalists have done for centuries, can provoke insightful questions and lead to new observations about their diets, behaviors, and biology. Watching a thrush forage along the ground, you might wonder how it decides where to probe for an earthworm. At the seashore, witnessing an osprey suddenly stop mid-flight and plummet to the water, you might ask how it determines when and where to fish.

In a tropical rainforest, some birds fly out to capture insects in the air, some specialize in probing in clusters of dead vegetation, while others restrict themselves to flipping fallen leaves. Still other birds consume mostly fruit, some feed only on large insects and small lizards, and others dive for fish in small streams. Why do bird species eat such different types of food? Why do some specialize on just a few kinds of feeding locations or prey types?

If you scrutinize the ground below a jacamar roost in a New World tropical rainforest, you might notice that in consuming its diet of large insects, the bird leaves behind a pile of butterfly wings, but never those of the locally abundant *Heliconius* butterflies, a group of slow-flying species that should be easy for a bird to catch. Why do these birds avoid some types of insects but not others? You might notice that small, foliage-gleaning birds such as warblers pop their heads up, scanning their surroundings even more often than they scan for food. How do birds avoid becoming prey themselves, and avoid other dangers associated with feeding?

While watching large flocks of terns, gannets, or boobies out over the ocean, or birds following army ants in a tropical rainforest, you might wonder how birds track their changing food patches from day to day and sort out who feeds where. You might observe that individual birds of the same species feed differently from one another. They possess the same species-typical morphology, so why do they not feed similarly?

These are examples of fruitful observations and questions that arise when watching foraging birds. The purpose of this chapter is to summarize the vast observations and literature on birds' diets, feeding behavior, and anatomical and morphological adaptations for foraging.

8.1 Basics: meeting energy and nutritional demands

A bird's metabolism largely determines how much food it requires (Chapter 7). All birds are **homeotherms** with a generally high metabolic rate. Homeothermy is energetically

Homeotherm: an organism that maintains its internal body temperature at a constant or nearly constant level regardless of environmental conditions.

Opposite: Two Lammergeiers (*Gypaetus barbatus*) fight over bone marrow. To break through and access the rich marrow, these birds—often referred to as "bonebreakers"—drop scavenged bones from great heights. The darker of the two birds is a juvenile. (Photograph by Magnus Elander.)

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Fig. 8.01 Clay as a nutritional supplement. Birds that regularly visit clay licks, such as these Red-and-green Macaws (*Ara chloropterus*), probably consume clay for its high sodium content. (Photograph © Frans Lanting, www.lanting.com.)

costly, necessitating frequent eating. Because of this high cost, most birds either eat high-energy plant foods—such as seeds, fruit, and nectar—or they gain high-energy protein and lipids from eating animals. The metabolic rate typically scales with body size, so that larger birds consume more food in total than smaller birds, but consume less food per unit of body mass (Chapter 7). Conversely, small birds have a higher metabolism per unit of mass, requiring a higher feeding rate; this in turn makes small birds more sensitive to feeding interruptions caused by challenges such as inclement weather.

8.1.1 Calories and nutrients

Aside from these general patterns, birds vary considerably in their energy needs. For example, birds that live in cold environments may need to elevate their metabolic rate just to maintain body temperature. Hot environments also may require increased energy expenditure as birds use evaporative cooling via panting and the wetting of body parts. For example, a pelican sitting in the sun on a hot day may visibly flutter the neck membranes of its gular pouch, an effective but energetically expensive form of evaporative cooling (Chapter 7).

Birds living in seasonal environments undergo annual changes in energy-demanding activities such as migration. Fats are the most efficient fuel for long-distance migration (Chapter 12). Many birds put on fat reserves to buffer themselves against inhospitable or unpredictable circumstances—such as blizzards, monsoons, or droughts—that reduce feeding opportunities. Birds that rapidly accumulate fat reserves by increasing their consumption rate are described as going through a period of **hyperphagia** that is often accompanied by increased metabolism. Some birds may also conserve energy by decreasing their metabolic rate and simultaneously dropping body temperature, entering a state of torpor (Chapter 7).

Scientists measure food consumption in energetic units of calories. However, certain nutrients can constitute a disproportional currency in birds' diets (Chapter 7). Willow Ptarmigans (*Lagopus lagopus*) of northern Europe and North America, for example, increase their intake of valuable nitrogen and phosphorus via their choice of particular plant foods. Geese and some ducks also feed selectively on the most digestible and high-nutrient plants and plant parts. Calcium is a chemical element that birds often seek in particular food types. Calcium is often in short supply for female birds that require it to create eggshells for their young. Birds frequently obtain calcium by eating snails, bones, or other calcium-rich foods that otherwise are not a major dietary component. A variety of seed- and plant-eating birds additionally consume soil at clay licks (a habit known as **geophagy**). Studies in South America, where clay licks are known as "colpas," have suggested that birds like macaws and their relatives visit them primarily as a source for sodium, an element that is rare in plants but important for animal physiology (Fig. 8.01). Evidence supporting this hypothesis includes the low sodium content of plants forming a major part of these birds' diet, the high-sodium clays selected by the birds, the location of colpas far inland and thus far from other natural sources of sodium (such as the ocean), the increased use of colpas by parent birds when feeding chicks who need dietary sodium

Hyperphagia: rapid feeding, as often exhibited by birds putting on pre-migratory fat.

Geophagy: the consumption of soil, clay, or sand.

for early growth (Brightsmith and Muñoz-Najar 2004; Powell et al. 2009), and signs of sodium limitation in other animals like ants living in the same regions (Dudley et al. 2012). The colpa clays consumed by birds may also help them detoxify the alkaline compounds contained in some seeds (Powell et al. 2009).

8.1.2 Feeding rates and food abundance

Given a nutritious and available food source, how does a bird's feeding rate change as prey availability, or concentration, increases? The simplest model of this feeding process, or **functional response** to the prey's availability, is direct and linear. Figure 8.02A shows prey (or victim) mortality corresponding to a linear increase in predator feeding rate with prey density. This curve is flat because more prey are eaten by the predator as prey density increases, so the percent eaten does not change with density until the individual is satiated and feeding stops. This type of functional response results from passive feeders, which are rare among birds.

A humped functional response curve is far more typical in birds and other predators (Fig. 8.02B). Such a curve indicates a rapid increase in consumption rate as prey density increases, but then a decreased feeding rate up to the point of satiation. This kind of relationship has been documented in Eurasian Oystercatchers (*Haematopus ostralegus*) feeding on mussels (Goss-Custard et al. 1996). The humped functional response to prey density typically arises when birds respond rapidly to visible or easily detected prey, but slow their consumption rate as handling time per prey item increases. In other words, searching is important at low prey densities, but prey-handling time takes over more of the consumer's time as prey density increases. Under these circumstances, the percentage of prey consumed declines with prey density.

Ecologists have observed a third type of functional response in bird foraging, one depicted graphically as an S-shaped or sigmoidal curve (Fig. 8.02C). This curve represents infrequent use of a rare resource, then a rapid increase in its exploitation with increasing density, and finally diminishing use as satiation is reached. Correspondingly, the percentage of prey consumed first increases, then decreases with increased prey density. One explanation for this pattern centers on the cognitive abilities of feeding birds, and proposes that as a bird increasingly encounters a cryptic prey type—such as a well-camouflaged caterpillar or moth—it develops a mental representation of that prey type that helps guide its search. With increased consistent exposure, a specific **search image** can make the bird far more efficient in finding it. A similar process occurs when human birders first scan an unfamiliar habitat with binoculars. Cryptic birds often are hard to spot, but after you discover a few, you develop a mental search image for them and start to see them "everywhere."

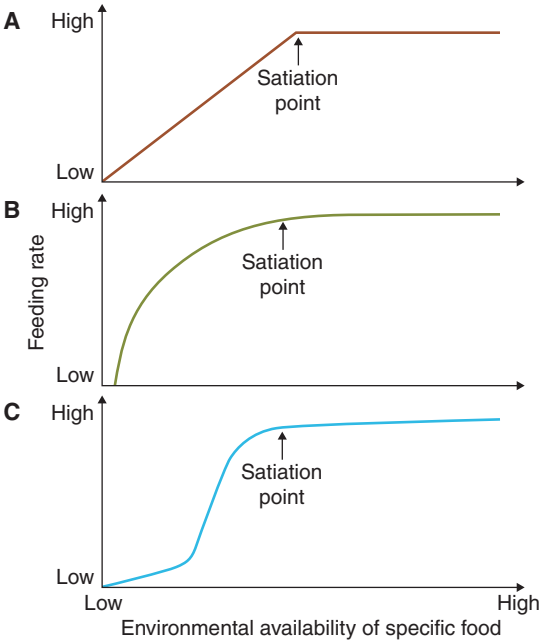


Fig. 8.02 Three alternative functional responses to prey availability. Arrows indicate satiation point. (A) Individuals may feed at a linear rate, regardless of prey availability, until they are satiated. (B) Alternatively, individuals may initially feed at high rates, then gradually become more selective as they near satiation and prey become easier to find. (C) Still other individuals may feed at low rates (reflective of low prey density), then rapidly increase their feeding rate as prey availability increases, and finally return to lower levels of prey exploitation as prey become highly abundant. (From Holling 1965. Reproduced with permission from Cambridge University Press.)

Alexandra Pietrewicz and Alan Kamil (1979) tested this experimentally in foraging birds. They projected images of cryptic moths to caged Blue Jays (*Cyanocitta cristata*) and measured the time it took for each bird to detect and peck at the image, getting a mealworm reward when each did so.

Functional response: in the context of avian foraging behavior, the graphical relationship between varying food or prey density and its consumption rate by a foraging bird.

Search image: a general idea or cognitive representation of an object or prey type being sought; if a bird has a search image for a particular type of prey, it is able to find that prey more easily than it can find prey for which it lacks a search image.

With consecutive exposure to images of the same moth species, the Blue Jays detected the images increasingly efficiently. However, when the researchers shuffled images of differently colored moth species, the birds showed little improvement in detecting any particular moth type. In effect, the sequential encounter of various different moth types prevented the development of an efficient search image for any particular moth.

This classic example illustrates a trade-off in which efficiency in detecting certain kinds of prey decreases the efficient detection of other types. A more recent example comes from Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) hunting crabs in New England intertidal and subtidal zones (Ellis et al. 2012). Both gull species detect and consume Jonah crabs far more frequently than predicted based on abundance, probably because this crab is far easier for the gulls to capture and handle than two other much more common crab species. The Blue Jay and gull examples both illustrate the widespread phenomenon of birds specializing to increase their foraging efficiency, a pattern illustrated by the classic proverb that a "jack of all trades is master of none."

8.2 Optimizing what, when, where, and how to forage

All birds must make foraging choices, such as deciding where to feed, what search path to follow, how long to persist in a food patch, what foods to pursue or bypass, whether to join a group, and how to balance feeding with other considerations such as avoiding predators. These decisions constitute the fundamental questions of foraging behavior. Researchers create models as tools to describe how animals make decisions, given assumptions and constraints about the foraging process, and then test these models using observations and experiments.

8.2.1 Optimal Foraging Theory

Optimization models are an important way to understand animal behaviors such as foraging, habitat use, and communication. **Optimal Foraging Theory** is an important subdiscipline of this general field. The underlying assumption of such models is that natural selection favors those individuals that perform best—as foragers, in the context of this chapter—because efficient foraging leads to higher survival and more offspring (Chapter 3). Optimal Foraging Theory thereby helps researchers make explicit predictions about how birds should behave.

Models of optimal foraging decisions typically have three components. First, what is the form of natural selection at work, and over what time period does it occur? For example, what matters more: to maximize the energy harvested over short time periods such as hours or days, or to minimize the likelihood of starvation or death over a longer season? Second, what behavioral options or choices are available to, and being exercised by, the bird? These options could include whether or not to attack a particular prey individual or how long to persist foraging in a resource patch. Third, what constraints are limiting the variety of foraging options? Limitations can arise from many sources, for example, **gape size** limits the maximal size of prey that birds can swallow, whereas lung capacity for oxygen constrains dive (search) times in diving birds. In fact, all factors that influence what birds actually consume relative to the food available are potential constraints in optimal foraging models.

One of the most basic decisions foraging birds make is whether to spend time and energy attacking a particular prey item they have already encountered, or instead to continue searching for more profitable prey. The very first optimal foraging models looked at the inherent trade-offs between the energy in each prey type, the search time needed to find it, and the handling time required to catch and consume it, comparing the costs and benefits of feeding as a generalist (attacking all items encountered) versus a specialist (passing over some items). In these models it is generally assumed that natural selection favors optimizing short-term energy gains, and the choice available to the forager is whether or not to pursue a particular prey item when encountered. The constraints include the overall abundance of the prey (which influences search time) and the profitability of the prey (which usually is assessed using handling time since more profitable items provide more energy per item and require less handling time). These models, formulated with simple algebra, predict, among other things, that foragers should ignore less profitable items as long as more profitable items are sufficiently abundant. The original prey choice models and their later variants now have been tested hundreds of times through observations of wild birds. These field studies typically support the prediction that greater overall food abundance favors greater diet selectivity.

Occasionally, predictions from optimal foraging models are not supported. This could mean either that birds do not always forage optimally, or that some assumptions of a particular model were not met under the circumstances in

Optimal Foraging Theory: models of foraging behavior in which it is assumed that animals maximize their food intake while minimizing the overall costs of obtaining it, such as energy and time devoted to searching, capturing, and processing.

Gape size: size of the mouth opening through which food items must pass.

which it was tested. The real world is not nearly as simple as optimal foraging models assume: prey often are not encountered sequentially, foragers often lack the perfect knowledge of all prey types needed to make optimal decisions, and foragers are selected for traits other than optimizing feeding rate over short time intervals. For example, birds might forage, seemingly suboptimally, on low-quality prey found near safe cover if moving out to forage on better quality prey would cause the foraging birds to become more vulnerable to predators.

In a classic study of optimal foraging, Reto Zach (1979) tested aspects of prey choice and harvesting behavior in Northwestern Crows (*Corvus caurinus*) along the coast of British Columbia, Canada. He noticed that the crows selected and broke open whelks by flying up and repeatedly dropping these marine snails onto rocks. A variety of birds drop food items onto hard substrates to access food: Golden Eagles (*Aquila chrysaetos*) drop tortoises, American Crows (*Corvus brachyrhynchos*) drop black walnuts, and Lammergeiers (*Gypaetus barbatus*) drop bones (Davenport et al. 2014). In this case Zach observed that the birds selected only the largest whelks and that the drop height was consistently about 5 meters. Zach questioned why the crows bypassed smaller whelks containing perfectly good meat and why the drop height was not lower, which would use less energy. To mimic this behavior, he performed his own whelk drops using a long pole equipped with a pulley that hoisted a small, tippable platform. Assuming the crows were foraging optimally, he predicted that the shells of larger whelks would break after fewer drops than those of smaller whelks, and that the likelihood of a shell breaking would increase little as the drop height rose above 5 meters. His results confirmed these predictions: larger whelks required fewer drops to break (and thus required less effort) than smaller whelks, regardless of drop height, and drops above 5 meters provided little improvement in breakage, regardless of whelk size (Fig. 8.03). These results support the idea that the crows adopted whelk-foraging tactics that optimize their short-term energy harvest. John Davenport et al. (2014) extended our understanding of this behavior in a study of Carrion Crows (*Corvus corone*) and Hooded Crows (*Corvus cornix*) in the UK. Their results similarly showed that the birds based foraging decisions on efficiency of mussel shell breakage rather than travel costs.

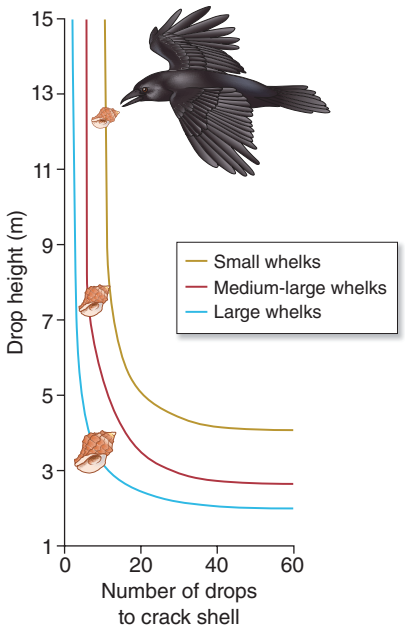


Fig. 8.03 Optimal foraging behavior. Northwestern Crows (*Corvus caurinus*) almost exclusively prefer to forage on larger shelled whelks (a type of mollusk). They drop shells onto rocks to crack them. Smaller whelks require more and higher drops (gold), whereas larger whelks can be dropped from lower heights with a higher rate of opening success (blue). There is an additional trade-off in the effort necessary to carry, drop, and retrieve various whelks; larger whelks are often stolen by other birds. For these crows, dropping medium–large whelks (red) from a height of 5 meters is optimal. (Adapted from Zach 1979. © Cornell Lab of Ornithology.)

8.2.2 Optimal prey searching strategies

Optimal Foraging Theory also addresses how birds should optimize the way they search for prey. For example, many birds capable of foraging over large areas of open ocean, like albatrosses and penguins, face the problem of detecting sparsely scattered prey patches. A major constraint facing such foragers is a paucity of information to guide them to high-quality feeding locations. One potential strategy animals employ in such circumstances is **Lévy flight**—named after a French mathematician who introduced the concept in 1937. Lévy flight is characterized by short, randomly oriented searches interspersed by occasional longer flights, and it provides a useful way to understand how some birds forage (Ornes 2013).

Several recent studies have explored how seabirds search for food over vast distances of open ocean. In one, researchers used GPS satellite data to track Wandering Albatrosses (*Diomedea exulans*) over antarctic waters. The locational data were coupled with temperature data-loggers placed in the birds' stomachs that allowed the biologists to determine the mass and timing of prey eaten (Humphries et al. 2012). This integrated approach showed that some albatrosses used Lévy-like flight patterns (Fig. 8.04), whereas others used random search paths, and some used a mixture

Lévy flight: a pattern of movement based on mathematical models that generates a mix of short random movements and occasional longer movements.

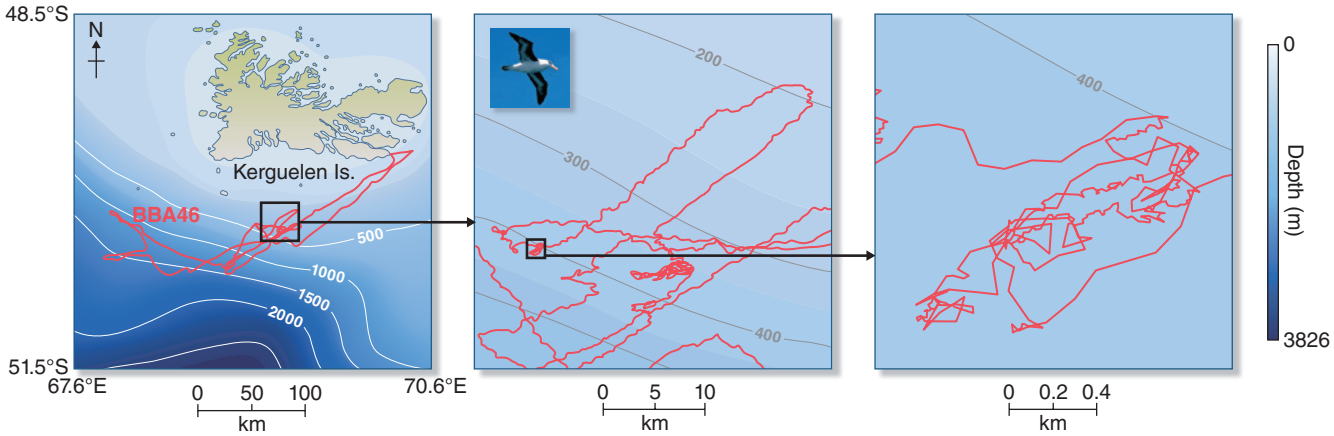


Fig. 8.04 Lévy flight foraging hypothesis. Black lines trace the flight path of an individual Black-browed Albatross (*Thalassarche melanophris*) foraging off the Kerguelen Islands in the southern Indian Ocean. These tracks reveal a Lévy-congruent flight pattern: short, randomly oriented searches interspersed with longer flights. Background color denotes depth (meters); areas within red squares are enlarged in adjacent right panels. (From Humphries et al. 2012. Reproduced with permission from National Academy of Sciences, USA.)

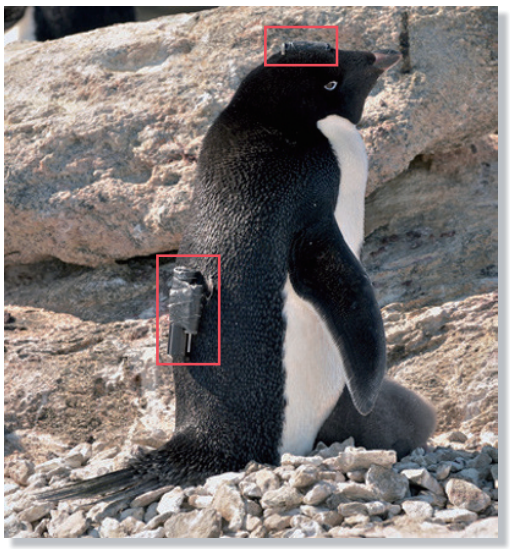


Fig. 8.05 Tracking foraging penguins. Researchers identified foraging patterns by fitting two motion detectors and a video camera (red rectangles) to Adelie Penguins (*Pygoscelis adeliae*). When hunting at sea, these penguins use a combination of long search trips with numerous short forays to find patchily distributed prey. (Photograph by Yuuki Watanabe.)

of the two. A different research group (Watanabe and Takahashi 2013) examined the search paths of Adelie Penguins (*Pygoscelis adeliae*) foraging on krill in the open ocean near Antarctica using cameras, data-loggers, and motion detectors attached to the penguins (Fig. 8.05). They found that these birds also had search patterns characteristic of Lévy foraging paths to optimize the discovery of patchily and sparsely distributed prey.

Optimal Foraging Theory also addresses how long a forager should stay in a particular patch of food. This situation is faced by foraging animals that discover that finding food becomes harder, with diminishing returns the longer they stay in a patch (Fig. 8.06A). Given the three components of such models, natural selection should cause the bird to maximize its long-term food gain rate. The bird's behavioral choice is how long to stay in the patch as determined by experience. The bird should adopt a "give-up time" rule that causes it to leave the patch when its rate of feeding diminishes to the average rate in the environment overall. The third component involves constraints, which in this model include both the diminishing return as the bird stays in a particular patch (Fig. 8.06A) and the time cost of leaving a patch to search for a new one. One prediction from this model, seen by comparing Fig. 8.06B and Fig. 8.06C, is that the longer the search-and-travel time span between patches, the longer the foraging bird should remain within a particular patch.

Working in the Gulf of St. Lawrence (Quebec, Canada), Ron Ydenberg and Magella Guillemette (1991) tested this model with Common Eiders (*Somateria mollissima*), which dive for invertebrates on the ocean bottom. The birds have to decide how long to stay on the bottom to forage in the food patch. In this example, unlike many cases of patch feeding in nature, the time between dives is spent coping with the physiological constraint of loading oxygen at the water's surface rather than searching for a new patch. The diminishing returns arise because longer dives require proportionately longer recovery times on the surface as well as longer travel times between the surface and the food. The graphic models (Fig. 8.06B, C) predict most simply that optimal foraging time should increase with dive depth. This prediction of the model was supported: the pause (or recovery) time at the surface indeed corresponds with dive time, most of which is spent foraging on the bottom (Fig. 8.06D).

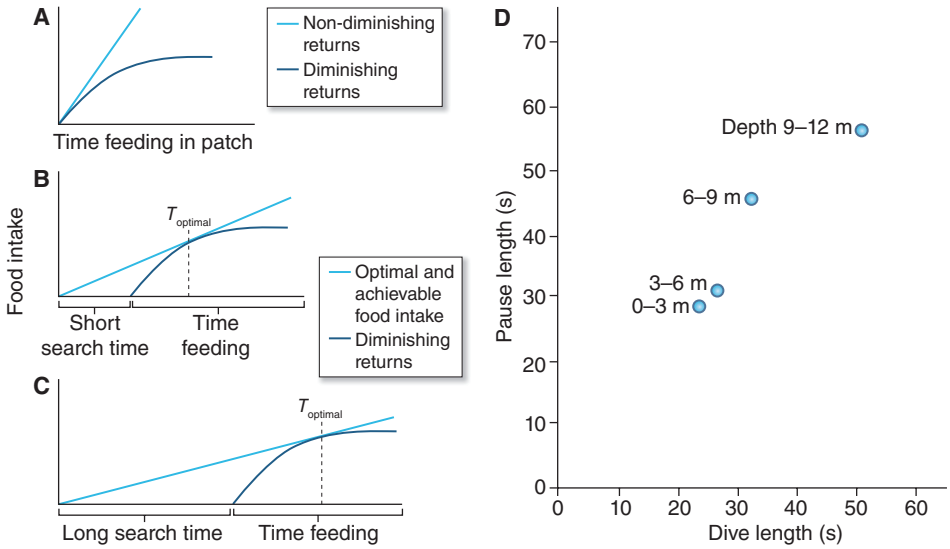


Fig. 8.06 An optimal foraging model for patch occupancy. (A) Food gain curves for feeding in a patch, with and without diminishing returns on time and effort. (B) Overall (net) rate of food gain: time feeding plus *short* search time. (C) Overall (net) rate of food gain: time feeding plus *long* search time. Note that despite identical diminishing returns curves in B and C, the optimal time to keep feeding in the patch is longer with a longer search time. (D) Actual dive times of Common Eiders (*Somateria mollissima*) foraging on bottom-dwelling shellfish are directly associated with the pause length (seconds) after foraging dives. As diving time increases, so does the subsequent pause between dives, showing diminishing returns of deeper dives. Error bars denote means and standard errors of the mean for grouped dive times (10-second groupings, *x*-axis). Circles represent mean pause lengths for dives at specific depths (meters). (A–C, reproduced with permission from Thomas W. Sherry. D, From Ydenberg and Guillemette 1991. Reproduced with permission from John Wiley and Sons.)

8.2.3 Foraging in groups

Birds foraging in groups may face additional decisions involving trade-offs between benefits and costs. Group-living individuals face questions including: (1) whether to join the group, taking into account the number of birds already in the group and food abundance; (2) how to forage and compete within the group; and (3) how to take advantage of or collaborate with other group members. Group living is complicated by the fact that the optimal behavior for an individual bird almost always depends on the choices made by other individuals, a scenario that can be modeled using evolutionary **game theory**. Consider, for example, a bird's choice either to locate its own food or to steal food from another individual in the group. If all other individuals in the group are locating food, then a thief does well in the absence of competition from other thieves; conversely, if all other individuals are thieves, then locators do best. Neither pure strategy is an **evolutionarily stable strategy** because an individual adopting a particular strategy does better when more individuals in a group use the other strategy. This situation should lead to an equilibrium that balances the frequencies of individuals using different strategies: the best foraging decision varies depending on the frequency of individuals in the group making alternative decisions.

One example of such scrounging behavior comes from aviary experiments involving Common Ravens (*Corvus corax*). Individual birds made decisions about when to recover cached food depending on whether or not potential competitor individuals had witnessed the food being cached (Box 8.01). In a laboratory study, Kieron Mottley and Luc-Alain Giraldeau (2000) constrained Scaly-breasted Munias (*Lonchura punctulata*), small Southeast Asian seed-eaters that typically feed in small flocks, to be either food finders or scroungers. In each flock of six individuals, the proportion of finders and scroungers was changed systematically from 6:0 (finders to scroungers) to 0:6. Although all individuals were trained to act as finders by pushing a bar that dumped seeds into a communal feeding dish, only the birds on one side of a partition—the finders—had access to the bar and could generate new resources. The birds on the other side were effectively scroungers, and relied on the finders to push the bar and make seeds available to

Game theory: mathematical cost–benefit models of alternative behavioral strategies involving conflict versus cooperation.

Evolutionarily stable strategy: an equilibrium strategy or behavior that, once established in a population, cannot be displaced by selection for an alternative strategy that gives individuals higher fitness.

Box 8.01 Cunning carnivores: wolves, carcasses, and the Common Raven

Common Ravens (*Corvus corax*), perhaps more than any other bird, use brain rather than brawn to make a living. The environments to which they are adapted are often harsh, from barren arctic ice to seasonal forests and deserts, locations where food—from flies to caribou carcasses—is boom-and-bust. Moreover, lacking the built-in tools of raptors to kill hide-bound animals, ravens instead rely on cunning cognition while facing stiff competition from other ravens, as well as from carnivores such as wolves and bears. These skills also help them avoid becoming carnivore snack-food themselves.

Common Raven behavior has been studied intensively in North America by naturalist Bernd Heinrich (1989, 1999). Heinrich's research methods are generally low tech: watching raven families reared in aviaries for close observation of individuals, continual experimentation with both captive and wild birds to distinguish among competing hypotheses, and tree climbing when necessary even in subzero weather to watch the birds close to a nest or a food-provisioning experiment.

Ravens are about as generalized in diet as any bird—eating nearly anything edible. This is not surprising given their challenging environments, but how they do so is rich with surprises. As young, in the company of family, ravens explore any new object. Ravens eat many berries and insects, but can also learn to kill relatively large animals, dragging trout out of the water by the tail, digging ground-squirrels or nesting petrels out of their burrows, driving flying kittiwakes to the ground where they are more easily pecked to death, and even killing reindeer calves and seal pups.

As ravens mature they switch to a deep suspicion of novelty, including avoiding carcasses unattended by carnivores such as wolves. Heinrich's (1999) initial expectation was that ravens avoided carcasses attended by wolves because of the competition and even the risk of being eaten by the wolves that created the carcass. Heinrich tested the raven's perplexing preference for feeding with wolves by putting down two meat piles at the same time, only one of which was accessible to wolves. The ravens invariably chose to feed at the meat pile with wolves. Heinrich argued that ravens evolved mutualistically with some of the carnivores with which they regularly share meat, such as wolves and human hunters, going back at least tens of thousands of years (Fig. 8.B1.01). The birds' fear of feeding on wolf-free food carcasses may have evolved in response to the human practice of poisoning carcasses as part of predator-control programs; wolves, with their acute sense of smell, usually avoid poisoned bait.

Common Ravens' cognitive toolbox includes manipulation by deceit. For example, ravens can plan ahead, such as when one individual feigns injury to lure a much larger bird, such as a swan, off a nest so another raven can sneak in to grab an egg. Ravens also communicate both acoustically and visually to diverse predators capable of killing large animals, seemingly alerting those predators about potential prey.

Confronting large food resources that they are forced to share with other carnivores has led ravens to cache meat, a challenging business when surrounded by other keen raven observers inclined to steal another individual's cache. Accordingly, ravens have sufficient memorization skills to recover caches many weeks later, and individuals can



Fig. 8.B1.01 Wolf and raven mutualism. Common Ravens (*Corvus corax*) occasionally lead wolves to dead animals via behavioral signals such as vocalizations and postures. Ravens cannot open carcasses and therefore need other predatory animals to do so—particularly in winter, when carcasses freeze solid. (Photograph by Bernd Heinrich.)

remember other individuals' cache sites, pretend-cache, and even re-cache when other ravens are not watching.

Ravens can judge not only how to avoid being eaten themselves by diverse predators at a kill site but also when to call in the reserves—other ravens! In one experiment, Heinrich (1999) released a wild-caught female raven, held for months in captivity and fitted with a radiotransmitter, in the evening at a freshly provisioned carcass within earshot of a night roost to which she traveled to spend the night. The next morning, she led the entire roost, which had been feeding elsewhere, directly back to the carcass. In other experiments he showed that a subordinate individual raven given the same opportunity to alert other individuals to a kill would not do so, safeguarding the food to consume it alone and uncontested. Heinrich was long confused as to why socially dominant ravens ever advertise the presence of carcasses already attended by other individuals, because any newly attracted ravens presumably would compete even more for the meat. By patiently inventing experiments to eliminate alternative hypotheses, he concluded that ravens most often summon outsider individuals to a carcass so as to overwhelm the territorial ravens that are trying to defend it.

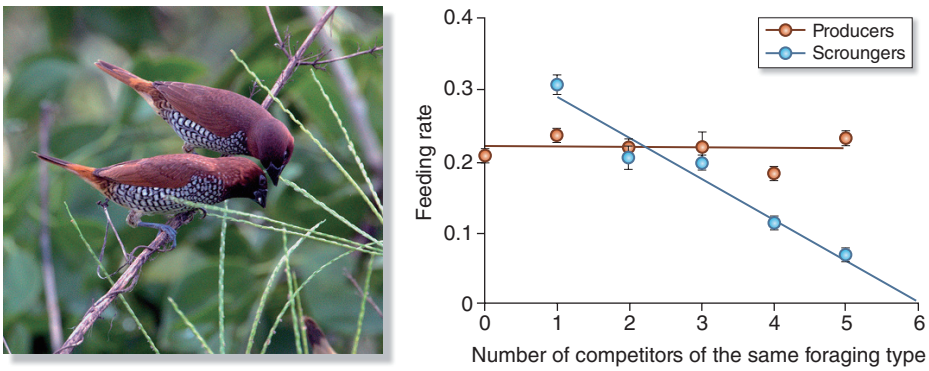


Fig. 8.07 Optimal producer and scrounger strategies. Laboratory flocks of Scaly-breasted Munias (*Lonchura punctulata*) were divided into two foraging strategies: "producers" that fed by jumping on a bar (which spilled out food) and "scroungers" that only fed on seed spilled by the producers. As predicted by theory, producers or finders (orange circles) fed at a consistent rate regardless of the number of scroungers. However, scroungers (blue circles) fed at high rates when few other individuals were scroungers, but experienced dramatically lower feeding success as the number of competing scroungers increased. A similar process may apply to wild birds that find or follow other individuals to new food sources. (From Mottley and Giraldeau 2000. Reproduced with permission from Elsevier. Photograph by Ravivaidya, https://en.wikipedia.org/wiki/File:Scaly_breasted_munia_feeding.jpg. CC-BY-SA-3.0.)

the birds on both sides of the partition. As predicted, scroungers fared worse in terms of feeding rate when there were more scroungers, whereas the finders' feeding rates changed little under the different ratios of feeding roles (Fig. 8.07). Notably, scroungers did best when they were rare, yet did not have a large effect on finders. Finders did best when they were rare, and the cost of competing with other finders did not change significantly as the number of scroungers increased. This result parallels that in nature, which tends to maintain a balanced equilibrium of both finders and scroungers. In a follow-up experiment, the researchers found that under less restricted conditions, individual Scaly-breasted Munias did in fact switch strategies to reach an equilibrium.

Optimal Foraging Theory has been used to explore many other aspects of foraging behavior. For example, the threat of predation means that birds often cannot simultaneously maximize feeding efficiency and safety (Cresswell 2008; Bonter et al. 2013). Consistent with this idea, Black-capped Chickadees (*Poecile atricapillus*) of North America carry food from an exposed birdfeeder back to cover (safety) more often when they perceive that staying at the feeder exposes them to predation risk and when carrying the food entails relatively little cost. This idea was first tested experimentally by simulating the presence of a predator using a model hawk "flown" past a birdfeeder on a wire (Lima 1985). For these chickadees, moving to cover had short-term costs, because the added transport time decreased their feeding efficiency, but it increased their long-term survival. Predators pose a threat to most birds, which are often particularly vulnerable or conspicuous during foraging.

8.3 Diversity of foods and foraging behaviors

Optimal foraging models attempt to understand how birds might generally optimize different aspects of feeding behavior given available choices and constraints. However, another way to understand avian diets and feeding is to

look at the many differences among birds. Birds eat virtually every kind of food imaginable, even some that are inedible to most other organisms. **Generalist** bird species eat diverse foods, but most bird species are **specialists** and eat only a narrow array of available foods. The diversity of birds' diets and foraging reflects selectivity by birds with different attributes and skills. However, an improved ability to detect, capture, handle, swallow, or digest one type of food often decreases a bird's ability to use other types.

8.3.1 New technologies for studying diets

Ornithologists use diverse methods to test hypotheses about foraging and determine what birds eat. Two new technologies deserve special mention because they are being applied widely to understand what birds eat when their diet is difficult to observe directly, such as when birds feed over vast ocean areas or feed on small items. The first such technology tracks diets using stable isotopes—chemical signatures derived from birds' food and stored in their tissues such as blood and bone. Stable isotopes are forms of an element that differ in atomic weight, and their relative frequencies after being incorporated into bird tissues provide signals about feeding. For example, stable isotopes of carbon vary naturally depending on latitude and plant productivity, and among types of plants with different types of photosynthesis. Stable nitrogen isotopes differ in ocean versus terrestrial environments, and change with trophic level. For example, researchers used carbon and nitrogen isotopes in the collagen (connective) tissue within bones (both fossil and recent) to show that endangered Hawaiian Petrels (*Pterodroma sandwichensis*) nesting on different islands forage in different regions of the Northeast Pacific Ocean, and that their diet has changed over time (Wiley et al. 2013).

The second technology uses DNA sequencing of organic fragments in the gut or feces of a bird, matched to unique DNA sequences for diverse prey types such as insect species. For example, Daniel Karp et al. (2014) used these genetic methods to identify which small insectivorous bird species in Costa Rica had consumed coffee berry borer beetles, the most economically important pest of coffee beans.

8.3.2 Diversity of avian foraging strategies

The diversity of birds' diets and foraging behaviors is evident in aspects of their anatomy—especially their beaks, feet, wings, and tails—that reflect feeding adaptations. Since "function follows form" in feeding, general physical characteristics of birds underline how distinctively different birds obtain prey. For example, various foliage-gleaning birds capture insects in and near vegetation; these birds typically hop rapidly, facilitated by long tarsi, through leafy vegetation, capture prey with short, tweezer-like beaks, and use small, rounded wings to move rapidly and hover within vegetation. In contrast, woodpeckers pound dead trees to disturb insects, and remove wood or flake off bark to reveal prey hidden within trunks and branches. Their strong, chisel-like bills, strong tarsi and toes for gripping tree trunks, tails for props, and shock-absorbing heads and necks are all adaptations that assist in these feeding behaviors. A very different set of adaptations is required for capturing fish and other aquatic animals in shallow water; for example, herons, egrets, and their relatives use long legs for wading; stalking, foot-raking, or stamping to reveal prey at the bottom of the water; and long necks with straight, pointed beaks for stabbing prey.

Birds do not simply pick items from a natural buffet table. Instead, essentially everything they ingest is living, or the product thereof, and thus what birds eat reflects not only their own anatomy and behavior, but also the behavioral and evolutionary responses of the food they consume (Box 8.02). Some plants have easily accessible nectar, fruit, and seeds, but other plant products and all animal prey are defended against birds in diverse ways. Birds generally have to work at foraging and feeding, and their adaptations to feeding must take into account their ecological and evolutionary interactions with their food. Hummingbirds provide one clear example: flowers of a particular shape favor the evolution of an appropriately shaped hummingbird bill (Chapter 14). When two species—in this case, predator and prey (or food source)—evolve traits in response to the other, the process is called **coevolution**.

A bird species' adaptation for food acquisition can be envisioned using the metaphor of "filters" between the total food potentially available to all birds in a particular environment and what each bird species actually consumes. Such filters operate at all stages of foraging, from the identification of food to feeding (Fig. 8.08), and involve all other species and the environment. For example, a specialized seed-eater's selection of a preferred food removes from

Generalist: an organism that is able to use a wide range of some type of resource; for example, birds with generalist diets eat many different kinds of foods.

Specialist: an organism that uses only a narrow range of some type of resource; for example, birds with specialized diets eat only one or a few kinds of food.

Coevolution: an evolutionary interaction between two (or more) species in which both species evolve adaptations in response to the other.

Box 8.02 Get a grip: prey handling by White-fronted Nunbirds

Puffbirds such as the White-fronted Nunbird (*Monasa morphoeus*) are among the tropical birds that have become evolutionarily specialized for eating large insects. This specialization raises challenges for these birds: finding their relatively rare prey, capturing and manipulating it, and finally swallowing it. Some puffbirds are solitary and spend large amounts of time sitting and scanning the foliage for prey. Others, like the White-fronted Nunbird, supplement the sitting-and-waiting strategy with foraging along with a flock of large birds that rummage in foliage, and thus stir up some insects that the birds can capture in flight.

Many tropical insects are far too large for nunbirds to swallow whole, and some also are protected by spines or enlarged body parts. Therefore, the nunbirds must process these insects using their beaks before ingesting them. For example, the Peruvian shield mantis (*Choeradodis rhombicollis*), a large insect that is readily eaten by nunbirds, has flaps just behind the head that are much wider than the bird's gape (Sherry and McDade 1982). Nunbirds can swallow this insect only after up to 12 minutes of continuous mandibulation to crush and soften the insect's flaps.

Although nunbirds can eventually swallow many such large insects, smaller birds would not be able to do so, and thus an adaptation like the shield mantis' flaps protects the insect against many avian predators. For example, another sit-and-wait predator on relatively large tropical insects, the Bright-rumped Attila (*Attila spadiceus*) of the neotropics, cannot eat the even larger insects that nunbirds can handle easily. Nunbirds themselves reject prey that are distasteful, too large, or shaped so that the birds cannot hold onto them. For example, the largest katydids are protected from nunbirds because the birds can neither grab them in flight nor pull them away from the vegetation because of these insects' strong legs.

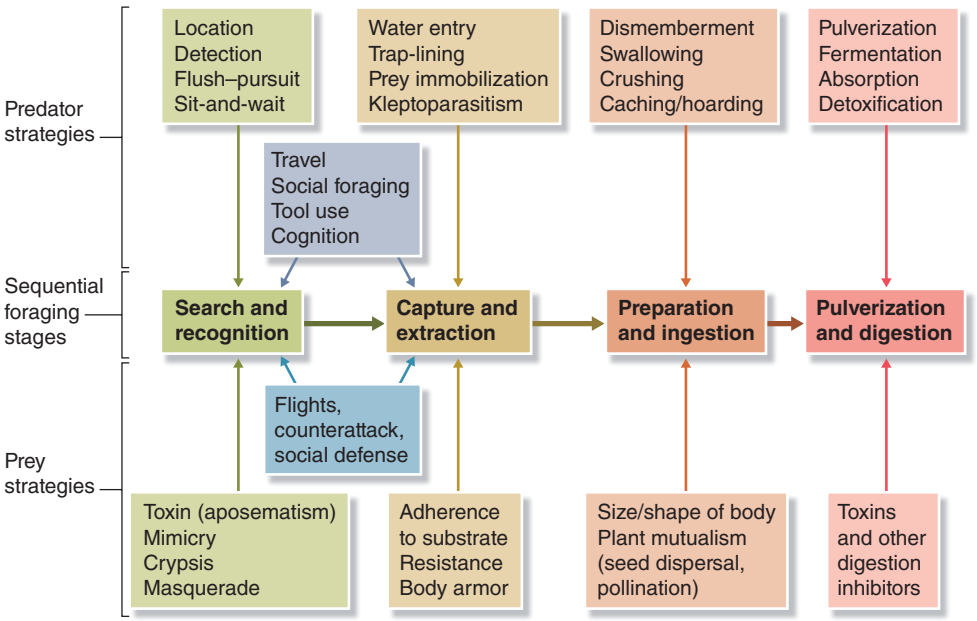


Fig. 8.08 Sequential stages of the foraging process. This schematic shows how both predators and prey use stage-specific ecological and evolutionary strategies (and counterstrategies) to forage, feed, and avoid becoming prey. (Reproduced with permission from Thomas W. Sherry.)

the environment (filters out) foods otherwise available to a less specialized seed-eater.

Another kind of filter comes from the coevolutionary arms race between birds and their animal prey: a bird species' adaptations leading to improved prey detection or capture also impose selection on their prey. Accordingly, birds' adaptations for capturing prey can result in adaptations such as stings or toxins in their prey. Similarly, birds' adaptations for handling and swallowing prey can put pressure on prey to develop anti-swallowing defenses like spines.

Insectivorous birds rummaging for prey in vegetation must remain continually vigilant for hawks, snakes, or other predators. The same fear response that helps protect these birds from predators has imposed selection for the eyespots seen in hundreds of species of butterflies and

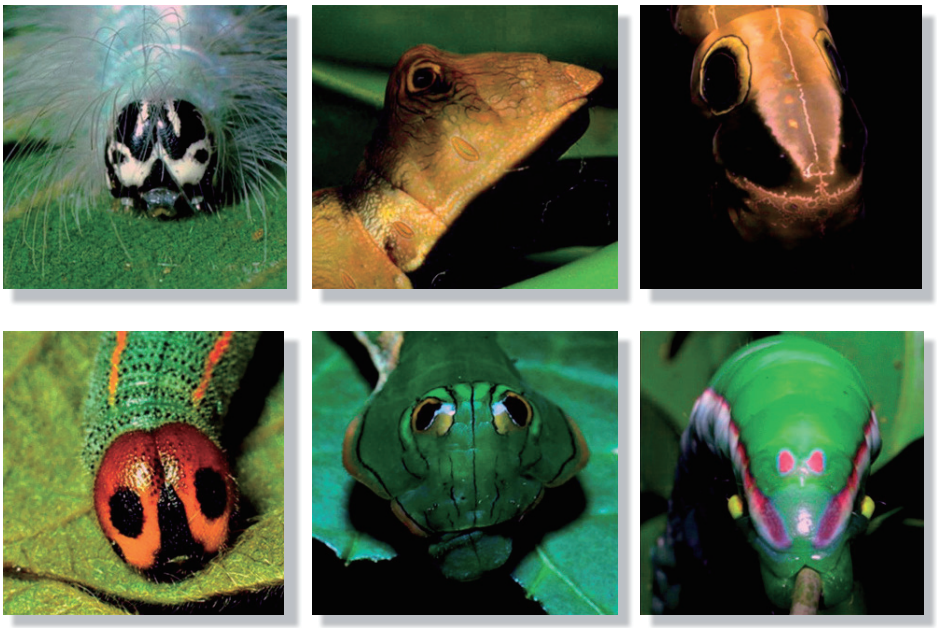


Fig. 8.09 Antipredator defense in arthropods. These caterpillars trigger avian flight (fear) responses with their large eyespots, which mimic those of snakes and other predators so well that the caterpillars often escape unscathed. (Adapted from Janzen et al. 2010. Reproduced with permission from National Academy of Sciences, USA.)

moths in Costa Rica alone (Janzen et al. 2010). These eyespots serve as a deceitful defense that helps these prey species appear to be predators (Fig. 8.09). Various prey also masquerade as inedible or innocuous objects to avoid predation, such as caterpillars—which are generally relished by birds—that mimic twigs or bird excrement. Recently, domestic chickens (*Gallus gallus*) were used as predators in laboratory experiments to show that chicks exposed to real twigs were more reluctant and took longer to attack two twig-mimicking caterpillar species than non-exposed chicks, even when the caterpillar prey were in plain sight (Skelhorn et al. 2010). Masquerade thus effectively deceives some birds, and its widespread manifestation by prey suggests a strong survival advantage in nature. Each successful counteradaptation by prey or a food plant filters out those birds that are not capable of detecting, capturing, handling, or digesting those prey or food sources.

8.3.3 Stages of foraging and consumption

Delineating stages within the feeding process helps to illustrate the diverse and subtle purposes of specific adaptations that birds use for particular food types. Although these stages may be delineated arbitrarily, because one stage grades into the next, many feeding adaptations are clearly stage-specific and integrate aspects of birds' anatomy, cognition, and behavior.

Search and recognition

The first problem that hungry birds face is locating appropriate foods. This process can involve active search, waiting for prey to come to the bird, provoking prey to move and disclose itself, or a combination of these and other search strategies.

Flying birds are able to search widely and so have an advantage in finding patchily or widely distributed foods. One obvious morphological adaptation to long-distance searching is high aspect ratio (pointed) wings, which enable efficient long-distance flights (Chapter 5). For example, albatrosses and other seabirds search large areas of ocean surface for small fish, squid, and crustaceans. Terrestrial birds such as swifts and swallows also have high aspect ratio wings and efficiently travel long distances seeking rich aggregations of flying insects such as termite swarms. Swallows often seek bodies of water to feed on ephemeral prey such as mayflies, midges, and caddis flies. Swifts and martins feed opportunistically on arthropods that constitute "aerial plankton" and are concentrated by updrafts associated with passing storm fronts (Russell 1999). Southern Carmine Bee-eaters (*Merops nubicoides*) of Africa often specialize on grasshoppers and other orthopteran insects disturbed into the open by bush fires, grazing mammals, people, or tractors.

For other birds, the food-searching process often involves scanning substrates such as leaves, tree trunks, and the ground. Small birds scan in different ways, with

subtle—and sometimes not-so-subtle—variations in morphology linked to their search methods. For example, foliage-gleaning warblers scan foliage with occasional hops and short flights, tree creepers creep up tree trunks clinging with large feet and a prop-like tail, and nuthatches walk headfirst down tree trunks.

Walking and running are also efficient ways for birds to search, chase, and subdue prey. Ratites such as the Ostrich (*Struthio camelus*) and Emu (*Dromaius novaehollandiae*) have long legs and strong toes that are well adapted for traveling long distances. Other long-legged birds that hunt primarily on foot include the bustards of Africa, Eurasia, and Australia; the Secretary-bird (*Sagittarius serpentarius*) of Africa; and the seriemas of South America. All of these birds live in relatively open grassland or desert environments that facilitate travel on foot.

One widespread avian search strategy is **flush–pursuit foraging**, a behavior that takes advantage of the innate startle response of insect prey such as flies and planthoppers. In this strategy, a bird hops and pirouettes animatedly through vegetation, simultaneously revealing brightly contrasting plumage patterns by suddenly spreading its wings and tail. A startled prey then flushes from its hiding place, and the bird pursues it in flight. A variety of Old World and New World flycatchers and redstarts use this behavior. Some of the best studied are the neotropical Painted (*Myioborus pictus*) and Slate-throated (*Myioborus miniatus*) Redstarts. Piotr Jabłoński (1999) and Ronald Mumme (2002) tested the efficacy of this foraging mode by experimentally darkening these birds' white tail feathers to eliminate the advantage of contrasting plumage. They found that the artificially darkened redstarts located prey less frequently and fed their nestlings less food than control birds with normal plumage (Fig. 8.10). These experiments thereby confirmed that the contrasting plumage pattern increases the effectiveness of these redstarts' flush–pursuit foraging strategy.

Other birds use a "sit-and-wait" strategy to capture prey that move infrequently. Examples of birds that wait patiently for an opportune moment include fish-eating birds such as kingfishers, wading birds such as herons that slowly stalk prey, and many raptors that perch and watch the ground closely. Some birds that specialize on relatively large insects—such as the puffbirds of Central and South America—also use a sit-and-wait strategy. This strategy is a bit perplexing because many of the puffbirds' prey are nocturnally active and hide during the day. What causes prey to move and reveal themselves to day-hunting

Flush–pursuit foraging: a foraging strategy in which birds first scare prey (usually insects) out of hiding and then chase and capture them.

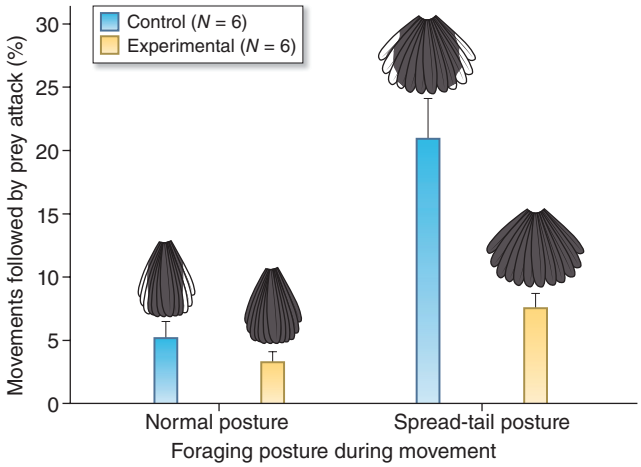


Fig. 8.10 Artificially darkened tails lower foraging success. Slate-throated Redstarts (*Myioborus miniatus*) flash their black-and-white tails to startle and subsequently catch prey. When the tails of some redstarts were experimentally darkened, typical flushing movements resulted in fewer attacks, suggesting that the white patterning enhances the ability to startle prey. (From Mumme 2002. Reproduced with permission from Auk.)

birds? One possibility is that heat from a moving patch of sunlight within the rainforest can cause an insect to change its position. Another is that ants moving continually through rainforest foliage occasionally irritate insects into making small motions that are then detected by the keen-eyed birds.

In an unusual but effective variation of the sit-and-wait strategy, some birds use tool-like enhancements to attract prey within striking distance. For example, herons may set out baits for fish (Fig. 8.11A), and Snowy Egrets (*Egretta thula*) vibrate their beaks rapidly just beneath the water surface to attract mosquito fish (*Gambusia*) (Kushlan 1973). Burrowing Owls (*Athene cunicularia*) surround their burrow entrances with bits of mammal dung, but are not slovenly housekeepers: the dung attracts dung beetles, which are a favored prey of the owls (Levey et al. 2004) (Fig. 8.11B). If one removes the dung piles experimentally, the Burrowing Owls replace them.

In addition to using diverse search strategies to locate prey, birds also employ a variety of sensory modes. Birds, like humans, rely heavily on color vision in feeding, but they also use a variety of other senses, and their sensory world differs significantly from ours (Chapter 7). For example, avian vision can be more acute than ours, allowing birds to detect prey from great distances, a trait well applied by raptors such as eagles and falcons. Eurasian Kestrels (*Falco tinnunculus*) perceive ultraviolet wavelengths, allowing them to detect the urine paths of voles that run through meadow grasses (Viitala et al. 1995). Nocturnal birds such as owls and nightjars have extremely acute vision in low light conditions, but even with this

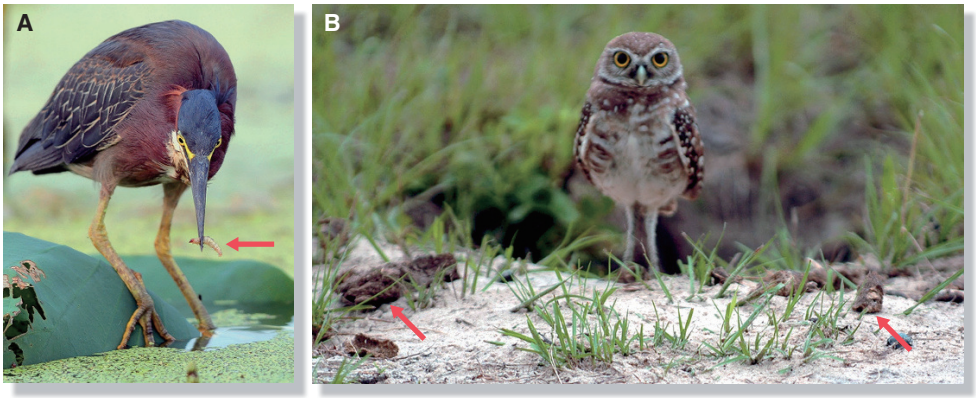


Fig. 8.11 Prey-attractant tools. (A) Green Herons (*Butorides virescens*) sometime use bait, such as insects (arrow), to lure fish within striking distance. (B) Similarly, Burrowing Owls (*Athene cunicularia*) place mammal dung (arrows) near their burrows to attract dung beetles. (A, photograph by Greg Lavaty. B, from Levey et al. 2004; photograph by R. C. Wolff.)

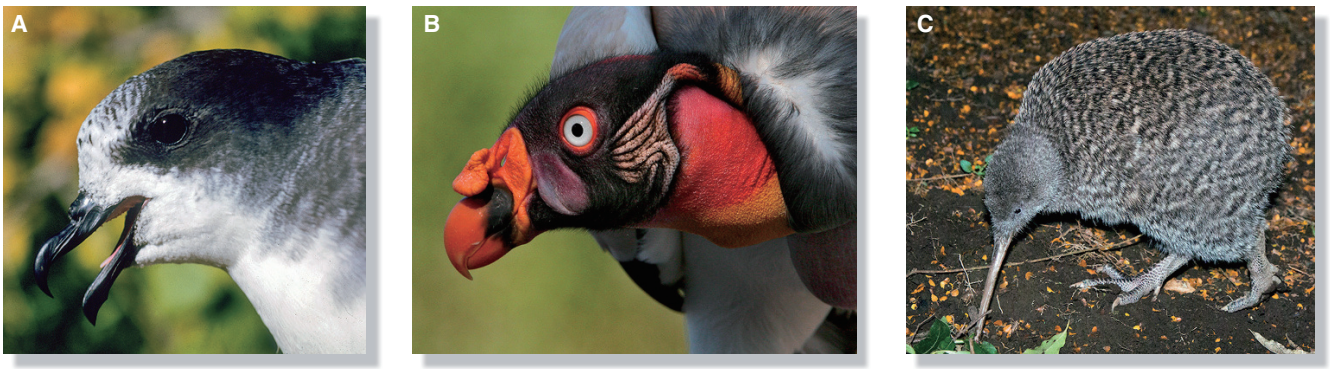


Fig. 8.12 Olfaction in foraging. (A) Bonin Petrels (*Pterodroma hypoleuca*)—like many petrels, shearwaters, and albatrosses—use their keen sense of smell to locate prey on the ocean surface. (B) King Vultures (*Sarcoramphus papa*), along with most New World vultures, use olfaction to locate carrion when foraging in forested habitats. (C) Great Spotted Kiwis (*Apteryx haastii*) and other kiwi species are nocturnal foragers, employing smell to locate earthworms and other prey underground. (Photographs by: A, Chandler S. Robbins; B, E. J. Peiker; C, Sharon Richards.)

ability, most species are generally **crepuscular**, foraging at dawn and dusk except when moonlight extends feeding activity times.

Owls have a particularly acute sense of hearing, and some have anatomically offset ears that allow the precise localization of the source of a sound using a two-dimensional map in the brain (Chapter 7). Great Gray (*Strix nebulosa*) and Snowy (*Bubo scandiacus*) Owls can detect sounds and successfully capture prey through as much as 30 centimeters of snow cover. To help them fly stealthily as they approach prey, most owls also have feathers that dampen the sound of air currents passing across them, giving potential prey less warning (Chapter 4). All these adaptations make owls formidable nighttime predators. Other birds, such as thrushes and the antpittas of Central and South America, have an acute sense of hearing to detect underground animals, and woodpeckers similarly listen for wood-boring insects.

Crepuscular: refers to organisms that are most active near dawn and dusk.

Although most birds have a poorly developed sense of smell (Chapter 7), especially as compared with mammals, some birds do use olfaction to find food, sometimes over great distances. For example, some seabirds search over large ocean areas, and once they discover a smell, move upwind to find its source. Researchers and birders wishing to attract such pelagic birds often take advantage of this behavior by leaving a slick of fish oil behind their boat; with luck, the smell of the oil lures in petrels, shearwaters, albatrosses, and other seabirds from downwind (Fig. 8.12A). Terrestrial birds that feed on rotting carcasses might be expected to have acute senses of smell, but the Old World vultures do not appear to locate their prey through olfaction. In contrast, some New World vultures, including King (*Sarcoramphus papa*) and Turkey (*Cathartes aura*) Vultures, have a strong olfactory sense



Fig. 8.13 Facial bristles. (A) Many species have facial bristles (arrows), but the type and function of these bristles differ. The American Redstart (*Setophaga ruticilla*) (left) and Royal Flycatcher (*Onychorhynchus coronatus*) (middle) likely use their bristles for detecting insect prey during aerobatic foraging. The White-necked Puffbird (*Notharchus hyperrhynchus*) (right) is thought to use its long bristles to protect its face and eyes from the spines of its large insect prey. (B) Other species use bristles for gathering sensory information. For example, North Island Brown Kiwis (*Apteryx mantelli*) (left) use facial bristles for sensing the movement of subterranean prey, as evidenced by the vibration and pressure-sensing Herbst corpuscles (black arrows), nerve bundles (black star), and muscles (white stars) near the bristle follicle (right). Scale bar = 5 mm in histological view. (Photographs by: A, left, Jennifer Malpass; middle, Andrew Snyder; right, Thore Noernberg; B, left, Tui De Roy, AUSCAPE; right, from Cunningham et al. 2011. Reproduced with permission from John Wiley and Sons.)

(Fig. 8.12B). Turkey Vultures can smell their way to rotting meat even when it is completely covered by leaves in dense tropical forest (Houston 1986). The nocturnally adapted kiwis of New Zealand also use olfaction for feeding (Fig. 8.12C). They are the only birds with nostrils at the very tip of the beak, and are capable of detecting scents at concentrations of only a few parts per million. Kiwis typically feed on invertebrates, especially earthworms, which they detect by probing their beaks into leaf litter and soil.

Some birds use tactile senses to locate prey at close range, employing pits near the bill end that are packed with cell receptors (Cunningham et al. 2010). Shorebirds such as snipe and woodcock use their long, sensitive beaks to detect earthworms and other invertebrates via touch in muddy spots. Some ibises detect crayfish with their long, decurved beaks, which they deploy in up-and-down, sewing-machine-like movements that both detect and grab prey. The Shovel-billed Kookaburra (*Clytoceyx rex*) of New Guinea rainforests plows its beak laterally through the soil to detect invertebrates.

Many birds have stiff, pin-like feathers called facial "bristles" that help them sense or capture prey. **Rictal bristles** are specialized rigid, whisker-like feathers that are usually evenly spaced at the base of the bill (Chapter 4). These bristles are most conspicuous in birds that pursue insects, including nightjars, flycatchers, and some New World warblers such as redstarts (Fig. 8.13A). Because many birds with bristles forage in dark locations, the bristles may have a tactile function to help the bird sense its prey's location as it closes in (Fig. 8.13B). Alternative hypotheses for the bristles' function are that they funnel prey into the bird's mouth (both physically and by providing tactile information, as mammalian whiskers do); that they help hold onto prey for manipulation once it has been caught; and that they protect the eyes and face from spiny appendages and other threats from prey. For example, the White-necked Puffbird (*Notharchus hyperrhynchus*) (Fig. 8.13A) of Central America feeds on many large insects, and correspondingly has a long, deep beak as well as well-developed bristles between the beak and eyes that likely protect its face from the large and sometimes spine-bearing prey species these birds catch and handle (Sherry and McDade 1982).

Rictal bristles: stiff, hair-like feathers projecting from the base of the beak in some birds.

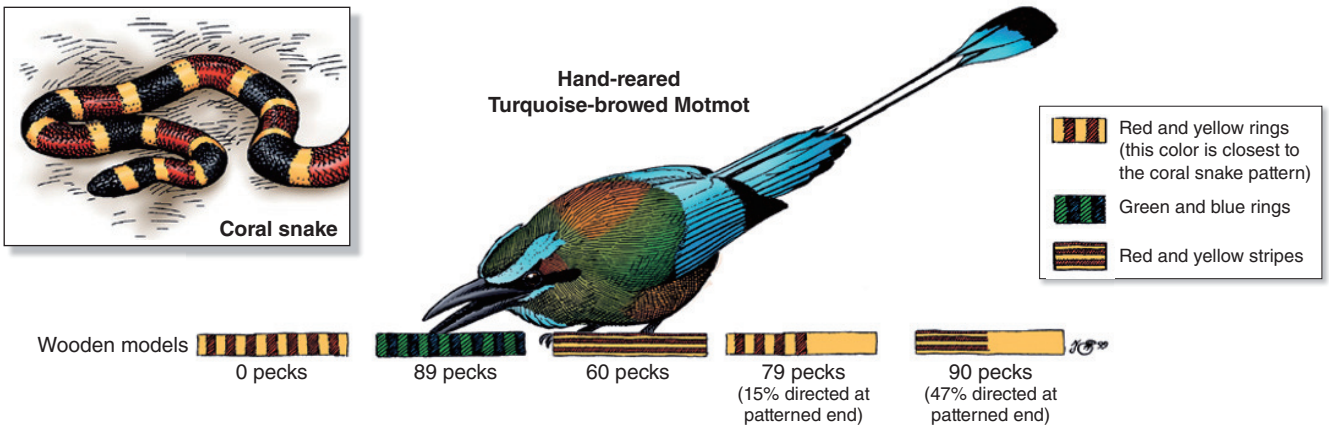


Fig. 8.14 Innate responses to coral snake warning colors. Turquoise-browed Motmots (*Eumomota superciliosa*) sometimes capture prey from the leaf litter, where they are vulnerable to venomous coral snakes. Experiments revealed that naïve motmots (hand-reared, with no experience in the wild) recognized and completely avoided (0 pecks) wooden models that resembled coral snakes, but pecked at other color and pattern combinations. (Adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology, and Smith 1975.)

Woodpeckers also have bristles that appear to protect their nostrils and face from woody debris. Surprisingly few experiments have tested the function of rictal bristles, although studies by Michael Conover and Don Miller (1980) suggested that the bristles of Willow Flycatchers (*Empidonax traillii*) serve a protective rather than a prey-capture function. The role of bristles likely varies among bird species, and more experimental studies are needed to clarify how rictal bristles function.

Cognitive skills help foraging birds learn what, where, and when to forage for the best foods. Individual hummingbirds may encounter hundreds to thousands of flowers that differ in nectar quality, renewal rates, and availability. Using both aviary and field experiments with Green-backed Firecrowns (*Sephanoides sephaniodes*) in Chile, Paulina González-Gómez and colleagues (2011a, 2011b) showed that most individual territorial male hummingbirds could distinguish and recall nectars of different quality (sucrose concentration), their location within a patch, and renewal intervals (to which they adjusted their flower visitation rates) even many hours after their original foraging experience.

Sometimes birds learn important foraging skills from their parents. For example, Common Ravens (*Corvus corax*) go through a juvenile phase of highly exploratory ("curious") behavior that helps them learn both from their parents and by trial and error about which foods are edible (Box 8.01). This apparently innate tendency to approach novel objects or environments appears most frequently in birds that forage broadly on many different types of food. In addition, parents may teach their young how to hunt, a behavior found most commonly in raptors and other carnivores requiring complex skills to capture prey. For example, parent Ospreys (*Pandion haliaetus*) sequentially bring dead prey to their youngest offspring, then bring live but incapacitated prey, and—as the young develop skills—live prey that requires recapture (Adams-Hunt and Jacobs 2007). In Costa Rica, Alexander Skutch (1976) described White-fronted Nunbird (*Monasa morphoeus*) parents holding a large insect conspicuously for their juvenile to practice snatching while in flight. The importance of learning to feed is suggested by local feeding traditions within a species; for example, a population of Peregrine Falcons (*Falco peregrinus*) in New Mexico (USA) specializes in capturing bats as they emerge from their roosting caves (Skutch 1976).

In addition to recognizing edible foods, searching birds must recognize and avoid inedible or dangerous items. Birds use both innate recognition mechanisms and learning to avoid dangerous prey. An experiment with Turquoise-browed Motmots (*Eumomota superciliosa*) (Fig. 8.14) and Great Kiskadees (*Pitangus sulphuratus*) demonstrated a dramatic case of innate recognition of danger. Both species are liable to encounter potentially deadly coral snakes while foraging. Coral snakes and a variety of other animals that are dangerous or noxious to potential predators display **aposematic coloration**: brightly colorful warning coloration that has evolved to get a predator's attention and thereby reduce unnecessarily injurious or life-threatening attacks. Susan Smith (1975, 1977) presented painted wooden dowels to hand-reared motmots and kiskadees that had no

Aposematic coloration: often known as "warning colors," conspicuous patterns or colors that signal to potential predators that an organism is potentially toxic or dangerous.

previous experience with venomous snakes. She found that both species innately feared most the combinations of red, yellow, and black rings that resembled the most common coral snake species in their area. In fact, young Great Kiskadees cowered in the farthest corner of their cages when presented with wooden models that even crudely resembled coral snakes. Other experiments showed that the birds exhibited no aversion to longitudinal stripes of the same color combinations or to alternating rings of other colors. Thus, even without firsthand experience, these birds appear to recognize and fear the particular aposematic color patterns of the snake species that are most dangerous to them.

A variety of venomous or potentially toxic prey, though not as dangerous as coral snakes, are readily handled by birds that have become specialized on those prey types. Some bee-eaters, for example, have an innate beating behavior by which they de-venom and de-sting these insects. An unknown physiological mechanism allows several species of *Pitohui* in New Guinea to tolerate dietary toxins (Chapter 4) and then incorporate those toxins into their own plumage (Dumbacher et al. 2004; Jønsson et al. 2008).

Some birds are reluctant to approach or feed on food sources that they have not experienced previously, perhaps sensing a general threat from unknown and dangerous hazards. For example, although young Common Ravens (*Corvus corax*) exhibit curiosity, older birds in contrast may exhibit generalized neophobia (Box 8.01).

Learning also is clearly important in many birds' responses to noxious prey. A classic study of such learning comes from studies of hand-reared captive Blue Jays (*Cyanocitta cristata*). The birds were presented with a meal of distasteful monarch butterflies (Brower 1969, 1984), which caused them to vomit (Fig. 8.15). This strong negative experience resulted in the jays later avoiding both monarchs and other similarly colored butterflies. Other animals that are not distasteful can benefit by evolving similar colors and gaining protection by deceit. This process can lead to elaborate mimicry complexes, in which toxic and non-toxic prey evolve similar appearances. In tropical forests, diverse predators and prey interact year-round (Chapter 14). The wealth of both model and mimetic insects at tropical latitudes poses a problem for bird species such as the New World jacamars that rely on these insects as prey, as they have to distinguish edible prey from very similar-looking inedible species (Box 8.03).

Capture and extraction

For many birds, locating food is a minor challenge compared with capturing the prey once it is found.

Just as wing structure can help birds find prey, it can enhance aerodynamic performance for capturing prey (Chapter 5). For example, *Accipiter* hawks use their short, rounded wings, coupled with a long tail, to maneuver through tight woodland spots to surprise and attack

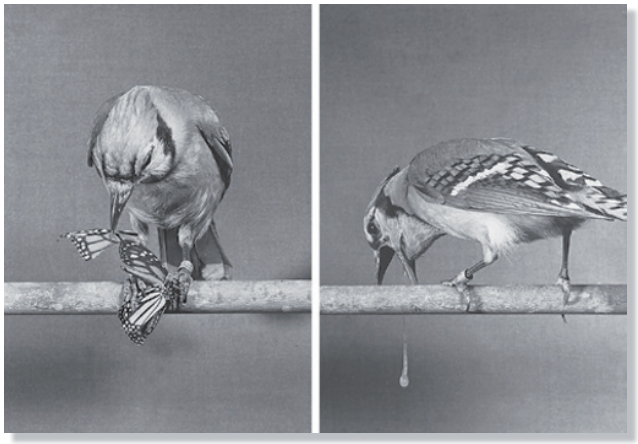


Fig. 8.15 Learning response to noxious prey. A captive Blue Jay (*Cyanocitta cristata*) consumes a toxic monarch butterfly for the first time and vomits in response to its unpalatable alkaloids. After just one bad experience, jays and other birds learn to avoid eating butterflies with the monarch's coloration and pattern. (Photographs by Lincoln P. Brower, Sweet Briar College.)

songbirds. Analogously, various insectivorous birds have converged on a set of traits that facilitate rapid acceleration from rest in order to have the advantage of attacking relatively wary insects by surprise. These traits include small body size; short, rounded wings; short tails that further reduce aerodynamic drag; long legs, probably to help jump at takeoff; and relatively long and flat-tipped beaks to extend reach at the moment of capture. Insectivorous birds with this combination of attributes include the todies of the Caribbean region, the phylogenetically distant tody-flycatchers of Central and South America, and the African Dwarf Kingfisher (*Ispidina lecontei*).

Pouncing birds take advantage of perches in order to scan the surrounding ground for potential prey to attack. An example of such birds' dependence on appropriate perches is illustrated by a study of perch limitation in Florida (USA), where Loggerhead Shrikes (*Lanius ludovicianus*) fly on average 6.5 meters to the ground from fencerows and 9.2 meters from higher perches on palmettos. These search distances were deemed to be the optimal search radius because shorter distances do not provide as much food, and longer distances involve lowered attack success and reduced efficiency. These presumed optimal search distances were used to show that a shortage of available perches was contributing to population decline in this species (Yosef and Grubb 1992, 1994); when high-quality perches were added experimentally to territories, birds decreased their territory size, more birds settled in those areas, and their overall body condition improved.

A predator's body size constrains what it can attack successfully, and most predatory birds select prey substantially smaller than themselves. However, some birds of prey can successfully attack and subdue prey much larger than their

Box 8.03 Baffling butterflies: how jacamars choose prey

Birds living in environments containing diverse, colorful prey face the challenge of how to recognize what is safe to eat. Some prey types are palatable, some are unpalatable, and many are deceitful mimics of the unpalatable. Researchers working in Costa Rica have studied this challenge by looking at the prey avoidance behaviors of Rufous-tailed Jacamars (*Galbula ruficauda*), testing both experienced adults and naïve young birds (Chai and Srygley 1990; Marden and Chai 1991; Chai 1996). As relatively specialized predators on butterflies, these jacamars must choose among the hundreds of butterfly species present in their habitat (Fig. 8.B3.01). How do they learn which butterflies are palatable?

In this series of studies, a single jacamar typically was released into a field cage containing live butterflies of diverse species. The scientists then watched the bird foraging, noting the identity and characteristics of the butterfly species attacked, the order of attack, and the bird's level of success.

Costa Rican butterflies themselves employ two divergent strategies to avoid predation by birds such as jacamars. Butterflies in one group protect themselves by using warning colors to advertise that they taste bad, or by pretending to do so by mimicking the colors and patterns of the unpalatable species. The unpalatable butterflies (and their mimics) also often flaunt their chemical immunity to predation by flying weakly and conspicuously. Butterflies in the second group are generally safe for birds to eat, and they protect themselves by being good fliers, with strong flight muscles and erratic flight activity that help them evade aerial attacks by birds.



Fig. 8.B3.01 Rufous-tailed Jacamars (*Galbula ruficauda*) are selective butterfly predators. Individuals learn which butterflies to avoid, and many can distinguish mimics from true toxic threats—even if they differ only slightly in hue. (Photograph by Flávio Cruvinel Brandão.)

The aviary tests showed that naïve young juvenile jacamars either innately ignore the distasteful butterflies and their mimics, or learn as adults to avoid them on sight after tasting and rejecting them. Learning is involved in recognizing which prey are suitable, with the jacamars appearing to adopt simple rules related to the body size, coloration, and style of flight of their potential butterfly prey species.

This is a not only a story of jacamars eating butterflies, but also a coevolutionary tale of butterflies being selected to improve their defenses and thereby their own survival. Butterflies that are distasteful clearly benefit from their chemical defense, and Rufous-tailed Jacamars quickly learn by tasting these individuals—often without even injuring the butterfly—to avoid these butterflies on sight, without trying to capture them. This avoidance provides an opportunity for imposters, the butterfly mimics, to benefit from a resemblance to distasteful butterflies. The problem that jacamars face is that the more mimics there are flying about, the more of a food resource there is that jacamars could use if they could discern the mimics from the species that actually taste bad. In other words, given the confusing arrays of tropical butterflies, jacamars that can make subtle color discrimination while foraging should be favored. Experiments on this same jacamar species in Bolivia (Langham 2004) reveal that many jacamar individuals can distinguish the distasteful local butterflies from species that are only slightly different in color hue. Recognizing these other morphs as different, jacamars attack them and are thus in a position to outwit the imposters. In contrast, non-specialist birds that occasionally eat butterflies, such as Blue Jays (*Cyanocitta cristata*) and Tropical Kingbirds (*Tyrannus melancholicus*), appear to be incapable of making such fine distinctions, but instead generalize about color patterns, avoiding species with patterns that even remotely resemble the distasteful species with which they have had a bad previous experience.

own body size. For example, Golden Eagles (*Aquila chrysaetos*) in the western USA sometimes chase adult pronghorn antelope, land on their backs, paralyze them, and pull them down. In Spain, these eagles can pull young ibex goats off cliff edges, using gravity and the rocks below to complete the kill.

Birds foraging in open water have special opportunities for capturing prey, but also encounter challenges including



Fig. 8.16 Bills of fish-eating birds. (A) The serrated bill of Red-breasted Mergansers (*Mergus serrator*) grips fish for easy handling. (B) The ridges of Atlantic Puffin (*Fratercula arctica*) bills have backward-pointing spikes, allowing them to hold many small fish at once. (C) American White Pelicans (*Pelecanus erythrorhynchos*) gulp large quantities of water into their enlarged pouches, pushing out excess water and retaining any fish. (D) Great Blue Herons (*Ardea herodias*) use their spear-like bills to pierce or clamp down on prey in shallow water. (A, © Cornell Lab of Ornithology. Photographs by: B, Sandy A. Flint; C, Lawrence I. Finkel; D, Marie Read.)

water's high viscosity, increased pressure and darkness associated with deeper water, and the reflectance and refraction of surface light that obscures objects below. Dabbling ducks avoid most of these problems by feeding on foods at or near the surface. Other birds, such as mergansers and puffins, have serrations on their bills for grabbing slippery fish (Fig. 8.16A, B). American White Pelicans (*Pelecanus erythrorhynchos*) scoop up fish from just below the surface along with the surrounding water (Fig. 8.16C), and then eject the water while sitting at the surface, leaving the fish trapped in the extendable pouch below their lower mandible. Herons use their spear-like bills to stab prey using a sit-and-wait strategy. They can also clamp down and use their bills as tongs to maneuver prey items into the most effective position before gulping them down in one seamless motion (Fig. 8.16D). Pied Kingfishers (*Ceryle rudis*) of Africa have wings adapted for hovering, which allow them to hunt far from shore without trees or other high perches from which to detect fish. Some pelagic birds of the southern oceans, such as the White-faced Storm-Petrel (*Pelagodroma marina*), feed far out at sea by facing into the strong winds and using rounded, outstretched wings; long, dangling legs that seem to walk on the water; and a small beak to pick tiny items such as crustacean plankton from the surface. Frigatebirds snatch flying fish and squid from the water surface during forward motion, often by adeptly tipping their heads back so that their long beaks stay in contact long enough to secure their prey. Black Skimmers (*Rynchops niger*) fly just above calm water, allowing their lower mandible to skim through the water; when they touch a fish, they snap their mandible shut, pinning the prey against the upper mandible (Fig. 8.17). Black Skimmers frequently cruise back through the ripples created by their first flight across water to snatch fish attracted to the disturbance.

Many seabirds plunge-dive to capture fish at great depths. Boobies and gannets are adapted to dive from tens of meters in the air, achieving water-entry speeds up to 95 kilometers per hour and dives as deep as 30 meters. Just before entering the water, they pull their wings back behind their streamlined bodies (Fig. 8.18). When diving seabirds such as gannets forage for fish they also have to overcome the physical properties of light reflection and refraction at the water surface. Because light reflected off a fish and into the air is refracted at an angle, to a flying predatory bird the fish appears to be in a different location than it actually is. Diving seabirds appear to learn from experience how to take into account the challenge of light refraction in determining where to dive.

Birds that actively pursue fish below the water surface must overcome the simultaneous problems of buoyancy and viscosity (resistance to movement). Solutions to both of these problems involve trade-offs with aerial flight ability, because the very adaptations that facilitate efficient flapping flight in air—the reduced body density from hollow bones and large wings—increase buoyancy and drag

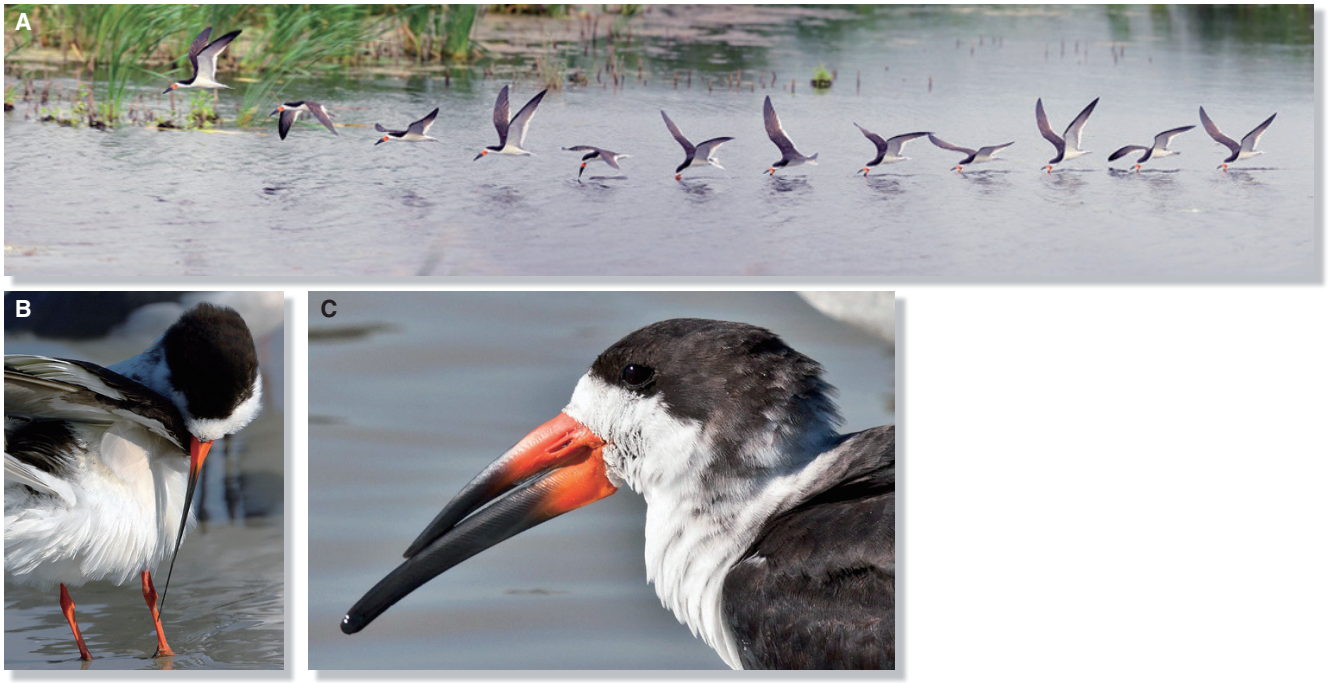


Fig. 8.17 Specialized bill and foraging strategy of the Black Skimmer (*Rynchops niger*). (A) This species captures fish by efficiently skimming the water surface with its lower mandible. (B) A dorsal–ventral view of its extremely laterally compressed bill. (C) In lateral view, the lower mandible is visibly longer than the upper, providing more surface area with which to contact fish near the water surface. (Photographs by: A, Tony Mills, www.photoartbytonymills.com; B, Dane G. Adams; C, © Laura L. Erickson.)



Fig. 8.18 Plunge-diving. To hunt, Blue-footed Boobies (*Sula nebouxii*) fly high into the air before plunging into the ocean, achieving great speeds both above and below water. Note that individuals near the surface have folded their wings tightly, giving their bodies a streamlined, torpedo-like shape that decreases drag upon water entry. (Photograph © Frans Lanting, www.lanting.com.)

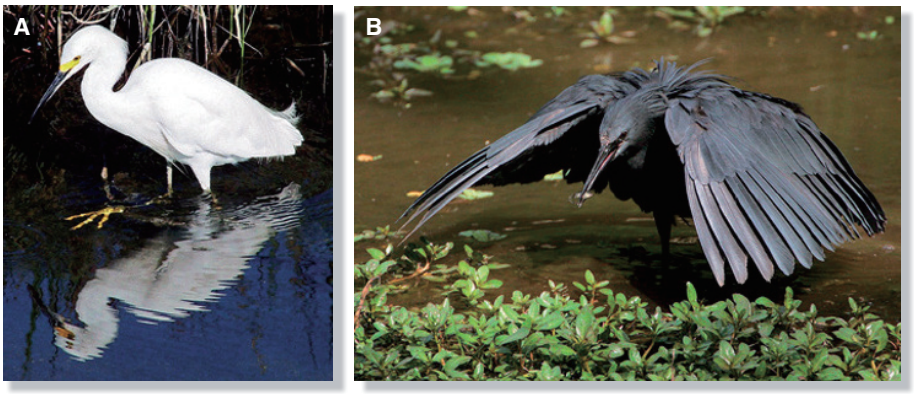


Fig. 8.19 Egret foraging strategies. (A) Snowy Egrets (*Egretta thula*) use their bright yellow feet to spot silhouettes of their prey in shallow water. (B) Black Herons (*Egretta ardesiaca*) outstretch their wings while foraging to disguise their shadow and reduce surface reflection. This technique, sometimes called canopy feeding, also tricks fish that seek shade for protection. (Photographs by: A, Hugh Ryono, Aquarium of the Pacific; B, Steve Garvie, https://en.wikipedia.org/wiki/File:Flickr_-_Rainbirder_-_Black_Egret_%28Egretta_ardesiaca%29.jpg. CC-BY-2.0.)

when birds are submerged. Thus, a variety of birds dive successfully via adaptations that sacrifice some or all of their flight ability. At one end of this spectrum are anhingas and cormorants, which fly well and dive to pursue fish in relatively shallow water using their long, snake-like necks. These birds have relatively dense bones but their large wings and tails help them retain a strong ability to fly. Cormorants and anhingas reduce their buoyancy by wetting their flight feathers; these must be dried out after a dive, and these birds are often observed with their wings outstretched in the sun (Chapter 4). Loons and grebes use webbed or fringed feet for rear propulsion, and also have heavy bones. Trade-offs are implicit in all compromises, and because loons' wings are relatively small for their body size, they experience difficulty taking off in flight from the water surface. The struggle sometimes causes loons to patter across a lake's surface for hundreds of meters while paddling with both feet and wings to gain sufficient take-off speed. Alcids such as auks, murres, and guillemots are even more specialized divers; they reach depths of more than 200 meters, stay down for several minutes at a time, swallow prey underwater, and propel themselves by paddling with their wings. Alcids have sacrificed efficient flight to dive well, and species such as guillemots must flap their wings vigorously and continuously to stay aloft—an energetic cost. Penguins are the most specialized of all diving birds: their wings are highly modified into efficient paddles that preclude flight altogether. Emperor Penguins (*Aptenodytes forsteri*) are pre-eminent divers even among penguins and can dive to a depth of 535 meters and remain underwater for 18 minutes. Their streamlined shape, heavy bones, and ability to reduce their metabolic rate (and thus conserve oxygen; Chapter 7) help them accomplish these underwater feats.

Birds that feed in shallow water also are well adapted for detecting and capturing prey. To reach aquatic invertebrates, dippers counteract the buoyancy from air bubbles trapped in their feathers by gripping the bottom of fast-flowing streams with their large feet and walking underwater. Herons and egrets fish from above, stalking shallow-water prey on long legs and using various feeding tactics such as sit-and-wait foraging. These birds also use their feet in a variety of ways to assist feeding, such as stirring up bottom muck to reveal invertebrates. The brightly colored feet of Snowy Egrets (*Egretta thula*) provide a contrasting backdrop that silhouettes and exposes their prey (Fig. 8.19A). Some waders like the Reddish Egret (*Egretta rufescens*) of the Americas and the Black Heron (*Egretta ardesiaca*) (Fig. 8.19B) of Africa use shade from their own outstretched wings to overcome the problem of light reflected from the water surface. This behavior is called canopy feeding, and might also attract fish that tend to hide in shade and shallow water.

An important challenge in capturing prey from water involves surface tension—the smaller the prey, the greater the pull. Some shorebirds that feed in shallow water, such as phalaropes, use the forces of surface tension to extract tiny invertebrates trapped in rows of water droplets and transport them up their beak (Rubega and Obst 1993). Manu Prakash and colleagues (2008) showed how these birds can vary the surface tension of the droplets by alternately opening and closing their beak, drawing the droplets up toward their mouth.

The problem of extracting prey from harder, protective substrates such as soil, trees, bones, and shells provides a diverse set of opportunities for avian feeding adaptations. For example, Oriental Honey-buzzards (*Pernis ptilorhynchus*) extract wasp grubs with a straightened claw while a well-feathered face protects them from stings. Snail Kites (*Rostrhamus sociabilis*) have long, decurved upper mandibles, an adaptation for extracting mollusks from their shells (as their name implies). A few species of birds use tools to



Fig. 8.20 Foraging extraction tool. Woodpecker Finches (*Camarhynchus pallidus*) use small twigs or spines to extract grubs from decaying wood. These birds carefully choose twigs depending on the dimension of the cavity and may reuse a preferred tool several times. (Photograph by Susan B. Wright.)

extract prey from tough substrates. The Woodpecker Finch (*Camarhynchus pallidus*) of the Galápagos Archipelago uses cactus thorns or twigs to pry insect larvae and other arthropods from holes and crevices in dead wood or mossy tangles (Fig. 8.20). Carrion Crows (*Corvus corone*) in Sendai City, Japan turn automobiles into nutcrackers, swooping down when stoplights at busy intersections are red to deposit an intact walnut or to harvest a cracked one. Under more natural settings, Northwestern Crows (*Corvus caurinus*) in Washington State (USA) drop shellfish onto rocks, whereas Egyptian Vultures (*Neophron percnopterus*) drop rocks to break open ostrich eggs (Adams-Hunt and Jacobs 2007; Bluff et al. 2007). New Caledonian Crows (*Corvus moneduloides*) demonstrate even more sophisticated cognitive abilities in the variety of tools they select and manufacture (Box 8.04).

Birds' beaks often have conspicuous adaptations for capturing foods. Shorebirds feed on a wide variety of food types in water, soil, mud, and sand. Their beaks correspondingly differ in their stoutness, length, curvature, and other features (Fig. 8.21) according to each species' probing method and foraging habitat.

Many shorebirds have a remarkable ability to seize and extract invertebrates with their beaks. Some can separate their bill tips (while the rest of the bill remains closed) like tweezers, an ability called **rhynchokinesis**. A variety of shorebirds have recently been shown to use rhynchokinesis to capture and transport small prey in both soil and open water (Estrella and Masero 2007) (Fig. 8.22). Other birds use cranial kinesis, defined as the movement of one component of the skull relative to another (Chapter 6). One of the most unusual cases involves hummingbirds, for although they are thought to feed largely on nectar, many hummingbirds also feed extensively on arthropods for added protein. Hummingbirds take prey in flight by flexing their upper beak upwards (via rhynchokinesis) and their lower

Rhynchokinesis: the ability of some birds to independently move or open the upper tip of a long bill, most often seen in birds that feed by probing in soil or mud.

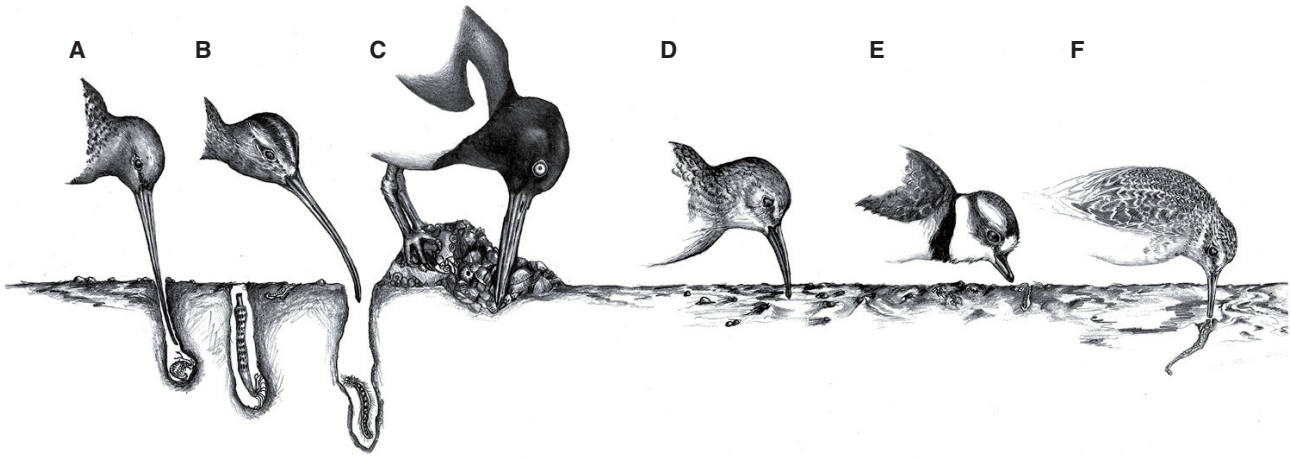


Fig. 8.21 Resource partitioning and bill variation. Shorebirds have bills adapted to access prey within specific substrate types and depths. (A) Marbled Godwits (*Limosa fedoa*) and (B) Whimbrels (*Numenius phaeopus*) use their long bills to forage for large invertebrates that often live far below the surface. The Whimbrel's down-curved bill also fits into the burrows of fiddler crabs, their primary food in the winter. (C) The American Oystercatcher (*Haematopus palliatus*) drills at shellfish attached to rocks with its chisel-shaped bill. (D) Dunlins (*Calidris alpina*) forage on coastal mudflats and sandbars via methodical probing, often compared to the motion of a sewing machine. (E) Semipalmated Plovers (*Charadrius semipalmatus*) hunt by sight on wet substrates, quickly snatching marine invertebrates and crustaceans with their small, blunt bills. (F) Least Sandpipers (*Calidris minutilla*) forage with their short, sharp bills by rapidly pecking the surface of wet substrates and/or quickly probing into mud. (© Cornell Lab of Ornithology.)

Box 8.04 Tool use by New Caledonian Crows

New Caledonian Crows (*Corvus moneduloides*) hold the distinction of being the pre-eminent tool users among birds. When foraging, these birds employ a variety of intelligent strategies, dropping hard nuts on rocks from particular perches and manufacturing at least three different types of tools, including straight tools made from twigs and leaf stems (Fig. 8.B4.01), hooked tools made from twigs or vines, and jagged tools torn from leaves. For example, the crows use small harpoon-like tools to remove beetle grubs from dead tree trunks (Hunt 2000). The bird inserts a twig or grass-stem tool into a beetle burrow and harasses the prey by poking it with the tool until the grub grabs the tool with its strong mandibles; the bird then pulls it out.

These beetle grubs are obtainable only by tool-using crows, but they form an important part of the diet of these birds (Rutz et al. 2010). The grubs are large and nutritious, and the crows can acquire all their daily energy needs from just a few such larvae. The value of this prey type may be an important factor favoring the ability of these birds to use tools.

Young crows are not skilled at these manipulations but improve with practice, in part by following and observing more experienced individuals. However, tool use in New Caledonian Crows is at least partially innate. Naïve crows studied far from their native island in the laboratories at Oxford University (UK) have demonstrated a tendency to pick up and use tools and to select appropriately shaped tools for particular tasks (Bluff et al. 2007). For example, one individual crow repeatedly manufactured and used hook-shaped tools from wires provided in the experiments.

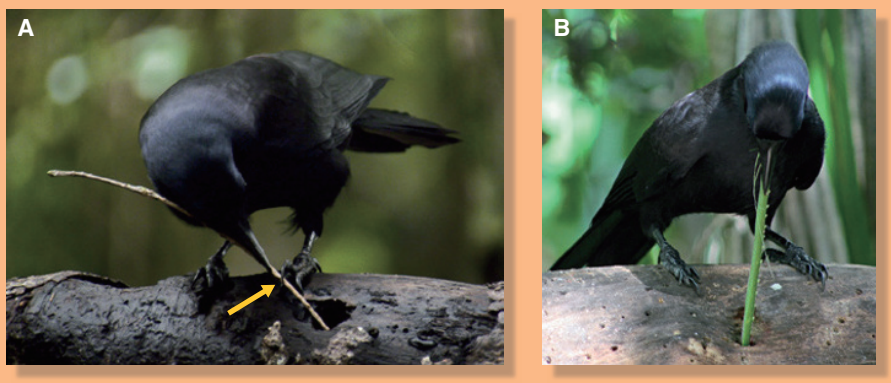


Fig. 8.B4.01 New Caledonian Crows (*Corvus moneduloides*) are pre-eminent tool-users. These crows have been observed using a wide variety of tools to access food. Here individuals have manufactured different types of tools, including (A) straight twig tools, steadied with help from its toe (arrow), and (B) natural or modified jagged tools made from stems or leaves. (Photographs by: A, Brian McClatchy; B, Mick Sibley.)

beak downwards (via cranial kinesis) to increase their fly-catching efficiency (Yanega and Rubega 2004).

Woodpeckers are pre-eminent extractors, and most species are able to chisel into wood to get at carpenter ants, wood-boring insect larvae, and other arthropods. Other woodpeckers, including flickers, use their long, extrusible tongue to forage for ants and other insects in subterranean tunnels (Fig. 8.23). The highly specialized Campo Flicker (*Colaptes campestris*) of southern South America feasts primarily on termites from large terrestrial mounds, which it extracts delicately using its tongue.

Some birds use beaks and tongues in tandem to extract food efficiently from various substrates (Fig. 8.24). For example, the Eurasian Nutcracker (*Nucifraga caryocatactes*) has an unusual bifurcated tongue that is a specialized adaptation for both prying open conifer cones to extract their seeds and for manipulating those seeds. The tongues of ducks and geese are often fringed with comb-like structures for straining small food items from water. Birds including sapsuckers and lorikeets have adaptations for nectar absorption, such as brush- or feather-like tongues, to increase the surface area for nectar uptake. Woodpeckers have long, narrow tongues with barbs at the ends to extract insects from deep within wood cavities after drilling into the cavities to get closer access. Flamingos have highly specialized beaks and tongues to filter large quantities of water, extracting planktonic algae and small invertebrates such as insects, mollusks, and crustaceans (Fig. 8.25).

Novel specializations of the beak and tongue in shorebirds like Western Sandpipers (*Calidris mauri*) and Dunlin (*Calidris alpina*) permit them to graze on foods too small to pick up individually (Elner et al. 2005; Mathot et al. 2010). Both of these species feed on biofilm, a thin layer of microbes, their secretions, and other organic matter found at the bottom of shallow, intertidal flats. Denticles, tooth-like structures that line the roof of the maxilla, are a specialized anatomical feature of these birds' beaks that may aid in scraping biofilm from the tongue. The tongue itself traps biofilm in water with microscopic, mucus-covered papillae (bumps) covered with microvilli. The dense bristles fringing and tipping the tongue work to trap biofilm just as the fringed tongues of nectar-feeding birds trap nectar.

The most specialized nectar-feeders, hummingbirds, take nectar feeding one step further. Their tongues are

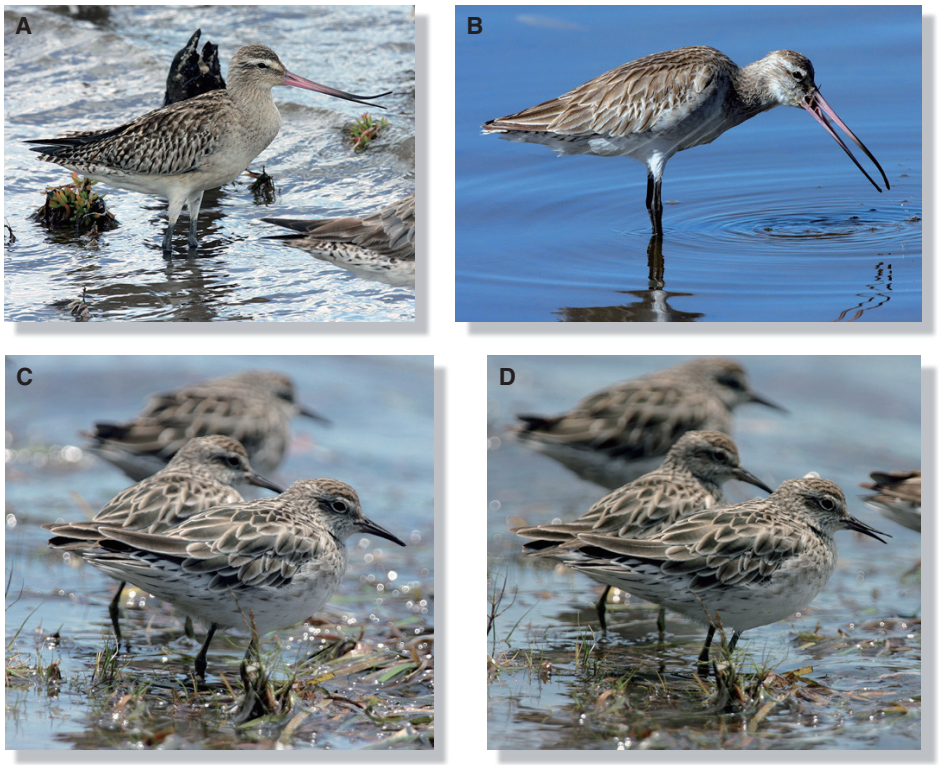


Fig. 8.22 Rhynchokinesis. Bar-tailed Godwits (*Limosa lapponica*) can bend their upper mandibles up (A) and down (B) to aid in food handling and capture. (C) Sharp-tailed Sandpipers (*Calidris acuminata*) can also flex their upper bill tip (D). (Photographs by Robert Inglis.)

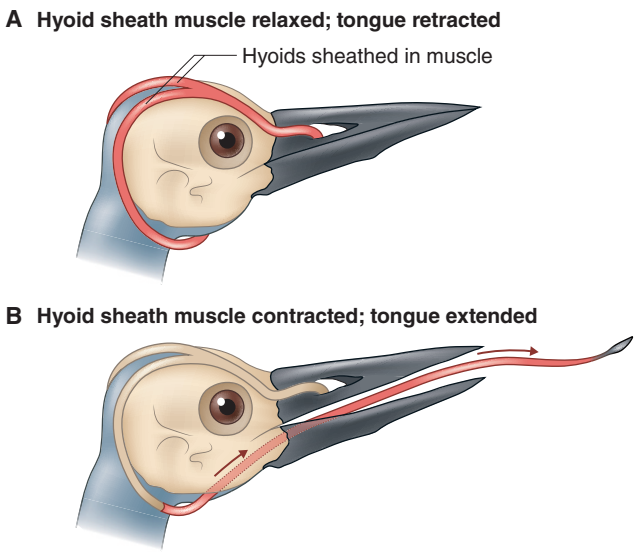


Fig. 8.23 Tongue protrusion in woodpeckers. The hyoid bone serves as an attachment site for muscles along the throat, head, and tongue in all birds. (A) Woodpecker hyoids have two bony extensions called "horns." Sheathed in powerful muscle, these hyoid horns are so long that they wrap around the back of the skull—sometimes into the nostril cavity, as shown in this Northern Flicker (*Colaptes auratus*). (B) To protrude their long tongues, woodpeckers contract the horn muscles, which hug the skull and push the hyoid forward. Equipped with such specialized tongue anatomy, woodpeckers adeptly extract prey from deep cavities. (© Cornell Lab of Ornithology.)

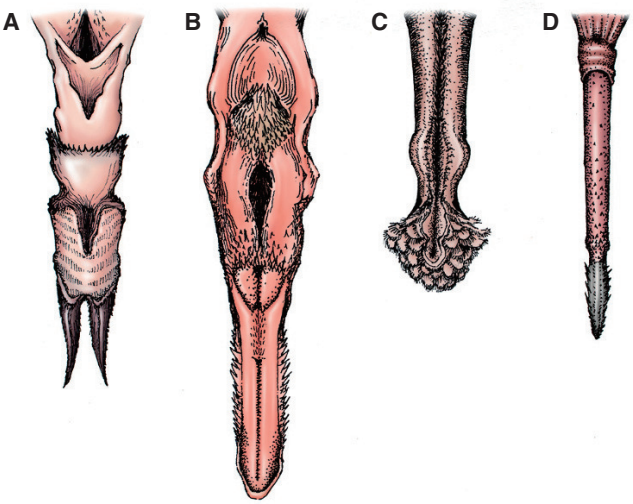


Fig. 8.24 Diversity of specialized bird tongues. (A) White-headed Woodpeckers (*Picoides albolarvatus*) have a bifurcated tongue tip for extracting seeds from pine cones. (B) Canada Geese (*Branta canadensis*) have tongues with spiny projections to help them sift through food in water. (C) Purple-crowned Lorikeets (*Glossopsitta porphyrocephala*) have tongues with specialized brush tips to capture nectar and pollen from flowers. (D) Hairy Woodpeckers (*Picoides villosus*) quickly extend their sticky, barbed tongues deep into excavated holes to impale and extract invertebrate prey. (© Cornell Lab of Ornithology.)

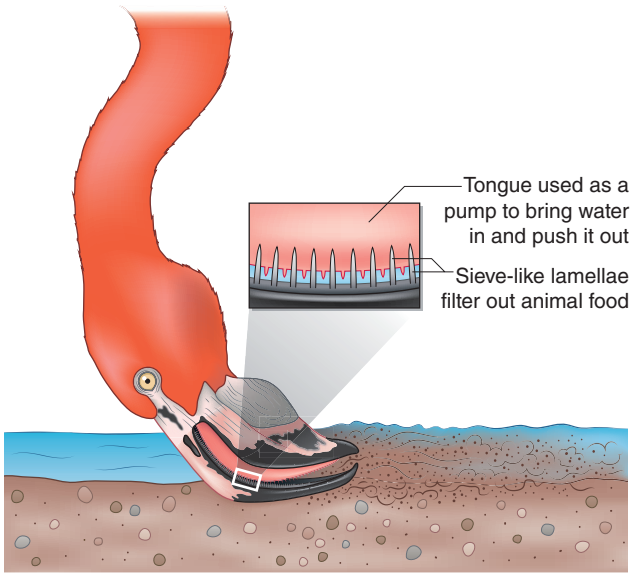


Fig. 8.25 Filter foraging. Equipped with a complex beak–tongue filtration system, Greater Flamingos (*Phoenicopterus roseus*) forage on tiny drifting animals in shallow water. Flamingos suck in muddy water and force it out with their muscular tongues via piston-like pumping. In the process, the water passes through numerous hair-like projections (lamellae) on the upper and lower mandibles, which capture prey like a sieve. (© Cornell Lab of Ornithology.)

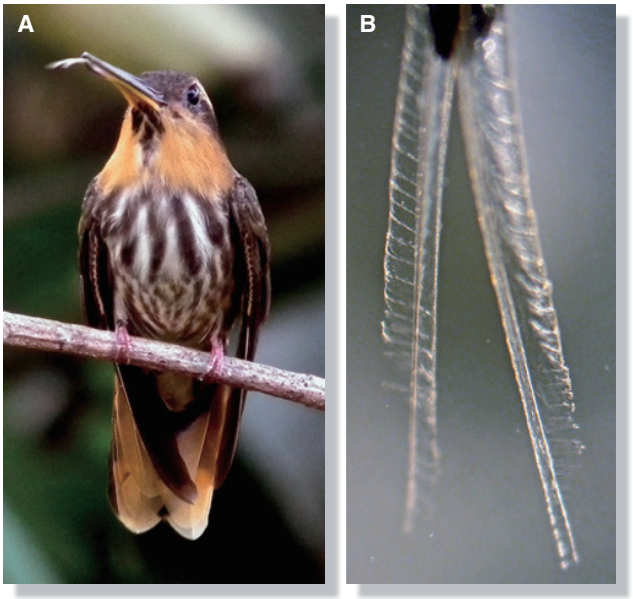


Fig. 8.26 Bifurcated tongue. (A) The tongue of this Saw-billed Hermit (*Ramphodon naevius*) splits into two parts when exiting the bill. (B) A close-up view of its forked tongue reveals tiny hair-like plates (lamellae). As the tongue retracts, the lamellae fold in and funnel captured nectar into the mouth. (Photographs by Alejandro Rico-Guevara.)

forked, tubular-like straws, and have flattish coils to increase the surface area for nectar absorption (Fig. 8.26). Until recently, scientists believed that capillary action sopped up liquids adhering to hummingbirds' delicately bifurcated, curled, and fringe-tipped tongues. Alejandro Rico-Guevara and Margaret Rubega (2011) discovered an alternative mechanism using high-speed (stop–action) videography of hummingbirds feeding through clear artificial tubes. They found that, when inserted into nectar, the curved lamellae (parallel hair-like structures) along the tongue tips of hummingbirds unfurl from their supporting pair of rods, while the elasticity of the rods and the opposing forces of the nectar's surface tension cause the rods themselves to separate (Fig. 8.27). The process of retracting the tongue and its lamellae past the liquid surface into the air causes the lamellae to refurl and trap a tube of nectar into each of the bifurcated tongue tips, which adhere to each other due to surface tension. This mechanism also explains why hummingbirds prefer sugary, viscous nectar, which is not easily extracted using capillary action (Kim et al. 2011). After collecting these nectar tubes, the bird unloads the nectar by squeezing (flattening) its tongue as it extrudes it back through its flattened beak.

Hummingbirds have a variety of other adaptations for exploiting nectar, including their unique wing and shoulder anatomy for hovering flight (Chapter 5), and diverse beak lengths and curvature, adapted to different flower sizes and shapes (Fig. 8.28). Some hummingbirds and other species also engage in **traplining**—visiting the same set of food sources on a regular basis to minimize competition and maximize availability. Research on the Purple-throated Carib (*Eulampis jugularis*) on eastern Caribbean islands (Temeles et al. 2006) illustrates the potential for competition within and among species. In this hummingbird, the relatively larger males outcompete females for the densest patches of flowers, defending these territories and thus forcing females to move around more widely. Experiments support the expectation that females employ traplining and are more efficient than males, minimizing travel costs by visiting flowers at longer intervals, thereby allowing the flowers to accumulate more nectar, and feeding from different flower types. Increasing levels of competition from other birds has the opposite effect: when female Purple-throated Caribs encounter flowers depleted by other hummingbirds (or experimentally depleted by scientists), they return more quickly so as to try and compete pre-emptively.

Traplining: foraging movements in which a bird rotates through a set of discrete food sources; most often applied to individual hummingbirds that visit a set flower patches in an established and repeated sequence, allowing the time in between for the flowers to replenish their nectar.

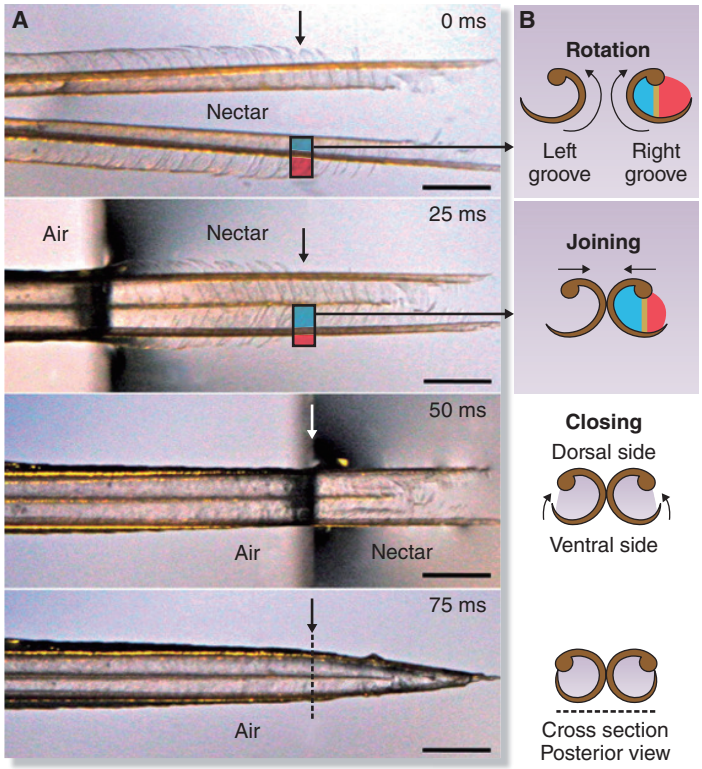


Fig. 8.27 Nectar extraction by a Ruby-throated Hummingbird (*Archilochus colubris*) tongue. (A) Dorsal views show the tongue tips fully immersed in nectar and then extracted from the nectar in stages, from totally immersed (top) at 0 milliseconds (ms), to outside the liquid (bottom). Arrows show the same reference point on the tongue in each image. (B) Cross-sectional diagrams indicate the changes in lamellae position at the reference point over time. From top to bottom: inside rotation of the entire structure (blue and red colors represent portions of visible lamellae along each side of the rod); tongue tips joining; and lamellae closing and closed. In the first two diagrams, the lamellae are inside the nectar; in the last two, the lamellae have been withdrawn but contain nectar trapped inside the grooves. Scale bars = 0.5 mm. (From Rico-Guevara and Rubega 2011. Reproduced with permission from National Academy of Sciences, USA.)

Predatory birds must hold onto and immobilize prey prior to ingestion. To hold onto different prey types, raptors and owls have talons. Other birds have bills that are either hooked (as in raptors, shrikes, ant shrikes, and some puffbirds) or serrated (mergansers and puffins) (Fig. 8.16A, B). Fish-eaters such as cormorants and penguins have backwardly pointing projections on their mandibles to help direct their slippery prey towards their esophagus. Birds such as jacamars and bee-eaters chase aerially fleeing insects and often have long, thin beaks that can close quickly at the tip and reach beyond an insect's fragile wings to secure the prey by its body.

Preparation and ingestion

Once a bird has successfully captured and secured food, processing often is needed to facilitate swallowing or digestion. Mammals use teeth to tear, chew, and grind their food before it enters the gut, but birds do not have teeth. Nonetheless, many birds process food extensively before ingestion and digestion. For example, raptors, vultures, and buzzards use their feet and beaks to dismember prey. Fish-eaters often numb or kill their prey by whacking it against a perch, and they generally swallow fish headfirst to avoid choking on spines that run along the dorsal fins. Insect-eating birds usually swallow their prey headfirst for the same reason.

Most birds other than parrots and raptors simply use their beak to immobilize and prepare food. With only a beak to handle prey, most birds are limited to food types that are small enough to fit through the gape of their mouth unless they can break up or soften larger food items. Good evidence for gape limitation comes from a study of nightjar species that found a correlation between the prey size and the size of the birds' mouths, rather than with the birds' overall body size (Holyoak 2001). As you might expect, the nightjar species with the largest gapes ate the largest insects. Gape size also limits the size of seeds and fruits consumed by many frugivores (Wheelwright 1985) and insectivores (Box 8.02).

In addition to shredding food with a beak and talons or softening it up with the beak, birds have additional ways of processing food. Once food is swallowed, many seed-eaters and some insect-feeders pulverize the food physically within their highly muscular gizzard (Chapter 6). Birds that feed on fruits containing seeds too large to pass through the gut may regurgitate the seeds after separating them from the surrounding fruit pulp, sometimes long after swallowing them. When birds transport viable seeds, the parent plant benefits, and plants have evolved nutritious fruits so that birds will be attracted to find, harvest, and disperse their seeds. For example, the Resplendent Quetzal (*Pharomachrus mocinno*), a spectacular iridescent green member of the Trogon family, plucks fruits of the avocado family while in flight and often regurgitates the large, uneaten seeds some distance from the parent plant. Seed dispersal by birds is an important ecological service in many tropical habitats.

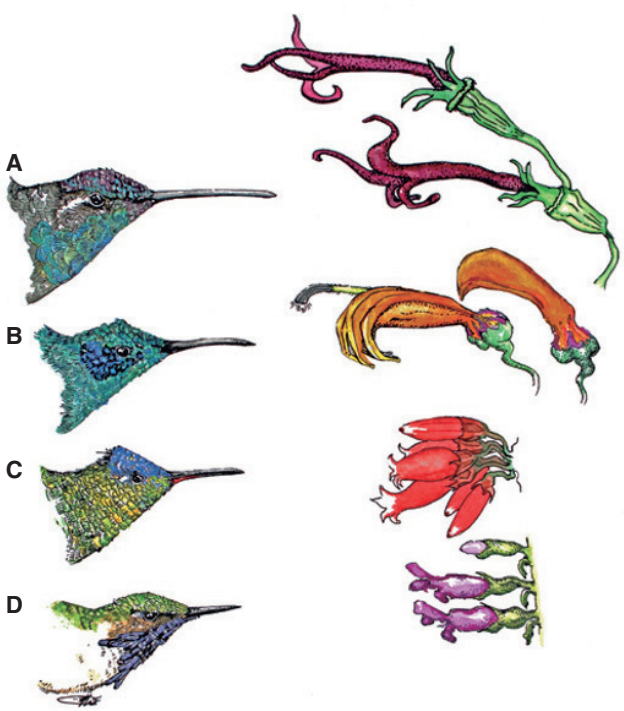


Fig. 8.28 Bill size corresponds to flower shape. The (A) Magnificent Hummingbird (*Eugenes fulgens*), (B) Green Violetear (*Colibri thalassinus*), (C) Fiery-throated Hummingbird (*Panterpe insignis*), and (D) Volcano Hummingbird (*Selasphorus flammula*) coexist in the mountains of Costa Rica, where each species has a bill adapted to different flower sizes and shapes. (© Cornell Lab of Ornithology, adapted from Wolf et al. 1976.)

Birds that feed directly on seeds often must process them by breaking open the seed coat or extracting them from cones or other protective structures. Perhaps the most pre-eminent avian seed-eaters are the blue macaws. The Hyacinth Macaw (*Anodorhynchus hyacinthinus*) of arid parts of Brazil specializes on palm nuts and other seeds with exocarps so hard that humans need sledgehammers to open them. These birds accomplish this feat by using the mechanical advantage from the short lever-arms of their powerful, deep beaks. The heavy-beaked Hawfinch (*Coccothraustes coccothraustes*) of Eurasia uses more than 45 kilograms of force to open cherry and olive stones. Other adept seed-crackers include large-billed species of bullfinches, grosbeaks, and cardinals.

Some birds that specialize on the seeds of conifer trees have evolved specialized morphologies to extract seeds from cones, leading to coevolution between the birds and trees. Some of the most compelling examples of this process come from studies of Clark's Nutcrackers (*Nucifraga columbiana*) and Red Crossbills (*Loxia curvirostra*) (Box 8.05).

Nectar-feeders are similar to seed-eaters in that they must work to extract food from plants. Thus, they have also evolved both mutualistic and parasitic relationships with plants (Chapter 14). Nectarivory has evolved in diverse bird groups along with striking convergences in beak shape. Nectar specialists include the New World hummingbirds, the African and Asian sunbirds, different groups of honeycreepers in Hawaii and Latin America, and the Australasian honeyeaters. Birds in all these groups participate in mutualisms with plants in which the bird is dusted with pollen while extracting nectar, and thereby moves

Box 8.05 Complex coevolution among crossbills and conifers

Birds that depend on conifer seeds have evolved specialized morphologies, often adapted to extract seeds from only one type of conifer cone. Scientists have used this specialization to explore the dynamic coevolution between birds and their food plants. To demonstrate coevolution, one must show both that the prey's (in this case, pines and other conifers) traits have influenced the evolution of the predator's (in this case, the bird) traits, and that in return the predator's traits, such as feeding behavior, have influenced the evolution of the prey's traits.

Red Crossbills (*Loxia curvirostra*) are specialized seed predators adapted to opening conifer cones to obtain the nutritious seeds within. Crossbills obtain seeds by first wedging their beak tips underneath open cone scales, next closing their crossed bill tips with powerful muscles and twisting the beak to separate the scale from the cone, and finally husking the seed using grooves in the palate of the upper mandible. Craig Benkman and colleagues have meticulously studied the coevolution of crossbills with conifers (Benkman 1993, 1999; Benkman et al. 2001, 2003), first to understand how the trees have influenced the birds. Particular conifer species provide the critical resources on which different Red Crossbill morphs are specialized; each of these conifer species produces cone crops reliably every year, and retain their seeds into late winter and spring when food is critical to the crossbills' survival and reproduction. These conifers also hold the seeds tightly enough with tough cone scales that generalist seed-eaters such as Pine Siskins (*Spinus pinus*) cannot extract the seeds. Each crossbill morph has evolved a bill size and shape that is suited to opening the cones and/or husking the seeds from a particular type of conifer (Fig. 8.B5.01). Moreover,

Continued



Fig. 8.B5.01 Red Crossbills (*Loxia curvirostra*) and cone specialization. Two (of many) examples of distinct crossbill types and the conifer species cones they prefer: (A) has a beak shape that is particularly adapted for opening ponderosa pine cones and (B) expertly opens western hemlock cones. (Photographs by Craig Benkman.)



Fig. 8.B5.02 The coevolution of Red Crossbills (*Loxia curvirostra*) and red squirrels. In areas with plentiful red squirrels, pines respond to seed predation by the squirrels by producing fewer and smaller seeds with wider and stronger cone scales. This selection gradient benefits Red Crossbills, which can access seeds faster in squirrel-adapted cones compared with cones in areas without red squirrels. (Photograph by Dewhurst Donna, US Fish and Wildlife Service.)

the efficiency of the different morphs declines steeply when feeding on other types of conifer cones (Benkman 1993). One link between morphology and fitness comes from survival estimates in one crossbill population, in which the birds with beak depths most efficient at foraging on lodgepole pine also experienced the greatest annual survival (Benkman et al. 2003).

What about the other half of crossbill–pine coevolution, the evolutionary impact of the birds on the pines? The more seeds the birds harvest from a tree, the lower the tree's fitness, and thus trees with traits that prevent easy seed harvesting should survive best and proliferate. Benkman and colleagues compared traits of lodgepole pine cones fed on by crossbills with nearby trees of the same species that the birds avoided and showed that the fittest trees, those that had crossbill-resistant cones, had larger, thicker scales that overlapped each other more.

However, both geography and other animals also influence the feeding success of crossbills. The well-adapted morphs of Red Crossbills coevolving with lodgepole pines described above occur on only a few small mountains, isolated from the main Rocky Mountain chain, in the South Hills of Idaho (USA). In the Rocky Mountains themselves, red squirrels also are important predators on lodgepole pine seeds. Red squirrels use their teeth to snip entire cones for storage and later extraction of the seeds and tend to strip their preferred lodgepole trees of cones, thus exerting a far stronger selective force on the pines than do crossbills (Fig. 8.B5.02). Where red squirrels have long been feeding on lodgepole pines, trees with fewer and smaller seeds and with wider and stronger cone scales at the base of the cone are favored. In response, the Red Crossbills' beak morphology is influenced by how lodgepole pines fight back against the squirrels: the local Red Crossbills' beaks are optimal for feeding on these squirrel-modified cones. For example, Rocky Mountain Red Crossbills are able to extract a seed in an average of 5 seconds when feeding on Rocky Mountain lodgepole cones, versus 7 seconds when feeding on South Hills cones. In contrast, South Hills Red Crossbills require 6 seconds per seed when feeding on South Hills cones, versus 13 seconds on Rocky Mountain cones. Each type of crossbill clearly does better when feeding on the type of cone to which its bill is best suited. One lesson here is that birds are not always the drivers in their interaction with the organisms they feed on, and thus understanding the adaptations of other key players in the environment (such as red squirrels in this case) helps us understand how birds are themselves adapted to feed.

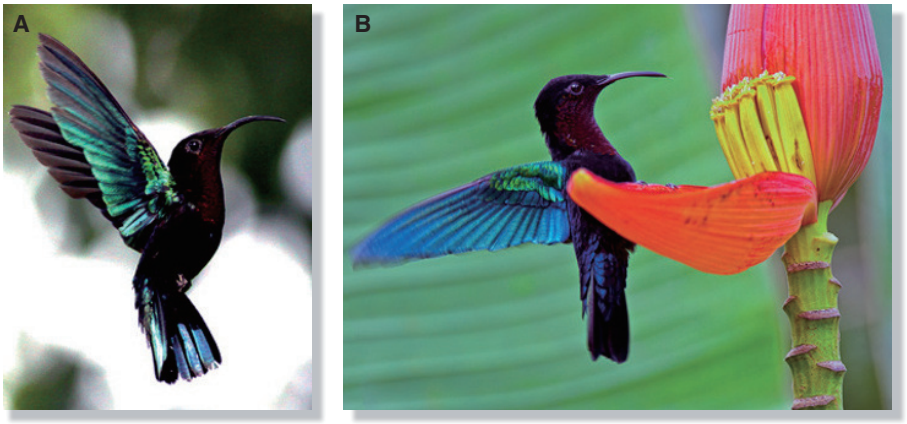


Fig. 8.29 Sexual dimorphism in bill anatomy. (A) Female Purple-throated Caribs (*Eulampis jugularis*) have longer, more curved bills compared with (B) males. Each sex is most efficient at extracting nectar from flowers that match its bill shape, and both employ different strategies to guard or search for flowers. (Photographs by: A, Stephen Daly; B, Fred D. Canter.)

pollen among flowers. These birds often are highly specialized in their choice of flowers. Plants have adapted to their avian pollinators in various ways. For example, New World plants pollinated by hovering hummingbirds often have flowers that are inaccessible to other birds, whereas Old World plants pollinated by sunbirds often have structures for the birds to perch on while feeding.

A wealth of evidence supports the idea that the beaks of hummingbirds are adapted to flower length and shape, based primarily on correlations between the two—for example, the tendency for short-beaked hummingbirds to visit short flowers. The longer term evolutionary question is whether flower length and shape actually cause specialized bird morphology by selectively restricting access to nectar rewards. This requires researching whether hummingbirds with different bill anatomy are more or less efficient when foraging for nectar on different flower species. A recent study tested the impact of different flowers on the Purple-throated Carib (*Eulampis jugularis*) (Temeles et al. 2009). These hummingbirds are **sexually dimorphic**, meaning that females and males have different morphology. In this case females have longer, more curved beaks than males (Fig. 8.29), and the sexes tend to feed on different flower types. By experimenting with both real and artificial flowers, these researchers showed that when females fed on long, curved flowers, they extracted nectar more efficiently than males. Males, on the other hand, used their shorter, straighter beaks more efficiently on short artificial flowers, particularly while hovering. This study provides a clear example of a trade-off in which one adaptation outcompetes another under one set of circumstances, and vice versa.

Sexual dimorphism: a situation in which males and females of the same species differ in aspects of their size, color, or form.



Fig. 8.30 Tree sap foraging. Yellow-bellied Sapsuckers (*Sphyrapicus varius*) drill and maintain a series of holes to access tree sap. Other species, like warblers and hummingbirds, have been known to visit these holes for the sugar and the insects attracted to it. (Photograph by Cameron Rognan.)

Although we typically associate nectar feeding with birds like hummingbirds that extract nectar from tubular flowers, birds have found other solutions for accessing nectar. For example, a group of neotropical tanagers called flowerpiercers are nectar robbers that poke a hole through the flower base to draw off nectar without helping the flower to transport pollen. Some hummingbirds with short, pointed bills do the same thing—so one cannot assume that hummingbirds with short bills feed only on shallow flowers. Sapsuckers in North America feed on sweet plant fluids in a different way: they drill neat rows of holes in tree bark to stimulate oozing sap (Fig. 8.30). It is still debated whether the sapsuckers feed primarily on the plant sap itself or on the insects that it attracts.

Ruby-throated Hummingbirds (*Archilochus colubris*) are able to migrate north in spring into areas in eastern North America before flowers are available because they parasitize both the sap and insects attracted to the holes made by Yellow-bellied Sapsuckers (*Sphyrapicus varius*). The hummingbirds even follow the hole-makers through the woods to learn the locations of the sapsuckers' feeding areas (Flaspohler and Grosshuesch 1996).

Finally, some birds process the foods they catch or find, and **cache** non-perishable seeds or frozen meat for later use. The most general definition of caching is handling food to save it for future use. This behavior usually has three components: deferring the immediate consumption of the food item; handling so as to deter its use by most other animals; and the diverse behaviors necessary to select, prepare, transport, place, conceal, and later retrieve the food (Vander Wall 1990). Birds that cache obviously benefit from having access to foods long after they were originally available. The caching of seeds can also benefit plants via the dispersal of occasional seeds that the birds never retrieve. Caching, hoarding, or storing food (all are synonyms) are beneficial enough to birds that this behavior has evolved in at least 15 bird families within four orders. Hoarding species can store food items either individually (scatter hoarders) or grouped (larder hoarders).

Two basic questions are important to understand hoarding behavior: (1) why is it beneficial; and (2) how do birds manage it? One of the most obvious advantages of hoarding is the ability to control the distribution of food in time and space, and accordingly most hoarding behavior follows natural rhythms: diurnal, tidal, or seasonal. Hoarding can reduce a bird's vulnerability to environmental fluctuations in food and reduce its vulnerability to worsening weather conditions that impede foraging. Some birds hide food early in the morning for use later in the day, hedging bets against inclement weather and making sure they have enough energy to survive cold temperatures during a long night. For example, New Zealand Robins (*Petroica australis*) store earthworms and insects in tree branch crotches and stump ends (Powlesland 1980). Other birds cache when food is only temporarily available, such as Northwestern Crows (*Corvus caurinus*) in British Columbia that cache shellfish during low tide to feed on later when the intertidal zone is inundated (James and Verbeek 1984).

Other birds hoard food for much longer periods, as a resource for future survival and reproduction. For example, Clark's Nutcrackers (*Nucifraga columbiana*) and Pinyon Jays (*Gymnorhinus cyanocephalus*) in the Rocky Mountains of North America hoard when pine seeds are abundant in the fall. The thousands of seeds that they cache keep well for months and provide up to 70–100% of their food in winter and early spring (Giuntoli and Mewaldt 1978). These saved food resources allow the birds both to persist in locations that otherwise would be inhospitable and to start breeding far earlier in spring than their potential competitors. Similarly, Eurasian titmice such as Willow Tits (*Poecile montanus*) and Crested Tits (*Lophophanes cristatus*) hoard in the fall. Their stored provender constitutes up to 50% of their diet later in the year when food is scarce and improves their chances of overwinter survival (Haftorn 1954; Jansson et al. 1981).

Some raptors, particularly falcons, may hoard the relatively large food items they catch, and use them weeks or months later. For example, American Kestrels (*Falco sparverius*) may store multiple mice in small trees or grass clumps (Stendell and Waian 1968; Toland 1984). Eleonora's Falcons (*Falco eleonorae*) store migratory songbirds they catch during the prey's fall flights across the Mediterranean Sea in shrubs, and even imprison them live in rock crevices, keeping them fresh (Vaughan 1961; Walter 1979; Qninba et al. 2015). A variety of owls hoard to supplement food both while breeding and during cold periods, times when energetic costs of survival increase and when food keeps well by freezing. Eurasian Pygmy-Owls (*Glaucidium passerinum*), for example, hoard more food during cold winter periods (Solheim 1984). Other predatory birds known for caching prey include the butcherbirds of Australia and New Guinea and the widely distributed shrikes. Many species in both of these groups impale animals—such as small mammals, birds, lizards, and grasshoppers—on thorns or on barbed-wire fences. This impaling behavior may have originated as a way for these birds to handle and anchor prey so that it could be torn and dismembered more easily (Fig. 8.31).

Caching: the behavior of storing food in an often hidden location (a "cache") for later retrieval and consumption.



Fig. 8.31 Impaling prey. Long-tailed Shrikes (*Lanius schach*) and other members of the family Laniidae impale prey on thorns or other sharp objects. Impaled prey is easier to dismember; some shrike species also impale prey as a form of caching. (Photograph by Eddy Lee Kam Pang.)

Box 8.06 Conifer layaway plans: seed-caching corvids

Corvids such as nutcrackers and jays have evolved diverse adaptations for hoarding and retrieving conifer seeds and other nutritious nuts. Many corvid species take advantage of these seasonally abundant crops by hoarding. Probably as a result of strong interspecific competition for pine seeds, the corvids in this seed-caching guild represent different degrees of ecological dependence and evolutionary specialization for food handling and caching (Vander Wall and Balda 1981; Vander Wall 1990; Adams-Hunt and Jacobs 2007). In North America, Clark's Nutcrackers (*Nucifraga columbiana*) and Pinyon Jays (*Gymnorhinus cyanocephalus*) assess seeds by manipulating and weighing them in their beak. Clark's Nutcrackers cache seeds in snow-free areas such as wind-swept ridges, cliff bases, and south-facing slopes; Pinyon Jays cache on the south sides of trees in a communal home range. In one trip to its caching area, a Clark's Nutcracker may transport seeds equivalent to 22% of its own body mass, and Pinyon Jays 16% of its mass. Corresponding morphological adaptations for seed transport include a large sublingual pouch in the nutcracker (Fig. 8.B6.01) and a distended esophagus in the Pinyon Jay. In one season, an individual Clark's Nutcracker may store 20,000–100,000 seeds, compared with the Pinyon Jay's 18,000–21,000.

The advantages of evolving specialized traits for caching and recovering seeds have resulted ultimately from competition for food. Conifer seed crops are highly seasonal in temperate and boreal environments, and individuals of any species that can pre-emptively stow away the bulk of the crop can benefit enormously relative to other individuals. By transporting more seeds per trip and by traveling further from the source trees, Clark's Nutcrackers and Pinyon Jays are able to grab a larger portion of the seed crop and stash it far from the eyes of potential marauders. To put it another way, food caching itself likely evolved as an adaptation to provide more efficient use of seasonal seed resources (Vander Wall 1990), and this adaptation allowed species, especially those that store for months and live at high elevations and latitudes, to exist in otherwise uninhabitable environments. These hoarders essentially have created their own food niche.



Fig. 8.B6.01 Sublingual pouch for seed transport. (A) The Clark's Nutcracker (*Nucifraga columbiana*) is one of two known species with a special seed-transporting morphology, handy for caching large numbers of seeds at one time. (B) Shown here in an X-ray, this species' pouch opens under the tongue and bulges into the throat region when stashed with pine seeds; it can hold up to 150 seeds of whitebark pine. (A, photograph by Steven Dijkshoorn. B, from Vander Wall 1990. Reproduced with permission from University of Chicago Press.)

These birds now use cached items as part of courtship, as supplemental food for other reproductive activities, and for surviving inclement weather. Some desert shrikes in North Africa have adopted an unusual variant of this impaling behavior and similarly cache date-palm fruits that help them survive dry, food-lean summer months (Parrott 1980).

When food is limiting, pre-caching competition provides another compelling advantage for hoarding. Caching food that is only temporarily available—such as a seed crop or a large animal carcass (Box 8.01)—helps keep it away from competitors. A variety of seasonally fruiting pine species with large and wingless seeds are esteemed by diverse corvid species in both the New and Old World temperate latitudes. These species show varying dependence as well as corresponding behavioral, morphological, and spatial cognition adaptations for caching and recovering seeds (Box 8.06). Competition for these seasonally abundant, nutritious, and long-keeping foods can be intense, so some bird species travel long distances to conceal their seed caches. The Gray Jay (*Perisoreus canadensis*) even uses

special salivary gland secretions to form compact food balls containing multiple seeds and fruits that they scatter on conifer foliage and bark (Dow 1965; Vander Wall 1990).

A final advantage of hoarding is to redistribute food for convenience, perhaps minimizing time spent foraging instead of other activities. In New Guinea, for example, male Macgregor's Bowerbirds (*Amblyornis macgregoriae*) store fresh, ripe fruit in shrubs and understory trees near their bowers, thereby increasing the time they can spend in courtship later (Pruett-Jones and Pruett-Jones 1985).

Pulverization and digestion

The final stages of feeding begin when food enters the esophagus from the oral cavity and continue into the processes of digestion. Since every stage of feeding influences what is eaten, physiology and digestion influence diet. Because the fate of foods in the digestive tract is the domain of physiology, this topic is covered in greater detail in Chapters 6 and 7.

One of the most obvious ways birds break down food to make it digestible is to pulverize hard items such as seeds in their gizzard. Since birds do not have molar teeth as mammals do, many birds ingest small stones to aid the strong muscles of their gizzard in grinding food (Chapters 6 and 7). Few birds eat plant leaves, probably because of the low nutritive value relative to birds' high metabolic demands, but the exceptions are informative about the trade-offs involved in specializing on leaves. The Hoatzin (*Opisthocomus hoazin*) of South America has a particularly unusual specialization of its digestive tract, which contains symbiotic microbes that break down the cellulose in leaves via fermentation (Chapters 6 and 7), similar to the rumenary action of cows and other ungulates. The plantcutters (*Phytotoma* species) of South America eat diets comprised of over 90% leaves. They benefit from feeding year-round on a few plant species with relatively high protein to fiber ratios, coupled with special enzyme activity throughout the length of their intestine that helps them digest proteins and sugars (Meynard et al. 1999; Bucher et al. 2003).

When considering feeding choices by frugivorous birds, it is important to recall that the evolutionary goal of fruiting plants is to make fruits attractive to seed-dispersing frugivores while deterring seed-destroying frugivores. Some plants appear to have accomplished this goal by producing compounds that are toxic to seed-destroying frugivores. For example, wild chili peppers use the compound capsaicin, which humans sense as the chili peppers' "heat," to influence which animals consume their fruits, and how long their gut retains the seeds (Tewksbury and Nabhan 2001; Levey et al. 2006; Tewksbury et al. 2008). These pepper plants pack their fruits with capsaicin and relatively high concentrations of oils and proteins. Mammals, which tend to macerate and thus destroy seeds with their molar teeth, can taste capsaicin, but birds lack the molecular receptor that capsaicin binds to, and so do not sense this pungency. Video observations of plants in nature document that mammals avoid eating these peppers, whereas some bird species (including thrushes, thrashers, and flycatchers) consume many. These same bird species are excellent seed dispersers for the plants, defecating the seeds unharmed after gut passage times of several hours.

8.4 Benefits and costs of social foraging

Birds join groups for many purposes, including nesting, roosting, mating, and feeding (Chapter 9). Even in groups formed only for feeding, such as foraging flocks, individuals benefit in the locating, subduing, and handling of prey. The diversity of flock types and circumstances raises questions about when it is advantageous for an individual to join a group. At what group size are diminishing returns from competition reached? Or when does the increased risk of predation outweigh the group benefits? Benefits typically derive from finding food and feeding more successfully and safely. Group feeding also carries unique risks, however, such as having food items stolen by other group members. It is also complex in that it involves decision processes that depend on what other group members do, and involves complex interactions with the prey or other food resources. The diverse benefits and costs of group foraging also depend on whether the other group members belong to the same or different species; whether they are strangers or relatives; whether the resource is permanent, seasonal, or ephemeral; and on the balance between competition versus cooperation.

The simplest types of avian feeding groups are aggregations that form temporarily around resources too abundant, ephemeral, or otherwise difficult for a single individual or mated pair to defend. Dominance hierarchies often form in these kinds of foraging groups. Such hierarchies occur among the individual House Sparrows (*Passer domesticus*) feeding on crumbs in an urban plaza as well as among the diverse bird species visiting a fruiting tree in a tropical forest. Such aggregations may form simply because individuals are attracted to sites where other individuals are foraging.

A well-studied class of avian aggregations involves seabirds diving into a frothing mass of prey below the water surface. Because schooling fish simultaneously try to evade predatory fish attacking from below and seabirds diving from above, they are easier to attack from both directions, creating a mutualism between the different fish-eating groups. Many species of seabirds—including petrels, shearwaters, gulls, terns, boobies and gannets, pelicans, cormorants, and frigatebirds—may join these foraging groups (Fig. 8.32). Some of the raucous screaming at such aggregations is not excitement, but rather fear from birds with prey being pursued by birds who would rather steal than



Fig. 8.32 Mixed-species foraging. Seabirds, such as cormorants and gulls, often forage for fish in mixed-species groups. As group size increases, so does hunting success and overall consumption. (Illustration by N. John Schmitt.)

catch their own food. Acquisition of food by force is known as **kleptoparasitism** (or piracy) and is a characteristic behavior of frigatebirds (so-named because they behave like aerial pirates), which harass boobies and tropicbirds in warm waters. Skuas and jaegers similarly steal food from terns and kittiwakes at higher latitudes (Chapter 14). This behavior is frequent in nature because the parasite is at an advantage while on the chase since it is unencumbered and has an aerodynamic edge over a victim slowed by carrying a heavy prey item. One consequence of kleptoparasitism is that it creates both an incentive for the parasite to join flocks and for the victim to avoid them.

Diverse bird species may aggregate at animal carcasses. These ephemeral banquets of carrion are traditionally provisioned by various large carnivores (Fig. 8.33). Humans supplement natural kills both inadvertently (by road kills and hunting) and deliberately (as in the case of lead-free carcasses provisioned to California Condors (*Gymnogyps californianus*) as part of a conservation effort; Chapter 15). The most species-rich feeding assemblages of avian scavengers involve eight or more species of African vultures in places where carcasses are continually generated by large mammalian carnivores such as lions. The scavenging birds typically arrive within hours of a kill, locating it from cues such as the presence of hyenas or other scavenging birds. Studies have documented that larger bodied species such as White-headed (*Trigonoceps occipitalis*) and Lappet-faced (*Torgos tracheliotos*) Vultures arrive first, because their larger and stronger beaks are capable of tearing through skin to get at the meat (Kruuk 1967; Houston 1975). These two larger African species also have relatively long necks that can reach deep into carcass holes and orifices, and tongues with tooth-like projections to help rasp meat off the bones. This creates a type of positive interaction between species known as trophic advantage, since smaller species later gain better access to food they can handle (Cortés-Avizanda et al. 2012). In contrast, a study of 639 cheetah kills of various animals in Serengeti National Park, Tanzania (Hunter et al. 2007) found that mammalian scavengers (lions, hyenas, and jackals) generally arrived within half an hour of a kill, but that vulture species did not arrive in a standard order. The arrival times of the vultures in this area may not have been distinguished by species because the abundant mammalian scavengers opened the carcasses quickly enough to make food promptly accessible to vultures of all sizes.

These and the many other avian feeding aggregations illustrate the benefits and costs of foraging in groups, especially competition within and among species. Competition within species contributes to broadening diets (Box 8.01). Competition among species leads to niche partitioning (Chapter 14), illustrated by the various depths different seabirds dive for prey, the existence of birds that catch their own prey and those that kleptoparasitize other birds, and carrion-feeders that specialize on different parts of a kill. These niche differences attest to the importance of

Kleptoparasitism: a parasitic interaction in which one bird steals prey or food from the individual who originally obtained it.



Fig. 8.33 Carcass aggregation. Different vulture species often congregate at the same large carcass, provisioned either by carnivores or humans (as a conservation measure). Here, critically endangered White-rumped (*Gyps bengalensis*) and Slender-billed (*Gyps tenuirostris*) Vultures flock to the carcass of a water buffalo in Cambodia. (Photograph by Yula Kapetanakos.)

interspecific competition; indeed, competition both among and within species is common in feeding aggregations simply because the individuals that feed most efficiently (often in groups) have the greatest fitness, and thus tend to survive and reproduce.

Feeding in a group also raises the question: When do the benefits of joining these groups outweigh the costs arising from competition? An experiment involving aggregations of multiple species of carrion-feeders in northern Spain addressed both costs and benefits of feeding on large carcasses (Cortés-Avizanda et al. 2012). Dead livestock carcasses were used to create "vulture restaurants" as part of a vulture conservation initiative. The study compared how birds used these predictable carrion sources versus experimentally reproduced ephemeral (unpredictable) carcasses more similar to those occurring naturally from unpredictable kills by predatory mammals. Although the same number of carrion-feeding bird species visited carcasses of both types, most of the spoils from the predictable treatment went to the largest species, the Eurasian Griffon (*Gyps fulvus*), because these socially dominant birds were easily able to find and exclude other competitor species from the vulture restaurants. At the ephemeral carcasses, by contrast, other carrion-feeder species often discovered the carcass first, and were less likely to be excluded from feeding by Eurasian Griffons. This study clearly showed how the unpredictability of prey occurrence contributes to the coexistence of multiple vulture species in this feeding assemblage.

Joining a flock potentially provides another benefit to the individual by increasing the time it can spend foraging (Chapter 9). At first glance, this benefit might seem counterintuitive, because squabbling and competing with flock members tend to reduce rather than increase foraging time. In many situations, however, birds in flocks are able to share the sentinel duties of watching for predators. Overall, a flock can have many more eyes looking for danger even if each individual bird spends less of its own time being vigilant. The enhanced vigilance benefit of foraging in a group probably is responsible for the various combinations of mixed-species flocks (Chapter 14) that occur in most parts of the world. Although mixed-species foraging flocks differ in their patterns of seasonality and in their social organization, they are widespread because most small birds are vulnerable to attacks by raptors and other predators. At north temperate latitudes, these flocks tend to form in fall when food becomes scarce and the relative benefit of increased surveillance contributes to feeding efficiency. In fall, groups of titmice, nuthatches, creepers, and woodpeckers travel actively together, scanning tree trunks and branches for small arthropods. In many tropical areas, mixed-species flocks form year-round and can comprise dozens of species each searching different substrates for prey.

Some bird species take on specialized roles within flocks, such as sentinels. This is most common in relatively open areas where predators can be scanned for and easily spotted, and an alarm call broadcast. In South America, White-winged Shrike-Tanagers (*Lanio versicolor*) serve as a sentinel species for canopy flocks. However, they occasionally use their alarm calls deceptively to obtain food from other flock members; this species essentially "cries wolf" to signal the need to dive for cover, even though no predator is present, thereby allowing the sentinel to retrieve the morsel (Munn 1986) (Fig. 8.34A). Fork-tailed Drongos (*Dicrurus adsimilis*), songbirds that forage in mixed-species flocks in the Kalahari Desert in Africa, use alarm calls

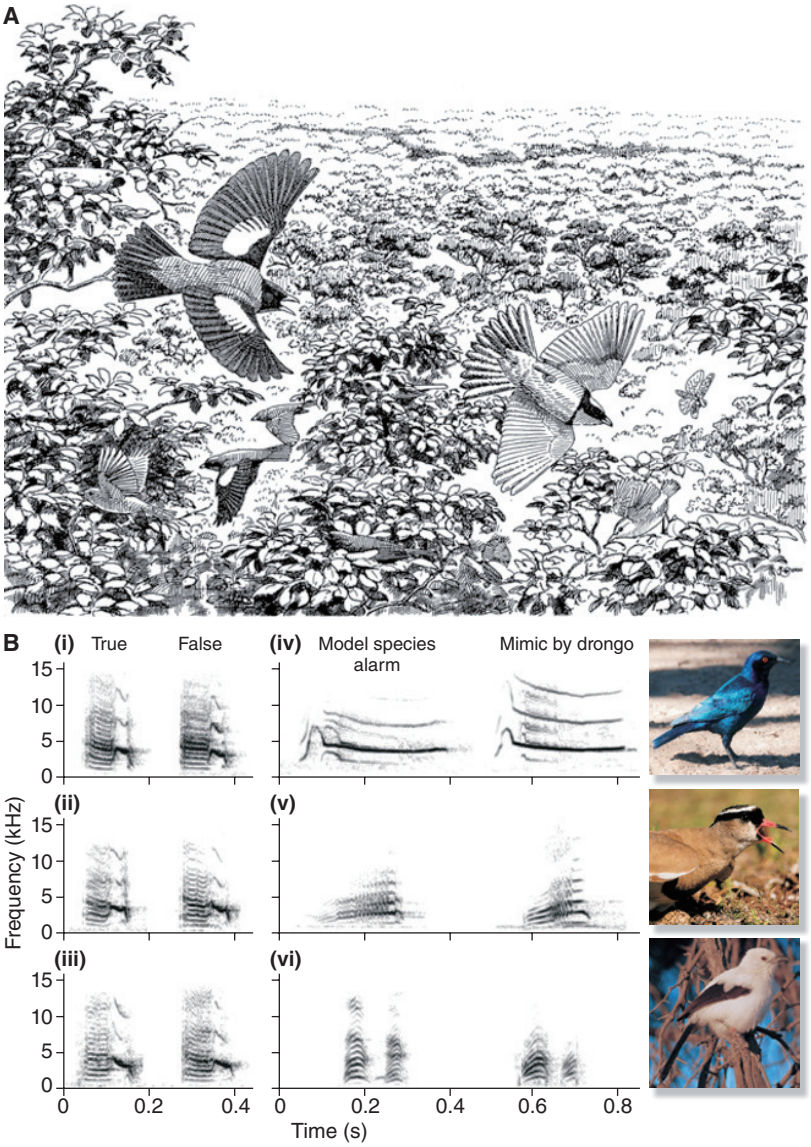


Fig. 8.34 Real and deceptive alarm calls. (A) White-winged Shrike-Tanagers (*Lanio versicolor*) often serve as sentinels in mixed-species flocks, alerting other species to avian predators—although sometimes they also sound false alarms to steal prey found by fleeing flock members. (B) Similarly, Fork-tailed Drongos (*Dicrurus adsimilis*) use drongo-specific "chink" alarm calls to alert other drongos of predators or to deceive conspecifics and steal their prey (three individuals in a, b, and c were recorded using their alarm calls in true and false contexts). Drongos also mimic heterospecific alarm calls that cause foraging birds to flee for cover, abandoning found prey. Drongos have been observed and recorded mimicking heterospecific alarm calls while watching other species forage, for example: d, Asian Glossy Starlings (*Aplonis panayensis*); e, Crowned Lapwing (*Vanellus coronatus*); and f, Southern Pied-Babbler (*Turdoides bicolor*). (A, illustration by N. John Schmitt. B, from Flower 2011. Reproduced with permission from the Royal Society/Tom Flower and Martina Boerner.)

honestly to protect other bird species from predators—as well as dishonestly—but also take deceptive alarm calls one step further. They take advantage of their ability to mimic different target bird species' alarm calls and change them regularly so that their victims do not become habituated to and ignore a particular call type (Flower et al. 2014) (Fig. 8.34B). The drongo can even change the alarm call used on a targeted individual—especially when a particular alarm call type has failed to elicit a prey drop by the victim (Chapter 10).

Sentinel species are often boisterous and provide flock cohesion for other species. The sentinel function of these boisterous species provides an incentive for non-sentinel species to join a flock. This is particularly important for birds like shorebirds and ducks that are vulnerable when feeding with their heads down, or for those like the antwrens in neotropical forests that search for prey hidden within clusters of curled, dead leaves. In a study of Amazonian mixed-species flock assemblages in Peru (Martínez and Zenil 2012), it was found that different types of foragers depend on sentinel benefits. In upland tierra firme habitat, a different *Thamnomanes* antshrike species served as the alarm caller to the one in nearby inundated forests, and different species of flycatchers and dead-leaf foragers were parts of these flocks in the two forest types. As predicted, the more vigilant species in each flock type, the flycatchers, responded more weakly and recovered more quickly in response to experimental playbacks of the antshrikes' alarm calls. The more vigilant flycatchers therefore seemed less reliant on the antshrike alarm calls compared with their more vulnerable flock-mates who were dead-leaf foraging specialists.

When food is abundant enough to sustain a large feeding group but is unpredictable relative to individuals' searching capacity, the ability to locate food using knowledgeable individuals—informants—minimizes the risk of starvation. This idea raises the question of whether some birds form breeding aggregations, such as a heron rookery or booby colony, or other kinds of social groups to gain information about where to feed. This idea is known as the "information center hypothesis." Despite its appeal, this idea has been well documented in only a few cases, including Cliff Swallows (*Petrochelidon pyrrhonota*) (Brown 1986), Common Ravens (*Corvus corax*), and Ocellated Antbirds (*Phaenostictus mcleannani*) (Box 8.07).

Cooperative hunting as a means to improve prey-capture efficiency is yet another benefit of group foraging in birds. This ability is exploited by some raptors and fish-eaters, and by at least one passerine songbird. In the simplest case, members of a mated pair or a small group hunt in a coordinated way to capture more or larger prey than would be possible otherwise, even after food is shared between the hunters. Ravens (the one passerine known to hunt cooperatively) often hunt in tandem (Box 8.01), as do Golden Eagles (*Aquila chrysaetos*) and Aplomado Falcons (*Falco femoralis*). Harris's Hawks (*Parabuteo unicinctus*) in New Mexico hunt in groups of two to six individuals, and capture animals such as jackrabbits that single hawks cannot subdue. For these hawks, hunting efficiency increases directly with hunting group size (Bednarz 1988). One tactic is for one or two group members to penetrate shrubbery cover to flush prey into the open, where other group members are waiting to make the kill. Among fish-eating birds, groups of American White Pelicans (*Pelecanus erythrorhynchos*) may form a line or semicircle of a dozen or more individuals and work to scare fish into shallow water where they can be more easily scooped up (Fig. 8.35).

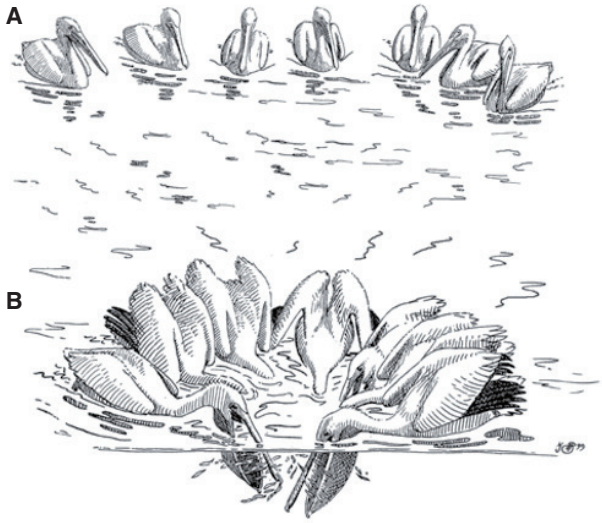


Fig. 8.35 Prey-capture efficiency in groups. (A) When a group of American White Pelicans (*Pelecanus erythrorhynchos*) comes upon a school of fish, they will form a line and/or splash with their wings to corral their prey into shallower water. (B) Sometimes pelicans will form a circle around their prey to increase fishing efficiency under water. (Illustration by N. John Schmitt.)

8.5 Feeding specialization and generalization

Feeding specialization and generalization are two ends of a behavior spectrum in which individuals range, respectively, from being highly selective in what they eat to being nondiscriminating. A hummingbird that feeds from the flowers of only a few plant species is clearly a specialist, and most ravens are clearly generalists (Box 8.01), as is the Cocos Finch (*Pinaroloxias inornata*) (Box 8.08). Understanding a species' specialization is important for interpreting feeding adaptations, because the more specialized a species is, the more likely it is that a particular adaptation is evolutionarily fine-tuned to help the bird exploit a particular resource. The beaks of crossbills (Box 8.05) and many hummingbirds are good illustrations of specialized morphologies that have evolved to help these species gain access to particular food resources that they could not use otherwise.

Feeding specialization also is important in the context of conservation, because particular food resources can disappear or become less available. Species with specialized diets are dependent on specific, potentially unreliable, resources and so are at higher risk of population decline or extinction (Chapter 15). Specialist feeders are even more vulnerable if their specialization involves evolutionary commitment via adaptations specific to a particular food or foraging substrate. The Ivory-billed Woodpecker (*Campephilus principalis*) of the southeastern USA provides a poignant example of how a specialization that is highly successful under some circumstances can quickly become a liability when conditions change. With their large beaks, these big woodpeckers could chisel into huge dead trees and extract large beetle larvae and other energy-rich invertebrates. Sadly, nearly all old-growth forests within its range in the southern USA were logged between 1850 and 1950. Although much of this area remained forested, the newly regenerating forest offered few of the dead and dying trees required by the Ivory-billed Woodpeckers. The shortage of mature trees precipitated rapid, habitat-induced range contraction and population decline, resulting in the woodpecker's widespread extirpation and ultimate extinction. Meanwhile, the superficially similar Pileated Woodpecker (*Dryocopus pileatus*), which lives in the same habitat but has a far more generalist diet and foraging behavior, remains abundant.

Thus, feeding specialization can be defined more formally as the consistent use and dependency on one or a few

Box 8.07 Avian professionals: Ocellated Antbirds trailing army ants

In Central or South American rainforests, *Eciton burchellii* army ants swarm across the jungle floor in a seething mass of tiny biting marauders, penetrating every nook of ground and low trees (Chapter 14). Few other natural phenomena evoke the ebullience of the neotropics as do these ants and the attendant flocks of birds that churr and jostle for the best feeding sites in pursuit of the arthropods and small vertebrates scurrying to escape the ants. Ant-following flocks comprise up to a dozen or so species of regular ant followers, birds that take at least 50% of their prey by joining these particular flocks. Dozens of other bird species join these flocks regularly, including about 50 species of typical antbirds and ground antbirds, plus a variety of cuckoos, treecreepers, and tanagers.

As army ants raid the forest for anything to munch on, birds take advantage of the food sources they flush up, arranging themselves according to social dominance, with smaller subordinate species further from the leading edge of the spreading ant swarm (Fig. 8.B7.01). For example, in Central America, the obligately ant-following Ocellated Antbird (*Phaenostictus mcleannani*) holds the best foraging location, perching low to the ground horizontally at the very front of the swarm (Fig. 8.B7.02). The smaller, more flexible Bicolored Antbird (*Gymnopithys bicolor*) perches higher above and further from the swarm front along with species such as the Northern Barred Woodcreeper (*Dendrocolaptes sanctithomae*) (which often finds prey fleeing up trees); these species take second pick. Still further

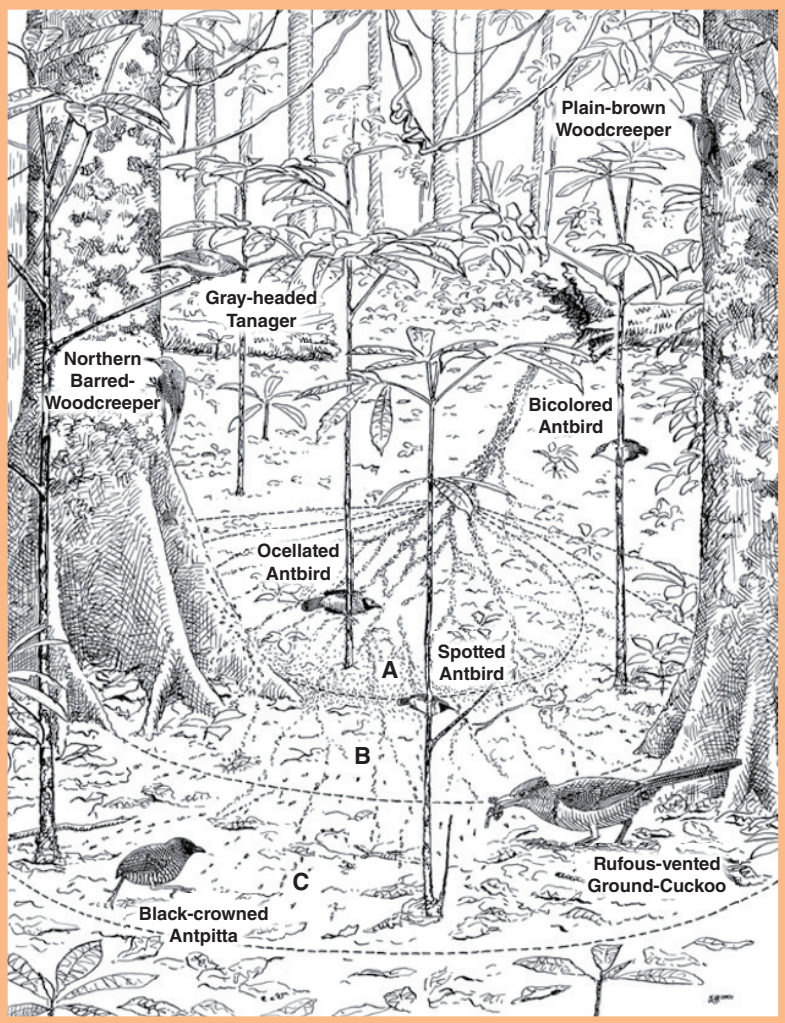


Fig. 8.B7.01 Dominance structure in ant-following foraging flocks. Many bird species follow army ants as they raid the forest floor and nearby vegetation, preying upon insects and small vertebrates flushed by the swarm. These avian ant followers arrange themselves according to social dominance—subordinate, often smaller species situate themselves further from the leading edge (dashed lines) of the spreading ant swarm, in zones B and C. Zone A is the area of highest dominance, directly over the swarm front where the greatest number of insect prey are found. (Illustration by N. John Schmitt.)

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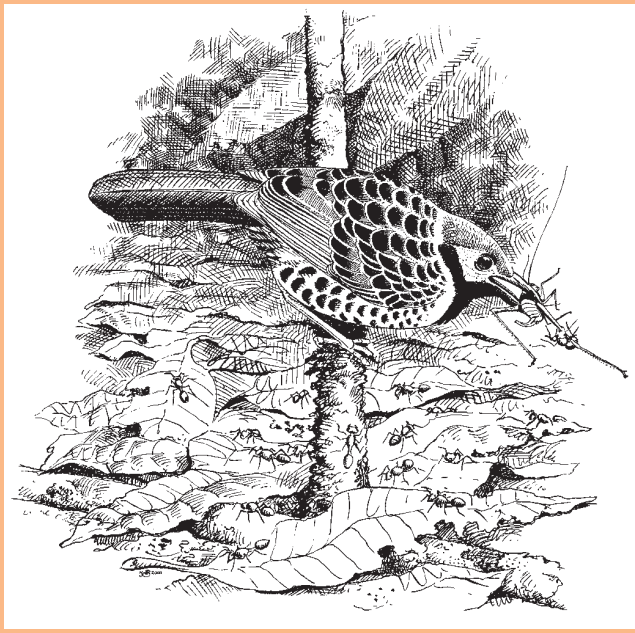


Fig. 8.B7.02 Ocellated Antbird (*Phaenostictus mcleannani*). This species holds the dominant position in some ant-following foraging flocks. These relatively large antbirds perch low to the ground, nearest to the raid (dominance circle A in Fig. 8.B7.01), in order to snatch flushed insects and small reptiles. (Illustration by N. John Schmitt.)

back where prey become more scarce, clinging species like the smaller Spotted Antbird (*Hylophylax naevioides*) and Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) search for any remaining prey. They typically associate with ground species like the Rufous-vented Ground-Cuckoo (*Neomorphus geoffroyi*) and Black-crowned Antpitta (*Pittasoma michleri*) while they fight for remaining prey that have not succumbed to the other birds or ants. A group of Gray-headed Tanagers (*Eucometis penicillata*) is often around, but these birds cannot cling horizontally to saplings as can the antbirds, thus they typically perch higher above the action zone, finding remnant food left by other birds and the ants.

An army-ant-following flock in some areas of Central America may contain 2 to 20 Ocellated Antbirds. Edwin Willis (1973) proposed that Ocellated Antbirds forage in kin groups, helping each other to the spoils. Recently, Costa Rican ecologist Johel Chaves-Campos assessed this idea along with the information center hypothesis by studying this species intensively in Costa Rica (Chaves-Campos and DeWoody 2008; Chaves-Campos et al. 2009; Chaves-Campos 2011). He radio-tracked individual antbirds, genotyped them to distinguish kin from non-kin, and conducted experimental playbacks to army-ant swarms to study individual birds' dominance relationships. He also doggedly pursued antbirds for hundreds of hours, day and night through the forest, to identify roosts and home range areas and to track and observe radio-tagged individuals for entire days to know how many ant swarms they would visit and under what circumstances. His results open a window into how complex the social interactions can be in permanent feeding societies such as army-ant-following birds.

Chaves-Campos discovered, first, that mated antbird pairs feed in home ranges that are often 50 hectares or more in extent—very large even for tropical rainforest birds—and that these home ranges overlap substantially with those of neighboring antbirds. The birds may feed at one to five (typically two) ant swarms daily, but generally stay all day at the first swarm they visit if it is active. Antbird pairs compete for the best foraging locations, and within the core of their own home range the local birds dominate all other Ocellated Antbirds that have commuted in from longer distances. These birds also may forage all day at swarms traveling through their immediate neighbors' core areas. Using song playbacks of neighbors and non-neighbors, Chaves-Campos showed that neighbors tolerate foraging in choice spots only by their own nearest neighbors and that antbirds foraged significantly more successfully on their own core areas or those of their nearest neighbors than elsewhere. Thus Ocellated Antbirds exhibit what behavioral ecologists term a "dear enemy" relationship, one in which neighbors cooperate, greatly increasing their ability to feed on this rich but ephemeral resource. The neighbors, moreover, were rarely close relatives, so that groups of many individual Ocellated Antbirds were not benefiting from the help of neighboring kin.

What is the fate of an Ocellated Antbird when no ant swarm happens to show up on a particular day in either its own or its neighbor's core area? This is when antbirds benefit from the information provided by other birds about more distant swarms; in other words, this is when antbirds benefit from being specialized. Chaves-Campos discovered that birds travel in pairs and small groups when they move among ant swarms. Birds vocalize when leaving a swarm but then travel silently through the rainforest, in single-file. Chaves-Campos also showed that birds traveled in direct paths from one swarm to another, as would be expected if one or more members of the swarm-hopping group knew the new swarm's location in advance of their trip. In short, he observed all the conditions necessary to show that a foraging group of these antbirds contains both informed and uninformed individuals, and that uninformed individuals used this shared information to find a new swarm. Thus, in effect, the feeding bird flocks themselves constitute mobile information centers.

food types because of foraging adaptations evolved specifically for such foods. Conversely, feeding generalization, or opportunism, is the absence of specialization. These seemingly simple definitions are not always easy to apply, and many birds cannot be classified easily. For example, a species can eat a narrow range of foods but do so using diverse behaviors, or conversely can eat a variety of foods but in a consistent, stereotypical way. Another complexity arises from the multiplicity of skills required to feed successfully, including encountering, recognizing, catching, handling, and finally digesting foods (Fig. 8.08): a bird may be specialized in one of these skills but not in others. With these confounders, one needs to define specialization carefully in a particular context.

8.5.1 Conditions favoring diet specialization

No general theory yet links the different components of specialization discussed above. Ecological conditions favoring specialization include a stable environment, competition from other species, and the availability of a distinctive resource.

One assumption underlying most cases of foraging and diet specialization in birds is termed the ecological **principle of allocation**; it holds that the energy or other resources an organism allocates to one aspect of its life history are unavailable for other aspects. In the present context, the more specialized an organism is for one resource, the less efficiently it can exploit other resources. Thus, for a bird to gain efficiency in a particular feeding technique, it generally needs to specialize in that technique, and that specialization decreases its efficiency in other techniques. For example, a thin beak with a forceps-like tip that is well adapted to gleaning small insects efficiently is likely to be incapable of cracking hard seeds, and, conversely, birds with massive bills that easily crack seeds are not likely efficient at gleaning small insects. Trade-offs are inherent to the principle of allocation: skill in one aspect of

Principle of allocation: the assumption of a trade-off in energy and other resources, such that those devoted to one aspect of life history (such as survival) thereby become unavailable for others (such as reproduction).

Box 8.08 Feeding cultures: Cocos Finch foraging specializations

Just as species are adapted to feed differently from each other, individual birds also can specialize. Ultimately, individual specialization probably arises for the same reasons as specialization among species, namely the increased feeding efficiency permitted by relatively predictable food resources. The advantages of individual specialization within a species probably depend on the balance of competitive pressures individuals encounter from other individuals of the same versus other species. When most of the competitors an individual encounters are members of its own species, it often is advantageous to specialize relative to those other individuals. This situation occurs on oceanic islands where the paucity of species allows those present to undergo ecological release (Chapter 13), becoming more abundant by acquiring adaptations to whatever resources are most abundant on the island.

One of the most dramatic cases of learned feeding specialization occurs in the Cocos Finch (*Pinaroloxias inornata*), the only species in the Darwin's finch group found not in the Galápagos Archipelago but instead on the tiny and isolated Cocos Island (Costa Rica) in the tropical eastern Pacific Ocean. The Cocos Finch is one of the most ecologically generalized of all bird species, largely free of interspecific competition because of the dearth of ecologically similar bird species sharing its island. All Cocos Finches have essentially the same "jack of all trades" bill morphology. Yet despite their lack of bill variation, individual Cocos Finches differ in how they feed. Based on many months of close observation of color-banded individuals, Tracey Werner and Thomas Sherry (1987) showed that individual Cocos Finches primarily use only a subset of the feeding behaviors used by all the nearby individuals on the island. Individual finches specialized on feeding by dead-branch gleaning and probing (like woodpeckers), leaf gleaning (like warblers), leaf-mine and nectar feeding (like honeycreepers), or flower feeding (like sunbirds) (Fig. 8.B8.01). Some individual finches even specialized on probing within dead leaves for cockroaches, crickets, and other juicy insects, much as some species of tropical New World antwrens do (Chapter 13).

Cocos Finches maintained their individual specializations even while moving through the same tree within minutes of each other, so the individual birds clearly were not feeding opportunistically on whatever food was present at a given time. Their specializations were not related to sex or age or to the slight morphological variation among individuals. Regular observations of juvenile finches following

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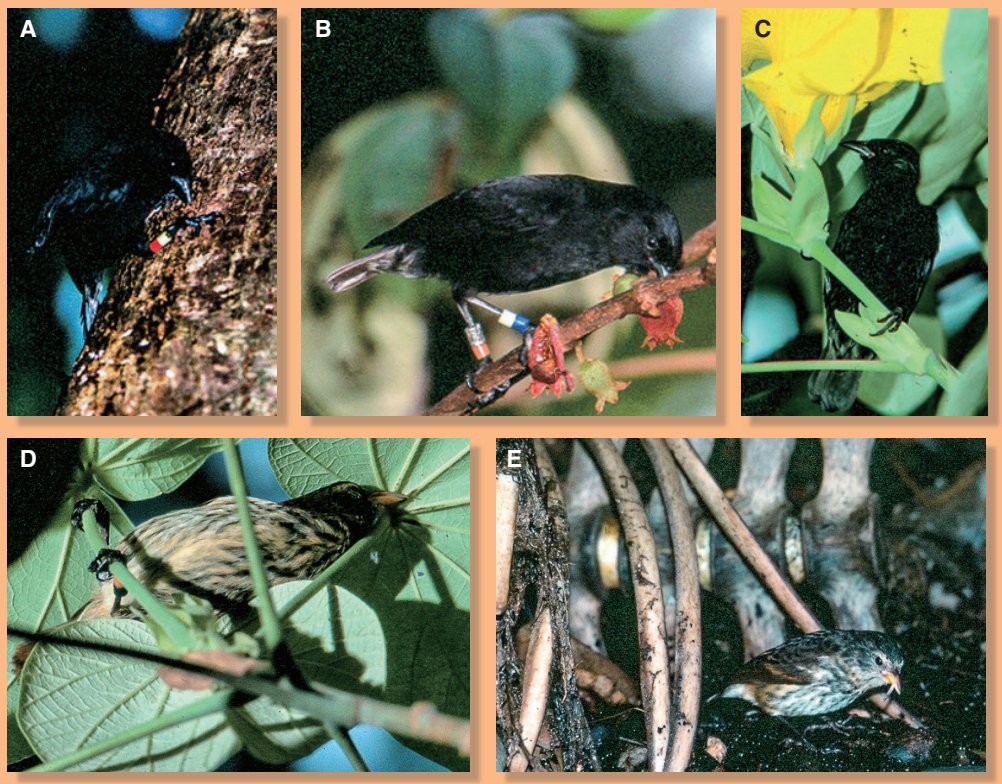


Fig. 8.B8.01 Learned feeding specializations. Although the Cocos Finch (*Pinaroloxias inornata*) is a dietary generalist as a species, individuals specialize in their foraging behaviors. (A) Finches may forage like treecreepers, searching for arthropods and beetle larvae hidden in bark crevices and rotten wood. (B) While some individuals feed on tree fruit, most forage on (C) nectar—and some even specialize on a few flower species. (D) Extrafloral nectaries, the dark slits beneath the central leaf veins, provide another source of nectar. This juvenile finch forages by running the tip of its beak and tongue back and forth in the slit. (E) Finches will also opportunistically feed on rarer food when it becomes available, as shown by this finch feeding on maggots in a decaying beached dolphin carcass. (Photographs by Tracey K. Werner and Thomas W. Sherry.)

an adult within a meter or so and imitating what the adult had done suggest that these specializations are learned. This kind of learning (and possibly teaching by adults) is a simple form of cultural transmission of information. The value of learning for Cocos Finches derives from their often awkward and inefficient foraging behaviors (such as falling off branches while trying to forage like woodpeckers). Cocos Finches can succeed as clumsy woodpeckers, to take just one example of their feeding behaviors, because their island contains no specialized woodpeckers that would outcompete individual Cocos Finches that adopt a woodpecker-like foraging style.

an organism's performance comes at the expense of skill in others. We already have encountered examples of trade-offs in which a bird gains efficiency in recognizing and handling particular prey types with the downside of reducing its efficiency in using other co-occurring prey types.

The most important general condition for specialization is a reliable, year-round food source, so that the specialist is not penalized by the disappearance of its preferred food. Conversely, highly seasonal or unpredictable environments are poor places to specialize. Not surprisingly, many of the most dramatic examples of avian foraging specialization come from the tropics, which are relatively predictable compared with seasonally variable, higher latitude environments. For example, groups of tropical forest insectivores in Peru have narrower foraging niches (thus, greater specialization) than do ecologically similar groups at temperate latitudes (Marra and Remsen 1997). This finding stems from a tendency for many year-round resident tropical insectivores to feed on a specific substrate, a behavior known as substrate-specific foraging. For example, many Central American woodcreepers and many Malaysian woodpeckers use only certain tree types (Sillett et al. 1997; Styring and Zakaria bin Hussin 2004). The year-round availability of hanging dead-leaf substrates colonized by

hiding insects such as cockroaches and crickets supports entire foraging guilds of tropical New World antwrens that specialize in foraging in this aerial leaf litter (Rosenberg 1990, 1993) (Chapter 14). Similarly, a large guild of Costa Rican flycatchers contains many species with unusually high diet selectivity and specialization, especially as compared with migratory flycatchers that feed seasonally in the same rainforest habitats (Sherry 1984).

Reliably constant, year-round resources likely explain the tendency for resident birds at higher latitudes, as well as in the tropics, to feed as specialists on particular substrates. Understanding why some resources are more constant than others in a given environment thus helps us understand not only the nature of resource specialization but also why some birds migrate and others do not. In any environment, some resources tend to be relatively buffered from fluctuations, whereas others vary across space and time. For terrestrial birds, buffered resources tend to be hidden and cryptic, or relatively difficult to reach, such as wood-boring beetle grubs in trees and arthropods under leaves or deep underground. Such prey tend to be relatively constant in abundance and require methodological searching strategies to find and extract, so their use favors specialized searching behaviors. Birds that reside on a feeding territory year-round are well suited to exploit such foods. In contrast, exploiting resources that are conspicuous and variable in space and time—such as foliage and flying insects, and many kinds of fruit and nectar—requires a different set of skills related to opportunistic search and foraging behaviors.

Sophisticated cognitive abilities also may help resident birds cope with temporary resource shortages as compared with the more opportunistic and plastic behavior of migrants. For example, Daniel Sol et al. (2005) showed that year-round resident birds in Europe, which must cope with shortages even of buffered foods, are particularly successful in exploiting novel foods, perhaps due to their methodological searching. Moreover, they found that resident birds tend to be relatively larger brained than migratory European songbirds, a trait that may facilitate the kinds of learning needed to find and exploit novel foods. A study of a group of Great Tits (*Parus major*) that systematically search out and kill bats wintering in a Hungarian cave, documented a novel foraging behavior (Estók et al. 2010). When these researchers experimentally provisioned these birds with alternative foods, their predation rate on bats decreased, supporting the idea that hunger provides a stimulus for such novel behaviors. A resident European bird, the Eurasian Blue Tit (*Cyanistes caeruleus*), provides another particularly famous example of novel foraging behavior. A population of these birds in the UK learned to open milk bottle caps to get at the cream, a trait that then spread culturally among nearby groups of tits. Intense competition for scarce winter food may even have contributed to the evolution of sex differences in cognitive, specifically memory, skills, illustrated in Great Tits: females exceed males in remembering the locations of food cached by another local titmouse species, which is thought to help females cope with losing out to socially dominant males in direct competition for food (Brodin and Urhan 2015).

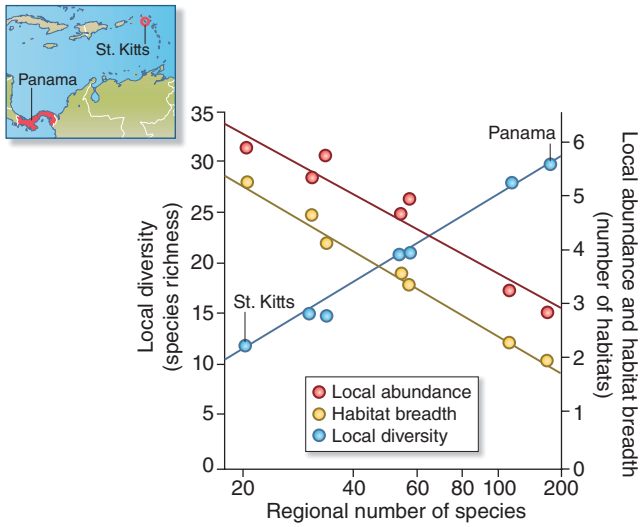


Fig. 8.36 Ecological release and habitat breadth. As both the local (blue line) and regional number of species increases—here comparing species-poor St. Kitts with biodiverse Panama—the breadth of habitats occupied per species (yellow line) and the local abundance of species within particular habitats (red line) decreases. This pattern is consistent with the idea that species are "released" from interspecific competition in species-poor regions and thus become more abundant in a wider range of habitats (as in St. Kitts). (Adapted from Ricklefs and Cox 1977, reproduced with permission from John Wiley and Sons; and Wunderle 1985, reproduced with permission from The Wilson Bulletin.)

The second general condition for feeding specialization is competition from other animals. The importance of interspecific competition in structuring species' niches has been debated (often contentiously) among ecologists, but today little doubt exists that competition is a critical factor in causing species to specialize (Chapter 14). The importance of interspecific competition is supported by the phenomenon of **ecological release**, in which species expand their feeding niche—becoming more generalized—when competing with fewer species. One of the best documented examples of ecological release involving many species comes from the Caribbean Islands. In these islands, there are fewer bird species and those that inhabit the islands can expand their range of habitats as compared with the same species residing in species-rich Panamanian forests where they must compete with many competitors (Ricklefs 2001) (Fig. 8.36).

Ecological release: a situation in which the absence of competitors allows a species to occupy an expanded niche compared to locations in which the competitors are present.

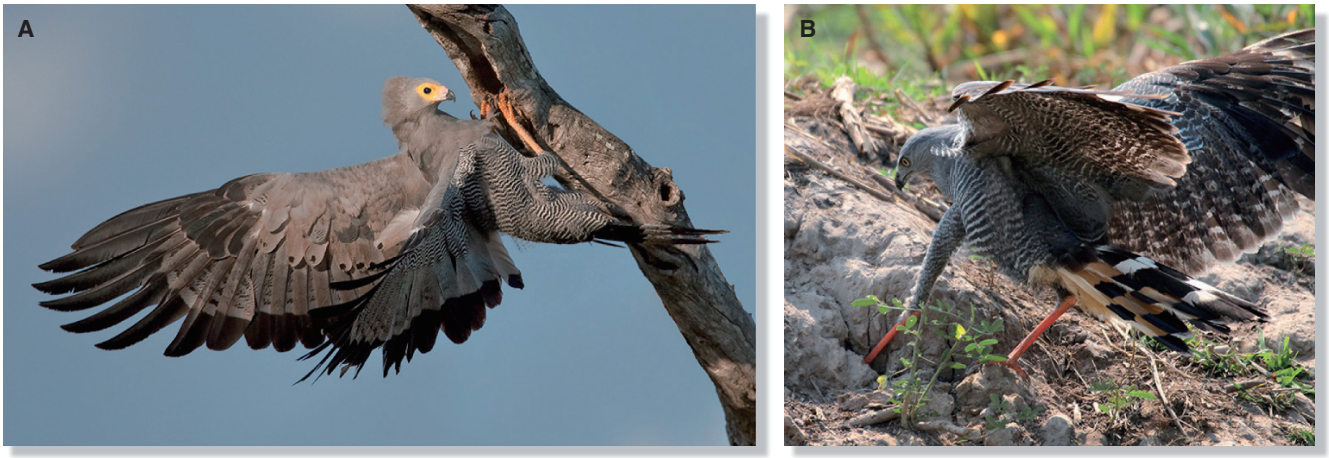


Fig. 8.37 Foraging adaptation convergence in raptor legs. (A) The African Harrier-Hawk (*Polyboroides typus*) and (B) the Crane Hawk (*Geranospiza caerulescens*) from the neotropics have independently evolved the ability to bend their knees in multiple directions. This adaptation permits them to grab prey from otherwise difficult-to-reach places, including cavity nests, burrows, and narrow crevices. (Photographs by: A, Marietjie Froneman; B, Andreas M. Schmidt.)

A conspicuous feature of many **foraging guilds**—sets of coexisting bird species that feed on similar resources in similar ways—is that each species becomes specialized in a way that reflects competition with the other guild species (Chapter 14). Dominant species may specialize on a specific resource, leaving others to feed opportunistically as social subordinates on leftovers or on resources that the specialists cannot monopolize completely. A classic example of such a guild is birds that feed on piñon pine seeds and cache them for future use (Vander Wall and Balda 1981) (Box 8.05). Other avian foraging guilds that are structured by competitive interactions include professional versus opportunistic army-ant followers (Boxes 8.08 and 14.08) and guilds of vultures and other carrion-feeders.

A third situation that promotes the evolution of specialists is food that requires particular anatomical adaptations for handling. As mentioned earlier in this chapter, the Snail Kite (*Rostrhamus sociabilis*) has a specialized bill that allows it to rely on one species of abundant, marsh-dwelling snail. As discussed in Box 8.05, different Red Crossbill (*Loxia curvirostra*) morphs have bill shapes and sizes that are fine-tuned to extract seeds from particular types of conifer cones. Both the African Harrier-Hawk (*Polyboroides typus*) and the Crane Hawk (*Geranospiza caerulescens*) from the New World tropics have double-jointed legs that allow them to reach deeply into tree holes and other crevices to extract amphibians and the nestlings of other birds (Fig. 8.37).

Foraging guild: a group of species in a community that use similar foraging behaviors and/or which feed on a generally similar type of food resource.

8.5.2 Individual feeding specializations

Some of the most surprising specializations arise when members of the same bird population feed on different resources, a phenomenon observed in a number of species (Bolnick et al. 2003). Some of these differences arise from genetic differences, but others are learned as the individuals mature. Within species, sexual dimorphism for feeding (as opposed to secondary sexual trait dimorphism driven by sexual selection—Chapters 3 and 9) is the most familiar and widespread genetically based feeding specialization. Examples of species in which the sexes feed on different resources include many woodpeckers, raptors, and the dramatically sexually divergent (and sadly extinct) Huia (*Heteralocha acutirostris*) of New Zealand (Fig. 8.38). In these and many other birds, sexual dimorphism in beak and/or body size results in sexual differences in prey types, sizes, or foraging habitats.

Learning underlies many other feeding specializations by individual birds. Learning by experience that improves feeding skills is widespread, especially in species requiring skill to catch and handle prey. Learned feeding skills especially benefit individuals in communities with few species. This circumstance favors broad diets—resulting from intraspecific competition—but diminishes feeding efficiency, as illustrated by the Cocos Finch (*Pinaroloxias inornata*) (Box 8.08). One of the best studied examples of learned feeding specialization within a species involves Eurasian Oystercatchers (*Haematopus ostralegus*) (Sutherland et al. 1996). Individual oystercatchers often feed on only one species of intertidal invertebrate, such as mussels, cockles, crabs, or polychaete worms. Oystercatcher individuals that feed on the same prey—such as mussels—may specialize further by technique as "stabbers" (inserting their beaks to pry the shell open) or "hammerers" (pounding a shell's weak



Fig. 8.38 Sexual dimorphism in bill shape. The two sexes of the extinct Huia (*Heteralocha acutirostris*) of New Zealand were once thought to be separate species, owing to the extreme differences in their bills. Pairs were reported to work together to optimize foraging: males had chisel-shaped bills, perfect for drilling holes in wood, while females used their long, decurved bills to probe under bark for insects. (Artwork by John Gerrard Keulemans, from Buller 1888, public domain.)

spot until it breaks to expose the meat inside). Hammerers may specialize even further on either the dorsal or ventral surface of a valve, and ventral hammerers may even specialize on a right or left valve. Why do oystercatcher individuals specialize to this high degree and pass over prey that other individuals find profitable? Part of the answer may be that these prey types are difficult for oystercatchers to find and handle, and the optimal search behavior for one prey type may cause individuals to overlook another. Likewise, oystercatchers must learn how to exploit each type of prey efficiently. Once learned, a particular feeding technique may require commitment, because a bird's beak becomes shaped to some extent by abrasion and makes a particular type of feeding more efficient. Individual feeding specializations allow birds to increase their efficiency while competing for resources, a battle where even the slightest increase in foraging efficiency might be the difference between life and death.

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Chapter 9 Avian Mating and Social Behavior

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Imagine that it is springtime in central Arizona (USA), and you are watching a male and female Abert's Towhee (*Melozone aberti*) in a suburban backyard (Fig. 9.01). With luck, you will see the female towhee exercising mate choice when she comes around to forage for seeds. She likely will arrive with a male companion by her side, because adult Abert's Towhees often form long-lasting social partnerships, and this pair is typical in that regard. The female appears practically attached to her partner as they hurry to the spot where scattered seeds await them. Once the birds have had their fill and have begun to hop toward the nearby shrubs, the female may stop and raise her long tail straight in the air. The male responds promptly to this signal by rushing to his partner and mounting her in a flurry of wing beats. After he succeeds in pressing his cloaca against hers for a few seconds, the mating is over. The two towhees then scurry off together under the shrubbery.

This sequence of social behaviors, which is typical of many songbirds, illustrates the topics covered in this chapter. First, the female towhee clearly takes an active role in determining which male will fertilize her eggs. She does not merely accept the sexual advances of a partner passively, but instead signals her receptivity by elevating her tail, facilitating cloacal access for the male that she has selected as a partner. Abert's Towhees are representative of birds in general in that females typically accept sperm only from particular males; such choices by females generate a host of questions, such as what are the attributes that females prefer in their mates, and what do they gain from their choices? These questions are at the heart of the first section of this chapter, which addresses the interrelated topics of behavioral mate choice and sexual selection.

Second, birds overall exhibit extremely diverse mating and social behaviors; these towhees provide an example of **social monogamy**, one of the most common avian **mating systems**. In Abert's Towhees, one male associates closely with one female throughout an entire breeding season (if not longer) in a pair-bond relationship that appears to restrict his reproductive options. Would a male be better off (that is, leave more surviving descendants) if he sought out several sexual partners in each breeding season? Males that fertilize the eggs of more than one female each spring would seem likely to pass on more of their genes than strictly monogamous males in the population. If so, monogamous tendencies in males would be eliminated over time in favor of

Social monogamy: in birds, a mating system in which one female forms a lasting pair bond with one male, though she may also copulate with other males.

Mating system: the pattern in which matings are distributed among males and females within a population, sometimes but not always involving longer term social bonds.

Opposite: A male Andean Cock-of-the-rock (*Rupicola peruvianus*) displays in a sunspot. This species is known for its lekking behavior; the most beautifully plumed male with the most appealing display area secures the most matings. (Photograph by Jason Rothmeyer.)

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Fig. 9.01 A pair of Abert's Towhees (*Melozone aberti*). This species often forms long-lasting social partnerships. (Photograph by John Alcock.)

a different mating system in which some males have several partners rather than only one at a time. This dilemma provides a starting point for the second section of the chapter, which explains why bird species range from purely monogamous to highly polygynous.

Third, these towhees also illustrate issues associated with social behavior in general. The birds clearly are social in the sense of remaining in each other's company and interacting regularly. They cooperate in the defense of their territory, their private real estate from which they expel other Abert's Towhees. Both members of this pair feed their young during the breeding season. Furthermore, they permit each other to feed freely on seeds offered to them, but frequently show aggression to the local House Sparrows (*Passer domesticus*) and other visitors that attempt to eat at the same bird table. What determines why the birds are cooperative in some contexts, but exhibit antisocial aggression in others? This question, along with other key puzzles linked to avian social behavior, is considered in the third and final part of the chapter.

9.1 Female mating preferences

Given what we know now about the sexual give-and-take between female and male birds, it is hard to believe that until the mid-1900s, many biologists believed that females in general (even in our own species!) lacked preferences for particular attributes in their potential mates (Milam 2010). The standard view used to be that males controlled the mating game by competing among themselves for passive females. Charles Darwin, in contrast, argued that females of many bird species had what he termed "aesthetic sensibilities" that they employ when considering would-be mates. Darwin knew that in pairs of birds where the sexes differed in traits such as singing ability, display dances, or the vividness of their plumage, the male would almost invariably be the sex with the greater capacity for song, the more bizarre courtship displays, and the more striking plumage. Darwin (1871) asked somewhat rhetorically whether "every male of the same species equally excite[s] and attract[s] the female? Or does she exert a choice, and prefer certain males?" He asserted that females do indeed have preferences for certain males.

In recent years, an explosion of research has demonstrated that Darwin was entirely correct in his observation that females are far from neutral bystanders when it comes to selecting mates (Jones and Ratterman 2009). Consider, for example, experiments that have shown how female Zebra Finches (*Taeniopygia guttata*) assess males via their songs (Woolley and Doupe 2008). When Zebra Finch males are singing in the presence of a female, they tend to produce songs that are faster and more standardized than the songs they sing when no females are nearby. By using two speakers to play back faster and slower songs, researchers can assess which of these variants the females prefer. It turns out that when female Zebra Finches are given this choice, they generally approach the speaker playing the faster song type, thereby demonstrating their preference for this kind of song. The underlying presumption of such an experiment is that under natural conditions, female Zebra Finches seeking mates would tend to approach and choose males able to sing the preferred song quality. This assumption also has been tested in experiments with captive finches: females given a choice between two caged males gave more raised-tail **copulation-solicitation displays** to the individual they visited more often (Witte 2006). In other words, a female's association preference reveals her sexual preference as well.

Many other experiments on how females respond to the sexual signals of males have shown that females often pay close attention to even subtle differences in male behaviors or other traits. Male vocalizations (Chapter 10) frequently are a component of the sexual displays that female birds use to assess their mates. For example, female Swamp Sparrows (*Melospiza georgiana*) in eastern North America are attracted to unusually fast trilling songs (Ballentine et al. 2004), whereas female European Serins (*Serinus serinus*), a small Eurasian finch, prefer songs that incorporate notes of exceptionally high frequency (Cardoso et al. 2007). The speed of sound production correlates with male mating success in the Magnificent Frigatebird (*Fregata magnificens*) of the tropical Atlantic, a species in which males attract females by generating a drumming sound via bill clacking that then resonates into an inflated, bright red gular pouch, which itself is a sexual signal

Copulation-solicitation display: a stereotyped posture adopted by female birds that indicates their readiness to copulate.

(Madsen et al. 2007) (Fig. 9.02). In the Brown Skua (*Stercorarius antarcticus*) of Antarctica, males try to produce calls with many notes per second while also generating notes over a relatively broad range of sound frequencies; it is particularly difficult to do both things at once, and the males best able to call near the upper limits of this performance trade-off have higher reproductive success than their less adept rivals (Janicke et al. 2007). These and other cases outlined in Chapter 10 illustrate the general rule that female birds prefer vocal performances that are challenging to produce.

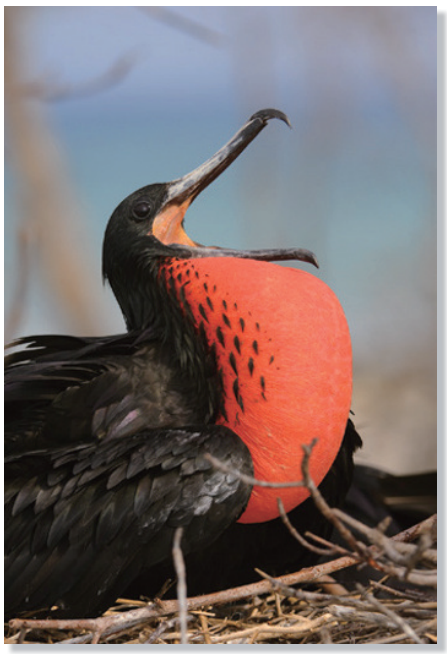


Fig. 9.02 Displaying male Magnificent Frigatebird (*Fregata magnificens*). Males of this species use both visual (inflated red pouch) and auditory signals (calling and bill clacking) to compete for access to reproductively active females. (Photograph by Gerrit Vyn.)

Although male song in general is a very common sexual signal in many groups of birds, the precise song traits preferred by females vary widely from species to species: some female birds assess males on the basis of their speed of signal production, others by the presence of favored sound frequencies. Still others prefer male vocalizations with a wide frequency range or a large total number of song types in a male's repertoire. None of these song attributes is favored universally across all birds. More remains to be learned about how a particular kind of signal preference by females of a given species translates into reproductive benefits for those females.

Just as no one acoustic element predominates in female mate preferences, so too no one visual aspect of courtship does the job across all bird species. In some birds, female preferences revolve around the intensity and frequency with which males perform visual displays that show off tail plumes, or wing feathers, or throat pouches. So, when Black Grouse (*Tetrao tetrix*) gather in groups in Finnish fields to compete for display territories visited by selective females, males differ in their overall activity, and the frequent displayers in relatively large central territories secure more mates than less active, peripheral males (Rintamäki et al. 1995) (Fig. 9.03). This finding suggests that the females evaluate their mates in part by the properties of their visual displays, which determine a male's territorial success and his ability to stimulate female observers.

For other species, the size of a special male **ornament** most strongly affects female mate choice. For example, some

Ornament: any physical trait that has been exaggerated for social display by sexual selection; usually refers to conspicuous traits involved in mate attraction.

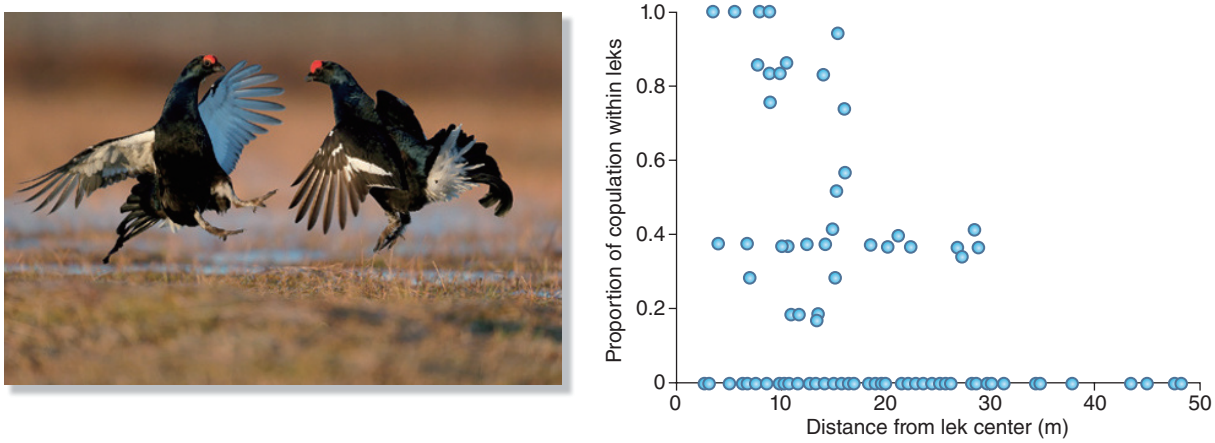


Fig. 9.03 Lekking display of a male Black Grouse (*Tetrao tetrix*). Males compete for access to mates by displaying their bright ornaments in groups termed leks. In this species, males that have display sites near the center of the lek tend to have higher mating success. (From Rintamäki et al. 1995. Reproduced with permission from Elsevier. Photograph by Mike Lane.)



Fig. 9.04 House Finch (*Haemorhous mexicanus*) color variation. Although male House Finches generally have red plumage (left), yellow males (right) also occur in the wild. Color differences are due to dietary carotenoid variation; redder males are directly signaling to females that they have had better access to dietary carotenoids and are in better condition. Females therefore prefer red males over dull or yellow males. (Photograph by Kevin McGraw.)

researchers have found a relationship between the length of the Indian Peafowl's (*Pavo cristatus*) amazing train and male reproductive success (Loyau et al. 2008). Peahens may attend to this aspect of the male or some other component of the train, such as the density of eye-spots, when making a decision about which of several males to select as a mate. Peahens are not the only females with such preferences. In the Eurasian Penduline-Tit (*Remiz pendulinus*), choosy females prefer males that have larger dark eye-stripes ("masks") over males with less prominent masks. As a result, males with large masks pair off more quickly than their less-well-masked rivals (Pogány and Székely 2007).

For other species, female mate choice may revolve around the extent to which a feathered body part reflects ultraviolet (UV) radiation, the yellowness of a patch of feathers, or the redness of a throat pouch (Chapter 4). In particular, carotenoid pigments, which make feathers appear yellow or red, are now believed to be a cue that females of many bird species use to evaluate the attractiveness of potential mates (Hill and McGraw 2006). The general rule—"the brighter, the better"—applies, for example, to the American Redstart (*Setophaga ruticilla*), an attractive wood-warbler that breeds across much of northern North America. In this species, males with more brightly colored reddish feathers on their flanks sire more of their mate's offspring than those with paler flank plumage (Reudink et al. 2009). Females of these songbirds sometimes exercise the option of seeking out redder neighboring males for extra-pair copulation, a widespread attribute in birds, as we shall see (Westneat et al. 1990). Likewise, when some House Finch (*Haemorhous mexicanus*) males were artificially made redder by the application of hair dye, these extra-bright males paired off with females more rapidly than those whose feather color had been made a paler red (Hill 1991) (Fig. 9.04). Studies of this sort make it clear that female mate choice occurs widely in birds (Box 9.01).

9.2 Pair bonds, courtship, and divorce

The sexual signaling that goes on when males court females may serve to induce a female to mate right away, but signals of this sort also can help establish a **pair bond** between a male and a potential mate as a prelude to eventual copulation and reproduction. In many birds, males and females form a social partnership that lasts for at least one breeding season, and sometimes for many more than one. In the Little Penguin (*Eudyptula minor*) of Australia and New Zealand, for example, some pairs remain together for as many as 13 years (Nisbet and Dann 2009).

One behavior that in some birds helps form and maintain a pair-bond relationship is **courtship feeding**, in which a male brings food to a female during courtship. These gifts may provide information that influences the intensity of the bond between the male and female and thus the female's sexual receptivity. The quantity of food delivered can have these effects on females, as studies in Poland have shown for the Northern Shrike (*Lanius excubitor*) (Tryjanowski and Hromada 2005). Male shrikes that offer their partners a large gift of food—that is, a sizeable sparrow or lizard rather than a small cricket—are more likely to be rewarded by a copulation. Likewise, long-term studies of Black-legged Kittiwakes (*Rissa tridactyla*) on the coast of France have found that in successive years females are more likely to re-pair with males who did a better job of courtship feeding in the previous year (Helfenstein et al. 2003).

Pair bond: the social bond between a mated pair (usually a male and female) in a socially monogamous species, usually lasting for one breeding attempt or longer.

Courtship feeding: a behavior in which one member of a pair (usually the male) presents his potential partner with food during courtship or before mating. The food item is sometimes termed a "nuptial gift" and this behavior is an important part of pair bonding in some bird species.

Box 9.01 Mate choice in bowerbirds

The bowerbirds of Australia and New Guinea provide a special case in which female mate choice is influenced by certain properties of the bower, which acts as an indicator of the male's qualities. Bowers built by some species are astonishing constructions that show off elaborate collections of fruits, flowers, beetles, and/or shells that males gather to decorate their display bower (Fig. 9.B1.01). In contrast, the male Satin Bowerbird (*Ptilonorhynchus violaceus*) builds a relatively modest bower that consists of two rows of incurved twigs; the male paints the interior walls with chewed berries or charcoal and saliva (Fig. 9.B1.02). Satin Bowerbird males also litter their bower entrances with bright objects collected from the forest, such as the blue feathers of a local parrot, the Crimson Rosella (*Platycercus elegans*). When females visit a bower with a male in attendance, they are treated to elaborate vocal and behavioral displays, which involve much wing-waving and noisy calls, including imitations of the songs of other local birds. In addition to observing the glossy blue-black males in action, female Satin Bowerbirds evidently pay close attention to the bower itself, because the owners of neatly made and well-decorated bowers are more likely to mate (Borgia 1985). In contrast, the male owners of bowers that are subject to frequent attack and destruction by neighboring rivals experience low reproductive success (Borgia and Gore 1986; Wojcieszek et al. 2007). Thus, the bower itself provides females with considerable information about the builder's behavioral competence, in terms of both his construction skill and his capacity to defend the structure against rival males. In effect, the bower is an extension of the male's display behavior, one that females can use to assess the quality of the bower builder.



Fig. 9.B1.01 Three of the world's most elaborate bowerbird bowers. (A) The magnificent bower of the Vogelkop Bowerbird (*Amblyornis inornata*) consists of a hut-like structure made of sticks with a large "lawn," decorated with meticulously placed collections of flowers, fruit, beetles, and other novel objects. (B) The Great Bowerbird (*Chlamydera nuchalis*) is the largest of all bowerbirds. Males build a complex "avenue bower," often decorated with stones, seashells, and colorful items. These bowers work as optical illusions that lure females into the runway (Kelley and Endler 2012). (C) Macgregor's Bowerbirds (*Amblyornis macgregoriae*) are known for their fantastic circular-runway bower structure made of gathered moss. Males build runways and central towers of small twigs over several years, stomping down the runway as they strut around. Food and decoration for the bower court are draped around for the female's approval. (Photographs by: A, Mengjan Shi; B, L. A. Kelley; C, Alexandra Class Freeman.)



Fig. 9.B1.02 Satin Bowerbirds (*Ptilonorhynchus violaceus*) at the bower. In this species, the bower is a simple structure, often embellished with bright blue objects (including, in modern times, human trash). Here, the female (left) examines the bower, while the male (right) adds a new object. (Photograph by Julian Robinson.)



Fig. 9.05 Nest stones as an indicator of male quality. As the mating season begins, Black Wheatear (*Oenanthe leucura*) males carry hundreds of stones to build the base of a nest mound. Females gauge a male's parental provisioning potential based on the quantity and quality of stones at a nesting site, laying more eggs with males that carry heavier stones. (Photograph by Manuel Soler.)

Although often it is popularly thought that many pairs of birds "mate for life," pairs in most species often break up between or even within breeding seasons. These breakups may happen after one member of the pair dies or when one or both members subsequently pair with a different individual. Behavioral ecologists generally refer to this switching between pair-bonded mates as **divorce**, and in birds the female usually takes the lead in switching mates. Female birds can initiate a split even in mid-season, as shown by an experiment involving Black-capped Chickadees (*Poecile atricapillus*) in Ontario, Canada. Two researchers, Ken Otter and Laurene Ratcliffe (1996), captured females that had paired with high-status (dominant) or low-status (subordinate) males. These females were held in captivity long enough to permit seven neighboring females to abandon their current mate and move to territories with the experimentally "widowed" males. Six of the seven divorcees paired off with a high-status male; only one accepted a member of the subordinate group. This elegant experiment shows that female birds often are aware of the dominance status of various nearby males, or perhaps are alert to the quality of their territories, and are prepared to divorce their current, lower quality mate should a better opportunity present itself.

Divorce: occurs when members of a socially mated pair of birds cease being pair bonded, often to re-pair with different individuals.

In other species, females may eschew divorce, but make the number of eggs they lay dependent upon the physiological state of a male. This is known to occur in Black Wheatears (*Oenanthe leucura*) (Fig. 9.05), a species found in southwestern Europe and northwestern Africa. In this species, females appear to wait until they have observed their partners carrying stones to their nest cavities before deciding how many eggs they will lay (Soler et al. 1996). Females produce more eggs when their mates have carted in many heavy rocks during the nest-building period, whereas males that cannot—or are unwilling to—carry large rocks to the nest caves are on average given fewer copulation attempts. Thus, a given male Black Wheatear's reproductive success appears to depend on his mate's decisions, which in turn are influenced by his behavioral performance.

Additional evidence helps explain why female wheatears cue in on stone carrying as an indicator of male quality. Males that carry very heavy stones have stronger immune systems (Chapter 7) than do males that only carry smaller stones (Soler et al. 1999). A healthy male may be able to help the female rear a larger clutch. Alternatively, a female with a healthy male may gain by working harder in a year when she has acquired a mate with "good genes" rather than holding back to increase the odds that she will survive to reproduce again in a future year. However, this pattern in which females paired with top males lay more eggs also might arise if the females in the best condition were to acquire stronger males as partners. This outcome would leave the females that are unable to produce a large clutch with lower quality males (Lebigre et al. 2007).

Female birds exhibit many other forms of mate choice, some of which are quite subtle. For example, Sjouke Kingma and colleagues (2009) have found that female Eurasian Blue Tits (*Cyanistes caeruleus*) at their study site near Groningen in the Netherlands adjust the amount of testosterone they contribute to their eggs in relation to the intensity of the UV coloration of their mate. Eggs containing the sons of high-UV males receive more testosterone from their mothers. These hormonal adjustments by egg-laying females may affect the attractiveness of their sons, in turn influencing the reproductive success of their mates, that is, the number of descendants that their partners contribute to the next generation. Females forced to accept lower quality males may gain by withholding testosterone from their eggs if the hormone is expensive to produce and if the sons of these males would be unable to use the biochemical in a developmentally advantageous manner.

At the most general level, we now know that any of a very broad spectrum of male attributes can affect the likelihood that a male will succeed in attracting a mate or in inducing her to lay more eggs, or eggs of higher quality. The cues used

Box 9.02 Same-sex pair bonds in Laysan Albatrosses

Pair bonds in birds generally involve a male and a female, but individuals of more than 150 bird species have been seen engaging in some form of same-sex courtship (MacFarlane et al. 2010). In most cases these same-sex mating behaviors are rare, but Laysan Albatrosses (*Phoebastria immutabilis*) breeding on Oahu and some other Hawaiian islands are an exception: more than 30% of their nests are attended only by a pair of adult females (Young et al. 2008) (Fig. 9.B2.01). Female albatrosses lay only a single egg per year, and the presence of two eggs in some nests was an initial tip-off to the researchers that something unusual was happening in this population. Albatross pairs, whether male–female or female–female, incubate only a single egg even if they start out with two. Female–female pairs are not nearly as successful as male–female pairs in hatching the egg in their nest, but the two kinds of pairs do equally well at raising their chick to fledging if the egg hatches. In many cases, the fathers of the chicks parented by two females are male albatrosses from the same colony that are pair bonded to other females.

Long-term studies have shown that some of these female–female albatross pairs remain together for long periods, with the record being two females that were pair bonded for at least 19 successive years. When these birds have raised chicks together in multiple years, often each of the females ends up being the mother of some of the offspring, although in different years. What conditions might cause these females to pair bond with other females? A likely possibility is that males are in short supply in these albatross breeding colonies, where surveys indicate that there are about three females for every two males. Although male–female pairs do better overall, females who are unable to obtain a male partner clearly can achieve higher reproductive success by pairing with another female than by foregoing nesting altogether.



Fig. 9.B2.01 A female–female Laysan Albatross (*Phoebastria immutabilis*) pair at their nest. In this species, pair bonds are formed for many years (and these birds are known to survive up to 62 years). Some colonies have skewed sex ratios, where females outnumber males three to two. In such cases, some females form same-sex pair bonds. (Photograph by Daniel W. Clark.)

by females may even vary between populations of the same species. As described in more detail in Box 3.03, a comparison of mate choice in the North American and European subspecies of the Barn Swallow (*Hirundo rustica*) showed that females in different populations may focus on different male ornaments. In North American populations of Barn Swallows, males whose ventral plumage is more heavily pigmented secured mates more rapidly than their duller rivals (Safran and McGraw 2004). In contrast, in Europe the males most attractive to females are those with unusually long and symmetrical tail streamers, and differences in plumage coloration play little role in mate choice (Møller 1988). This example illustrates that although female mate choice, broadly defined, may be standard practice in birds, the nature of the preferences can vary markedly from species to species and sometimes from population to population within the same species (Box 9.02).

9.3 Male mating preferences

Many fewer studies have considered whether male birds, like females, are choosy about their partners. As Darwin himself noted, this relative lack of attention to mate choice by males stems from the fact that males are much more likely to court females than the other way around. Therefore, it has made general sense to focus first on the cues females use when evaluating courting males rather than to investigate the intuitively less likely phenomenon of mate choice by males.

Nonetheless, theoretical reasons exist for thinking that male mate choice happens too. Social monogamy is extremely common among birds, and to the extent that males limit themselves to one social and sexual companion per breeding season, they certainly could gain by selecting a superior partner, one with whom a male



Fig. 9.06 Plumage variation as a signal of female quality. In some populations of the European Pied Flycatcher (*Ficedula hypoleuca*), variation in forehead patch size is a signal of individual quality. For example, females with white forehead patches (right) occupy better territories, where they face fewer parasites and have higher chances of producing more offspring. (Photographs by Judith Morales-Fernaz.)

is likely to rear an above-average number of surviving offspring. In an impressive diversity of birds, monogamous males cooperate with their mates in sharing most or all of the tasks associated with reproduction (except, of course, egg laying). For such a male to maximize the return on his paternal investments, he may benefit by identifying an especially fertile female or one that is an unusually good parental partner. For example, in the European Pied Flycatcher (*Ficedula hypoleuca*) population in central Spain, only some females have a white patch on the forehead, and these individuals raise more fledglings on average than do females that lack this patch (Morales et al. 2007) (Fig. 9.06). If males preferred white-patched females, they might well derive a reproductive benefit from their preference.

In a good many bird species, females do look rather like males, and this resemblance suggests that the sexes may be engaged in mutual mate choice based on appearance cues. This statement may be particularly true when males vary greatly in their attractiveness so that some males have the option of rejecting certain females in favor of others. One experiment that definitively documented male preferences explored the mating patterns in the Eurasian Blue Tit (*Cyanistes caeruleus*), whose males tend to associate more with females whose crown feathers reflect UV radiation and associate less with females whose UV plumage has been experimentally diminished (Hegyi et al. 2007). Males in this species therefore select females on the basis of a plumage trait, just as females often choose males with special feather ornaments. Likewise, another study—this one on the Rock Petronia (*Petronia petronia*), a relative of the exceedingly widespread and more somber House Sparrow (*Passer domesticus*)—documented that females with an experimentally reduced yellow breast patch were courted less often, and mated at a significantly later date than those with a larger breast patch (Griggio et al. 2005). Such studies demonstrate that male mate choice is a reality in at least some bird species and suggest that overall it is more common than generally realized.

9.4 Adaptive value of mate choice

What might choosy females (and choosy males) gain from their preferences for partners capable of providing them with attractive songs, ornaments, displays, and the like? This question really concerns the adaptive value of mate choice and addresses the long-term evolutionary causes of a choosy female's or male's behavior, not the immediate short-term physiological causes of a given individual's behavior. The distinction is considered essential by most behavioral biologists, who distinguish between two kinds of questions (Box 9.03): namely, **proximate questions** that deal with the internal mechanisms that enable individuals to carry out certain actions, versus **ultimate questions** that examine the longer term evolutionary explanations for behaviors.

The remainder of this chapter focuses primarily on the ultimate causes of bird behavior; on why, for example, individuals that prefer certain attributes in their partners are more likely to leave surviving descendants than if they had different preferences. Research on the adaptive value of animal characteristics complements—but does not replace—studies on the proximate causes of behavior. Both are needed to paint a complete picture of animal behavior (Box 9.04).

Proximate questions: in biology, questions that pertain to immediate, internal, and/or mechanistic processes, often addressing "how" the process is produced by physiological, behavioral, or other means.

Ultimate questions: in biology, questions that pertain to long-term evolutionary processes, often addressing "why" a particular trait arose within a species or higher taxonomic group.

Box 9.03 Proximate and ultimate levels of analysis

Ever since Niko Tinbergen (1963) published a classic paper on the different questions underlying behavioral research, behavioral biologists have understood that there are different ways to explain any trait of interest. On one level, we can look into the immediate reasons why an individual does something. Thus, in the example that leads off this chapter, when a female Abert's Towhee (*Melozone aberti*) invites her male companion to copulate, her behavior is caused by such things as her breeding state and the interaction between certain hormones circulating in her blood and her nervous system. These are the immediate or proximate causes of her behavior. To study these proximate reasons for her behavior, we have to consider what is going on inside the female, such as how certain physiological systems operate in her body. In addition, these physiological mechanisms developed over time within a female as a result of interactions between her genes and her cellular environment. If we are to understand the connections between development and behavior, we also must carry out proximate research on the internal mechanisms possessed by the animal.

At the same time, these properties of the developmental, endocrine, and nervous systems of female Abert's Towhees have arisen via natural selection acting on females in past towhee generations. These traits resulting from long-term evolutionary processes are responsible for the ultimate causes of her behavior. Over evolutionary time, some female towhees happened to have special proximate mechanisms, whether genetic–developmental, hormonal, or neural, which helped them leave relatively more surviving descendants. These reproductively successful females gradually shaped the species in their image, endowing the present generation of females with internal systems that have been linked to reproductive success in the past. To understand fully the behavior of a female towhee living today, we must figure out both how her internal mechanisms work and why these mechanisms promote successful reproduction by the individuals that have these devices.

Box 9.04 Potential adaptive benefits of being choosy when selecting mates

There are five major benefits that birds may gain by having strong preferences about their mating partners.

Mate choice that results in genetic benefits

- Preferred mates supply genes for the development of sexually attractive offspring.
- Preferred mates supply genes for the development of healthy, viable offspring.

Mate choice that results in material benefits

- Preferred mates supply food or other resources to their partners.
- Preferred mates do not carry infectious diseases or communicable parasites.
- Preferred mates offer superior parental care to their offspring.

9.4.1 Genetic benefits from mate choice

There are many reasons why a female might derive reproductive benefits from her choice of a partner or partners. When studying female mate choice, we must consider the possibility that female preferences are not actually adaptive, but instead arise via selection that favors those males best able to persuade females to mate with them. This "empty advertisement hypothesis" suggests that females are lured into accepting sperm from persuasive partners that really have nothing of value to offer them, only courtship that activates the proximate mechanisms (Box 9.03) underlying female mating behavior. However, under this scenario, even if the females gain nothing directly from a sexual partner, the females that prefer the most stimulating males may tend to have sons that have inherited that preferred trait and that therefore are especially capable of acquiring mates in the next generation. Given these conditions, the empty advertisement hypothesis is converted into the more widely accepted **sexy son hypothesis**, with choosy females gaining attractive sons (even if nothing else) from their mate

Sexy son hypothesis: the idea that breeding females can achieve higher fitness by mating with particularly attractive males because their sons are thereby more likely to inherit those attractive traits and be reproductively successful themselves.

preferences (Weatherhead and Robertson 1979). One example that supports the sexy son hypothesis comes from European Starlings (*Sturnus vulgaris*) studied in southern Germany, where the sons of polygynous fathers defend more nest boxes and produce more courtship songs than the sons of monogamous fathers (Gwinner and Schwabl 2005). In other words, the sons' apparent inheritance of their fathers' mating behaviors would enable females to produce sexy sons by mating with males that are able to acquire several mates rather than just one social partner.

The sexy son hypothesis is not the only adaptive explanation for mate choice that focuses on a possible hereditary benefit from the behavior. For example, a choosy female could get sperm from a hereditarily healthy male whose genes—when passed on to his offspring—will help them develop a strong immune system. Females that made mate choices based on cues of male health could give their progeny a **genetic benefit**.

Likewise, when male plumage coloration is reflective of the carotenoid content of foods consumed, a female preference for bright reds or yellows in potential partners would lead females to mate with birds that are good foragers. If this ability has a hereditary component, selective females might be securing partners with genes that promote skillful foraging in their offspring.

Some of the clearest evidence for genetic benefits comes from species in which males provide no parental care after mating with the female. Females in these species often are highly selective about which males they choose as mates, presumably to obtain the best genes for their offspring. In the Black Grouse (*Tetrao tetrix*) of Europe, for example, females carefully observe many displaying males before choosing one to fertilize their eggs (Fig. 9.03). The same male often is chosen by several females, whereas most males in the display area are never selected by any visiting females. The most reproductively successful males are those that dominate other males while keeping their tail ornaments from being damaged in fights. They usually are also the males that occupy central display territories, an achievement that often requires years of intense competition (Höglund et al. 1994; Rintamäki et al. 2001).

The female preference for central-territory grouse strongly suggests that they gain good genes for their offspring from these males, genes that promote the development of attractive and/or healthy offspring. In the Great Snipe (*Gallinago media*), a shorebird of Europe and northern Asia, the males chosen most often by females have a stronger immune response than their less successful neighbors, suggesting that they are in the best overall body condition (Ekblom et al. 2005) (Fig. 9.07). Once again, this result suggests an indirect (genetic) benefit from mate choice, although the finding does not absolutely rule out a direct (material) benefit in the form of a reduced risk of acquiring a contagious disease or parasite from preferred sexual partners.

Genetic benefits: benefits of mate choice that stem from the high-quality genetic variants inherited by offspring of partners that choose genetically high-quality mates.



Fig. 9.07 Male Great Snipe (*Gallinago media*) display. Leks of polygamous species like this one may have 5–30 males competing for females simultaneously. (Photograph by Dmitry Yakubovich.)

With respect to the benefits to males from mate choice, recall that, as described earlier in this chapter, male Eurasian Blue Tits (*Cyanistes caeruleus*) prefer females with relatively intense UV-reflecting crowns. In one study, females of this sort survived better than those with less UV reflectance in their feathers (Doutrelant et al. 2008). Moreover, female Eurasian Blue Tits with brighter yellow (carotenoid-based) plumage produced larger clutches and had higher fledging success than females with duller yellow coloration. To the extent that males have a choice between bright and dull females as mates, this study suggests that a male preference for brighter females would translate into more progeny for the male. This conclusion also may apply to the Rock Petronia (*Petronia petronia*), in which females with a larger yellow breast patch weighed more and had more broods per year than conspecifics with a naturally smaller yellow patch (Griggio et al. 2005). Male mate preferences, like mate selection by females, appear to have the potential to raise the reproductive success of choosy individuals.

Moreover, just as females can exercise a kind of mate choice after pairing with a male by modifying their investment in offspring depending on the quality of their partner, so too some male birds appear to adjust their investment in parental care in relation to the quality of their mate. For example, variation in the color of eggs laid by female Spotless Starlings (*Sturnus unicolor*) in Spain affects male decisions about the care of the resulting offspring. Female starlings that have had some wing feathers removed—thus lowering their condition by making it more difficult for them to fly—lay



Fig. 9.08 Egg color signals mate quality. In the Gray Catbird (*Dumetella carolinensis*), males are more likely to provide parental care to their offspring when eggs are a vibrant shade of cerulean-blue (a sign of female condition). (Photograph by Elizabeth A. Sellers.)

paler blue eggs than do control birds with a full complement of primaries. Males paired to females that laid pale eggs were less active parents when they started to provision their brood (Soler et al. 2008). Similar male responses to egg color have been documented in the Gray Catbird (*Dumetella carolinensis*), a North American species that also lays blue eggs (Hanley et al. 2008) (Fig. 9.08). Females in these and other species probably are under pressure to provide signals that encourage their social partners to work hard for their progeny.

9.4.2 Material benefits from mate choice

In the realm of mating decisions, **direct benefits** are those that return an advantage directly to the choosy individual. For example, females might prefer males that give them greater nutritional gifts via courtship feeding. In the case of the Yellow-legged Gull (*Larus michahellis*) studied on islands off northwestern Spain, females that had been consistently well fed by their courtship partner were less likely to move during copulation, so the male was more likely to transfer sperm during the mating and thus was more likely to sire the offspring of that female (Velando 2004). By making effective copulation contingent upon her mate's ability to provide her with food, a female could use mate choice to acquire a material benefit, namely, the calories and nutrients needed to enhance her personal condition or

Direct benefits: tangible benefits that a mate derives directly from their partner, such as food, access to a good territory, protection from predators, or a high-quality nest site.



Fig. 9.09 Courtship feeding. Particularly common in species for which food resources are inconsistent or hard to find, courtship feeding—a pair-bonding activity before nestlings hatch—demonstrates to females that a mate is capable of providing food to future young. Here, a male Osprey (*Pandion haliaetus*) returns with a fish for his mate. (Photograph by Barbara Rich.)

her capacity to produce offspring. Likewise, in British Columbia, Canada, the rate at which male Ospreys (*Pandion haliaetus*) provide their partners with fish during the courtship phase is related to the probability that the female will lay a clutch (Fig. 9.09). Moreover, the frequency of courtship feeding by the male, which is a function of his fish-catching ability, is correlated with the rate at which he later provisions his offspring. Thus, by evaluating the nature of a male's courtship feeding, female Ospreys can secure a competent forager as a partner in the feeding of their offspring (Green and Krebs 1995).

Moreover, a highly successful forager is likely to be in generally good health and therefore unlikely to pass a contagious debilitating disease to his partner or her offspring. Depending on the bird species, a male's appearance, the quality of his plumage ornaments, the brightness of the reds and yellows in his feathers, the intensity of his behavioral displays, the number of large rocks he carries to his partner, the nature of his songs, and even the size of the nest he builds for his partner all provide potential indicators of his past, current, and even future physiological condition, and thus of his health and capacity for parental care. For example, in American Kestrels (*Falco sparverius*) studied in Saskatchewan, Canada, males with bright orange skin (the product of high levels of carotenoids) about the base of the bill (Fig. 9.10) are less likely to have blood parasite infections later during the breeding season when male parental care becomes important to offspring survival. Therefore a preference for males with this coloring would help



Fig. 9.10 The Cere can indicate mate quality. In American Kestrels (*Falco sparverius*), males with the brightest orange cere (bill skin, arrow) are most likely to be the best providers late into the nestling period, when offspring survival is critical but food can be harder to find. (Photograph by Patricia Donald.)

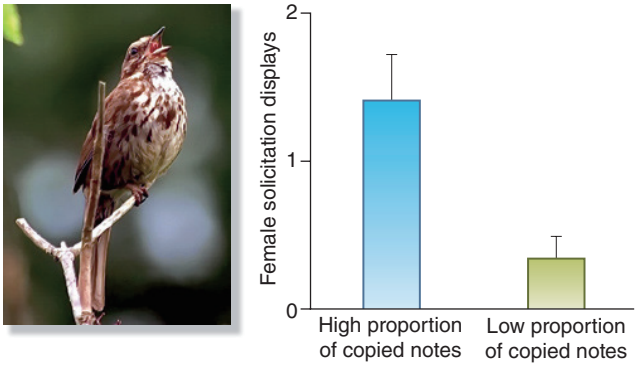


Fig. 9.11 Song production reveals male quality. Male Song Sparrow (*Melospiza melodia*) nestlings that experience stress during song learning in early development will produce poorer quality songs (with a low proportion of copied notes) compared with non-stressed males (that produce a high proportion of copied notes). Females prefer songs that are reproduced with accuracy, regardless of the tutor song structure. (From Nowicki et al. 2002. Reproduced with permission from the Royal Society. Photograph by Hector Chu-Joy.)

females acquire capable partners (Dawson and Bortolotti 2006). Likewise, in an experiment in which male House Finches (*Haemorhous mexicanus*) were inoculated with an infectious bacterial pathogen, birds with redder plumage recovered more quickly than birds with paler, yellower feathers (Hill and Farmer 2005). Because female mate choice in this species is biased in favor of redder males, females could pair off with males able to be better parents because they were resistant to certain diseases.

The quality of a male's song sometimes serves as another potential indicator of his paternal ability. In this context, it is striking that a male's ability to learn songs early in his life often is very sensitive to the conditions experienced at that time (Chapter 10). For example, nestlings that receive relatively little food might be handicapped when it comes to imitating their species' song(s). As a result, a female listening to an adult male sing might learn something about his past developmental history, which in turn might influence his current health and capacity for competent paternal behavior. In this regard, a series of careful laboratory studies have shown that young Song Sparrow (*Melospiza melodia*) males that are in good condition learn and copy the songs they hear more accurately than do young sparrows that are in poor condition. These better songs later provide information to mating females: when adult female Song Sparrows that have been dosed with hormones to make them sexually responsive listen to taped songs, they are more likely to elevate their tails into the precopulatory position when they hear accurate copies of their species' song than when they hear the poorer imitations made by disadvantaged males (Nowicki et al. 2002) (Fig. 9.11). This kind of preference could lead the female to mate and bond with a better-than-average male, one with a good copy of his species' song, which correlates with his ability to provide better-than-average assistance to the female and her brood.

9.5 Sexual selection and mating systems

Mate choice, whether by females or by males, has evolutionary consequences if the differences among the individuals subject to choice are hereditary. Individuals with the favored hereditary attributes may experience greater reproductive success than others of their species. Over time, the genetic basis of the ability to sing a particular kind of song, or to exhibit a particular ornament, or to engage in certain courtship displays, or to supply mates with their favored foods can spread through the species.

Sexually appealing traits generally come with costs: songs can attract predators as well as mates, ornaments make individuals more conspicuous to their enemies, animals focused on displaying to potential partners are less alert to danger, and individuals that offer food to their mates expend valuable time and energy in collecting what they later give away. Charles Darwin (1871) realized that such survival-reducing traits required a special explanation, which he supplied in the form of his theory of **sexual selection**. He argued that elaborate ornaments, for example, might put a male at special risk of attack by predators and thus might be thought to

Sexual selection: a special form of natural selection that involves the differential reproductive success of individuals that arises specifically from competition over mating opportunities; this can involve direct competition with members of the same sex or competition to attract members of the opposite sex.

be maladaptive, but if these ornaments also increase the odds that a male will acquire a mate and reproduce successfully, then sexual selection favoring the ornaments could trump natural selection against them. The same argument can be applied to any attributes that appear to function strictly in terms of the competition among individuals for mates, whether these are sexually attractive characteristics or traits that enable individuals to prevail over others of the same sex in mating-related struggles.

As covered in more detail in Chapter 3, sexual selection now is generally considered to be one component of natural selection, in that the conditions required for both forms of selection are fundamentally similar. Both natural and sexual selection act on hereditary variation among individuals in their ability to pass on their genes, but sexual selection does so in the narrow context of competition for access to mates. Nevertheless, sexual selection theory is valuable because it helps focus attention on the significance of pure reproductive competition (Andersson 1994). One of the benefits of this perspective is that researchers alert to the theory can identify puzzles that they otherwise might ignore, particularly those when males or females appear to behave in ways that on first glance might seem to reduce their chances of acquiring mates. As discussed earlier in the chapter, monogamy by males is one example of this sort of puzzle, because the truly monogamous male appears to forego opportunities to mate with more than one female.

9.5.1 Solving the puzzle of male monogamy

Bird mating systems are wonderfully diverse, ranging from monogamy (one male mates with one female) to polyandry (one female mates with several males) to polygyny (one male mates with several females) (Box 9.05). One would think that sexual selection would favor polygynous males, those that acquire more than one mate in a breeding season and thereby increase their chances of fertilizing eggs and leaving many descendants. Because most birds appear to be monogamous, behavioral researchers have wondered whether, under certain special conditions, polygyny actually might reduce, rather than increase, a male's reproductive success.

One such condition involves **reproductive retaliation** by abandoned females so that if a male were to leave one partner in order to secure another, his original mate might copulate with another individual. In keeping with this hypothesis, females of many species of birds are sexually receptive to males other than their partners. Indeed, one of the most significant findings in behavioral ornithology during the past several decades is that most bird species previously assumed to be strictly monogamous are not nearly so faithful as researchers had thought. Not so long ago, the British ornithologist David Lack (1968) famously stated, "Well over nine-tenths (93%) of all passerine subfamilies are normally monogamous … Polyandry is unknown." Now, however, we know from genetic investigations that in about 90% of all birds, at least some females mate with males other than their social partners. This behavior is termed **extra-pair copulation**, with the outcome sometimes resulting in **extra-pair fertilization** of eggs (Box 9.06).

Given the generally high prevalence of extra-pair mating, it is the rare cases of true monogamy that require special explanation. Monogamy would likely be rarer still if males of some species did not attempt to monitor and control their partner's behavior in order to reduce her opportunities to copulate with other males. Active **mate guarding** is a common feature of male behavior in many birds, with males following their partner closely, especially during the female's fertile phase. The fact that male Abert's Towhees (*Melozone aberti*) (from the introduction to this chapter) remain so close to their mates is consistent with a guarding function: when the male stays within centimeters of his partner, it must be hard for her to slip away for a clandestine meeting with another male.

The consequences of mate guarding have been assessed experimentally in field studies of many bird species. If active guarding by males does reduce the probability that the female partner will engage in extra-pair copulations, then temporary removal of the male **social mate** should lead to a higher probability that his mate will go elsewhere to copulate. This generally turns out to be the case, as shown by experiments on Bluethroats (*Luscinia svecica*), an attractive Eurasian songbird. When Bluethroat males were held in a cage for only one morning during their

Reproductive retaliation: a behavior in which one member of a pair provides less parental care in situations where the offspring in the nest may not be their own and/or when their mate also provides less care.

Extra-pair copulation: matings between two members of a population who are not pair bonded, usually when each is socially pair bonded to a different mate.

Extra-pair fertilization: the fertilization of eggs resulting from matings between two members of a population who are not pair bonded.

Mate guarding: a behavior in which a male attends closely to his mate during her fertile period to help ensure that she does not mate with other males.

Social mate: the individual with which a bird has a pair bond.

Box 9.05 The diversity of avian mating systems

The mating systems of birds are remarkably varied, with different forms of monogamy, polyandry, and polygyny (Fig. 9.B5.01).

Social monogamy

Individuals pair off with one member of the opposite sex for one to several breeding periods. Rarely, species may be genetically monogamous, where they mate exclusively within their pair.

- *Mate-guarding monogamy*—males associate with a female to prevent her from mating with other males.
- *Mate-assistance monogamy*—males associate with a female to help her increase the number of offspring reared per breeding season.
- *Female-enforced monogamy*—males associate with a female that is capable of preventing her partner from seeking other mates.

Polyandry

Females accept sperm from more than one male per breeding season.

- *Male-enforced polyandry*—females are forced to copulate with sexually aggressive "partners."
- *Convenience polyandry*—females mate with more than one male because the costs of rejecting secondary suitors is too high.
- *Material benefits polyandry*—females mate with more than one male to secure the resources or the parental care that secondary partners provide.
- *Fertility insurance polyandry*—females mate with more than one male to reduce the probability that a primary partner's sperm are defective.
- *Genetic benefits polyandry*—females mate with more than one male to secure purely genetic benefits from their partners, such as more compatible gene combinations for their offspring or greater heterozygosity for their progeny.

Polygyny

Some males are able to gain sexual access to two or more females.

- *Deception-based polygyny*—males induce secondary females to pair with them by behaving as if they were monogamous.
- *Female-defense polygyny*—males defend and monopolize groups of potential mates against rival males.
- *Resource-defense polygyny*—males defend and monopolize valuable resources that attract several mates to them.
- *Lek polygyny*—males defend a small display territory where they may persuade visiting females to mate with them.

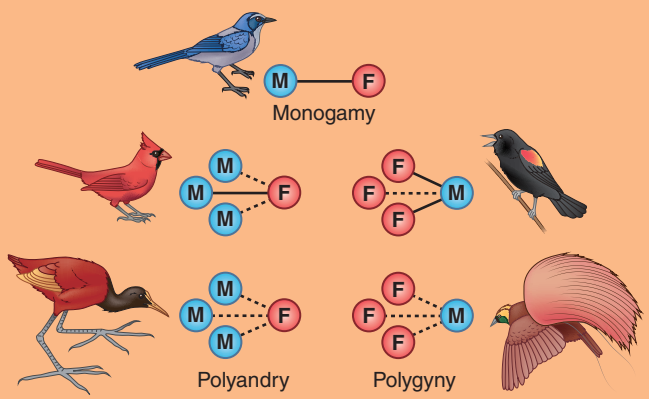


Fig. 9.B5.01 Avian mating systems. These diagrams represent the range of avian mating systems, from genetic and social monogamy (top) to lek-based polygamy (bottom right). Solid lines denote social pair bonds; dashed lines indicate copulations that do not lead to further social interaction, mate guarding, or parental care. Additional combinations of genetic and social pairings are possible in polyandrous and polygynous species. (Illustration by Andrew Leach © Cornell Lab of Ornithology.)

mate's fertile period, the proportion of extra-pair offspring in her next clutch was twice that of females whose males had not been prevented from guarding their mate (Johnsen et al. 2008).

Jan Komdeur and his colleagues (2001, 2007) have used similar experiments to show that male mate guarding is highly effective in the Seychelles Warbler (*Acrocephalus sechellensis*). In this island species, the male typically remains vigilant and close to his mate for several days before egg laying, in the period when an egg can be fertilized. Female Seychelles Warblers lay only a single egg, and therefore if a male can sexually monopolize his partner as that egg is being formed and laid, he greatly improves his chances of fertilizing it. Once the egg is laid, however, males no longer guard their partners and instead may attempt to find a neighboring female with whom to mate. Komdeur and company put false eggs into the nests of females that had yet to lay, duping their mates into relaxing

Box 9.06 Genetic parentage testing

Genetic testing to determine the parentage of offspring has become one of the most important tools of modern behavioral ornithology. Before the development of these techniques, researchers had to measure a male's reproductive success indirectly by counting the number of females with whom he copulated or the number of offspring produced by his mate or mates. However, these measures were called into serious question by the discovery that the females of socially monogamous birds often engaged in extra-pair copulations. If a female mates with more than one male, the problem becomes how to establish which of her various partners sired which of her various offspring.

The adult birds in any wild population invariably have some degree of genetic variation. By comparing the particular genetic variants found in an offspring with those found in a series of candidate parents, researchers can determine which two individuals really are that young bird's parents. For most birds, it is straightforward to determine the mother using non-genetic methods—she is the adult female attending the nest. So genetic techniques are used most often to determine paternity, identifying which male is the father. The same approach works well, however, when the mother's identity is uncertain also, as in species in which females lay eggs in the nests of other females, or in which multiple reproductively active females occur within the same social group.

Any form of heritable genetic variation can be used to determine parentage, but researchers most commonly have used regions of DNA called microsatellites for this purpose. Microsatellites have unusually high mutation rates, so any population of birds is likely to have a high degree of microsatellite variation, and these differences among individuals allow researchers to match the genetic variants found in offspring with those seen in potential parents. Genetic parentage testing has become a standard tool for behavioral ecologists, so that now it usually is much more challenging to collect the genetic samples from the full pool of candidate parents in the field than it is to do the subsequent laboratory work.

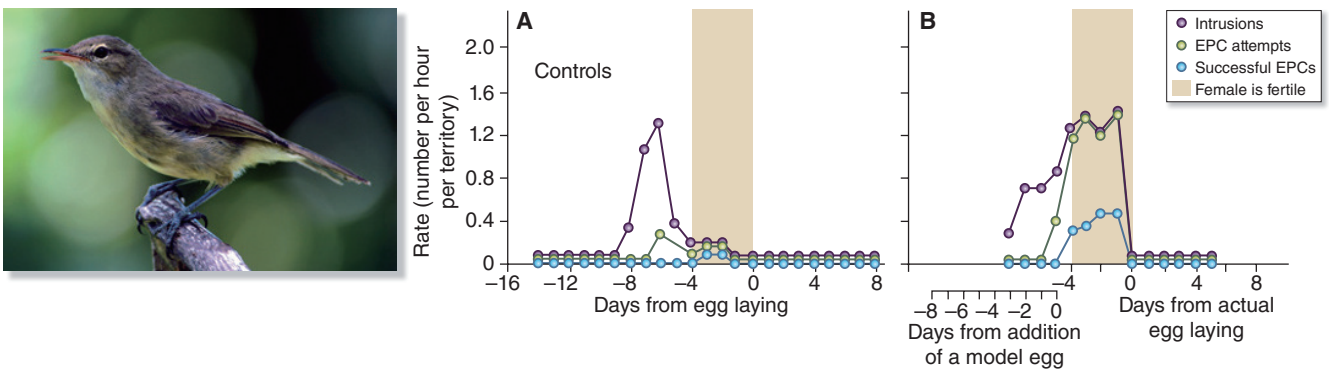


Fig. 9.12 Pre-breeding mate guarding and extra-pair copulation (EPC). Male Seychelles Warblers (*Acrocephalus sechellensis*) fiercely mate guard during the female fertile period to avoid EPCs. (A) In control pairs, the rate of territorial intrusions by other males, EPC attempts, and successful EPCs drops off during the female fertile period, as expected. (B) When males were experimentally fooled into thinking that their mate was past her fertile period (via the addition of a model egg in a newly lined nest), they left her unguarded, allowing other males to engage in more territorial intrusions and gain more EPCs. (From Komdeur et al. 1999. Reproduced with permission from the Royal Society. Photograph by Jonathan Hornbuckle.)

their mate guarding even though their females were still fertile. Neighboring males were quick to take advantage of the situation by sneaking into the territory of the unguarded female and copulating with her (Fig. 9.12). As a result, the rate of extra-pair copulations was much higher for poorly guarded females than for those with an alert protector.

One point to consider here is that when mate guarding is necessary and effective, the potential for female infidelity can push males towards monogamy, because they must forgo opportunities to mate with other females while guarding their own mates. Another point is that **social monogamy**—the pair bonding typical of so many birds—does not always,

Social monogamy: in birds, a mating system in which one female forms a lasting pair bond with one male, although she may also copulate with other males.

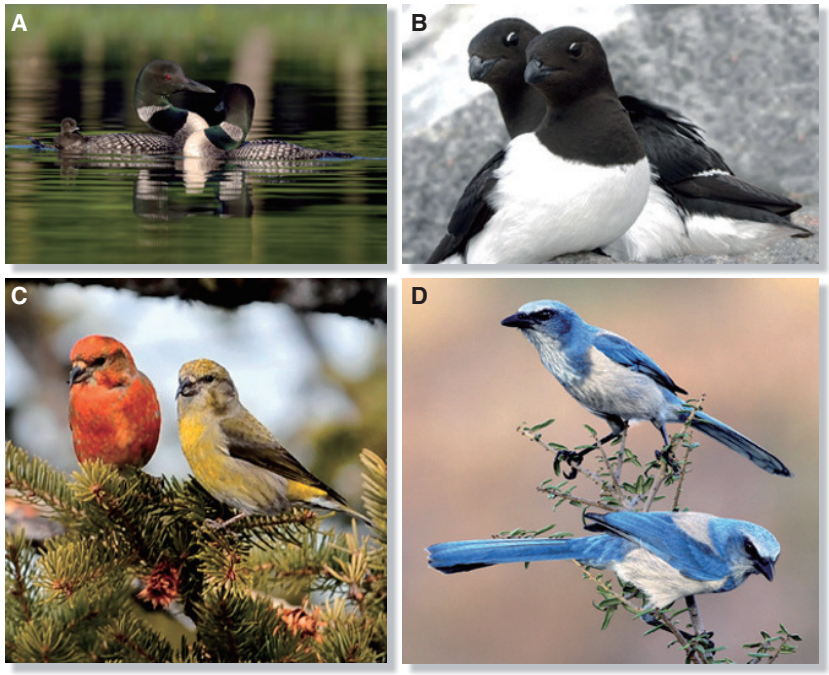


Fig. 9.13 Reproductively monogamous bird species. The following species are among those that form socially and genetically monogamous pair bonds: (A) Common Loons (*Gavia immer*), (B) Dovekies (*Alle alle*), (C) Red Crossbills (*Loxia curvirostra*), and (D) Florida Scrub-Jays (*Aphelocoma coerulescens*). (Photographs by: A, Mary Anne Pfitzinger; B, Leo Roos; C, Christine Pentecost; D, Matthew Studebaker.)

or even often, equate with **genetic** (true) **monogamy** in which a socially monogamous couple only has offspring of their own. Such genetic monogamy does occur sometimes, however (Fig. 9.13). For example, Common Loons, the widespread bird known in Eurasia as the Great Northern Diver (*Gavia immer*), apparently never engage in extra-pair copulations (Piper et al. 1997). Likewise, in the colonial Dovekie (*Alle alle*), the species known as the Little Auk in Eurasia, males occasionally attempt an extra-pair copulation with a neighboring female, but these females make cloacal contact all but impossible and almost never produce offspring with a male other than their social partner (Wojczulanis-Jakubas et al. 2009). A few songbirds also are represented in the small truly monogamous contingent; for example, a genetic study of a Norwegian population of the Red (aka Common) Crossbill (*Loxia curvirostra*) found that all offspring were sired by the male that was socially bonded to their mother (Kleven et al. 2008). Similar genetic monogamy occurs in the Florida Scrub-Jay (*Aphelocoma coerulescens*), a species whose complex social behavior is discussed later in this chapter (Townsend et al. 2011).

Far more common, however, is the finding that a number of the offspring produced by pair-bonded males and females have a father other than the female's social companion. In some species, extra-pair paternity is relatively low; for example, in a Finnish population of Eurasian Three-toed Woodpeckers (*Picoides tridactylus*), fewer than 10% of the nestlings sampled had been sired by a male other than the female's social partner (Li et al. 2009). On the other hand, fewer than 50% of Reed Bunting (*Emberiza schoeniclus*) chicks possessed the genes of their mother's social partner (Dixon et al. 1994). Although not quite so eager for extra-pair copulations as Reed Buntings, female California Towhees (*Melozone crissalis*)—a socially monogamous species in which males and females stay in close contact, like their relatives the Abert's Towhees (*Melozone aberti*)—nevertheless engage frequently in extra-pair copulations, with more than 40% of all nests having at least one egg sired by an extra-pair male (Benedict 2008). In such cases the puzzle of male monogamy can be partly resolved by noting that monogamous males actually are would-be polygynists who readily take advantage of opportunities to sire additional offspring by mating with extra-pair females (Box 9.07).

Nonetheless, in explaining why males of so many birds spend most of their time and energy associating with a single female in a pair-bonded relationship (instead of trying to mate with as many females as possible), we need hypotheses that focus on the benefits of social monogamy. The mate-guarding hypothesis is not the only such explanation, which is fortunate because it cannot explain, for example, why male Purple-crowned Fairywrens (*Malurus coronatus*) in Australia remain close to their females at all times, whether they are fertile or not (Fig. 9.14), nor why they fail to court other females that they happen to encounter (Hall and Peters 2009). In this species and others, monogamy seems driven by the female's voluntary fidelity to a social partner, not

Genetic monogamy: a mating system in which a female mates with only one male.

Box 9.07 Extreme infidelity in fairywrens

Among all socially monogamous birds studied so far, the small, brightly colored fairywrens of Australia hold the record for their extraordinarily high levels of extra-pair mating. In most fairywren species well over half of the offspring are sired by males from outside the pair bond, and in one species—the Superb Fairywren (*Malurus cyaneus*) (Fig. 9.B7.01)—up to 80% of the nestlings in a population can be sired by extra-pair males, and nearly all nests have at least one extra-pair nestling.

Why do some female fairywrens engage in such high levels of extra-pair mating? Part of the answer might be that their cooperative social system renders breeding females less dependent on the help of their social mates. These fairywrens typically occur in small, cooperative groups, which most often comprise a female, her social mate, and a number of male offspring from previous seasons. The lingering sons aid their mother in later breeding attempts, for example by bringing food to the nestlings (which are at least half-siblings of the helping son, if not full siblings). The dominant, socially mated male in each group helps less and less with breeding duties as the number of other helpers in his group increases. With many helpers around to fill in for the social male, the breeding female is buffered against retaliation by her social mate should her infidelities lead him to reduce his investment in parental care of nestlings that may not be his own offspring (Mulder et al. 1994) (Fig. 9.B7.02).

Another explanation for this mating behavior is that patterns of dispersal in these species may lead females often to pair socially with an undesirable male. First, female fairywrens typically disperse from the territory in which they were born to become breeders themselves, but open territories are in short supply. It might make sense for a dispersing female to grab any territorial opening that she encounters, even if it means pairing with a lower quality male who owns that territory. Similarly, when a female's mate dies, the breeding vacancy typically is filled very quickly (often in less than an hour) by a dispersing helper male from a neighboring territory (Pruett-Jones and Lewis 1990). Thus, fairywren females may have little opportunity to choose their social mates, and extra-pair mating may allow them to mate with males of higher (genetic) quality than their



Fig. 9.B7.01 A male Superb Fairywren (*Malurus cyaneus*). In this species, females constantly seek copulations with promiscuous high-quality males, but retain a monogamous social bond. Females receive most of their nest provisions and protection from subordinate helper males. (Photograph by Marjorie Kibby.)

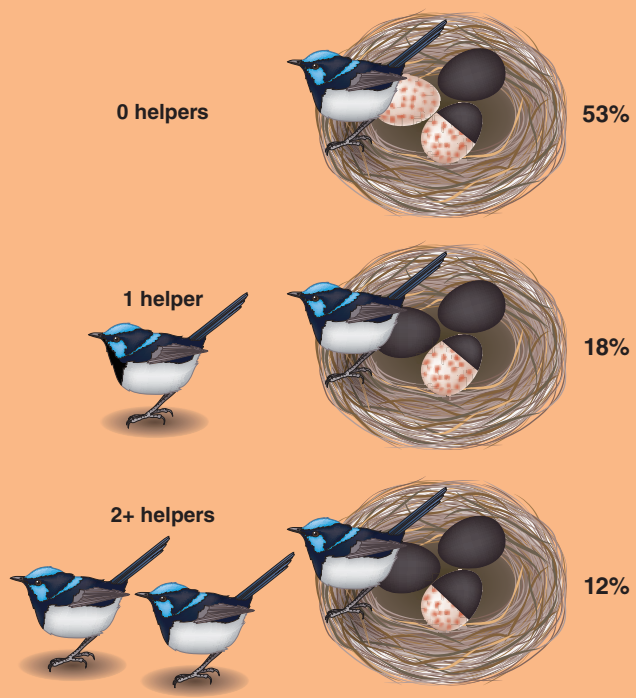


Fig. 9.B7.02 Paternity is negatively correlated with the number of helpers. Female Superb Fairywrens that rely more on plentiful helper individuals tend to engage in more extra-pair copulations, trading tighter social and mating bonds with one male for the genetic benefits of mating with many males. Note that percentage paternity per nest (given at right) decreases as helper number increases (at left). (Illustration by Amellia Formby. Reproduced with permission.)

Continued

own mate. This opportunity may be particularly important in fairywrens because their natal dispersal distances are unusually short, leading to high levels of relatedness within social neighborhoods; consequently, a female often may end up being paired to a close genetic relative. Thus, female fairywrens may use extra-pair matings to avoid the deleterious effects of inbreeding (Brooker et al. 1990; Tarvin et al. 2005).

Long-term studies of Superb Fairywren social behavior have been conducted in the Australian National Botanic Gardens in Canberra by Andrew Cockburn and his colleagues (Dalziell and Cockburn 2008). By closely following the birds in this population, the research team discovered that female fairywrens gain their extra-pair matings just before dawn during short forays into other territories, when their social males would likely have a hard time following them to mate-guard. This also is the time of day when the breeding males engage in a dawn chorus (Chapter 10), advertising their own availability to females on other territories in a sort of hidden lek (Cockburn et al. 2009). The male fairywrens therefore face a trade-off between a potentially futile attempt to guard their own pair-bonded mate versus staying at home and singing with the possibility of attracting extra-pair females.



Fig. 9.14 Purple-crowned Fairywren (*Malurus coronatus*) pair. Males of this species guard their partners despite the negligible risk of extra-pair copulation. (Photograph by Alwyn Simple.)

by the male actively preventing his partner from engaging in extra-pair copulations.

Let us consider still another explanation for monogamy, that a pair-bonded male can boost the production of his own surviving offspring by helping his social partner rear a brood of baby birds. This hypothesis makes intuitive sense, because many male birds clearly have the potential to be helpful parents by building a nest, incubating eggs, brooding nestlings, or feeding fledglings. The "mate-assistance hypothesis" for monogamy generates a number of predictions, one of which is the expectation that the paternal male will have sired a least some of the offspring he helps rear. Genetic studies have upheld this prediction for the great majority of socially monogamous bird species, in which the female's social partner typically has sired at least some of the offspring of his mate.

A second prediction of the mate-assistance hypothesis is that females who lose part or all of the assistance of their pair-bonded partner will rear fewer surviving progeny than females who retain their helpmate through the breeding season. This prediction also has broad support, because the male's contribution to parenting has been shown to be valuable in many cases. In European Starlings (*Sturnus vulgaris*), for example, males vary in how much they contribute to the incubation of their mate's eggs, with some males incubating much of the time and others less so. The males that are the most faithful incubators help their mates keep the eggs at a higher average temperature during the incubation period. These higher egg temperatures promote more rapid development of the embryos within, which is advantageous for the offspring and therefore for both parents (Komdeur et al. 2002).

The importance of males to their mates also has been shown through experimental removal of the partner, which often has a negative effect on the number of fledglings produced at nests cared for by widowed females. If, for example, the male partners of Snow Buntings (*Plectrophenax nivalis*), a bird of the Arctic, are removed early in the incubation period when males often feed their mates, the widowed females rear fewer offspring than those that are widowed late in the incubation phase (Lyon et al. 1987).

Another kind of test of the mate-assistance hypothesis for social monogamy comes from a comparative study of a group of European warblers in the genus *Acrocephalus*. In this genus, monogamous species tend to occupy poor habitats where rearing offspring is difficult, whereas polygynous species occur in resource-rich environments (Leisler et al. 2002). These trends suggest that, when social

monogamy has evolved in this group, it is because having a helpful male partner substantially increases the production of surviving offspring when birds occupy a challenging habitat.

Generally speaking, findings of this sort indicate that paternal males derive benefits from their social monogamy, although it often remains difficult to tell whether these benefits (including reduced partner infidelity and increased offspring production) really outweigh the overall costs (a smaller number of females inseminated).

9.5.2 Polygyny: the puzzle of female participation

It makes intuitive sense from the female perspective to have a socially monogamous, paternal male around to assist in various ways, perhaps especially in the feeding of nestlings and fledglings. In the European Starling (*Sturnus vulgaris*) and in other species such as the House Wren (*Troglodytes aedon*) (Soukup and Thompson 1998), females lose paternal care for their offspring when their social partner acquires an extra-pair mate (Fig. 9.15). Therefore, in the starling and other socially monogamous species, females often react aggressively toward prospecting females that enter their territory. In fact, female European Starlings and House Wrens have been observed destroying the eggs of other females that attempt to breed with their partner. In so doing, a female can try to force monogamy on her partner, making it advantageous for him to care only for her own brood. Given the successful attempts of females of many bird species to monopolize the paternal care offered by a social partner (Slagsvold and Lifjeld 1994), it seems odd that in other species females accept a polygynous male even though the female must share her male's parental care with his other sexual partners or even lose his assistance altogether.

Of course it is possible in some cases that polygynous males may not alert some partners that they have already acquired another mate. For example, this "deceit hypothesis" may apply to the European Pied Flycatcher (*Ficedula hypoleuca*), in which males that have established a territory and attracted a mate sometimes attempt to acquire a second territory with a second female. These dual territories can be up to 3 kilometers away from one another, and the secondary female may not know that her newfound male already has a mate elsewhere. Once she begins to lay eggs and incubate, her now polygynous partner typically returns to his primary mate, whose offspring will be the beneficiaries of all or most of his parental care. The secondary female and her brood lose out (Alatalo and Lundberg 1984). Perhaps secondary females are not really deceived by their partners but instead are simply making the best of a bad situation arising from their late arrival on the breeding grounds. Alternatively, they may voluntarily accept a polygynous male whose special attractiveness increases the odds that they will produce sons that inherit his appeal, thereby increasing their number of grand-offspring (the sexy son hypothesis discussed earlier in the chapter) (Huk and Winkel 2006).

In any event, polygyny is not surprising from the male perspective. Males that can inseminate more than one female successfully typically fertilize more eggs than they would if they restricted themselves, or were restricted by aggressive partners, to a single mate. What conditions enable males to practice polygyny successfully despite the apparent costs to their mates?

Consider the Montezuma Oropendola (*Psarocolius montezuma*), a Central American species in which several to many females build their long hanging nests from the same tree (Webster 1994) (Fig. 9.16). Under these circumstances, some males can acquire a number of mates by

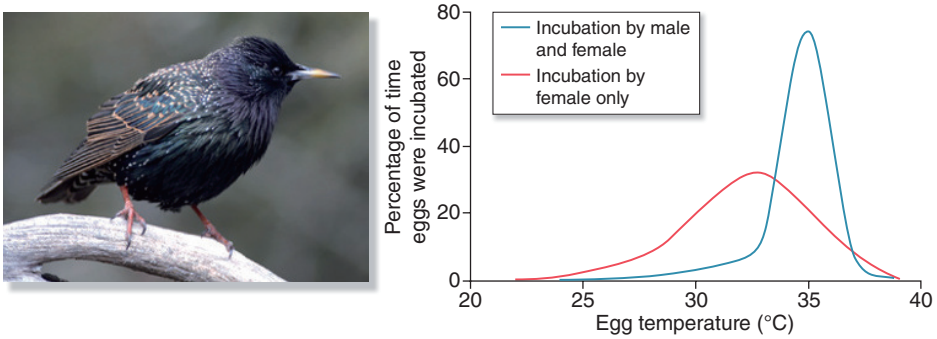


Fig. 9.15 Offspring gain a developmental benefit from attentive fathers. When male European Starlings (*Sturnus vulgaris*) contribute to incubation, eggs spend more time at temperatures optimal for development (blue line) compared with instances in which only the female incubates (red line). (From Reid et al. 2002. Reproduced with permission from Springer Science + Business Media. Photograph by Carrie L. Johnson.)



Fig. 9.16 Montezuma Oropendula (*Psarocolius montezuma*) nest colony. To court females, males spread their wings and make a series of loud trickling-sounding calls before hanging upside-down near one of many pendulous nests. (Photograph by William David Grimes.)

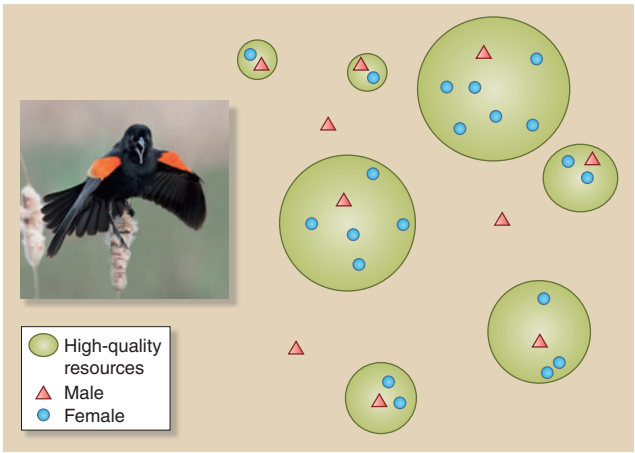


Fig. 9.17 Resource defense polygyny. This mating system arises in Red-winged Blackbirds (*Agelaius phoeniceus*) and other species that occupy a patchy nesting habitat with limited resources. Males (red triangles) occupying superior territories with better nest sites and resources (green circles) generally secure more mates (blue circles), while males on inferior territories attract few or none. Some males do not have territories at all as good habitat is limited. This mating system offers a trade-off between resources and parental care: females on better territories have access to more food but get less help from their mate. (© Cornell Lab of Ornithology. Photograph by Nick Saunders.)

monopolizing the group of females at a nest tree. Indeed, males compete with one another to prevent rivals from approaching the nest tree. Successful males presumably gain more through polygyny than they could by guarding one female or assisting a single partner in the rearing of her brood. To the extent that powerful territorial males can pass their attributes on to their sons, females could gain by accepting top males as their partners, thereby increasing the odds of having reproductively successful sons. The result of male competition for pre-existing groups of females has been labeled **female defense polygyny**, a mating system that is common in mammals but relatively rare among birds.

A far more common kind of avian polygyny can occur if some males invest in the defense of resources rather than in direct parental care. **Resource defense polygyny** is practiced, for example, by the Red-winged Blackbird (*Agelaius phoeniceus*) of North America (Fig. 9.17). As males divide up a marsh or abandoned farm field into a set of breeding territories, some individuals may be able to acquire real estate of exceptional value; that is, a territory with unusually large amounts of insect food that could be supplied to nestling blackbirds, or one with unusually safe, well-concealed nest sites. Unmated female Red-winged Blackbirds then can be faced with options that include joining an unpaired male who holds a territory with only modest resources or joining an already-paired male whose territory is of considerably higher quality. Under these circumstances, it can pay for the female to enter into the polygynous arrangement if the difference between the territories of the two males is sufficiently great (Orians 1969).

This explanation for why female Red-winged Blackbirds often accept polygynous partners has been tested experimentally. Researchers gave some males extra cattail reeds placed over water and others a reed supplement of the same size placed over dry land. Faced with a choice between a safer over-water location in a territory that already had attracted one female and a less safe one owned by a male without a mate, the female blackbirds in this study almost universally chose the safer over-water option, even though they had to share a territory with another female and also share whatever parental care was offered by their partner (Pribil and Searcy 2001).

Female defense polygyny: a mating system in which one male is the predominant mate for multiple females, through defending that group of females against other males.

Resource defense polygyny: a mating system in which one male is the predominant mate for multiple females, through defending against other males a high-quality territory or other valuable resource that attracts a group of breeding females.

9.5.3 Lek polygyny

The most striking form of polygyny exhibited by birds and other animals occurs at **leks**, places where males gather in display arenas or guard small display territories, often very close to those of their rivals, in order to court and mate with visiting females. The polygynous males are the fortunate ones that acquire multiple sexual partners during one breeding season. Although only a small fraction of bird species have a lek-based mating system, this mating behavior has evolved independently in many avian lineages. Lekking species include the Black Grouse (*Tetrao tetrix*) and Great Snipe (*Gallinago media*) mentioned earlier in this chapter, as well as some other grouse, sandpipers, and hummingbirds. Lekking also has evolved among the songbirds, where it is exhibited by many manakins, birds-of-paradise, bowerbirds, cotingas, and tyrant flycatchers, among others. In leks, the male's display territory does not contain any resource of direct value to the female: it has no nesting site, no food—only the male himself. Because the only thing a male has to offer a given female is his genes, sexual selection via male–male competition (Chapter 3) generally is acute in lekking species, which in turn have evolved some of the most dramatic and spectacular physical ornaments and display behaviors.

Leks can have many spatial configurations. Males in some species gather only in loose aggregations; in these **exploded leks** males usually display in the same general area but not necessarily within view of one another. The Satin Bowerbird (*Ptilonorhynchus violaceus*) (Box 9.01) is an example of this kind of lekking species. Males of that species generally build their bowers about 250–300 meters apart (Reynolds et al. 2009).

At a classic lek, the displaying males are very close together and spend considerable time and energy behaving aggressively toward one another as they compete for spots within the lek favored by visiting females. Black Grouse offer an example of this sort of mating system. In this European species, 10 or 20 males may attend a single display site, with the nearest neighbors spaced only a few meters apart. When female birds visit classic leks, they generally watch the males interacting and displaying before sometimes moving toward a particular individual. As a female approaches a male, he responds with elaborate courtship, often combining both visual and acoustic components. These courtships often involve demonstrations of the extraordinary feather ornaments that many lekking species possess: Greater Sage-Grouse (*Centrocercus urophasianus*) in North America fan their tails and puff out the breast feathers that surround their brilliantly orange vocal sacs; Victoria's Riflebirds (*Ptiloris victoriae*) in eastern Australia wave their extended wings from one side to the other in a carefully timed ritual; and the Blue Bird-of-Paradise (*Paradisaea rudolphi*) of New Guinea hangs upside down from a limb while shimmering a fan of blue body feathers (Fig. 9.18).

Lek: an aggregation of males that engage in competitive mating displays toward visiting females.

Exploded lek: a loose aggregation of males that engage in competitive mating displays toward visiting females; exploded leks are more spread out in space than are classic leks.



Fig. 9.18 Blue Bird-of-Paradise (*Paradisaea rudolphi*). Males of this species hang upside down and fan out their feathers as part of a lekking courtship display. (Photograph by Fabien Pekus.)

Subtle differences among males may have big effects on the reproductive success of lekking individuals. In the male Golden-collared Manakin (*Manacus vitellinus*), the brightness of the yellow collar greatly affected male reproductive success in one population studied in Panama (Fig. 9.19). Here, as in other brilliantly plumaged birds, the intensity of feather colors is linked to physiological condition, with brighter males tending to be in better physical condition (Stein and Uy 2006). Perhaps because they are in such good shape, bright males may be better performers for visiting females. Indeed, some male Golden-collared Manakins are faster than others in getting their "beard" of throat feathers extended upon landing on a perch after a period of energetic bouncing from a sapling to the ground and back. In one study, the fastest males resumed their extended throat feather pose in 43 milliseconds, but the slowest males required 63 milliseconds to adopt the correct posture (Schlinger et al. 2001). Needless to say, these and other behavioral differences are tiny in absolute terms, but some ornithologists believe that female manakins can detect the differences as males run through their routines and that



Fig. 9.19 Golden-collared Manakin (*Manacus vitellinus*). Males display by rapidly flaring out their golden throat feathers. Females assess males based on their display, throat color (which indicates condition), and position in the lek. (Photograph by Marie Read.)

they use this information to make decisions about who does and who does not get to mate.

There is no question that behavioral differences among males play a critical role in female mate choice in other lekking species. For example, the way in which male Satin Bowerbirds engage in courtship clearly determines their success with females. Males that dance very vigorously, even aggressively, before the female are more likely to mate than those whose actions are less intense. In addition, males that are able to moderate the degree to which they charge at the female do better than males less capable of adjusting their display in response to whether the visiting female flinches, crouches down, or remains in place during a male performance (Patricelli et al. 2002).

From the male's perspective, lekking represents an investment in courting many females with the possibility of fathering a great many offspring. At most leks, most or all females choose the same male to inseminate them, conferring very high reproductive success on the favored male. The corollary is that the reproductive output of the other, less attractive males is very low (during a given year). For example, at leks of the Golden-collared Manakin in Panama, three to eight males competed for the attention of visiting females, but only one or two of these males secured almost all the copulations during one breeding period (Schlinger et al. 2008). This pattern of great variation in mating success among individuals is termed high **reproductive skew** (the alternative pattern where all members of a given sex have equal mating success is termed low reproductive skew). One review of this kind of variation among lekking bird species found that 10–20% of the males at leks customarily account for 70–80% of all matings (Mackenzie et al. 1995) (Box 9.08).

Given that a tiny fraction of the males at most leks monopolize most mating opportunities in any given year, what can the other males do to secure at least some copulations? Males of some species have evolved a behavioral flexibility in which low-status males employ alternative tactics that help them make the best of a bad situation. For example, at study sites in Sweden, Great Snipe (*Gallinago media*) males that are excluded from prime territories by highly dominant, highly attractive males sometimes establish territories immediately adjacent to the sites held by their superior rivals. These satellite males occasionally may get a chance to intercept and mate with a female headed toward a prime male on his super-territory (Höglund and Lundberg 1987).

Another tactic has evolved in the Ruff (*Caladris pugnax*), a large Eurasian sandpiper, in which actively lek-displaying males have brightly colored plumage in a variety of color morphs. Other Ruff males lack this distinctive plumage and instead mimic the drab appearance of females. By posing as females, these sneaker males may be permitted to enter a very attractive male's domain. Yet a third kind of male adopts male plumage but does not hold a territory on the lek; these satellite males linger on the periphery and attempt to mate with females as they are passing by (Fig. 9.20). All three of these strategies are sometimes successful, though the lekking males generally sire the most offspring (Jukema and Piersma 2005).

Still another tactic that males can use under certain circumstances is to associate with relatives who may concede a few matings to their brothers or nephews. In the Satin Bowerbird, for example, males tend to build their bowers fairly close to that of a relative. These birds avoid attacking the bowers constructed by relatives in favor of going after those owned by unrelated males (Reynolds et al. 2009). The generous behavior exhibited by relatives toward one another makes evolutionary sense in the context of kin selection (Chapter 3). When males help relatives, they help the portion of their own genes present in these other kin.

A final reason why low-ranking males may participate in lek mating systems requires us to take a long-term perspective. Males may copulate rarely, if ever, when they are low-ranking members of a lek, but if they are fortunate to survive a number of years, they eventually may secure an

Reproductive skew: refers to the degree to which reproduction is limited to only a few adults in the population (high skew) or is more equal among all adults in the population (low skew).

Box 9.08 Tracking mating success in Lance-tailed Manakins

Observant researchers have spent many thousands of hours patiently waiting for female birds to visit leks so they can record which male each visiting female chooses as a sexual partner. Do the matings observed at leks represent the entire story, or do females sometimes mate with other males at times and places where they are not being observed by scientists? A direct way to track the mating success of males is to sample all the newly hatched birds in a population and use genetic techniques to determine which males sired which offspring (Box 9.06). This approach might seem to be easy, but simply finding the nests of most lekking species usually is a great logistical challenge, because females leave the lek after mating to nest alone somewhere in the surrounding environment (Fig. 9.B8.01A).

These difficulties are even greater in tropical forests, where finding cryptic nests within the lush vegetation is particularly daunting. Nevertheless, while studying Lance-tailed Manakins (*Chiroxiphia lanceolata*) in western Panama, a hard-working team led by Emily DuVal (2007) was able to find hundreds of nests and genetically match the offspring they contained to the males that sired them. Lance-tailed Manakins have a display system very similar to that of the Long-tailed Manakins (*Chiroxiphia linearis*) described elsewhere in this chapter and Box 9.09. In both species, pairs of males partner together to perform a tightly coordinated display. Each lek usually has one pair of dominant displaying individuals and 10 or more subdominant males who do not engage in displays. A female usually visits many leks and then mates with the alpha male at one lek. Beta males seem to mate very rarely, even though they partner actively with the alpha in their joint display (Fig. 9.B8.01B).

DuVal's genetic studies confirm that Lance-tailed Manakin alpha males get most of the mating opportunities: of the 413 nestlings she tested, more than 92% were fathered by an alpha male, and most of the remainder were sired by males that were on their way to gaining alpha status in the next year (DuVal and Kempenaers 2008). Although beta males rarely mated, they had a reasonably good chance of moving up to alpha status if the alpha male disappeared (either through natural causes or when he was temporarily removed by the researchers).

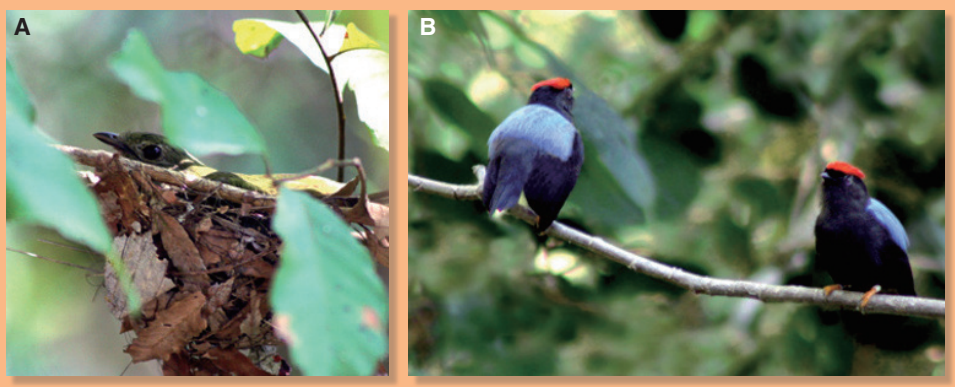


Fig. 9.B8.01 Lance-tailed Manakins (*Chiroxiphia lanceolata*). (A) A female sits quietly in her nest. (B) Two males—an alpha and beta—sit on a display branch. (Photographs by Carla C. Vanderbilt.)

alpha position and all the mating opportunities that go with being a dominant male. However, only males that persistently participate in the lek have a chance to move up the ladder to the top. This argument has been demonstrated to be correct for lekking Long-tailed Manakins (*Chiroxiphia linearis*). In this species, some males display to help others attract females. The subordinate males often wait years for the payoff that comes when the more dominant individual dies, enabling the patient helper to move up to the top spot. Only then do they have a chance to leave copies of their genes to the next generation (McDonald and Potts 1994).

9.5.4 Absence of male parental care and the lek paradox

Male Golden-collared Manakins (*Manacus vitellinus*) spend many months each year at their lek, with individual manakins returning year after year to exactly the same set of saplings where they reconstruct their display arena. Should a male be so fortunate as to mate, he does not accompany that female when she departs; instead he returns to the dance floor to continue his efforts to persuade other females to copulate with him. The mated females are left to do the hard work of nest building,



Fig. 9.20 Reproductive morphs of male Ruffs (*Calidris pugnax*). Satellite males do not engage in lekking behavior or territory defense. Instead, they linger near the periphery of the lek and try to mate with females as they pass through, or when the lekking males are busy displaying or fighting. Here, the satellite (left) was detected and must suffer the consequences as the dark-plumed male (right) fiercely defends his territory. (Photograph by Dominique Halleux.)

incubation, nestling feeding, and fledgling chaperoning completely on their own.

Why do male manakins, and males of the many other lekking species, not help their sexual partners rear their offspring? Why do female birds choose to mate with males whose only contribution to the next generation is their sperm? One possibility is that lekking tends to evolve in species in which biparental care is not essential or even is harmful, and hence male care would do little or nothing to boost the reproductive output of either the male or female. This possibility could apply to species such as grouse and sandpipers with precocial offspring (Chapter 11) that are not fed directly by their parents after hatching. Biparental care may be a handicap in some tropical forests and other situations where predators that raid nests are abundant, and where the increased number of visits by an attendant male would increase the chances of a predator finding the nest.

Given that lekking males and their territories provide no parental care or food for females or their offspring (Höglund and Alatalo 1995), it seems reasonable to assume that female mate choice in these birds probably revolves around securing good genes, although, as previously mentioned, females also might benefit from mating with healthy, non-parasitized, non-infectious partners. If the ecology of the species is such that male assistance either has little benefit for females or provides few benefits for males, then females may be forced to participate in a system in which the best that they can do is to choose a healthy mate or one with good genes.

The good genes theory, however, does generate a major puzzle, which goes as follows: if females select mates on the basis of their genetic makeup, then in relatively short order, genetic variation in the male population will be drastically reduced. Why? Because if only a small group of males gets to pass on their genes, soon the gene pool will be filled with the particular genetic variants possessed by the small number of popular males of the past. In the absence of hereditary variation among males, females gain nothing by being choosy. But in avian leks today, females of most species continue to be highly selective about their choice of sexual partners. This conundrum is known as the **lek paradox**.

Many solutions to this paradox have been suggested (Kotiaho et al. 2008), most of which are based on rather arcane mechanisms that could maintain genetic variation in a population even when females consistently choose males with a particular genetic makeup. For example, if female choice favors males that are heterozygous (that is, males that have two different forms of many different genes rather than two copies of the same allele of these genes), then by choosing the most intrinsically diverse males, females select for the maintenance of genetic variation among males over time.

9.5.5 Polyandry: why do males accept polyandrous mates?

Another puzzling feature of avian mating systems involves the rare cases in which males voluntarily participate in **polyandrous mating systems** in which males mate with females that have more than one sexual partner. Particularly surprising are the instances in which several males act as helpers to the same female, whose sexual favors they must share. In the Galápagos Hawk (*Buteo galapagoensis*), for example, as many as eight unrelated males may pair bond with a single female on a territory, which all defend jointly. The polyandrous female copulates with all her partners more or less equally, meaning that the males are essentially taking part in a fertilization lottery (DeLay et al. 1996). Why might male Galápagos Hawks tolerate this competition within their territory rather than trying to defend a territory on their own? One possible answer is that suitable hawk territories are in very short supply on some islands in the Galápagos, and generally there are many males competing for each suitable location. If several males join together

Lek paradox: a theoretical conundrum where, in a population in which all females mate only with the rare highest quality males, all offspring will inherit the traits that make those males so attractive, and hence over a few generations there will be little genetic variation among males in those important traits.

Polyandrous mating system: a mating system in which one female mates with multiple males.



Fig. 9.21 Sex-role reversal in Wilson's Phalaropes (*Phalaropus tricolor*). In this species, females (right) exhibit brighter plumage and aggressively compete for males (left), which incubate eggs and provide parental care without female help. (Photograph by Larry Jordan.)

and cooperate in defending valuable real estate that a female will accept, they can win out over single males that try to defend a solo territory. Under these constraining circumstances, a male in a group has at least some possibility of fertilizing an egg and thus does better than a solo male without a suitable territory.

The Galápagos Hawk is unusual but not unique among birds in engaging in social polyandry, with more than one male behaviorally pair bonded with the same female. An even better known example of polyandry in birds involves the phalaropes, three species of small shorebirds that breed primarily in the Arctic. In the phalaropes, a sex-role reversal has occurred so that females compete aggressively with one another for mates while courting males (Fig. 9.21). The males they court in turn assume all parental duties once the eggs have been laid in their nests. Some female phalaropes achieve **sequential polyandry** by abandoning an initial partner after supplying him with a clutch and then securing another mate that will care for a second batch of eggs. When polyandrous females leave their partners, the male's only good option is to continue to accept the parental role because he can incubate a clutch of eggs successfully by himself. Later, the newly hatched, precocial chicks feed themselves on an abundance of insect food (Reynolds 1987). Males that retaliate against female abandonment by also abandoning their nests would leave no descendants at all. As we might predict given the unusually high male parental investment by phalaropes, genetic studies have shown that only a very small percentage (<2%) of all phalarope chicks are sired by a male other than their caretaker (Schamel et al. 2004). The paternal male phalarope thereby enjoys a direct genetic payoff in return for his attentiveness to his nest.

One of the ways male Red Phalaropes (*Phalaropus fulicarius*) increase the odds that they will produce offspring with their own genes is to increase the frequency with which they copulate with their one partner during her fertile period (Schamel et al. 2004). Male birds that provision offspring also generally make this activity contingent upon sexual access to the mother of those offspring, a fact that some polyandrous females use to "encourage" paternal behavior on the part of all their mates. For example, the Dunnock (*Prunella modularis*) is a drab little European bird that exhibits a rich diversity of mating systems (Davies 1985). In some cases, a polyandrous female lives with two male partners with whom she copulates at frequent intervals. Socially polyandrous Dunnock females tend to solicit matings from the male that thus far has had fewer copulations, thereby activating the male's psychological mechanisms that push him (unconsciously of course) toward paternal behavior when the nestlings have hatched and need to be fed. Because copulation frequency correlates with egg fertilizations, males that mate often with a female are likely to have sired at least some of her offspring. A polyandrous female that skillfully partitions matings between two males gains two caretakers for her progeny, a clearly advantageous consequence for the female in this species in which the additional paternal care increases the number of offspring they can rear in a breeding season.

When a polyandrous female gets her partners to care for her offspring, she derives an obvious material benefit from copulating with more than one male. However, many socially monogamous females solicit extra-pair copulations from males that cannot or will not be available when the eggs hatch. The added parental care hypothesis for polyandry does not apply to these situations. A reproductive benefit that could lead females to mate with multiple partners is that receiving sperm from several males provides **fertility insurance** against the possibility that their social partner's

Sequential polyandry: a mating system in which one female mates with multiple males within a breeding season, but with only one male during each successive nesting attempt.

Fertility insurance: mating with multiple males to help ensure that at least one partner is sexually fertile.

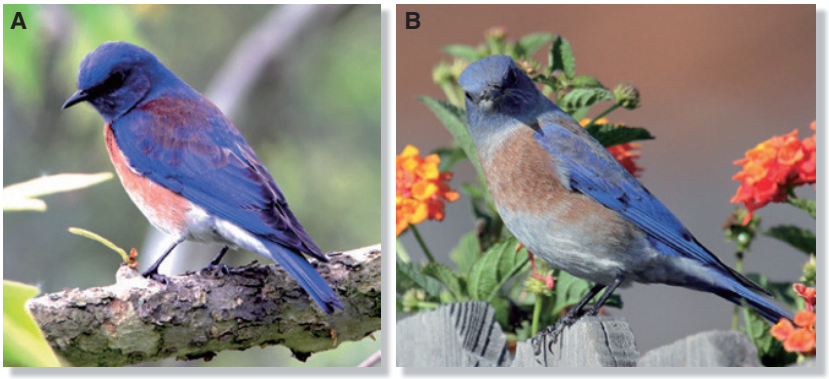


Fig. 9.22 Western Bluebird (*Sialia mexicana*) plumage differs with age. Females can judge the age of a male by the intensity of his feathers. (A) Males with deeper blue feathers are typically older, demonstrating their potential fitness and ability to survive. (B) Younger males are generally duller and provide less parental care for their broods. (Photographs by: A, Chris Morrison; B, Andrew A. Reding.)

sperm are inadequate or defective. Studies of a few species have found that a small but measureable percentage of male songbirds are infertile; the mates of these individuals certainly would benefit by receiving sperm from a fertile extra-pair partner. Thus, although 2–4% of Eurasian Blue Tit (*Cyanistes caeruleus*) and related Great Tit (*Parus major*) males tested in one study were infertile, the females mated to these individuals nonetheless produced six to nine offspring, demonstrating that their extra-pair copulations provided them with plenty of viable sperm (Krokene et al. 1998).

By far the most popular explanation for why females with a helpful social partner nevertheless mate outside the pair bond is the **good genes hypothesis** (Chapter 3). Polyandrous females in at least some species make choices that apparently provide them with good genes. For example, in the Reed Bunting (*Emberiza schoeniclus*), a boldly patterned black, white, and brown European finch, females are more likely to seek out males whose color pattern reveals that they are older than their social partners. To the extent that these older males possess hereditary traits that promote survival, females that select them as sperm donors may gain those valuable attributes for their offspring (Bouwman et al. 2007). Perhaps this is why female Western Bluebirds (*Sialia mexicana*) whose social mates have been removed temporarily are more likely to accept sexual advances made by neighboring males when those males are considerably older than their missing social partner. Because relatively old males have brighter blue head plumage (Fig. 9.22), females use this as a signal when deciding whether to accept or reject an extra-pair partner (Budden and Dickinson 2009). Other evidence suggests that these older bluebird males on average sire heavier offspring; heavier nestlings in general have a better chance of surviving to adulthood.

Good genes hypothesis: the idea that individuals choose mates based on an assessment of their potential genetic contribution to their mutual offspring, either directly by demonstrating components of the mate's fitness or indirectly by being able to survive and compete despite exaggerated sexual ornaments.

There are other possible benefits from extra-pair copulations, some of which may have the function from the female perspective of increasing the genetic diversity of their offspring. Some researchers have suggested that females prefer males that differ from them genetically to a greater extent than their social partners. Indeed, female Reed Buntings have been found to engage in extra-pair copulations with males that were more genetically dissimilar to them than their partners, with the result that their extra-pair young were more heterozygous (more likely to have two different copies of a given gene) than the offspring they produced with their social mate (Suter et al. 2007). Greater heterozygosity generally is believed to be developmentally advantageous, and, in fact, the extra-pair bunting offspring weighed more than their maternal half-siblings upon fledging.

The Reed Bunting experiment compared the properties of offspring that had different fathers but the same mother and the same rearing conditions, because they grew up in the same nest at the same time. This experimental technique has been applied to other species, including the Bluethroat (*Luscinia svecica*), the attractive Eurasian songbird mentioned earlier. In one population of this species about a quarter of all offspring are the products of extra-pair matings. One sample of these extra-pair offspring was more heterozygous than their maternal half-siblings who had the mother's social partner as a father. Moreover, the immune response of the extra-pair offspring was greater than that of within-pair offspring (Fossøy et al. 2008). These results support the hypothesis that extra-pair matings can confer genetic benefits to the resulting offspring, making extra-pair copulations adaptive for female birds of at least some species. However, results vary across studies,

with some not finding any support for the genetic benefits of extra-pair matings. At present, it remains hard to generalize about the type and impact of the genetic benefits arising from extra-pair matings across bird species, and this subject therefore remains an active area of research in behavioral ornithology.

9.5.6 Mating systems and sexual conflict

When two male Dunnocks (*Prunella modularis*) are paired with the same female, the odds are that they both will make parental investments in some offspring that, genetically speaking, are not theirs. The risk of cuckoldry is often substantial in socially monogamous species because, as noted already, the most common form of avian polyandry involves extra-pair matings by females that have a single social partner with whom they also mate. Although it is possible that females participate willingly in extra-pair matings and so are voluntary polyandrists, it also is likely that at least in some cases males harass females so severely that they either are forced to mate or do so as a way of ending the harassment. Indeed, some (but not all) behavioral ecologists have concluded that some cases of avian polyandry are entirely the result of male sexual drive and redound to the advantage of the male rather than the female (Arnqvist and Kirkpatrick 2005).

Most birders are likely to have observed male Mallards (*Anas platyrhynchos*) and other ducks aggressively pursuing apparently reluctant females across the water. Sometimes several sexually motivated male ducks simultaneously clamber onto the back of a harassed female, driving her underwater and potentially even drowning her as they all attempt to copulate (Fig. 9.23). Because these assaults occur more often when females are about to lay their eggs, and because they can result in successful sperm transfer and egg fertilizations, forced copulations of this type are likely to be a part of an adaptive male sexual strategy (McKinney et al. 1983). It seems less likely that they are advantageous to females, which may accept an unwanted mating only to terminate a potentially costly interaction. Cases of this sort have been labeled "convenience polyandry," with females mating with more than one male because they might be harmed if they refuse.

Note that this example of sexual conflict between males and females of the same species reflects what appears to be a general rule: individuals do what is in their own genetic interest, even if it harms others of their species and even if it reduces the reproductive success of a sexual partner. Such a view is derived from a modern understanding of evolution by natural selection, which occurs when individuals (not species as a whole) differ in their ability to pass on their genes (Chapter 3). As a result, exploitative, manipulative, or aggressive traits that advance individual reproductive success can spread through a population even if they generate severe conflicts of interest within that population.

One such example is seen in the Stitchbird (*Notiomystis cincta*) of New Zealand, a species in which paired males regularly enter nearby territories in pursuit of other males' females, which they often grasp in unusual face-to-face pairings accompanied by attempted copulation (Fig. 9.24). To this end, the male Stitchbird has a very large cloacal protuberance—the avian intromittent organ analogous to a penis (Chapter 6)—which facilitates the junction of the male cloaca with that of the female, which is necessary for sperm transfer. Researchers studying Stitchbirds have noted that these birds are perfectly capable of mating in the standard avian position, in which the male mounts a cooperative female as she stands still (Low 2005). The face-to-face matings involve behavioral and structural adaptations of males that seem designed to circumvent female mate choice and impose polyandry on females.

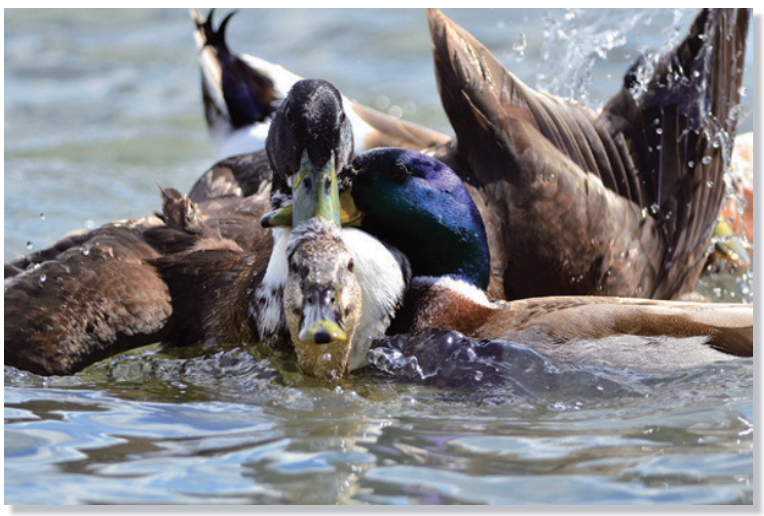


Fig. 9.23 Forced copulation in the Mallard (*Anas platyrhynchos*). Males in many duck species often violently force themselves upon females, sometimes even in groups. Females can drown or die of injuries related to these forced copulations. (Photograph by Don Bantum.)



Fig. 9.24 Forced copulation in the Stitchbird (*Notiomystis cincta*). This is the only bird species known to copulate face-to-face (rather than typical back-mounting), seeming to negate female choice. Here the arrow points to the tail and belly of the female, positioned on her back on the ground, beneath the male. Several forced copulation postures have been documented in Stitchbirds. (Photograph by Matthew Low.)

9.6 Costs and benefits of social behavior

Sexual interactions between males and females are merely one of many kinds of social interactions that occur among birds. Avian social behavior embraces a broad spectrum of activities, ranging from highly aggressive acts (as in the forced copulations of the Stitchbird and Mallard) to highly cooperative ones (as in the mutual parenting of a brood of nestlings by a pair of Abert's Towhees). In analyzing this diversity of behaviors, researchers have been assisted by a cost–benefit approach that is based on the premise that all interactions potentially have both a downside and an upside in terms of their effects on the fitness of the interactors. So, for example, when a male bird slips out of his territory to look for a mating opportunity with another female, his behavior has costs, such as the risk of being attacked by a mate-guarding male and the chance that his own social partner will mate with a sexual intruder during his absence. Likewise, when a socially paired female accepts or invites an extra-pair copulation, she may derive a benefit in the form of egg fertilization insurance or better genes, but she also may incur costs including the loss of paternal care that her cuckolded mate now withholds, physical assaults by her disgruntled social partner, or a heightened risk of acquiring sexually transmitted pathogens from her extra-pair partners.

The application of the cost–benefit approach to sociality has led to insights at several levels. For one thing, researchers now feel confident that highly social species are not inherently superior to more solitary ones; rather, these social species live under conditions in which the benefits of sociality are relatively great compared with the costs. For example, social aggregations are more likely to evolve in bird species whose predators can be better detected, repelled, or overwhelmed by groups of individuals than in species in which the antipredator benefits of sociality are too small to compensate for the costs of social living. Often, these costs are substantial. For example, Cliff Swallows (*Petrochelidon pyrrhonota*) in North America often nest in large colonies where their mud nests are packed side by side. The high density of these nests facilitates the spread of blood-sucking swallow bugs, which harm the growth and development of the nestlings they infect (Fig. 9.25). Not only are infestations and contagious diseases more likely to spread in densely packed groups, but competition for food also becomes more intense in an area in which many individuals are foraging (Brown and Brown 1986).

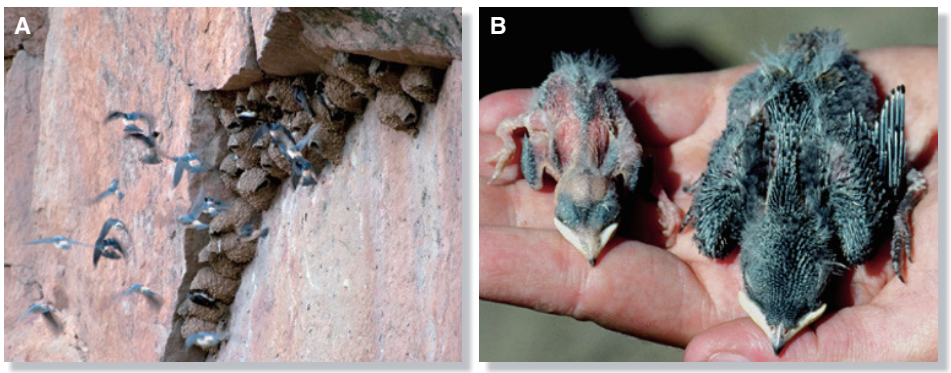


Fig. 9.25 A cost of sociality. (A) Colonies of Cliff Swallows (*Petrochelidon pyrrhonota*) occur among steep, rocky outcrops (as shown here) and on man-made structures. High-density colonies are more susceptible to the spread of nest parasites that impact the fitness and survival of the young. (B) The smaller nestling (left)—from a dense, infested nest colony—was attacked by blood-sucking swallow bugs, slowing its development and stunting its growth. The larger nestling (right) came from a nest fumigated with insecticide and so developed without the damage caused by swallow bug parasites. (Photographs by: A, Sharon Jue; B, Charles R. Brown.)

9.6.1 Territoriality and aggressive social behavior

The cost–benefit approach helps explain avian **territoriality**, which is based on aggressive social interactions as one or more individuals attempt to keep others away from a piece of real estate. The territory may be as small as the square meter display court of a Black Grouse (*Tetrao tetrix*) or Golden-collared Manakin (*Manacus vitellinus*), or as large as the hunting ground of a Golden Eagle (*Aquila chrysaetos*) or Northern Goshawk (*Accipter gentilis*), which usually spans thousands of hectares (Fig. 9.26). The costs of territory defense obviously include the time and energy expended in displaying to and chasing off intruders, as well as the risk of injury should a territory holder be hurt in a fight with a determined rival. The display costs alone are not trivial, especially for species in which males sing to deter competitor males from entering their territory (Chapter 10). For example, male Great Reed-Warblers (*Acrocephalus arundinaceus*) expend about three times more energy when singing than they do when resting quietly. During spring in central Sweden, some such warblers have been recorded singing nearly continuously for 20 hours a day (Hasselquist and Bensch 2008). Likewise, male Willow Warblers (*Phylloscopus trochilus*) generally sing from exposed song posts in Scotland where they are subject to heat loss, especially on cool, windy days. They also lose heat as they exhale at an elevated rate when singing, which they do at a rate of five songs a minute for hours at a time. The combined thermoregulatory costs of singing raise these males' metabolic rates (Chapter 7) by 20% (Ward and Slater 2005).

Many other potential costs are associated with territoriality. A displaying male Vermilion Flycatcher (*Pyrocephalus rubinus*)—a species found across much of the Americas—flies upwards slowly with its brilliant red plumage fluffed, while singing to draw attention to itself. The fact that this behavior appears to be triggered by a neighbor's display indicates that males use the flight display as part of their territorial defense system. This display behavior has clear costs in terms of time and energy; moreover, the conspicuousness of the behavior presumably makes the flycatcher at least somewhat more vulnerable to predators such as hawks and falcons, which often are common in the flycatcher's environment. The same costs may apply to the flashy ornaments of many other male birds, which are used as signals in territorial interactions in part because of their conspicuousness, an attribute that may expose the owner to unwelcome attention (Chapter 3).

Given the costs of territoriality, we can predict that it should evolve only when the fitness benefits more than compensate the territorial individual for the price it pays to monopolize its patch of real estate. Researchers have tested this claim by demonstrating, for example, that in lekking species the possession of a prime display territory boosts male reproductive success. Moreover, when individual males are incapable of acquiring an attractive territory, they often either drop out of the competition altogether for a time (thus saving the costs of trying to be territorial) or employ an alternative mating tactic that does not carry the full costs of territoriality.

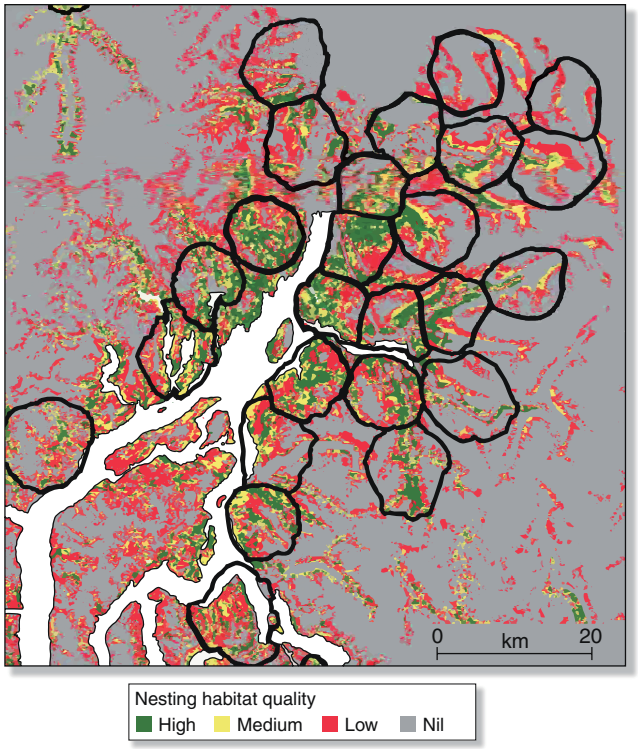


Fig. 9.26 Map of Northern Goshawk (*Accipiter gentilis*) territories. As typical for a resource-based territorial species, each nesting pair defends a food-based territory. Since these large predators need to secure a great deal of food for their nestlings, their territories are very large (often over a kilometer in diameter). Territories (rough black circles) with poorer habitats tend to be larger, as more space is necessary to support the adequate amount of resources. (From Smith and Sutherland 2008. Reproduced with permission from TimberWest Forest Corporation.)

Most avian territories are much larger than those of lekking species. In these cases, a potential benefit that comes from owning a territory is access to the food that the defended area contains. We thus might predict that larger species will tend to have larger territories, because a nesting pair of a large species generally requires more food for themselves and their young than two adults and their

Territoriality: a behavior in which an individual defends an area against other individuals.

brood of a small species. This prediction seems to hold across most birds, because it has long been known that large birds, particularly predatory ones, do require very large territories if they are to nest successfully (Schoener 1968).

A prime benefit to males that comes from owning a food-rich breeding territory is the attraction of a receptive female (or females) to the territory and the male defender. We can predict that males able to control more food-rich territories will acquire mates more quickly, as has been shown for the Blue Grosbeak (*Passerina caerulea*) in Alabama (USA). Male grosbeaks in better physical condition are able to produce brighter blue feathers and are more likely to acquire territories with abundant food resources; females prefer these males and pair off with them more quickly (Ballentine and Hill 2003).

Another prediction derived from the cost–benefit approach to territoriality is that individuals in relatively resource-poor sites should abandon them more often than males in high-quality territories. In keeping with this expectation, in both Spotted Owls (*Strix occidentalis*) in western North America and Red-backed Shrikes (*Lanius collurio*) in Switzerland, individuals were significantly more likely to leave poor territories than were competitors that secured better sites (Blakesley et al. 2006; Pasinelli et al. 2007).

It also is true that when individuals of a given species are unable to acquire a resource-rich territory, they often stop trying to do so for a breeding season or two. Although this behavior once was interpreted as an adaptation for the "benefit of the species" because it supposedly helps prevent overutilization of critical resources, dropping out of the breeding competition now is viewed, in light of the cost–benefit approach, as an adaptation that directly benefits the dropouts themselves. Birds that are smaller, less physiologically fit, less experienced, or slightly weaker than average have little to gain from costly attempts to acquire a territory, especially if the good places already have been claimed by stronger rivals and the remaining unoccupied slots are resource poor. These individuals may gain more by conserving their energy so that they can try again when conditions become more favorable or when they are older and more competitive. For example, in migratory populations of the Black Kite (*Milvus migrans*), a graceful mid-sized hawk of Europe and Australasia, territories usually are taken by older birds in such good condition that they can arrive early on the breeding grounds. Younger kites become **floaters**, birds that move about while postponing their territorial and reproductive ambitions (Sergio et al. 2009).

In most territorial bird species, some individuals are non-territorial floaters. Those that have the good fortune to find a territorial vacancy can be predicted to take advantage of the opportunity that an opening implies. Indeed, floaters in the Eurasian Oystercatcher (*Haematopus ostralegus*) responded quickly to the experimental removal of established residents by entering a vacant territory and switching tactics, provided that they had intruded into this site previously (Bruinzeel and van de Pol 2004). Presumably, during their earlier secretive incursions, these floaters had acquired information about territory quality that they can use to good advantage if they find that the site now lacks a defender.

9.6.2 Dominance hierarchies

Many species of birds do not defend territories, and even those that do frequently are non-territorial during some parts of their annual cycle. There are simply times and places where territoriality is precluded by features of the environment, or where the costs of being territorial are much higher than the benefits. For example, when a potentially territorial individual must face large numbers of competitors, the value of being territorial decreases because of the heightened costs of defense. In a large flock of birds, for example, if any one bird were to attempt to keep all the others out of a patch of food, the costs of doing so probably would overwhelm any benefits the would-be territory holder could generate from its territorial exclusivity. Therefore, traditional territoriality does not occur when groups of birds gather together either for their mutual defense or to forage more safely.

This diminished territoriality does not mean that all competition ends when groups of birds assemble for one or another reason. Indeed, the competition continues but leads to an evolutionary result that is different from the kind of aggressive territoriality exhibited by many nesting birds. Instead, as individuals within a flock jockey for valuable resources such as space and food, the standard result is a **dominance hierarchy**, which is sometimes labeled a "pecking order." This secondary term comes from early studies of chickens in which some members of the flock displaced others by administering a peck or two, or simply by approaching or even looking at a subordinate (Schjelderup-Ebbe 1935).

A special case of dominance hierarchies sometimes occurs among chicks within a nest. These sibling hierarchies are particularly obvious in groups such as herons, seabirds, owls, and raptors, in which successive eggs within a nest hatch on different days (Chapter 11), giving the oldest

Floaters: in largely territorial bird species, individuals that do not hold a territory and instead "float" among territories or less optimal habitats.

Dominance hierarchy: a ranking of social status among members of a group.

chicks a decided size advantage over their younger and smaller nest mates. Competition for the food brought by the parents sometimes is acute, and the larger chicks may bully their younger siblings aggressively to the point that these unfortunate subdominant birds simply crouch in the nest rather than begging to be fed. In breeding seasons when food is short, these lower ranked nestlings usually die. In Cattle Egrets (*Bubulcus ibis*), a bird now found throughout the Americas as well as in much of the rest of the world, the last of the chicks to hatch probably lives longer by not fighting back, since its oldest sibling is three times its weight. Admittedly, such battered subordinates almost always die eventually, sometimes from starvation, or by being forced out of the nest (Fig. 9.27). But on rare occasions, when it becomes the only nestling survivor because of the destruction of its dominant siblings by predators or weather, this once-subordinate individual will have a chance to be fed. Thus, the last-hatched nestling may be lucky enough to reach adulthood, but only if it has managed to hold on long enough to take over upon the disappearance of its bullying nest mates (Mock 2004; Mock et al. 1990). Although this system may seem cruel, the nestling dominance hierarchy caused by the asynchronous hatching of eggs is thought to be an adaptation that increases the fitness of the parents: when times are good, more of the chicks survive, but when times are bad there is a way to dispose of the lower ranking members of the brood that allows the more dominant offspring to fledge successfully (Drummond 2006).

Dominance relationships also are apparent in winter-foraging flocks of songbirds, although their interactions usually are far less dramatic than those that occur in an egret nest. Birds join winter flocks primarily for protection against predators (a benefit), but the birds that live together may experience heightened competition for food (a cost). When there is competition for food, individuals that have become dominant to others displace subordinates from food resources. Thus, in a study of Great Tits (*Parus major*) in Spain, researchers found that at a cold, high-elevation site where insect food was scarce, dominant individuals frequently chased low-ranking members of the winter flock away from feeders (Carrascal et al. 1998).

Given the reality that not all members of a flock of birds are equal competitors, subordinates may avoid overt conflict and concede desired items to their superiors without question. They do so not because the group as a whole benefits from less violent conflict, but rather because the subordinates gain as individuals when the dominant members allow them to remain in the group. There they are more likely to survive long enough to become dominant themselves someday, with all the benefits that high status will confer upon them. In contrast, subordinates that are injured, driven off, or killed outright because of their refusal to accept their low status leave relatively few descendants.



Fig. 9.27 Dominance hierarchies in siblings. The first-born Brown Booby (*Sula leucogaster*) chick—crouching comfortably in the shade of its parent—has driven its younger and much smaller sibling (circled) into the blaring sun, a lethal act. (From Alcock 2013. Reproduced with permission from Sinauer Associates.)

9.6.3 Helpful social behavior

The emphasis in this chapter thus far has been on the competitive aspects of avian interactions, those that occur when individuals attempt to monopolize valuable resources such as food, space, or mates. However, it also is common to observe birds interacting with one another in ways that seem to provide benefits for all parties.

In some cases, birds involved in these **mutualisms** derive their benefits simply by assembling in groups, the better to reduce the risk for any one flock member of being attacked by a predator. Thus Common Redshanks (*Tringa totanus*), a Eurasian sandpiper, sometimes are hunted by raptors while foraging or resting on beaches on their wintering grounds. These birds often are found in groups, and if their flocks have formed for defensive purposes, the vulnerability of individuals to predators should decline as group size increases (Fig. 9.28). Field studies have shown that redshanks in larger flocks indeed are less likely to be killed when a predator comes hunting. Because these birds'

Mutualism: an ecological relationship involving multiple individuals or species in which all parties benefit in some way from the other.

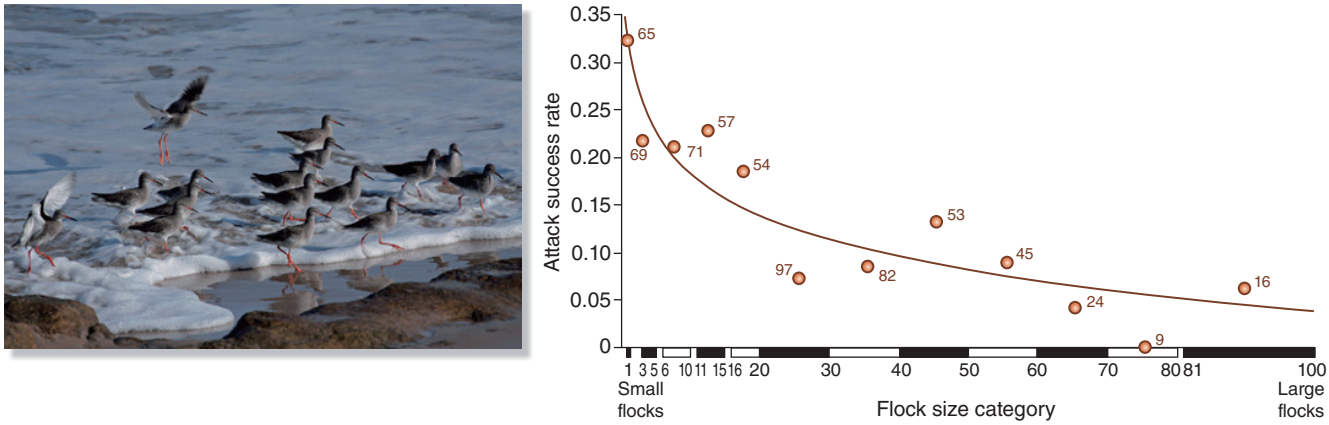


Fig. 9.28 Safety in numbers. A small flock of Common Redshanks (*Tringa totanus*) on a tidal flat. Predatory hawks are less likely to capture Common Redshanks in larger flocks. The numbers by the data points represent the number of attempted attacks on flocks of a given size range. (From Cresswell and Quinn 2011. Reproduced with permission from John Wiley and Sons and the authors. Photograph by Rob Woolf.)

foraging success declines as their flocks increase in size, these defensive benefits are likely the main reason that redshanks only form winter flocks (Whitfield 2003).

When redshanks cluster together, they are being helpful to one another even if they take no mutual action beyond joining others of their species to form a flock. The defensive benefit gained could be as simple as a reduction in the odds of being selected by a predator as a function of the increasing number of prey in the group. If, for example, each group of redshanks is attacked successfully by a raptor on average once per day, regardless of how many redshanks are in the group, then for an individual redshank the risk of dying will be 10 times greater in a flock of 10 birds than it would be in a flock of 100.

Birds may derive other antipredator benefits from flocking, such as the increased vigilance that comes from having many eyes scanning for predators. If one member of a flock spots an enemy and flees, others that had not yet seen the attacker also can react by flying off sooner than they would otherwise. The heightened vigilance hypothesis predicts that members of large groups should be more likely to avoid capture than members of smaller groups when under surprise attack from a predator. Data gathered by Will Cresswell and John Quinn (2010, 2011) on the outcome of sneak attacks by Eurasian Sparrowhawks (*Accipiter nisus*) on Common Redshanks support this prediction. Sparrowhawks were about three times more likely to make a kill when swooping onto a group of less than 10 sandpipers than when they launched an attack on flocks of 40 or more. The greater protection enjoyed by members of larger groups almost certainly results from the improved combined vigilance of the birds in the bigger flocks.

Of course, mutual benefits also can be gained by individuals engaged in much more active forms of cooperation than merely choosing to be part of a large group of conspecifics. The **mobbing** of a predator by a group of birds is one of the most familiar examples of avian cooperation, as illustrated by the willingness of some prey species to join others in calling loudly while swooping about a dangerous hawk or owl. The costs of group mobbing include the time and energy spent in the activity and the risk that the predator being mobbed will retaliate by attacking and capturing one of its harassers. However, the substantial benefits of the behavior have been demonstrated as well. In Australia, Powerful Owls (*Ninox strenua*) mobbed by up to 22 Pied Currawongs (*Strepera graculina*) sometimes flew from their roost, presumably reducing the chance that the mobbing individuals that lived near that site would be attacked by the predator in the night (Pavey and Smyth 1998). Predators that depend on surprise to make a kill have little to gain by remaining in an area where they have been discovered and are now surrounded by noisy mobbers. Moreover, relatively small predatory species, such as small owls or snakes, also may benefit by departing when noisily mobbed if larger hunters—such as Great Horned Owls (*Bubo virginianus*) in North America—take advantage of the information provided by mobbers to locate and kill the smaller predators. In any event, the fact that mobbing can cause a formidable predator to flee supports the "move-on hypothesis," which seeks to explain why prey species would risk everything to make a scene around a dangerous predator.

Mobbing: behavior in which a number of birds (sometimes of different species) swoop and dash at a potential predator, often while broadcasting loud calls to alert and potentially recruit other birds into the mobbing flock.

No matter who participates in mobbing, the benefits of this behavior are enjoyed by all the birds living in the area from which the roosting owl or hunting snake has departed. This universal benefit raises a fundamental question: why join others in risky mobbing rather than simply letting one's neighbors do the dirty work? One explanation is that joiners make it more likely that when they begin to mob an enemy, the individuals that they have helped in the past will return the favor and come to their assistance. An ingenious experiment conducted with a Latvian population of European Pied Flycatchers (*Ficedula hypoleuca*) has provided evidence in support of this "reciprocity hypothesis" (Krams et al. 2008). Working with sets of three pairs of flycatchers whose nest boxes were in close proximity, the researchers caught and temporarily removed one pair before placing a stuffed owl near one of the two other nests. As a result, the captured pair was unable to join the other four birds in mobbing the predator. An hour after releasing the two flycatchers that had been held in captivity, the ornithologists placed a stuffed owl at the nest of the previously captured pair and also at the nest of the earlier "helpful" pair. Under these circumstances, the original pair whose nest had been threatened had a choice of whom to join in harassing an owl, and they consistently chose to go to the aid of the pair that had helped them earlier. This result supports the idea that European Pied Flycatchers favor those that have helped them in the past when making decisions about whether to join others in mobbing a mutual enemy (Box 9.09).

9.6.4 Cooperative breeding and avian altruism

Another form of helpful behavior in birds is termed **cooperative breeding**, a form of sociality in which some individuals do not reproduce personally but instead assist others in chick rearing. Cooperative breeding is not common, occurring regularly in less than 5% of all bird species, but many species of cooperative breeders have been studied intensely because of their theoretical importance. The broader significance of the behavior stems from the fact that the non-reproducing helpers appear to be making a sacrifice on behalf of other individuals. Self-sacrificing behavior—altruism—always is intriguing to biologists familiar with Darwinian theory because it is hard to see how the hereditary basis for altruism can persist if the individuals acting altruistically fail to reproduce (Box 9.10).

Cooperative breeding: a breeding system in which adults other than the social breeding pair aid in rearing the offspring.

Cooperative breeders exhibit a variety of social arrangements, and in some cases all the various group members have at least some chance of reproducing. This occurs, for example, in some joint-nesting species such as the Greater Anis (*Crotophaga major*) studied in Panama by Christie Riehl (2010), in which multiple females lay eggs in a communal nest that then is attended by all the males and females in the group. In such cases, helping behaviors that benefit the group also are likely to benefit the helping individual directly, because the helper potentially is the parent of at least some of the offspring. A similar situation occurs when subordinate helper males in a cooperative group occasionally are able to mate with the breeding female and thereby sire some of the offspring. These forms of direct benefit may be hard to document without careful genetic testing to determine which individuals in the group actually are reproducing (Box 9.06), but they clearly are not altruistic.

Direct reproduction by helpers is unusual in most cooperatively breeding birds, so direct benefits cannot fully explain the general evolution of this social system. In nearly all cooperative bird species, most of the helpers within a group are young adults that are earlier offspring of the breeding pair, so they are helping to rear their brothers and sisters. For example, in a cooperatively breeding population of American Crows (*Corvus brachyrhynchos*) that lives on the campus of Cornell University in New York (USA), the majority of helpers are offspring of the breeding pair, although a very few are brothers of the male breeder (Townsend et al. 2009). Likewise, in the White-fronted Bee-eater (*Merops bullockoides*) of Kenya, older sons help their parents rear more siblings (Emlen et al. 1995). This pervasive pattern of offspring remaining at home to help their parents provides some clues to the various ways that this behavior might be a good strategy for the helpers.

If territories, mates, or other critical resources are in very short supply, young birds actually might not be sacrificing much when they stay and help instead of trying to breed on their own. This general explanation for helping behavior is termed the "ecological constraints hypothesis," because it focuses on the aspects of the environment that constrain a young bird's options in ways that render breeding on its own costly, risky, or impossible. Ecological constraints appear to be intense in some cooperative breeders such as the Florida Scrub-Jay (*Aphelocoma coerulescens*) (Box 9.10), in which all suitable breeding habitat usually is already occupied by breeding jays, and young adults may have to wait several years before the death of a nearby breeder opens a territorial vacancy.

Another possibility is that by staying in their natal territory, helping birds eventually might inherit their parents' territory, in which case their temporary period of celibacy may have a big payoff when they secure a location where reproduction is clearly possible. This "delayed payoff hypothesis" deals with cases in which a cooperative individual boosts another's reproductive success, but only

Box 9.09 The evolution of reciprocity

European Pied Flycatchers (*Ficedula hypoleuca*) with carefully calibrated mobbing behavior seem to be making an initial sacrifice when they go to the aid of neighbors confronted by a predator. However, the behavioral costs of being helpful are repaid if the helpers themselves later receive assistance from their neighbors. A general rule in behavioral ecology is that when some individuals appear to be making a sacrifice, they likely are gaining something for themselves, even if the benefit is not immediately obvious. Flycatchers that join their neighbors in trying to make life unpleasant for an owl gain a small immediate benefit if the owl leaves the area altogether, reducing the threat not only to the neighbor but also to themselves and their offspring. The joiners also benefit by increasing the probability of reciprocity if the individuals they helped are now primed to come to their assistance when a new predator is nearby.

Reciprocity can supply eventual reproductive benefits for helpers. Although the phenomenon is not especially common in birds, it does occur occasionally in situations other than mobbing. For another example, consider the cooperative courtship of lekking Long-tailed Manakins (*Chiroxiphia linearis*) (Box 9.08). Males of these small tropical birds form duos that work together to produce elaborate, coordinated acoustical displays for females. One element of the joint display consists of a male leaping over the other on their perch, a horizontal segment of a liana; as soon as one male has completed his leapfrogging flight, the other does the same, and on and on, as a female watches from the sidelines (Fig. **9.B9.01**). The integrated behaviors of the two males are extraordinary, but to a biologist the really striking feature of the manakins' display occurs when a female announces her receptivity after observing both males in action: one of the two male partners retires from the scene while the other copulates. Should the pair attract another female, the male that left previously departs this time as well, leaving his companion to inseminate the new female. In other words, one male derives all the reproductive benefits from the hundreds of hours the two manakins spend calling and dancing together on the display court! Indeed, some second-ranked males help their partner for up to 10 years, during which time the dominant male does all the mating (McDonald and Potts 1994).

The apparently unrewarded cooperation on the part of the reproductively inactive members of these manakin pairs constitutes a major puzzle. The solution comes from long-term studies of banded male manakins that enabled researchers to determine what happened upon the demise of the dominant male of the duo. When the top male dies, his subordinate male partner became the dominant, reproductive member of a new duo. Thus, the one male that had been permitted to display more often with the alpha manakin inherited the alpha manakin's display court along with his top status. This case can be considered an example of reciprocity in which subordinates that do good work for a dominant male eventually are rewarded when they move up the ladder to the alpha position and thus have a chance to reproduce (McDonald 2007).



Fig. 9.B9.01 Long-tailed Manakins (*Chiroxiphia linearis*) display for a female at a lek. Males of this species display with flashy plumes and repetitious vocalizations, along with a famous dance. In the dance, two (or more) males will position themselves on a horizontal twig or branch. While one male flies up and backwards in a semicircle, the male positioned further from the stationary female (far left) will then hop forward, pass under the other male dancer, then fly backwards, landing again behind the other male (like juggling). If the female shows interest, she always mates with the alpha male of the cooperative pair. (Photograph by Marie Read.)

Box 9.10 Cooperative breeding in Florida Scrub-Jays, Acorn Woodpeckers, and Superb Starlings

Florida Scrub-Jay (*Aphelocoma coerulescens*)

One of the earliest research projects on a cooperatively breeding bird was led by Glen Woolfenden and John Fitzpatrick, who worked with the Florida Scrub-Jay (Woolfenden and Fitzpatrick 1984). These jays have a relatively simple cooperative system in which a pair occupies a territory where they nest and rear their offspring—often, but not always, with the assistance of several non-breeding helpers that defend the territory, attack predators, and feed the nestlings produced by the breeding pair. Some helpers remain in this role for up to 6 years, although helpers usually leave the area after 1 or 2 years in an attempt to set up a territory of their own elsewhere. Helpers generally are the mature offspring of the breeding pair that they are helping. The finding that helper Florida Scrub-Jays really do assist their parents to produce more siblings of the helpers has been similarly documented in many subsequent studies of other cooperative breeders.

Acorn Woodpecker (*Melanerpes formicivorus*)

The Acorn Woodpeckers observed by Walt Koenig and his colleagues in central coastal California have a more complex cooperative social system. Multiple breeding woodpeckers—up to four males and two females—defend a joint territory containing a tree in which all group members store acorns (Fig. 9.B10.01) and a single nest. The brood produced by the group can have both mixed paternity and mixed maternity. The offspring are fed by the breeding adults and up to nine auxiliaries, which are sexually mature adults that have not contributed eggs to the nest. The helpers tend to be offspring that were produced by some of the breeding adults in earlier years (Koenig and Mumme 1987).

Superb Starling (*Lamprotornis superbus*)

Cooperative breeding is taken to the extreme in species like the Superb Starling of eastern Africa where joint territories are defended by a group of up to 35 birds, including multiple breeding pairs that nest separately and that are assisted by a flexible cadre of helpers. Studies on a Kenyan population of Superb Starlings by Dustin Rubenstein (2011) have shown that individuals in these groups have dynamic roles.



Fig. 9.B10.01 Acorn Woodpeckers (*Melanerpes formicivorus*). Family groups use granary trees to stash their food for the future, long after trees have cropped acorns. (Courtesy of Elkhorn Slough Foundation.)

In rainy years, when insects are abundant, several pairs within each group nest simultaneously, whereas in dry years only the dominant pair within each group attempts to breed. Predation rates on starling nests are high and some breeders switch to helping at a relative's nest after their own nest is destroyed. These starling groups have complicated networks of kinship, with the males in each group generally being more closely related to one another than to the females, because female starlings generally disperse to other groups before starting to breed. This social system in which a territorial group contains multiple breeding pairs is termed "plural cooperative breeding." The Mexican Jays (*Aphelocoma wollweberi*) of the Chiricahua Mountains in southeastern Arizona (USA) are another well-studied plural-cooperative species in which offspring often remain at home to help their parents or relatives and as many as three breeding pairs place their separate nests within the same group-defended territory (Brown 1994).

temporarily. This type of benefit seems to apply to species such as the Gray-crowned Babbler (*Pomatostomus temporalis*) studied in New South Wales, Australia (Blackmore and Heinsohn 2008), in which territorial openings are usually filled by helpers that are already present in that babbler group. However, one complication for these babblers and other family-living birds is that only one breeder is likely to die at a time, and if all the helpers are the sons or daughters of the remaining breeder, behavioral incest avoidance may preclude them from pairing with their widowed father

or mother. In the Gray-crowned Babblers and most other cooperative species, helpers pair with a surviving breeder only when they are not closely related.

All the various hypotheses for cooperative breeding discussed thus far involve benefits to helpers via their own direct reproduction. What is the explanation for instances in which helpers have little or no chance of ever reproducing personally? Helpers with no hope of becoming parents would seem be engaged in maladaptive altruism to the extent that their helpful behavior reduces whatever chances they have of breeding independently. In these situations, indirect benefits via kin selection (Chapter 3) are likely to be present. As William D. Hamilton (1964) first pointed out, if altruists direct their assistance to close relatives in ways that raise the reproductive success of these relatives, then, in effect, the altruists have passed on copies of their genes indirectly via the extra relatives they have helped to survive. Hamilton's genius was to see that genetic information can be copied and transmitted both directly in the bodies of one's offspring, which in sexually reproducing organisms carry 50% of each parent's genome, and indirectly via the reproduction of relatives. If individuals have little chance of reproducing themselves, the altruism option can become their most adaptive strategy. Adaptive altruism generally requires that helpers focus their efforts on close relatives, because these relatives share a relatively large proportion of their genes with the helpers. This approach generates an obvious prediction, namely, that helpers will promote the breeding success of their closest relatives.

As noted already, helpers at the nest often are offspring of the parents whose progeny they are feeding or protecting. Sometimes, however, unrelated individuals join cooperatively breeding groups. For example, Carrion Crows (*Corvus corone*) in Spain leave their natal territory and join other crow families as helpers at their nests. Researchers tracking these crows found that emigrating birds interacted regularly with more than one breeding pair before settling down at one location, a site that rarely was next to the territory in which they were reared. In other words, the birds were not simply selecting a group to join on the basis of the proximity to their natal territory. However, the territory chosen by the dispersing males typically contained a fairly close relative, so that the average genetic similarity between a new helper at the nest and the male resident at this site was about one-quarter, the same as that shared by an uncle and his nephew. Male Carrion Crows somehow are able to identify their relatives, and they use this ability when searching for individuals with whom to form a cooperative association (Baglione et al. 2003).

Hamilton's explanation for altruism generates another critical prediction: helpers must have a positive effect on the survival or reproductive success of their close relatives. Some studies have demonstrated that helpers really do increase the survival of their younger siblings. Feedings by helpers at the nest in the Bell Miner (*Manorina melanophrys*), an Australian honeyeater, increase the body mass and physical condition of the nestlings (te Marvelde et al. 2009) (Fig. 9.29). In the Social Weaver (*Philetairus socius*) of southern Africa, helpers boost the rate at which nestlings are provisioned; such help may be particularly important during droughts when food is scarce (Covas et al. 2008). In the cooperatively breeding Carrion Crow, the larger the group, the lower the probability that the nest will be parasitized by the Great Spotted Cuckoo

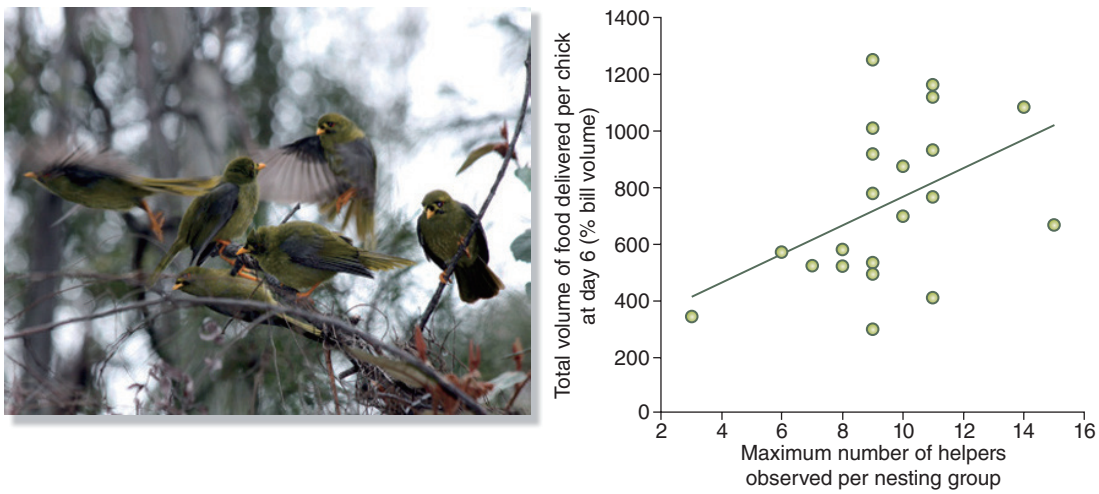


Fig. 9.29 Helpers improve nestling condition. Bell Miners (*Manorina melanophrys*) forage and breed in family groups. More food is delivered to each chick when there are more helpers in a group. (From te Marvelde et al. 2009. Reproduced with permission from Elsevier. Photograph by Marlene Lyell.)

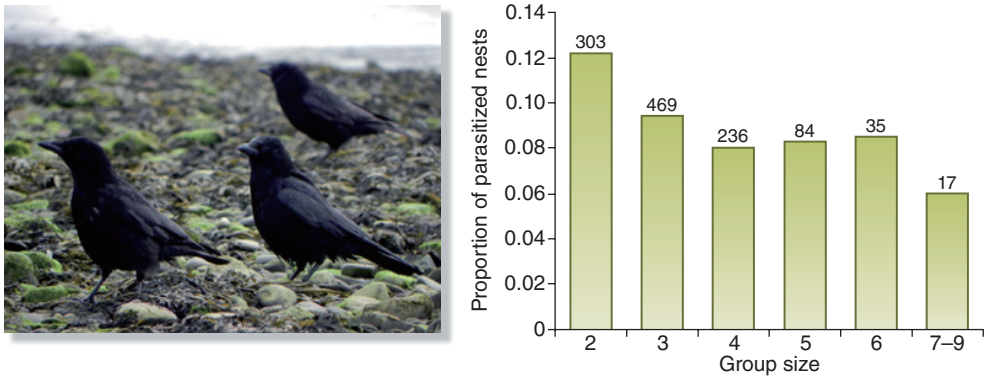


Fig. 9.30 Larger groups experience lower rates of brood parasitism. Carrion Crows (*Corvus corone*) are cooperative breeders. Larger groups of this species are less likely to fall victim to brood parasitism by Great Spotted Cuckoos (*Clamator glandarius*), one benefit of avian sociality. Sample sizes of nests per group size category are shown above the bars. (From Canestrari et al. 2009. Reproduced with permission from Elsevier. Photograph by W. Keith Milne.)

(*Clamator glandarius*) (Fig. 9.30). More directly still, very young nestling crows received more food when cared for by a larger number of helpers, leading to a relatively greater output of fledglings by large groups of these crows (Canestrari et al. 2009).

Even when the presence of helpers does not result in more or higher quality offspring, helpers may provide other kinds of benefits. For example, in the Superb Fairywren (*Malurus cyaneus*) (Box 9.07), helpers are often the sons of the breeding pair, and their work at the nest enables the adult female to bring less food to the nestlings than she would otherwise have to (Cockburn et al. 2008). Helpers in effect do what the breeding female would do, thus permitting her to conserve her energy and avoid risky foraging, potentially translating into a longer life and more breeding attempts for her. When a helped female reproduces again, and again, she generates more siblings of her cooperative sons. In other words, avian altruists that provision their siblings or boost parental survival are doing what evolutionary theorists predict they should be doing: they are making indirect contributions of their genes to the next generation.

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Chapter 10 Avian Vocal Behavior

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Birds are noisy animals. This noisiness is a boon to birdwatchers, who often rely on sounds to detect birds that would otherwise remain unnoticed as they forage in dense foliage, lurk in tall grass, or fly high overhead. Birders also benefit from the specificity of birds' sounds, as birds of almost any species can be identified solely by the sounds they make. These practical benefits of bird sounds, however, pale in comparison with the aesthetic ones. Who can fail to be impressed by the symphonic beauty of the dawn chorus in a temperate woodland, the overwhelming cacophony of a seabird nesting colony, the mysterious mood music of a tropical forest as dusk falls, or the virtuoso individual performances of many songbirds?

Bird sounds did not, of course, evolve for the convenience and pleasure of humans. Birds use sounds to communicate, and scientific investigation of bird vocalizations has focused on questions related to this function. What information is transmitted by vocalizations? Why do individual birds produce so many different sounds? Why are some bird vocalizations so complex and elaborate? How and why do the vocalizations of a given species vary? How do birds produce their sounds? How does a developing bird gain the ability to produce the sounds of its species? The aim of this chapter is to address these questions about bird vocalizations.

Throughout this chapter you will find references to songs and calls that will help you understand vocal behavior in birds. To get the most of out of this material, it is important to listen to the associated sounds while reading it. To animate and listen to these sounds online, go directly to the following site: **birdbiology.org/vocalbehavior**.

10.1 Studying bird sounds: the investigator's toolbox

In the not too distant past, ornithologists interested in studying bird vocalizations undertook their research equipped with nothing more than their own ears and perhaps the ability to transcribe the sounds they heard into musical notation. Today, scientific investigation of bird vocalizations is aided by digital recorders, sensitive microphones, and computerized tools that augment our senses and allow us to make measurements that otherwise would be impossible. We describe some of these tools below, after a brief description of the physical properties that they measure.

Opposite: A Taiwan Barbet (*Psilopogon nuchalis*) sings from its nesting tree. Endemic to Taiwan Island, this species has a song reminiscent of a high-pitched frog trill. (Photograph by Sushyue Liao.)

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10.1.1 Physical basis of sound

Consider the way in which a drum produces sound (Fig. 10.01). Pounding on the tightly stretched membrane of the drumhead causes the membrane to vibrate. As the vibrating membrane moves outward, the air molecules near it compress. When the vibrating membrane moves inward, nearby air molecules move to fill the space vacated by the membrane, thereby spreading further apart. Thus, the air near the drumhead is alternately compressed and thinned out, forming alternating high-pressure and low-pressure bands. As air molecules near the drumhead interact with those a bit further away, the pattern of alternating high- and low-pressure bands is transmitted to air increasingly distant from the drum and thus forms a sound wave traveling through the air.

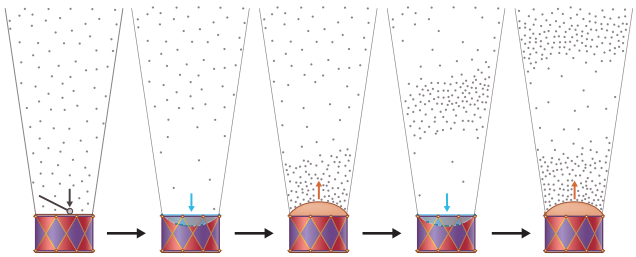


Fig. 10.01 Sound waves are generated by moving air molecules. Just before a stationary drum membrane is struck (left), air molecules are more or less evenly distributed. Once struck, the drum membrane moves down (downward arrows) and air molecules spread out to fill the low-pressure space. When the membrane oscillates back up (upward arrows), it adds pressure to the air above, forcing air molecules to compact. This process repeats, creating waves of pressure changes that are detected and translated into audible sound by the ear. (© Cornell Lab of Ornithology.)

If a sound wave reaches a human eardrum, the eardrum vibrates in response, initiating a chain of events that converts the vibrations into an electrical signal that the brain interprets as a sound. Our sound perception capabilities allow us to discriminate among different sounds; for example, some sounds are high pitched and others are low pitched (Box 10.01). These differences in perceived pitch result from differences in how fast the object that generated the initial sound wave was vibrating. For example, on a piano the heavy wires that produce the lowest C vibrate only 32.7 times per second, and the thin wires that produce the highest C vibrate more than 4000 times per second. These vibrations generate sound waves; the higher the rate at which waves are generated, the higher the resulting sound's perceived pitch. The rate at which a sound's waves are produced is called its frequency, which is measured in cycles (waves) per second, or Hertz (Hz), named after Heinrich Hertz, a pioneer in the study of sound.

Box 10.01 How well can a bird hear?

To find out how well a bird can hear, an experimenter typically begins by training a captive bird to peck at a lever when it hears a tone. The bird is then exposed to tones of varying frequency and loudness; by observing whether or not the bird pecks the lever, the experimenter can determine which tones the bird can hear, and can construct an "audiogram" graph that shows the softest sound a bird can hear at a given frequency. Alternatively, these hearing thresholds may be measured by using electrodes to record activity in a bird's auditory brainstem as the tones are played. Audiograms have been derived for about 50 different bird species, and the collective data show that bird hearing generally is most acute at frequencies between 1000 Hertz (or 1 kilohertz (kHz); 1 kHz = 1000 Hz) and 5000 Hz (5 kHz) (Dooling 2002). At frequencies below and above this range, bird hearing ability declines substantially. For example, no bird tested so far can detect sounds higher than 15 kHz. In general, birds' ability to hear very low- and very high-frequency sounds is poorer than that of humans; most of us can hear sounds with frequencies as low as 20 Hz and as high as 20 kHz.

Although birds do not hear as well as people (and other mammals) according to standard measures of hearing acuity, birds have some special auditory abilities that far exceed those of humans. For example, Budgerigars (*Melopsittacus undulatus*) and Zebra Finches (*Taeniopygia guttata*) have been shown to be about three times better than humans at distinguishing very small differences in the structure of acoustically complex sounds (Dooling et al. 2002; Lohr et al. 2006). These species also are far better than humans at distinguishing tiny differences in timbre, the harmonic quality of a sound (the characteristic that makes an oboe, for example, sound different from a flute, even when both instruments play the same note) (Lohr and Dooling 1998). These findings suggest that birds listening to the vocalizations of other birds are able to distinguish small differences and rapid changes that are inaudible to humans. This ability allows birds to distinguish and respond to the subtle acoustic variability that characterizes many avian vocalizations.

Box 10.02 Using website sound recordings

This chapter is augmented by many animated recordings of bird sounds; you can find them on the Handbook website at **birdbiology.org** or go directly to these recordings at **birdbiology.org/vocalbehavior**. The recordings illustrate concepts, descriptions, and species mentioned in the text. All of the spectrograms included as figures in this chapter have online versions where you can listen to the sound and follow along visually at the same time. In some cases, sounds that are impossible to show as a static figure—like the dawn chorus of a North American forest (Fig. 10.38)—are included only in this online supplement.

The website also provides many additional recordings of birds from around the world, illustrating the concepts presented in this chapter.

These recordings are part of the Macaulay Library at the Cornell Lab of Ornithology. The Macaulay Library is the world's largest archive of animal sounds, with well over 230,000 recordings (both audio and video) of animal behaviors that you can access at no cost via the web at **macaulaylibrary.org**. On the full Macaulay Library website, you can browse the entire sound and video collection, search for a favorite species, create your own spectrograms, and get tips on how to record bird sounds yourself.

10.1.2 Visualizing sounds as spectrograms

One way to supplement our hearing and enhance our listening skills is to use computer programs that convert bird sounds to visual representations that we can see and study (Box 10.02). Traditionally, ornithologists often visualized bird vocalizations in the form of a **spectrogram** (also called a sonogram), illustrated here using a simple whistled song of North America's Black-capped Chickadee (*Poecile atricapillus*) (Fig. 10.02A). The spectrogram's vertical axis represents sound frequency, measured in kilohertz (kHz); the horizontal axis represents time. This chickadee song is often described in field guides as sounding like "*hey-sweetie*," with the first part slightly higher in frequency than the second. Sure enough, the spectrogram shows two whistled notes separated by about 0.2 seconds of silence. The first whistle begins at about 4.0 kHz, roughly the frequency of the highest C on a piano, and descends to about 3.5 kHz. The second note is about 400 Hz lower, at approximately 3.6 kHz.

In a black-and-white spectrogram, however, relative loudness (sound intensity) is not demonstrated clearly. For example, in this chickadee song, there is a very brief break in the second whistle where there is a subtle but clear drop in the loudness (sound intensity) near the middle of the whistle. The black-and-white spectrogram does not clearly reveal this drop in loudness. The relative loudness of these sounds is shown more clearly in a second type of graph, an **oscillogram** (Fig. 10.02B). As in a spectrogram, the horizontal axis of an oscillogram represents time, but an oscillogram's vertical axis shows sound intensity: the louder a sound, the greater the height of the wave on its oscillogram.

Today, ornithologists often use a colorized spectrogram that merges these two kinds of information to help us visualize both patterns of frequency and patterns of sound intensity (Fig. 10.02C). The spectrograms used throughout this chapter show time on the horizontal axis, sound frequency on the vertical axis, and relative loudness using colors: from white/gold (loud) to purple/pink (less loud). Experienced researchers can often look at a spectrogram and imagine clearly the associated song, but this skill requires practice. Be sure to take advantage of the web resources associated with this chapter, where you can watch animated versions of most spectrograms depicted while simultaneously listening to the sounds they portray (Box 10.02).

Spectrogram: a graphic representation of a recorded sound (like a bird song) that includes information on both frequency and loudness, usually by plotting frequency against time and indicating intensity by shading or colors.

Oscillogram: a graphic representation of a recorded sound (like a bird song) where sound intensity (loudness) is plotted against time.

10.1.3 Using your eyes to assist your ears

By using spectrograms to help us "see" bird sounds, we can begin to appreciate the finer details of what we hear. Consider another example of a song with pure whistles, the "*poor old sam peabody peabody peabody*" song of the White-throated Sparrow (*Zonotrichia albicollis*) (Fig. 10.03). This song, evocative of the northern North American forests in which this species breeds, is introduced by two or three relatively long whistles, each on a slightly different frequency, denoted

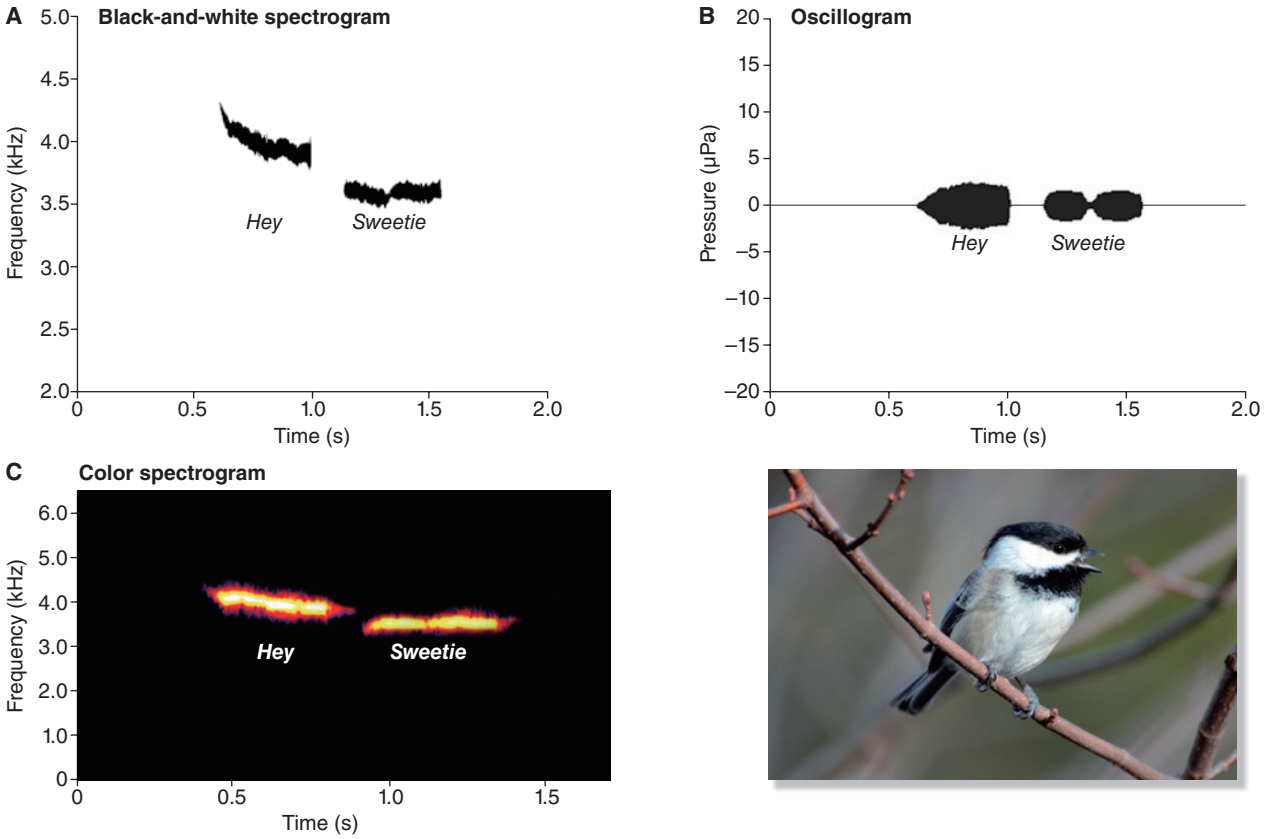


Fig. 10.02 Three ways to visualize a vocalization. Here, the "*hey-swee-tie*" song of a Black-capped Chickadee (*Poecile atricapillus*) is represented three different ways. (A) In a black-and-white spectrogram, a sound's frequency is plotted against time. (B) An oscillogram displays changes in a vocalization's loudness over time; the vertical axis represents sound intensity (the louder the song, the more vertical space the plot will occupy). (C) Modern spectrograms often use color to represent sound intensity (the brighter the color, the higher the intensity). ***Listen online.*** (Recordist: Matthew D. Medler. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Peter Brannon.)

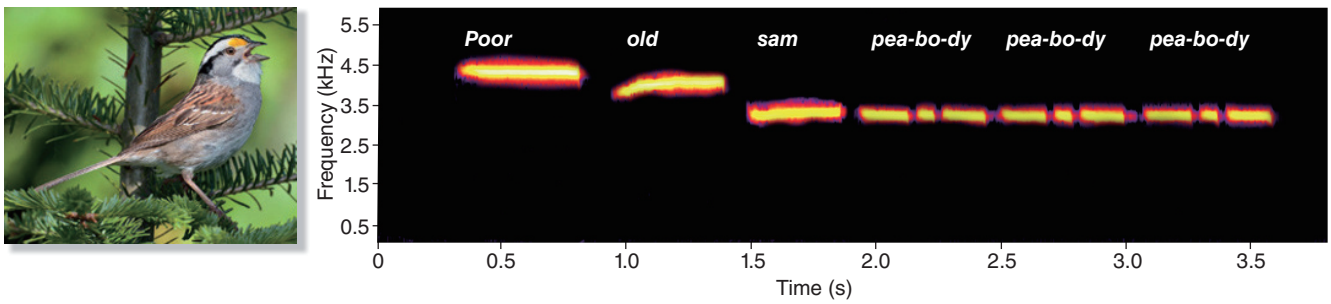


Fig. 10.03 Pure whistles in the song of the White-throated Sparrow (*Zonotrichia albicollis*). Males sing whistled notes of distinct frequencies that are traditionally transcribed as "*poor old sam peabody peabody peabody.*" The individual triplet notes within each "*pea-bo-dy*" are easy to distinguish in the spectrogram, but more difficult to hear. ***Listen online.*** (Recordist: Geoffrey A. Keller. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Jim Zipp.)

by the different words "*poor old sam*." In some individuals, successive notes rise in frequency, and in some they fall, but the overall pattern is unmistakable. Look at the last portion of the spectrogram and find the triplet notes represented by the three syllables in the word "*pea-bo-dy*." When you listen to the song, it is hard to distinguish the three notes in "*peabody*," but their separation is considerably more apparent in the spectrogram.

In sharp contrast to whistled sounds, such as the chickadee's "*hey-sweetie*" and sparrow's "*peabody*," are "noisy" sounds, which include a broad span of simultaneously produced frequencies. Noisy sounds appear on a

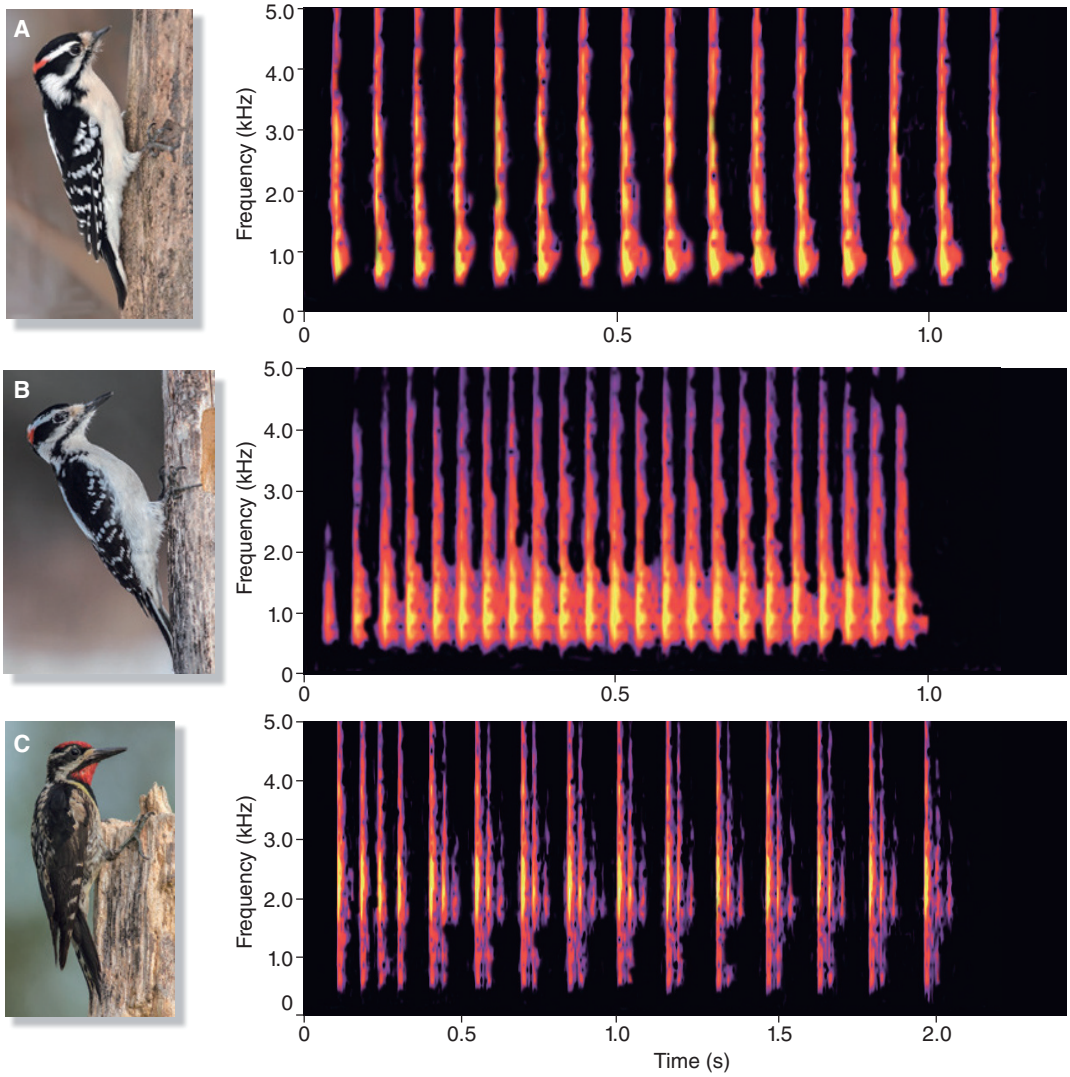


Fig. 10.04 Woodpecker drumming differs by species. Many woodpeckers drum at a species-specific rate that is easily discernible in spectrograms. Note the wide frequency range of the noisy sounds in the territorial drums of three different species: (A) Downy Woodpeckers (*Picoides pubescens*) drum at a rate of about 15 drums per second. (B) Hairy Woodpeckers (*Picoides villosus*) drum at a faster rate of 26 drums per second. (C) Yellow-bellied Sapsuckers (*Sphyrapicus varius*) have variable drumming rates, often slowing down at the end of a series of drums. ***Listen online.*** (Recordists: A and C, Gregory F. Budney; B, William W. H. Gunn. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photographs by: A, Rafael Garciá Sánchez; B and C, Bill McMullen.)

spectrogram as vertical lines, rather than horizontal ones. The snap of a finger and the slam of a door are examples of noisy sounds. Similarly, a woodpecker tapping on a tree produces noise because different parts of the tree vibrate at different frequencies.

The drumming sounds of three North American woodpecker species nicely illustrate this and show how patterns of noise can be highly distinctive. The first two species—the Downy Woodpecker (*Picoides pubescens*) (Fig. 10.04A) and Hairy Woodpecker (*Picoides villosus*) (Fig. 10.04B)—are similar in appearance but can be distinguished by their different sizes or by their distinct vocalizations. They differ, too, in the rate at which they drum. Surprisingly, the larger Hairy Woodpecker drums faster than the Downy. Counting the number of pulses in a second shows that the Hairy Woodpecker has about 26 drums per second and the Downy only 15. The third species, the Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Fig. 10.04C), adds a unique rhythm to its drumming, delivering taps that start fast and end in a slower rate, unlike the Downy and Hairy Woodpeckers.

Spectrograms can help us visualize more complex sounds, too. Consider, for example, the song of the Common Yellowthroat (*Geothlypis trichas*), a wood-warbler species found throughout most of North America. The field guides render the yellowthroat's song as "*witchity-witchity-witchity*," suggesting that we should search a spectrogram for a repeating

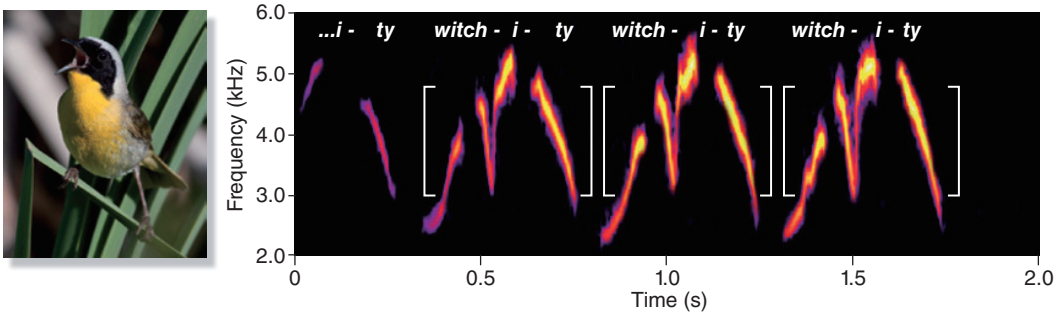


Fig. 10.05 Dissecting the components of a Common Yellowthroat (*Geothlypis trichas*) song. In the spectrogram, repeated "*witchity*" phrases (white brackets) are easy to discern. Each phrase can be further divided into three notes, "*witch-i-ty*." Online you can hear these features even more clearly by comparing the normal song to recordings that have been slowed to half and quarter speeds. Note that slowing the speed causes the pitch to drop. ***Listen online.*** (Recordist: Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Bill Bouton. CC-BY-SA 2.0.)

pattern of individual notes. In line with our expectation, spectrograms of yellowthroat songs show that each "*witch-i-ty*" consists of three or four notes, and successive "*witchities*" appear to be identical (Fig. 10.05). This pattern occurs in almost every yellowthroat song. When the songs are slowed to one-half or one-quarter speed, we can more easily hear each note, especially while following along in the spectrogram. Halving the speed also halves the frequency, so the song sounds lower pitched.

One final example illustrates the usefulness of a spectrogram in seeing the diverse components of song. The song of the Pacific Wren (*Troglodytes pacificus*) of western North America has been described as "the pinnacle of song complexity" (Kroodsma 1980) (Fig. 10.06). The songs of these wrens are truly remarkable; they can be 10 seconds long or even longer, but during that time the wren sings successive notes so rapidly that all we hear is a blur. Once we slow the song down, however, we can appreciate all the fine details and begin to hear what we can see in the spectrogram. At one-half and especially at one-quarter normal speed, the listener can identify each note the wren produces.

10.2 Vocal repertoires

Our experience tells us that birds produce a tremendous variety of sounds (Box 10.03). How can we begin to make sense of this great diversity? The best way is to start with an individual bird. Researchers who study bird sounds often mark a bird, usually with a distinctive combination of colored leg bands, and then follow it, often for days at a time and sometimes year after year. Researchers record sounds that the bird makes and carefully document the context in which each sound was recorded. Next, they make spectrograms of each recording so that the anatomy of each sound can be studied in more detail. Finally, they sort all the spectrograms by shape and combination of notes to establish the entire vocal repertoire of that individual.

This approach has revealed that an individual bird usually has a relatively limited selection of **vocal signals**. A signal is a trait that influences the behavior of other individuals and that evolved for that function. Consider again the Black-capped Chickadee (*Poecile atricapillus*). Extensive research has shown that chickadees have about 14 different kinds of vocalizations (Hailman 1989; Hailman and Ficken 1996). Three of these sounds are frequently used, are highly distinctive, and are readily recognized by anyone who watches chickadees for even a short time. One of these is the "*hey-sweetie*" whistle song (Fig. 10.02), usually sung loudly from an exposed perch. Another vocalization, the one for which the bird was named, is the "*chick-a-dee*" call, often heard in winter flocks and near birdfeeders (Fig. 10.07A). These birds give this call in a variety of contexts, including when they seem mildly alarmed. The third common vocalization is the "gargle," a complex sound used mostly by males during aggressive interactions (Fig. 10.07B).

10.2.1 Songs

One type of avian vocal signal—the **song**—has received special attention from researchers. Song has been defined in numerous ways, but it is generally accepted that songs are long, loud vocalizations, typically delivered from an exposed perch, with the presumed function of attracting

Vocal signals: vocalizations that influence the behavior of other individuals.

Song: an often loud and sometimes complex vocalization used to attract mates or compete with members of the same sex.

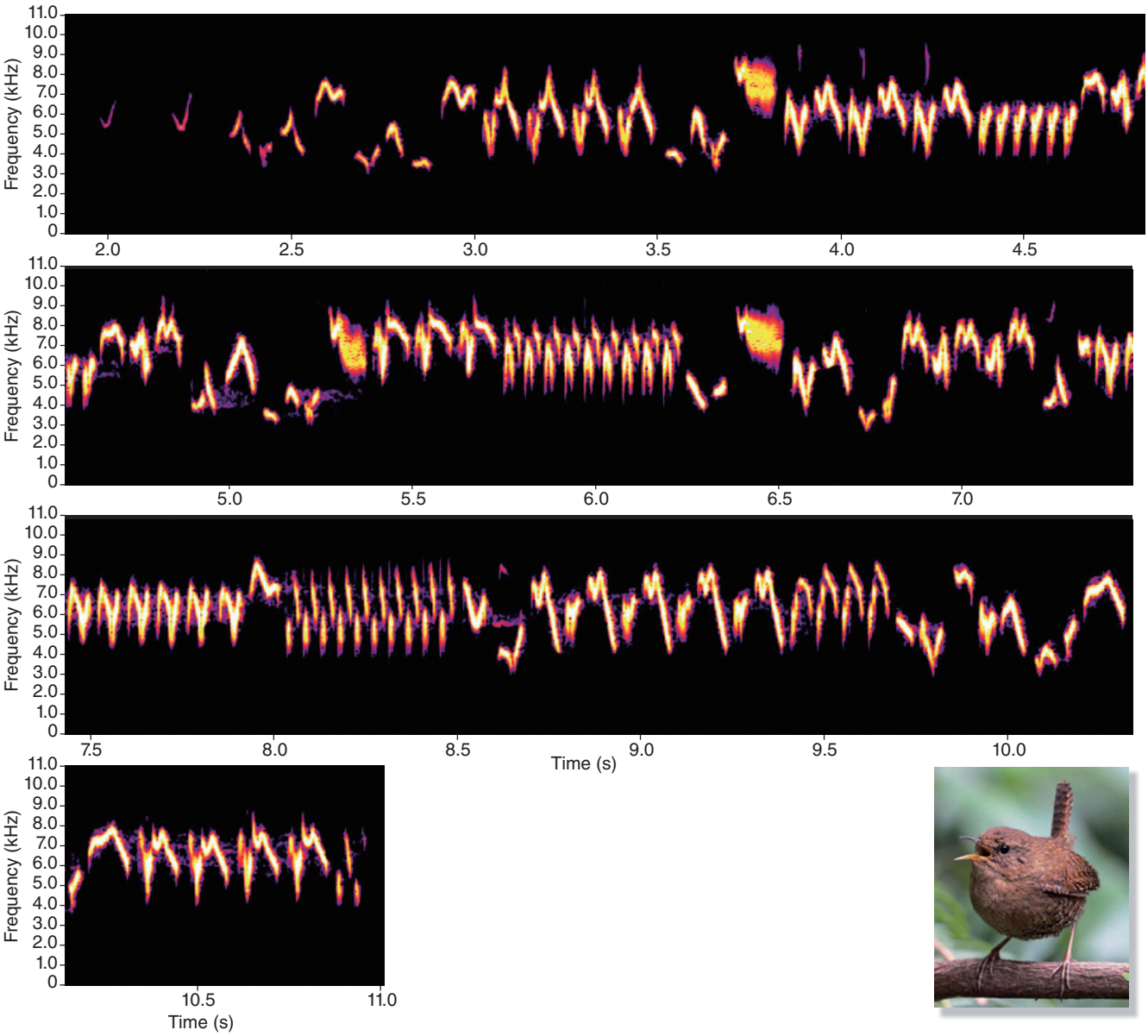


Fig. 10.06 Pacific Wren (*Troglodytes pacificus*) songs are remarkably complex. This spectrogram shows the diversity of elements in this tiny wren's long and complicated song. Web content includes both regular and slowed (half and quarter) speeds, which reveal even more astounding detail. ***Listen online.*** (Recordist: Geoffrey A. Keller. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Liron Gertsman.)

mates or repelling territorial intruders. This definition of song is not very precise, and indeed the distinction between songs and other types of bird vocalizations is somewhat arbitrary. Nonetheless, this general definition is appropriate in many situations because most birds use special, conspicuous vocalizations to attract mates or defend territories. Because songs are often sung loudly and persistently, they are often the most noticeable of the vocalizations that we hear from birds.

The complexity of song varies widely among bird species. In some, such as the Superb Lyrebird (*Menura novaehollandiae*) of eastern Australia (Fig. 10.08), the song is by far the most complex vocalization produced. In other species, however, the song can be less complex than other vocalizations. For example, the "*hey-sweetie*" song of Black-capped Chickadees (*Poecile atricapillus*) is much simpler than their gargle call.

Song is often thought of as a behavior of male birds, but females and males both sing in many bird species, especially in tropical habitats. For example, females sing even more than males in the Streak-backed Oriole (*Icterus pustulatus*) (Fig. 10.09A) and the Stripe-headed Sparrow

Box 10.03 Non-vocal sounds

In addition to the songs and calls that seem to dominate avian acoustic communication, birds produce a variety of non-vocal sounds. Some, such as the whooshing sound we hear when a flying bird passes nearby, are probably just side effects of a bird's normal movements. However, many non-vocal bird sounds appear to be evolved signals that function in communication. Woodpecker drumming, for example, occurs mainly during the breeding season, and drumming birds choose to drum on surfaces that yield especially loud and long-lasting sounds when struck repeatedly (Eberhardt 1997). These observations hint that a woodpecker's percussive performances generate long-distance signals that function in territory defense or courtship, much like the songs of passerine birds.

The rapid drumming of a woodpecker is made possible by a suite of special anatomical features that allow it to bang its head forcefully on a tree many times per second without losing consciousness or sustaining brain damage (Chapter 6). At least one non-woodpecker species without these adaptations nonetheless manages to produce percussive sounds by using tools to strike hollow tree trunks. Palm Cockatoos (*Probosciger aterrimus*) in New Guinea and northern Australia use their bills to craft a drumstick from a small branch (Wood 1984) (Fig. 10.B3.01). The bird then grasps the stick with its foot and bangs it rhythmically against a hollow tree. The resulting drumming sound is audible to human listeners more than 100 meters away.

Many non-vocal bird sounds are produced by feathers, most commonly by wing or tail feathers. For example, feathers are responsible for many of the sounds produced by displaying hummingbirds and manakins (Chapter 4), and for those produced during the aerial courtship display of the American Woodcock (*Scolopax minor*) (Fig. 10.B3.02). The twitter audible during a displaying woodcock's ascent is produced by air moving over its rapidly flapping wings and vibrating three specially modified, narrow wing feathers.

The conclusion that woodcock twittering is produced by wing feathers arose mainly from close observation of displaying birds and an assumption that the three strangely modified wing feathers must be involved. In recent years, however, this kind of educated guesswork has been superseded by more sophisticated methods of establishing the mechanisms by which non-vocal sounds are produced. A key advance in this endeavor has been the advent of the high-speed video recorder, a tool that allows researchers to record videos that can be played back in super-slow motion. In one study, for example, researchers placed the outer tail feathers of museum specimens of Common Snipes (*Gallinago gallinago*) in a wind tunnel and made high-speed video recordings as air moved rapidly over the feathers (van Casteren et al. 2010). In the wind tunnel, the feathers emitted the distinctive "*winnow*" sound that living Common Snipes (and other snipe species) make during the high-speed dives that are part of their courtship display



Fig. 10.B3.01 Palm Cockatoos (*Probosciger aterrimus*) use tools to drum. Some individuals of this species use sticks to strike hollow trees, producing loud percussive sounds. (Photograph by Glenn Walker.)

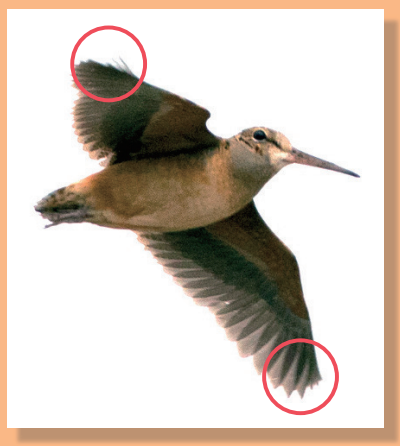


Fig. 10.B3.02 Flight feather sounds. Birds of some species produce non-vocal sounds with specialized sound-producing flight feathers, which vibrate during rapid movement through the air. When an American Woodcock (*Scolopax minor*) flaps its wings during an aerial display, air flows through small slits in three outer primary feathers (red circles), producing a high twittering sound. Access the web content to hear this sound (as well as the "*peent*" call that the male woodcock produces prior to the aerial display). ***Listen online.*** (Photograph by Sam Galick.)

(Fig. 10.B3.03). Analysis of the video revealed that the vanes on one side of each outer tail feather flapped rapidly up and down once the wind speed became fast enough. The flapping produced the characteristic sound, probably by a mechanism similar to the one by which a flag flapping in the wind produces sound.

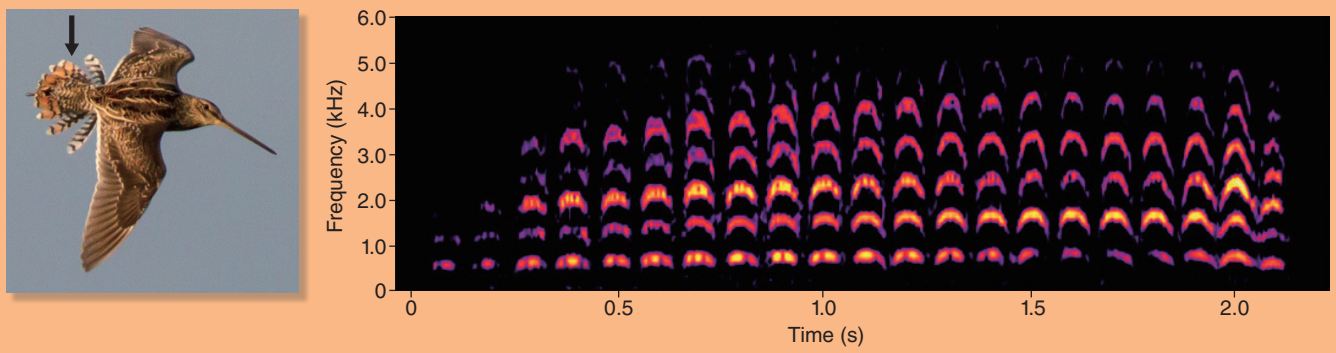


Fig. 10.B3.03 Tail feather sounds. During the high-speed dive portion of a Common Snipe's (*Gallinago gallinago*) courtship display, its outer tail feathers produce a distinctive "*winnow*" sound as the outer tail feather vanes (arrow) flap rapidly back and forth, much like a tethered flag in the wind. The online recording features Wilson's Snipe (*Gallinago delicata*), a closely related species that also produces a "*winnow*" sound as part of its aerial display. ***Listen online.*** (Recordist: Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Ómar Runólfsson.)

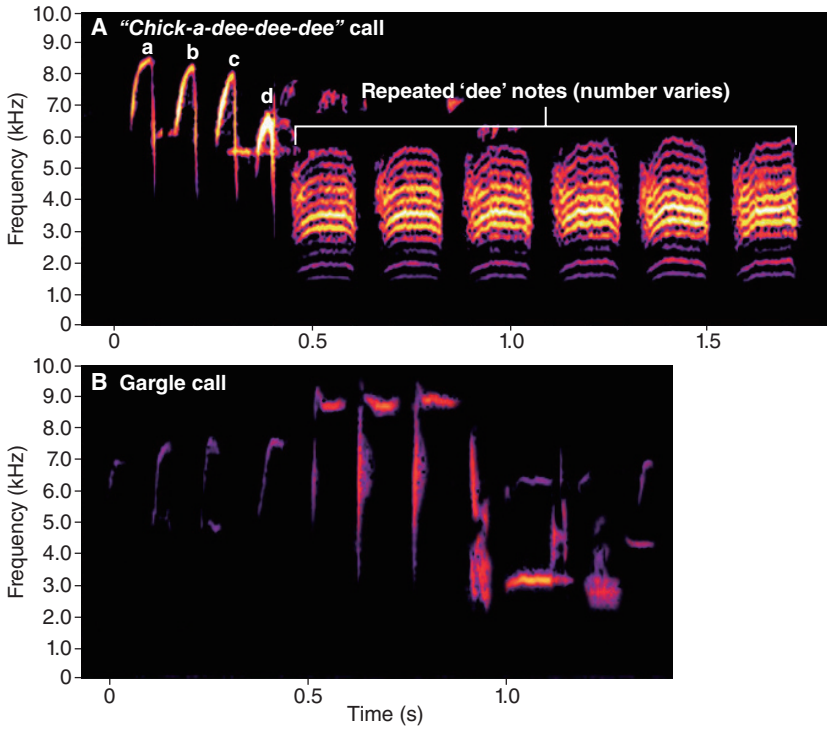


Fig. 10.07 Calls of the Black-capped Chickadee (*Poecile atricapillus*). In addition to the "*hey-sweetie*" song illustrated in Fig. 10.02, chickadees have other vocal signals. (A) The "*chick-a-dee*" call is often associated with flock identity. Although this call consists of the same component notes (a–d) in addition to the characteristic "*dee*" sequence, individuals modify the note order and/or repetition according to the call variety specific to their flock. (B) Gargle calls are typically given by males during aggressive interactions. ***Listen online.*** (Recordists: A, Matthew D. Medler; B, Gerrit Vyn. Courtesy of Macaulay Library © Cornell Lab of Ornithology.)



Fig. 10.08 The Superb Lyrebird (*Menura novaehollandiae*). Lyrebirds are famous for their vocal mimicry of both biotic (other animals) and abiotic (including chainsaws and car alarms) sounds. ***Listen online.*** (Photograph by Alex C. Maisey.)

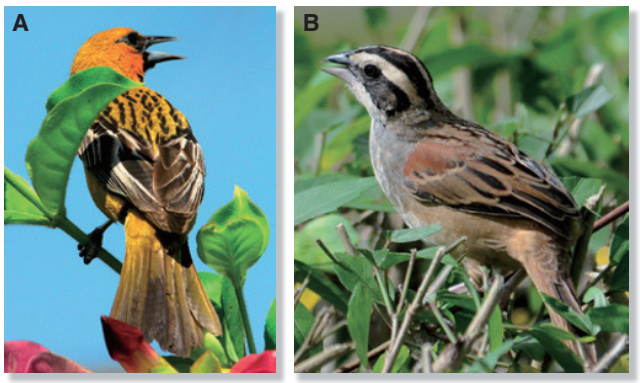


Fig. 10.09 Both sexes may sing. Females sing more than males in (A) the Streak-backed Oriole (*Icterus pustulatus*) and (B) the Stripe-headed Sparrow (*Peucaea ruficauda*). Both sexes sing in many tropical bird species. (Photographs by: A, Jay Ailworth; B, Jean-François Hic.)

(*Peucaea ruficauda*) (Fig. 10.09B), both of which are found in Mexico and Central America (Price et al. 2008; Illes and Yunes-Jimenez 2009). Ways in which female birds use song are covered later in this chapter.

Songs are especially prominent among the 4600 or so species in the **oscine** subgroup of the order Passeriformes (Chapter 2). The oscines, known informally as the songbirds, are renowned for their singing ability. Unlike most other birds, songbirds learn many components of their songs, which therefore can be quite complex. One aspect of this complexity is the number of different song types an individual sings, a number that varies immensely among songbird species. Many songbird species have multiple song types in their repertoires. A European male Common Chaffinch (*Fringilla coelebs*), for example, may sing up to six different "*chip chip chip chooee chooee cheeoo*" song types (Slater et al. 1980). Each song type has a distinctive structure and sequence of notes; the differences are visible on spectrograms and are audible to anyone who listens carefully (Fig. 10.10). A male Common Chaffinch typically sings 2 to 15 or so renditions of one song type, but then he switches abruptly to another type, and eventually to another, until he returns to sing, with great fidelity, the initial type (Riebel and Slater 1999). Song Thrushes (*Turdus philomelos*), another European songbird, are more impressive: each male has about 100 different song types (Ince and Slater 1985). Likewise, Common Nightingales (*Luscinia megarhynchos*) may sing 100–200 different song types (Kiefer et al. 2006) (Fig. 10.11A). The largest repertoire found so far, however, is that of the Brown Thrasher (*Toxostoma rufum*) (Fig. 10.11B) of North America. When thousands of spectrograms of one male Brown Thrasher were sorted into different categories, he was estimated to sing well over 2000 different songs (Kroodsma and Parker 1977).

Although songbird song repertoires can be large, songbirds of some species use very simple song repertoires. For example, as noted earlier in this chapter, the Black-capped Chickadee uses one basic "*hey-sweetie*" song. Except for slight differences in frequency, all "*hey-sweetie*" songs look basically the same on spectrograms. Other North American species with simple song repertoires include Chipping Sparrows (*Spizella passerina*), Indigo Buntings (*Passerina cyanea*), and White-crowned Sparrows (*Zonotrichia leucophrys*). Eurasian species with similarly basic repertoires include Redwings (*Turdus iliacus*), Short-toed Treecreepers (*Certhia brachydactyla*), Meadow Pipits (*Anthus pratensis*), and Willow Tits (*Poecile montanus*). Members of all these species use one basic song type, and the sequence of notes in their songs remains essentially unchanged from one song to the next.

10.2.2 Calls

The term **call** is applied to any bird vocalizations that—compared with songs—are shorter, generally simpler, and less likely to function exclusively in mate attraction or territory defense. Although the distinction between calls and songs is not always clear-cut, in practice a given vocalization usually can be readily classified as either a song or a call.

Oscine passerines: the "true songbirds," one of the two groups within the order Passeriformes, the most diverse avian order.

Call: an avian vocalization that is shorter and simpler than a typical song.

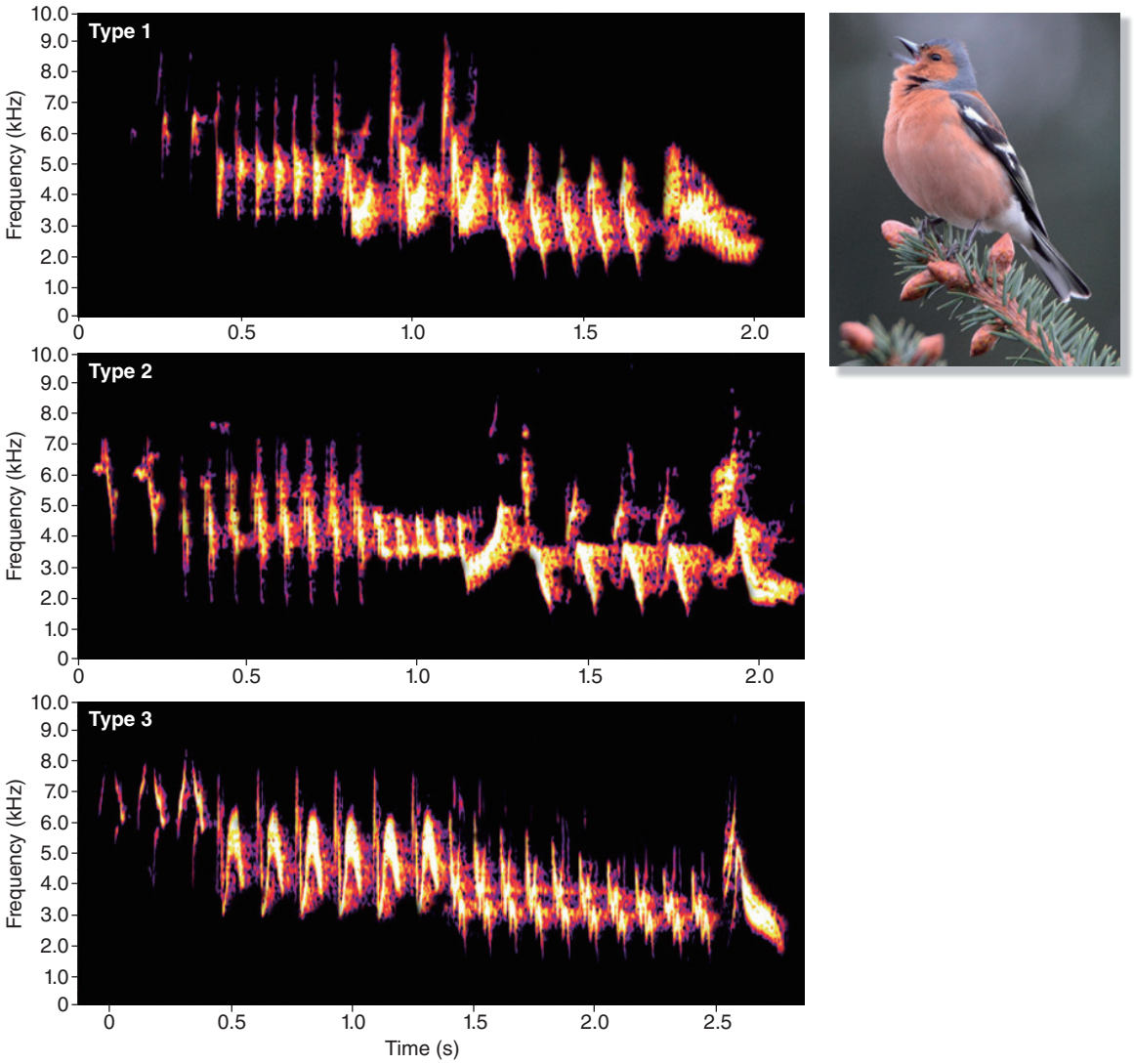


Fig. 10.10 Repertoires. Many species are capable of singing several song types, which together form a repertoire. Compare the spectrograms of three Common Chaffinch (*Fringilla coelebs*) song types; each has a distinctive structure and sequence of notes. ***Listen online.*** (Recordist: Krzysztof Zyskowski. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Jim Almond.)

Most bird species have vocal repertoires that include both calls and songs.

Overall, calls play a large role in facilitating the myriad interactions that characterize a bird's social life. Calls have a variety of communicative functions, with different calls of a species frequently serving different roles (Box 10.04). Contact calls help members of a flock or pair maintain contact with their companions. The flight calls of nighttime migrants probably serve a similar function. Food calls attract offspring or flock mates to a newly discovered source of food. A nestling's begging calls induce its parents to feed it. Alarm calls warn other birds of approaching predators. Mobbing calls attract other birds to join in harassment of a predator. Aggressive calls help resolve conflicts between birds.

10.2.3 Influences on vocal structure

Bird song researchers often refer to the "structure" of a bird vocalization, by which they mean a combination of all the features that form the sound, many of which can be seen on a spectrogram. These features include the duration of the sound, its main frequency, whether the sound is a relatively pure whistle or reaches across a broad spectrum of frequencies at once, whether individual sound units are repeated, and so on.

To some extent, the structure of a vocalization is dictated by its function. For example, the alarm calls that small birds produce when a hawk flies overhead are usually high, narrow-bandwidth sounds that begin softly, grow louder, and then fade away. Sounds with these characteristics, such

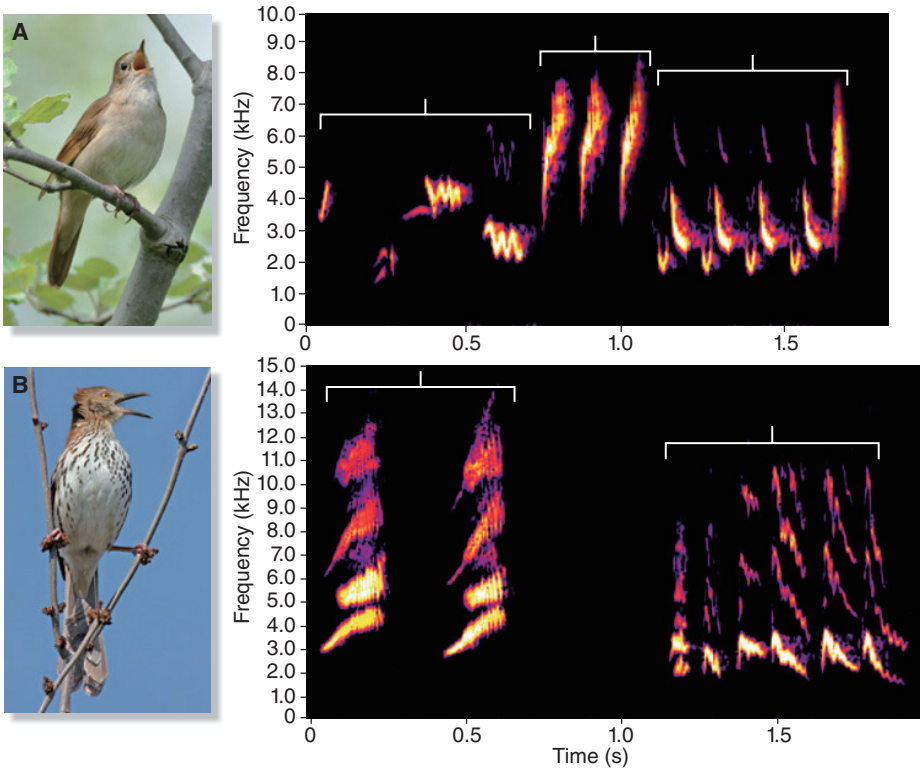


Fig. 10.11 Species with large repertoires. (A) Common Nightingales (*Luscinia megarhynchos*) can sing hundreds of song types. Each bracket indicates a phrase; together the phrases form a song. (B) Brown Thrashers (*Toxostoma rufum*) hold the record for the most song types: one male may sing more than 2000 song types. Each bracket indicates a song. ***Listen online.*** (Recordists: A, Arnoud B. van den Berg; B, Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photographs by: A, Wouter Marck; B, Nick Saunders.)

as the high "*zee*" of many birds, are difficult for a predator to locate (Marler 1955; Klump and Shalter 1984) (Fig. 10.12). In contrast, the mobbing calls that songbirds broadcast as they dive and swoop at a predator often consist of harsh, broadband noise; these sounds are more easily located, thereby revealing the location of the predator and perhaps encouraging other birds to join the mobbing attack (Ficken and Popp 1996) (Fig. 10.13). More generally, sounds associated with aggression are often broadband noise emphasizing low frequencies, whereas appeasing sounds are higher in frequency (Morton 1977).

The structure of complex songs may also be influenced by the type of habitat in which a bird sings. The sound characteristics that are optimal for long-distance transmission of vocal signals vary among different habitats, and song structure may evolve to maximize transmission effectiveness in a particular habitat. For example, songs of the Great Tits (*Parus major*) that breed in Great Britain differ consistently in dense forests versus more open woodlands; forest songs are simpler, lower in frequency, and contain purer tones (Hunter and Krebs 1979). Similarly, Satin Bowerbirds (*Ptilonorhynchus violaceus*) living in dense rainforests in Australia use vocalizations that are lower pitched and have fewer trills compared with bowerbirds living in more open habitats (Nicholls and Goldizen 2006).

Bird species that live near the ground often use songs dominated by low-frequency, fairly pure tones, as reflections off the ground cause sounds that are higher than 1 or 2 kilohertz to transmit poorly. Thus, the low frequency, often tremulous whistles that are conspicuous components of tropical forest soundscapes are, in many cases, voiced by ground-dwelling birds such as tinamous (Fig. 10.14).

10.2.4 What do bird sounds mean?

Many of the researchers who document and study the vocal repertoires of birds worry that the way humans classify birds' signals may not match the classifications used by the birds themselves. Our main tools of analysis, such as spectrograms, are relatively crude ways to picture a sound, showing only selected features of this extremely rich form of communication. The visualized features may be important, but in reality we usually do not fully understand which features the birds themselves really attend to.

In fact, birds may make use of a far greater variety of sounds than we appreciate. Reconsider the Black-capped Chickadee's (*Poecile atricapillus*) seemingly simple "*chick-a-dee*" call (Fig. 10.07A). The initial part of this call consists of four different notes: 'a', 'b', 'c', and 'd'. Most "*chick-a-dee*" calls contain these four notes, but the birds

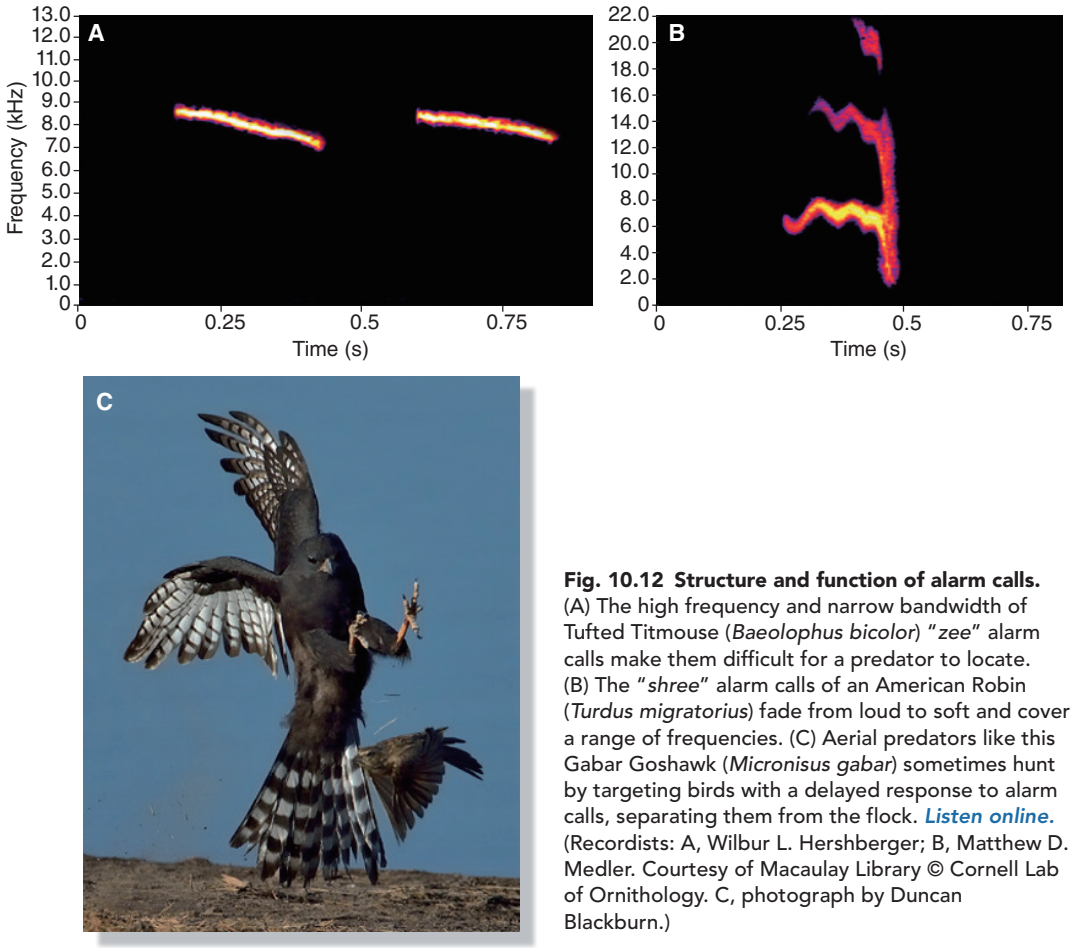


Fig. 10.12 Structure and function of alarm calls. (A) The high frequency and narrow bandwidth of Tufted Titmouse (*Baeolophus bicolor*) "*zee*" alarm calls make them difficult for a predator to locate. (B) The "*shree*" alarm calls of an American Robin (*Turdus migratorius*) fade from loud to soft and cover a range of frequencies. (C) Aerial predators like this Gabar Goshawk (*Micronisus gabar*) sometimes hunt by targeting birds with a delayed response to alarm calls, separating them from the flock. ***Listen online.*** (Recordists: A, Wilbur L. Hershberger; B, Matthew D. Medler. Courtesy of Macaulay Library © Cornell Lab of Ornithology. C, photograph by Duncan Blackburn.)



Fig. 10.13 Mobbing. Many songbird species (here, European Starlings, *Sturnus vulgaris*) will mob—chase and harass—larger birds perceived as a threat (here, an Osprey, *Pandion haliaetus*). In contrast to alarm calls, mobbing calls are harsh, broadband sounds that reveal the location of the calling birds, presumably to induce others to join the mobbing group. (Photograph by John Dustan.)



Fig. 10.14 Ground-dwelling species use low-frequency vocalizations. In dense forest habitats, ground-dwelling birds like this Great Tinamou (*Tinamus major*) have evolved low-frequency songs, optimized for transmission near the ground. ***Listen online.*** (Photograph by Jacques Erard.)

Box 10.04 Call notes and their functions

Birds employ a tremendous diversity of vocalizations. These diverse signals can be classified into two broad but useful categories: songs and calls. Calls are generally softer, shorter, and less complex than songs. Although calls may be less conspicuous than songs, they are important components of birds' vocal repertoires. Let us take a closer look at some examples of calls.

Waxwings

Not all songbirds sing. Apparently, some species do not need a loud, complex vocalization that is broadcast far and wide. The waxwings (genus *Bombycilla*) of the northern hemisphere, for example, have no recognizable "song," at least as we have come to know song in other species. Their sounds have been broadly classified into two categories, the "*bzeee*" call (Fig. 10.B4.01A) and the "*seee*" call (Fig. 10.B4.01B). In Cedar Waxwings (*Bombycilla cedrorum*), the difference in these two sounds can be heard easily because the "*bzeee*" has a buzzy or rattling quality, and the "*seee*" is a high-pitched, hissy whistle. However, careful analysis reveals that the birds use a great diversity of subtle variants. Some variants are given during flocking, some when the male and female are nest building, some during courtship feeding, some by nestlings, and so on (Howell 1972).

Red-winged Blackbirds

Red-winged Blackbirds (*Agelaius phoeniceus*) in North America use a tremendous variety of calls. Especially intriguing are the various calls that the males use as they perch on their territories. Investigators have established seven broad categories of these sounds: "*check*," "*chuck*," "*chick*," "*chonk*," "*chink*," "*peet*," and "*cheer*." Neighboring males tend to use the same call, such as the "*check*," simultaneously, but then they all seem to switch to another call, and eventually another (Beletsky et al. 1986). Waves of call usage spread throughout the marsh, like shock waves spreading out from an epicenter. Do any of the different sounds convey a special meaning about a particular circumstance within the marsh? Or perhaps the vocalization itself has no special significance, but rather the change from one vocalization to the next has particular meaning. Female Red-winged Blackbirds also have some

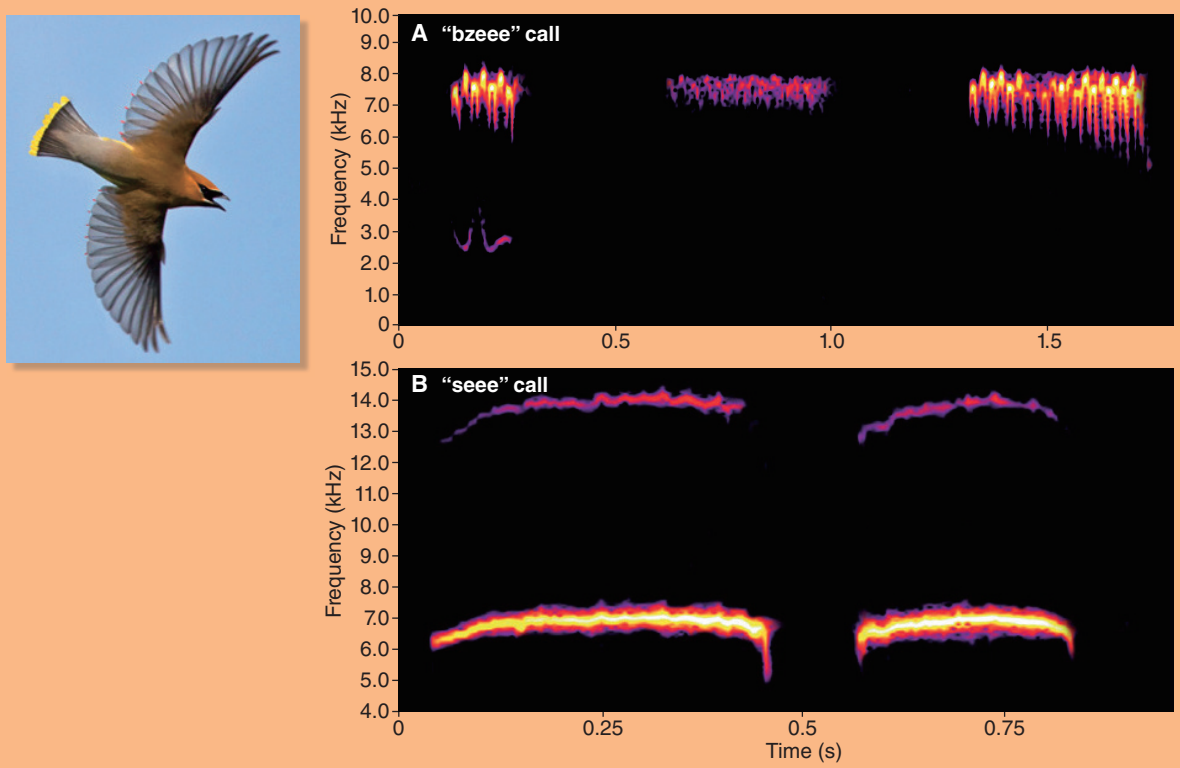


Fig. 10.B4.01 Communicating with calls. Some species, like the Cedar Waxwing (*Bombycilla cedrorum*), communicate with calls rather than songs. (A) This species' buzzy "*bzeee*" call is easily distinguishable from (B) its high, hissing "*seee*" call. ***Listen online.*** (Recordists: A, Gregory F. Budney; B, Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Michaela Sagatova.)

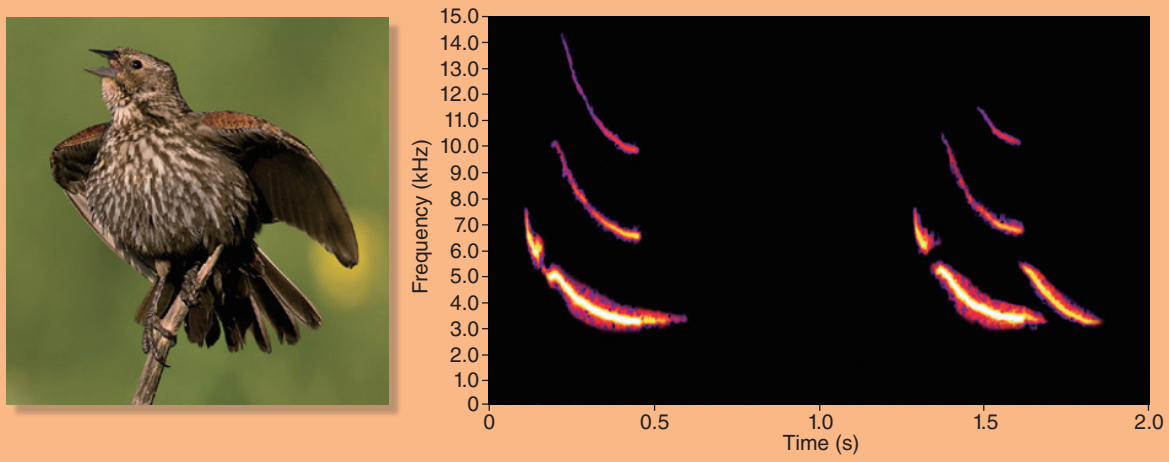


Fig. 10.B4.02 Female calls in Red-winged Blackbirds (*Agelaius phoeniceus*). Females of this species use aggressive "*cheer*" calls to warn other females to stay away. The spectrogram shows the call's short, whistled elements. ***Listen online.*** (Recordist: Randolph S. Little. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Larry J. Kaufman.)



Fig. 10.B4.03 Mimicry in Greater Racket-tailed Drongos (*Dicrurus paradiseus*). Drongos act as sentinels in mixed-species flocks, sounding alarm calls to alert flock mates when predators approach. Mimicry improves the effectiveness of this alarm, as drongos produce the alarm calls of other species as well. (Photograph by Krzysztof Błachowiak.)

loud vocalizations. One is the "*chit*," which is often delivered immediately after the male's song, so that the two vocalizations overlap; this duet between males and females is heard frequently in marshes throughout North America. The "*chit*" seems to encourage the male to guard the female's nest against predation and to discourage him from harassing her (Beletsky and Orians 1985). The female has a second loud vocalization, the "*cheer*," which she uses in aggressive encounters with other females (Fig. 10.B4.02).

Greater Racket-tailed Drongos

Calls can sometimes communicate across species boundaries. In Sri Lanka, Greater Racket-tailed Drongos (*Dicrurus paradiseus*) (Fig. 10.B4.03) spend much of their time in mixed-species flocks that typically include 40 or so birds belonging to a dozen or more species. A drongo uses a variety of calls, including alarm calls that it utters when it detects an approaching predator, such as a hawk. Birds of other species in the flock tend to scatter when they hear a drongo alarm call (Goodale and Kotagama 2005). That is, the drongo's flock-mates treat it as a kind of sentinel and scramble to safety when the drongo signals its alarm. The drongo enhances its effectiveness as a sentinel by mimicking the alarm calls of other species in the flock and mixing the mimicked calls in with its own alarms (Goodale and Kotagama 2006). On occasion, a drongo may produce an alarm call when no predator is in the vicinity (Satischandra et al. 2010). Other birds respond to these false alarms as if they were real. The drongo's foraging success increases after it gives a false alarm, probably because startled birds of other species drop or abandon food that the drongo then snaps up (Chapter 8).

Eastern Phoebes

The vocalizations of the Eastern Phoebe (*Sayornis phoebe*) of North America provide a final example illustrating the diversity of calling behaviors among passerines. The most common phoebe call has been described as a "clear, sweet, weak chip" or simply a "*tp*," and it is given in a variety of contexts (Smith 1969). It typically is used in aggressive encounters, but it is also used by lone birds when foraging during migration or on non-breeding grounds. If a predator is encountered near the nest, this call becomes more emphatic. The same vocalization seems to serve a variety of purposes, and thus the actual meaning of the vocalization may depend on the circumstance in which it is used.

deliver the notes in different combinations, and with differing number of repetitions, to form hundreds of qualitatively different kinds of calls (Hailman et al. 1985). In addition, each note's structure is variable, so each different note combination itself has dozens of potential variants.

Do chickadees send different messages with all these different combinations and variations? This is a challenging but intriguing question. Building on an earlier discovery that chickadees produce "*chick-a-dee*" mobbing calls in response to the presence of stationary or perched (but not flying) predators (Ficken et al. 1978), researchers have discovered that the number of notes in a call differs depending on the size of the predator (Templeton et al. 2005). In an experiment, smaller predators such as Northern Pygmy-Owls (*Glaucidium gnoma*) and Merlins (*Falco columbarius*) elicited "*chick-a-dee*" calls that contained more "*dee*" notes than did the calls produced in response to larger predators such as Great Horned Owls (*Bubo virginianus*) and Gyrfalcons (*Falco rusticolus*). Thus, longer calls with more "*dee*" notes might serve to indicate the greater threat posed by smaller predators (which are more likely than larger predators to prey on small birds such as chickadees). Do chickadees actually use variation in the number of "*dee*" notes to communicate this kind of information? Perhaps so: when experimenters played recorded "*chick-a-dee*" calls through a hidden speaker, responding birds approached more closely and stayed longer (as if aggressively mobbing) in response to calls with many "*dee*" notes than to calls with fewer "*dee*" notes.

Our understanding of the meanings of avian vocalizations to other birds is truly in its infancy. Our current classifications may bear little resemblance to how birds actually hear and use their vocal signals, and we must remember that our ultimate goal is to ascertain how they do this.

10.3 Vocal development

Birds produce a variety of sounds, but how do they acquire the ability to do so? The first sounds made by most newly hatched nestlings are soft peeps, given perhaps in response to siblings or to parents who provide warmth and food. The nestling grows and eventually becomes a fledgling, a yearling, and finally an adult. During this development, the bird's vocal repertoire also develops, with various vocalizations appearing in turn to enable the growing bird to manage its social environment. How does the bird know each vocalization and when to use it? Are its vocalizations encoded in its genes, to be uttered automatically in the appropriate circumstances? Or is development more complex, with the young bird learning much of what it knows from other individuals, much as young humans learn language from adults?

Birds in a few groups—parrots, hummingbirds, and songbirds—clearly do learn during vocal development. This learning process is intriguing to researchers who have studied it intensively, primarily in songbirds. In all songbirds that have been studied, researchers have discovered some kind of vocal learning. Just as in humans, this learning involves listening to a model sound, memorizing the model, and practicing until the sound matches with great fidelity the young bird's memory of the original sound.

10.3.1 Song development in songbirds

Among birds, the songbirds are especially diverse. Comprising about 4600 of the world's roughly 10,000 bird species, they are one of two subgroups within the order Passeriformes (Chapter 2). The songbirds are well known for their complex, often beautiful (at least to human ears) songs (Fig. 10.15). Not all songbirds produce conventionally

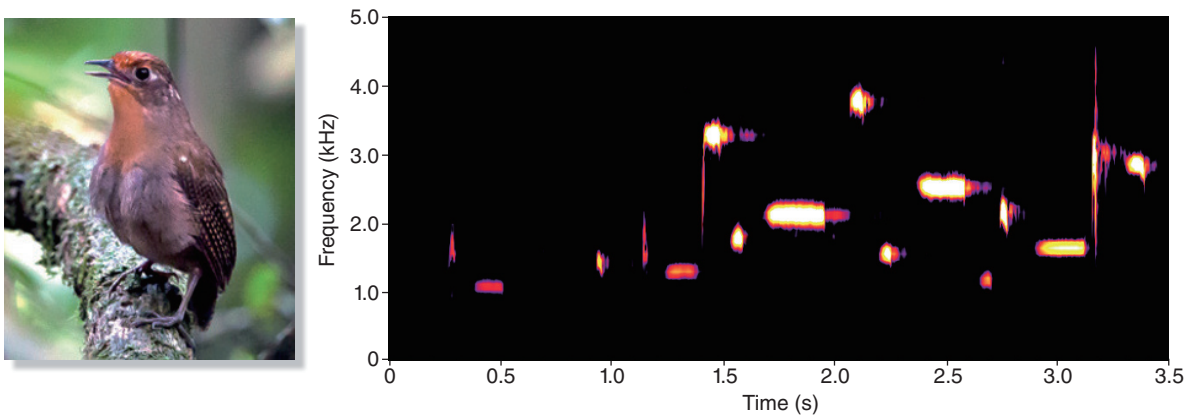


Fig. 10.15 A complex song. The song of the Musician Wren (*Cyphorhinus arada*) is among the most melodious of bird songs. ***Listen online.*** (Recordist: Curtis A. Marantz. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by João Sérgio Barros Freitas de Souza.)

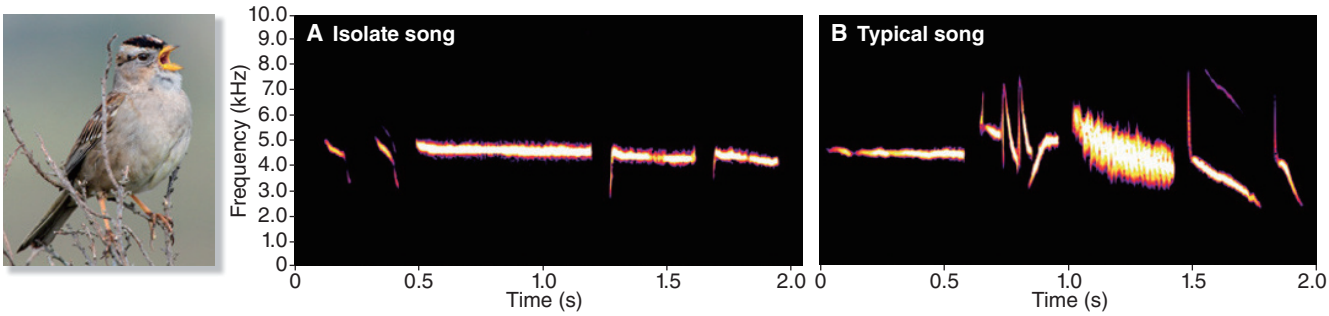


Fig. 10.16 Songbirds learn their songs. (A) White-crowned Sparrow (*Zonotrichia leucophrys*) nestlings raised without exposure to adult songs develop abnormal songs. (B) Adult sparrows sing songs that they memorized early in life. ***Listen online.*** (Recordists: A, Masakazu Konishi; B, Geoffrey A. Keller. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Pat Ulrich.)

beautiful songs—consider the unmelodious songs of most species of crows, jackdaws, or ravens—but most songbirds earn their name by singing frequently and conspicuously.

In the laboratory, we can readily demonstrate the song-learning potential of developing songbirds. In North America, the White-crowned Sparrow (*Zonotrichia leucophrys*) has been a favorite study species for researchers interested in how songbirds learn their vocalizations. When researchers remove a male sparrow from its nest at 8 or 9 days of age and keep him in a laboratory where he cannot hear adult males, he develops a highly abnormal or "isolate" song (Fig. 10.16A). However, a lab-reared male exposed at an early age to recordings of wild adults will learn to sing the details of the tutor song (Marler and Tamura 1964) (Fig. 10.16B). Regardless of where the young bird was born, he can learn a wide range of White-crowned Sparrow songs, taken from anywhere in the geographic range of the species (Petrinovich 1985). The youngster's song matches the song with which he was tutored, detail for detail.

Most songbirds have a **sensitive period** for song learning, a relatively brief time during which they are best equipped to memorize the details of a tutor's song. For a White-crowned Sparrow, model songs broadcast from a loudspeaker in the laboratory have the greatest influence from day 15 of a bird's life to about day 50; the birds have a much more difficult time learning songs heard after day 50 (Marler 1970). If the young bird also is provided with a live bird to interact with, learning after day 50 becomes somewhat easier but never as easy, it seems, as during those early weeks of life (Petrinovich and Baptista 1987). Other songbirds that learn best during a sensitive period early in life include Swamp Sparrows (*Melospiza georgiana*) (Marler and Peters 1988) and Marsh Wrens (*Cistothorus palustris*) (Kroodsma and Pickert 1980) in North America; Common Chaffinches (*Fringilla coelebs*) (Thorpe 1958; Slater and Ince 1982) in Eurasia; and Zebra Finches (*Taeniopygia guttata*) (Immelmann 1969; Braaten 2010) in Australia. Generally, birds of species with a well-defined sensitive period develop a repertoire of sounds during their first year of life and then rarely, if ever, modify it in later years.

Some birds, however, are much less constrained by sensitive periods and retain the ability to learn new songs well into adulthood or even throughout their lives. These **open-ended learners** include the Northern Mockingbird (*Mimus polyglottos*) of North America (Derrickson 1987), the Common Nightingale (*Luscinia megarhynchos*) and European Pied Flycatcher (*Ficedula hypoleuca*) of Eurasia and Africa (Todt and Geberzahn 2003; Eriksen et al. 2011), the Village Indigobird (*Vidua chalybeata*) of Africa (Payne 1985), the Saddleback (*Philesturnus carunculatus*) of New Zealand (Jenkins 1978), and the cosmopolitan European Starling (*Sturnus vulgaris*) (Eens et al. 1992).

Songbirds are selective in what they learn. A young male White-crowned Sparrow, for example, does not learn just any bird song it hears. Instead, the young bird tends to imitate only sounds that match, to some extent, his innate knowledge of the characteristics of his own species' song. If he hears both Song Sparrow (*Melospiza melodia*) and White-crowned Sparrow songs, for example, he will learn the White-crowned Sparrow songs (Marler 1970). This inherent bias toward songs of his own species helps prevent him from mistakenly learning the songs of other species that may be singing in his vicinity. This protection mechanism is not perfect, however. For example, when experimenters housed a young White-crowned Sparrow only with a singing adult Song Sparrow, the young bird's physical and vocal interactions with the adult overrode his inborn tendencies,

Sensitive period: the period of time during a songbird's neural development when it is able to learn songs after hearing a tutor.

Open-ended learners: songbirds that remain able to learn new songs throughout all or most of their lives.

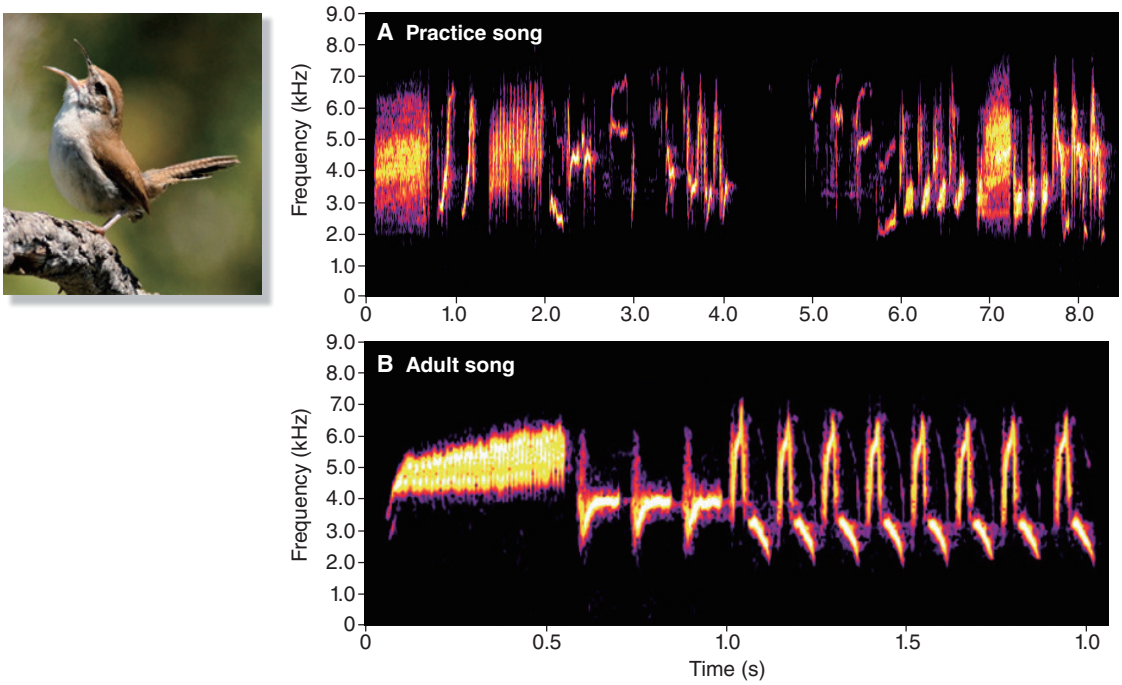


Fig. 10.17 Oscine song development requires exposure and practice. In songbirds, song learning often begins in the nest, but song development is not completed until later. In Bewick's Wrens (*Thryomanes bewickii*), newly fledged males choose a territory, where they are exposed to the songs of their neighbors. (A) Young males begin practicing the songs of their new neighbors shortly after dispersing. (B) After much practice, an individual's song matches those of his neighbors. ***Listen online.*** (Recordist: Donald E. Kroodsma. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Susan Teefy.)

and the White-crowned Sparrow learned to sing Song Sparrow songs (Baptista and Petrinovich 1986).

10.3.2 Process of song development

The process by which songbirds learn to sing unfolds in stages. A young songbird first memorizes a song, which it can do as early as 15–20 days of age. Days, months, or even a year later, the bird recalls that early memory as it practices singing and tries repeatedly to produce an imitation of what it remembers. Listening carefully to its own practice songs, the bird makes successive corrections to the practice sounds that eventually result in a near-perfect copy of the remembered song.

Nestlings of many species begin to practice singing shortly after leaving the nest, often at about 3 weeks of age. The earliest practicing, known as **subsong**, is barely detectable, even by someone listening very carefully from a short distance away. Among birds hand-raised in the laboratory, subsong often occurs in a fledgling that recently has been fed. The youngster perches, resting comfortably, even appearing to doze with eyes closed and head tilting to one side. All the bird's systems appear to be completely at rest, but soft whispers, accompanied by barely perceptible throat movements, reveal that inwardly the future singer has begun to practice. If this resting state is disturbed by a sibling (or a curious human), the young bird breaks abruptly from its apparent slumber, becomes fully alert, and halts its practice singing.

Subsong: the quiet practice songs made by young birds that are just learning how to sing.

As the fledgling grows older, its practice songs gradually become louder, more persistent, and more structured. The sounds begin to resemble the adult song. This transition was evident in a study of the non-migratory Bewick's Wren (*Thryomanes bewickii*) in Oregon (USA) (Kroodsma 1974). In the study population, a typical young male wren left his parents' territory at 4–5 weeks of age, and a few weeks later was already defending the territory he would hold for the rest of his life. On that territory, the quality of his practice singing gradually improved (Fig. 10.17A) until his songs matched, detail for detail, the songs of his adult neighbors. Although the young male was capable of learning his father's songs during the first 4 or 5 weeks of his life (when he was cared for by his parents), he instead learned the songs of males adjacent to his later territory (Fig. 10.17B).

The practice singing (subsong) of a young Bewick's Wren or other songbird is remarkably similar to the practice speaking (babbling) through which humans progress as

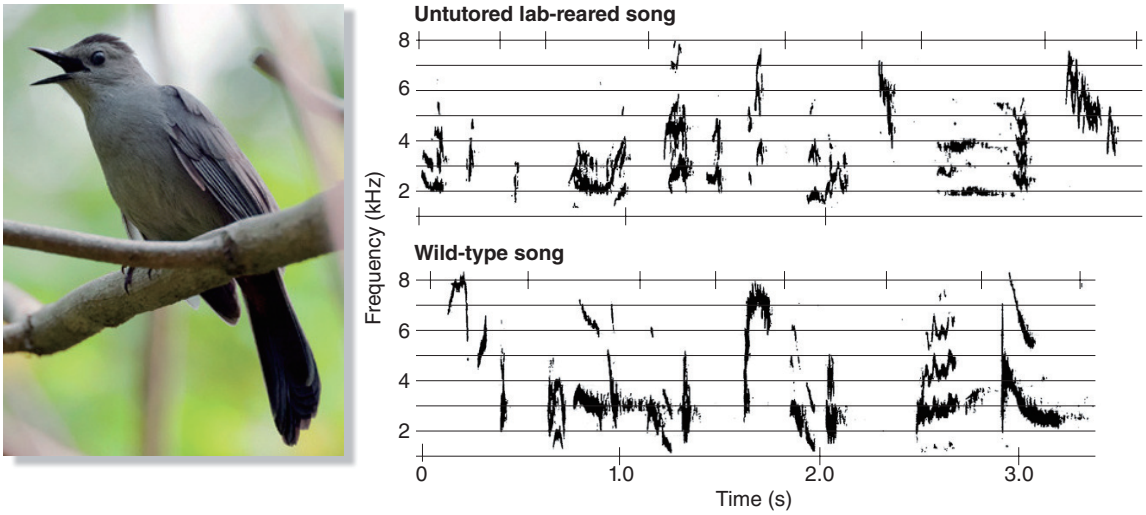


Fig. 10.18 Not all species learn by imitation. Some species, like the Gray Catbird (*Dumetella carolinensis*), do not require exposure to adult song. Compare the songs of an untutored, lab-reared male (above) to those of a wild bird (below). The untutored bird sings a complete wild-type catbird song without exposure to conspecific recordings. (From Kroodsma et al. 1997. Reproduced with permission from Elsevier. Photograph by Michael Hogan, hoganphoto.com.)

toddlers. Each young male Bewick's Wren must master a vocabulary of about 16 different song types, copied from his adult male neighbors. Eventually, he will be able to choose one of those 16 song types and sing it 20–50 times in succession, giving each rendition crisply and consistently, with no mistakes or wavering. Then he will introduce another of the 16 songs, and eventually another, until slowly, methodically, over several hours, he has worked his way through his entire song repertoire.

But the practicing young wren gets much of this wrong. Like a babbling human toddler, he takes bits of sound out of context and strings them together in a continuous, nonsensical sequence. The sounds lack the crispness and confidence of an adult wren's vocalizations, and no two attempts at the same sound are alike. Eventually, however, this young wren will be as competent as his father, just as we master spoken language.

Wherever you live, chances are you will be able to hear young birds practicing if you listen very carefully during times of the year when juvenile birds are becoming independent. Practice songs are less structured and more rambling than the adult male song.

10.3.3 Diversity of song development in songbirds

With well over 4000 species of songbirds, trying to generalize about how "the songbird" develops its song is difficult. Perhaps the only valid general statement we can make is that evidence of learning has been found in all songbird species studied to date. But how this learning occurs varies considerably among species.

Natural selection (Chapter 3) has molded the developmental process so that individual birds develop vocalizations that function appropriately in the communication system of their own species. In some cases, this evolutionary process has yielded developmental programs characterized by high-fidelity imitation. For example, young Swamp Sparrows (*Melospiza georgiana*) must hear adult songs in order to later produce normal songs of their own, which generally are near-perfect imitations of the songs they heard earlier (Marler and Sherman 1985). The young sparrows fail to develop normal songs if they are prevented from hearing adult songs to imitate. In other species, however, imitation plays a much smaller role. A laboratory study of young Gray Catbirds (*Dumetella carolinensis*), for example, showed that they do not require exposure to normal catbird song (Kroodsma et al. 1997). Catbirds isolated from adult songs, even starting at the young age of 8 days, later developed seemingly normal repertoires of hundreds of typical catbird song types (Fig. 10.18).

Nevertheless, observations in the laboratory and of wild birds suggest that Gray Catbirds can imitate the songs of both their own and other species, so vocal learning certainly does occur in catbirds; however, imitating other adult catbirds does not dominate the song development process as it does in many other species. Overall, we can picture song developmental programs as falling along a continuum, from species at one extreme that acquire songs strictly by precise imitation during an early sensitive period, to species at the other extreme that rely almost exclusively on invention and improvisation of songs that continues throughout life. Between these extremes lies a range of developmental programs that vary in the relative importance and fidelity of

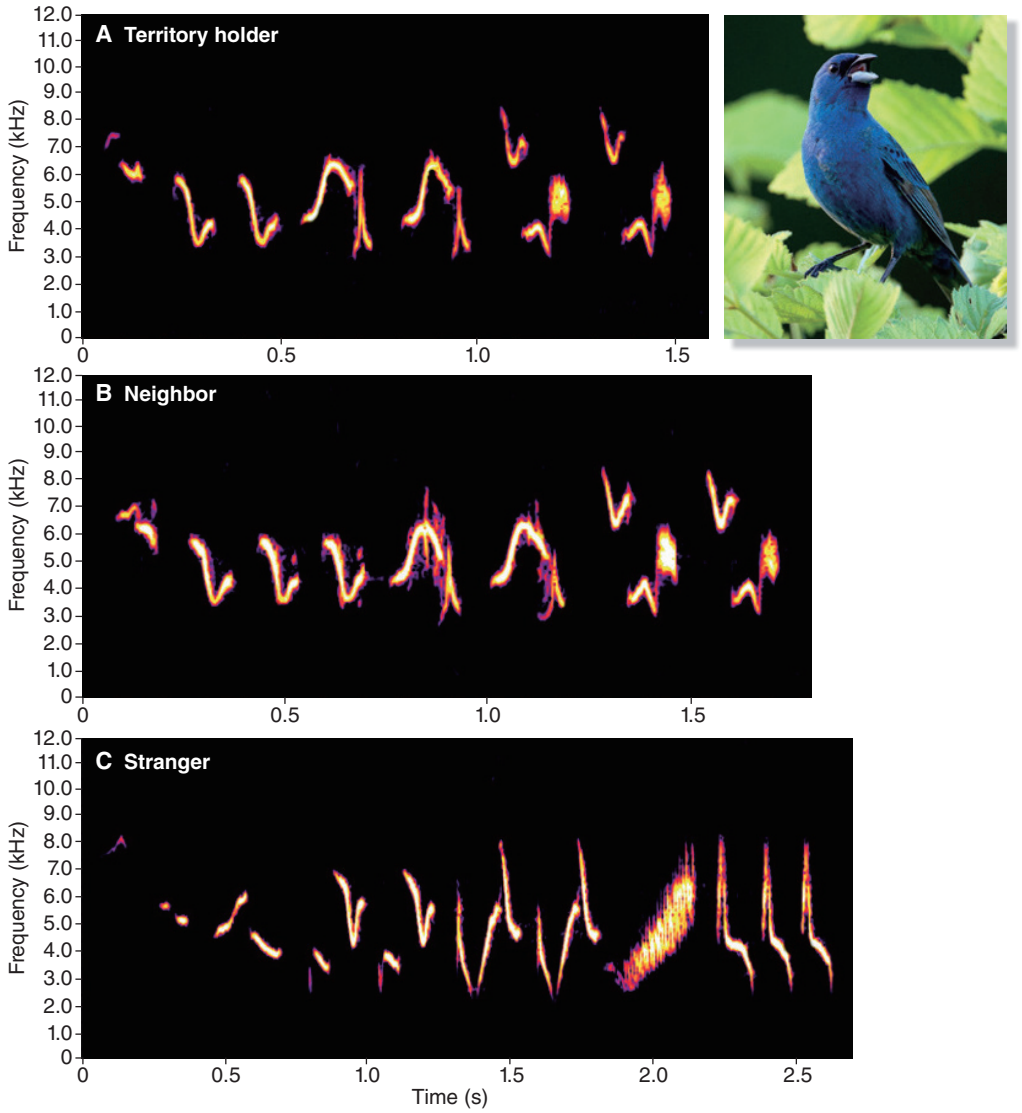


Fig. 10.19 Local dialects and song development. Young male Indigo Buntings (*Passerina cyanea*) gradually transition from singing song components developed on their natal territories to songs that match the details of their territorial neighbors. Compare the virtually identical songs of (A) one territorial adult and (B) his neighbor with (C) a conspecific recorded in a different neighborhood. ***Listen online.*** (Recordists: A and B, William W. H. Gunn; C, Geoffrey A. Keller. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Mike Martin.)

imitation, in the timing of and limits on song acquisition, and in the number of different songs acquired.

Why do young birds of some species imitate their neighbors so perfectly, while the young of other species improvise unique repertoires? To better understand these differences, we need to know something about the social life of the species in question and how they use songs during social interactions.

In a number of studies of how songbirds acquire and use songs, young birds have been found to be especially good at learning the songs of other adults in their immediate neighborhood. For example, research on Indigo Buntings (*Passerina cyanea*) in Michigan (USA) has shown that these birds live in small "neighborhoods" in which the resident males share the same song type (Payne 1981, 1983). Young males and females typically breed in neighborhoods other than the one in which they were hatched. When a young male settles on a territory during his first breeding attempt, he usually has an odd song, one that is unique to him and that typically bears little resemblance to his father's song. Over time, however, he changes his song to match the song details of an immediate territorial neighbor, thereby perpetuating the local neighborhood of songs (Fig. 10.19). A young male Indigo Bunting must gain some social advantage by

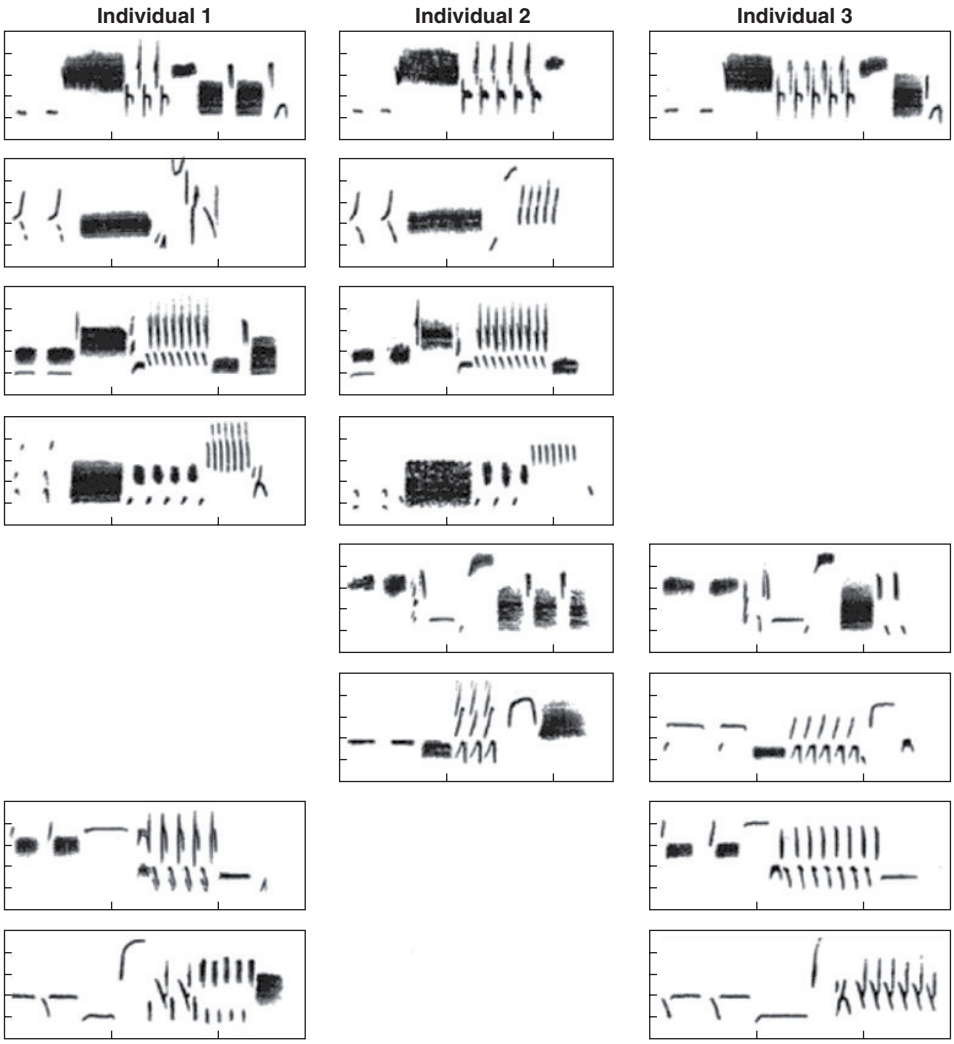


Fig. 10.20 Song learning can lead to song type sharing. Young male Song Sparrows (*Melospiza melodia*) acquire repertoires of several song types by imitating their neighbors. After establishing a territory, they learn some of the common neighborhood song types, thus ensuring that they share some song types with all or most of their territorial neighbors. The three columns in the figure contain the song repertoires of three neighboring birds. Rows show similar (shared) song types. (From Beecher 2008. Reproduced with permission from Elsevier.)

using the same song type as his immediate neighbors, and his song development program ensures that he is able to sing the local shared song type.

Young Song Sparrows (*Melospiza melodia*) develop their songs in much the same fashion as Indigo Buntings, but the process is more complex because each sparrow has a repertoire of 8–10 different song types. In non-migratory populations, young male Song Sparrows do not settle down immediately, but rather spend some time late in their hatch year ranging over an area that includes the territories of four or five adults (Arcese 1989). In a well-studied population in Washington State (USA), a young male learns songs from the adults in his small neighborhood and seems to follow two rules in his learning process (Beecher 2008). First, each song type he acquires is a complete song copied from a particular bird; unlike birds of some other species, a young Song Sparrow does not create amalgamated songs by linking together pieces from different songs or different males. Second, he preferentially learns the song types most common in his neighborhood, so if all five adults in the neighborhood share a particular song type, the youngster is especially likely to learn it; songs unique to a single adult are far less likely to be learned (Fig. 10.20).

These rules for learning maximize the chance that a Song Sparrow male settling in for his first breeding season will share some song types with all or most of his neighbors. Sharing song types with neighbors enhances a Song Sparrow's ability to interact with and influence other birds in his social environment, in part because male Song Sparrows in this population resolve conflicts by means of a



Fig. 10.21 Matched countersinging. Male Marsh Wrens (*Cistothorus palustris*) engage in singing contests in which one male matches each song type sung by the other, while cycling rapidly through multiple song types. ***Listen online.*** (Photograph by Ron Dudley.)

communication system that requires that a singer selectively use song types of varying degrees of similarity to those used by his opponent (Beecher et al. 1996; Burt et al. 2001).

A comparison of Marsh (*Cistothorus palustris*) and Sedge (*Cistothorus platensis*) Wrens provides an additional illustration of how song development programs ensure the acquisition of a signal repertoire appropriate to a species' communication system. Laboratory studies have shown that Marsh Wrens acquire their large song repertoires (more than 100 song types per male) by imitation (Kroodsma and Pickert 1984; Kroodsma 1986). In western North America, many Marsh Wren populations are resident year round and, as in the Song Sparrows of Washington State, imitation tends to yield neighbors with similar song repertoires. But in western Marsh Wrens, the vocal similarity between neighboring males is more extreme, and neighbors may have nearly identical repertoires. They often use these repertoires to perform a display called **matched countersinging**, in which two males engage in a kind of call-and-response battle of matching songs (Verner 1976). A bout of matched countersinging might start with one male singing song type A, which his neighbor counters with A; the first male immediately switches to type B, and the neighbor replies with B; type C is followed by C, and so on through many dozens of song types. Successive song types in the exchange are different enough that a human listener can readily distinguish them and follow the matching interplay (Fig. 10.21).

In contrast to Marsh Wrens, Sedge Wrens in North America generally do not engage in this intricate countersinging. They communicate not with matching song types but with generalized songs that declare their identity as a "Sedge Wren." In fact, matched countersinging usually is impossible for Sedge Wrens in North America, because no two males in a population share identical song repertoires (Kroodsma and Verner 1978). This lack of song-type sharing is related to the Sedge Wren's different mode of song development. In the laboratory, Sedge Wrens do not imitate songs the way Marsh Wrens do, but rather they mostly improvise, with each bird inventing 100 or more of its own song types (Kroodsma et al. 1999a).

Why have Sedge Wrens evolved improvisation and unshared song types, whereas closely related Marsh Wrens evolved imitation and matched countersinging? These differences may stem from differences in the two species' lifestyles. The Sedge Wrens of North America are somewhat nomadic, unpredictable in their breeding locations in different years and sometimes moving even within a year. As a result, neighboring males are often strangers to one another and are not involved in the kind of long-term social relationships that favor communication with matching sounds. In these circumstances, improvisation may be the most effective mode of developing a repertoire of many song types. In contrast, Marsh Wrens resident in western North America live in stable communities whose members interact with one another repeatedly over many months or years. Such repeated interactions with the same individuals may foster communication with shared identical songs, which in turn favors careful imitation of those songs.

A connection between social stability and song imitation is also apparent in Sedge Wren populations resident in the tropics. Unlike their nomadic North American relatives, tropical Sedge Wrens are non-migratory and remain on their territories year round. Research on resident Sedge Wrens in Costa Rica and Brazil has shown that, in contrast to the absence of song-type sharing among North American Sedge Wrens, neighboring males in those places tend to share many song types, an indication that the birds have learned their songs through imitation of their neighbors. Birds in Brazilian populations even exhibit matched countersinging, a sure sign of song imitation (Kroodsma et al. 1999b, 2002).

10.3.4 Song development in suboscine passerines

We can better appreciate song development in songbirds by understanding how songs develop in other bird groups. Consider the close relatives of the oscine songbirds, the **suboscine passerines**. Suboscines and oscines together

Matched countersinging: a behavior in which rival males respond to one another's songs, with both males matching different song types one after another.

Suboscine passerines: the group within the order Passeriformes in which song learning is rare or absent.

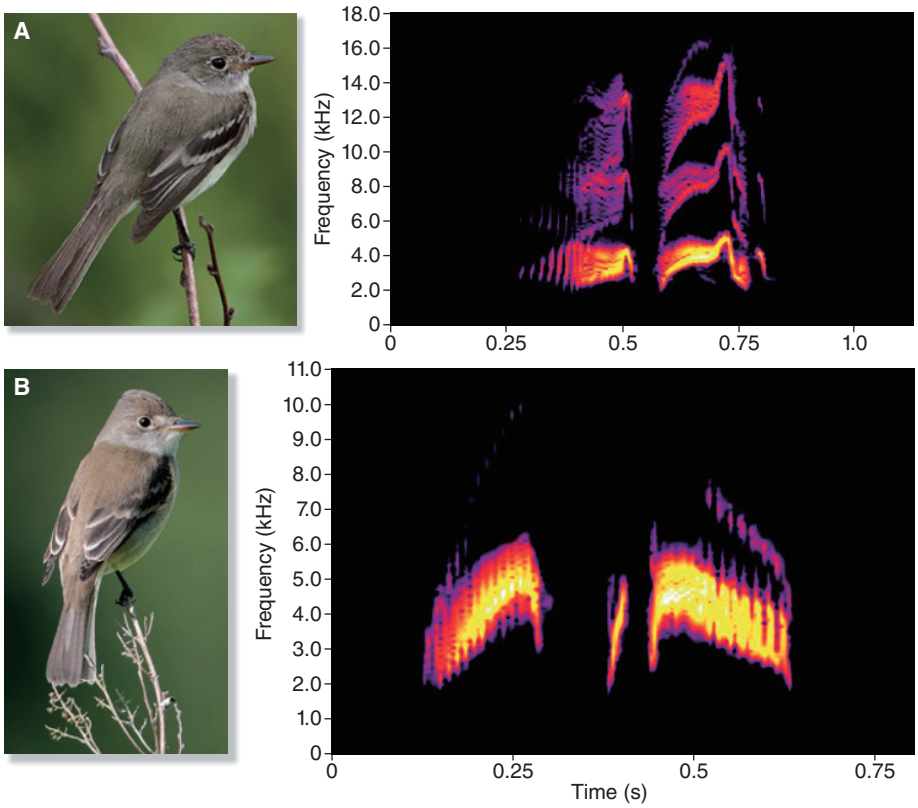


Fig. 10.22 Suboscine song development. In contrast to oscines, suboscine passerines typically develop normal songs without learning or experience. For example, (A) Alder Flycatchers (*Empidonax alnorum*) and (B) Willow Flycatchers (*Empidonax traillii*) develop songs typical of their species even when exclusively exposed to songs of a different species as young birds. Although the two species look very similar, their songs are quite distinct. ***Listen online.*** (Recordists: A, Michael J. Andersen; B, Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photographs by: A, Simon Pierre Barrette, http://en.wikipedia.org/wiki/File:Empidonax_alnorum_CT2.jpg. CC-BY-3.0; B, Wes Aslin.)

form the order Passeriformes (Chapter 2). Only a relative handful of suboscine groups—such as the broadbills and the pittas—live in the Old World. About a thousand suboscine species, however, reside in the New World, including groups such as the antbirds, antpittas, woodcreepers, cotingas, and flycatchers.

The striking differences in song development between the oscine songbirds and suboscines are clearly illustrated by studies of song development in two very similar species found in eastern North America, the Alder (*Empidonax alnorum*) and Willow (*Empidonax traillii*) Flycatchers. These two species are essentially identical in appearance, and the only reliable way to identify them in the field is by their songs and calls: the Alder Flycatcher sings a song that sounds like "*fee-BEE-o*" (Fig. 10.22A), and the Willow Flycatcher sings a "*FITZ-bew*" song (Fig. 10.22B).

In an experiment to determine how these suboscine flycatchers develop their songs, young Alder and Willow Flycatchers were taken from their nests at about 10 days of age and moved to the laboratory (Kroodsma 1984). The young Willow Flycatchers were then trained with Alder Flycatcher songs played over loudspeakers, and Alder Flycatchers were trained with Willow Flycatcher songs. Although the young Willow Flycatchers heard only Alder "*fee-BEE-o*" songs, and the young Alder Flycatchers heard only Willow "*FITZ-bew*" songs, the birds were not confused. Unlike songbirds, these young flycatchers developed perfectly normal songs of their own species. The young flycatchers did not imitate the songs they heard, and their experience with the wrong songs caused no problems.

In the wild, young Alder Flycatchers usually remain near each other in a small family flock during their first few days out of the nest. If the fledgling brothers and sisters get separated, they use a particular vocalization as a contact call, as if to keep tabs on each other and perhaps announce their location to their parents, who are still feeding them. This call is an unmistakable, although scratchy and uncertain, rendition of what will eventually become the adult song, the "*fee-BEE-o.*" Thus, as soon as young Alder Flycatchers leave the nest, they are already uttering what clearly will

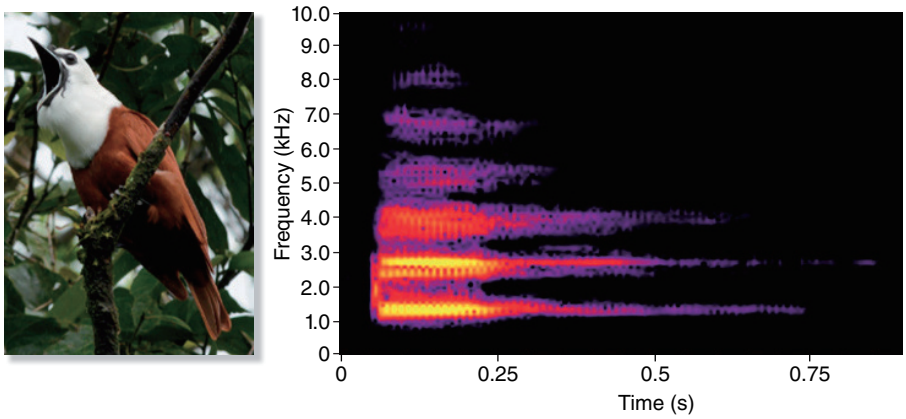


Fig. 10.23 Some suboscines may learn their songs. Long-lived Three-wattled Bellbirds (*Procnias tricarunculatus*) modify their songs from year to year. These changes occur in concert among all birds in a population, strongly suggesting that the birds are imitating one another. Bellbird songs contain some incredibly loud elements. ***Listen online.*** (Recordist: David L. Ross, Jr. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Eduardo Chang.)

become their adult song. In the laboratory, the process is the same: a young bird that has just left the nest gives this call repeatedly when separated from its siblings. This call is already being used at 14 days of age, the age at which young songbirds are just beginning to memorize the sounds they will later produce.

An additional experiment shows just how different suboscine flycatchers are from songbirds (Kroodsma and Konishi 1991). Eastern Phoebes (*Sayornis phoebe*) were brought into the laboratory at 10–12 days of age, before the birds were old enough to sing. The young birds were anesthetized and surgically deafened. The deafened birds developed normal song, even though they could not hear themselves practice. In contrast, songbirds must hear themselves vocalize in order to compare their practice sounds with their remembered model sounds. Phoebes, with their innate songs, do not require this kind of auditory feedback.

Eastern Phoebes, Alder Flycatchers, and Willow Flycatchers are only three of the more than 1000 species of suboscine birds, so generalizing from them to the whole suborder might be unwise. Nonetheless, clues from other suboscine species, such as the contact calls used by young birds and the lack of geographic variation in song form, suggest that the song development of most suboscines may resemble that of these flycatchers. At the same time, however, research has revealed evidence of song learning in at least one suboscine species, the Three-wattled Bellbird (*Procnias tricarunculatus*) (Fig. 10.23). These bellbirds are rather long-lived—wild bellbirds can live more than 20 years—and careful study of marked birds in Costa Rica has shown that individuals alter their songs from year to year, with all the birds in an area making the same change in concert (Kroodsma 2005). This observation strongly suggests that the birds are copying songs from one another, although no one knows which bird first changes its song, or why.

10.3.5 Vocal development in non-passerines

Vocal development has been less well studied in the other orders of birds. Extensive vocal learning seems to occur in only two other orders, the parrots (order Psittaciformes) and the hummingbirds (order Apodiformes).

Parrots, of course, are renowned for their ability to imitate human speech in captivity, and captive parrots of some species, such as Budgerigars (*Melopsittacus undulatus*), modify their calls to match those of their mates or other flock members (Farabaugh et al. 1994; Hile et al. 2000). In addition, captive Budgerigars have been induced to imitate calls played through a loudspeaker (Manabe et al. 2008). Experiments have shown that wild parrots also may imitate the vocalizations of other individuals of their species. For example, in the Galah (*Eolophus roseicapilla*), an Australian cockatoo, many wild birds responded to playback of unfamiliar calls by using calls that changed steadily over successive utterances, becoming progressively more similar to the playback call (Scarl and Bradbury 2009). Wild and captive Orange-fronted Parakeets (*Eupsittula canicularis*) in Costa Rica also changed their calls in response to playback, but in this species the changes sometimes made the calls increasingly similar to the playback, sometimes increasingly dissimilar, and sometimes by turns increasingly similar and dissimilar (Balsby and Bradbury 2009). Both parrot species clearly alter their vocalizations in response to the vocalizations they hear, and many of the changes are imitative. What is the function of these rapid vocal changes? Perhaps the ability to modify calls quickly to match (or "anti-match") other birds facilitates the social interactions and negotiations that ensue when a flock encounters another, perhaps unfamiliar, flock.

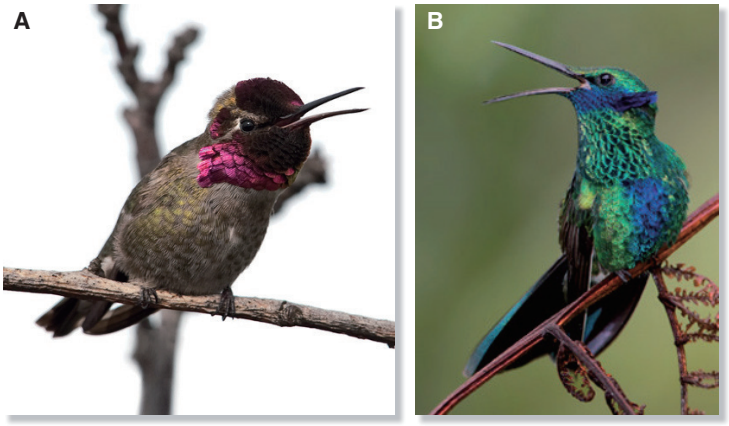


Fig. 10.24 Hummingbirds learn their songs. (A) Anna's Hummingbirds (*Calypte anna*) and (B) Sparkling Violetears (*Colibri coruscans*) acquire their songs through imitation. Many hummingbird species have regional dialects, an indicator of song learning. (Photographs by: A, Johanna van de Woestijne; B, George Scott.)

Vocal imitation by hummingbirds was first demonstrated in California (USA) by raising young Anna's Hummingbirds (*Calypte anna*) (Fig. 10.24A) in the laboratory (Baptista and Schuchmann 1990). In this experiment, the songs of a hand-reared hummingbird that had been raised in isolation were compared with the songs of three other hand-reared birds, one of which had been housed with singing adults for 8 weeks before being moved to live with the other two youngsters. The isolated bird ultimately developed only highly abnormal songs, but the songs of birds in the other group were fairly normal and very similar among group members, suggesting that they had imitated one another. Additional evidence of song imitation comes from the existence of hummingbird dialects, in which birds in an area sing similar songs that differ from those of birds in other areas. For example, among Sparkling Violetears (*Colibri coruscans*) in Ecuador, the songs of territorial neighbors are very similar, but the songs of non-neighbors are not, and each bird's songs are more similar to those of birds in its geographic area than to those of birds that live farther away (Gaunt et al. 1994) (Fig. 10.24B). This kind of song-type clustering caused by imitation also has been documented in Wedge-tailed Sabrewings (*Campylopterus curvipennis*) in Mexico (González and Ornelas 2009). There, a breeding group of sabrewings was found to be arranged in three adjacent "song neighborhoods," each with it own distinctive songs. The song neighborhoods persisted for at least 4 years, suggesting that a neighborhood's song types might be passed to successive generations by song learning.

Vocal development in other groups of birds is more like that of suboscines and seems to involve little, if any, imitation. Doves and pigeons, for example, develop normal vocalizations without learning them from adults (Nottebohm and Nottebohm 1971). In addition, the hybrid offspring of mating between members of different dove species produce vocalizations intermediate to those of the two parents, again suggesting that vocal development is encoded in the genes and does not involve imitation of adults (Lade and Thorpe 1964). Similarly, hybrid offspring of two Common Quail (*Coturnix coturnix*) subspecies with different crowing calls produce intermediate calls (Derégnaucourt 2010). Roosters (male domestic chickens, *Gallus gallus*) develop normal crowing calls even if they cannot hear, suggesting that no vocal learning is taking place (Konishi 1963). Although researchers have studied vocal development in relatively few non-passerine groups, most believe that vocal learning is unlikely to be found outside of the passerines, hummingbirds, and parrots.

10.4 Production and control of song

A bird may produce a variety of calls and sometimes hundreds or even thousands of different songs. How are these vocal sounds produced? How does the brain acquire and store knowledge of them? These questions have inspired substantial research and some fascinating discoveries.

10.4.1 Sound production apparatus

The organ that birds use to produce vocal sounds is known as the **syrinx** (Fig. 10.25). This avian equivalent of the mammalian voice box lies within a bird's chest, located at the junction where the trachea (windpipe) splits to form the two tubular bronchi that lead to the lungs (Chapter 6).

The details of the syrinx's structure differ among groups of birds (Chapter 6), but, as you might expect, the anatomical

Syrinx: the primary sound-producing organ of birds, located at the point where the trachea divides to form the two bronchi.

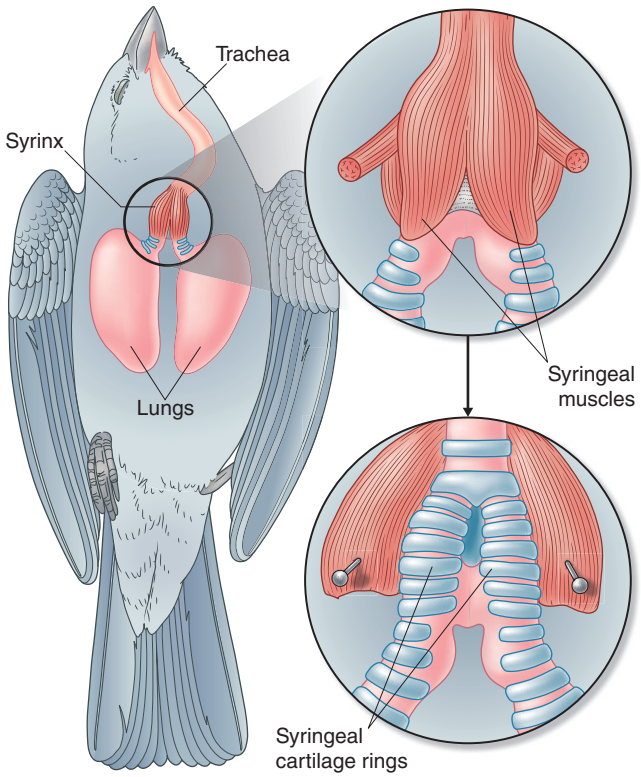


Fig. 10.25 The syrinx. Situated near the junction of the trachea and the bronchi, the avian voice organ typically consists of a pair of chambers held open by rings of cartilage. Songbirds can control the muscles on each side of the syrinx independently, allowing them to produce two sounds simultaneously. (Adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology.)

complexity of the syrinx is greatest in the songbirds. In the songbirds, the syrinx includes small pads of tissue, known as labia, located in each bronchus. Six pairs of muscles in the syrinx control the movement of the labia, and when the labia are extended into the bronchial cavity, exhaled air passing over them causes them to vibrate. These vibrations are the source of the sound waves that constitute bird vocalizations. The pitch, timing, and other aspects of the sound are altered and modulated by movements of the labia, trachea, and beak, which change the rate of airflow through the syrinx and the shape of the space that the sound waves pass through on their way to the outside environment.

The multiple muscles of the songbird syrinx provide very fine control of the sounds produced, making possible the extraordinary vocal gymnastics of many species. In addition, the songbird nervous system controls the muscles on each side of the syrinx independently. Thus, the two sides can produce different sounds at the same time. Some bird songs clearly demonstrate this dual control of the two sides of the syrinx. In the songs of the Wood Thrush (*Hylocichla mustelina*) of North America, for example, one side of the syrinx produces the higher pitched sounds and the other side produces the lower pitched sounds (Borror and Reese 1956); in essence, a Wood Thrush can sing a duet with itself. Other species in which researchers have found vocalizations generated by a similar "two voice" mechanism include the Brown-headed Cowbird (*Molothrus ater*), domestic Island Canary (*Serinus canaria*), Brown Thrasher (*Toxostoma rufum*), and Australasian Magpie (*Gymnorhina tibicen*) (Suthers and Zollinger 2004; Suthers et al. 2011) (Fig. 10.26).

10.4.2 Neural basis of song perception and production

One of the great success stories in contemporary neuroscience has been the identification of songbird brain pathways involved in learning and producing songs. As a result of this success, songbirds (or at least a few species of songbird) have become important model systems for studying the neural basis of a complex, learned behavior. The domestic Zebra Finch (*Taeniopygia guttata*), a cage bird whose wild counterparts are widely distributed in Australia, is the model species in which the neurobiology of singing behavior has been studied most intensively.

Neurobiologists have identified two key brain pathways associated with songbird singing. One of these is known as the motor pathway; the other is the anterior forebrain pathway. Each pathway includes a set of brain nuclei (groups of interconnected neurons at particular locations in the brain). Neural connections between the nuclei constitute the pathway. Both the motor pathway and the anterior forebrain pathway include the nucleus known as HVC (Fig. 10.27).

In the motor pathway, information specifying how to produce a learned song travels from HVC through several other nuclei to the nuclei that control the nerves of the syrinx and respiratory system. Thus, output from HVC guides the motor processes that produce songs. In the anterior forebrain pathway, HVC and other nuclei process the sounds that the bird hears and, in developing birds, store memorized sounds. Subsequently, the pathway evaluates the sounds of the bird's own singing and guides an appropriate adjustment of motor output until the developing bird perfects its adult song. In adult birds, the pathway may evaluate and classify the sounds that the bird hears and also helps ensure that the bird's own song types stay stereotyped and do not deteriorate.

In many species, the overall size of the song-control nuclei in the brain is proportional to the size of the bird's song repertoire. For example, in Cassin's Finches (*Haemorhous cassinii*) of western North America, females sing very little, and the song-control centers of the female are less than half the size of those of the male (MacDougall-Shackleton et al. 2005). Male Carolina Wrens (*Thryothorus ludovicianus*) of eastern North America have robust song-control nuclei, but in females of the species, which do

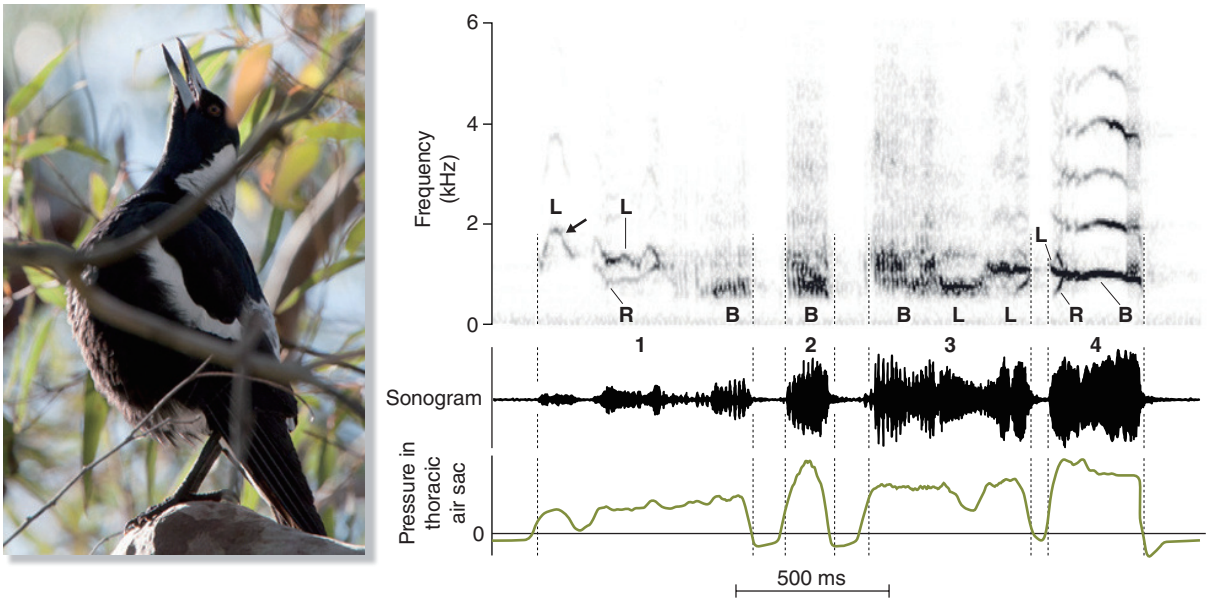


Fig. 10.26 Dual syringeal control. Australasian Magpie (*Gymnorhina tibicen*) songs include sounds produced using both sides of the syrinx together (B), as well as by the left (L) or right (R) syrinx alone. The high variability in each of the song syllables (labeled 1–4) relates to changes in the thoracic air-sac pressure before and after syllable production, as new air passes through the thoracic sac before reaching the lungs. ***Listen online.*** (From Suthers et al. 2011. Reproduced with permission from Springer Science+Business Media. Photograph by Thomas Cullen.)

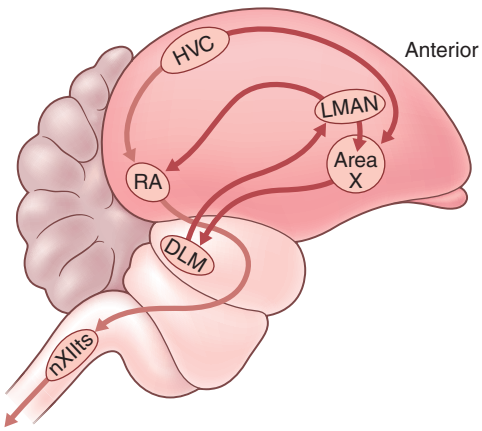


Fig. 10.27 Brain pathways for bird song learning and production. Two main pathways are highlighted in this schematic of a passerine bird brain. In the motor pathway, song is produced when signals from the nucleus called HVC are transmitted to the archistriatum (RA) and ultimately to the 12th cranial nerve (nXIIts), which controls the muscles that produce songs. The anterior forebrain pathway processes and evaluates the songs that a bird hears, and it guides song acquisition as signals from the HVC are transmitted to area X, the dorsolateral medial nucleus (DLM), and the lateral magnocellular nucleus of the neostriatum (LMAN). (From Nottebohm 2005. © 2005 Fernando Nottebohm. CC BY 4.0.)

not sing, the nuclei are so minuscule that researchers had difficulty detecting them (Nealen and Perkel 2000). In species in which females do sing extensively, these brain nuclei are correspondingly larger, although usually they still are smaller than those of males. For example, in the Forest Weaver (*Ploceus bicolor*) of southern Africa, females sing just as much as males and with similarly sized repertoires, but a male's brain nuclei nonetheless are about 1.5 times as large as a female's (Gahr et al. 2008). In addition to such between-sex differences, the size of song nuclei may vary among males of a species, so that males with more songs have larger nuclei. Thus, for example, male Sedge Warblers (*Acrocephalus schoenobaenus*) with larger song repertoires tend to have larger song-control nuclei than do males with smaller repertoires (Airey et al. 2000). In addition, species with huge song repertoires such as the Brown Thrasher (*Toxostoma rufum*) also tend to have enormous song-control nuclei (DeVoogd et al. 1993).

In many songbirds, the song-control centers change with the seasons, shrinking during the non-breeding season and enlarging again during the breeding season when singing increases dramatically (Nottebohm 1981; Brenowitz 2008). Careful work has also shown that new neurons are created in some of these song-control nuclei, even in adults (Goldman and Nottebohm 1983; Paton and Nottebohm 1984). This genesis of new neurons in the brains of adult songbirds was a surprising and important discovery, because neurobiologists had previously thought that the brains of adult vertebrates were incapable of developing new neurons. Additional research that followed this finding in birds has revealed that adult neurogenesis occurs in all vertebrates, including humans.

The main song-control nuclei have been found in all major groups within the songbirds. What about other types of birds? The brains of suboscines that do not learn their songs lack the song-control nuclei found in songbirds. Of course, some neural network must control suboscine vocalizations, but nothing similar to the pathways of the songbird brain has been found. Parrots and hummingbirds have brain structures analogous to those of the songbird pathways, but their brain anatomy is sufficiently different from that of songbirds that vocal learning and its neural machinery likely arose independently in these three groups (Striedter 1994; Jarvis et al. 2000).

10.5 Song variation in space and time

Bird songs vary in many ways: among species, among places, among individual birds, and even among the songs of a single individual. You can hear a lot of this variation yourself (Box 10.05). Song researchers have long been intrigued by this variation. Why do species differ in how their signals vary from one population to the next (over space) and in how their signals vary from one generation to the next (through time)? To answer such questions, researchers must first document patterns of variation and then try to understand the relationship between the observed patterns and song function. The goal is to understand both proximate questions of *how* sounds come to vary and ultimate questions of *why* they vary the way they do (Chapter 9, Box 9.03).

10.5.1 Differences among species

Why does each bird species have its own distinctive songs? During a bird's normal daily activities, it typically interacts mainly with other members of its own species, because they are the ones with which it must cooperate or compete most directly to survive and reproduce successfully. Producing signals that influence members of other species would often be a waste of time and energy.

Humans take advantage of these differences between species in a variety of ways. The sounds are indispensable in bird survey work, for example. In many habitats, especially in dense forests, few birds are seen but many are heard. Thus it is the birds' voices that enable us to determine the relative abundance of different species in different habitats. Or consider those who survey migrating birds. Most small birds migrate at night, when they are invisible, at least to our eyes, but many of them call, and the calls they use in flight are distinctive enough that they can be used to identify species (Evans and O'Brien 2002; Lanzone et al. 2009).

10.5.2 Individual distinctiveness

We humans can identify each other easily, as is to be expected, given that recognizing individuals is the foundation for social relationships. Birds, too, rely on social relationships, so we might expect that they, too, can recognize individuals. One way that people can recognize one another is by our distinctive voices, and research shows that many birds can recognize each other by voice, too.

The first evidence that songbirds might have this ability came from research on the Ovenbird (*Seiurus aurocapilla*), a wood-warbler that breeds in forested areas of eastern North America. Each male Ovenbird has his own unique rendition of the species' characteristic "*tea-CHER*" song. Differences in the songs of individual Ovenbirds can be seen clearly in spectrograms, and a field playback experiment demonstrated that the birds use those differences to distinguish familiar from unfamiliar individuals (Weeden and Falls 1959). In the experiment, a speaker was placed on the territory of a male Ovenbird. When the songs of a neighboring male were broadcast, the resident male acknowledged them with a few songs in return. But when songs from an unfamiliar male were broadcast from the same location, the territorial male responded much more aggressively, presumably because a newly arrived, unfamiliar male poses a bigger threat than does a neighbor going about his usual activities.

The Ovenbird experiment showed that a male can distinguish the familiar songs of his neighbor from the unfamiliar songs of a stranger. To determine if a bird's abilities go beyond distinguishing neighbors from strangers and extend to true individual recognition, a more sophisticated experimental design was required. An ingenious extension of the individual recognition experiment was first performed on White-throated Sparrows (*Zonotrichia albicollis*) (Falls and Brooks 1975). Territorial sparrows were tested twice (Fig. 10.28). When a neighbor's song and a stranger's song were broadcast on the boundary between the territories of the focal bird and the neighbor, the focal bird responded more aggressively to the stranger's song. However, when the neighbor/stranger playback test was repeated at a different territorial boundary, away from the normal location of the neighbor, the focal bird responded very aggressively to both playbacks, presumably because the abnormal location of the simulated out-of-place neighbor makes him just as threatening as a stranger. Because the White-throated Sparrow's responses to its neighbor's songs differed depending on the location from which the songs were broadcast, we can infer that that the sparrows recognized that the songs belonged to a particular individual (the neighbor). Apparently, males defending territories come to know their neighbors and the songs they sing.

Individual recognition is especially easy for White-throated Sparrows, because each male has a single, distinctive song type. Thus, the memory needed to recognize all of

Box 10.05 Listening on your own

All too often, bird enthusiasts stop listening to a singing bird once they have identified it. By keeping your ears tuned in a bit longer, you can discover the variety of songs that a particular bird sings and some of the ways they use their songs. Here we describe several ways to increase your listening enjoyment. In the description, we mention recordings of particular species that you can use to hone your listening skills, both by referring to the online materials and by searching out birds in your area. If you live in a part of the world where these example species do not occur, you can gain these same skills by practicing with these recordings and then going outdoors to listen to the birds of your area.

Individual variety

As you listen to a singing bird, try to hear the variation in a single individual's song. To practice, identify the two song forms in a recording of an Eastern Phoebe (*Sayornis phoebe*), the "*phoe-be*" and "*phoe-bree*" types. Both songs start with essentially the same sound, the "*phoe*," but one ends in a raspy "*be*" (Fig. 10.B5.01A) and the other ends in a stuttered, higher "*bree*" (Fig. 10.B5.01B). At dawn, males tend to alternate the songs, but later in the day more and more of the songs are of the "*phoe-be*" type. In the field, this same exercise can be done with any species in your area that has a modestly sized repertoire, including Eastern Towhees (*Pipilo erythrophthalmus*) (Fig. 10.B5.02),

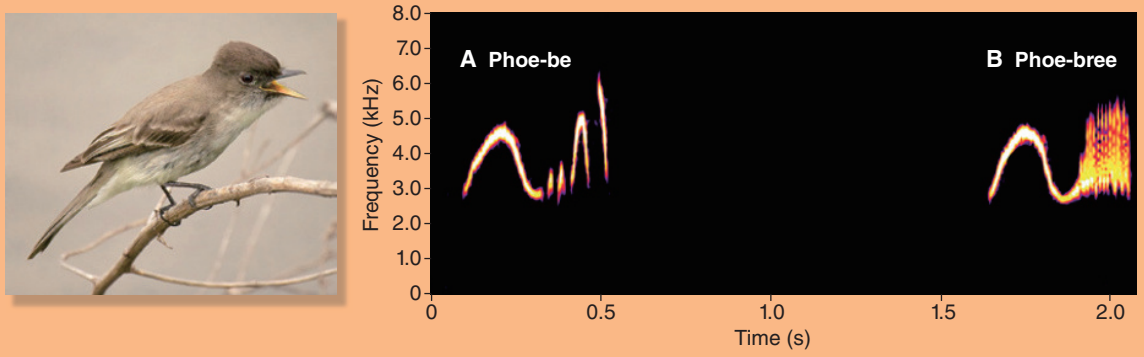


Fig. 10.B5.01 Individual variety. An Eastern Phoebe (*Sayornis phoebe*) sings two song forms: (A) "*phoe-be*" and (B) "*phoe-bree.*" ***Listen online.*** (Recordist: Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Jane Kaufman.)

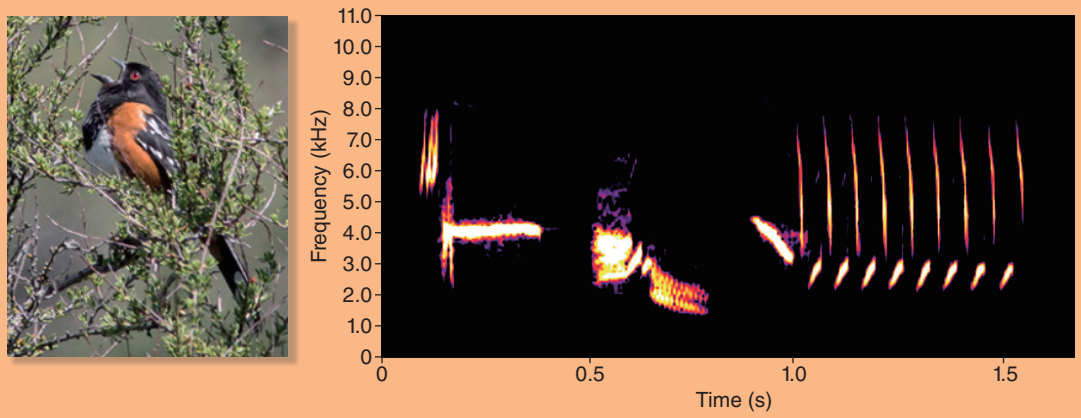


Fig. 10.B5.02 Medium-sized song repertoires. The song repertoire of an Eastern Towhee (*Pipilo erythrophthalmus*) provides an opportunity to practice your song discrimination skills. In the various online recordings of one individual, see if you can hear the differences apparent in the spectrograms. ***Listen online.*** (Recordist: Wilbur L. Hershberger. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Sue Barth, ChirpsAndCheeps.com.)

Continued

Great Tits (*Parus major*), Common Chaffinches (*Fringilla coelebs*), and Pied Bushchats (*Saxicola caprata*).

Wood Thrush song repertoires

Wood Thrushes (*Hylocichla mustelina*) provide special opportunities to challenge your listening skills and identify their repertoire size. Each song consists of three parts: a few barely audible notes at the beginning, a loud middle portion, and a softer concluding section. Focus on the loud, highly musical middle portion of the song (Fig. 10.B5.03). Each male has a repertoire of four to eight phrases he may use here, and he uses one per song. He often (but not always) sings songs with different "middles" in a regular order. If a male's four types of phrases are identified as A, B, C, and D, for example, the first song will have A, the second B, and so on. By listening carefully, you can learn to identify the different sounds and to determine, by ear, the repertoire size of those middle portions of the song.

Baltimore Oriole

Once your ears are sharpened up, try challenging yourself with a species that has a larger repertoire. For example, Baltimore Orioles (*Icterus galbula*) usually have large song repertoires, but you may be able to estimate the number of different song types each male sings (Fig. 10.B5.04). These birds tend to sing with immediate variety, cycling through their whole repertoire before repeating any song type. Listen carefully to an individual singer and pick out an especially distinctive song. Then count how many other songs occur before you hear the same song again. Repeat this process several times for that unique song, and then calculate the average number of songs that occur before your song is repeated. Now repeat the entire process for several other songs that you have come to recognize. Calculate the grand average, and you will have a rough estimate of how many different songs the individual sings.



Fig. 10.B5.03 Estimating repertoire size. A Wood Thrush (*Hylocichla mustelina*) typically sings several song types, which differ in the phrases they contain. When listening to the web content, pay particular attention to the middle portion of each song. How many different versions of the middle portion do you hear? ***Listen online.*** (Photograph by Ed Schneider.)



Fig. 10.B5.04 Large song repertoires. Baltimore Orioles (*Icterus galbula*) often switch rapidly between the songs in their repertoires. In the web content, listen for a song type you can remember and count how many songs are uttered before your memorized type is repeated. ***Listen online.*** (Photograph by Miguel de la Bastide.)

one's neighbors is limited, and distinguishing neighbors is straightforward. However, individual recognition also has been demonstrated in species with much larger repertoires. Song Sparrows (*Melospiza melodia*), for example, may have up to 10 different songs apiece, but they still can recognize their neighbors, even though collectively the neighbors may have more than 50 song types (Stoddard et al. 1991). Overall, playback experiments have detected neighbor–stranger discrimination or individual recognition by song in about three dozen songbird species of varying repertoire size, as well as in the North American suboscine Alder Flycatcher (*Empidonax alnorum*) (Lovell and Lein 2005) and in some non-passerine species such as Little Owls (*Athene noctua*) in France (Hardouin et al. 2006) and Green Woodhoopoes (*Phoeniculus purpureus*) in South Africa (Radford 2005).

Birds also use vocalizations other than territorial song to recognize individuals. Bank Swallows (*Riparia riparia*) live in colonies, and once the young leave the nest, they mix with other young (Fig. 10.29). Parents use the distinctive

calls of their offspring to locate them within large flocks of other young Bank Swallows (Beecher et al. 1986).

Numerous experiments show that in many species, mates recognize each other. Sometimes they do so under conditions that seem overwhelmingly difficult to us, such as in a huge colony of seabirds or penguins. Consider, for example, the King Penguins (*Aptenodytes patagonicus*) of Antarctica. Instead of building nests, they incubate a single egg as it rests atop their feet. These penguins breed in dense colonies that may contain tens of thousands of birds, and an individual may move around the colony as it incubates. Thus, when a member of a pair returns from a foraging trip and is ready to take over the incubation duties, finding its mate can be a challenge. The returning bird calls and awaits a return call from its mate, suggesting that pair members are able to recognize one another's calls. Field experiments have confirmed this ability: a King Penguin is much more likely to call in response to playback of the calls of its mate than to playback of the calls of other colony members (Lengagne et al. 2000). Similar experiments on colonial Magellanic Penguins (*Spheniscus magellanicus*) show that females of this species respond more strongly to recordings of their mate's display calls than to such calls recorded from other males (Clark et al. 2006).

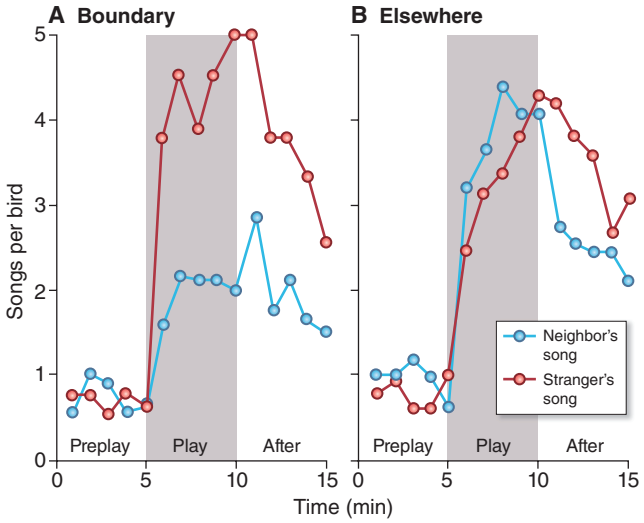


Fig. 10.28 Testing individual recognition in White-throated Sparrows (*Zonotrichia albicollis*). (A) Territorial males respond more aggressively (with greater song output) to playback of a stranger's song (red) than to playback of a neighbor's song (blue) when the songs are played on the territory border between the focal male and his neighbor. (B) However, the focal male responds with equal aggression to neighbor playback if the songs are played at a location other than the border, presumably because the defending male realizes that his neighbor—now singing from a different location—seems to be encroaching on his territory. The focal bird's ability to respond differently to his neighbor's song when presented in different contexts suggests that he can recognize and identify his neighbor by song alone. (From Falls and Brook 1975. © Canadian Science Publishing or its licensors. Reproduced with permission.)

10.5.3 Geographic variation

One distinctive feature of the vocalizations of most songbird species is their tendency to differ from place to place. One particular form of geographic variation in the songs of songbirds—**dialects**—has attracted special attention from researchers. We humans have dialects in our speech, of course, and astute listeners can often pinpoint a person's place of origin by the subtleties of their accent. Songbirds

Dialects: in birds, regional variants of the songs of a particular species.

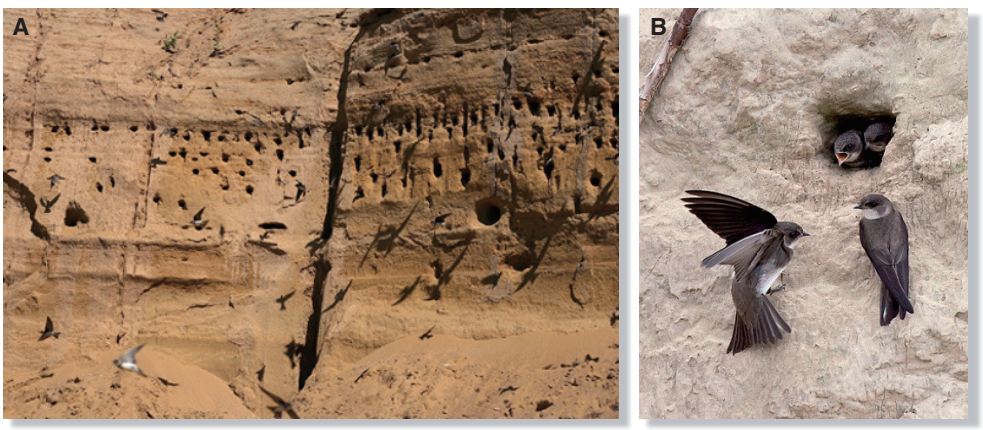


Fig. 10.29 Call recognition in colonial birds. (A) Bank Swallows (*Riparia riparia*) nest in large colonies. (B) Parents learn the distinctive calls of their offspring during the nesting period and later use them to identify their young when they gather in large flocks after fledging. (Photographs by: A, Shkumbin on Flickr, https://commons.wikimedia.org/wiki/File%3ARiparia_riparia_colony.jpg. CC-BY-2.0; B, Bruce Van Valen.)

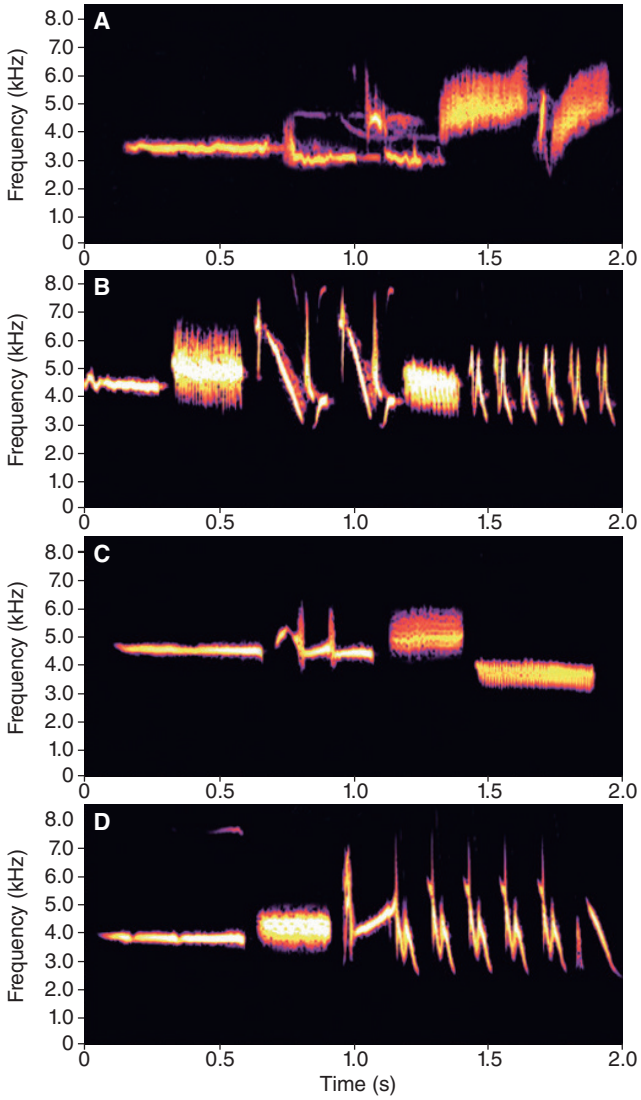


Fig. 10.30 Distinguishing dialects. White-crowned Sparrow (*Zonotrichia leucophrys*) songs occur in dialects; the form of a male's song depends on where he lives. Each song form occurs within one particular area. Spectrograms A through D illustrate four different White-crowned Sparrow dialects. ***Listen online.*** (Recordists: A, Arthur A. Allen and Peter Paul Kellog; B, Arthur A. Allen and David G. Allen; C, Leonard J. Peyton; D, Geoffrey A. Keller. Courtesy of Macaulay Library © Cornell Lab of Ornithology.)

have dialects as well, and dialects in both human speech and bird song are a consequence of vocal learning. If individuals generally remain near the location where they learned their vocal signals, then the individuals in that geographic area come to use the same local dialect.

In reference to birds, the term dialect signifies any spatial clustering of similar vocalizations. Song dialects thus can include only a few birds or many thousands, depending on how learning and dispersal affect the distribution of vocalizations in a particular species. Each small neighborhood of like-singing Indigo Buntings (*Passerina cyanea*) could be called a dialect, as could the entire population of millions of Black-capped Chickadees (*Poecile atricapillus*) living from the eastern USA to western Canada who all sing very similar versions of the "*hey-sweetie*" song.

Distinguishing song dialects requires a good ear, but a skillful listener can hear dialect differences in the songs of many songbird species. Dialects have been especially well studied in the White-crowned Sparrows (*Zonotrichia leucophrys*) of the coastal chaparral in California (USA). There, boundaries between dialects are so sharp that in some places a listener can stand facing the Pacific Ocean and hear songs of one dialect to the left and another to the right (Baptista 1975). Distinguishing dialects is especially easy in this species because each male uses a single song form, and one song thus identifies a male's dialect (Fig. 10.30).

Just how do these sparrow dialects form? The chaparral in California is a fire climax community. Vast stretches of the habitat routinely burn, temporarily destroying good sparrow habitat. The destruction is part of normal renewal, however, and when pockets of suitable habitat again become available, the sparrows re-inhabit them. Founding birds can have songs that are incompletely learned or in some way different, and these odd songs then can become the basis for a new dialect. As suitable habitat areas expand, they eventually contact other nearby areas of suitable habitat. Boundaries between dialects form at these areas of secondary contact (Fig. 10.31).

The formation of dialects in this fashion is relatively straightforward. More controversial is the issue of how dialect boundaries are maintained once they have formed. The central question is: How socially and genetically isolated are the birds in different dialects? The degree of isolation is determined in large part by when and where young sparrows enter a breeding population and learn their songs. We know that many dialects tend to remain stable (Trainer 1983; Nelson et al. 2004), so two possibilities exist. First, males may learn the songs of their home area early in life and later settle there, within their fathers' dialect region. Alternatively, young males may disperse to new dialect areas and then modify their songs to match the local dialect.

Exactly what young White-crowned Sparrows do, however, remains unclear. Laboratory experiments show that young males learn most readily early in life, during a period in which wild birds still live on their parents' territory. However, laboratory experiments also show that, under the right social conditions, birds can modify their songs later in life. Banding studies in the field show that some young males remain in their natal dialect area, but some move across dialect boundaries to settle (Baker and Mewaldt 1978; Petrinovich et al. 1981). Merely knowing that a young male may opt for either choice does not address the critical question: Does the dialect boundary in any way inhibit dispersal? Genetic analyses suggest that birds in some

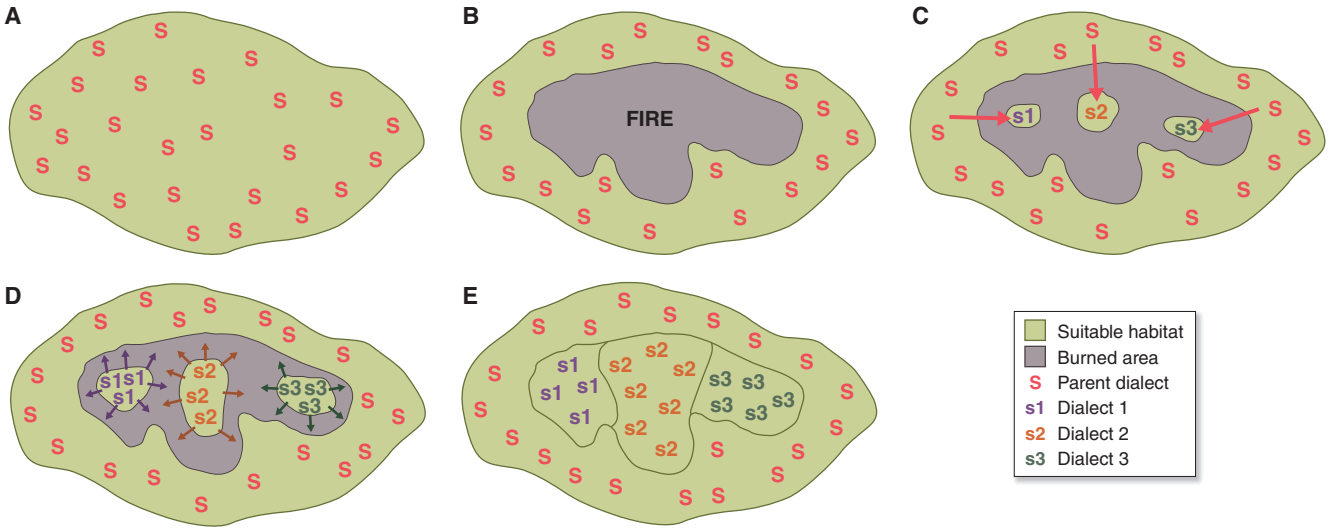


Fig. 10.31 Local dialect formation in White-crowned Sparrows (*Zonotrichia leucophrys*). When some of the vegetation in an area containing White-crowned Sparrows (A) that share a song dialect (represented as "S") burns down (B), new dialects (s1, s2, s3) may form as small areas of suitable habitat regenerate (C). If the new areas are colonized by birds singing distinctive song types, these dialects may be spread by learning as the population in the new area grows (D). As the vegetation in the burned area continues to regenerate, formerly isolated populations come into contact, forming new dialect boundaries (E). (© Cornell Lab of Ornithology.)

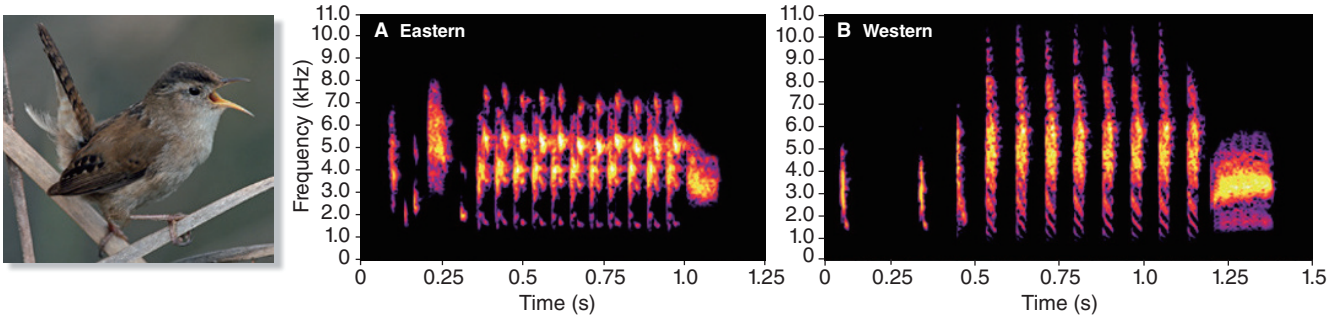


Fig. 10.32 Regional dialects. (A) Marsh Wrens (*Cistothorus palustris*) in eastern North America sing songs that begin with a nasal buzz, followed by repeated melodious notes. (B) In the western half of their range, Marsh Wrens produce coarse, buzzy songs that often contain raspy notes. ***Listen online.*** (Recordists: A, William W. H. Gunn; B, Kevin J. Colver. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Ron Wolf.)

White-crowned Sparrow populations disperse freely out of their home dialect area but that dispersal may be restricted in other populations (Baker et al. 1982; MacDougall-Shackleton and MacDougall-Shackleton 2001; Soha et al. 2004). Additional research is necessary before we can fully understand how dialect boundaries affect dispersal and mating opportunities in the White-crowned Sparrow.

Dialect patterns often occur at geographic scales larger than the local dialects found in White-crowned Sparrows. The Marsh Wren (*Cistothorus palustris*) provides a good example. Field guides typically identify a single species of Marsh Wren across most of North America, but careful listening reveals two distinctly different Marsh Wren song variants (Kroodsma 1989). In eastern North America, male Marsh Wrens typically introduce their songs with a nasal buzz and then produce a relatively musical series of repeated notes (Fig. 10.32A). Among eastern birds, this basic song pattern is used consistently; even though a male sings 50 or more different song types, each type is of this basic formula. The songs of western Marsh Wrens are very different from those of their eastern relatives (Fig. 10.32B). The songs of these birds are raucous, buzzy, noisy, and coarse, and some include loud, penetrating whistles modulated rapidly in frequency. Western songs are never introduced by the faint buzzy note of the east, and they include or end with a raspy, noisy note.

The simplest explanation for the origin of these regional differences lies in the distribution of habitats during past periods of North American glaciation. When glaciers advanced, they may have isolated two Marsh Wren populations, one in the west and the other in the east. Over thousands of years, the song differences we hear today developed

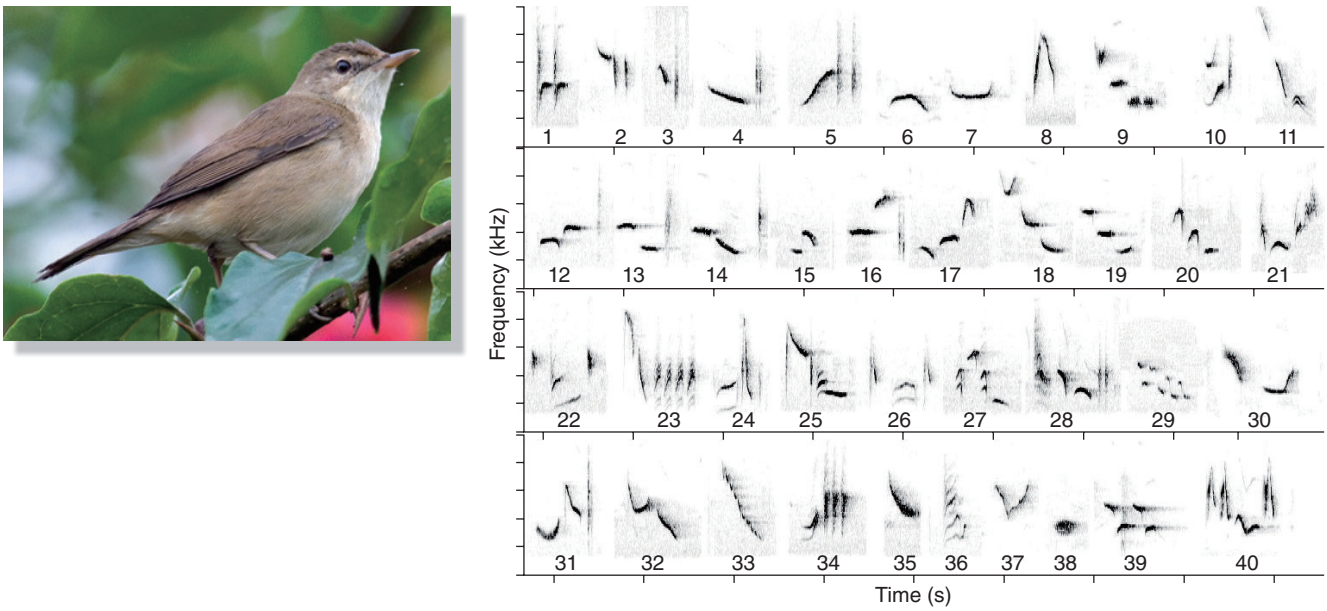


Fig. 10.33 Widespread song types. Some species sing song types that recur across their entire geographic range. For example, even though Blyth's Reed-Warblers (*Acrocephalus dumetorum*) within a local neighborhood do not typically share songs, the individual song types found in that area may also occur in distant populations. Each number here corresponds to a different song type found throughout this species' range. (From Marova et al. 2010. Reproduced with permission from Springer Science + Business Media. Photograph by Shankar70, https://commons.wikimedia.org/wiki/File:Blyth%27s_Reed_Warbler.jpg. CC BY-SA 3.0.)

in these two isolated populations. As the glaciers receded, the available habitat increased, and the two populations then met in the central Great Plains. Even though males of the two groups can learn each other's songs, as has been shown in the laboratory (Kroodsma and Canady 1985), in nature they tend to maintain their distinctiveness, and few hybrid singers occur.

10.5.4 Diversity of geographic patterns

In some songbird species, the same song types recur throughout the geographic range of the species. Within any population of Blyth's Reed-Warblers (*Acrocephalus dumetorum*), for example, many different song types exist with little sharing among males, but the song types found in one population generally occur in other populations across the species' wide breeding range in Asia and Europe (Marova et al. 2010) (Fig. 10.33). Also widely distributed are the hundred or so components from which Indigo Bunting (*Passerina cyanea*) songs are constructed; local dialects in buntings are formed not so much by the types of elements used, but by their particular combinations (Baker and Boylan 1995).

The whistled "*hey-sweetie*" of the Black-capped Chickadee (*Poecile atricapillus*) has an especially puzzling geographic distribution. The chickadee uses the same song across continental North America. Across this huge geographic area, patterns of whistles are the same in both frequency and sound intensity, and birds use the same rules to transpose their songs in frequency (Ratcliffe and Weisman 1985; Weisman et al. 1990; Horn et al. 1992). Such consistency in a learned song across an entire continent is remarkable. How the chickadees maintain such a stereotyped learned signal over such a vast geographic expanse remains a mystery. The more typical songbird pattern is to show at least some form of local variation.

Some intriguing local chickadee populations do have song forms other than the "*hey-sweetie*," however. One is on Martha's Vineyard, a small island off the coast of Massachusetts (USA). There, males also whistle, but the two whistles are on the same frequency, with no drop between the first and second whistles in each phrase (Kroodsma et al. 1999c). Furthermore, song dialects occur on the island, so that males in the eastern and western parts of the island use different songs. A second pocket of chickadee song differentiation occurs near Fort Collins, Colorado (USA), where three different non-standard whistle songs occur, and each male uses a repertoire that includes two or all three of the local song types (Gammon and Baker 2004). In addition, males in coastal Oregon and Washington (USA) sing a variety of whistled songs (Kroodsma et al. 1999c).

How do these regional differences in song arise? Martha's Vineyard is about 11 kilometers off the coast of New England, so birds there may be relatively isolated

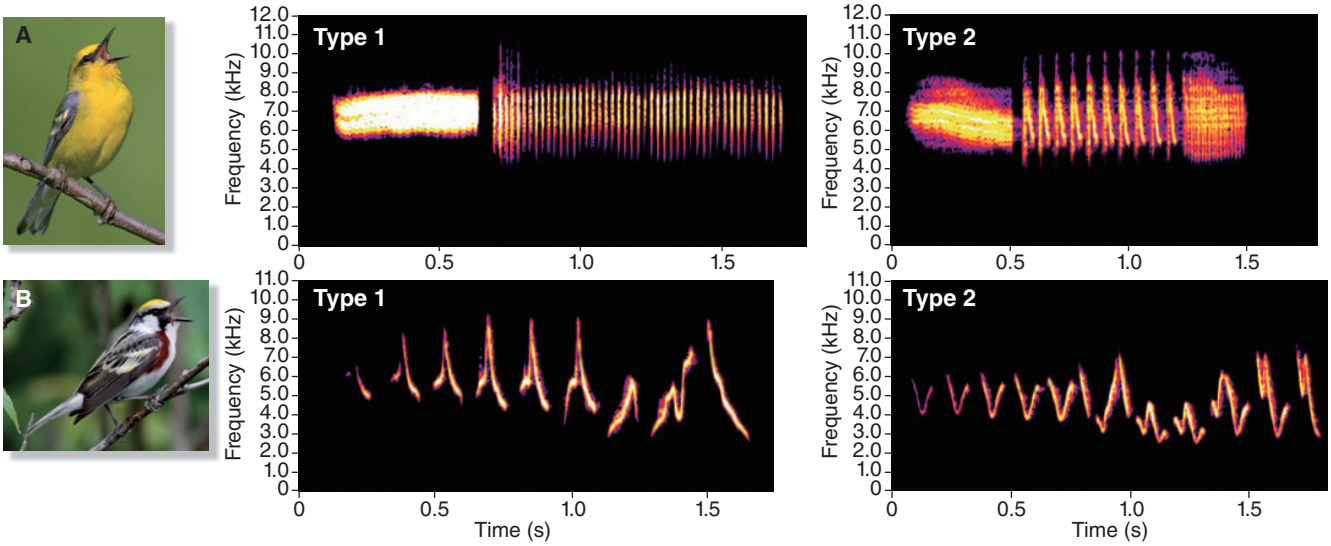


Fig. 10.34 Different song types can serve different functions. In some species, such as (A) Blue-winged Warblers (*Vermivora cyanoptera*) and (B) Chestnut-sided Warblers (*Setophaga pensylvanica*), songs in the first category (type 1) function in mate attraction, whereas songs in the second category (type 2) function in male–male aggression. ***Listen online.*** (Recordists: type 1, Geoffrey A. Keller; type 2, Wilbur L. Hershberger and Matthew D. Medler, respectively. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photographs by: A, Jim Zipp; B, Larry Gridley.)

from mainland North America. Perhaps isolated pockets of chickadees also occurred in some western states, so songs in those areas had a chance to diverge from the standard "*hey-sweetie*." We do not know whether these vocally distinct populations are genetically distinct or if a female of one song tradition would accept a male from another.

Work with Black-capped Chickadees in the laboratory has only enhanced the mysterious nature of chickadee song. If male chickadees from normal "*hey-sweetie*" populations are tutored with normal "*hey-sweetie*" songs in the laboratory, they nonetheless develop highly abnormal songs, unlike anything one would expect from a chickadee in nature (Kroodsma et al. 1995). Although the whistled tonal quality remains, the songs consist of from one to seven or more different whistles on a variety of frequencies. Furthermore, males develop repertoires of up to three different song types. Groups of laboratory males isolated from one another even develop different "dialects." Over most of the North American continent, some social factors must restrict chickadee song variation to the simple "*hey-sweetie*" form; those factors are absent in the highly artificial laboratory environment. What are these social factors? Perhaps it is the female chickadee that sets standards for what songs are to be sung, as happens in other birds. For example, female Brown-headed Cowbirds (*Molothrus ater*) respond differently to the various songs of males, and in that way "instruct" males about which songs to sing to be especially successful in acquiring a mate (West and King 1988). Perhaps the female chickadee also has certain inviolate standards for her mate's song.

The diverse patterns of geographic variation are puzzling, but some hints as to why songs vary in these ways are found in certain North American wood-warblers. In a number of wood-warbler species, males have two categories of songs (Spector 1992). One category contains songs that seem to be used especially to attract females. For example, both the "*beee-buzzzz*" of the Blue-winged Warbler (*Vermivora cyanoptera*) (Fig. 10.34A1) and the "*pleased-pleased-pleased-to-MEETCHA*" of the Chestnut-sided Warbler (*Setophaga pensylvanica*) (Fig. 10.34B1) are used to attract mates. Spectrogram analyses show that these mate-attraction song forms vary little over the entire geographic ranges of these species (Byers 1996; Kroodsma 1981). These species also use a second category of song at dawn and in highly aggressive situations, when males are countersinging with one another, especially near territory boundaries (Fig. 10.34A2, B2). These songs occur in dialect patterns, with songs often changing over short distances.

Among these wood-warblers, it seems that a male attempting to attract a female succeeds best if he has a highly stereotyped signal that all females can recognize. Females of many songbird species tend to disperse further than males (Chapter 12), so an especially stereotyped male signal will be unmistakably recognizable to all females, no matter where they fledged. When males address other males on neighboring territories, however, some advantage must accrue to having a local signal. Vocalizations employed by wood-warblers in more aggressive contexts accordingly vary from place to place, in dialects.

10.5.5 Geographic variation in suboscine vocalizations

Dialects occur widely in learned vocalizations such as the songs of songbirds, but how much do non-learned vocalizations change over geographic space? In most species vocalizations stay relatively constant over space. For example, the songs of the Pale-edged Flycatcher (*Myiarchus cephalotes*) are very similar throughout the species' range in South America, and the same is true for many other species of *Myiarchus* flycatchers (Lanyon 1978). No detectable local variation occurs in the songs of Long-tailed Manakins (*Chiroxiphia linearis*) in Costa Rica (Trainer and Parsons 2001) or Acadian Flycatchers (*Empidonax virescens*) in Maryland (USA) (Payne and Budde 1979). The same general pattern is found among most other suboscines. The songs of these birds are not learned but instead seem to be innate, developing mainly under genetic control.

Because suboscine songs are a good indicator of a bird's genetic background, the songs of suboscine birds can help us determine which populations of birds belong to which species. During the 1960s, for example, investigators discovered that the North American species then known as "Traill's Flycatcher" actually includes two subgroups whose songs differ consistently, suggesting that the two groups do not interbreed (Stein 1963). This song difference helped researchers recognize that "Traill's Flycatcher" was actually two species, the Alder Flycatcher (*Empidonax alnorum*) and the Willow Flycatcher (*Empidonax traillii*). More recently, researchers recognized that the closely related "Western Flycatcher" similarly consists of two different groups, each with its own distinctive songs (Johnson 1980). Further investigation of genetic variation showed that the song differences identified genetically distinct populations (Johnson and Marten 1988), which subsequently were recognized as distinct species, the Pacific-slope Flycatcher (*Empidonax difficilis*) and the Cordilleran Flycatcher (*Empidonax occidentalis*).

Song differences still serve as indicators of the limits of suboscine species, especially when used in conjunction with information on the genetic differences between populations that sing different songs. For example, researchers who investigated geographic variation in the calls of a neotropical antbird noticed that the songs of birds living in Panama and Costa Rica sounded different than those of similar-looking birds living further east and south in Colombia (Cuervo et al. 2007). The researchers suspected that the song differences indicated that the two populations in fact were different species. Analyses of genetic differentiation supported this suspicion, as the genetic differences between the populations are large enough to suggest that each population should be classified as a separate species, the Dull-mantled Antbird (*Myrmeciza laemosticta*) and the Magdalena Antbird (*Myrmeciza palliata*) (Chaves et al. 2010). In addition, the researchers identified song characteristics that are diagnostic of each proposed species. Thus, songs can serve as valuable clues to direct the efforts of systematists, who often are faced with the challenge of defining species in suboscine groups such as antbirds (Fig. 10.35), woodcreepers, and flycatchers in which different species can be very similar in appearance.

10.5.6 Change over time

Because oscine songs are learned, they have a high potential to change over time as well as over space (Box 10.06). The Indigo Bunting (*Passerina cyanea*) of eastern North America is among the few species in which song changes in a population have been tracked over a long period (Payne et al. 1981, 1988). As you may recall from earlier in this chapter, each male Indigo Bunting sings a single song type, which he acquires by copying an adult male in his neighborhood. However, not all buntings make perfect copies of their tutor's song. Thus, as songs are copied from male to male, changes accumulate in the songs present in a given area. In addition, new songs may be introduced to an area when older males from other locations immigrate into the population. In Indigo Buntings, these factors contribute to a rapid turnover of song forms within local populations. Over time, many songs are introduced, and many songs are lost, and only a few are copied and maintained for long periods of years. Over 10 years, the song types in a population turn over almost completely. Similarly steady, rapid change over time also has been found in the songs of Corn Buntings (*Emberiza calandra*) (Holland et al. 1996), European Starlings (*Sturnus vulgaris*) (Adret-Hausberger 1986), and Common Chaffinches (*Fringilla coelebs*) (Ince et al. 1980) in Europe, and in Singing Honeyeaters (*Gavicalis virescens*) in Australia (Baker et al. 2001).

In some other songbird species, song form does not change at such a rapid pace. For example, in a population of Wood Thrushes (*Hylocichla mustelina*), song elements remained unchanged over a 9-year period (Whitney 1992). Similarly, the trills that define White-crowned Sparrow (*Zonotrichia leucophrys*) song dialects have been shown to persist for up to 34 years in some sparrow populations (Trainer 1983; Chilton and Lein 1996; Nelson et al. 2004). In the Galápagos Archipelago of Ecuador, the well-studied population of Medium Ground-Finches (*Geospiza fortis*) on the island of Daphne Major (Chapter 3) used the same set of four song types for six consecutive years (Gibbs 1990) and in a population of the same species on nearby Santa Cruz Island, some song types persisted for 38 years (Goodale and Podos 2010).

Some species even exhibit these rapid-turnover and slow-change patterns simultaneously. In Chestnut-sided Warblers (*Setophaga pensylvanica*) of eastern North America, songs of one category (the category used in aggression between

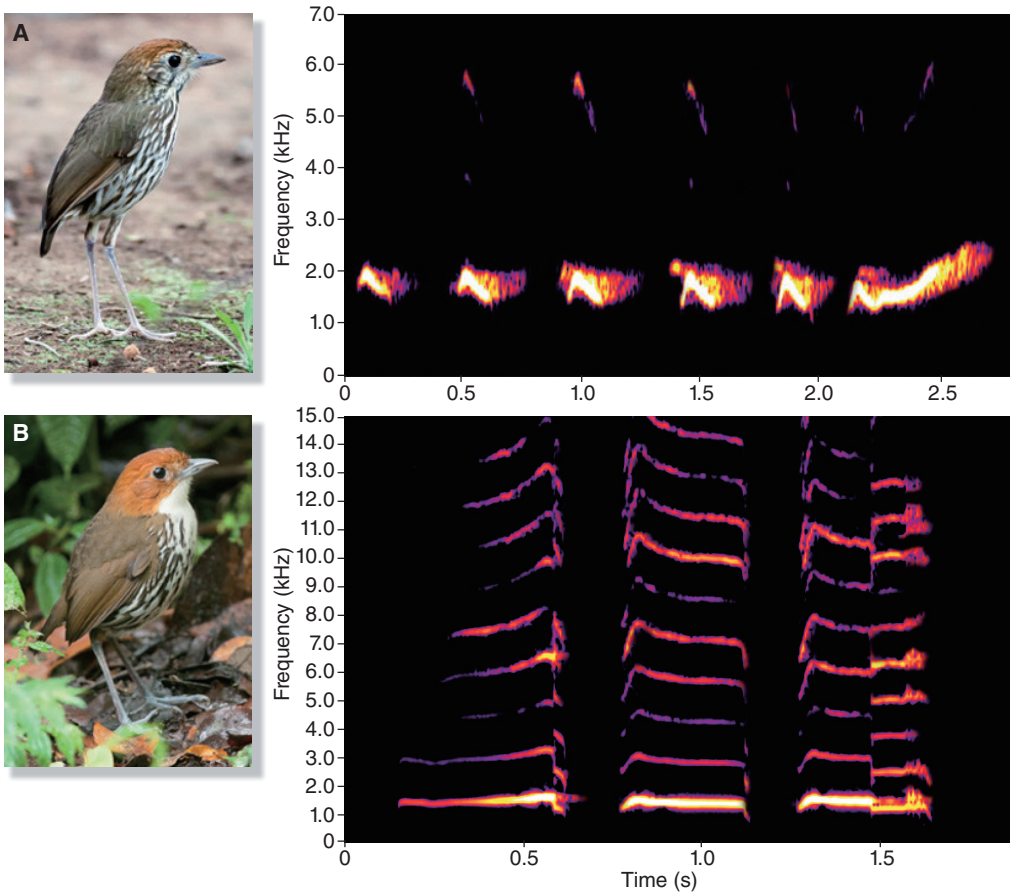


Fig. 10.35 Songs help us recognize suboscine species. Differences in song can help systematists identify cryptic species. For example, although (A) Watkins's Antpittas (*Grallaria watkinsi*) and (B) Chestnut-crowned Antpittas (*Grallaria ruficapilla*) occur in overlapping geographic ranges and are similar in appearance, they can be distinguished by their distinct songs. ***Listen online.*** (Recordists: A, Linda R. Macaulay; B, Paul A. Schwartz. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photographs by: A, Robert Lewis; B, Arthur Grosset.)

Box 10.06 Singing in noisy places

The songs of birds that live in cities or near busy roads may differ from the songs of individuals of the same species that live in quieter environments. Human-generated noise can impede bird communication by making it more difficult for avian listeners to detect songs, so urban birds may compensate by altering their songs for better detectability. For example, city-dwelling Common Nightingales (*Luscinia megarhynchos*) in Berlin (Germany) have been shown to sing loudest where the surroundings are noisiest (Brumm 2004).

Singing louder is perhaps the most obvious possible adjustment to noisy conditions, but birds also seem to make other kinds of accommodation. European Serins (*Serinus serinus*), for example, sing more songs during noisy periods than when it is quieter, presumably thereby improving the odds that a listener will detect the songs (Díaz et al. 2011). Birds in noisy places also may sing at higher frequencies. Most human-generated urban noise is at frequencies below 2 kilohertz, so in principle a bird could reduce the masking effect of noise by singing higher frequency sounds. Researchers have found that birds of many species sing higher-frequency songs in noisy environments than in quiet environments. For example, in Mexico City (Mexico), House Finches (*Haemorhous mexicanus*) in noisy areas sing at higher frequency than do individuals in quieter places (Bermúdez-Cuamatzin et al. 2009), and the same is true for Great Tits (*Parus major*) in Leiden (the Netherlands) (Slabbekoorn and Peet 2003). Similar patterns are apparent in comparisons of urban and rural populations of a species. Great Tits in 10 cities in continental Europe and 20 cities in the UK sing at higher frequencies than do individuals in nearby rural areas (Slabbekoorn and

Continued

den Boer-Visser 2006; Mockford and Marshall 2009). Likewise, the songs of Eurasian Blackbirds (*Turdus merula*) in the noisy city of Vienna (Austria) are higher pitched than those of Eurasian Blackbirds in the quieter Vienna woods (Nemeth and Brumm 2009).

How do urban birds achieve their higher frequency songs? City birds might preferentially imitate high-frequency songs during their early period of song development. Or perhaps the sound-production apparatus of birds in urban populations has been evolutionarily modified by natural selection imposed by noisy environments. Or individual adult birds simply might modify their learned songs in response to noisy conditions. These possible mechanisms are not mutually exclusive, and researchers are not yet ready to rule out any of them. However, recent field experiments have shown that, in at least some species, individuals can modify their singing quickly in response to noisy surroundings. For example, when experimenters played city-like low-frequency noise through a loudspeaker placed near singing Great Tits, the song type that the birds sang immediately afterward was invariably higher pitched than the one they had been singing before the playback (Halfwerk and Slabbekoorn 2009). It appears that, when their environment suddenly became noisy, the birds selected from among the song types in their repertoires the ones whose transmission would be least affected by the noise.

Not all urban birds modify their songs in response to city noise. Researchers who recorded the songs or calls of 12 bird species in the city of Melbourne (Australia) and in the quieter surrounding countryside found that only five of the species sang at higher frequency in the city (Hu and Cardoso 2009). The species that failed to shift their songs tended to have songs that were ordinarily high pitched, so perhaps their songs were well suited for transmission in a noisy environment without further modification. Some species may simply be unable to modify their songs in response to noise, perhaps because of physical constraints that place an upper limit on song loudness or frequency.



Fig. 10.36 Simulated intrusion experiment with Townsend's Warblers (*Setophaga townsendi*). Here, a male (top) attacks a decoy (below, on branch) during a territorial intrusion experiment; recorded songs were broadcast through speakers near the decoy, within the pictured male's territory, to assess his aggressive response. (Photographs by Scott Pearson.)

males) changed rapidly and continuously during a 20-year study, but songs of a second category (the category used by males to attract females) did not change appreciably over that span (Byers et al. 2010). In fact, some Chestnut-sided Warbler songs from this second category recorded in 2010 are identical to those recorded in the 1950s.

10.6 Functions of bird song

What do birds use their vocalizations for? Most investigations of the functions of bird vocalizations have focused on songbird songs. These are among the most extravagant and noticeable sounds birds make, and it is no wonder that they have attracted so much attention. Researchers now generally agree that singing has two main functions: to help defend a territory and to help attract and stimulate a mate.

10.6.1 Territorial defense

Territoriality is common among birds and song often plays an important role in avian territorial behavior. One indication of this role is the manner in which a territorial male songbird responds to the songs of another male. If a recording of a species' song is broadcast within the territory of a conspecific, the resident male often responds aggressively; he may even go so far as to attack the loudspeaker or an associated decoy (Fig. 10.36). Such song playback has been shown to elicit

aggressive behavioral responses in many species. This aggressive response suggests that a territorial male interprets a rival's song as a signal of his intention to claim some turf. But would singing in return help keep an intruder out?

Evidence that songs help to keep other males out of a territory comes from "speaker replacement" experiments. In these experiments, researchers temporarily remove a male from his territory and replace him with recordings played through a series of speakers. For example, experimenters in Pennsylvania (USA) removed male Song Sparrows (*Melospiza melodia*) from their territories, performing the removals two at a time to create pairs of nonadjacent, unoccupied territories (Nowicki et al. 1998). One of the empty territories in each pair served as a silent control. On the other territory, the experimenters placed two speakers from which Song Sparrow songs were broadcast, alternating between the two speakers to simulate the presence of the territorial male. These simulated males, consisting only of songs, deterred potential interlopers; speaker-inhabited territories were much less likely to be reoccupied by intruders than were the silent controls. Song does seem to send the message to "keep out" to other birds that are prospecting for potential territories.

The role of song in territorial defense is further confirmed by muting experiments. In one such experiment, territorial male Seaside Sparrows (*Ammodramus maritimus*) in Florida (USA) were temporarily muted by surgery on one of their air sacs (McDonald 1989). A male with a disabled air sac cannot maintain enough pressure in his respiratory system to produce songs. In the experiment, the muted males lost their ability to defend their territories; intruders were far more likely to invade and successfully claim all or part of a muted male's territory than to invade the territory of a control male who could sing. When the air sacs healed and the muted males regained their songs, most were then able to regain their temporarily lost territory.

Vocalizations other than songs also can serve as keep-out signals. For example, birds of species that defend territories during the non-breeding season, when singing declines or disappears in some species, may then use a simpler call to broadcast territorial rights. For example, migratory Yellow Warblers (*Setophaga petechia*) may defend individual feeding territories on their non-breeding grounds in Mexico. When neighboring warblers confront one another at a territorial border, they utter a rapid succession of short "chip" calls (Greenberg and Ortiz 1994). Additional evidence that chip calls play a role in territorial conflict among Yellow Warblers comes from a field playback experiment (Neudorf and Tarof 1998) in which non-breeding, territorial Yellow Warblers in Panama mounted an aggressive response to a playback of Yellow Warbler chips but not to chips of the Northern Waterthrush (*Parkesia noveboracensis*), another wood-warbler species present in the area.

10.6.2 Mate attraction

Bird song also functions in mate attraction. One piece of circumstantial evidence that male songbirds use songs to attract females is that males generally sing more frequently before they acquire a mate than they do afterwards. At a study site in France, for example, male Common Nightingales (*Luscinia megarhynchos*) sing extensively at night when they are unpaired but cease nocturnal singing once they acquire a mate (Amrhein et al. 2002). During the day, unpaired nightingales sing steadily throughout the breeding season, but a paired male substantially decreases his singing once his mate lays eggs and is thus no longer reproductively available to other males. In Sedge Warblers (*Acrocephalus schoenobaenus*) breeding in Great Britain, a male's copious singing declines to almost none immediately after pairing (Catchpole 1973). Studies of numerous other species have shown that, typically, unpaired males sing all day long and paired males sing far less often, and that if a paired male loses his female, he reverts to abundant singing. The amount of song coming from a male is therefore often a good indication of his pairing status.

Additional evidence that male song attracts females comes from field experiments with species such as European Starlings (*Sturnus vulgaris*), European Pied Flycatchers (*Ficedula hypoleuca*), and House Wrens (*Troglodytes aedon*) (Eriksson and Wallin 1986; Mountjoy and Lemon 1991; Johnson and Searcy 1996). In these experiments, speakers were placed near the openings of nest boxes, and songs of the focal species were played through the speakers at some boxes, while the speakers at other boxes remained silent. In all three species, females were far more likely to approach or enter nest boxes with songs than silent boxes. This result seems to indicate that females used songs to identity potential mating opportunities.

In the laboratory, female birds often seem to find male songs appealing. To test the attractiveness of a song to females, researchers can monitor the females' **copulation-solicitation display**, the tail-up posture that initiates copulation in many species (Fig. 10.37). In copulation-solicitation experiments, females typically display more in response to songs of their own species than to songs of other species. For example, in a laboratory experiment with female Red-winged Blackbirds (*Agelaius phoeniceus*), researchers compared the number of displays performed in response to playback of typical blackbird songs with the number performed in response to a mockingbird's imperfect imitation of blackbird songs (Searcy and Brenowitz 1988).

Copulation-solicitation display: a stereotyped posture adopted by female birds that indicates their readiness to copulate.



Fig. 10.37 Copulation-solicitation display. A male (top) Lark Sparrow (*Chondestes grammacus*) responds to a female's tail-up solicitation display (bottom) by initiating copulation. In the lab, females will sometimes display in response to male song. (Photograph by Ron Dudley.)

The mockingbird songs induced far fewer displays than did the songs of the females' own species. The strong sexual response to own-species song suggests that females regard the songs as sexual signals.

10.7 Signal values of differences among singers

As noted earlier in this chapter, individual songbirds of a given species tend to have individually distinctive songs and singing behavior. Thus, birds listening to a singer's attempts to defend a territory or attract a mate might be reading cues more subtle than the simple presence or absence of singing. For example, an avian listener can probably judge the location of the singer (how distant it is) by the loudness and degree of degeneration in the sound quality of its songs. If a singer is of a species that uses different song types or different styles of singing in different contexts, its songs give clues about its motivational state. When songs vary geographically, a bird's song identifies the region in which it acquired its songs. Similarly, if a male's songs match those of his local neighborhood, he reveals that he probably has lived in the neighborhood long enough to establish his local identity. In species in which birds add to their song repertoires in successive years, singing reveals a bird's age. Differences in singing may also reveal to listeners differences in the intrinsic qualities of the singer. The singing emanating from a territory might indicate the relative health or genetic quality of its owner, information that might be useful to potential mates or rivals.

10.7.1 Song output

Differences among singers could be revealed by something as simple as the number of songs produced in a day. A male in possession of a territory rich in food might be able to acquire energy more quickly than a male on a poorer territory and therefore be able to sing more actively. One way to test this hypothesis is to provide wild birds with extra food and see how their singing is affected. For example, when researchers provided mealworms to territorial New Zealand Robins (*Petroica australis*), the birds' song output was greater on the days on which they received this extra food than on the days just before and just after (Barnett and Briskie 2011). A similar experiment on Australian Reed-Warblers (*Acrocephalus australis*) evoked a similar result: territorial males sang more songs when experimenters supplied blowfly maggots than when none were provided (Berg et al. 2005). Black-capped Chickadees (*Poecile atricapillus*) provided with a daily helping of mealworms produced more songs and began singing earlier in the day than did comparable chickadees that received no extra food (Grava et al. 2009). These experiments, and others like them, suggest that a female seeking a mate could use the amount of song produced by a male to judge his ability to obtain a good territory, or perhaps to indirectly judge the quality of the territory itself, which might be important as a food supply for herself and her young. A male seeking to establish a territory could use the amount of song to judge the likelihood that a rival male is too healthy and robust to be challenged successfully.

There is some evidence that avian listeners do attend to quantity of song output. For example, in a Swedish population of Snow Buntings (*Plectrophenax nivalis*), males that produced more songs nested earlier, an indication that females chose them ahead of males with lower song output (Hofstad et al. 2002). Early mating also was associated with high song output in an Austrian population of Blackcaps (*Sylvia atricapilla*) (Hoi-Leitner et al. 1995). In this case, the researchers also showed that males with higher song output had higher quality territories with denser vegetation and better-protected nest sites. Thus, singing a lot of songs helped male Blackcaps both to secure a better territory and to attract a better (or at least an earlier) mate. In comparisons between males on territories of similar quality, high-output males still reproduced earlier, suggesting that females based their mate choice on the song output rather than by directly assessing the territory.

10.7.2 Song performance

In addition to differences in the quantity of songs produced, males may differ in more subtle aspects of song performance. For example, the songs of different males can differ in the rate at which similar syllables are repeated within a song (the trill rate), in the frequency bandwidth of their songs, or in the pitch (frequency) at which a shared

song type is produced. Males also may differ in their ability to sing consistently; researchers have documented between-male variability in ability to maintain consistent pitch across consecutive syllables in a song, in the ability to maintain a consistent time interval between the songs in a bout of singing, and in the ability to maintain a constant between-syllable frequency ratio across the songs in a bout.

Research findings suggest that such differences in how songs are performed influence the ability of males to attract mates and win contests with other males. For example, male Chestnut-sided Warblers (*Setophaga pensylvanica*) in eastern North America differ in their ability to maintain constant pitch and timing across successive songs in a bout, and the most consistent singers have the largest number of extrapair offspring (Byers 2007). Moreover, when a female has an offspring fathered by a male other than her social mate (Chapter 9), the genetic father almost always sings more consistently than the female's social mate. These findings suggest that a female seeking an extrapair partner makes her selection by comparing males' song performance consistency. In a population of Tropical Mockingbirds (*Mimus gilvus*) in Colombia, dominant males sang more consistently than subordinate males. In dominant "alpha male" mockingbirds, a bird's rendition of a given syllable type varied only a little (Botero et al. 2009), and these consistent singers had more offspring than did more variable singers.

A different kind of song performance seems to be important in other species whose songs include rapid trills. Trills require rapid, coordinated movements of the beak, syrinx, and respiratory system, and these movements are especially hard to execute when the trill spans a high bandwidth, with a big difference between its highest and lowest frequencies. A bird that sings an especially rapid trill with a high bandwidth is executing a physically challenging task. For example, female Swamp Sparrows (*Melospiza georgiana*) judge males on the basis of their ability to sing such high-performance trills: in a laboratory test, female sparrows performed more sexual displays in response to playback of high-performance songs than to playback of low-performance songs (Ballentine et al. 2004).

Why would avian listeners be impressed by a male that sings rapid, high-bandwidth trills or bouts of highly consistent songs? Probably because performing those difficult vocal feats may require unusually good stamina and coordination. Thus, males whose singing performance is excellent may be especially healthy or vigorous, and song performance therefore may be a good indicator of a mate worth choosing or a rival worth avoiding.

10.7.3 Song repertoire size

A species' mode of song development influences the size of its song repertoire. Species that do not learn songs, such as most suboscine passerines, tend to have small repertoires. In contrast, song learning has enabled some songbirds to evolve huge repertoires. A Five-striped Sparrow (*Amphispiza quinquestriata*) has 75 different song types, a Tropical Mockingbird (*Mimus gilvus*) has 130 types, a Common Nightingale (*Luscinia megarhynchos*) has 200 types, and a Brown Thrasher (*Toxostoma rufum*) has 2000 types. Why do some songbird species have huge song repertoires, whereas in other species each male uses only a single song type? Efforts to answer to this question have focused, not surprisingly, on what we presume to be the two main functions of bird song: territory defense and mate attraction and stimulation.

In some species, larger repertoires might help males display their prowess and defend their territories. Marsh Wrens (*Cistothorus palustris*) in western North America, for example, seem to duel with their large repertoires. The complexity of interactions can be dizzying. Marsh Wrens have been shown to match a sequence of as many as 10 different song types broadcast from a loudspeaker, but because males in the local marsh sang songs in a predictable sequence, the males could sing each song type in the sequence even *before* the tape recorder played it (Verner 1976); the male could anticipate which song would come next and sing it before the simulated intruder did. The singing of Common Nightingales in Europe also includes predictable song type sequences and anticipatory matching (Todt and Hultsch 1996). This kind of matched countersinging might be important in directing threats to particular individuals or in mediating interactions. Likewise, females somehow might be impressed by the way a singer uses his repertoire.

Some evidence supports the idea that large repertoires function in mate attraction. In the laboratory, females of some species respond more strongly to a greater variety of song. In one experiment, captive female European Pied Flycatchers (*Ficedula hypoleuca*) could simultaneously hear recordings of two singing males, one of which used a larger repertoire of song types than the other (Lampe and Sætre 1995). The females who built nests placed them closer to the large-repertoire speaker than to the small-repertoire speaker. In other species, however, a female's response in laboratory experiments does not seem to depend on the diversity of songs to which she is exposed. For example, researchers found no preference for larger repertoires among female European Starlings (*Sturnus vulgaris*) that could choose to elicit playback of one of two different male song bouts by choosing between two different perches (Gentner and Hulse 2000).

Measuring a female's responses in nature is more difficult, and most field studies instead test for an association between the properties of a male's songs and his success in attracting or fertilizing a female. Some field studies have found a relationship between a male's repertoire size and his mating success. A study of a German population of polygynous Great Reed-Warblers (*Acrocephalus arundinaceus*), for example, found that the number of mates a male acquired was correlated with the size of his song repertoire

(Catchpole 1986). However, a later study of the same population found no correlation between repertoire size and number of mates (Forstmeier and Leisler 2004). More generally, most field studies of repertoire size and female mate choice have found no effect of repertoire size. Overall, the inconsistent results of research on song repertoires and female mate choice suggest that we cannot yet reach a firm conclusion about whether females use variation in repertoire sizes to evaluate potential mates.

In at least two species, the Great Tit (*Parus major*) of Eurasia and the Song Sparrow (*Melospiza melodia*) of North America, males with larger repertoires survive longer than males with smaller repertoires (Lambrechts and Dhondt 1986; Reid et al. 2005). One is tempted to conclude that having a large song repertoire somehow causes a male to live longer, but perhaps it is more likely that good health permits both the longer life and the development of a larger repertoire in youth. Young male Bewick's Wrens (*Thryomanes bewickii*), for example, learn more songs if they hatch early in the breeding season than if they hatch late; early-hatching birds have more time to learn songs before their first winter, and they may have a chance to select the best territory too (Kroodsma 1974). In some species, birds with larger repertoires are older, because males continue to add songs to their repertoires throughout life. For these reasons, males with larger repertoires are more likely to be healthier and better at surviving, and both males and females might be attentive to these vocal indicators of success.

10.8 Other remarkable features of singing behavior

No overview of bird vocalizations would be complete without mention of some especially striking and intriguing manifestations of avian vocal behavior that long have delighted naturalists. In this section, we describe the pre-sunrise burst of singing that greets early-rising bird watchers, the singing abilities of many female birds, the coordinated singing performance conducted by mated pairs of some species, the propensity of some birds to mimic the sounds of species other than their own, and the gymnastic efforts of birds that sing in flight.

10.8.1 Dawn chorus

Some of the most remarkable avian singing occurs at dawn (Fig. 10.38). Most day-active birds are silent throughout the night, presumably roosting quietly somewhere on their territory. Beginning an hour or so before sunrise, birds of many species begin their dawn chorus. Typically, the chorus begins with a burst of songs from the earliest singing species. As the dawn progresses, other species join the chorus in a rather predictable sequence. The order in which species join may be determined by differences in how well species can see in dim light. According to this hypothesis, a bird will not begin singing until there is enough light for it to see well enough to do whatever it must be able to do while singing, such as detecting predators that might notice a singing bird. Evidence in support of the hypothesis comes from a study that measured the size of the eyes of representative individuals of each of 57 passerine species (Thomas et al. 2002). Birds with larger eyes have larger pupils to let in light, so birds with bigger eyes are able to see better in dim light. The researchers also measured the time, relative to sunrise, at which each species began singing at several sites in Europe. These data revealed that species with larger eyes began singing earlier, presumably because they were able to see well earlier. A similar study of a tropical dawn chorus in an Ecuadorian forest revealed a somewhat more complex pattern (Berg et al. 2006). There, the earliest passerine singers were species that lived high in the forest canopy, where light first penetrated at dawn. Singing began progressively later at lower levels in the forest vegetation, and began latest in species that foraged on the heavily shaded forest floor. Within each level of the forest, however, start time and eye size were correlated, just as in the temperate forest.



Fig. 10.38 Dawn chorus. Each day, birds begin to sing in the darkness before dawn. Try to pick out different species in this dawn chorus, recorded on a spring morning in western Oregon (USA). ***Listen online.*** (Photograph by Janet Dodson.)

The quantity and often the quality of singing during the dawn chorus differ markedly from singing during the rest of the day. In many species, singers use the same kind of songs that they sing later in the day but sing them at a markedly faster rate. For example, a Buff-breasted Flycatcher (*Empidonax fulvifrons*) in a neotropical forest sings the same song types throughout the day, but its dawn singing is four times faster than its singing later in the day (Lein 2007). Other species, such as the Chipping Sparrow (*Spizella passerina*), give dawn performances that are

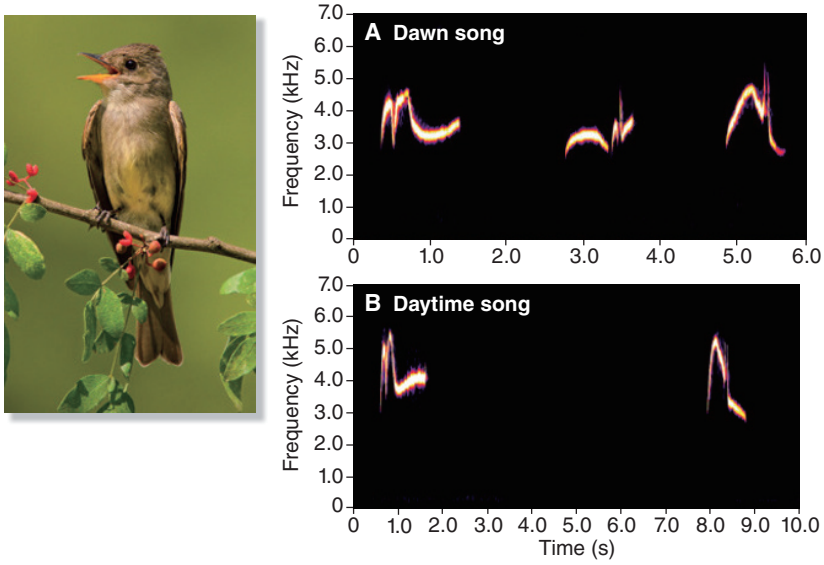


Fig. 10.39 Temporal variation in suboscine song. Some New World flycatchers, such as Eastern Wood-Pewees (*Contopus virens*), sing (A) distinctive song types at dawn compared with (B) the rest of the day. ***Listen online.*** (Recordist: Geoffrey A. Keller. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by Bob Dunlap.)

qualitatively different from their daytime singing (Liu and Kroodsma 2007). At dawn, a male sparrow often sits on the ground near a male from a neighboring territory and delivers bursts of song as if they were being shot from a machine gun. He will sing two or three elements of a song, pause very briefly, sing another burst followed by a pause, and so on. This dawn vocal display seems highly energized, even frantic. In contrast, during daytime singing, a male Chipping Sparrow sits on an exposed perch high in a tree and produces a longer version of his song that lasts about 2 seconds. Between songs, the sparrow pauses for 10 seconds or more, producing a more leisurely, relaxed display.

Reed Buntings (*Emberiza schoeniclus*) in Europe also sing differently at dawn than they do later in the day (Suter et al. 2009; Brunner and Pasinelli 2010). At dawn, a paired male sings a nearly continuous stream of 2.5-second songs, with only a brief, 0.5-second pause, or even no pause at all, between songs. Later in the morning, this fast-paced dawn bout gives way to singing at a more relaxed pace. During daytime singing, males sing much more slowly (pausing 5–10 seconds between songs) and also sing shorter songs (about 1.5 seconds long).

Other species use entirely different songs at dawn than during the day. Certain North American wood-warblers that have two song categories use their aggressive songs for the first 30–60 minutes of the morning and then lapse into a slower-paced delivery of their other song. A male Yellow Warbler (*Setophaga petechia*), for example, uses about 12 song types delivered with immediate variety during his dawn chorus, and after half an hour or so he switches to his single daytime song type (Spector 1991). The male reverts to songs of his aggressive dozen during daytime encounters with other males, but the singing is never as energized as at dawn. Some New World flycatchers, such as the Eastern Wood-Pewee (*Contopus virens*) (Fig. 10.39) and the Vermilion Flycatcher (*Pyrocephalus rubinus*), also use qualitatively different songs at dawn (Allard 1934).

The dawn bout is a truly extraordinary display. Why is there such a burst of energetic singing at dawn? Researchers have proposed many ideas for why dawn singing is so dramatic. Perhaps males sing at dawn because that is the best time to attract females. Also, conditions at dawn are often calm, so song at that time may carry over the maximum possible distance. Furthermore, the dawn chorus occurs at a time of day too dark for effective foraging, so singing then rather than later is an efficient use of time. Or perhaps singing at dawn is especially important for territory defense; dawn follows the longest period of inactivity, and predation occurs at night, too, so dawn might be an important time for a bird to proclaim, "I am still alive" and "This territory is still mine." The dawn chorus probably serves multiple purposes, with the relative emphases undoubtedly varying from species to species. More generally, the dawn chorus may serve as a ritualized display that establishes hierarchies and broadcasts information about them. Avian listeners can glean the information they need to establish and monitor the social relationships that form the basis of their complex societies.

10.8.2 Female song

A common misperception—especially among people who spend most of their time in the north temperate zone—is that song is primarily a behavior of male birds. This incorrect perception that song is solely a male trait also arises in part because most bird song research has been conducted on species that breed in the north temperate zone, where male-only song is more prevalent. Overall, song is indeed more common in male birds, but females of hundreds of bird species also sing as part of their normal activities.

Many of the functions of female song parallel those of males: females use song to defend territories against members of both sexes, for attracting and communicating with their mates, and for advertising their availability and condition. For example, studies of Alpine Accentors (*Prunella collaris*) in France have shown that females use song to attract male mates, and that the males can distinguish between songs of females and males (Langmore et al. 1996). Female song is particularly prevalent in birds in tropical regions around the world. In many such species, females sing less frequently or more quietly than males, but in other species the songs of females are common and conspicuous (Langmore 1998).

Some functions of song are particular to females. Female birds may use song to communicate about their reproductive state by letting potential mates (both their own social mate and other nearby males) know when they are in their fertile egg-laying period. For example, studies of the Pied Bush-Chat (*Saxicola caprata*) in Uttarakhand (India) have shown that females sing in various contexts, including in duets with their mate and during antagonistic interactions with other females. Their songs are most common during the early parts of the breeding cycle, with female Pied Bush-Chats singing only rarely once they are incubating eggs (Sethi et al. 2012).

At a later state of the nesting cycle, some female birds may similarly use song to communicate with multiple fledglings that have left the nest. In Black-headed Grosbeaks (*Pheucticus melanocephalus*) at a breeding site in Utah (USA), family groups of parents and fledglings start to wander away from their home territory about 3 weeks after the young birds leave the nest. These family groups use vocalizations—including songs from both parents—to stay together as they move through thick vegetation, and experiments have shown that the young birds are more responsive to songs of their own parents than to songs of unrelated grosbeaks (Ritchison 1983).

10.8.3 Duetting

The members of a mated pair of birds communicate with one another frequently, and in many species the communication includes vocal signals. In some species these vocal exchanges are simply overlapping bouts of calling, but in others they involve coordinated singing (Fig. 10.40). Such coordinated **duets** differ among the species in which they occur. The difference can be in how often mates join in duets, in the relative complexity of the male and female sounds, in how precisely the vocal exchanges are timed, and in the nature of the overlap between the male and female songs (from synchrony to antiphony, in which the male and female rapidly alternate their contributions).

The Carolina Wren (*Thryothorus ludovicianus*), a common songbird of the eastern USA, has a simple form of duet (Shuler 1965). Male Carolina Wrens sing a loud, resounding "*teakettle-teakettle-teakettle*," each song consisting of a complex syllable ("*teakettle*") repeated several times. On occasion, the female appends to this song a coarse rattle or "*churr*"—unmistakably the female Carolina Wren announcing her social bond to her mate (Fig. 10.41). The quality of male and female utterances differs markedly: females are only occasional participants, and the timing of the male and female contributions does not appear to be well coordinated.



Fig. 10.40 Coordinated duets. Pairs of Bearded Barbets (*Lybius dubuis*) produce duets so well synchronized that they sound as if they are being made by a single bird. (Photograph by Nathan Rupert.)

Far more extraordinary are the complex, highly coordinated duets sung by some related wren species. So coordinated are some of these singing efforts that it is impossible for a human listener to differentiate between the male and female contributions unless the two singing birds are separated by a considerable distance. Among the *Cantorchilus* wrens of the neotropics, the Buff-breasted (*Cantorchilus leucotis*), Bay (*Cantorchilus nigricapillus*), Riverside (*Cantorchilus semibadius*), and Plain (*Cantorchilus modestus*) Wrens sing duets of this sort (Levin 1996; Mann et al. 2003, 2009). In these duets, male and female contributions are equally complex, exchanges are highly coordinated and precise, and both sexes participate frequently.

Most duetting bird species live in the tropics, where duetting also occurs in various species of parrots, woodpeckers, bushshrikes, fairy-wrens, whipbirds, drongos, antbirds, flycatchers, monarch flycatchers, shrikes, and weavers, among others. The occurrence of duetting in these settings is almost certainly related to the long-term pair-bonds of many tropical species. In these species, pairs maintain prolonged monogamous bonds and remain on their territory year round. The two members of a pair thus have a long-lasting relationship and a long-term shared investment

Duets: coordinated songs performed simultaneously by two individuals, usually a mated pair of birds.

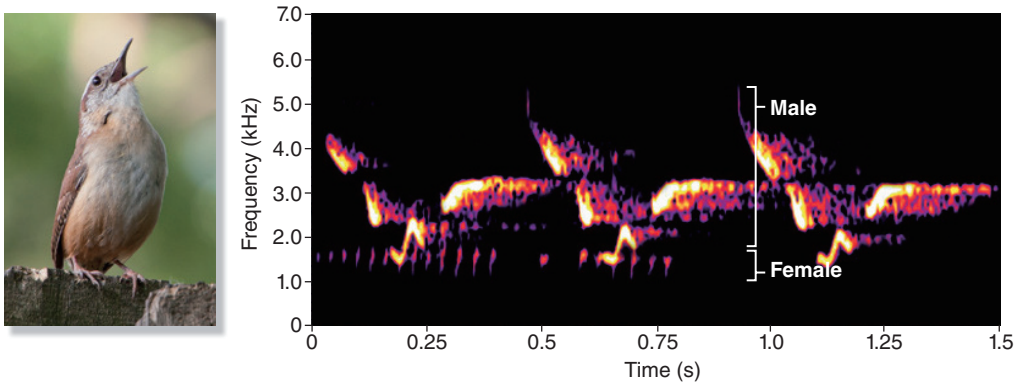


Fig. 10.41 A simple duet. Male and female Carolina Wrens (*Thryothorus ludovicianus*) perform a simple duet without tight choreography. A male repeats a loud phrase several times, while his mate occasionally adds a low-frequency rattle. ***Listen online.*** (Recordist: Gerrit Vyn. Courtesy of Macaulay Library © Cornell Lab of Ornithology. Photograph by David Mozzoni.)

in a territory; these factors may foster a communication system in which both partners benefit from sending highly coordinated signals that help defend their joint territory and maintain their pair bond.

10.8.4 Mimicry

Mimicry is a fascinating consequence of song learning: birds of some species learn not only their own songs but also the songs of other species. In North America, the Northern Mockingbird (*Mimus polyglottos*) is perhaps the best-known example of an accomplished mimic: male mockingbirds sing up to 200 different song types, and a considerable number are clearly copied from other bird species. Renowned mimics elsewhere include the lyrebirds of Australia and Lawrence's Thrush (*Turdus lawrencii*) in South America (Fig. 10.42).

Species not typically thought of as mimics also occasionally learn the vocalizations of other species. In North America, Blue Jays (*Cyanocitta cristata*) imitate the calls of various species of hawks, for example. European Starlings (*Sturnus vulgaris*) are excellent mimics. A study of starlings in five European populations documented high-fidelity mimicry of more than 70 different sounds, including a cat's meow, a frog's call, a squeaky door, and the vocalizations of bird species ranging across the taxonomic spectrum, from owls, gulls, ducks, and sandpipers to thrushes, warblers, finches, cuckoos, and more (Hausberger et al. 1991).

In some species, mimicry occurs only very rarely and seems to be a maladaptive side effect of song learning. Well-documented examples from North America include a Vesper Sparrow (*Pooecetes gramineus*) singing songs of the Bewick's Wren (*Thryomanes bewickii*) (Kroodsma 1972), a Chestnut-sided Warbler (*Setophaga pensylvanica*) singing Indigo Bunting (*Passerina cyanea*) songs (Payne et al. 1984), and a Cerulean Warbler (*Setophaga cerulea*) singing Hooded Warbler (*Setophaga citrina*) songs (Boves et al. 2010). In all of these cases, the males who learned the wrong species' songs remained unpaired, thereby paying a fitness price for their learning error.



Fig. 10.42 Vocal mimicry. Lawrence's Thrush (*Turdus lawrencii*) is a skilled mimic of other forest birds in South America. ***Listen online.*** (Photograph by Daniel Lane.)

For species in which mimicry is routine and normal, researchers have proposed a number of hypotheses to explain its occurrence. One hypothesis is that mimics use other species' songs to help exclude those species from the mimics' territories. This possibility has not yet been thoroughly investigated. Or perhaps learning the songs of other species is simply an easy way for a songbird to develop a diverse repertoire of novel sounds, which might be used to impress a female. This idea is supported by studies of Marsh Warblers (*Acrocephalus palustris*) at breeding sites in Belgium; these warblers learn and mimic both the songs of other local breeding birds and those of species that they encounter only on their overwintering sites in Africa during their non-breeding season (Dowsett-Lemaire 1979).



Fig. 10.43 Flight song. In lengthy displays, Eurasian Sky Larks (*Alauda arvensis*) spiral into the sky while repeatedly singing whistled notes. At the peak height of their display, they turn and rapidly descend into their territory while continuing to sing. ***Listen online.*** (Photograph by Susanne Rintelen.)

10.8.5 Flight songs

Although most birds sing while perched, some sing in flight. Many shorebirds produce long, complex songs in flight above their breeding grounds (Miller 1983; Miller et al. 1988). Sky Larks (*Alauda arvensis*) impress us by delivering their seemingly unending soliloquy from great heights (Fig. 10.43). Hummingbirds, too, often combine flight and sounds—which can combine vocalizations with sounds produced by their wings and tail (Clark 2011)—in their impressive courtship displays (Fig. 10.44).

Flying is a physically demanding activity, so singing in flight is undoubtedly more difficult than singing from a perch. Why do some birds do it? In open country, birds may have few high perches from which to broadcast their songs, so singing in the air may be the best available option. Hence, most birds with flight songs are birds of grasslands or the arctic steppe. The extra energy required to deliver the songs in flight must be rewarded by an increase in the area over which the song can be heard.

However, some flight-singing species do not quite fit this neat explanation for flight songs. The Ovenbird (*Seiurus aurocapilla*), a common warbler of forests in northeastern North America, is a prime example (Lein 1981). Its flight song may be heard near dawn and dusk, sometimes even in the middle of the night, when an Ovenbird launches itself from near the forest floor up into the canopy and sometimes beyond. Elements of the normal Ovenbird song are embedded in the long, jumbled stream of the flight song, but this bird's vocal performance in flight is very different from its normal earthbound sounds.

The Ovenbird's flight song is just one of a multitude of astounding avian vocalizations. The evolutionary "goal" of a bird—to survive and leave offspring—is rather simple,

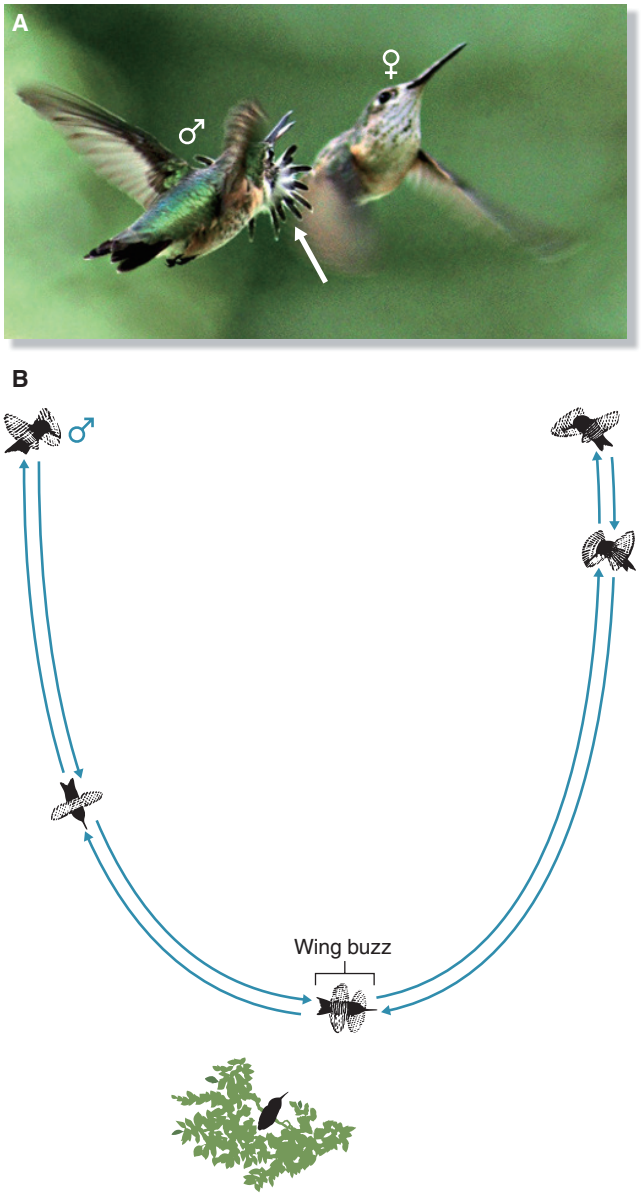


Fig. 10.44 Aerial hummingbird displays. Hummingbirds of many species produce both vocal and non-vocal sounds during aerial courtship displays. (A) This male Calliope Hummingbird (*Selasphorus calliope*) fans his neck feathers (arrow) in mid-air, which creates vibrations in addition to a spectacular visual display—all while simultaneously singing—to court a nearby female. (B) Male Ruby-throated Hummingbirds (*Archilochus colubris*) perform U-shaped flight displays that include a wing buzz at the bottom of each arc. This auditory and visual display can deter competing males or attract receptive females. (A, photograph by Tania Simpson. B, adapted from illustration by N. John Schmitt © Cornell Lab of Ornithology.)

but the role of sound in achieving this mission is extraordinary. A human listener hears short songs, long songs; simple songs, complex songs; musical songs, harsh songs; duets and solo performances; simple repertoires, huge repertoires; and much, much more. Young songbirds are learning,

practicing, and babbling as they copy older birds, which pass traditions on to future generations, creating sounds that we have come to recognize and love.

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Chapter 11 Breeding Biology of Birds

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Birds are adapted to breed in an amazing diversity of habitats, and avian breeding biology is correspondingly varied and complex. To appreciate some of this wonderful diversity in how birds reproduce, consider for a moment the lives of three kinds of birds from very different environments around the globe.

First, imagine that it is the middle of the winter just outside the French antarctic station in Terre Adélie. A group of male Emperor Penguins (*Aptenodytes forsteri*) stands huddled together in the freezing, howling wind. These birds will remain at this location for over 100 days, each incubating his single egg atop his feet within a thick insulated flap of flesh and feathers. The egg will hatch just as sunlight is returning in the antarctic spring, giving the new penguin chick most of the highly productive summer to grow, develop, and fledge before the sun disappears again.

Next, imagine yourself in a wet coastal forest as you watch a male Australian Brush-Turkey (*Alectura lathami*) poking its bill into the top of a giant pile of dirt and leaves. This male is the builder, tender, and protector of this impressive mound. Inside, the process of decomposition generates heat to incubate the eggs that female brush-turkeys have laid and buried within the mound. As soon as they hatch, these eggs will produce the most self-reliant of young birds, chicks that will walk, or fly, off into the forest for a life on their own.

Finally, imagine that you are in a grove of fan palms on the bank of an African river, where you see an African Palm-Swift (*Cypsiurus parvus*) returning to its unusual nest. The female palm-swift has used her sticky saliva to glue a shallow shelf of plant fluff and feathers to the side of a down-hanging palm leaf, and then she has similarly glued her eggs into this minimal nest. She and her mate take turns incubating these eggs by snuggling up next to them on the palm frond. As soon as they hatch, the chicks will grasp onto this precarious nest and remain there for weeks; meanwhile, their parents will return hundreds of times to provision the chicks as they grow mature enough to forage for flying insects on their own.

These are just three of the many ways that different birds have evolved to raise their offspring in different environments. We arguably know more about the breeding biology of birds than about any other single aspect of their lives, and this chapter outlines some of the generalities shared by all breeding birds along with some of the fascinating variation in the reproductive strategies of different avian groups.

Opposite: Great Crested Grebe (*Podiceps cristatus*) parents often carry their young chicks on their backs.
(Photograph by Wim Boon.)

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11.1 Timing of breeding

Most birds breed within a limited window of time that depends on the seasonality of the local environment and on aspects of that bird species' natural history such as its diet, predators, nest type, and habitat. Most birds in temperate regions must breed within the resource-rich period in the spring that is driven by a seasonal flush in vegetation, the hatching of insects, and the oncoming summer warmth. Seasonal temperature fluctuations become less dramatic towards the equator, and in many tropical habitats it is seasonal variation in rainfall that drives annual cycles in resource availability. Therefore, timing of breeding is often less constrained for birds that breed in the tropics, where some species breed exclusively during a dry season, others find optimal conditions during the transition between dry and wet seasons, and a few are able to breed year-round.

The timing of availability of food for their young is the factor that seems to have the greatest overall influence on when birds breed. Ideally, nestlings will hatch just when those food resources are most plentiful. Birds often must lay eggs while food supplies are still rising, especially in environments with strong seasonal changes in resource availability. Since many species—particularly passerines—feed primarily insects to their nestlings, these avian parents often lay eggs just before peak insect abundance. In the most extremely seasonal locations towards the earth's poles, the breeding season of avian insectivores may last only a month or so due to the correspondingly brief period of insect abundance in arctic habitats.

Bird species that feed their chicks on food other than insects often breed at different times than insectivores in the same avian community. For example, American Goldfinches (*Spinus tristis*) of North America rely almost exclusively on thistle seeds to feed their young (Fig. 11.01), and this species therefore breeds in mid-summer when thistle seeds ripen, rather than earlier in the spring. Elsewhere, many honeyeater species in Australia breed when and where they can find the abundant blossoms of key *Eucalyptus* tree species. Likewise, Eleonora's Falcons (*Falco eleonorae*) in the eastern Mediterranean lay eggs in late summer, insuring that the peak food demands of their nestlings coincide with the parents' prime hunting season during the fall landbird migration (Chapter 13).

The more regular the seasonal changes, the easier it is for a potentially breeding bird to predict them. In most environments, year-to-year fluctuations are minor enough that the breeding season falls within a predictable period within each year. Most birds' reproductive systems are primed to be active only during these months. The avian internal clock relies on changes in day length, or **photoperiod**, which cue a cascade of physiological preparations for breeding (Chapter 7). Birds generally use photoperiod to establish their general breeding period, but often rely on other cues to fine-tune the initiation of breeding. For example, in the wet forests of Panama, the presence of live insects helps stimulate male Spotted Antbirds (*Hylophylax naevioides*) into high breeding condition (Hau et al. 2000). The more closely an environmental cue relates to a critical environmental feature, the better it serves as the basis for reproductive scheduling. For example, many birds that nest in arid environments, such as the Red-billed Quelea (*Quelea quelea*) of Africa (Chapter 12), are driven to breed after a heavy rainfall (Cheke et al. 2007). The same is true for many desert-nesting birds, such as Zebra Finches (*Taeniopygia guttata*) of central Australia and several species of ground finches in the arid lowlands of the Galápagos Islands (Chapter 3). For all of these species, rainfall is a cue that predicts the future availability of seeds and insects related to plants that grow only when water is available.

A few non-insectivorous birds have evolved to avoid regular breeding seasons altogether. Although they breed most commonly in the spring and summer, Rock Pigeons (*Columba livia*) of many cities worldwide can breed year-round on a diverse diet of seeds and city scraps. The crossbills of the northern hemisphere initiate reproduction based on the availability of their key resource—pine and spruce seeds. Because the seed production of these



Fig. 11.01 Breeding season and food availability. American Goldfinches (*Spinus tristis*) breed later in the summer than most insectivorous birds occupying the same habitat, as they rely on the ripening seeds of thistles and other plants to build their nests and feed their young. (Photograph by Stan Tekiela, www.NatureSmart.com.)

Photoperiod: the amount of a 24-hour day in which birds are exposed to light; or the relative lengths of light and dark periods of the day.

trees varies greatly from place to place and from year to year, crossbills may breed as soon as they find an adequate food supply (Hahn 1998), no matter what month of the calendar it happens to be. Birds like crossbills that remain ready to breed upon encountering favorable conditions must pay the costs of maintaining their reproductive systems throughout the year. In contrast, the majority of birds, particularly those in strongly seasonal environments, shut down their reproductive system during the non-breeding season (Chapter 7).

11.2 Breeding territories

Nearly all birds defend some kind of territory during the breeding season (Chapter 13). Although expensive in terms of time, energy, and personal risk, the benefits of defending a territory often outweigh these costs. The size and richness of a territory's resources frequently influence mate choice and subsequent breeding success. Males of many species therefore defend large, multipurpose territories to attract one or more females and supply enough food for chick rearing. For example, females of both marsh-nesting warblers in Eurasia and blackbirds in North America may choose mates on the basis of a male's territory size. Similarly, female Purple-throated Caribs (*Eulampis jugularis*) of the Lesser Antilles prefer males with a higher availability of nectar on their territories. Males in this hummingbird species defend much more nectar than they need for their own use, reserving parts of their territories for females (Temeles and Kress 2010).

Territories also reduce the chance that other individuals of the same species will interfere with the territory owner's breeding activities. This kind of breeding interference is a large problem for some species. For example, male bowerbirds of Australia and New Guinea craft elaborate structures to attract females, often by stealing rare bower materials from bowers made by neighboring males; if left unguarded by its male owner for just one day, a bower may disappear entirely (Pruett-Jones and Pruett-Jones 1994). Many birds may also attempt to destroy the eggs of nearby competitors. For example, in North America, both Marsh Wrens (*Cistothorus palustris*) and House Wrens (*Troglodytes aedon*) routinely puncture the eggs of conspecifics and other potential nest-site competitors; Crimson Rosellas (*Platycercus elegans*) do the same in Australia (Krebs 1998). Breeding birds often mitigate the risk of this kind of disturbance by guarding their nests. For example, in northern South America, Green-rumped Parrotlet (*Forpus passerinus*) pairs guard their eggs diligently. To test the rate of clutch destruction without parental defense, researchers set up experimental nest boxes filled with replicas of this species' eggs. These false nests were undefended, and nearby Green-rumped Parrotlet groups destroyed 40% of these clutches within 3 days. By comparison, invading parrotlets destroyed only 5% of clutches in real nests that were actively defended (Beissinger et al. 1998).

11.3 Nests and nest building

Only insects surpass birds in the diversity and sophistication of their nests. A tremendous amount of literature, mostly from the nineteenth century, describes the nest-building behavior of birds. Yet across the entire spectrum of bird species—from common backyard birds to exotic species in far-off lands—aspects of the nesting biology of most species have yet to be studied. In terms of construction and placement, each type of bird nest incurs its own costs (such as parental effort and risk of predation or sabotage) and benefits (including greater nest safety and thermoregulatory efficiency). To explore these various costs and benefits, it is necessary to appreciate the functions that nests serve and the diversity of ways these aims are achieved.

11.3.1 Functions of nests

Most birds construct nests primarily to hold and protect their eggs, and to keep them together so that a parent bird can incubate them at the proper temperature for development. A simple scrape in the ground can serve as an adequate nest for some birds. A few birds that lay only one egg at a time have forgone nests altogether and incubate their single egg in other ways. However, most birds build some kind of nest. Nests sometimes serve additional functions: a few birds roost in their nests even beyond the breeding season, whereas others construct nests as a type of display to attract mates. For some species, mutual nest building is a common component of pair formation and bonding (Chapter 9). Nevertheless, nearly all nests must primarily provide a safe haven from predators and the elements.

A successful nest usually thwarts predators via its concealment and/or inaccessibility. The nests of most bird species are therefore purposefully difficult to find. For example, the risk of nest predation is particularly high in many tropical forest habitats, and many tropical passerines accordingly construct notably small nests that are inconspicuous when not attended. Most birds construct nests with common materials, generally avoiding brightly colored substances. To further enhance camouflage, some species affix lichens or bits of bark to a nest's exterior. The nests of some passerines include a long, trailing pendent, perhaps to break up the visual profile of the nest shape. Most bird species are also quite adept at constructing out-of-reach nests. For example, birds in groups as diverse as vireos, broadbills, and herons often prefer to nest

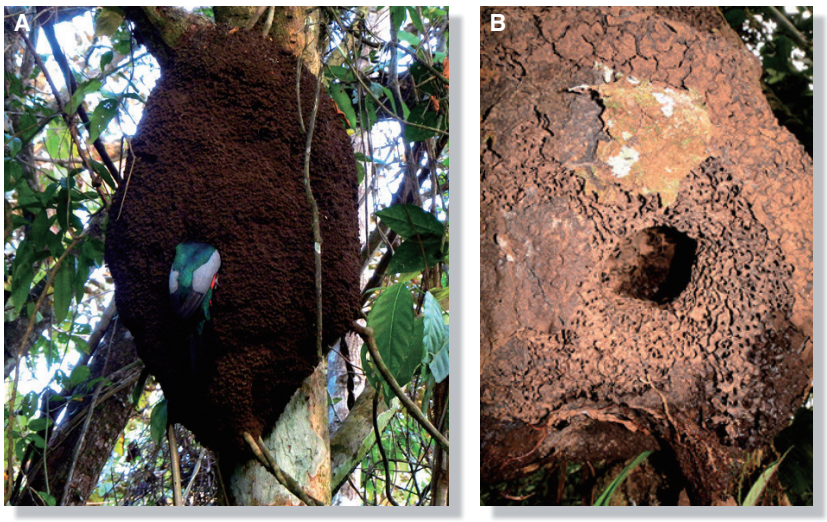


Fig. 11.02 Cavity nesting within active wasp and termite nests. Some birds dig cavities within social insect nests, most likely a strategy to deter predators. (A) A Slaty-tailed Trogon (*Trogon massena*) entering a nest hole within an arboreal termite nest. (B) The entrance of a Black-tailed Trogon (*Trogon melanurus*) cavity that the birds have excavated within an active arboreal termite nest. (Photographs by: A, Jenn Sinasac; B, Rebecca Brunner.)

precariously on the tips of long, high branches—places that most climbing predators like rodents or snakes are unable to reach. Other birds commonly build nests in tree cavities, within cliff nooks, or high on the walls of buildings.

Among the most interesting nest locations are those constructed near animals that deter predators (Chapter 14). Many tropical birds lay their eggs within or very near the nests of aggressive wasps (Joyce 1993) or ants (Young et al. 1990), both of which will attack an approaching predator. In the neotropics, some species of trogons, kingfishers, and parrots dig nest tunnels within active termite or ant mounds (Fig. 11.02). How (or why) these nesting birds are spared the insects' attacks remains a mystery.

Nests also provide shelter from the elements. The microclimate around and within many nests is much more favorable for eggs and nestlings than is the surrounding environment. For example, temperate-nesting hummingbirds often choose nest sites under overhanging trees to minimize heat loss at night (Calder 1973). Some gulls place their nests in the shade to reduce the risk of their nestlings overheating or becoming dehydrated (Winnett-Murray 1980). Similarly, in the desert, where vegetation is scarce and solar radiation intense, many birds build enclosed nests to provide shade for their eggs and themselves. Nests may also prevent eggs and young from rolling out. New World orioles and oropendolas, Old World weavers, and Asian broadbills all build deep, enclosed nests at the tips of long, thin branches. This combination of nest structure and site works in tandem: the structure keeps the eggs from falling out as the nest swings wildly in the wind, and the location prevents access by predators like monkeys.

11.3.2 Diversity of nest locations and nest-site selection

Birds nest in almost every terrestrial and shallow-water habitat on Earth—from the surfaces of lakes to rock niches above the timberline, from the howling, frozen barrens of Antarctica to forests and deep caves in the tropics. The sites that birds occupy within these habitats are similarly diverse. Featureless cliff faces, holes and cracks of every type, branches of all diameters, bare ground, and myriad human constructions (skyscrapers, bridges, telephone poles, signs, oil pumps, old boots and hats, and even active ferries)—nearly anything that can support a nest has been used by birds at some time.

Beyond protection from predators and the elements, birds often choose nest sites that are close to a food supply. Nesting sites generally correspond with the ecology of the parent. For example, Crab Plovers (*Dromas ardeola*) nest in burrows in the sand, not far from the sandy tidal flats on the Indian Ocean where this species prefers to feed; the treeswifts of Asia nest high on thin branches in the midst of their aerial habitat. However, there are many exceptions: both the Secretary-birds (*Sagittarius serpentarius*) of Africa and the two long-legged seriema species of the South American savanna nest atop small trees, despite spending most of their lives running and walking on the ground. Similarly, the Black-and-white Warbler (*Mniotilta varia*) of North America nests on the ground, despite being a specialized forager on the surfaces of tree trunks and branches.

Although some birds have very specific requirements for their nest sites, others show substantial flexibility.

Ospreys (*Pandion haliaetus*) generally nest in treetops, but on islands free of predators they will nest on the ground if no trees are available. Many species with long breeding periods build nests in different sites as their breeding habitat changes across the season. For example, American Robins (*Turdus migratorius*) breeding in North America often place their first nests of the season low in protected evergreen trees, whereas robins breeding later usually choose higher sites in newly leaved deciduous trees (Sallabanks and James 1999). As the weather becomes progressively hotter in the Arabian Desert, Greater Hoopoe-Larks (*Alaemon alaudipes*) similarly shift their nesting preferences from open areas to shadier, shrubby sites (Tieleman et al. 2008).

Increasing evidence suggests that birds pay a great deal of attention to the disturbance and predation risks associated with a given habitat. For example, Rufous-bellied Thrushes (*Turdus rufiventris*) in Argentina build a greater proportion of their nests in protective bromeliads when nesting in sites disturbed by human traffic (Lomáscolo et al. 2010). Birds must balance the benefit of a well-hidden spot with the risk that the same mode of concealment may obscure an approaching predator from view. Playback experiments have shown that when exposed to the recorded calls of larger nest predators, Siberian Jays (*Perisoreus infaustus*) in northern Sweden chose nest sites in denser vegetation than those chosen by control birds that were not exposed to such recordings (Eggers et al. 2006). Some host species respond similarly to the presence of **brood parasites** (Chapter 13) that might lay eggs in their nest. For example, in an experiment in Montana (USA), researchers played calls of brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) during the territory establishment periods of their potential host species. The hosts responded by settling in lower densities, compared with other areas where the cowbird calls were not played. Non-hosts, to whom the presence of cowbirds offered no threat, established territories of equivalent density in both the test and control areas (Forsman and Martin 2009).

Closely related and ecologically similar bird species often compete for nest sites at least as much as they compete for food. Competition for nest holes can be particularly intense in some habitats. Moreover, nest predators often develop a search image after finding multiple nests with similar attributes. Thus, within any given patch of habitat, competition persists both within and among bird species to build nests in less occupied locations.

The males of some species display for a mate from a potential nest site, as do many weavers, herons, and wrens.

Brood parasite: a female bird that lays its eggs in the nest of another individual of the same or different species.



Fig. 11.03 Display on a breeding territory. Male birds like this Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) attract mates by defending a high-quality territory with many potential nest sites. (Photograph by Herman H. Giethoorn.)

Others display on a territory where the male has identified likely nest sites, as do marsh-nesting blackbirds (Fig. 11.03). Species that exhibit these behaviors generally build nests that are demanding to construct or defend, or must nest within sites that are limited in space or resources. In other species, such as gulls, many passerines, and even some polyandrous birds such as jacanas, choosing a nest site appears to require a negotiation between the male and female; each considers sites identified by its mate. This early decision stage of the nesting cycle is hard to study because birds tend to be less committed towards the beginning of a breeding attempt, and slight disturbances caused by human observers may cause the pair to abandon a potential nest site. Therefore, ornithologists do not yet understand as much about this establishment stage of nesting as they do about later parts of the breeding cycle.

11.3.3 Diversity of nests

Nests vary wonderfully in composition and structure. They can be classified in many different ways; each nest type described below is classified primarily by its shape.

In a number of species, nesting involves site selection but no further nest construction whatsoever. Murres lay their single eggs directly on exposed rock ledges, and New World vultures and condors lay their eggs on the bare floors of shallow caves. White Terns (*Gygis alba*) of tropical seas lay a single egg on bare branches (Fig. 11.04), as do the potoos of the neotropics. The absence of a nest may be advantageous to these species for different reasons: parents need not waste time and effort nest building, exposed eggs may be less conspicuous to predators, and ectoparasites may be less of a problem when chicks are not restricted to the same soiled spot. Male Emperor Penguins (*Aptenodytes forsteri*) build no nest, and instead have evolved an incubation

pouch that is formed by a loose bulge of skin above their feet; after a female lays her single egg for the season, she passes it to her mate for safe keeping while she leaves for a long period to feed in the distant ocean. All brood parasites also fall into the "nestless" category, as they lay their eggs in nests built by other birds.

The nests of some species consist of a simple **scrape**, in which birds displace loose gravel or sand on the ground to provide a slight depression for the eggs (Fig. 11.05). For example, many plovers, terns, and skimmers nest in a very shallow scrape, perhaps lined with a few flat pebbles or nothing at all. Some scrape-nest species do not even create a depression at all if the substrate at their nesting site is too hard, but they may still arrange flat pebbles and twigs to create a very rudimentary nest.



Fig. 11.04 Some birds do not build nests. White Terns (*Gygis alba*) precariously lay a single egg on bare branches. (Photograph by Duncan Wright, US Fish and Wildlife Service.)

Platform nests consist of a mound with a very shallow depression on top. Different birds build platforms on the ground, floating in water, or within trees or shrubs. Platform nests vary tremendously in complexity, from the flimsy platforms of twigs thrown together by most doves (Fig. 11.06) to massive structures—sometimes containing thousands of large sticks—built by storks or large birds of prey like Ospreys (*Pandion haliaetus*) and eagles. Birds may build platform nests anywhere they find a strong enough support. Many herons, cormorants, storks, and raptors build platform nests in trees, but will use the same types of sticks to nest on the ground if no trees are available. Oilbirds (*Steatornis caripensis*) build platform nests inside South American caves (Box 11.01). Flamingos build short pedestals of mud, and grebes and some terns build floating rafts of aquatic vegetation to support their shallow nests (Fig. 11.07). The Horned Coot (*Fulica cornuta*) of South America builds an interesting variant of this type of platform nest: occupying high Andean lakes with limited aquatic vegetation, these birds pile stones in the water, building a shallow nest of vegetation upon the stones at the surface (Fig. 11.08). The accumulation of stones built up by several pairs over a few years can reach up to 1 meter high and 4 meters in diameter, weighing up to a metric ton (Ripley 1957).

The majority of bird species build **cup nests**, structures with depressions on their top surfaces that are at least half as deep as they are wide. Birds place cup nests in a broad variety of sites: on the ground, in trees, beneath waterfalls,

Scrape nest: a shallow depression created for use as a nest; scrapes usually contain little or no nest material.

Platform nest: a nest consisting of a shallow depression on the top of a mound of nest material.

Cup nest: as the name implies, a nest in the shape of a cup that is at least half as deep as it is wide.



Fig. 11.05 Scrape nest. Some species like this Ladder-tailed Nightjar (*Hydropsalis climacocerca*) scrape an indentation in the substrate for their eggs. In these cases, the incubating adult generally blends in well with its surroundings. Here, the nightjar has just barely modified its nest site, placing this nest type at the boundary between a scrape nest and no nest at all. (Photographs by Rebecca Brunner.)

Box 11.01 The strange nesting biology of Oilbirds

Secluded caves in the tropical forests of northern South America provide nesting sites for the bizarre Oilbird (*Steatornis caripensis*). Young Oilbirds are so lipid-rich that they were once harvested and boiled down for oil—hence their common name (Fig. 11.B1.01A). Oilbirds eat only fruit (Fig. 11.B1.01B), a diet that distinguishes them from related birds; every other species in the order Caprimulgiformes eats nectar or insects. Parent Oilbirds even incorporate fruit seeds into their nests, along with pulp and feces, and use saliva to reinforce these materials. Since pairs reuse and add materials each year, older nests become cone-like in shape. Oilbird nesting caves often support large colonies of these birds.

Oilbirds lay one to three spherical eggs, with an uncommonly long interval of 2–9 days between layings. This timeframe likely relates to their diet: because fruit does not contain much protein, female Oilbirds may need time to gather enough resources to form each egg. Incubation begins with the first egg laid, so the chicks in a nest hatch at different times. When feeding their chicks, parents often leave and return to the nest together, frequently in synchrony with neighboring pairs in the colony. These feeding visits occur five to six times per night immediately after hatching, trailing off to three or four visits during the later part of the chicks' development. Despite this generous feeding regime, Oilbird chicks develop slowly and do not fledge until they are 3–4 months old—a lag that is also likely related to the limited protein content of fruit.

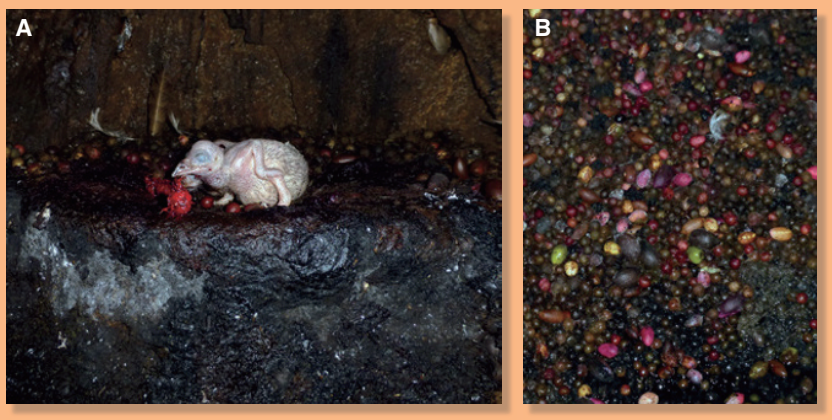


Fig. 11.B1.01 Oilbird nesting biology. (A) This Oilbird (*Steatornis caripensis*) nestling sits at the edge of its nest on a ledge inside a South American cave. (B) Oilbirds are obligate frugivores; their nesting sites are filled with mounds of seeds and other inedible fruit parts. (Photographs by Peter LaBelle.)



Fig. 11.06 Platform nest. Most dove species, such as this Wompoo Fruit-Dove (*Ptilinopus magnificus*), build flimsy platform nests made of sticks. (Photograph by Deane Lewis, http://dl.id.au.)



Fig. 11.07 Vegetation raft nest. Grebes and other aquatic species, like this Black Tern (*Chlidonias niger*), construct floating rafts of vegetation to support their nests. (Photograph by Jean Troalen.)

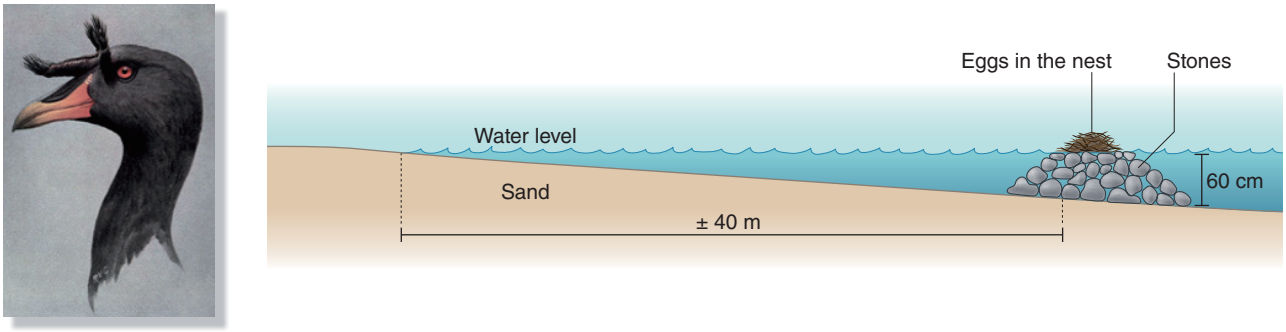


Fig. 11.08 Elevated nesting mounds. Horned Coots (*Fulica cornuta*) create nest mounds in shallow Andean lakes. These birds gather hundreds of stones until the top of their mound rises above the water surface; they then place debris and vegetation on top as a cushion for their eggs. (Artwork by Robert V. Clem, from Ripley 1957.)

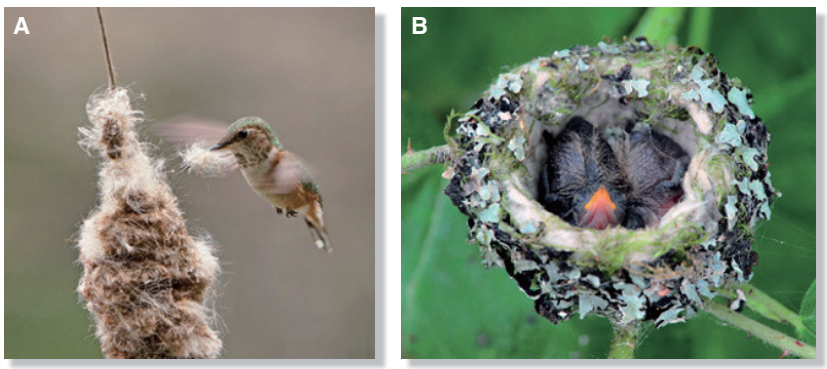


Fig. 11.09 Cup nest. Rufous Hummingbirds (*Selasphorus rufus*) gather spider webs, lichens, and "vegetable down" from seeds (A) to construct tiny, insulated cup nests (B). (Photographs by: A, Penny L. Hall; B, David H. Wong, Vancouver, Canada.)

and within nest cavities of all kinds. Cup nests come in an equally diverse array of sizes and materials, although they are most commonly made of small twigs, dried grass, or mud. Crows and ravens build the largest cup nests; hummingbirds construct the smallest, often by securing lichens and soft fibers from seeds together with carefully collected spider webs (Fig. 11.09). As outlined below, ornithologists often categorize cup nests based on the nature of their support.

Simple, hard surfaces—the ground, a niche on a cliff, or, most commonly, tree branches—support "statant cups," structures supported primarily from below. Oftentimes, gravity alone holds the nest in place. Bobolinks (*Dolichonyx oryzivorus*) of the New World build statant cups directly on the ground. Horned Larks (*Eremophila alpestris*) do the same in open country, with a slight twist: in order to keep their eggs slightly below ground surface to avoid foot traffic from large mammals, Horned Larks commonly build their statant cups within hollows of hardened cow or horse hoofprints. Most nests built in shrubs and trees are also statant cups, ranging from the loose piles of twigs and grass built by some songbirds to the heavy mud nests built by the Magpie-larks (*Grallina cyanoleuca*), White-winged Choughs (*Corcorax melanorhamphos*), and Apostlebirds (*Struthidea cinerea*) of Australia (Fig. 11.10).

"Pensile cups" hang by their rims, which are often securely attached to thin branch tips or reedy vegetation in marshes. New World blackbirds, vireos, and many other songbirds in Australia and Asia build pensile cups.



Fig. 11.10 Statant cup nest. Constructed with mud, this Apostlebird (*Struthidea cinerea*) statant cup nest is supported by the tree branch from below. (Photograph by Irby Lovette.)



Fig. 11.11 Pendulous cup nests. The long, sock-like nest of this Altamira Oriole (*Icterus gularis*) represents an extreme example of a pensile cup, supported only by its rim. (Photograph by Greg Page.)



Fig. 11.12 Adherent cup nest. Grey-rumped Treeswifts (*Hemiprocne longipennis*) and many other treeswift species use saliva to attach their minuscule nests, containing just one egg, to the sides of branches. After hatching, the nestling must balance in the nest or on the adjoining branch for several weeks. (Photograph by Johnny Wee.)

The nest's belly hangs unsupported, and the lack of sturdy structures surrounding pensile cups often minimizes predator access from below. Pensile nests with deeper centers are considered "pendulous cups." Birds enter from the top of such nests, which are usually woven from plant strips or fibers. Pendulous cups are characteristic of New World orioles (Fig. 11.11), oropendolas, and caciques, as well as some Old World weaver species.

Usually made mainly of mud and/or saliva, "adherent cups" attach securely to vertical surfaces. Barn Swallows (*Hirundo rustica*), which breed throughout the northern hemisphere, build adherent cups by mixing mud with straw. Asian treeswifts use saliva to glue their tiny nests to the sides of branches (Fig. 11.12). The African Palm-Swift (*Cypsiurus parvus*) even goes so far as to glue its eggs to a pad-like vertical nest, incubating in a vertical position. White-nest Swiftlets (*Aerodramus fuciphagus*) of Southeast Asia build perhaps the most extreme adherent cups, which often consist entirely of saliva. As their former common name "Edible-nest Swiftlet" suggests, the nests of this species are the main ingredient in an Asian delicacy called "bird's-nest soup." People have long harvested these nests in vast caves, climbing rickety skyscraper-like scaffolds of bamboo to reach them. More recently, harvesters have instead constructed artificial caves for these birds—these structures resemble human houses, with the upper floor open to the air and the comings and goings of swiftlets. A swiftlet pair will often hurriedly build another nest if the first is removed, but these replacement nests usually contain bits of vegetation (as well as saliva) and are thus much less desirable as human food.

Some bird species, especially those that nest on the ground amid vegetative cover, build **domed nests**. The woven dome, integrated with the woven cup, conceals the eggs or nestlings. In North America, meadowlarks build domed nests in grassy areas, and wood-warblers called Ovenbirds (*Seiurus aurocapilla*) build them in forests (Fig. 11.13). In the Old World, many grass-nesting species similarly build domed nests.

Globular nests are completely enclosed (with the exception of a small side entrance). Built in shrubs or trees, these nests are characteristic of most wrens. For example, Cactus Wrens (*Campylorhynchus brunneicapillus*) of North America build grassy spheres, often within the spiny arms of a *cholla* cactus. In the same desert habitats, Verdins (*Auriparus flaviceps*) build smaller globe nests with spiny twigs, orienting the spines to the outside for extra protection. Black-billed (*Pica hudsonia*) and Eurasian (*Pica pica*) Magpies build larger globular nests of thorny twigs, sometimes inserting short strands of barbed wire. Broadbills in Asia and some New World flycatchers and South American

Domed nest: a cup nest with an overhead dome that helps conceal the eggs and nestlings.

Globular nest: a spherical dome nest with a top that completely encloses the nest, usually entered through a hole on one side.



Fig. 11.13 Domed nest. The Ovenbird (*Seiurus aurocapilla*) is named for the domed shape of its nest, which resembles an old-fashioned oven. (Photographs by: left, Peter Caulfield; right, Scott R. Loss.)

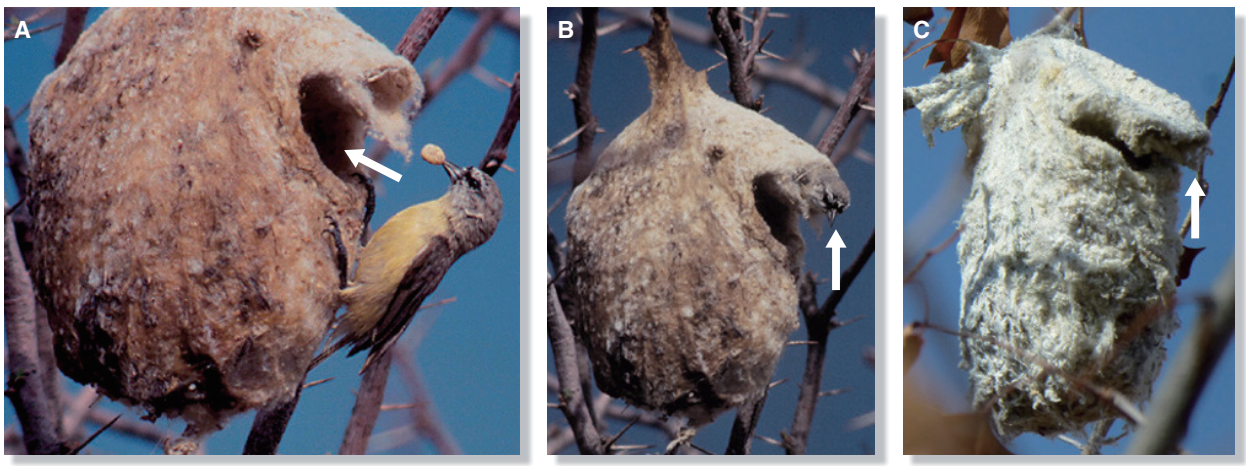


Fig. 11.14 Globular nest with false entrance. (A) Southern Penduline-Tits (*Anthoscopus minutus*) build nests in which the larger, more obvious nest opening (arrow) is actually a false entrance. (B) The real nest chamber entrance is located above the false one (arrow). (C) When not occupied, the entrance tunnel lies flat, ending in a concealed slit (arrow). (Photographs by: A and B, Mike Soroczynski; C, Peter LaBelle.)

ovenbirds deter predators by building their globular nests at the ends of long vines or tendrils. Southern Penduline-Tits (*Anthoscopus minutus*) of Africa build pendent globular nests with a false entrance to foil predators. A prominent hole on the side of the nest is actually a fake entrance leading to a dead-end chamber; the true entrance is a concealed slit in the roof of the false entrance that closes behind the parent as it enters and exits the real nest chamber (Fig. 11.14).

A globular nest with an entrance tunnel is called a **retort nest** (Fig. 11.15). These nests are common among the mud-nesting swallows, many African weavers, and some swifts. The lengths of these tunnels can vary from a few centimeters to more than a meter. Retort nests built with mud, especially those with very thick-walled tunnels, can be very difficult for all predators except snakes to access.

A few species build **mound nests**, which generally consist of large piles of nest material on the ground or in large trees. Megapodes—the most famous mound nesters—are the only birds that use the nest itself, rather than a parent's body, as the source of heat for developing embryos (Box 11.02). Only a few passerine species build true mounds: Palmchats (*Dulus dominicus*) on the island of Hispaniola and several species of African social weavers build colonial mound nests—resembling large, suspended haystacks—in palms or trees. Monk Parakeets (*Myiopsitta monachus*) use sticks to build colonial mound nests in their native Patagonia. The odd, heron-like Hamerkop (*Scopus umbretta*) of Africa builds an enormous nest

Retort nest: a globular nest with an entrance tunnel.

Mound nest: a nest comprised of a pile of material, usually with a chamber in the middle for the eggs.



Fig. 11.15 Retort nest. Birds like this Baya Weaver (*Ploceus philippinus*) build retort nests, which have a globular nest chamber with a distinct entrance tunnel. (Photograph by Con Foley.)

mound more than 2 meters high and wide, usually in a large tree (Fig. 11.16). Hamerkop nests may contain up to 8000 sticks and weigh up to several hundred kilograms. The nest chamber lies in the center of the mound, connected to the outside by a mud-lined tunnel.

A tree hole is likely the most familiar sort of **cavity nest**. All woodpeckers are capable of excavating their own nest cavities (Fig. 11.17), sometimes even in healthy tree trunks, thanks to a host of adaptations (Chapter 6). Although woodpeckers are adept at creating nest cavities in trees, many species of parrots, barbets, toucans, nuthatches, and tits are capable of modifying pre-existing holes to suit their needs. As mentioned earlier, some trogons and other tropical birds dig nest cavities within arboreal termite nests.

When cavities in the ground are longer than they are deep, they are generally termed **burrow nests**. Numerous

Cavity nest: a nest located in an empty space within a larger substrate, such as the cavities excavated by woodpeckers or the nest boxes provided by humans.

Burrow nest: a cavity nest in the ground that is longer than it is high; usually accessed by an entrance tunnel.

Box 11.02 The unique incubation of megapodes

Megapodes are turkey-like birds from Australia and New Guinea with extraordinary incubation strategies. At 10–20% of the female's total weight, megapode eggs are among the largest in the avian world relative to female body size. But rather than sitting on the eggs to provide warmth, each species of megapode locates or creates an external heat source for incubation. In volcanically active regions, some megapode males dig burrows for their eggs in moist sands warmed by volcanic vents, while others tend to eggs laid directly on black volcanic beaches heated by the sun. In forested habitats, some megapodes bury their eggs within forest banks, where the process of decomposition provides enough heat for incubation. Male Australian Brush-Turkeys (*Alectura lathami*) exploit this type of heat production by gathering vegetation into a mound the size of a large car (Fig. 11.B2.01); as it rots, this compost pile heats the eggs. Male brush-turkeys constantly tend to their mound, adding new materials and monitoring the internal temperature.

Among the megapodes, Malleefowl (*Leipoa ocellata*) engage in perhaps the most complicated of external incubation strategies (Fig. 11.B2.02). First, a male Malleefowl will dig a pit into the sandy soil of its open woodland habitat. Then, both the male and female fill the pit with vegetation until it overflows. Decomposition begins shortly after the materials are soaked by rain, at which point the female leaves in search of enough food to produce roughly two dozen eggs. She returns briefly to lay each of her eggs,



Fig. 11.B2.01 Brush-Turkey mound. Male Australian Brush-Turkeys (*Alectura lathami*) construct enormous mounds out of leaves and branches. Females lay their eggs within the mound, where the heat of decomposition is sufficient to incubate the eggs. (Photograph by Ian Withnall.)

Continued



Fig. 11.B2.02 Malleefowl mound. Male Malleefowl (*Leipoa ocellata*) construct crater-like mounds in which the central pit contains decomposing vegetation. Males tend their mounds carefully, adding and removing vegetation and sand to ensure that the internal temperature remains within the range suitable for incubation. (Photographs by Graeme Tonkin, South Australia.)

leaving the male solely responsible for incubation duties—he will monitor and modify the pit for up to 11 months, employing a remarkable range of strategies to maintain proper nest temperature. On cool nights, the male covers the decomposing nest with sand for insulation; as the season warms and decomposition wanes, he increasingly exposes the nest to the sun, even adding sand at mid-day when temperatures get too hot. As the solar-heating season wanes, males use sun-warmed sand to keep the nest warm through cooler nights. When the sun ceases to heat the nest through the night, the male removes the old materials from the pit and refills it with fresh vegetation. This routine of nest modification may be the most complex annual cycle of engineering displayed by any bird.

Multiple females typically lay eggs within the same megapode mound, provided that they mate with the tending male. Intriguingly, the eggs of different megapode species have occasionally been found in the same megapode mound, presumably a form of brood parasitism. This is a particularly cunning strategy, considering megapode males rarely encounter the eggs themselves and megapode adults do not provide any parental care once the chicks hatch.



Fig. 11.16 Mound nests. This Hamerkop (*Scopus umbretta*) mound nest is in the process of being built in a tree. When finished, these nests can span more than 2 meters. (Batra, https://en.wikipedia.org/wiki/File:Hammerkop_Nest_Kenya_2012.jpg. CC-BY-SA 3.0.)



Fig. 11.17 Cavity nest. Woodpeckers like this Red-headed Woodpecker (*Melanerpes erythrocephalus*) are able to excavate their own nest cavities, sometimes even in healthy trees. Other cavity-nesting species must find pre-existing holes (sometimes drilled by a woodpecker in the past); competition over these valuable nesting cavities can be intense. (Photograph by Stephen Patten.)



Fig. 11.18 Burrow nest. This Common Kingfisher (*Alcedo atthis*) excavates its nest in a clay bank by loosening soil with its bill and clearing the resulting tunnel with its feet. (Photograph by Andy Holt.)



Fig. 11.19 Cavity adopters. Rock Nuthatches (*Sitta neumayer*) construct their nests in natural cliff crevices that they expand and enclose using clay and mud. Most other cavity adopters are less capable of modifying their nest sites, requiring fully formed cavities created by woodpeckers or natural weathering. (Photograph by Amir Ben Dov, Israel.)

species in many different avian families excavate burrows in sandy soil or moist sand. In contrast to the physical characteristics required to excavate in wood, soil excavators do not usually have specialized adaptations for this task. Examples from the temperate zone include the Bank Swallow (*Riparia riparia*) and the Common Kingfisher (*Alcedo atthis*); both loosen soil with their bills and clear a tunnel with their weak feet (Fig. 11.18).

Cavity adopters occupy nest cavities created by other animals or through forces such as decay or erosion. Most cavity adopters throughout the world nest in naturally occurring tree holes or rock niches. Some birds that nest in adopted tree cavities rely on other species, usually woodpeckers, to create their holes (Chapter 13). Most artificial nest boxes placed out by humans are intended for cavity-adopting species that typically nest in old woodpecker cavities. Australia has a particularly high proportion of cavity adopters even though no woodpeckers are found there; the *Eucalyptus* trees that dominate the Australian landscape develop natural cavities through fungal activity on scars resulting from dropped limbs. All nuthatches are cavity adopters, and many nuthatch species use mud to narrow the entrance to a hole in a tree branch or under a flap of tree bark. True to their name, Rock Nuthatches (*Sitta neumayer*), and the closely related Persian Nuthatch (*Sitta tephronota*), nest in rock face niches rather than trees. For added protection, these nuthatches construct a large mud nest within their rock cavity (Fig. 11.19). Many other birds also use mud to modify adopted cavities, and most design the entrance so that the parents may enter and exit with ease. In most hornbill species of Africa and Asia, females use mud and feces to seal themselves inside a nest cavity and remain there for months (Box 11.03). The male is solely responsible for supplying food to the female and their nestlings through a small slit in the mud wall of the cavity opening. In some hornbill species, mother and young emerge together; in others, the female emerges after the chicks are fairly well developed—in which case the nestlings seal themselves back in while both parents continue to feed them.

Cavity adopter: a bird that does not construct its own nest cavity, but rather uses cavities created by other animals or by forces such as decay or erosion.

Some unusual birds build nests that do not fall cleanly within a single category of nest type. For example, the Rufous Hornero (*Furnarius rufus*) from South America builds a cup nest of grasses enclosed within a snail-shaped sphere of hardened mud, complete with separate entrance and egg chambers (Fig. 11.20). In central Africa, Forest Swallows (*Petrochelidon fuliginosa*) build mud retorts within tree cavities. The Common House-Martin (*Delichon urbicum*) of Eurasia builds the walls of its mud cup all the way up to an overhanging surface, incorporating the overhang as the top of its nest. The extremely small entrance presumably limits predator access.

11.3.4 Nest linings

Many, if not most, bird nests are lined with materials different than those used in constructing the outer structure. Birds use a great many kinds of materials to line their nests. A bowl of sticks is usually lined with softer materials, such as plant fibers, mammal hair, or dried grass. A tree cavity

Box 11.03 Solitary confinement: the extreme dedication of female hornbills

Many birds minimize predation risk by building nests out of reach or sight, but hornbills go to unusual lengths to modify the nest itself as an additional precaution. Hornbills occur across the tropical regions of the eastern hemisphere, from the dry thorn-scrub of the Kalahari Desert to the warm rainforests of New Guinea. All species are cavity nesters, usually within trees. Although cavities are among the safest of nest types in general, hornbills still face predators such as raptors, mongooses, cats, mustelids, and monkeys. As a result, hornbills seal the cavity hole of their nest almost completely, encasing the female inside with her eggs. The female's confinement is a voluntary one: she initially fills the hole with mud and finishes sealing from within, using feces and leftover bits of uneaten food, leaving only a tiny vertical slit in the cavity opening that is just large enough for the male to pass food through (Fig. 11.B3.01). Both mother and chicks eject their feces out of this slit as well. The female relies completely on the male to deliver food through laying, incubation, and chick rearing—she even molts her flight feathers while inside the cavity.

Female hornbills lay eggs at variable time intervals, ranging from 1 to 6 days. Because incubation begins with the first egg, the chicks hatch asynchronously. This creates quite a size disparity among the nestlings, and the smallest young commonly die of starvation. Females of the smallest and largest hornbill species emerge when their chicks are about one-third to half grown, but in most hornbill species the female remains in the nest with the young until they are ready to fledge. When the female emerges, she hammers at the nest slit to enlarge the opening and squeezes out of the nest, first with her head, then one wing at a time, and finally the rest of her body. In species where the chicks remain in the cavity a bit longer, one of the larger chicks will reseal the slit after the mother's departure. As each chick reaches fledging age and breaks out of the nest, the younger remaining chicks re-close the opening.

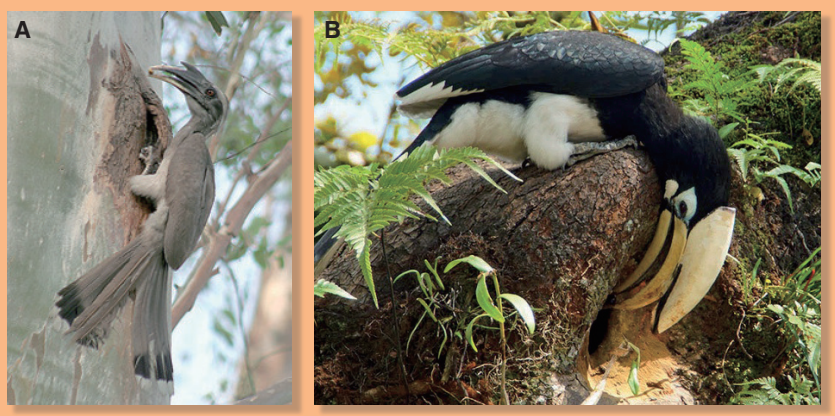


Fig. 11.B3.01 Hornbill nesting biology. Female hornbills use mud and feces to wall themselves inside their nesting cavity for most or all of the nesting cycle. Here, a female (A) Indian Grey Hornbill (*Ocyceros birostris*) and a female (B) Oriental Pied Hornbill (*Anthracoceros albirostris*) are being fed by their mates through small holes in the walls of their nesting chambers. (Photographs by: A, J. M. Garg, https://commons.wikimedia.org/wiki/File:Indian_Grey_Hornbill_I_IMG_4051.jpg. CC-BY-SA 3.0; B, Ng Chan Chiew.)

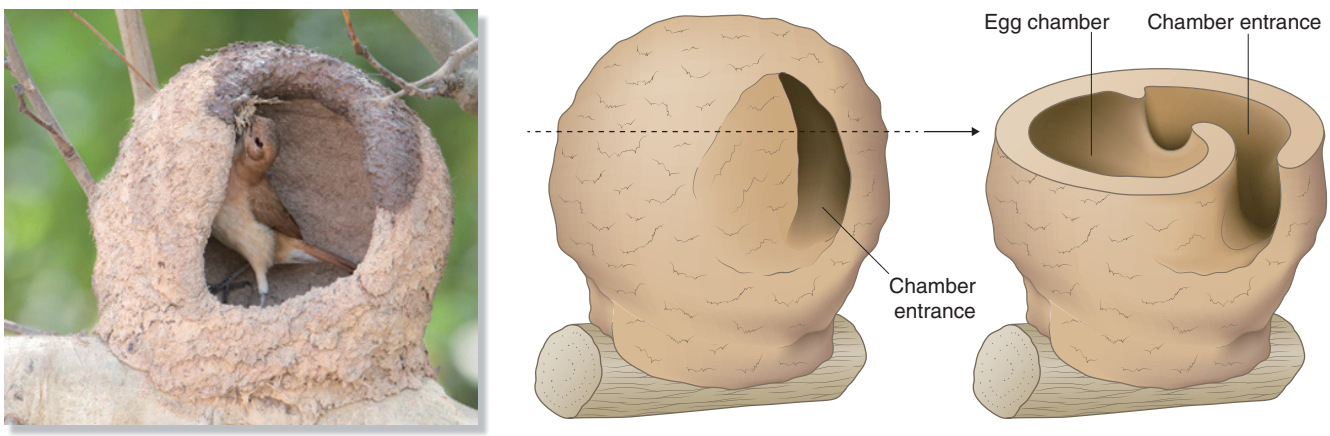


Fig. 11.20 A Rufous Hornero (*Furnarius rufus*) nest under construction. This species builds a cup nest of grasses enclosed in a statant sphere of hardened mud, creating a separate entrance and egg chambers. These nests often harden to the consistently of cement; they generally last for many years and are sometimes occupied by cavity-adopting species in subsequent years. (Photograph by David W. Winkler. Illustration © Cornell Lab of Ornithology.)

may have fur, bark strips, moss, or feathers covering the bottom. The likely primary function of most nest linings is to help insulate the nest and its living contents and prevent chicks from getting tangled in the coarser outer nest materials.



Fig. 11.21 Nest lining with fungus fibers. (A) Horse-hair fungus is one of the most common nest lining materials worldwide. (B) For example, Bicknell's Thrush (*Catharus bicknelli*) nests are often lined with filaments of this fungus. (Photographs by K. P. McFarland, Vermont Center for Ecostudies.)

Many species line their nests with various combinations of natural materials. Most thrushes build a nest of twigs, grass, and leaves cemented together with mud and lined with soft, fine grasses. The Song Thrush (*Turdus philomelos*) of Eurasia forms the mud portion of its nest into a hard, smooth lining—sometimes using rotten wood, dung, or peat. Most of the wood-warblers of the New World line their nests with fine dried grasses, but the Worm-eating Warbler (*Helmitheros vermivorum*) of North America lines its nest with the spore capsule stalks of hair moss (Vitz et al. 2013). A surprising number of bird species worldwide line their nests with thin, hair-like fungus fibers (Fig. 11.21): one survey found filaments of horse-hair fungus (*Marasmius*) in the nests of 98 bird species, spanning 27 families throughout tropical and nearctic regions (Aubrecht et al. 2013). Some previous reports citing the use of "animal hair" in nests likely mistook horse-hair fungus as real animal hair—an easy mistake, given how closely they resemble one another (McFarland and Rimmer 1996).

Many birds also use feathers to line their nests. Most female waterfowl line their nests with down plucked from their own breasts, while several songbird species line their nests with feathers that are not their own. The Long-tailed Tits (*Aegithalos caudatus*) of Europe could be considered the champions of feather collecting, often lining their oval nests with between 1000 and 2000 feathers (Fig. 11.22).

A variety of species, ranging from raptors to starlings, line or adorn their nests with green plant material. Early biologists, failing to see a function for this "decoration," wondered if these birds simply might be expressing an aesthetic sense. However, research on European Starlings (*Sturnus vulgaris*) suggests that the green plants used as nest lining contain chemicals that repel or kill avian ectoparasites (Wimburger 1984; Clark and Mason 1988). Subsequent research on Spotless Starlings (*Sturnus unicolor*) suggests that the compounds in these plants may affect the hormones of the attending female, and perhaps even the sex ratio of the offspring reared in the nest (Polo et al. 2010).



Fig. 11.22 Feather nest lining. (A) This Long-tailed Tit (*Aegithalos caudatus*) has collected the feather of another species to line its nest. (B) A nest of this species has been torn open by a predator, revealing the great number of feathers incorporated into its lining. (Photographs by: A, R. Zap; B, Ros Wood, LRPS.)



Fig. 11.23 The stitchwork nest of the Common Tailorbird (*Orthotomus sutorius*). This bird builds a cup nest within a "cradle" of one or more large leaves, which it sews together using pliable grasses, cobwebs, or silk. In the left photo, note how the bird stitches through the leaf, much as a person using a sewing needle would stitch through a piece of cloth. (Photographs by: left, Anton Croos, http://commons.wikimedia.org/wiki/File:Nest_of_tailorbird.jpg. CC-BY-SA 3.0; right, Adityamadhav83, http://commons.wikimedia.org/wiki/File:(Orthotomus_sutorius)_Common_Tailorbird_nests_at_Madhurawada_04.JPG. CC-BY-SA 3.0.)

11.4 Nest-building behaviors

Nest-building behaviors vary based on the complexity of the nest structure, the availability of materials, and the number of birds involved in the construction of the nest. Clearly some nest types involve more investment and skill to construct than do others. For example, scrape nesters probably spend much more time locating a suitable site than in forming the simple nest depression itself.

When building platform nests, most birds lay a foundation of coarse sticks across branches or another supporting substrate, then add additional sticks until the bulk of the platform is built, and finish with finer sticks and a lining, if any. Building a cup nest often requires more specialized techniques. As in platform construction, birds often start with coarse material for the nest foundation, adding finer materials as they work upward and inward toward the cup. To pack and solidify the nest, the building bird may sit and turn in the center, thrusting its legs and pressing its breast against the surrounding materials. Once the cup is coherent and strong, the bird will often add lining—either by packing it down via continued breast lunges, body rotations, and belly quivers, or by using its bill to weave the lining into existing materials. The aptly named Common Tailorbird (*Orthotomus sutorius*) of Southeast Asia adds an extra step at the beginning of this process by sewing a funnel-shaped cradle, and then building its soft cup nest inside, under its cover: first, it pierces a series of small holes near the edges of two large, living leaves. Then, it inserts plant fibers, cobwebs, or cocoon silk through the holes and draws the leaves together (Fig. 11.23).

Pendulous cup nesters exhibit even more intricate building behaviors. With incredible dexterity, these avian weavers often hold onto structural material with their feet, using their bills to weave strands together and form knots. These expert builders flit their heads back and forth, over and under, meticulously positioning supple fibers—usually freshly gathered grass or other green and pliant plant fibers—into a pendent formation. As the fibers dry, the nest walls solidify with considerable integrity and tensile strength. The globular and retort nests of African weavers are created using perhaps the most impressive and elaborate of all avian weaving techniques. These birds use a variety of knots in their constructions, producing nests of remarkable durability and unrivaled intricacy (Fig. 11.24). The orioles and oropendolas of the western hemisphere—quite distant relatives of the African weavers—use most of the same knots (Heath and Hansell 2002).

Mud-nesting birds also employ a great variety of construction methods. The most common technique involves dipping dried vegetation into mud before applying it to the inner nest layers. Many species incorporate mud in this way. Certain swallow species represent the only birds that build adherent nests solely of pure mud (Fig. 11.25). Selecting the right consistency of mud to meet the extraordinary engineering demands of these nests must require considerable discernment.

11.4.1 Sex roles in nest building

Males and females play various roles in nest construction, depending on the species. However, responsibilities tend to be fairly consistent within certain groups. For example, in hummingbirds and most other lekking avian groups in which there is strong sexual selection on males (Chapters 3 and 9), the female builds the nest entirely on her own. The opposite is true for polyandrous species, such as phalaropes and jacanas, in which the male builds the nest. In many sexually dimorphic species with brighter males, the female often assumes responsibility for most of the nest

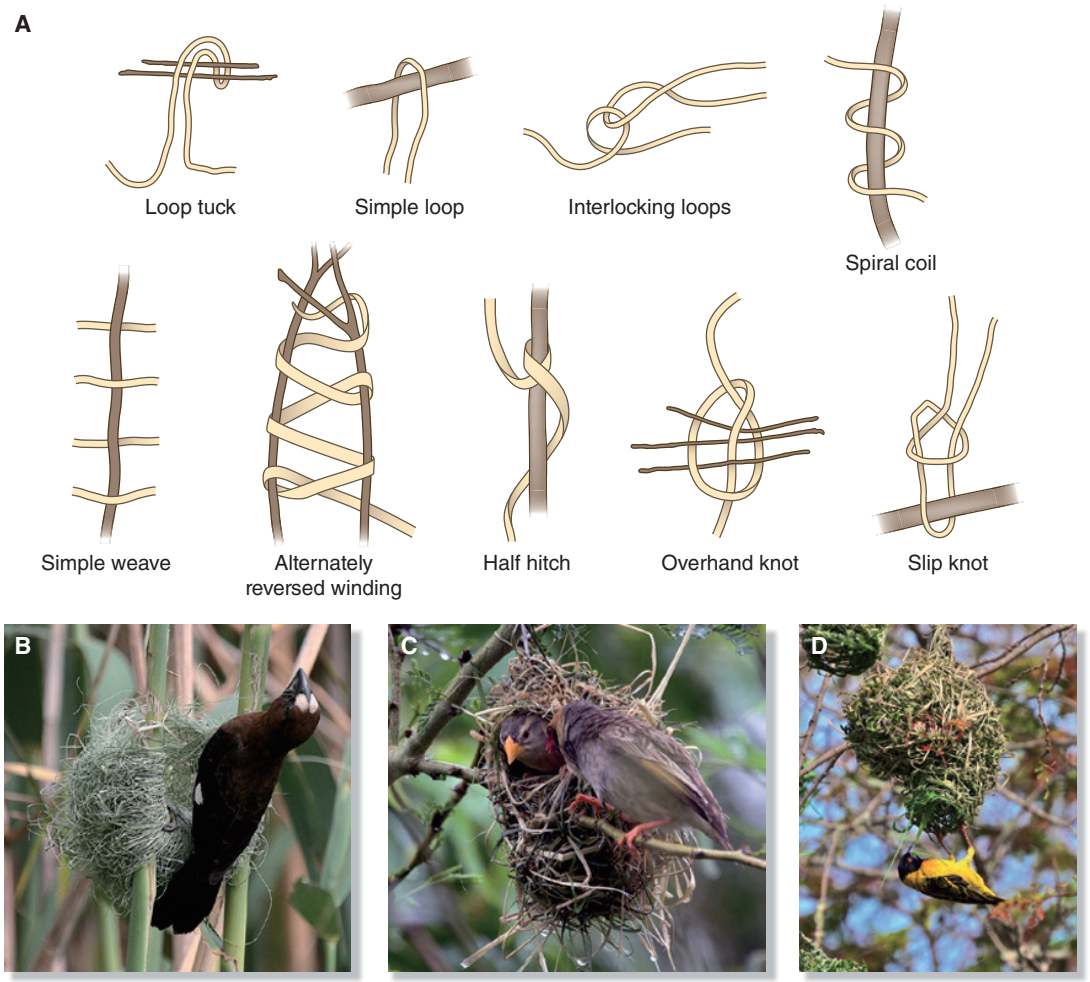


Fig. 11.24 Avian weaving techniques. (A) African weavers employ a variety of patterns and knots during nest construction. (B) The Grosbeak Weaver (*Amblyospiza albifrons*) constructs its nest with simple loops and tucks. (C) Red-billed Queleas (*Quelea quelea*) use spiral coils in their crudely woven nests. (D) The Village Weaver (*Ploceus cucullatus*) uses more sophisticated stitches, including alternately reversed winding, simple weaves, and half hitches. Overhand and slip knots are even more complex. (A, from Collias and Collias 1964. Courtesy of Karen Collias Whilden. Photographs by: B, Robert Lewis; C, Susan Knodle; D, Alexander Yates.)



Fig. 11.25 Mud nests. Cliff Swallows (*Petrochelidon pyrrhonota*) transport mouthfuls of mud to build and attach their nests to walls and cliffs. Most other mud-nesting birds use a combination of mud and vegetation. (Photographs by: left, Cameron Rognan; right, Mike's Birds, https://commons.wikimedia.org/wiki/File:Cliff_Swallow_building_a_nest_(4737045414).jpg. CC-BY-SA 2.0.)

construction, perhaps because her duller colors help avoid detection of the nest location by predators. When the male and female are similar in appearance, they often each take a nearly equal share in nest building—as in many gulls, corvids, and herons. In these species, the male may gather most of the material while the female builds the nest. In other birds, males take the lead in nest building and the female then adds the lining when the nest is finished.

Many male wrens, and some raptors and weavers, construct surplus nests on their territories. Although the function of these extra nests is open to debate, they may allow rapid re-nesting if a first nest is lost to predators or competitors. Extra nests may also help attract females: a study of Eurasian Wrens (*Troglodytes troglodytes*) in the UK showed that the more nests a male had on his territory, the more likely he was to obtain multiple mates—a few such males with multiple nests attracted as many as five females (Evans and Burn 1996). In other species, females evaluate males based on the craftsmanship of their nests. Red-billed Queleas (*Quelea quelea*) establish nests and pairs at about the same time, forming enormous colonies very rapidly. To attract a mate, a male builds the first half of a nest and displays from it; if a female deems the half-nest worthy, the pair builds the rest together.

11.4.2 Duration of nest building

The amount of time required for nest building depends on the type of nest (more elaborate nests take longer), the stage of the breeding season (construction often takes less time as the season progresses), and the weather (rain and snow often cause delays). A songbird in a temperate zone typically spends about 6 days building its simple cup nest—3 days on the outer layer and 3 days on the lining. With shorter breeding seasons, temperate birds must generally build faster than their counterparts in the tropics. For example, a tiny antwren in Panama may spend 10–15 days to build a comparable cup nest. Great Kiskadees (*Pitangus sulphuratus*), a type of neotropical flycatcher, build bulky, domed nests over several weeks; Chestnut-headed Oropendolas (*Psarocolius wagleri*) require about a month to construct their long, pendulous nests. While building a nest, birds also forage, familiarize themselves with their territory and/or mate, and interact with neighbors. Hamerkop (*Scopus umbretta*) pairs can build their enormous nests in as little as 20–25 days, but they typically spend only a few hours intensively nest building on each of those days (Wilson and Wilson 1986).

11.4.3 Nest appropriation and reuse

Most birds construct a new nest every year, especially if a previous nest supported young all the way through to fledging. After a single use, constructed nests often become flattened and misshapen. Used nests may also be littered with feces, uneaten food, the debris of nestling feather sheaths, and perhaps even the carcass of a chick that did not survive to fledging. These components produce odors that might attract nest predators; used nests also support a wealth of bacteria and invertebrates, some helpful and others harmful. Even most woodpeckers, whose cavities take much effort to excavate, usually create new nests every year. However, starting from scratch each year is not a universal rule; for example, raptors and other large birds with exposed nests may reuse them for generations, and many seabirds will return to the same rock ledge or burrow for their entire lifetimes.

Reusing old nests must provide an advantage for some birds, because many species appropriate the used nests of other species. For example, small gulls and some sandpipers that nest in northern boreal forests appropriate the old nests of landbirds in small spruce trees. Great Horned Owls (*Bubo virginianus*) of North and South America often adopt large nests of other species such as hawks, crows, or even squirrels. The large, thorny nests of South American thornbirds (Fig. 11.26) are known to be re-used by at least 11 other bird species (Lindell 1996). Sometimes an old nest is simply used as a physical support for a new nest: in North and Central America, Mourning Doves (*Zenaida macroura*) may place their flimsy stick nests on almost any elevated support, including the old nests of robins, grackles, or thrashers. The Little Swift (*Apus affinis*) of Africa adopts old mud retorts originally constructed by swallows, often affixing white feather "decorations" around the entrance.



Fig. 11.26 The well-defended nest of the Chestnut-backed Thornbird (*Phacellodomus dorsalis*). Thornbirds build large globular nests out of sticks; later, these nests are often reused by other species. (Photograph by Fabrice Schmitt.)

11.5 Eggs

Birds are the only major vertebrate group without at least one live-bearing species: fish, amphibians, reptiles, and mammals each include at least a few live-bearing species. Exactly why no live-bearing birds have evolved remains a bit of a mystery, but one compelling idea is that bearing live young would weigh down the female bird throughout gestation, and thereby either hinder her flight ability or limit her brood size. However, the fact that female bats successfully bear live young while flying competently through their entire pregnancy presents an argument against this hypothesis. Laying external eggs also allows both avian parents to at least potentially aid in their care, as well as the opportunity to abandon the eggs if conditions or circumstances are adverse—thus providing a chance for the parents to survive and rear broods in the future.

All avian eggs have the primary function of protecting the embryo inside as it develops. Yet the eggs of various bird species differ extensively in size and shape, shell coloration and structure, and the relative proportions of albumen and yolk. From the smooth white of some domestic chicken (*Gallus gallus*) eggs to the granulated, avocado-like capsule of the Emu (*Dromaius novaehollandiae*), bird eggs present a dazzling array of diversity. The study of egg diversity is a specialized branch of ornithology termed oölogy (Chapter 13).

11.5.1 Egg structure

The eggs of fish and most amphibians can survive only in water, tying these animals to an existence dependent upon aquatic environments. Bird eggs, in contrast, are able to retain their aqueous contents and develop on dry land across a great range of environmental conditions. Ancestral archosaurs (Chapter 2) first evolved a hard-shelled egg with internal membranes. Because their eggs contained the watery medium required by embryos to develop, these animals no longer needed to live in or near water; thus began the long evolution of one large branch of land animals, including birds.

Bird eggs are large, especially when compared with shell-less human eggs, which are about the size of the period at the end of this sentence. The only mammals with eggs at all similar to birds are the monotremes—the four species of echidnas (spiny anteaters) and the Platypus (*Ornithorhynchus anatinus*)—that lay soft, leathery eggs instead of giving birth to live young. Embryos contained within the large external eggs of birds, reptiles, and monotremes must be entirely resource-independent during early development—unlike all other mammals, whose mothers internally provide sustenance to the embryo. Thus, a bird egg must be packed with all of the protein, carbohydrates, fats, and water that the embryo will need until it hatches.

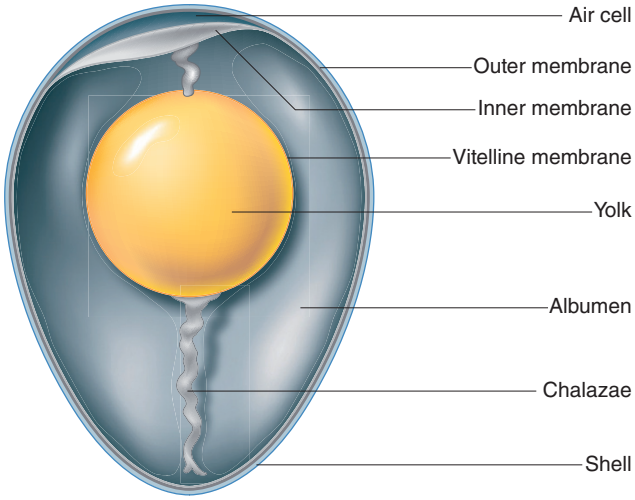


Fig. 11.27 Basic egg anatomy. This cross-section schematic shows some of the major internal components of an avian egg. (Illustration by Andrew Leach © Cornell Lab of Ornithology.)

One way to understand the structure of an egg is to follow it through the developmental process (Chapter 6). Initially, the ovum is pushed out of its surrounding follicle cells in the ovary, and it is generally fertilized by a sperm as it begins its journey across the infundibulum into the oviduct. As the egg moves down through the oviduct, it passes through a succession of glandular cells that secrete successive layers of albumen and shell membranes; the shell is added last, very near the terminus of the oviduct. Because not one of these added layers involves the addition of new cells with their own nuclei, the egg of an Ostrich (*Struthio camelus*)—with its single nucleus protected by layers of non-cellular material—is one of the largest living cells we can observe today.

To acquaint yourself with the major features of an egg, envision or explore a chicken egg from your kitchen (Fig. 11.27). As you crack a chicken egg, notice how a thin membrane holds the brittle mineral shell together, adhering to its inner surface, somewhat akin to the layers of auto safety glass. This membrane sticks tightly to the shell. Another membrane surrounds the **albumen**, or egg white; this layer can be frustrating to peel off a hard-boiled egg. Once you have broken through these two outer membranes, you are able to spill the contents of the egg into a bowl; you can see the yolk surrounded by the white, now released from its membrane. Although difficult to see, the yolk itself is surrounded and held together

Albumen: commonly known as "egg white," the clear regions of a freshly laid egg that are comprised primarily of water and protein.

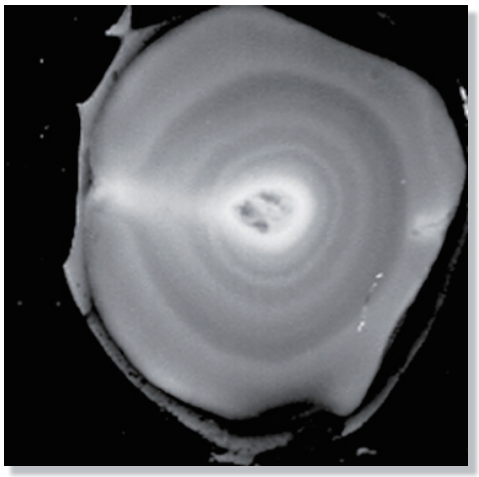


Fig. 11.28 Yolk rings. Over the course of several days, the yolk is deposited within the vitelline membrane in alternating bands of darker and lighter color. In this cross-section image through a yolk, the paler band cutting across the rings terminates at the germinal spot on the yolk surface, where the embryo will eventually develop. (Photograph by David W. Winkler.)

by the **vitelline membrane**; this membrane is what you rupture if you "break" a yolk. You may notice that the yolk rotates so that a circular, white spot on its surface is upward in the dish. This tissue, termed the **blastoderm**, would develop into the embryo if the egg were fertilized. If you ever have tried to separate a yolk from the white of a broken egg, you have encountered the gelatinous, stringy parts of the albumen that often are twisted and milky white in color. Hard to separate from the yolk, these tissues are the **chalazae**. Before the egg was cracked open, the chalazae were connected to the inner face of the shell at the distant ends of the egg, thus suspending the yolk in the center of the albumen, protecting it and holding it in place within the egg.

Now we will consider the structure and function of each component in greater detail, beginning with the yolk. The yolk contains all of the lipids (fats) and most of the protein needed to nourish the developing embryo until it hatches. The relative sizes of the yolk and white vary among groups of birds: yolks tend to make up a larger proportion of the total egg mass in species with precocial chicks, which are very well developed at hatching (such as waterfowl, shorebirds, and pheasants), compared to species with altricial young (such as passerines) in which the yolks are smaller. This difference arises from the fact that precocial chicks usually develop in the egg for a longer period of time and therefore require more sustenance, and thus a larger yolk.

The yolk is the first part of the egg produced by the laying female. Before the yolk passes down the oviduct for the addition of albumen and shell, it undergoes rapid growth over a period of about 5 days to 2 weeks. However, many birds—especially songbirds—usually lay one egg per day (and never more). Because yolk preparation requires more than a day, females often prepare yolks in enough ova for a complete clutch before laying their first egg. During this preparation period—sometimes called the "yolking up" stage—the yolk is deposited within the vitelline membrane in alternating bands of darker and lighter yolk, producing a structure that resembles growth rings in a tree when viewed under special laboratory conditions (Fig. 11.28). Because these bands alternate on a daily cycle (dark bands are deposited during the day, when the female ingests food rich in pigments), the yolk ring structure reveals how long each female needs to prepare its yolks for laying. The only structure that interrupts these concentric rings is a cylinder of light-colored yolk that stretches from the yolk's core to its surface, where the **germinal spot** sits. The embryo will develop here, beginning as the flattened disk-like blastoderm. Since the germinal spot and its column are lighter than the rest of the yolk, the developing embryo always floats to the top, no matter which way the egg is turned.

The yolk would float up against the shell if the chalazae did not suspend it at the center of the egg. The albumen, which varies in viscosity depending on the proportion of water and protein within it, consists of a series of layers around the yolk. A very thin layer of viscous albumen surrounds the yolk and extends into the chalazae, followed by a thin layer of watery albumen, a thick layer of more viscous and variably fibrous albumen (the largest component), and finally a thin layer of watery albumen right beneath the shell. In addition to providing nearly all of the water and much of the protein for the developing embryo, these layers of albumen serve admirably to protect the embryo from physical damage, provided the shell is not broken.

The shell is the developing embryo's outer line of defense (Fig. 11.29). Avian eggshells are much thicker and stronger than the shells of other egg-laying vertebrates. However, this increased thickness renders gas exchange across the shell more difficult. The growth and respiration of a developing embryo require oxygen and produce carbon dioxide.

Vitelline membrane: the transparent membrane that surrounds the yolk.

Blastoderm: a flattened disk of dividing cells that lies on the upper surface of the yolk in the first stages of the developing avian embryo.

Chalazae: the gelatinous, stringy coils of albumen that surround and protect the egg yolk and that suspend it in the middle of the egg.

Germinal spot: the site on the egg yolk where the embryo will develop; it sits atop a cylinder of light-colored yolk that runs from the yolk's core to its surface.

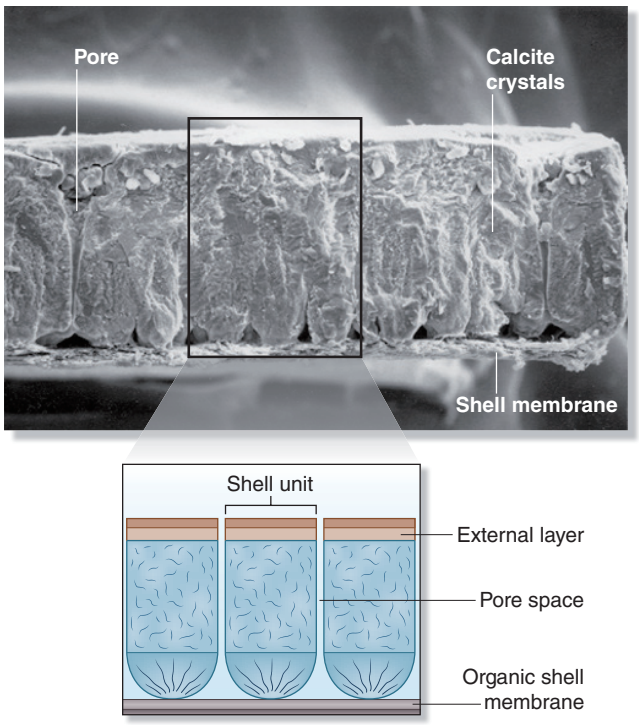


Fig. 11.29 Eggshell composition. This micrograph of an eggshell, paired with an enlarged schematic, shows the location of pores and the internal shell membrane. (Micrograph courtesy of University of Colorado Museum of Natural History Paleontology Eggshell Collection UCM # HEC 563-C; illustration by Shaena Montanari.)

The egg cannot contain all of the oxygen needed to fuel the embryo's metabolism, nor can it hold all of the carbon dioxide and wastewater produced by the embryo before it hatches. Therefore, the developing embryo must be able to "breathe" through pores in its shell. An egg loses, on average, 18% of its mass between laying and hatching (Rahn and Ar 1974), mostly from water loss across the shell.

The eggshell's porosity also can put the embryo at risk. Pollutants such as oil can enter the egg and poison the embryo or coat the egg's surface, cutting off gas exchange. Over 90% of Mallard (*Anas platyrhynchos*) embryos died when their eggshells were exposed to only one-tenth of a drop of crude oil (Hoffman 1978).

If you were to open a fertile chicken egg at an advanced stage of embryonic development, the entire inner surface of the shell would be covered with a membrane engorged with blood vessels that facilitate gas exchange. This **chorioallantoic membrane** (Fig. 11.30) is formed by the fusion of two embryonic sacs, the **chorion** and the **allantois**, which are both connected to the core inner organs of the developing embryo—very much analogous to a human embryo's connection to its mother's placenta via the umbilical cord. The chorion is the outer membrane that surrounds the entire avian embryo; it is evolutionarily homologous to the membrane of the same name in mammals, which forms much of the mammalian placenta. The allantois holds any metabolic waste that cannot evaporate through the shell, such as uric acid crystals. As a fusion of these membranes, the chorioallantoic membrane serves as the functional equivalent of the embryo's lungs throughout its development within the egg.

The chorioallantoic membrane covers more and more of the shell's inner surface as the embryo develops. In a newly laid egg, the membrane enclosing the albumen adheres directly to the membrane just below the shell—except at the blunt end of the egg, where a small air space occurs. This is the same air space you may encounter while peeling a fresh hardboiled egg. As the water within the egg evaporates through the shell or is consumed by the developing embryo, this air space between the two membranes gradually expands (Fig. 11.30). The buoyancy imparted by this growing air space is valuable to field ornithologists who need to check the developmental progress of an egg: the extent to which the egg floats or sinks when placed in water often indicates how much longer the embryo must develop before hatching.

11.5.2 Egg size

The egg of the Ostrich (*Struthio camelus*)—measuring roughly 18 by 14 centimeters and weighing about 1.4 kilograms—is the largest of any living bird. However, Ostrich eggs seem small compared with those of the extinct Elephant Bird (*Aepyornis maximus*) that roamed Madagascar until only a few hundred years ago—its eggs measured up to 37 by 24 centimeters and weighed as much as 12 kilograms. By way of comparison, at least 150 domestic chicken (*Gallus gallus*) eggs could have fit inside one Elephant Bird egg. The eggs of the smallest bird in the world, the Bee Hummingbird (*Mellisuga helenae*) of the West Indies, are

Chorioallantoic membrane: the membrane that forms during embryonic development from the fusion of the chorion and allantois. As it grows to cover the entire inner surface of the eggshell, inside the inner shell membrane, its rich blood capillaries allow the embryo to exchange oxygen and carbon dioxide through the pores of the eggshell.

Chorion: the membrane inside the egg that surrounds the entire avian embryo and the other three extra-embryonic membranes (the allantois, amnion, and yolk sac).

Allantois: a membrane inside the egg that forms a sac into which the developing embryo shunts all the metabolic wastes that cannot evaporate through the shell (such as uric acid).

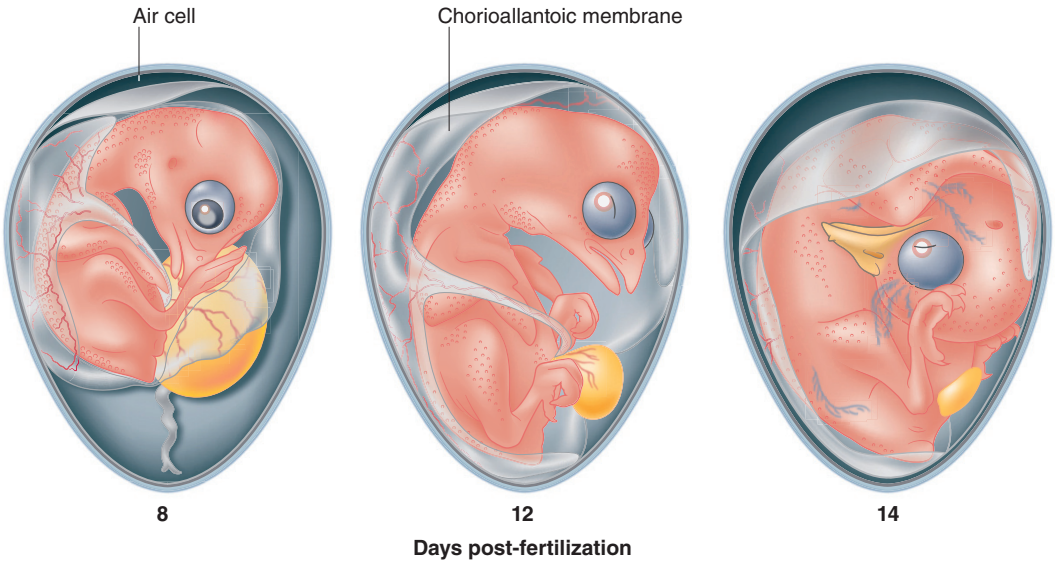


Fig. 11.30 Membrane anatomy changes as the embryo develops. Infused with blood capillaries, the chorioallantoic membrane is connected to the inner organs of this chicken (*Gallus gallus*) embryo. The air space at the top of the egg gradually expands as water content decreases via consumption by the embryo and evaporation through the permeable shell. (Illustration by Andrew Leach © Cornell Lab of Ornithology, adapted from Murray et al. 2013.)

only 10–13 millimeters in length and weigh less than 1 gram; approximately 75 of these hummingbird eggs could fit inside one large chicken egg (Fig. 11.31).

As a general rule, larger birds tend to lay larger eggs. However, when comparing egg size with adult body size, the eggs of larger species are proportionally quite small: an Ostrich egg is only 1.7% of the weight of an adult female Ostrich, whereas a wren's egg is 13% of the female's weight. The kiwis of New Zealand lay the largest eggs by relative size, with single eggs that are 25% of the female's body weight. Not surprisingly, female kiwis generally only lay one egg per season, although on very rare occasions they may lay up to three. Conversely, some brood parasites—the Common Cuckoo (*Cuculus canorus*) of Eurasia, for example—lay very small eggs relative to their body size. This may be advantageous for multiple reasons: smaller eggs may more closely resemble those of their hosts; it may increase the likelihood that the parasitic chick hatches first, since larger eggs usually take longer to develop; and it may enable brood parasites to lay more eggs per season, increasing the likelihood that some of their young will hatch and survive.

Egg size also varies among birds in other ways. In general, birds that lay large clutches generally produce small eggs relative to their body size. During their first nesting attempts, females of many species lay eggs that are smaller than those of more experienced breeders. The eggs of precocial birds tend to be larger than altricial ones, even when the adults are similar in size. For example, adult cranes and eagles weigh about the same, but the eggs of cranes, which have precocial young, are about 4% of the adult female's body weight, whereas the altricial eggs of eagles are about 2.8% of the adult's weight.

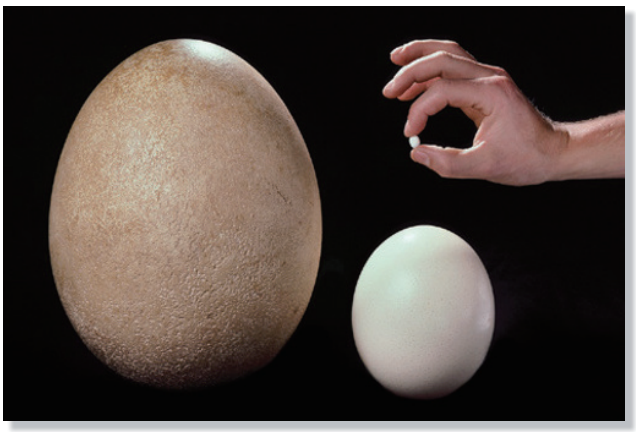


Fig. 11.31 Egg size extremes. The largest egg shown here is from the recently extinct Elephant Bird (*Aepyornis maximus*). To its right is an Ostrich (*Struthio camelus*) egg, the largest of all bird species living today. The tiny white egg is from the smallest of living birds, the Bee Hummingbird (*Mellisuga helenae*). (© Frans Lanting, www.lanting.com.)

11.5.3 Egg shape

Although bird eggs are usually approximately oval, their shapes vary from long and pyriform (pear-shaped) in some species to nearly spherical in others. The diameter and muscular tension of the oviduct during eggshell formation

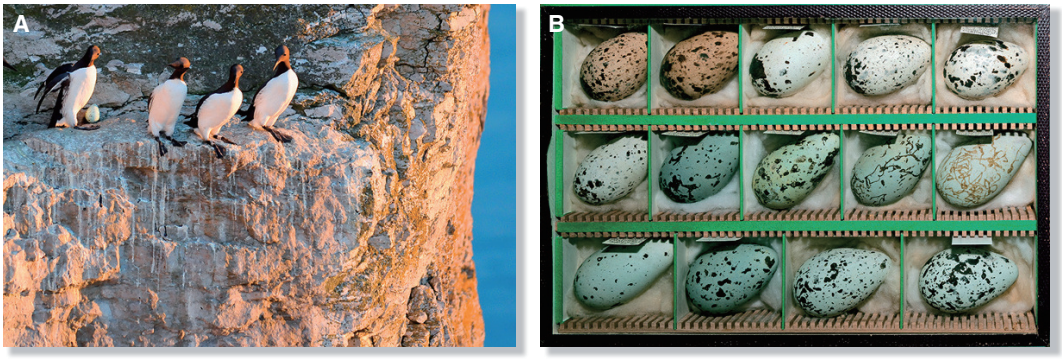


Fig. 11.32 Eggs of cliff-nesting murres. (A) Common Murres (*Uria aalge*) nest close together on precarious cliff ledges and lay eggs that are sharply tapered, a shape that serves as a safeguard against rolling off narrow ledges. (B) Murre eggs are also remarkably variable in color and pattern, which may be an adaptation that helps parent murres recognize their own eggs in a tightly packed nesting environment. (Photographs by: A, David Thyberg, Shutterstock.com; B, Didier Descouens, http://commons.wikimedia.org/wiki/File:Uria_aalge_MHNT_Box_Rouzic.jpg. CC-BY-SA 4.0.)

determine the egg's shape. Oviducal dimensions and contractions have presumably evolved to match egg shape with the environmental needs of each species. Owls often lay near-spherical eggs, which may allow efficient packing within their often deep nest cavities. Murres place their single eggs directly on narrow, often slanting, ledges high above the sea. Their eggs are long, with an almost straight side; one end is remarkably pointed, the other forms an obtuse arc. This strange shape ensures that the eggs always roll in a tight circle—a distinct advantage for eggs vulnerable to rolling off perilous ledges (Fig. 11.32). All shorebird eggs also have a pointed shape, even for species nesting in flatlands where the eggs are not in danger of rolling away. This pointed shape may increase incubation efficiency: shorebirds usually lay four eggs, which fit symmetrically and compactly when the pointed ends align toward the center of the clutch. If the eggs become disheveled, the parent shorebird points them all inward again before resuming incubation. Considering that shorebirds lay large eggs in proportion to their body size, and that many nest in cold environments, efficient heat transfer from parent to eggs may be particularly important for these birds.

11.5.4 Eggshell color and texture

After the eggs of most species leave the female's shell gland, pigment glands in the walls of the oviduct deposit successive layers of color on them. The background color of the egg is usually deposited first; any spots, streaks, or other darker markings are added later. The variation in egg coloration and pattern across species is usually correlated with breeding environment. Many birds, particularly those that nest in the open, lay cryptically colored eggs to avoid detection by visual predators. In North and Central America, for example, the color and speckled markings of Killdeer (*Charadrius vociferus*) eggs, together with the small, flat stones or wood chips used to line the nest, help the nest and its contents blend into the surroundings (Fig. 11.33). In the tropics, Chilean Tinamous (*Nothoprocta perdicaria*) lay glossy, chocolate-colored eggs with a purple hue; cassowaries of Australia and New Guinea lay pitted, avocado-colored eggs. Although striking when seen out of context, these colors actually blend in quite well in their nests on the forest floor.

Colorful eggs do not always provide camouflage, however. Although tinamou eggs are among the most beautiful in the world (they are shiny and come in many colors), those of some tinamou species do not blend in well with their surroundings. For example, the Great Tinamou (*Tinamus major*) of Central and South America lays bright, blue-green eggs that stand out against the generally dark ground. It has been hypothesized that such conspicuous egg coloration deliberately heightens vulnerability to



Fig. 11.33 Well-camouflaged eggs. Killdeers (*Charadrius vociferus*) and other birds that nest in the open often lay eggs with colors and patterns that blend in with the surroundings. (Photograph by William Sproul Sweet.)

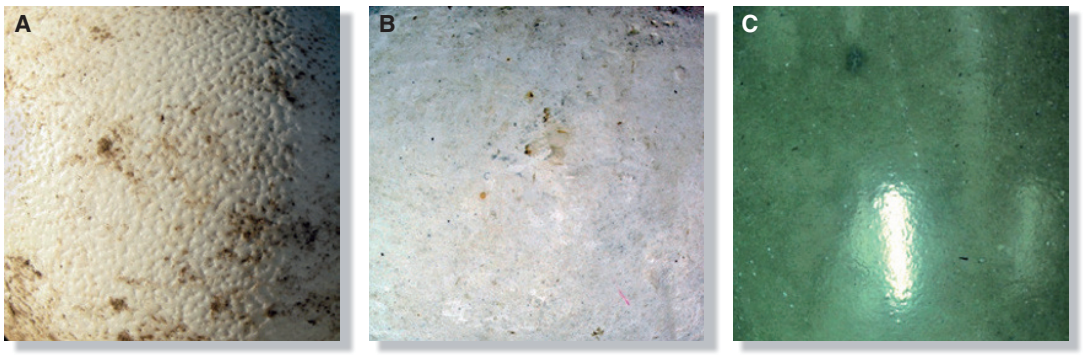


Fig. 11.34 Variation in egg texture. Although most avian eggshells are smooth, some species lay eggs with (A) pitted, (B) chalky, or (C) glossy surfaces. (Photographs by: A, Paul André Betancourt; B, Klaus Rassinger and Gerhard Cammerer, Museum Wiesbaden, https://commons.wikimedia.org/wiki/File:Phoenicopterus_roseus_MWNH_0940.JPG. CC-BY-SA 3.0; C, Klaus Rassinger and Gerhard Cammerer, Museum Wiesbaden, https://commons.wikimedia.org/wiki/File:Tinamus_major_MWNH_0076.JPG. CC BY-SA 3.0.)

predation or brood parasitism in order to incentivize the male to incubate more attentively. Alternatively, vibrant egg coloration may have evolved to provide benefits to the developing embryo, possibly involving protection from ultraviolet radiation, mediation of photoperiodic synchronization, or antimicrobial defense.

Some birds lay white eggs without any other markings. These species generally nest in dark holes (such as petrels, kingfishers, and woodpeckers), begin incubation with the first egg (such as hawks and owls), or cover their eggs when they leave the nest (such as grebes and some ducks). Because these eggs are hidden from predators hunting by sight, they do not need colors for camouflage. Additionally, pigments may be metabolically expensive to produce or may require dietary precursors that are hard to obtain. For hole-nesting birds, the white color may provide the added advantage of helping the eggs be more visible to the parents in their dark setting.

Egg coloration and markings are fairly consistent in most bird species. However, there are a few species in which egg color varies considerably—even dramatically—among individuals. Individual Common Murres (*Uria aalge*), for example, may produce eggs that are deep blue-green, bright pinkish, warm ocher, pale blue, cream, or white; their egg patterns vary from blotches to lines, with splashes of light yellow-brown, bright red, dark brown, or black, to no markings whatsoever (Figure 11.32). This variation may help each murre to recognize its own egg among dozens of others within their densely packed breeding colonies. Similarly, the females of several species of African weavers lay eggs in a great variety of colors and spot patterns. This variety seems to facilitate discrimination among a female's own eggs and those of another of her own species (Jackson 1992) or a brood parasite, such as a cuckoo (Lahti and Lahti 2002).

Bird eggs also vary in texture. Most eggshells have a smooth, matte finish like that of a chicken egg, but there are numerous exceptions. Cassowary and stork eggs are deeply pitted (Fig. 11.34A); grebe and flamingo eggs are chalky (Fig. 11.34B); tinamou eggs are glossy, resembling glazed porcelain (Fig. 11.34C). The greasy surface of most duck and goose eggs may be water resistant. The eggs of the Greater Ani (*Crotophaga major*) of the neotropics have a chalky white covering that abrades away during incubation to reveal a deep blue color underneath (Fig. 11.35). Anis live in groups in which multiple females lay and incubate eggs in a communal nest, so this change in egg appearance over time provides a ready mechanism by which the incubating caregivers might recognize eggs recently laid by another group member (Riehl 2010).

11.5.5 Egg laying

Once all the membrane layers have been deposited and the shell and pigmentation are complete, the egg passes through the cloaca. Although precise laying times for most species are not known, a pattern seems to hold: the larger the egg, the longer the laying process. Brood parasites have evolved to lay their eggs remarkably quickly, before the host returns to its nest. Common Cuckoos (*Cuculus canorus*), for instance, can lay an egg in another bird's nest and disappear in less than 10 seconds (Seel 1973).

The time required for the oviduct to secrete the layers around the ovum determines the interval between laid eggs. Small shorebirds, domestic chickens, woodpeckers, rollers, and most passerines lay eggs about 24 hours apart. In contrast, birds such as ostriches, rheas, herons, storks, cranes, bustards, gulls, doves, owls, hummingbirds, swifts, kingfishers, as well as some accipiter hawks and cuckoos, generally lay eggs every other day. Larger species tend to need more time between eggs, perhaps because the secretion processes in the oviduct take longer for larger eggs. Among waterfowl, for instance, many duck species lay eggs every day, whereas large geese and swans lay every other day.



Fig. 11.35 Chalky eggs of communally nesting Anis. (A) Freshly laid Greater Ani (*Crotophaga major*) eggs appear completely white; the chalky covering abrades away during incubation to reveal a blue shell underneath. (B) Unrelated females form breeding groups and lay eggs around the same time in one communal nest, sharing incubation duties. Egg color change over time is likely an adaptation that allows incubating individuals to discern new eggs from older ones, which in turn helps them identify eggs laid by other females in the group. Based on color, the eggs in this nest have been incubated for roughly the same amount of time—except for the fresh white one, which was added more recently to the nest. (From Riehl 2010. Reproduced with permission from Elsevier.)

Parrots, even the smaller species, lay their eggs 1–3 days apart. Penguins take 3–6 days between eggs, and the Masked Booby (*Sula dactylatra*) of tropical seas worldwide lays its two eggs as much as a week apart. Species that lay very large eggs for their size also tend to need longer intervals between eggs: megapodes wait 4–8 days between eggs, whereas kiwis, in the rare event that they lay multiple eggs within a season, need 14–30 days. Most bird species appear to lay successive eggs at approximately the same time of day, usually in the early morning—although some herons, bitterns, and parrots lay at intervals that are decidedly not multiples of 24 hours.

11.6 Clutch size

A **clutch** is the total number of eggs laid in an uninterrupted series, during a single nesting period, by one female bird. In the early days of ornithology, egg collectors from all over the world amassed large collections of bird eggs (Box 13.04). Clutch size is therefore often the only core avian life history trait for which any quantitative data exist; as a result, there has been considerable interest for almost a century in trying to understand patterns of variation in clutch size. During the 1940s, David Lack at Oxford University (UK) began studies on the clutch sizes and life histories of several local bird species. Many of these studies continue to the present day, providing contributions to avian life history theory that are covered in Chapter 13.

Clutch: a complete set of eggs laid in an uninterrupted series, during a single nesting period, by one female bird.

Closely related birds tend to have clutches of similar size. For example, all tubenosed seabirds (such as albatrosses and petrels) lay a single egg, virtually all hummingbirds lay two eggs, shorebirds do not lay more than four eggs, and so forth. Most songbirds lay between two and six eggs, although some tits in Eurasia lay extraordinarily large clutches of up to 17 eggs.

11.6.1 Clutch size and food availability

Food availability may be the most important factor influencing clutch size. Among non-passerines, birds that feed their young (such as gulls and storks) tend to lay fewer eggs than those whose young forage on their own (such as pheasants, grouse, quail, megapodes, and most shorebirds and waterfowl). The availability of food for the laying female is often an important limitation; since laying an egg is energetically costly for the female—even in places with abundant resources—doing so without an adequate food supply threatens a female's survival or her subsequent reproductive efforts. Thus, even though females are still physiologically capable of laying more eggs, they often limit their egg production (and thus clutch size) when food is scarce.

The amount of available food for chicks also limits the clutch size of many species. When female birds can anticipate future food conditions at the time when they are laying eggs, they may adjust their clutch size accordingly. Owls and arctic-nesting raptors are good examples of this flexibility, as their clutch sizes vary dramatically among years with abundant versus scarce prey. For example, female Snowy Owls (*Bubo scandiacus*) breeding high in the Canadian Arctic lay 7–11 eggs in rich lemming years, and only 3–5 in low lemming years (Parmelee 1992) (Fig. 11.36).



Fig. 11.36 Clutch size flexibility. Snowy Owls (*Bubo scandiacus*) are among the many bird species that lay larger or smaller clutches depending on prey availability in a given year. (Photograph by Gerrit Vyn.)

11.6.2 Clutch size, geography, and incubation

Both within and among species, birds that nest in the tropics tend to lay smaller clutches than those at higher latitudes. For example, House Wrens (*Troglodytes aedon*) lay an average of seven eggs per clutch in Saskatchewan (Canada) but average only three and a half eggs in Costa Rica (Young 1994). This established pattern has generated a number of interesting explanations, most of which involve ecological hypotheses addressing varying resource availability or seasonality across latitudes (Chapter 13). However, other factors may partly explain this pattern. For instance, environmental temperatures during the laying period tend to be warmer for tropical species than for temperate breeders. This difference, it turns out, seems to place many tropical species in a cruel bind. In the tropics, the higher ambient temperature at the nest may induce embryos to start developing even when the eggs are not being actively incubated. Yet embryos that begin development at ambient temperatures are less likely to hatch than those incubated directly by the female at somewhat warmer and better regulated temperatures; thus, birds in the tropics may lay smaller clutches so that they can begin active incubation sooner, rather than waiting until after many eggs are laid (Stoleson and Beissinger 1999).

11.6.3 Clutch size and nest type

In general, cavity nesters lay larger clutches than birds nesting in the open. This pattern has been attributed to the lower predation rates generally experienced by cavity nesters (Slagsvold 1982). Nestlings tend to draw attention to themselves by moving around, begging for food, or simply standing out against their surroundings. Because a smaller number of young in a nest potentially lessens the risk of attracting predators, the more vulnerable open nesters raise fewer young per clutch. The young of open nesters also tend to develop faster, reducing the amount of time they are exposed to predation risk in the nest. If parents can provide only a given amount of food at a given rate, they can either use that food to rear fewer young faster, or a greater number of young more slowly. It logically follows, then, that cavity nesters have larger clutches with longer development times, and open nesters have comparatively smaller clutches with shorter development times.

11.6.4 Clutch size, female age, and time of season

Birds that produce multiple broods each season, such as Eastern Bluebirds (*Sialia sialis*) in North America and Dunnocks (*Prunella modularis*) in Europe, tend to lay small clutches early in the season, their largest clutches mid-season, and then smaller clutches again later in the season. In contrast, for single-brooded species, clutch size tends to be largest for birds laying at the beginning of the season and declines steadily for birds laying thereafter. Exactly what drives this pattern is still unclear. In some places, it seems likely that food supply declines as the season progresses, and that smaller clutches may therefore be a response to declining food for the laying female or for the forthcoming chicks. However, in other cases, a female may curtail egg production during the warmer parts of the breeding season so that she can incubate her eggs directly rather than have them develop partially under environmental temperatures. Another possibility is that earlier birds lay larger clutches because they are simply in better condition or of higher quality.

In many species, young females lay smaller clutches than older birds. Additionally, younger females often begin nesting later in the season, but even when younger and older females begin laying on the same date, the younger bird often lays a smaller clutch. There are several potential reasons for this pattern. Individual females may gradually improve in their reproductive efficiency, or they may invest more effort into reproduction later in life (Chapter 13). Alternatively, perhaps individuals themselves do not change over their lifetime: at any given time, the younger age classes may include many inferior individuals that will die relatively early and thus are selected out, whereas the older birds in the population are higher quality individuals that have been more effective at both surviving and producing offspring all along. Teasing these possibilities apart requires long-term studies of many marked individuals throughout their lifetimes. One such study on Black Kites (*Milvus migrans*) in Spain found evidence for both individual improvement and age class selection (Blas et al. 2009), but a study of Common Terns (*Sterna hirundo*) in northern

Box 11.04 Research innovations on Common Tern islands

Places where large numbers of birds breed together and can be monitored without disturbance allow ornithologists to gather very large datasets on aspects of breeding biology, as in Peter Becker's studies of Common Terns (*Sterna hirundo*) nesting on specially designed artificial islands in Wilhelmshaven (Germany). These floating islands provide the terns with nesting sites that are inaccessible to mammalian predators, safe from flooding, and surrounded by waters rich in small fish. This research team has outfitted the birds and islands with RFID (radio frequency identification) tags and recorders that detect returning adults and monitor their attendance at active nests. Some RFID recorders are even placed on artificial perch sites fitted with electronic scales that record the identity and weight of each tern that rests on them. This combination of approaches has allowed these researchers to monitor the breeding and development of the terns in great detail. For example, by tracking the weights and fates of newly fledged birds, the biologists discovered that body mass gain or loss after fledging is the best predictor of survival to breeding age (Braasch et al. 2009), whereas factors such as weight at fledging, date of hatching, or date of colony departure are less important. In other words, the survival prospects of a newly fledged tern seem best predicted by how well that bird continues to develop and grow after fledging.

Germany concluded that almost all of the perceived reproductive superiority of older females resulted from their steady improvement as they grew older (Rebke et al. 2010) (Box 11.04).

11.6.5 Number of broods per season

When comparing the clutch sizes of birds in temperate zones versus the tropics, it is important to note that most tropical species have much longer breeding seasons than species at higher latitudes. Tropical landbirds often may lay eggs over a period of four or more months (and occasionally all year long), whereas species in temperate zones typically lay within a period of less than 2 months. Arctic species lay within an even shorter timeframe—generally, less than a month. Longer breeding seasons at lower latitudes allow birds living there many more breeding attempts per season than their counterparts at higher latitudes. The same effect appears within temperate latitudes of the northern hemisphere, with birds further north laying larger clutches but fewer clutches per season, and with overall fecundity probably varying little with latitude (Böhning-Gaese et al. 2000).

11.7 Clutch and egg replacement

Most birds will replace their clutch if it is destroyed, but many single-brooded species will not re-lay if the hatched offspring are lost. The laying of a replacement clutch usually requires the female's hormonal system to cycle back into laying mode, and the rapid yolking up phase of preparing ova for ovulation must be completed—this requires 5–8 days in most passerines and longer in larger birds.

However, if only one egg is removed from the nest, birds respond in diverse ways. **Determinate layers** lay a fixed number of eggs and will not lay a replacement egg if one is removed from the clutch during the laying period, whereas **indeterminate layers** will lay replacements until the clutch reaches a particular size. Some indeterminate laying species are capable of prodigious feats: for example, the regular removal of one egg every day from the nest of a Northern Flicker (*Colaptes auratus*) in Massachusetts (USA) induced the bird to lay 71 eggs in 73 days (Phillips 1887), whereas the normal clutch size of this species is six to eight eggs. Domestic chicken (*Gallus gallus*) hens, which have been artificially selected over many hundreds of years for egg production, can lay as many as 352 eggs in 359 days. Chicken hens, like all other birds, will stop laying eggs if they are allowed to sit upon a full clutch and begin incubation.

Some species act as indeterminate layers only at a certain point in the laying process. For example, some gulls will lay replacement eggs only if the eggs are removed before the female can sit on two or more. Variation also exists in how different birds determine that a "complete" clutch has been laid; some species seem to count the eggs visually, whereas others seem to rely upon the feel of the eggs beneath them.

Determinate layer: a bird species that will not lay additional eggs if any are removed from a clutch during the laying period.

Indeterminate layer: a bird species that will lay additional replacement eggs if any are removed from its clutch during the laying period.

The propensity of many birds to replace eggs taken from the nest during the laying period may have helped save some from extinction. Wildlife biologists have been able to "double clutch" many endangered species by removing some eggs to rear in the laboratory while the birds concurrently rear their replacement eggs in the wild. This approach has been an important part of captive-breeding programs for many endangered bird populations (Chapter 15).

11.8 Incubation

All birds lay external eggs that must be kept in the proper temperature range throughout their development; this temperature is maintained by a process called **incubation**. The precise temperature necessary for embryonic development varies among bird species, but most avian embryos require temperatures close to 37 °C or 38 °C. Because few environments have constant air temperatures at or above this level, almost all bird species must provide a source of warmth for their eggs. Most species use their own body heat by sitting on top of the eggs, but two groups employ other methods: brood parasites leave the incubation of their eggs to their hosts, and megapodes provide alternative sources of heat through a broad variety of methods (Box 11.02).

In rare cases, birds must cool their eggs to keep them in the appropriate temperature range. Due to their extremely hot breeding habitats along the Gulf of Mexico, Wilson's Plovers (*Charadrius wilsonia*) dip their breast feathers in water and run over to cool their eggs with the moisture. Along sandbars of African rivers, Egyptian Plovers (*Pluvianus aegyptius*) go one step further—in addition to cooling the eggs with wet breast feathers (Fig. 11.37), adults may also bury their eggs (and later sometimes their chicks) in sand to protect them from the sun. One pair of Black-necked Stilts (*Himantopus mexicanus*) nesting in hot and arid southern California (USA) soaked their belly feathers and carried the cooling moisture back to the nest 953 times in one day (Grant 1982). Seabirds with open nests on tropical islands or coastal deserts often spend more time standing over their eggs to provide shade than they do incubating.



Fig. 11.37 Cooling eggs in hot temperatures. This Egyptian Plover (*Pluvianus aegyptius*) has soaked its breast feathers (arrow) and will use the water to cool its eggs. (© Jabruson, naturepl.com.)

11.8.1 Brood patches and brooding

A few days before a female lays the first egg of her clutch, some of the feathers on her breast and belly fall out; that bare patch of skin develops through egg laying, becoming swollen via the expansion of blood vessels and the retention of water. This area is called a **brood patch** or an incubation patch (Fig. 11.38). The brood patch can be a single large region that spans much of the area of the belly and breast, or it may consist of a few smaller, distinct bare regions separated by areas that retain their normal feathering. To incubate, birds push the adjoining feathers aside, so that bare skin rests directly on the eggs.

Most birds continue to incubate their young even after they have hatched, providing heat until the chicks have developed the feathers and metabolism necessary to control their own body temperature. This post-hatching incubation, called **brooding**, involves much less pressing of the brood patch to the chicks, since newly hatched chicks can be smothered if the parent sits too tightly. Once brooding is over, the feathers in the brood patch grow back (often before the next body molt), the blood vessels shrink to their normal size, and the swelling of the skin subsides.

11.8.2 Incubation period

The **incubation period** begins when the parents start to incubate the eggs in earnest, with one of the parents incubating most of the time and with the temperature of

Incubation: the behaviors by which parent birds keep their eggs within the temperature range for proper embryonic development.

Brood patch: a patch of skin on the breast and belly of a bird that has lost its feathers and has become swollen and vascularized to increase the efficiency of heat transfer to the eggs.

Brooding: sitting on hatched young, or sheltering them under the body or wings, to keep them warm and/or protect them from sun, rain, or predators.

Incubation period: the number of days from the start of regular incubation of the eggs until hatching.

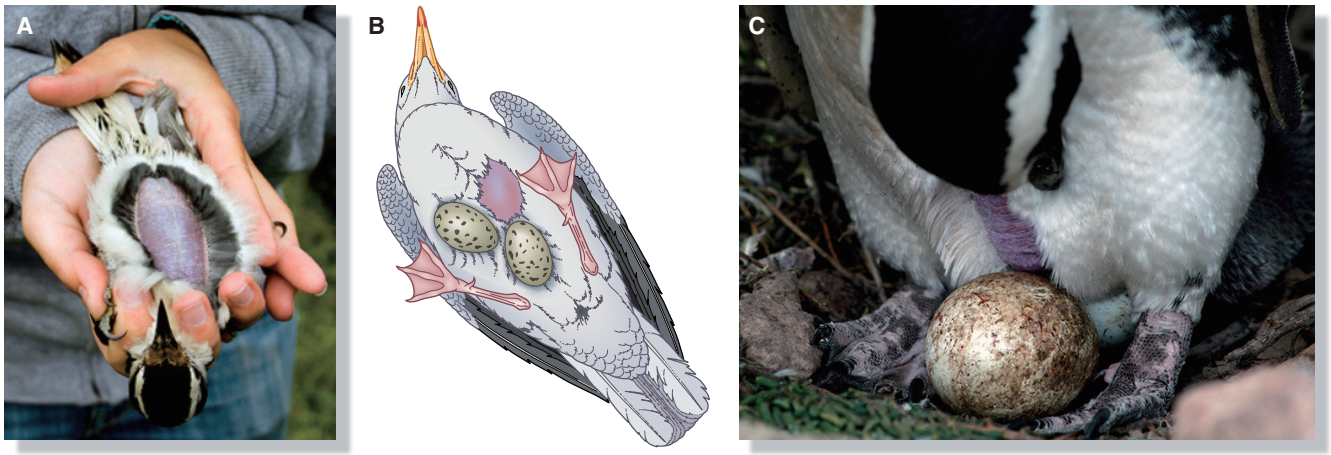


Fig. 11.38 Brood patches. (A) This Hairy Woodpecker (*Picoides villosus*) is clearly in reproductive condition: its feathers have been gently blown away from its breast to reveal a bare brood patch. Note the redness of the skin—the extensive blood supply to this area helps the parent bird warm its eggs. (B) Shorebirds and gulls often have multiple, separate brood patches associated with each egg they lay in a clutch, as shown in this drawing of a Herring Gull (*Larus argentatus*). (C) The Magellanic Penguin (*Spheniscus magellanicus*) has a pouch-like fold of bare skin on its lower abdomen that encloses, protects, and warms its egg. (Photographs by: A, Jennifer Scott Schlick; C, R. Roscoe, Photovolcanica.com. B, adapted from Proctor and Lynch 1993. Reproduced with permission from Yale University Press.)

the eggs being maintained near the optimal temperature, with only brief cooling periods. The incubation period ranges from about 11 days in some of the smaller finches to about 80 days in the larger albatrosses. Bigger eggs generally take longer to hatch. However, considerable variation exists among groups of birds; for example, hummingbird eggs take much longer to hatch (14–23 days) than might be expected from their tiny size. So do the large eggs of storm-petrels, petrels, and albatrosses: the eggs of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) are similar in size to those of the American Kestrel (*Falco sparverius*), but the incubation period of the storm-petrel (38–50 days) is considerably longer than that of the kestrel (about 30 days).

Although incubation periods are generally similar within species, they may vary somewhat from nest to nest in a population. Long bouts of inclement weather sometimes force adults to interrupt incubation to forage to ensure their own survival. After the eggs hatch, the presence of active nestlings acts as a stimulus, indicating the need for adults to switch from "incubation" to "care of the young" behavior. Without that signal, birds sometimes have a hard time knowing when to stop incubating if the clutch is defective: if all the eggs in a clutch fail to hatch, a bird may continue to incubate them for two or even three times its normal period before finally deserting them. For example, Northern Bobwhites (*Colinus virginianus*) have been known to incubate inviable eggs for as long as 75 days, considerably beyond their normal incubation period of 23–24 days.

11.8.3 Start of incubation

Different species initiate incubation at different times during the laying cycle. Some birds start to incubate after laying their first egg. Although immediate incubation helps protect the egg, this strategy ties the incubating bird to the nest site for a longer period, increasing the adult's exposure to predators. Additionally, this immediate incubation means that the embryos of the earliest laid eggs will start to develop before the later eggs are laid, resulting in staggered hatching and eventually a brood with young of different ages, a phenomenon called **asynchronous hatching**. Especially in species with large clutches, this variance in hatching dates can result in a strong hierarchy of sizes and begging abilities among the offspring. Pelicans, cormorants, herons, storks, eagles, hawks, cranes, parrots, and owls are among the birds that use this strategy of immediate incubation (Fig. 11.39).

Raising young of different sizes gives parent birds a systematic way to adjust the number of young to the amount of food available. By first feeding the most vigorously begging chick completely before moving on to another nestling, parents may help ensure that at least some

Asynchronous hatching: a pattern of hatching in which the eggs within a clutch hatch over a period of many days, rather than on or near the same day, resulting in a brood of chicks of different ages and sizes.



Fig. 11.39 Asynchronous hatching. In some species like Burrowing Owls (*Athene cunicularia*), parents begin incubation immediately after laying the first egg; nestlings hatch accordingly at different times. The resulting disparities in age and size often lead to unequal competition among them—older nestlings have an advantage, especially in breeding seasons when food is scarce. (Photograph by Jan Maguire.)

young will survive in years when food is in short supply. If food is scarce, the younger and more recently hatched nestlings, too small to beg competitively, will starve. This phenomenon is known as **brood reduction**. When food is abundant, however, parents are often able to feed all of their young, even the youngest. Despite the advantages of this strategy, relatively few species have asynchronous hatching; instead, most birds delay the onset of incubation until they lay the last or next-to-last egg. For precocial young, synchronized hatching is essential since a full nest of mobile and vocal young birds presents quite a target for predators, and most precocial broods leave the nest very soon after hatching.

11.8.4 Incubation by male and female birds

In many bird species, both members of a pair incubate. Generally, both parents share this task about equally, switching at frequent intervals, although the female most often incubates through the night. Members of a pair may perform a species-specific "greeting ceremony" when they exchange duties at the nest. These ceremonies can be spectacular among some of the large species such as albatrosses and boobies, but in most birds they are more subdued. For instance, when she hears an approach song from her mate, an incubating female Northern Cardinal (*Cardinalis cardinalis*) will sing from the nest, a seemingly counterintuitive response that could risk revealing the nest's location to predators. Her response, however, communicates information regarding whether she is hungry, and if not, the brightly colored male does not approach unnecessarily (Halkin 1997). An incubating bird usually appears more than ready to exchange incubating duties with its mate, but sometimes birds like gulls and plovers engage in pushing matches in which the relieving bird attempts to dislodge the previous incubator from the eggs.

In many other species, only one parent incubates. In groups such as ducks, geese, hummingbirds, most owls, and many passerines, the female usually is the incubating parent. Male geese and owls are fully engaged in defending or gathering food for the female while she incubates, but in the other species the male is emancipated from parental duties and spends his time seeking other breeding opportunities (Chapter 9). On the other hand, only the male incubates the eggs in a few species such as the polyandrous phalaropes and jacanas.

In species in which only a single parent incubates, the roles usually are predictable, with either the male or female always taking care of incubation. The Eurasian Penduline-Tit (*Remiz pendulinus*) is an exception. In this species, both sexes are fully capable of incubation, but only one parent generally takes on this duty at a particular nest. Apparently, both parents prefer to leave incubation to their mate in order to pursue other breeding opportunities, and therefore they engage in a serious contest. The female hides her eggs in the lining of the nest to prevent the male from discovering that she has begun laying (Fig. 11.40), because the appearance of a nearly complete clutch may tell the male that his mating opportunities in the current nesting attempt are finished and that this would be the best time for him to desert. By hiding her eggs until she is ready to abandon the nest to the male's care, the female can be the one to flee the current nest and search out another breeding opportunity elsewhere. In one well-studied Austrian population, female Eurasian Penduline-Tits ended up incubating their first clutch about 50% of the time. Although males solely incubated the clutch 20% of the time, it is also common for neither parent to incubate if the female is the one who leaves: both parents abandoned the nest altogether about 30% of the time (Valera et al. 1997).

Brood reduction: a behavior in which, during a time of limited food or other resources, a nesting bird directly or indirectly allows one or more of its eggs or nestlings to die, thereby reallocating their available resources to the remaining offspring.

11.8.5 Patterns of attentiveness

Incubating birds soon adopt a fairly regular rhythm, alternating periods on the nest (attentive periods) with periods off the nest (inattentive periods). Many birds tend to extend their attentive periods when environmental conditions are harsh, both because the eggs need extra care and because

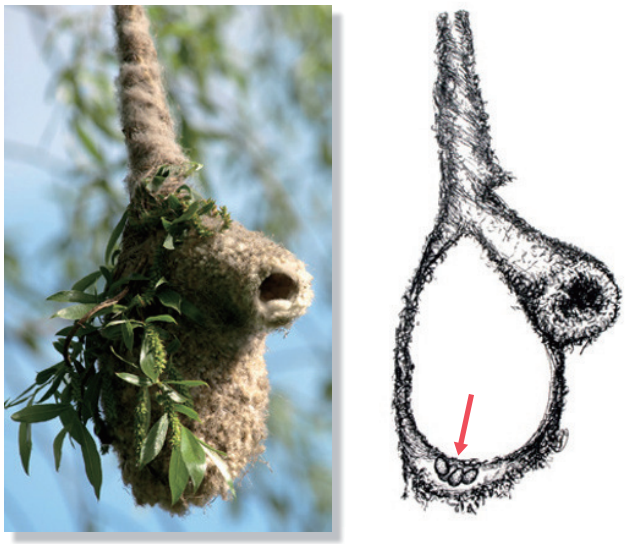


Fig. 11.40 Conflict over incubation between parents. In the Eurasian Penduline-Tit (*Remiz pendulinus*), the female and male compete to shirk incubation duties. Females often bury their eggs in the nest lining (arrow) to prevent male partners from discerning that a clutch is about to be completed—a perfect time to abandon and seek other breeding opportunities, forcing the other sex to provide sole parental care. (Photograph by Tomasz Przechlewski, http://commons.wikimedia.org/wiki/File:Remiz_pendulinis_6.jpg. CC-BY-2.5. Illustration © Cornell Lab of Ornithology.)



Fig. 11.41 Egg-turning during incubation. Many birds regularly rotate their eggs during incubation, as demonstrated by this Whooper Swan (*Cygnus cygnus*). (Photograph by Helen Haden.)

foraging is less productive. Birds tend to leave the nest when they will be able to feed efficiently and return promptly. Thus, most incubating passerines sit on the nest at the beginning and end of the day (the overnight bout usually is uninterrupted) and whenever conditions outside the nest become cooler and wetter. The male Emperor Penguin (*Aptenodytes forsteri*) endures the longest attentive period, incubating his egg through the latter half of the antarctic winter in one uninterrupted stretch of 64 days, living entirely off his stores of body fat. At the other end of the spectrum, the Karoo Prinia (*Prinia maculosa*) of southern African deserts has an incubation attentiveness of only about 49% of daylight hours (Chalfoun and Martin 2007).

Species that must forage far from their nest generally have longer attentive periods. In many pelagic seabirds such as fulmars, shearwaters, and many petrels, each parent typically incubates for 1–5 days while its mate forages far away at sea. For Northern Fulmars (*Fulmarus glacialis*) in the UK and arctic Canada, each shift of incubation can last from 1 to 14 days, depending on the distance and quality of foraging conditions (Mallory et al. 2008). Other birds have adopted unusual incubation rhythms in response to challenging environments. For example, in the high mountains of China, female Blood Pheasants (*Ithaginis cruentus*) leave their nests unattended each morning for one long period each day—usually lasting more than 6 hours—because it takes such a long time to find the mosses distinctive to their diet (Jia et al. 2010).

11.8.6 Behavior during incubation

The incubating adult usually is very quiet at the beginning of any attentive period, often seeming to doze off for long periods. As the bout wears on, the incubating bird may become more restless, changing its position, turning the eggs, or meddling with the vegetation in or around the nest. When the parent leaves or returns to the nest, it usually does so secretively and deliberately, especially if it is the only bird incubating. Ground-nesting species leaving their nest often thread their way through the nearby vegetation before flying up; species leaving elevated nests often drop nearly to the ground and fly level for a short distance before rising to their normal height.

In addition to providing warmth, parents care for their eggs in other ways. An incubating bird will sometimes raise its body slightly, reach down among the eggs with its bill, and gently turn them (Fig. 11.41). Although this turning behavior may help prevent the adhesion of embryonic membranes to the shell, embryos of species that do not turn their eggs, such as megapodes and palm-swifts, seem to suffer no adverse effects. Occasionally, ground-nesting birds such as gulls and waterfowl will retrieve their eggs if they accidentally roll out of the nest; most birds roll them back with their beaks, but adults with long bills, such as rails, may lift the eggs back into the nest.

The behavior of the incubating bird often changes as the incubation period advances. Nuthatches, usually noisy, become quiet and secretive in the vicinity of the nest. Defensive birds, such as owls, raptors, gulls, and shorebirds, become much more belligerent as hatching approaches, whereas cryptically colored birds remain on the nest for a longer period in the face of intruders. For example, American Woodcocks (*Scolopax minor*) in North America sometimes do not flush from the nest until touched. Evolutionary biologists have interpreted these behavioral changes as reflecting the increasing fitness value of the clutch as it nears hatching. Not only are more developed eggs more likely than just-laid eggs to produce fledglings, but a replacement clutch also becomes less likely to succeed as the breeding season progresses. It therefore makes evolutionary sense that birds are much more likely to abandon a breeding attempt early in the cycle than they are after the young have hatched. In extreme emergencies, however, parent birds may abandon the clutch or brood at any stage; in doing so, adults preserve their capacity to breed again by saving themselves and leaving their young to their fates. When birders and researchers observe nests, it is crucial that they keep disturbances to an absolute minimum, especially early in the nest-building cycle, and that they consider how visiting a nest at any time can leave scents or other cues that may attract or guide predators to a nest.

You may have seen a pair of raptors perform a food-exchange ceremony in which the female flies from the nest to receive food from the male in mid-air, either taking it directly from his talons or catching it as it falls. These characteristic displays have long been considered important for helping these birds establish a pair bond during courtship and maintain it throughout parental care. However, studies of many species also indicate that females who receive more food from their mates lay larger clutches. For example, in both Common Terns (*Sterna hirundo*) and Black-legged Kittiwakes (*Rissa tridactyla*), females that are fed more by their mates during their laying periods lay larger clutches (Nisbet 1977; Helfenstein et al. 2003). Providing food for a female mate most likely improves a pair's chance of raising more young: because the female does not have to spend as much time foraging, she can spend more time incubating the eggs, and eventually invest more energy into feeding the young, while staying in better condition herself.

11.9 Hatching

In preparation for hatching, bird embryos develop an **egg tooth**, a short, pointed structure on the tip of the upper beak (and sometimes on the lower beak as well) (Fig. 11.42). While in the egg, the avian embryo generally sits in a "fetal position," with its head bent forward towards its belly. When it is ready to hatch, the fully developed embryo pulls its neck back and up (often using muscles developed especially for this task), rubbing its egg tooth against the inner wall of the shell, which has already been somewhat weakened by the absorption of calcium from it by the developing embryo. Embryos of most bird species rotate in the egg while repeating this motion many times. Eventually, the chick manages to create a small hole in the eggshell, at which point the egg is **pipped**. Soon thereafter, the chick begins to puncture the shell with a series of holes—sometimes connected, sometimes not—that nearly encircle the blunt end of the egg. Once the shell is sufficiently weakened, the chick pushes off the end and struggles free, away from the egg membranes. This emergence appears to require a great deal of exertion, and immediately after they hatch most hatchlings lie quite still. Once dry, most nestlings weigh about one-third less than the fresh, whole egg from which they started. A few days after the young have fully hatched, the egg tooth sloughs off or is reabsorbed.



Fig. 11.42 Egg tooth. To break out of their shells, most bird embryos develop an egg tooth on the tip of the upper beak, visible on this newly hatched Masked Lapwing (*Vanellus miles*). The egg tooth reabsorbs or rubs off within a few days of hatching. (Photograph by Kell Nielsen.)

Egg tooth: a short, pointed structure on the tip of the beak that develops in avian embryos shortly before hatching, and which the hatching bird uses to break through the eggshell.

Pipped: the condition of an egg that is approaching hatching, in which the embryo within has punctured the first small hole through the shell.

The length of time between pipping and hatching varies among species. Many passerines complete the process in only a few hours, but some larger birds may need as long as 4 days. In many precocial species, siblings coordinate the synchrony of their hatching quite precisely by vocalizing to one another from inside their eggs. Once each soon-to-be hatchling breaks the membrane of the air cell in the blunt end of its egg, it begins calling with rapid clicks or peeps produced several times per second, usually from a day or two before hatching until the time of hatching.

11.10 Altricial and precocial young

Newly hatched birds vary widely in their readiness for life outside the egg. **Altricial** chicks hatch naked or very scantily feathered with down, with no ability to generate enough heat for thermoregulation, and totally dependent on their parents for food. In contrast, **precocial** chicks are already well feathered when they hatch, with substantial powers of thermoregulation and locomotion, and a considerable degree of independence from their parents for feeding. These two categories—altricial versus precocial—are endpoints on a continuum of developmental types, and quite a few species have chicks that are intermediate blends of these modes of development (Starck and Ricklefs 1998).

11.10.1 Appearance

No one is likely to describe a young altricial bird as attractive. A newly hatched altricial nestling appears to be all abdomen and head, with two large eyes bulging against closed lids. Soon after hatching, it lifts its head on its wobbly neck and opens its mouth (Fig. 11.43). Swollen **gape flanges**, equipped with nerve endings, extend from the corners on either side of the mouth and taper toward the tip of the bill; touch one of these flanges and the nestling's mouth is likely to spring open like a mechanical toy. The colors in the area of the mouth are often bright and contrasting, transforming it into a target into which the parent birds place food. The flanges typically are white or vivid yellow; the lining of the mouth is often a vibrant red, orange, or yellow. Some nestlings, especially in estrildid finches and some cuckoos, also have colored patterns on the roofs of their mouths or on their tongues. In nestlings raised in cavity nests, the colors around the mouth tend to be even more intense, presumably to help the parents find the chick's mouth in low light conditions.

An altricial nestling's skin, mostly pink from the muscles and blood vessels beneath it, is very thin and oily in appearance (Fig. 11.44A). The internal organs and an almost empty yolk sac, resorbed back into the embryo as it developed, show through the skin of the distended abdomen. If the nestling hatches with any down, it is usually most abundant on the top of the head and on the back. The color and length of the down varies by species and may or may not follow the outline of the definite feather tracts soon to emerge (Chapter 4). The first true feathers soon push out the down, although a chick often retains wisps of the natal down on the tips of its juvenal feathers. The juvenal feathers begin development beneath the skin, first visible as small bumps on the skin and showing as dark bands before they erupt into the pin feathers that will emerge throughout the chick's development. In most altricial chicks, pin feathers appear first in the feather tracts of the head, back, and wings, and later on the underparts. For most birds, the wing feathers grow continuously until full powers of flight are achieved at or after fledging.



Fig. 11.43 Begging for food. The left-hand chick in this recently hatched Brown-headed Nuthatch (*Sitta pusilla*) brood has started to beg for food. Its bright white gape flanges and inner mouth region serve as a target for food placement by its parents. (Photograph by c aubrey wiggins iii.)

Altricial: the condition of young birds that hatch relatively undeveloped and in many cases naked or with sparse down; such helpless young require complete parental care.

Precocial: the condition of chicks that are already well feathered with down when they hatch, with substantial powers of thermoregulation and locomotion, and a considerable degree of independence from the parents for feeding.

Gape flanges: brightly colored enlargements around the base of the bill in nestlings of species in which parents feed the chicks.

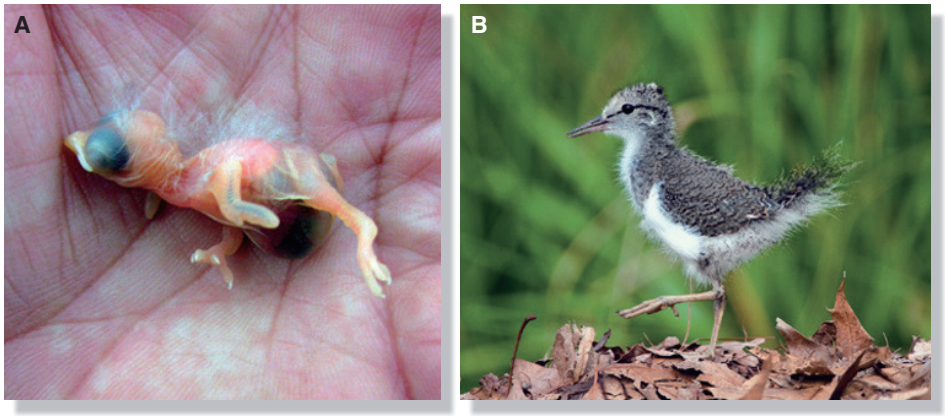


Fig. 11.44 Altricial versus precocial chicks. (A) Altricial chicks like this Tree Swallow (*Tachycineta bicolor*) hatch at an early stage of development and are highly dependent on their parents for warmth, protection, and food. (B) Precocial chicks like this Spotted Sandpiper (*Actitis macularius*) hatch at a later stage of development that allows them to walk and forage within hours or days of hatching. (Photographs by: A, Chris Gates; B, Navjot Singh.)

Because precocial embryos spend much more time developing in their eggs than do those of altricial species, precocial chicks are much more developed at hatching. Perhaps the most familiar image of a young bird is that of a newly hatched chicken, which well typifies precocial young. The chick's downy covering, wet from embryonic fluids, dries within 2 or 3 hours, taking on the fluffy appearance that makes the chicks of precocial species so endearing. The motor and sensory capabilities of a newly hatched chicken, after being in the egg for about 22 days, are about as well developed as those of an altricial chick that has spent 12 days in the egg and 10 days in the nest after hatching. As soon as they emerge from the egg, precocial hatchlings, with their eyes already wide open, respond immediately to external stimuli, are remarkably adroit in walking and maintaining their balance, and promptly begin exploring their environment with pecks at unfamiliar objects. This early neuromotor sophistication is one of the hallmarks of precocial chicks.

At hatching, the precocial chick's abdomen still contains up to one-third of the original contents of the yolk sac, and its digestive tract is essentially fully functional. The egg tooth is conspicuous, flanges are either reduced or not present along the margin of the bill, and the color of the mouth lining usually is plain—similar to that of the adult—because most precocial young feed themselves and thus have no need to send begging signals to their parents. Precocial chicks generally have large feet and legs along with well-developed muscles for walking and producing heat for thermoregulation (Fig. 11.44B). The most precocial of all birds, the megapodes ("pod" is a root word meaning "foot"), are the only birds whose embryos break out of their shells using their extremely large and powerful feet instead of an egg tooth (Jones et al. 1995). Megapode chicks are also distinctive in receiving no parental care (Box 11.02). These chicks simply walk off into the surrounding forest soon after they emerge from their incubation mounds, and their wings are fully feathered at hatching, allowing them to flutter away from any threats they encounter outside the mound.

11.10.2 Temperature regulation

A newly hatched altricial nestling is unable to regulate its body temperature. By brooding, the parents keep the nestling's body temperature high, near the levels at which digestive and growth enzymes work best. As the nestling grows, its surface area-to-volume ratio becomes more favorable for heat retention, and it begins to grow its insulating coat of downy and juvenal feathers. Eventually the nestling can convert the food brought by its parents into energy and use that energy for thermoregulation (Chapter 7). In most passerine birds, the parents begin to brood less around the time their nestlings' eyes open; most altricial young acquire full powers of thermoregulation about the time their wings are half grown.

In contrast, precocial chicks hatch with a thick covering of down, one of nature's best insulating materials (Chapter 4). Precocial chicks generally are larger than the average altricial nestling; thus, with a more favorable surface area-to-volume ratio, precocial chicks lose relatively less heat from their bodies. In fact, they can partly control their body temperature at hatching (well before altricial young can do so), although most still require some brooding. After hatching, however, their temperature control develops much more slowly than in altricial nestlings; some precocial chicks do not attain full temperature control until about 4 weeks of age. The feather coat of each precocial species develops in a pattern suited to its environment. Upland species, such as grouse and shorebirds, generally are more vulnerable to upward radiative heat loss, so they first develop feathers on

their back and upper surfaces. Aquatic species, such as loons, grebes, and waterfowl, first develop long, thick feathers on their body's undersurface that help insulate the chicks when they are floating on cold water.

11.10.3 Weight gain

After an initial lag of a day or two to allow the digestive system to become ready, altricial nestlings develop explosively, often doubling in mass several times during the first 10 days after hatching. For example, the chick of an American Crow (*Corvus brachyrhynchos*) weighs only 15 grams at hatching, but after 18 days of growth it will have increased to over 300 grams (Ignatiuk and Clark 1991)—a 20-fold increase. Growth tends to slow as nestling development continues; by the time most passerine young leave the nest, they usually weigh 70–80% as much as their parents. Once they reach independence, most birds are the same size as their parents; a young bird that can fly and behave like an adult may have a distinctive plumage, but there is usually nothing about its body measurements, except perhaps the length of its wing feathers, that distinguishes it from older birds.

In some altricial species, the nestlings put on so much weight late in development that they temporarily weigh more than their parents. This extra stored energy may help to nourish young birds through the challenging period when they must learn to forage on their own. In other altricial species, however, the fat stores are mostly depleted by the time the young leave the nest. Good examples of this weight recession can be found among seabirds. The chicks of the Gray-headed Albatross (*Thalassarche chrysostoma*) on South Georgia Island in the Southern Ocean, for example, temporarily weigh up to 30% more than adults before this weight is lost prior to fledging (Reid et al. 2000). In albatrosses, this phenomenon is believed to ensure adequate resources for chicks during the crucial period of feather growth preceding flight. A similar growth pattern occurs in swifts; the excess weight in these nestlings is associated with the developmental costs of exceptionally large and crucial wing feathers along with fine-tuned adjustments of their mass to optimize flight ability at fledging (Wright et al. 2006).

Most precocial young, particularly those that feed themselves, are somewhat inept at acquiring and ingesting food immediately after they hatch. For their first few days out of the egg, chicks sustain themselves primarily on the large amount of egg yolk still in their abdomens. They may lose weight during this transitional period, but once they begin to feed themselves efficiently, they gain weight in a pattern similar to that of altricial birds. As chicks grow, their metabolic rates also increase. Although overall patterns of weight gain are similar in precocial and altricial birds, their metabolic rates increase in strikingly different ways. The metabolic rate of precocial species increases in two distinct phases: a rapid initial phase that shifts quite abruptly into a slower phase about halfway through development. In contrast, the metabolic rate of altricial chicks increases fairly continuously as they develop.

11.10.4 Sensory and motor development

An altricial nestling's sensory and motor abilities develop as its body does. At hatching, it is all but helpless, able to stay upright only by leaning against the nest. Nevertheless, it gapes, swallows, digests, and defecates—the four behaviors crucial to obtaining and converting food into a rapidly developing young bird. With most of this energy going into growth, altricial nestlings also need to sleep, which they alternate with feeding. Most altricial chicks cannot even give begging calls during their first day or so, but these calls soon develop, becoming louder and more persistent as the nestling grows. At about one-fourth of the way through the nestling stage, their eyes open, allowing them to gape at visual stimuli (the parent, a human hand, or even forceps holding food). Then nestlings begin to grasp objects with their feet, although their balance generally is still poor. When defecating, the nestling raises its posterior and moves it from side to side, making it easy for the parents to retrieve the fecal sac; many species also back up to the edge of the nest. A few days after their eyes open, most altricial nestlings develop a crouching response to strange visitors at the nest, and in many species they develop the same reaction to the alarm calls of their parents. By the time most of their feathers have emerged, their begging behavior may have become quite aggressive. As the feathers continue to unfurl from their shafts, the nestlings begin their first preening movements, and they often begin stretching their wings up, to the side, and back.

Precocial chicks, although further along in their sensory and motor development at hatching, still require time to adjust to their new environment outside of the egg. Even megapode chicks must pause underground after hatching, often resting there for more than a day before they begin their ascent up through the layers of mound material above them. For example, the chicks of one well-studied megapode, the Australian Brush-Turkey (*Alectura lathami*), are born with their eyes closed and are unable to raise their heads for several hours. In captivity, once the head is raised, however, chicks quickly begin to preen, removing feather sheaths and making the plumage clean and dry. After 10 hours, chicks begin to respond to light stimuli with open eyes. In the wild, brush-turkeys begin digging to the surface after this initial period of resting and adjustment, and they develop as they proceed upwards. Along the way, the chicks develop the ability to feed themselves, pecking at soil invertebrates they find in their paths. Within 24 hours, these brush-turkey chicks



Fig. 11.45 Fledging before flight. The chicks of some seabirds, like this Guadalupe Murrelet (*Synthliboramphus hypoleucus*) swimming between its parents, leave the nest long before they can fly. These chicks then move out to sea, where their parents continue to feed them until they reach full independence. (Photograph by Tim Melling.)

have attained thermoregulatory abilities. As digging continues, the young brush-turkeys become more and more efficient, covering greater distances in shorter amounts of time until finally they emerge ready for life on their own (Göth 2002).

11.10.5 Leaving the nest

Most passerines leave the nest (fledge) about 9–12 days after hatching (the shorter periods are for species nesting in the open). Long before they are capable of sustained flight, many fledgling passerines disperse into denser foliage nearby, communicating their location to their parents through a series of soft calls. By spreading out in vegetation, the chicks are safer than they were in the nest. Altricial fledglings often sit on a protected perch, begging for food only when a parent gets quite close. As their feathers continue to develop, fledglings are fed less and less often until they are independent of parental care. During this transition, fledglings develop many new skills for finding and catching food: they begin pecking at objects, picking up food, catching insects, working at grass seed heads, scratching the ground, and probing in bark furrows. They also begin bathing.

The nestlings of some seabirds like guillemots, murres, and murrelets often leave the nest long before they have functional flight feathers; these young birds continue to develop at sea where the proximity to marine food allows one parent to feed the chick for several more weeks until it can fly (Ydenberg 1989) (Fig. 11.45). In other birds, parents sometimes help fledglings improve their prey-catching skills; raptors such as Northern Harriers (*Circus cyaneus*) of North America may drop mice for their young to catch in mid-air. Some kingfishers may similarly drop recently killed or battered fish into the water as easy targets for their fledglings' first few dives. American Woodcock (*Scolopax minor*) chicks, whose bills at first are too short and weak to probe in the soil for earthworms, rely on their mother to obtain them. As she probes and pulls up the worms, the chicks take them directly from her bill. Although the young of many diving species go underwater to escape predators, they are very reluctant at first to dive for food, so much so that the adults initially bring food to the surface for them. Adult grebes, loons, and alcids feed their young for up to 10 weeks, first in the nest and later as the young accompany them on the water's surface or on one of the parent's backs.

Most precocial chicks leave the nest shortly after they hatch and their feathers dry, reducing the chance that the entire brood will be found and eaten by a predator. The adult parent provides security for its chicks, and a strong social bond often holds them together. Perhaps because they receive essentially no parental care in the nest, chicks of precocial species are generally not referred to as "fledglings." Various vocalizations keep family members in touch with one another: adults make assembly calls to summon their young, alarm calls voiced by either the adult or young instantly trigger a crouching or freezing response from the chicks, and distress calls made by the young draw adults to their vicinity. As the chicks mature, a social hierarchy usually develops within the group, and siblings often challenge each other. In large precocial species, such as Canada Geese (*Branta canadensis*), a family may stay together throughout the subsequent winter. Similarly, Upland Geese (*Chloephaga picta*) in southern South America remain under the protection of their parents from hatching in November until eviction by their parents the following August (Summers 1983). In Tundra Swans (*Cygnus columbianus*) of northern Europe, the parents defend offspring in two ways: the parents react aggressively when their offspring are threatened, and, more subtly, the very presence of the adults seems to reduce the chances of offspring being threatened by other adult swans. Although second- and third-year offspring are no longer actively defended by their parents, they still may benefit in this way by remaining close to their parents (Scott 1980). In smaller waterfowl like ducks, parental defense is usually less imposing, and the family bond usually is weaker; young may follow their mother at first and a different female later, forming large groups, termed **creches**, of young from several broods. In these species in which direct defense from the adults is less important,

Creche: a group of the still-dependent young of two or more breeding females, attended by one or more adults.



Fig. 11.46 Precocial chicks are able to leave the nest site after hatching. Precocial chicks often follow a parent away from the nest shortly after hatching, decreasing the risk of predation. For example, Lesser Rhea (*Rhea pennata*) family groups often wander together in search of food shortly after the chicks hatch. (Photograph by Sergio Bitran Mogilevich.)

ducklings gain by safety in numbers: the more ducklings there are in a group, the less likely it is that any single duckling will fall prey to a predator (Chapter 13).

In addition to helping avoid predation, leaving the nest soon after hatching allows developing precocial young to move to areas of abundant food. Over the course of their development, for example, goslings (young geese) may walk many kilometers from their nest site in search of rich grass and other non-woody plants; many species of ducklings gather on productive water bodies; sandpiper and plover chicks congregate with their parents along rich stretches of shore; and groups of young Ostriches (*Struthio camelus*) in Africa and rheas in South America often wander widely through their respective desert and steppe habitats (Fig. 11.46).

11.10.6 Developmental periods and independence

Among altricial birds, the time from hatching to independence ranges from approximately 25 days to several months. The young of most passerine species, however, become efficient fliers at about 17 days and are independent of parental care in about 28 days. Large altricial non-passerines have long periods of nestling life: young Bald Eagles (*Haliaeetus leucocephalus*) of North America require 10–12 weeks in the nest before fledging, young Blue-and-yellow Macaws (*Ara ararauna*) in South America require more than 3 months, and young California (*Gymnogyps californianus*) and Andean (*Vultur gryphus*) Condors take as long as 5 months before leaving the nest, but may not become entirely independent of parental care for months afterward. Larger penguins brood their young for about 6 weeks, at which point the hatchlings huddle close together with other young in large groups (also called creches) where they continue to be fed by their parents for up to nine additional months.

Generally, altricial birds with short incubation periods tend to have short nestling periods, and those with long incubation periods usually have long nestling periods. It almost seems as though the growth rate of the developing young has a single setting for both within and outside the egg. The length of time that eggs and young spend in the nest is related to the safety of its location. For instance, many ground-nesting birds have short incubation and nestling periods in general, speeding the young bird through its time of greatest vulnerability to predators.

Young that stay in the nest and receive parental care there for long periods of time are termed **nidicolous**; those that leave the nest soon after hatching, although usually far from independent, are **nidifugous**. All altricial young are nidicolous (they are incapable of leaving the nest soon after hatching). In contrast, most precocial young (except many of the seabirds mentioned above) are nidifugous, and their nestling period thus is very short. In altricial birds, the fledging period (the time from hatching to leaving the nest) often can serve as a comparative measure of developmental rate, although even among altricial birds there is considerable variation in how well developed the chicks are when they leave the nest. However, the variation in precocial birds is even greater, with a clear difference between nidicolous and nidifugous species. In any event, the transition to independence may be less jarring for precocial species than for altricial species, because precocial chicks never require as much or as many kinds of parental care as do altricial chicks. As in so many other aspects of young birds' development, there is considerable variation in the length of dependency of precocial chicks. Young shorebirds and ducks may become independent and ready for a long southward migration without their parents within a few short weeks of hatching; the offspring of large geese and swans may stay with their parents through migration and well into the following winter.

Throughout the transition to independence runs the fundamental parent-versus-offspring conflict between what is best for the parent bird and what is best for its offspring. Parents feed the chicks less frequently once

Nidicolous: the condition of chicks that stay in the nest for long periods after hatching.

Nidifugous: the condition of chicks that leave the nest soon after hatching.

they have fledged, and, as the fledglings become more capable of taking care of themselves, the parents become less attentive to their demands. Each offspring eventually finds that it is easier to find food for itself than to try to obtain it from its parents, and then it is off on an independent life.

11.11 Recognition among parents and their young

Even before young birds hatch, they often have social contact with the parent (or parents) attending the nest. Young of some species peep from inside their egg, loudly enough to be audible from the outside. They apparently can hear their parents in return, as many will stop peeping after hearing a vocal response from the adult. Some species, such as Northern Bobwhite (*Colinus virginianus*), even learn to recognize their own mother's call while still in the egg (Lickliter and Hellewell 1992).

Nonetheless, only some kinds of parent birds are able to recognize their own young. Researchers can interchange the young of most passerine species without the parents realizing that any change has occurred: the adults usually seem willing to feed any chick that is begging in the nest. Adults of many non-passerine species, especially colonially nesting birds, however, are not fooled so easily. For example, for 2 or 3 days after their young hatch, most gulls will accept tiny young from other nests as their own, whether the young happen to wander in naturally or arrive as part of a biologist's experiment. After this short period during which the adults become accustomed to the nestlings in their own territory, they refuse any others; in fact, the adults will chase and peck stray young until they leave the territory or die. This developmental change in recognition likely reflects changes in the probability of getting offspring confused: very young gull chicks are not nearly as likely to wander into foreign territories as are older chicks, and young chicks are therefore far more likely to be the adult's legitimate offspring.

Most young birds do not recognize their parents for some time after hatching. Altricial nestlings beg from nearly any bird that comes near the nest—even from a predator such as a hawk—unless they are frightened by the size or behavior of the newcomer or the parent gives a warning call. As they grow older, however, nestlings learn to recognize their parents and save their begging energy for the times when it is most likely to lead to a delivery of food. In contrast, the young of many colonially nesting birds recognize the calls of their own parents at an early age. This recognition allows them to prepare quickly to receive food when the parent arrives and, in some species, prevents them from begging from the wrong adults, which may react aggressively. Nestlings recognize their parents' calls by 6 days of age in Laughing Gulls (*Leucophaeus atricilla*) of the Atlantic coast of North America (Beer 1969), by 3 days in Thick-billed Murres (*Uria lomvia*) being raised on cliffs over the Arctic Ocean (Lefevre et al. 1998), and by at least 14 days (7 days before fledging) in Pinyon Jays (*Gymnorhinus cyanocephalus*) of the American southwest (Balda and Balda 1978). In virtually all birds, begging vocalizations grow more intense when the chicks are hungrier, but in some colonially nesting passerines, such as Golden-backed Weavers (*Ploceus jacksoni*) of Africa, offspring vocalizations carry information about the identity of the chicks as well (Reers and Jacot 2011). For most species whose young gather into creches, the young recognize their parents' calls by the time these groups form; this is true for Australian Galahs (*Eolophus roseicapilla*), Adelie Penguins (*Pygoscelis adeliae*), and American White Pelicans (*Pelecanus erythrorhynchos*).

11.12 Parental care

All altricial nestlings and most precocial chicks require some form of parental care. From the moment they hatch until they reach independence, altricial young depend heavily on their parents. Parents of altricial young find and feed their nestlings copious amounts of food, often keep the nest clean by disposing of their feces, and defend them against predators. Even most precocial chicks, which usually feed themselves, rely on their parents for vigilance against predators and protection from the elements.

11.12.1 Feeding their young

Parents of altricial young must regularly bring food to their growing offspring. To feed nectar to her bee-sized young, a female hummingbird thrusts her bill down each of their throats, often probing so vigorously that it seems as though she might poke right through them. The offspring of boobies, penguins, and cormorants often seem to attack their parents when they return home with a load of food, scrambling to ensure access to the fresh harvest.

Some birds bring back large prey items that must be torn up to be fed to nestlings, at least when they are recently hatched. It is no surprise that birds such as raptors bring one large prey item back to the nest at a time, but birds that catch smaller prey often employ a different strategy. Puffins, for example, are adept at bringing a well-organized file of many small fish, stacked up along the bill, to their nests (Fig. 11.47). Most storm-petrels gather tiny red crustaceans from the ocean's surface by day and store them in their esophagus. At night, they return to the nest, when predatory gulls and falcons are much less of a threat. Once safe in their burrows, adult storm-petrels disgorge a band of crustacean paste—resembling pink toothpaste—to feed their ravenous nestling.



Fig. 11.47 Provisioning chicks. This Atlantic Puffin (*Fratercula arctica*) returns to its burrow, its beak full of small fish for its single chick. (Photograph by Harold Moses.)

Birds accomplish some impressive feats while feeding their young. Parents of altricial passerines in the northern temperate zone commonly bring food to their nests hundreds of times per day. For example, Great Tits (*Parus major*) in Japan, which have broods of seven or eight young, bring one prey item at a time to their nestlings at rates of 300–400 feedings per day (Royama 1966). In North America, one Eastern Phoebe (*Sayornis phoebe*) with four young made 8942 visits to its nest over the course of 17 days (Kendeigh 1952). If a species brings more than one prey item per visit, it generally comes to its nest fewer times, but it may deliver food at an awe-inspiring rate.

Most seabird parents forage across vast home ranges. Although many have precocial chicks capable of thermoregulation from an early age, their food is often available only far from the nest and requires great skill to gather; parents therefore must feed their young until they are capable of long-distance flight and effective foraging. Extraordinary among such seabirds are the albatrosses that nest on tiny islands in the southern oceans and forage for fish, squid, and shrimp for up to 10 days at a time at distances of almost 2000 kilometers from the colony (Pinaud et al. 2005).

A few kinds of avian parents are able to produce food internally for their nestlings rather than harvesting it directly from the environment. For example, for the first week after their chicks hatch, pigeons and doves feed their young **crop milk**, a rich, thick liquid substance made of epithelial cells from the lining of the parent's esophagus. Flamingo parents of both sexes also routinely feed their young an esophageal milk-like substance (Ward et al. 2001). Although it is not always necessary, male Emperor Penguins (*Aptenodytes forsteri*) can produce a thick milk from their esophagus for the first week or so of their chick's development if the female is late in returning to the nest to begin feeding.

Some birds carry water as well as food to their young. For example, Common Ravens (*Corvus corax*) and Anhingas (*Anhinga anhinga*), among others, deliver water to their nestlings beak-to-beak. The sandgrouse of deserts and arid grasslands in Africa and Asia use special sponge-like breast feathers to transport water from distant water holes to their young (Cade and Maclean 1967).

11.12.2 Defending their young

Parent birds defend their nests and young with varying levels of aggression. Raptors and large ratites may do so with dangerous effectiveness, whereas small passerines may offer only symbolic displays of agitation. Few, if any, birds are more potentially dangerous than an Ostrich (*Struthio camelus*) or cassowary—with their long and powerful legs—but actual accounts of these birds aggressively defending young are rare. However, few people attacked near the nest of an aggressive raptor or large owl will forget the experience. Large waterfowl, such as swans and large geese, almost always stand and defend their nests or broods, hissing and flapping their powerful wings. If a predator comes too close, they will strike with their wings and scratch with their feet. Smaller waterfowl rely on cryptic behavior to evade predators. The same is true for shorebirds: very large plovers such as lapwings often defend their young aggressively. Smaller shorebird species rely on camouflaged nests, eggs, and young, as well as on distinctive predator distraction displays that often involve the feigning of an injury by the parent bird (Fig. 11.48). The adult may hunch its back and drag one wing half-open to the side, creating the illusion that it could easily be captured and eaten. As soon as the potential predator is lured far enough away from the eggs or young, the seemingly crippled parent undergoes a transformative "recovery" and runs or flies away with ease.

Some birds remove their young from danger when threatened. If their bills are large enough, rails will carry their young to safety; jacanas transport their young under their wings. Male Sungrebes (*Heliornis fulica*) of the neotropics carry their young to safety, even in flight, by placing them in a pouch under each wing (Fig. 11.49).

Although the young of most species are effectively defenseless, some can simulate a threat or at least promise

Crop milk: a nutritious, milk-like substance produced by pigeons and doves from cells sloughed from the lining of their crop.



Fig. 11.48 Predator distraction displays. This Semipalmated Plover (*Charadrius semipalmatus*) is feigning injury in order to lure a potential predator away from its nest site. (Photograph by Andy Johnson.)

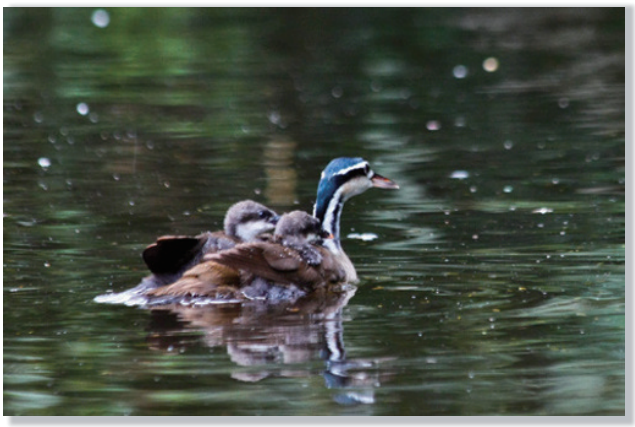


Fig. 11.49 A unique way to transport young. Sungrebes (*Heliornis fulica*) and other aquatic bird species commonly allow their chicks to ride on their backs as they swim. Male Sungrebes even have special pouches within the folds of their wings that allow them to carry their chicks during flight. (Photograph by Catalina Castillo.)

a disgusting encounter. Within a cavity nest, a brood full of tits or wrynecks can skillfully imitate a hissing snake when a predator comes to investigate their home. Young gulls and many other seabirds may release a barrage of feces and regurgitated food when molested by a predator. Fulmar chicks are notoriously revolting in this respect because their stomachs contain a vile smelling oil; the vomit of fulmar chicks is very difficult for a predator to clean from its fur, feathers, or scales—or for unfortunate researchers to clean from their clothes and hair.



Fig. 11.50 Fecal sac. Most passerine chicks produce packets of waste called fecal sacs that can either be eaten or carried away from the nest by the parent, as demonstrated by this female Red-winged Blackbird (*Agelaius phoeniceus*). (Photograph by Gary Seloff.)

11.12.3 Nest sanitation

Because young altricial birds often spend many days or weeks in the nest, parents often have behaviors that keep the area free of materials that might cause disease or attract predators. As soon as the young hatch, most parents remove the broken eggshells. In addition, the young of most passerines produce their feces, at least initially, in a tough, flexible bag called a **fecal sac** (Fig. 11.50). These sacs make the removal and disposal of feces easy: many parents simply carry them some distance and drop them. Some species drop these fecal sacs over water; nuthatches and wrens place them on tree branches. The duration of fecal sac production varies among passerines. The young of many species consistently produce their feces in these tidy packets until they leave the nest, so that the nest is nearly without feces even after all the young have fledged. In contrast, the nestlings of other species stop producing their fecal sacs about midway through nestling life, leaving behind a matted mess of feces and nest material after they fledge.

Although sanitation may be a principal reason for fecal sac production, the sacs also allow some birds to recycle scarce resources: parents of some bird species eat the sacs rather than disposing of them. Both the sacs themselves

Fecal sac: a tough, flexible bag enclosing the feces of most passerine nestlings that allows the parents to remove these wastes from the nest area.

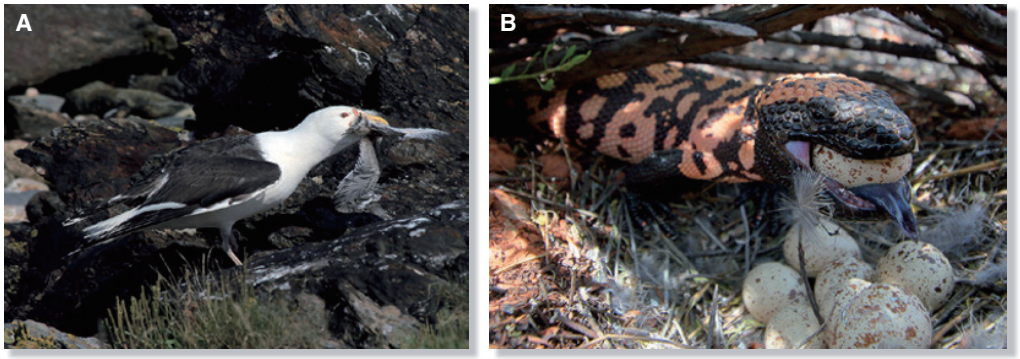


Fig. 11.51 Nest predators. Parent birds—as well as eggs and chicks—are vulnerable to many types of predators while incubating or attending to nestlings. Nest predators like this (A) Great Black-backed Gull (*Larus marinus*) and (B) gila monster are a common cause of nesting failure for birds in most habitats. (Photographs by: A, Brette Soucie, US Fish and Wildlife Service; B, Cameron Rognan.)

(made of a protein–sugar mixture) and their contents contain valuable nutrients that the parents can consume and potentially reuse (McGowan 1995). Younger chicks, in particular, are relatively inefficient at digesting the food they are fed, and the sac contents thus retain food value that the parents' more efficient digestive systems can recover.

Spotting a parent bird disposing of a fecal sac is a valuable find for a field ornithologist. A bird carrying a fecal sac is an unequivocal indicator of an active nesting attempt. Because the glistening white sacs are easy to see from a distance, the act of carrying one draws attention to the bird; once spotted, the adult may provide clues regarding the location of its nest, which can be particularly helpful to researchers searching for the nests of cryptic species.

The young of many large bird species rapidly become adept at directing their waste outside of the nest. For example, an Ornate Hawk-Eagle (*Spizaetus ornatus*) chick in Guatemala was able to begin defecating over the side of its large nest when it was 3 days old (Lyon and Kuhnigk 1985). Areas around some raptor nests soon become whitewashed with splattered feces—so much so, in fact, that one sometimes can estimate the number of young present without even seeing them. The sheer volume of feces within pelican, cormorant, and heron colonies soon whitewashes and often kills the surrounding vegetation.

11.13 Survival and reproductive trade-offs

A central idea of life history theory is that adults face a fundamental trade-off between allocating resources (such as energy and time) for reproduction versus their own self-maintenance, as covered in more detail in Chapter 13. A Eurasian Blue Tit (*Cyanistes caeruleus*) may produce more than 15 fledglings in one summer, but that adult likely has (at best) a 50% chance of surviving through to the next year. In contrast, a Royal Albatross (*Diomedea epomophora*) of the vast Southern Ocean produces one young only every 2 years, but the adult's annual survival rate is about 95% (Robertson 1993).

11.13.1 Meeting threats to offspring survival

One of the ways that birds can increase their lifetime reproductive output is to increase the survival prospects of their young. The most pervasive threat to the survival of most birds is predation. Most adult birds experience relatively high survival rates for their size because they are able to escape from predators through flight. From this perspective, the act of residing in a single spot to rear young is a risky departure from the typical avian lifestyle. Indeed, for some highly mobile birds, the breeding season is the only significant period they spend on land. Many nest predators will take adults as well as eggs or young, so incubating birds of most species are particularly vulnerable when they are nesting (Fig. 11.51).

Although the loss of an incubating parent is relatively rare, eggs and young often are consumed at a high rate: for example, predators commonly destroy half or more of the nests of most forest-nesting passerines. Much of the breeding biology of many birds seems to revolve around an effort to evade or fool predators. As we have seen earlier in this chapter, swifts build their nests on cliffs and under waterfalls, Killdeer (*Charadrius vociferus*) and other plovers lure predators away from their nest by feigning injury, lapwings and geese attack predators that approach too closely, and birds such as penduline-tits build nests with false openings. Notoriously effective nest predators include raptors, monkeys, raccoons, weasels, cats, opossums, and arboreal snakes; various other birds often can be dangerous nest predators as well. The top nest predators in marine habitats typically are birds such as skuas, jaegers, gulls, and frigatebirds.

Other sources of mortality for young birds tend to be much less constant. Weather is probably the most significant after predation. High rainfall, tides, or winds can cause the wholesale destruction of nests—especially for marsh-nesting species or colonial birds on low islands. Bad weather also may force parents to leave the nest for extended periods in search of food to maintain their own health, causing them to lose their eggs or young to exposure or starvation. In tropical and desert areas, fledgling production often is severely depressed by unpredictable periods of extended rain or drought, effects often associated with large-scale climatic oscillations such as El Niño (Jaksic and Fariña 2010). The arrival of El Niño can result in nearly total reproductive failure for seabirds in coastal Chile and Peru.

Brood parasites often cause substantial mortality for birds nesting in a more dispersed fashion (Chapter 13). For example, in a study in Illinois (USA), Brown-headed Cowbirds (*Molothrus ater*) were found to parasitize up to 100% of Wood Thrush (*Hylocichla mustelina*) nests (Robinson and Wilcove 1994), and parasitism by cuckoos in the Old World can foil more than 60% of the nesting attempts of their hosts (Moskát and Honza 2002). Many of these host populations cannot sustain such a high rate of parasitism.

11.13.2 Adult and offspring survival

After considering all the threats they must face, it may come as no surprise that immature birds nearly always experience lower survival rates than birds that have reached reproductive age. For example, in their first few years, most gulls have average annual survival rates of 30–50%, whereas about 80% of older birds survive each year. This pattern likely arises because the transition from being fed to feeding oneself requires the rapid development of foraging skills and predator vigilance. A study of Barn Swallows (*Hirundo rustica*) in Switzerland by Martin Grüebler and Beat Naef-Daenzer (2010) found that the extent of post-fledging parental care had a very large effect on post-fledging survival: young receiving care for up to 6 days after fledging experienced a survival rate of 23% over 3 weeks, whereas those receiving care for at least 14 days had a survival rate over the same period of 57%.

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Chapter 12 Avian Migration and Dispersal

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The movements of birds are among their most captivating traits. The regular seasonal movements of avian migrants are remarkably diverse: phalaropes (*Phalaropus* species) from the high Arctic spend their non-breeding season in upwelling areas on open tropical seas; Northern Wheatears (*Oenanthe oenanthe*) traverse most of the northern hemisphere in their back-and-forth movements to ancestral wintering areas in Africa; and Resplendent Quetzals (*Pharomachrus mocinno*) travel from one side of Costa Rica's mountainous spine to the other and back again in their annual search for fruiting trees. Birds migrate great distances to find suitable habitats, and they also engage in dispersal from the location where they hatched to their adult breeding sites.

Every avian migratory pattern is the result of an adaptive molding of a species' movements to variation in its environment. Even among similar species in the same habitat, some birds may migrate while others do not. For example, consider the woodpeckers present in summer and winter in the woods outside nearly any town in the northern hemisphere. Woodpeckers in the temperate zone range in size from that of a small thrush to the size of a crow, and in most woods three to five different species occur. The various members of this family share a good deal of their overall biology—chisel-shaped bills to excavate wood, a brain so well secured that it can stand the blasting that comes with wood chipping, claws that ensure firm grips on trunks and branches, and a stiff tail that helps to support their bodies against the trunks—but the different species have quite different patterns of annual movement. Often only the largest and smallest of these woodpecker species remain in the north for the winter. Closer inspection reveals that the species that leave for the winter are those that have particular food requirements. For example, Northern Flickers (*Colaptes auratus*) in the northern half of their North American range can no longer excavate ants in snow-covered frozen ground, and Yellow-bellied Sapsuckers (*Sphyrapicus varius*) in northeastern North America can no longer harvest the flowing sap of trees, so both species migrate to areas where their distinctive foraging habits can be pursued for the rest of the year.

Among migrants, differences in migratory routes can involve important differences in physiology. On the northeast coast of North America in fall, two of the songbirds that are captured most commonly in migratory mist-netting stations are Yellow-rumped (*Setophaga coronata*) and Blackpoll (*Setophaga striata*) Warblers. These closely related songbirds follow very different paths once the breeding season is over. The Yellow-rumped Warblers will migrate south and winter in the southern USA and Central

Opposite: Regular migrations of birds have represented seasonal change for millennia. This flock of migrating White Storks (*Ciconia ciconia*) exemplifies the spectacle of avian migration. (Photograph by Dov E.)

Handbook of Bird Biology, Third Edition. Edited by Irby J. Lovette and John W. Fitzpatrick.
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America, while the Blackpoll Warblers will spend the non-breeding season in northern South America. The more northern non-breeding range of the Yellow-rumped Warbler is reached by fairly short flights over land, whereas the Blackpoll Warbler reaches South America with one long, non-stop flight that lasts up to 3 days. The Blackpoll Warblers follow prevailing winds out over the Atlantic Ocean past the island of Bermuda until they encounter the trade winds that bring them back to the Caribbean shore of South America. Many ornithologists were very slow to accept the proposition that these small birds were making such long transoceanic flights, but many lines of evidence, including recent tracking of individual birds, now support this conclusion (DeLuca et al 2015). The most striking evidence, visible in the hand when birds are captured before departure, is that the Blackpoll Warbler amasses such huge stores of fat to fuel its journey that it doubles its pre-departure mass.

Dispersal, the process of discovering and moving to a new breeding home, occurs in all birds, even non-migratory birds from less seasonal environments. Dispersers must leave their natal territory, where their parents raised them, and get to know their surroundings well enough to find a mate and a breeding locale of their own. Compared with the distances traveled during many migrations, these dispersal movements are small in scale, yet the exploratory movements of dispersal are fraught with uncertainty, and as many birds likely fail to disperse successfully as die in migration. In any particular species, most dispersers stay fairly close to their natal home, yet other individuals may disperse across an entire continent. Dispersal, like migration, comprises a continuum of movements, from the local to the global.

12.1 Types of movements

Avian movements include **migration**, two-way trips that bring individual birds back and forth between breeding and wintering sites each year, and **dispersal**, a departure from the site where birds hatched or bred to find a breeding location elsewhere. In places where a bird species can persist year round, natural selection will likely not favor long-distance annual movements, with all of its attendant risks. In contrast, birds living in highly seasonal environments may have no choice but to move to distant locations to avoid the harshest seasons or to find a breeding opportunity. Both staying and moving have costs and benefits, and whether an individual bird stays in one place or moves depends on which strategy is more likely to ensure its survival and reproduction.

Migration: the regular, seasonal movement of individuals away from, and back to, the breeding grounds.

Dispersal: the movement of an individual from one breeding site to another.

Philopatry: the tendency to return to the same location in successive years.

12.1.1 Philopatry

One of the surprising facts about birds—even the migrants that cover tens of thousands of kilometers in their annual journeys—is that most individuals return annually to the same areas where they bred the year before. This site faithfulness is termed **philopatry**, a term derived from the ancient Greek words *philos* (loving) and *patria* (fatherland).

Most adult birds are philopatric in successive breeding seasons, returning to the same breeding site (or a site nearby) as long as they survive the intervening period. Thus, shearwaters and albatrosses travel the oceans of the world but often return each breeding season to the very same nest scrape or nesting burrow. Some Arctic Terns (*Sterna paradisaea*) make annual journeys of almost 100,000 kilometers as they migrate from high-latitude northern breeding sites to non-breeding areas in the Antarctic region (Fig. 12.01); they return to the same breeding sites more than 98% of the time (Devlin et al. 2008; Fijn et al. 2013). Bobolinks (*Dolichonyx oryzivorus*) make a round-trip journey from their grassland breeding areas in northeastern North America to non-breeding areas in southern South America, and exhibit more than 80% site faithfulness when they return to the breeding grounds (Fajardo et al. 2009).

Philopatry often occurs in the non-breeding season too. For example, individually marked American Redstarts (*Setophaga ruticilla*), Black-throated Blue (*Setophaga caerulescens*), and Black-and-white (*Mniotilta varia*) Warblers in the Dominican Republic often return to the same territory winter after winter (Wunderle and Latta 2000). Indeed, some early experiments on the homing abilities of wild birds involved transporting them away from their winter home ranges, to which they proved philopatric in later years. For example, ornithologist Richard Mewaldt (1964) displaced some of the White-crowned Sparrows (*Zonotrichia leucophrys*) that wintered in his California backyard by sending them east across the North American continent as air cargo to Louisiana and Maryland, where they were released. These displaced sparrows did not return immediately, but many came back to his California yard the next winter, presumably after having flown first to their more northerly breeding locations in the intervening spring (Fig. 12.02).

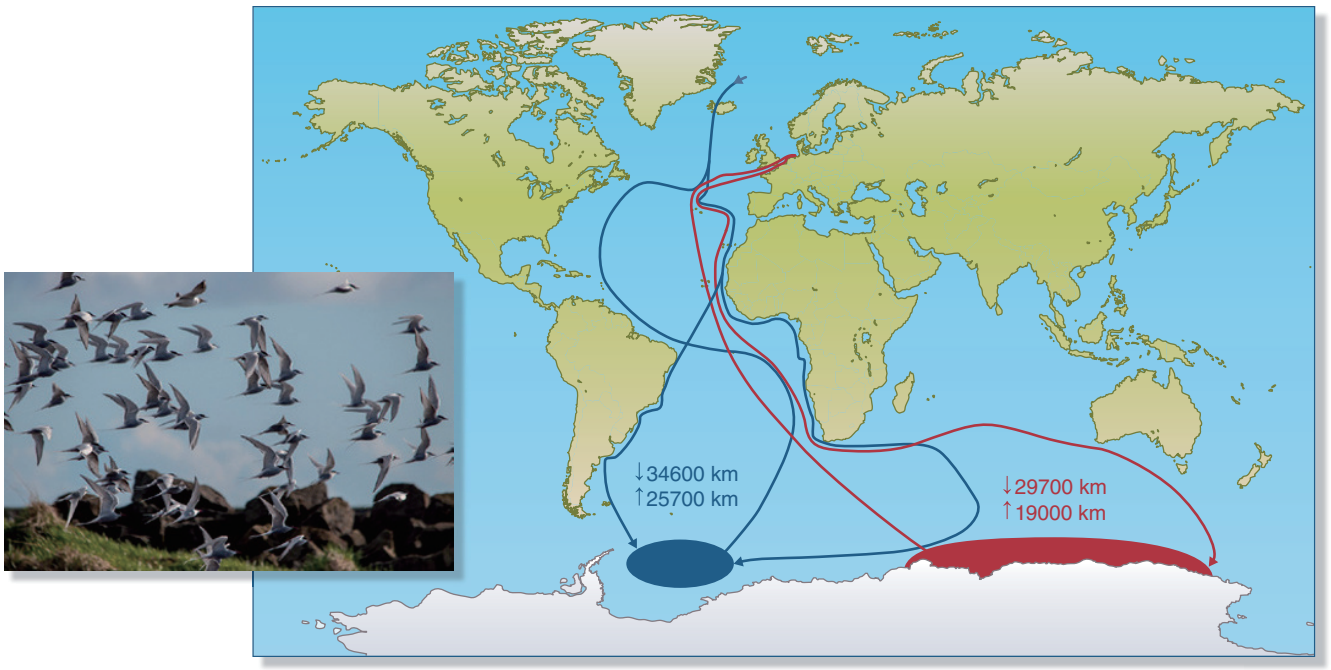


Fig. 12.01 Long-distance migration. Arctic Terns (*Sterna paradisaea*) breed in the Arctic and spend their non-breeding season in or near the Antarctic region. This map depicts the incredibly long migratory tracks (red and blue lines) of two individuals that were tracked throughout their annual cycle. (From Fijn et al. 2013. Reproduced with permission from ARDEA. Photograph by Örn Óskarsson.)



Fig. 12.02 Winter site fidelity. In a classic experiment, White-crowned Sparrows (*Zonotrichia leucophrys*) overwintering in California were transported (dashed lines) and released in two distant locations in Louisiana and Maryland (USA). Despite the unexpected uprooting, these individuals likely migrated north to breed (shaded area) and then returned to their original overwintering sites in California the next year. (From Mewaldt 1964. Reproduced with permission from AAAS. Photograph by Jack Sutton.)

12.1.2 Local movements, migration, and dispersal

Birds are very mobile creatures and there are many ways to classify their movements. One way to distinguish types of movements is by identifying what they accomplish for the bird. At the short end of the timescale are the **local movements** associated with daily foraging, flights to and from roost sites, and other daily activities. Migration, by contrast, is an annually repeated seasonal movement away from the breeding area and then back to it, usually over a far greater distance than an individual's local movements. Birds generally undertake migration to avoid times when resources are scarce and conditions are harsh, or, conversely, to exploit sites and seasons where the benefits of conditions there far outweigh the costs. Migrating birds usually are clearly migrating and doing little else at the same time: a migration is a means to cover distance and reach a new area to live for a season. The final general type of avian movement, dispersal, is a movement to find a place to breed. In most birds, dispersal movements occur on a smaller spatial scale than does migration, and dispersal will

Local movements: the non-migratory movements involved in the daily activities of birds.

generally occur only once or a very few times in an individual bird's life.

The distinction between local movements and migrations cannot be made solely on the basis of the distance traveled: some types of birds move farther during daily foraging than others do during seasonal migration. For example, Imperial Eagles (*Aquila heliaca*) in Spain can travel up to 114 kilometers in a single day's foraging (Fernández et al. 2009) and Short-tailed Shearwaters (*Ardenna tenuirostris*) may fly up to 15,000 kilometers during 3-week-long foraging trips in the vast Southern Ocean before returning to their nest (Phillips et al. 2008).

The local movements of birds are usually dictated by their habitat and by their need to feed and to avoid being eaten themselves. Many birds stay within a territory or home range when making most of their local movements. Dippers (*Cinclus* species) that live along fast-flowing streams worldwide have accordingly long, linear territories along which they move back and forth daily in search of food. Most oystercatchers, and many coastal and riverine birds (some shorebirds, swallows, sungrebes, screamers, etc.), are similarly tied to shoreline habitat, and their daily movements are generally up and down shores rather than across country.

Birds with less restrictive habitat requirements undertake movements that may extend in all directions, up to the edges of their defended space. Still, their movements tend to be concentrated within their territories, spending most of their time in areas that provide abundant food, shelter from predators and the elements, or key areas for displaying and singing. Fairy wrens (*Malurus* species) in Australia retain small territories for much of the year, and they restrict their movements even closer to the nest when they are feeding nestlings (Tidemann 1990). Swainson's Warblers (*Limnothlypis swainsonii*) in Arkansas (USA) (Anich et al. 2012) and Chestnut-backed Antbirds (*Myrmeciza exsul*) in Costa Rica (Marcotullio and Gill 1985) concentrate their activities in the most densely vegetated parts of their territories, probably because those areas provide the safest foraging opportunities. Like many other male songbirds, male Cerulean Warblers (*Setophaga cerulea*) remain close to the trees they favor for singing from during the early part of the breeding season in eastern North America (Barg et al. 2006).

In contrast, other birds may have very little attachment to a single prescribed territory during any part of their annual cycle. Birds that forage on the seas or in the open sky often have feeding conditions that are highly unpredictable and food sources that are diffuse and impossible to defend. Thus these birds often forage over very large distances, and their local movements can occur over a vast scale, as in many pelagic seabirds. Similarly, many swifts and swallows range over broad distances even while feeding young in a nest. Once the constraint of feeding young is removed, these broad foragers become even less limited. Tracking studies of Alpine Swifts (*Apus melba*) have shown that these birds remain in the air after leaving their breeding

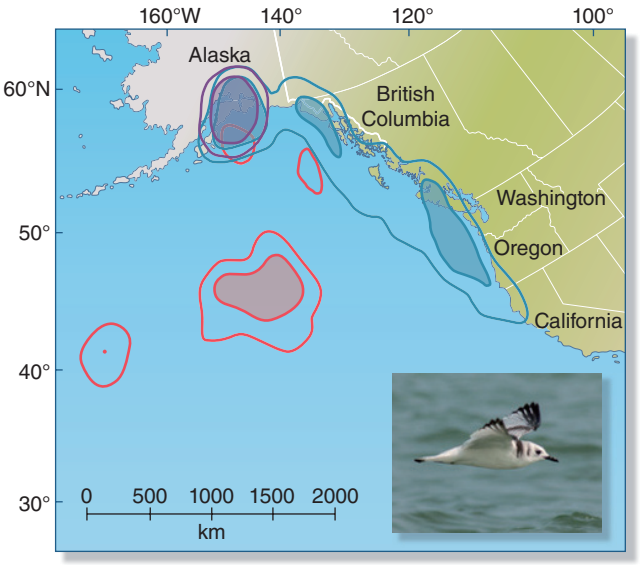


Fig. 12.03 Movements in the non-breeding season. Individual Black-legged Kittiwakes (*Rissa tridactyla*) from the same breeding colony in Alaska (USA) move to different locales in the non-breeding season: some remain near the colony (purple), others move southeast along the coast (blue), and some overwinter at sea (red). (From McKnight et al. 2011. © 2011 Inter-Research. Reproduced with permission. Photograph by Bernie Monette.)

sites, flying non-stop for at least 6 months as they migrate to sub-Saharan Africa and back (Liechti et al. 2013). When the small seabirds called Black-legged Kittiwakes (*Rissa tridactyla*) finish the breeding season in southern Alaska (USA), they show a variety of movements: some kittiwakes stay near the breeding colony all winter, others move up and down the nearby coast, and a third contingent spends much of the winter over the open ocean (McKnight et al. 2011) (Fig. 12.03).

In migratory birds, daily patterns of local movement can vary greatly at different times across the annual cycle. Red Knots (*Calidris canutus*) range over hundreds of square kilometers of mudflats in the Dutch Wadden Sea (Piersma et al. 1993), but when they arrive on their non-breeding grounds on the mudflats of Banc d'Arguin, Mauritania, where the availability of food is much more predictabe than in the Netherlands, they limit their ranging to less than a single square kilometer (Leyrer et al. 2012). Recent developments in tracking technology are helping ornithologists explore the local movements of these birds in ever greater detail (Box 12.01).

12.2 Patterns in migration

Each of the world's species of birds has adapted to the seasonality of resources across the earth's surface. Some birds find conditions around their breeding area to be sufficient for living year round, and these species often

Box 12.01 Tracking devices for studying bird movements



Fig. 12.B1.01 Radio-tracking devices for studying avian movements. (A) Researchers can attach small radio tags to a bird, here on the back feathers of a Clark's Nutcracker (*Nucifraga columbiana*), to monitor its movements. (B) Radio receivers and large antennas allow researchers to pinpoint a tagged bird's whereabouts after it is released back into the wild. (Photographs by Pocholo Martinez.)

For well over a century, ornithologists have been devising ways to track bird movements. The simplest and still most widely used markers are individually numbered metal leg bands; once placed on a bird, these leg rings usually stay on for the remainder of the bird's life. Based on the unique code, an individual bird can be identified whenever it is captured again, or if it is found dead. In situations where the bird's identification needs to be recognized from a distance, ornithologists may also attach a unique arrangement of colored plastic leg rings, or a wing tag, leg flag, or neck collar with a prominent number.

Starting in the early 1960s, these passive types of markers began to be augmented by an increasingly sophisticated set of electronic tracking devices. These devices generally weigh more and cost much more than simple numbered rings, but they have the great advantage of allowing birds to be tracked directly. The main challenge in deploying electronic tags is that most birds cannot carry a heavy tracking device. Ornithologists generally agree that any device attached to a free-flying bird should weigh no more than about 4% of the bird's mass. Thus, even a light tag of only 1 gram in total weight cannot be used on small birds like warblers, kinglets, wrens, and thornbills.

The first type of electronic devices widely used for tracking birds were radio transmitter tags that produce small frequency-modulated beeps when listened to through an FM radio receiver tuned to the tag's frequency. Newer radio tags that transmit individual digital codes have the advantage that many tags can all transmit on a single frequency. These simple beeper tags are still one of the best ways to keep track of the whereabouts of a moving bird, as long as the researcher can get a receiver into the transmission range of the tag and use triangulation to estimate the location of the bird (Fig. 12.B1.01).



Fig. 12.B1.02 Geolocators. Here, a Painted Bunting (*Passerina ciris*) is outfitted with a geolocator tag that records the timing of light and dark each day, which researchers will later use to reconstruct the bird's migration path over time. Obtaining data from this type of tag requires recapturing the bird at a later time. (Photograph by Tyler Michels, Oklahoma Biological Survey.)

For tracking birds globally, ornithologists have used tags that transmit radio signals to polar orbiting satellites,

Continued

which then transmit the locations back to the researchers. Satellite tags are very expensive and relatively heavy, but they have been used to make remarkable discoveries about the movements and migrations of birds as small as cuckoos and shorebirds.

Tags with on-board Global Positioning System (GPS) receivers and software allow the tag itself to determine its precise location, altitude, and ground speed just as today's smart phones and car navigation systems do. Some GPS tags are also equipped with a transceiver that can send data remotely and accept new measurement programs while the tag is on the bird.

Geolocators are even lighter tags that include a power source, an electronic clock, a light sensor, and an internal memory (Fig. 12.B1.02). By recording the time of sunrise and sunset where the bird is located, researchers can reconstruct the rough latitudes and longitudes of the bird's locations throughout its migrations.

When working with geolocators and some GPS tags, the researcher must recapture the bird and download the saved data. Despite these constraints, these small tags are now being used to study the movements of hundreds of kinds of birds, providing a much more detailed look at their patterns of annual migration.

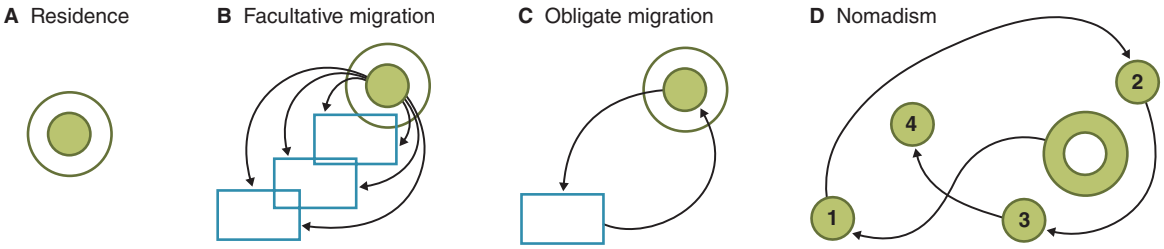


Fig. 12.04 Categories of avian residency and migration. Open shapes represent non-breeding areas, shading represents breeding areas, and arrows denote movements that link them. (A) Residents remain in the same location throughout the year, and are thus not migratory. (B) Facultative migrants move varying distances in different years, usually depending on conditions in the non-breeding season. (C) Obligate migrants undertake regular, predictable movements during their annual cycle. (D) Nomadic birds track environmental conditions in all seasons, often breeding in different locations in successive years. (From Greenberg and Marra 2005. © 2005 Smithsonian Institute. Reproduced with permission from Johns Hopkins University Press.)

remain in those areas permanently. But for a surprisingly large number of species, conditions are sometimes better elsewhere, and these species engage in various kinds of large-scale annual movements. Annual migrations can be as long as the globe-spanning journeys of Arctic Terns (*Sterna paradisaea*), or as short as the shift of a hummingbird or sunbird a few kilometers up and down a tropical mountain. Patterns in the migrations of birds are affected by many different biological influences, and, in turn, patterns in migration often have fascinating implications for other aspects of avian biology.

Luckily for birds, a large proportion of environmental variation is relatively predictable. The single-most important driver of environmental variation on earth—seasonal variation—exists because the earth's axis of rotation is not perpendicular to the sun. It is a cosmic accident that the earth's present axis of rotation is at an angle of 23.5° to the vertical: because of this tilt, the earth has seasons. In the northern winter, the northern hemisphere leans away from the sun, receiving less solar energy per hour and for fewer hours per day; in the northern summer, the balance is redressed, and the northern hemisphere basks in long days and short, warmer nights. Indeed, towards the North and South Poles, the summer sun does not set for many weeks at a time and winter darkness lasts equally long.

Birds breeding in high latitudes must contend with this seasonal variation, either by remaining throughout the winter or by moving away. To profit from the period of summer abundance, a migratory bird must both arrive and leave at the appropriate time, which requires the ability to move quickly, accurately, and relatively cheaply. With the ability to travel back and forth over large distances, migrating birds can enjoy a suite of favorable environments that occur sequentially at different locations during earth's annual cycle.

12.2.1 Types of annual movements

One of the most useful ways to categorize migration is by defining different seasonal patterns of movement (Fig. 12.04). Readers who live in the northern or southern temperate zone may take it for granted that many of the



Fig. 12.05 Minimal annual movements. Some resident birds like the Chowchilla (*Orthonyx spaldingii*) of Australia rarely venture more than a few hundred meters from their hatching site. (Photograph by Gerard Satherley.)

birds around them disappear for a large part of every year, often cherishing the **residents** that can make a living throughout their annual cycle even in locations with harsh winters. These resident birds have the simplest pattern of annual movement—that is, no annual movement at all. Once a resident settles down, it tends to remain in the same general area for the rest of its life, and for some birds this area may be quite small. In the tropics, residency is more common than migration. For example, Chowchillas (*Orthonyx spaldingii*) (Fig. 12.05) in the wet forests of eastern Australia occupy home ranges of less than 2 hectares (Jansen 1999); individual birds likely remain within an area only a few hundreds of meters across for their entire lives. Many resident tropical birds have home ranges only a little larger than those of the Chowchilla; Ivory-billed Woodcreepers (*Xiphorhynchus flavigaster*) in tropical Mexico are on the large end of this range, with home ranges of about 15 hectares (Rivera et al. 2003).

For other tropical birds, especially those that forage by commuting among widely scattered and ephemeral fruiting or flowering trees, daily movements may encompass tens of kilometers. For example, Wreathed Hornbills (*Rhyticeros undulatus*) in Thailand have a year-round home range of 2800 hectares (Poonswad and Tsuji 2008). In the tropics, seasonal conditions often vary more in terms of rainfall than in temperature, and most birds do not need to migrate long distances to find suitable year-round conditions. Thus, over much of the earth, there are more resident bird species than migrants.

Facultative migrants are birds that migrate only under certain conditions, rather than on a more predictable annual cycle. They may sometimes remain on their breeding grounds throughout the winter, moving elsewhere only in years when conditions are particularly harsh. Although their general migratory routes may be similar every year, the distances that facultative migrants travel along those routes can vary from year to year. Facultative migrants show similar variation in the timing of their movements, as they often linger in the breeding areas long after all the obligate migrants have departed on their fall migrations.

Facultative migration is usually triggered by deteriorating environmental conditions, such as a declining food supply or worsening weather. In northern temperate areas, facultative migrants include species such as shorebirds like the Northern Lapwings (*Vanellus vanellus*) of Eurasia, American Robins (*Turdus migratorius*) and Eastern Bluebirds (*Sialia sialis*) of North America, and European Blackbirds (*Turdus merula*) and European Starlings (*Sturnus vulgaris*). Members of all of these species sometimes remain in the breeding areas throughout a mild winter, but they move south or coastward when prey become unavailable in extremely cold weather. In North America, some populations of Yellow-rumped Warblers (*Setophaga coronata auduboni*) are facultative migrants that track their winter food supply: when a cold front reduces insect availability, densities of Yellow-rumped Warblers drop in Arizona, and the birds become more abundant to the south in Mexico (Terrill and Ohmart 1984) (Fig. 12.06).

Obligate migrants undertake predictable annual migrations to distant non-breeding grounds, sometimes traveling thousands of kilometers each season. In obligate migrant species, no individuals stay behind on the breeding grounds, and all of the migrants usually depart at similar times each year, often well before conditions begin to deteriorate. Most songbirds that breed in the northern parts of North America, Europe, and Asia fall into this category.

Many obligate migrants are site faithful in the winter, often showing as much territoriality and predictability in their winter behavior as on the breeding grounds. For example, both male and female Willow Flycatchers (*Empidonax traillii*) defend small territories throughout the winter in Costa Rica, and they are highly faithful to these sites from year to year (Koronkiewicz et al. 2006). In obligate migrants, many aspects of migration seem to be genetically controlled, resulting in very similar patterns across years. For example, these migrants move by a

Residents: birds that remain in the same area year round.

Facultative migration: a pattern in which the timing and distance of migration changes from year to year in response to varying environmental conditions.

Obligate migration: a pattern in which individuals migrate to the same areas on the same schedule every year.

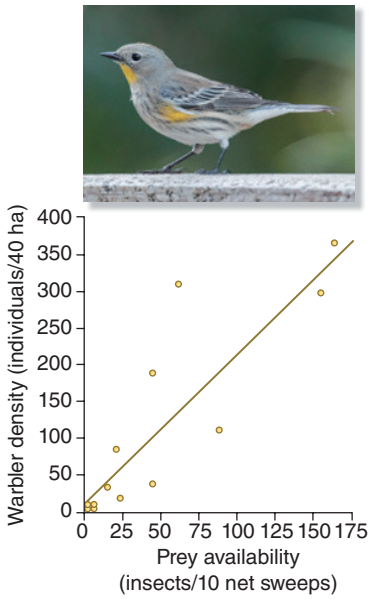


Fig. 12.06 Facultative migrants. Yellow-rumped Warblers (*Setophaga coronata*) in some regions move in response to prey availability. As the graph shows, fewer warblers remained at this winter study site when insect abundance declined—in this case, because of cold weather. (From Terrill and Ohmart 1984. Reproduced with permission from American Ornithologists' Union. Photograph by Jim Scarff.)

calendar that appears to be "hard-wired" in the sense that it is more sensitive to changes in photoperiod than to temporary local variations in weather conditions. Even the smallest bird species can be obligate migrants: for example, Ruby-throated Hummingbirds (*Archilochus colubris*) breed as far north as central Canada, then migrate long distances to the southern USA, Mexico, and Central America, sometimes buzzing across the Gulf of Mexico in a single flight.

Partial migrants are species in which some individuals within a population leave long in advance of winter, but others stay behind. This category does not appear in Figure 12.04 because it really represents a mix of different migration patterns within one population of birds. The complexity of partial migration can be seen in the distribution map of the European Blackbird (Fig. 12.07). In the northeastern part of this species' range, all blackbirds are obligate migrants, with birds present only in the summer months. Conversely, there is a band along the coast of North Africa and in Iran where this species only occurs in the winter months. A broad region occurs between these areas where at least some blackbirds are present in all seasons. Yet in winter, these intermediate areas may harbor a mix of obligate migrants that arrived from the north in early fall, facultative migrants that arrived later in the fall and early winter as conditions deteriorated to the north, and individuals that remained as residents.

Nomadic bird species move less predictably from one breeding ground to the next, sometimes in great numbers, and often are quite flexible in where and when they breed. Some birds in this group are on the move for much of their lives. This mode of movement is limited almost entirely to birds of the tundra and coniferous forest of the far north, and to birds of the dry steppes, shrublands, and woods of the arid tropics. In these relatively simple ecosystems, fluctuations in the populations of a single type of food often can drive birds to move long distances between breeding sites. For example, Snowy Owls (*Bubo scandiaca*) in the high arctic tundras concentrate their foraging on lemmings, the populations of which are highly variable from year to year and from place to place. As a result, these owls have very little attachment to a single breeding site, and they may wander over many thousands of kilometers between breeding sites in successive breeding seasons (Therrien et al. 2014). In Australia in particular, a great variety of birds—from songbirds such as honeyeaters, trillers, and woodswallows, to larger birds such as kites and ducks—are quite flexible in when and where they breed, responding to great variation in water levels and the flowering of key food species of plants. Likewise, the Red-billed Quelea (*Quelea quelea*) of Africa—a weaver—is famous both for the massive flocks that breed in ephemeral colonies and for the irregularity of their timing and location (Fig. 12.08). Queleas are nomadic because they feed on the seeds of unpredictable annual grasses that grow lushly only in locations and seasons with good rainfall (Cheke et al. 2007).

Partial migration: a pattern in which some individuals within a population or species are migrants and others are non-migratory residents.

Nomadic: refers to birds that move irregularly, rather than in a predictable migration, usually in response to highly variable food resources or other environmental variation.

Migratory connectivity: the degree to which individuals breeding in a particular region migrate to the same overwintering region.

12.2.2 Migratory connectivity

The term **migratory connectivity** refers to the degree to which a population of birds breeding in a distinct region remains cohesive as individuals move to a distinct region in the winter (Webster et al. 2002). In species with the strongest migratory connectivity (Fig. 12.09A), all members of a particular breeding population winter in the same well-defined area. Conversely, where migratory connectivity is low, individuals from different breeding



Fig. 12.07 Partial migrants. In different locations, European Blackbirds (*Turdus merula*) are year-round residents, facultative migrants, or obligate migrants. Even within the region where blackbirds are present year round (green), the population includes full-time residents, facultative migrants seeking refuge and resources because conditions farther north became unsuitable, and obligate migrants that migrate south every winter regardless of conditions in the north. (Map courtesy of www.xeno-canto.org. Adapted from BirdLife International and NatureServe 2014. Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA. Photograph by Rinus Motmans.)

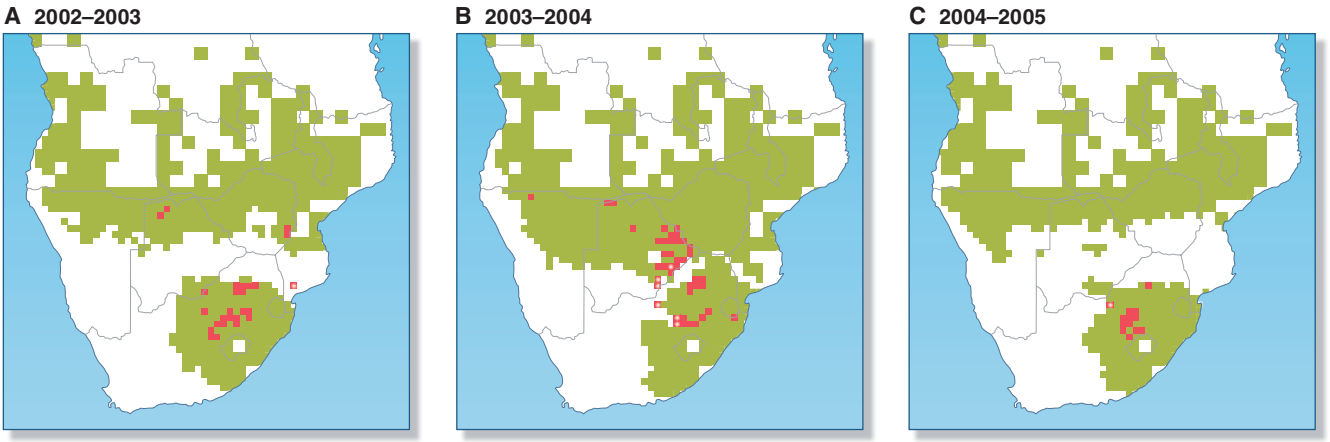


Fig. 12.08 Nomadic breeding. Massive colonies of Red-billed Queleas (*Quelea quelea*) breed in locations that receive enough rainfall to produce grass seed (green), which serves as food and nesting material. Quelea colonies (red) move to different areas in different years. (From Cheke et al. 2007. Reproduced with permission from John Wiley and Sons.)

populations share the same non-breeding sites (Fig. 12.09B). Confusingly, the term **population connectivity** is also used in reference to migrant birds, and as the tightness of migratory connectivity between breeding and non-breeding areas increases, the population connectivity between adjacent

Population connectivity: the degree to which two breeding populations are connected by dispersal and gene flow.

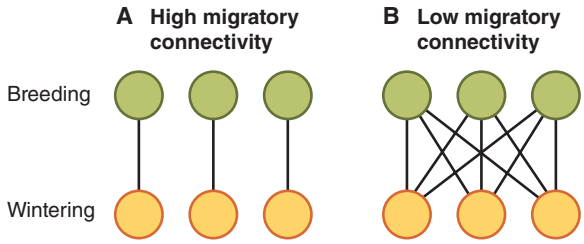


Fig. 12.09 Migratory connectivity. (A) In species with high migratory connectivity, individuals from each breeding region migrate to distinctive non-breeding areas. (B) When migratory connectivity is low, individuals from different breeding regions intermix during the non-breeding season. (© Cornell Lab of Ornithology.)

breeding subpopulations via interactions at the wintering grounds grows weaker.

Studies of two threatened bird species in Europe provide contrasting examples of migratory connectivity patterns. Individual Hoopoes (*Upupa epops*) from the same breeding population spend the winter in very different parts of Africa (Bächler et al. 2010), showing very weak migratory connectivity (Fig. 12.10). In contrast, Eurasian Wrynecks (*Jynx torquilla*) from breeding sites in Germany have quite restricted winter ranges in Africa, with greater migratory connectivity compared with Hoopoes (Reichlin et al. 2010).

12.2.3 Migratory paces and paths

Different bird species undertake migratory journeys of varying length and duration. Most species travel in many short bouts of migratory flight interspersed with short periods when they rest and refuel; that is, they "hop." Others make a few long-distance non-stop flights interspersed with periods of refueling; that is, they "skip." Finally, in some of the most spectacular migratory feats, some species travel in one very long migratory flight—a "jump."

Each of these strategies has advantages and disadvantages. Traveling in one big jump, as the Bar-tailed Godwit (*Limosa lapponica*) does from Alaska to New Zealand, can save flight time during transoceanic flights and reduce the risk of predation in staging areas (Gill et al. 2009). However, such long flights require exceptional physiological adaptations, and, if the weather turns against them, these migrants take great risks making non-stop flights over large expanses of water. The Hudsonian Godwit (*Limosa haemastica*)—an only slightly less extreme migrant—usually stops at just one site in central USA on its northward flight from Patagonia to central Alaska, and at three sites on its way back to Patagonia in the northern fall (Fig. 12.11). The longest non-stop leg of the northward flight, more than 15,000 kilometers from Chile to Nebraska (USA), takes 4–8 days; the birds follow that leg of the migration with a refueling stop of up to 3 weeks before making another multi-day non-stop flight to Alaska (Senner et al. 2014).

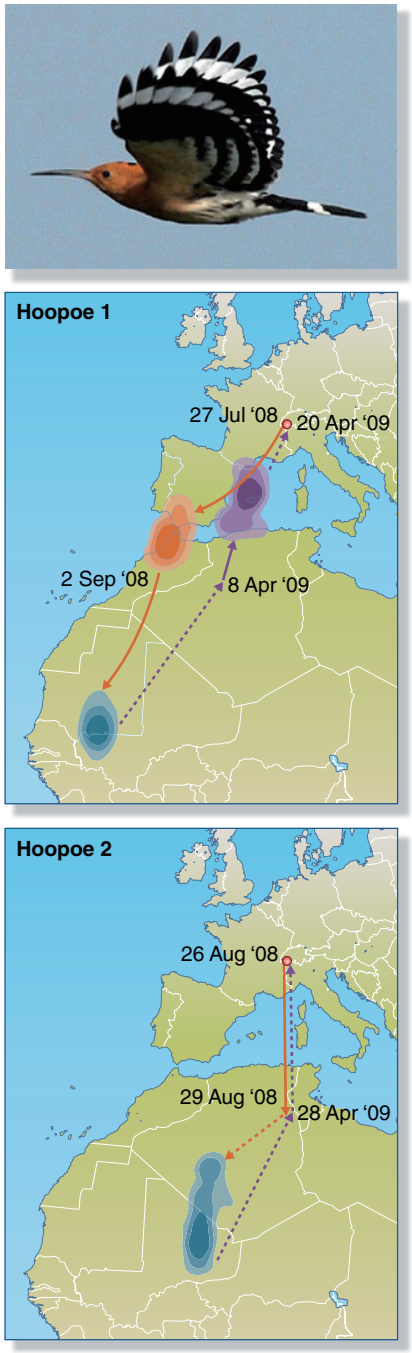


Fig. 12.10 Low migratory connectivity. Two Hoopoes (*Upupa epops*) originating from the same breeding population (red ring) migrated along different routes to different overwintering locations (blue areas). Orange arrows represent flight paths to the wintering area; purple arrows depict flight paths back to the breeding area. Shading of orange and purple represent stopover locations. (From Bächler et al. 2010. © 2010 Bächler et al. CC-BY-4.0. Photograph by Umang Dutt.)

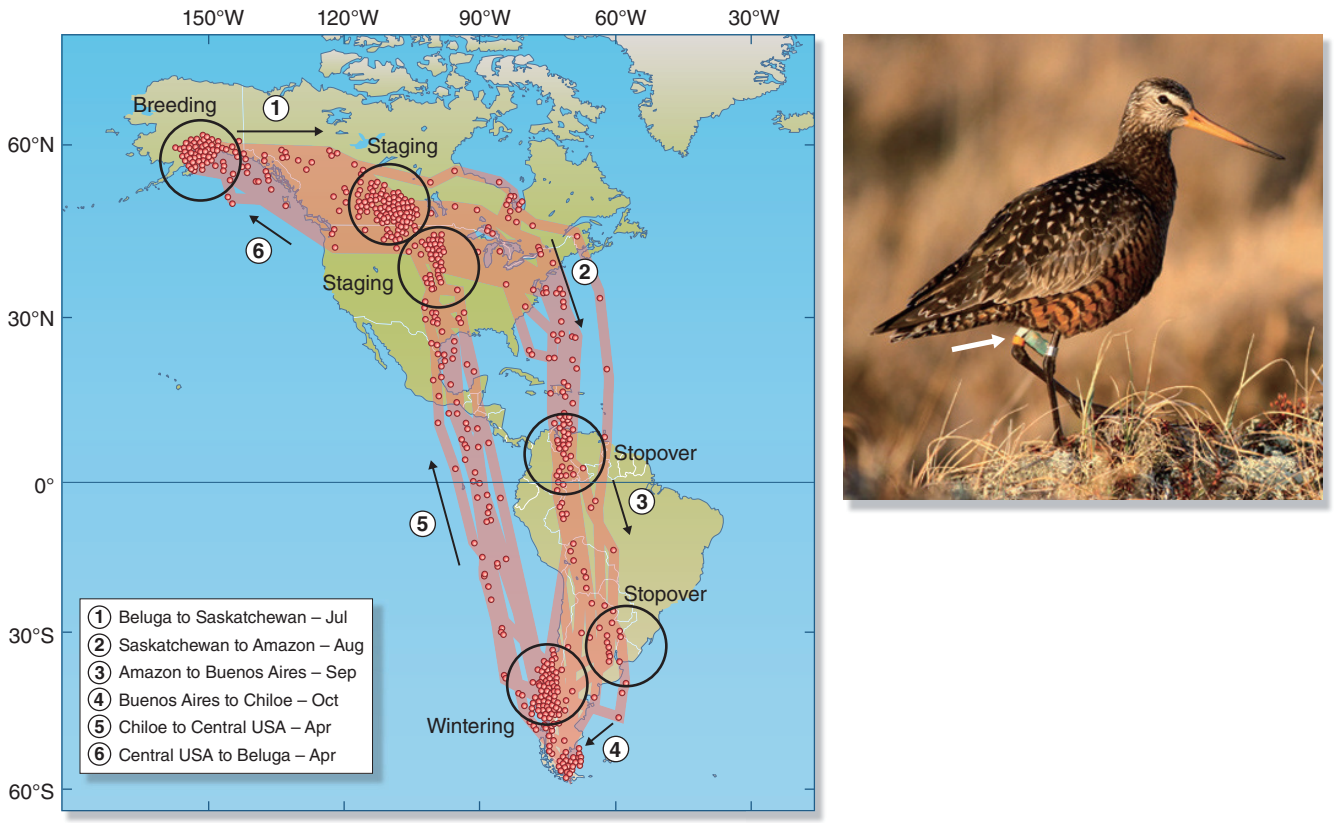


Fig. 12.11 Long-distance migration. Researchers attached geolocators (arrow in photo) onto Hudsonian Godwits (*Limosa haemastica*) to track their movements throughout the year. Individual godwits breed in Alaska, stopping at only a few sites during their annual migrations to and from southern South America. Circles indicate staging and stopover sites where birds rest and refuel, usually for multiple days, awaiting favorable migratory weather conditions. (From Senner et al. 2014. © 2014 Senner et al. CC-BY-4.0. Photograph by Andy Johnson.)

While migrating, most birds make adjustments in their paths in response to changing flight conditions and geography. The Great Snipe (*Gallinago media*) is an exception in that it migrates from Scandinavia to sub-Saharan Africa in one rapid bolt, passing non-stop over habitats both good and bad, in an almost direct path, with seemingly little regard for winds aloft (Klaassen et al. 2011a). It flies fast (with ground speeds nearing 100 kilometers/hour) and covers distances of up to 6800 kilometers in 3–4 days.

Stopping frequently can reduce the risk of exhaustion and the need for extreme physiological adaptations, but it may result in a relatively slow pace of migration and a larger period of vulnerability during frequent refueling stops. For example, Swainson's Thrushes (*Catharus ustulatus*) break their northward spring migration across the USA into three or more short legs, stopping at different wooded areas (Wikelski et al. 2003) and thus encountering different predators with different habits at each stop. Individual Lesser Black-backed Gulls (*Larus fuscus*) vary greatly in their migratory pace, but many of the individuals tracked from a breeding colony in the Netherlands did not seem to be in a hurry during their fall migration: they stopped often, sometimes only briefly and other times for several weeks (Klaassen et al. 2011b).

Although one might expect birds simply to follow the same back-and-forth migration route in the fall and spring, many species clearly choose different paths in different seasons. Migration routes that differ predictably between seasons often are termed "circle" or "loop migrations" and usually result from strikingly different relative wind directions during the south-bound and north-bound migrations. For example, several species of soaring migrants flying from Europe to eastern Africa migrate through the Arabian Peninsula in the fall, but further to the west via the Suez and Israel in the spring. Tracking studies have similarly revealed that Red-backed Shrikes (*Lanius collurio*) cross the Mediterranean Sea in fall but circumvent it via Arabia in spring (Tøttrup et al. 2012), whereas European Common Cuckoos (*Cuculus canorus*) execute a tight loop during their annual migrations south and north across the Sahara (Willemoes et al. 2014) (Fig. 12.12).

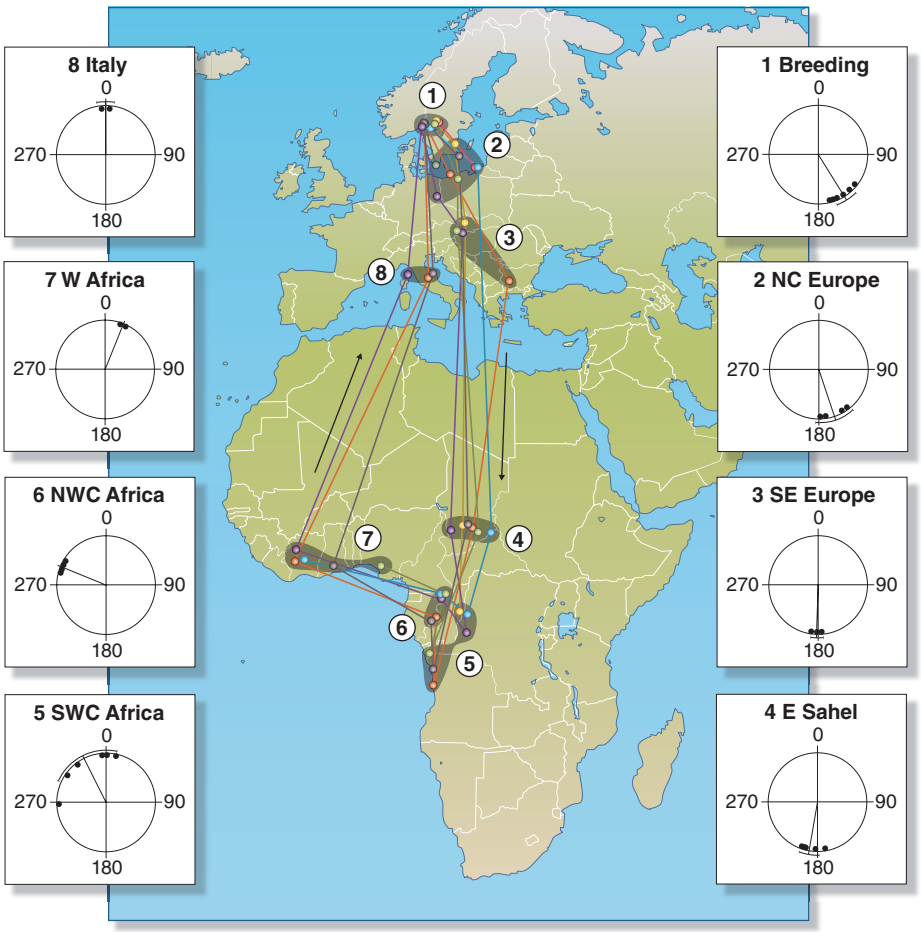




Fig. 12.12 Loop migration. Each year, Common Cuckoo (*Cuculus canorus*) individuals (colored lines) follow a clockwise path from their breeding grounds in Scandinavia to central Africa and back. The compass circles next to each site show the directional bearings of cuckoos being tracked as they began their flights to the next sites in their migratory circles. (From Willemoes et al. 2014. © 2014 Willemoes et al. CC-BY-4.0. Photograph by Vogelartinfo, https://commons.wikimedia.org/wiki/File:Cuculus_canorus_vogelartinfo.jpg. GFDL 1.2.)

Leapfrog migration occurs in species with a broad breeding range, in which the individuals breeding the farthest north or south migrate to the most distant wintering areas, traveling farther and passing over birds that breed in intermediate areas that move shorter distances to winter. Among songbirds, one of the best known examples of leapfrog migration occurs among the different races of the Fox Sparrow (*Passerella iliaca*) in western North America. Fox Sparrows are year-round residents in areas on the central Pacific coast. The subspecies that breeds in central British Columbia (Canada) spends the non-breeding season far south in Oregon (USA). The subspecies breeding even farther north spend the non-breeding season farther and farther south (Fig. 12.13). Leapfrog migration is also seen in the Yellow Wagtail (*Motacilla flava*): northern European breeders migrate to Africa south of 10°N, passing over and beyond populations from the Mediterranean that migrate only to areas north of 11°N (Bell 1996). Leapfrog migration may evolve when conditions in the north become increasingly favorable and the edge of a species' breeding distribution moves further and further north. Those most northerly breeders may then face greater competition when they return to mix in the non-breeding areas with birds from southerly populations; since the northern birds are already migrating long distances, natural selection favors their extending their southbound journey to winter in areas with less competition (Buehler et al. 2006).

Leapfrog migration: a pattern in which the individuals at the extreme of the breeding distribution migrate farthest, in the process traveling past birds that breed and winter in intermediate locations.

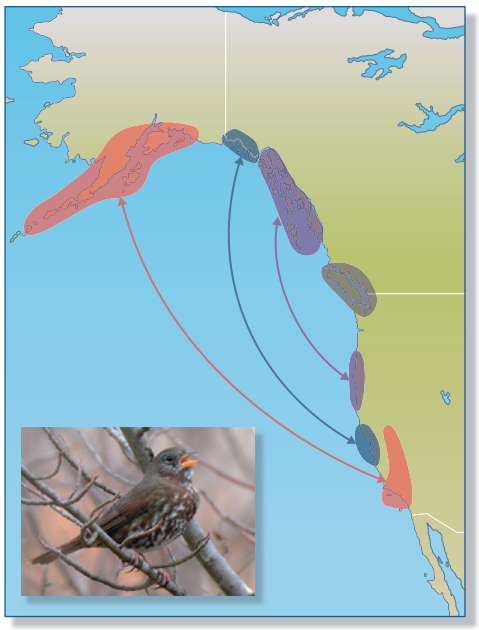


Fig. 12.13 Leapfrog migration. Along the Pacific coast of North America, the most northerly breeding Fox Sparrows (*Passerella iliaca*) winter farthest south, passing over individuals with intermediate breeding and wintering ranges. Arrows connect summer and winter ranges and do not represent migratory flight paths. (From Bell 1997. Reproduced with permission from Cooper Ornithological Society. Photograph by Jerry Ting.)

12.2.4 Sex and age differences in migration

Within a bird species, individuals of different ages and sexes often have somewhat different migration routes, non-breeding areas, and/or migration schedules. In many species, males and females depart from the breeding area at different dates, with departure delayed for the sex that cares for the chicks up to their independence. For example, males of several northern-breeding species of ducks leave the breeding grounds before the females, which stay until their young have become independent. In some of these same northern habitats, female phalaropes depart before males, since in phalaropes the males provide all parental care to the chicks (Chapter 9).

During the spring migration of many species—especially songbirds—males travel ahead of females and arrive earlier at the breeding grounds, where they can get a jump on competition for breeding territories. In a comparison of 22 species of European landbirds, males returning on their spring migration arrived 3–19 days before females (Saino et al. 2010).

Individual birds often change their patterns of movement with age. Some young shorebirds remain on the non-breeding grounds during their first year, not returning to the breeding grounds until their second year of life. This pattern of delayed return is even more pronounced in many gannets, gulls, terns, eagles, and condors, all birds that take many years to reach sexual maturity. In most migratory species, adults leave the breeding areas before juveniles. Young Eurasian Spoonbills (*Platalea leucorodia*) that have just fledged begin their southward migration later than the adults, and spoonbills that fledge late in the season do not migrate as far south as do earlier-fledging birds (Lok et al. 2011). Similarly, during their first fall migration, young Reed Warblers (*Acrocephalus scirpaceus*) pass through Israel about 3 weeks later, on average, than do older birds (Merom et al. 2000). In spring migration, birds on their first journey to breeding grounds tend to lag behind birds making repeat migrations; in 12 species of passerines passing through Ontario, Canada, all but one species showed later passage dates for younger birds of both sexes (Stewart et al. 2002).

12.2.5 Movements on the non-breeding grounds

Once in the non-breeding areas, birds do not necessarily remain at one site, as most species do during the breeding season. Both White (*Ciconia ciconia*) and Black (*Ciconia nigra*) Storks may move around their non-breeding range in Africa, sometimes spending several weeks in "pre-wintering areas" before moving farther south for the rest of the northern winter (Van den Bossche 2002; Bobek et al 2008). Gulls of many species also often move from site to site in winter, as typified by a study of the movements of a single Lesser Black-backed Gull (*Larus fuscus*) from breeding areas in the Netherlands to non-breeding areas in France, Portugal, and Spain, and back again (Klaassen et al. 2011b). Similarly, European raptors such as the Lesser Spotted Eagle (*Clanga pomarina*) often move among several locations in Africa during the winter period (Meyburg et al. 2004). Non-breeding populations of geese and waterfowl that spend the northern winter in northwestern Europe may suddenly evacuate an area during extremely cold winters with heavy snowfall, or when water bodies freeze, migrating to alternative sites farther south.

Data on the winter movements of smaller birds have become available as tracking devices have grown lighter, and it has become clear that many small birds also shift locations during the winter season. Common Swifts (*Apus apus*) tracked with tiny geolocators shifted their non-breeding areas in the Congo Basin of Africa within a single winter (Åkesson et al. 2012). Studies using similar tracking technology found that some Swainson's Thrushes (*Catharus ustulatus*) also move among multiple non-breeding sites in Mexico, Guatemala, and Honduras (Delmore et al. 2012). Similarly, several different species of kingbirds (*Tyrannus* species) visit a succession of non-breeding sites in Brazil during the non-breeding season

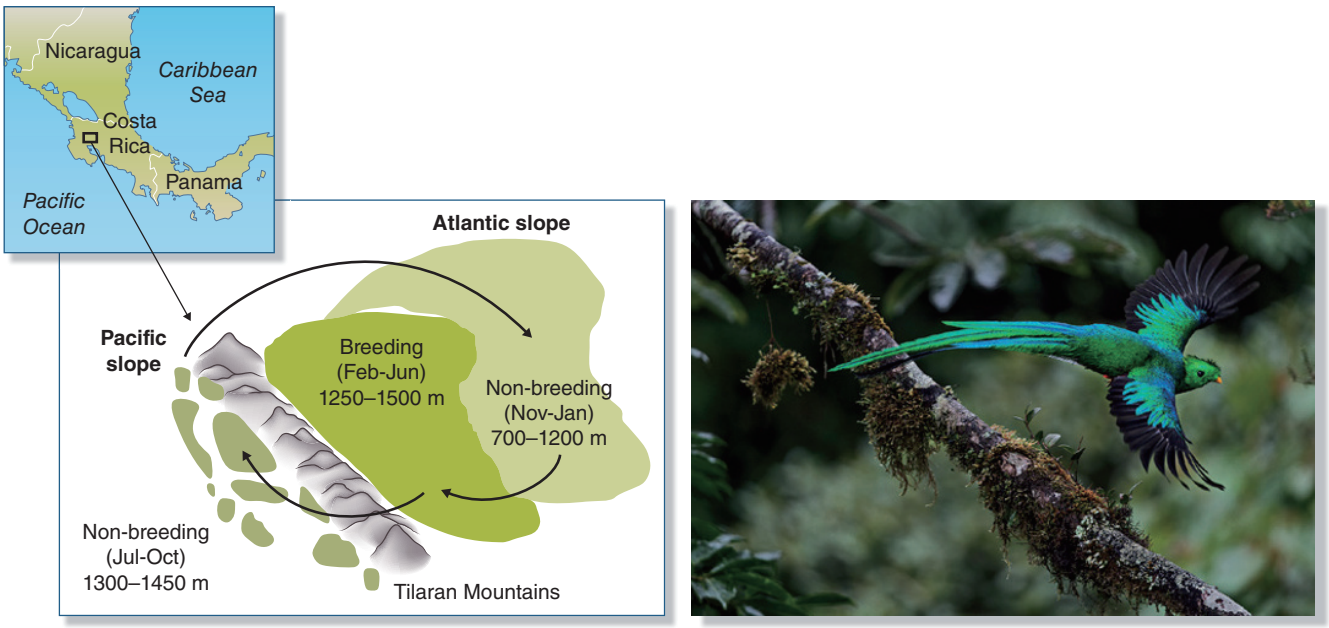


Fig. 12.14 Altitudinal migration. Resplendent Quetzals (*Pharomachrus mocinno*) migrate to different elevations and slopes in Costa Rica during different parts of the year. (From Powell and Bjork 1994. Reproduced with permission from Cambridge University Press. Photograph by Jan Pedersen.)

(Jahn et al. 2013). A large proportion of the Tree Swallows (*Tachycineta bicolor*) from eastern North America form enormous nocturnal roosts in late fall in sugarcane fields in Louisiana (USA), scattering to non-breeding sites further south when the cane fields are harvested in November (Laughlin et al. 2013).

12.2.6 Altitudinal migration

Many birds that live in mountainous areas undertake **altitudinal migration**, usually breeding in higher elevations and moving to lower elevations during the non-breeding season. They may not travel far in terms of overall distance, but by changing their elevation they can exploit new resources under different environmental conditions, just as another bird might do by migrating much farther to a different latitude. For example, Common Quails (*Coturnix coturnix*) in Catalonia on the eastern edge of Spain migrate to higher elevations during the summer, following the seasonally rising wave of newly ripened grass seeds, their favored food. These grasses mature later in the season at higher altitudes, and the quail work their way from altitudes of about 200 meters to about 1200 meters over a period of about 2 months before heading downslope again for the winter (Prats et al. 1996).

Altitudinal migration is particularly common in birds of tropical mountains that forage on fruit or nectar. For example, the Resplendent Quetzal (*Pharomachrus mocinno*) of Central America breeds in montane cloudforests, migrates downslope to pre-montane wet zones on Pacific slopes, and then moves across the continental divide to low Atlantic slopes (Fig. 12.14), spending several months in each area before returning to its cloudforest breeding areas (Powell and Bjork 1994). Many species that undertake altitudinal migrations are facultative migrants: not all members of the populations migrate, and a given individual may not migrate every year.

12.2.7 Austral migration

If one of the main drivers of migration is deteriorating living conditions during the winter, one would expect that birds breeding at high latitudes in the southern hemisphere would migrate north to warmer non-breeding areas, following a migration schedule offset by 6 months from that of the northern hemisphere. Although this kind of **austral migration** does occur, surprisingly little is known about it because most migration research has focused on the birds that breed in the northern hemisphere.

Compared with their northern counterparts, austral migrants experience some interesting geographic influences

Altitudinal migration: seasonal migration up or down mountain slopes.

Austral migration: refers to seasonal migration in the southern hemisphere, in which birds typically move north in the fall and south in the spring.

on their movements. One of these is visible on any map of the world's continents and oceans: the landmass area of the southern hemisphere is very heavily weighted toward the tropics, with the land areas of the southern temperate and antarctic zones much smaller than the corresponding zones in the northern hemisphere. Thus, relatively fewer birds in the southern hemisphere live in locations with extreme seasonal variations in temperature. In addition, most austral migrants do not have to cross forbidding ecological barriers to reach adjacent tropical areas. The distances that austral migrants travel are therefore generally much smaller than the distances traveled by long-distance migrants that breed in the north.

In South America, for example, more than 200 bird species are known to undertake austral migrations. Many migrants originating in temperate South America move north in the austral winter to warmer areas in temperate or subtropical parts of that continent, but some travel farther north to winter in tropical Amazonia. New World flycatcher species account for approximately 33% of these South American austral migrants, and for more than half of all the individual birds that migrate (Chesser 1994).

The migrant birds of both Australia and southern Africa also include species that visit these southern continents in the non-breeding season and return to breeding areas in the northern hemisphere. Among the birds that breed in these two regions, directed seasonal movements are little known, with most species displaying nomadic or irregular movements in response to variation in environmental conditions. For example, in a review of the movements of honeyeaters in Australia, Keast (1968) estimated that 35% of the species were strict residents, 15% were residents that made local movements, 39% were nomadic, about 6% were altitudinal migrants, and fewer than 5% were latitudinal migrants within Australia. In both Africa (Cumming et al. 2008) and Australia (Roshier et al. 2008), waterfowl do not display large-scale latitudinal movements as in the northern hemisphere. Rather, their movements appear to be coordinated with unpredictable changes in water levels and habitat availability over regional scales within both continents.

12.2.8 Migratory divides

Migratory divides arise where distinct breeding populations of the same bird species meet, yet birds from each side of the divide have different migration pathways. Migratory divides have been particularly well studied in some European songbirds. For example, a migratory divide across central Scandinavia separates two populations of Willow Warblers (*Phylloscopus trochilus*) (Bensch et al. 1999). In fall, birds from the southern population migrate to tropical West Africa, whereas birds from the northern population migrate to East and South Africa (Fig. 12.15). Similar migratory divides in thrushes (Box 12.02) and warblers occur across the Rocky Mountains in North America and around the Tibetan Plateau in central Asia.

Migratory divides: locations where two populations of the same species with different migratory orientations meet and potentially interbreed.

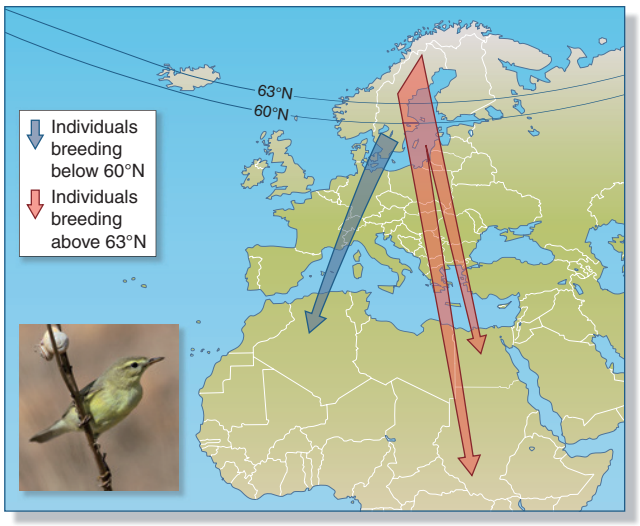


Fig. 12.15 A migratory divide. In their fall migration, Willow Warblers (*Phylloscopus trochilus*) breeding in Sweden segregate according to the latitude at which they nest: individuals that breed below 60°N (blue) winter in northwestern Africa, whereas breeders above 63°N (red) take a southeastern route to winter in eastern Africa. (From Bensch et al. 1999. Reproduced with permission from John Wiley and Sons. Photograph by António A. Gonçalves.)

At a migratory divide, parent birds from opposing sides of the divide may sometimes pair up and mate. For example, a pair of White Storks (*Ciconia ciconia*) breeding along a migratory divide in eastern Germany was tracked for 10 years using satellite telemetry. Every year the female migrated along the eastern route through Turkey and Israel to South Africa, whereas her mate took the western route and migrated a relatively short distance to southern Spain (Kölzsch and Blasius 2008). Tracking the offspring of such partners could provide researchers with the opportunity to dissect the genetic basis for migratory behaviors, since the migratory behaviors of the different parents can be compared with that of their hybrid offspring. Researchers pursued such an opportunity in the lab by captive-breeding European Blackcaps (*Sylvia atricapilla*) from either side of their central European migratory divide. Matings of birds from the same side of the divide produced offspring with orientations like their parents, while crosses of parents from across the divide produced hybrid young with intermediate migratory directions (Helbig 1996) (Box 12.03).

Box 12.02 Migratory divides and speciation in the Swainson's Thrush

The hauntingly melodic song of the Swainson's Thrush (*Catharus ustulatus*) can be heard in coniferous woodlands across much of North America in spring, from the redwood-studded streamsides of California (USA) to the spruce forests of Labrador (Canada). This thrush is a long-distance migrant nearly everywhere that it breeds. Its range is subdivided into two distinct migratory populations: one that breeds near the Pacific coast of North America and migrates along a western route to wintering areas in Central America, and another that spans the remaining inland and eastern parts of the breeding range and travels along a longer and often more circuitous eastern route to southerly wintering areas in South America (Ruegg 2008) (Fig. 12.B2.01).

These two migratory forms meet in a classic migratory divide at breeding sites in the mountain valleys of northwestern North America, where individuals from the two populations may pair up and produce hybrid offspring. In-depth genetic analysis and field studies of one of these hybrid zones in the Coast Mountains of British Columbia (Canada) have shown that, despite this ongoing hybridization, gene flow between the two forms is limited (Ruegg 2008). Further, an analysis of genetic variation in this species—including genes related to migration, song, and plumage coloration—suggests that differences in migratory behavior may be one of the main factors maintaining the barrier to gene flow (Ruegg et al. 2014). These two populations may therefore be on the path to becoming separate species, with their differences in migratory behavior helping to catalyze this process of evolutionary divergence.

There are several hypotheses to explain how differences in migratory behavior may lead to speciation in these and other birds. One is that differences in the timing of arrival on the breeding grounds may reduce the opportunity for mixed pairing in hybrid zones between distinct migratory forms (Ruegg et al. 2012). Another possibility is that hybrid offspring are less fit than their parents as a result of their intermediate migratory behavior. Recent improvements in tracking technologies soon may make it feasible to test this possibility directly.

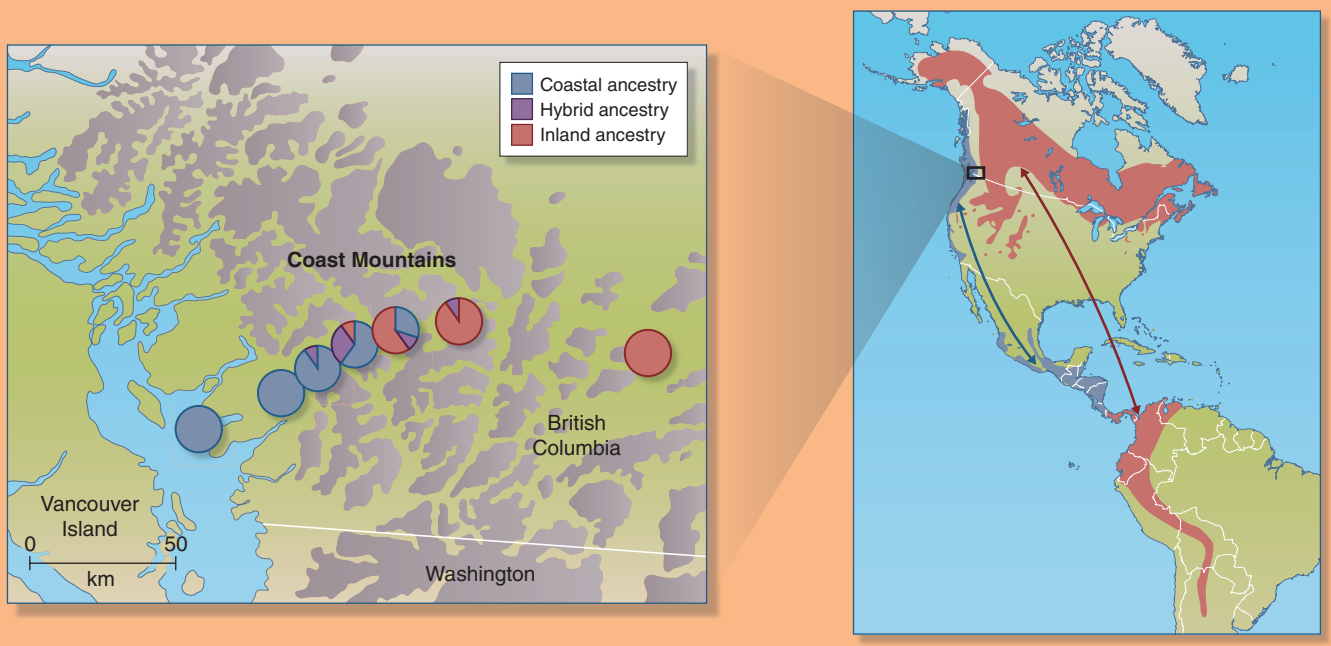


Fig. 12.B2.01 The migratory divide of Swainson's Thrush (*Catharus ustulatus*). Coastal (blue) and inland (red) populations use different migration routes to separate wintering grounds in the neotropics. The pie charts depict the fraction of breeding population types at study sites near the migratory divide, where the two forms come into contact and sometimes interbreed (purple). (From Ruegg 2008. Reproduced with permission from John Wiley and Sons.)

Box 12.03 Movements of the European Blackcap: studies in migratory evolution

The European Blackcap (*Sylvia atricapilla*) (Fig. 12.B3.01)—a warbler that breeds commonly in woodlands throughout Europe—is capable of a wide range of migratory strategies, including residency and short- and long-distance migration. Its populations exhibit several migratory divides, and some breeding populations consist of a mix of both residents and migrants. Coupled with the fact that blackcaps can be bred and raised in captivity, this wide range of movement behaviors has helped make this species a useful model for investigating the genetic basis of many different traits involved in migration.



Fig. 12.B3.01 The European Blackcap (*Sylvia atricapilla*). This species has been the subject of classic studies that demonstrate a genetic basis for migratory orientation and duration. (Photograph by Juan Emilio, Las Palmas de Gran Canaria, Spain, https://commons.wikimedia.org/wiki/File:Curruca_Capirotada.(_Sylvia_atricapilla_heineken)(%E2%99%82)_(5215354550).jpg. CC-BY-SA 2.0.)

Blackcaps from populations with differing migratory strategies have been cross-bred in captivity, and their hybrid offspring exhibit traits that are intermediate between the parent populations in the occurrence of migratory restlessness (*Zugunruhe*), its duration, and its direction (Berthold and Querner 1981; Berthold 1991; Berthold and Helbig 1992; Helbig 1996). By selectively breeding other captive blackcaps, researchers have similarly changed the occurrence and intensity of *Zugunruhe* and its timing through artificial selection (Pulido et al 2001; Pulido and Berthold 2010) (Chapter 3). These studies clearly show that many subtle details of blackcap migratory behavior have a genetic basis that has been molded over time by natural selection.

Recent changes in the migratory behavior of the blackcap population breeding in central Europe show that, even outside the laboratory, change in these behaviors can be swift. This population traditionally spent the winter in the Iberian Peninsula and northern Africa, but it has recently found sufficient winter food on bird tables in the UK and Ireland to spawn a subpopulation with a new migration route there. This new population of migrants returns to the breeding sites earlier than their counterparts spending the non-breeding season farther south. As a result of their different timing, birds wintering in Africa tend to breed with one another, and birds wintering in the UK likewise tend to breed with one another (Berthold and Helbig 1992; Bearhop et al. 2005), possibly setting the stage for future speciation.

12.2.9 Concentration points and staging areas

Many studies of migratory biology have been conducted in places where migrating birds are concentrated by the local topography or other environmental forces. Often these narrow migratory concentration points are utilized by staggering numbers of birds, making them wonderful places to observe and band migrants. One of the largest such migratory concentrations occurs in Veracruz, Mexico, where an aerial "river of raptors" is an annual spectacle (Fig. 12.16). This concentration results from the narrowing of Mexico's eastern coastal plain near the Isthmus of Tehuantepec. The entire world population of several birds, including the Mississippi Kite (*Ictinia mississippiensis*) and Swainson's Hawk (*Buteo swainsoni*), travel over Veracruz during migration, and count estimates from hawk-watching stations there are used to estimate the total number of individuals of the entire species (Ruelas Inzunza et al. 2010). Other locations where great numbers of raptors pass overhead during migration include Batumi, Georgia (where the birds are concentrated by the Black Sea); Bosporus, Turkey (where migrants cross from Europe into the Middle East); Israel (where they are concentrated by the Mediterranean Sea to the west and vast deserts to the east); and the Straits of Gibraltar that separate Spain from Morocco (where they are concentrated by the Mediterranean and the Atlantic on either side) (Bildstein 2006) (Fig. 12.16).

Migratory concentrations also occur in areas where food is especially abundant, and many species of migratory birds spend substantial time at **staging areas** to refuel before continuing their migrations. Well-known staging sites include Delaware Bay on the mid-Atlantic coast of North

Staging areas: locations where migrating birds fuel up just before, or in a pause during, migration.



Fig. 12.16 Migrating raptors concentrate in narrow overland corridors. This map depicts the five main raptor migration routes worldwide. (From Bildstein 2006. Reproduced with permission from Cornell University Press.)

America, which serves as a major staging area for migrating shorebirds that feast on the eggs of horseshoe crabs. This abundance of food allows these shorebirds to increase their weights by 70–80% in a few weeks (Baker et al. 2004). Disrupting these critical areas may cause dramatic population declines of the birds that rely on them for refueling: commercial exploitation has decreased the number of horseshoe crabs in Delaware Bay, resulting in a concomitant decline in numbers of Red Knots (*Calidris canutus*) (Baker et al. 2004; Niles et al. 2009). Other important staging sites that host huge aggregations of shorebirds include the Copper River Delta in Alaska, the Wadden Sea in western Europe, and the Yellow Sea in eastern Asia. Shorter pauses during migration occur at **stopover sites**, locations where migrating birds take a break to rest, eat and drink for maintenance, and/or await favorable migratory conditions.

The philopatry (site faithfulness) seen in the more sedentary parts of the annual cycle of many migrants sometimes extends to migratory staging and stopover sites, as some birds use the same route from year to year. Three warbler species (*Sylvia atricapilla*, *Sylvia borin*, and *Phylloscopus collybita*) passing through the Iberian Peninsula during spring and fall migrations show moderate levels of philopatry to their stopover sites (Cantos and Tellería 1994). A fourth species, the Reed Warbler (*Acrocephalus scirpaceus*), is a specialist of reed beds, a habitat which has a naturally patchy distribution. Likely because of this more specialized habitat requirement, Reed Warblers are more highly philopatric during migration, and some migrating Reed Warblers are known to have stopped over at the same site in Israel for up to five successive migrations (Merom et al. 2000).

12.2.10 Flyways

Flyways are established routes used year after year by large numbers of migrants, with many bird species often converging to use similar flyways. Flyway designations can be useful in bird conservation for establishing international collaborations, coordinating research efforts, and prioritizing areas for conservation. Whether it is for public health concerns about the spread of bird-borne diseases or conservation concerns about the status of habitat in distant non-breeding grounds, they serve as a tangible reminder of the way migrating birds create connections between continents and countries. For example, raptors breeding in Europe and Asia use several major flyways, with south-bound birds in fall funneling through concentration points from the Straits of Gibraltar in the west, through Italy, Israel, the Arabian Peninsula or the peninsulas of southern Asia in the east, to non-breeding areas in Africa or the Malay Archipelago. Similarly, for the shorebirds of the world, eight major flyways have been described linking North with South America, North America with Europe and Africa, Europe and Asia with Africa, and Asia and Alaska with Australia (Fig. 12.17).

The concept of flyways can also be linked to migratory connectivity, as flyways are likely to be more distinct and identifiable for species or populations with strong migratory connectivity. Yet not all birds use clearly defined flyways during migration. In contrast to species that concentrate in huge numbers during migration, many songbirds migrate across very broad areas without clear spatial delineations—a phenomenon termed **broad-front migration**. Migratory flyways are more difficult to delineate for such species (La Sorte et al. 2014).

Stopover sites: locations where migrating birds take a short break to rest, eat and drink for maintenance, and/or await favorable migratory conditions.

Flyways: general routes used by large numbers of migrants of many species.

Broad-front migration: a pattern in which the migrating individuals of a species are spread across a wide area rather than concentrated into narrower flyways.

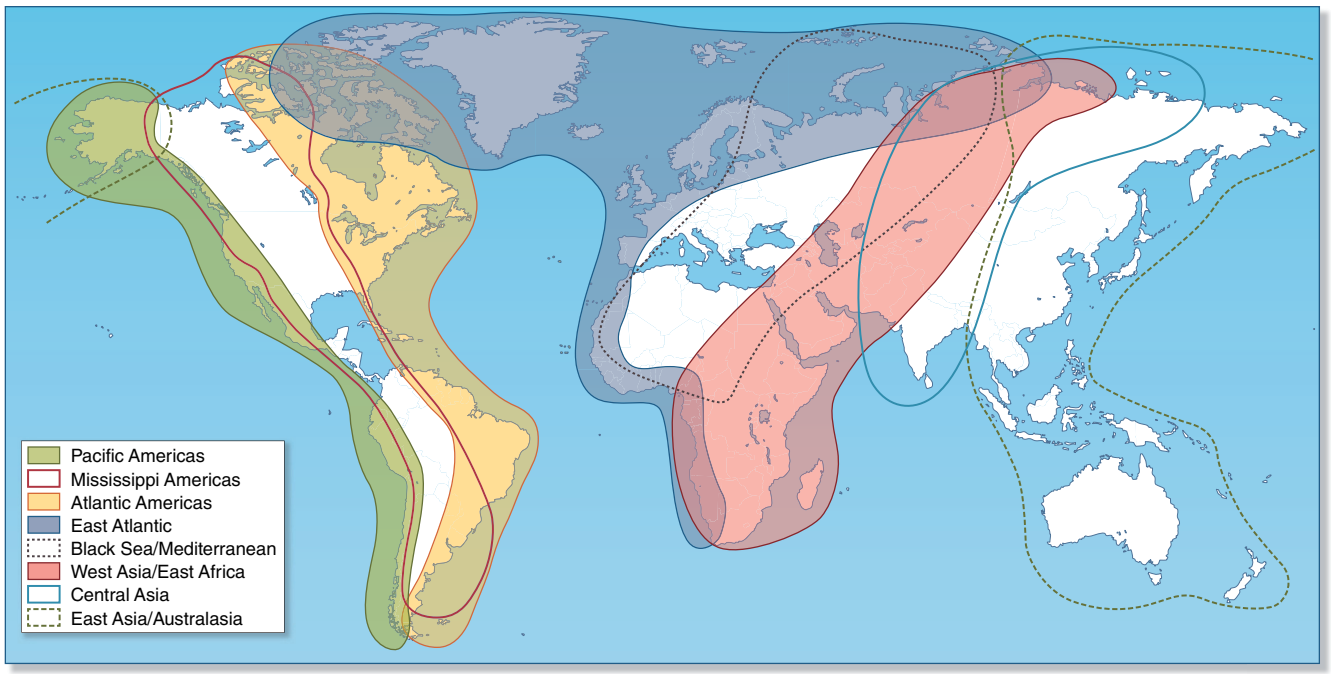


Fig. 12.17 The eight major flyways of migrant shorebirds. Many shorebird species annually migrate along particular flyways between breeding and non-breeding locations. (Courtesy of International Wader Study Group.)

12.2.11 Irruptive migration

Irruptive migrants are usually birds of arctic and boreal regions that generally stay far north during the winter but occasionally "irrupt" into lower latitudes. When they do, birders throughout the northern temperate zone delight in seeing finches and owls in places where they rarely occur. Irruptive species tend to be facultative migrants or nomads that depend on variable crops of tree seeds (mostly birch, alder, or spruce), or on fluctuating populations of northern rodents such as voles and lemmings. When the availability of these foods at northern latitudes fails, the birds wander further south in search of food. These mass movements build anticipation in birders because they often can be predicted on the basis of changes of conditions in the north or the movements of birds elsewhere. These movements are a type of facultative migration because the birds are responding to local declines in food availability rather than engaging in preprogrammed movements away from breeding areas.

Irruptive migrants: birds that occasionally move in large numbers beyond their usual range, usually in response to poor food supplies in their typical habitats.

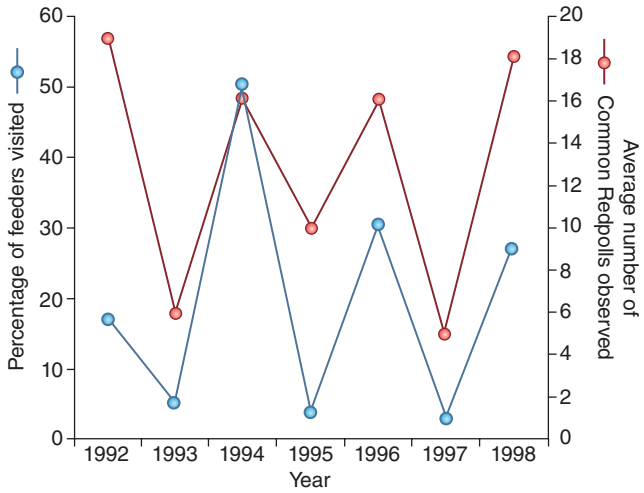


Fig. 12.18 Cyclic abundance of an irruptive migrant. Winter observations of Common Redpolls (*Acanthis flammea*) at feeders in the northeastern USA reveal that this species appears to follow a 2-year cycle of alternating abundance and scarcity. In years when redpolls are rare at these feeding sites, they seem to remain farther north during the winter. (© Cornell Lab of Ornithology.)

These irruptive movements often show remarkable cycling across years. For instance, the irruptions of some northern finches sometimes alternate regularly: every other year, redpolls or siskins are likely to show up at feeders in the northeastern USA (Fig. 12.18). Among the owls and raptors that feed on arctic and boreal rodents, the time

between southward irruptions is often closer to 4 years. This periodicity breaks down now and again, and sometimes it is not synchronized among different regions.

12.3 How birds time their migrations

For a migrant to match its movements to its environment, it must make its journeys at the appropriate times of year. A flight across the Sahara or the Pacific Ocean would doom the migrant unless it timed its flight to take advantage of supportive weather conditions (Gill et al. 2014) and arrived at its destination at a time when resources there were plentiful.

12.3.1 Migratory restlessness

When songbirds are ready to migrate, they literally cannot sit still. German ornithologists first noticed this migratory restlessness and gave it a name, ***Zugunruhe***, which migration biologists still use today. Because it is easily recognized and measured, *Zugunruhe* can serve as a reliable indicator of the strength of migratory preparedness and motivation: migrants, when kept in cages at night, usually jump in the direction that you would expect them to fly if they really were initiating their migratory journeys. Early researchers designed special circular cages that registered the hops of birds in *Zugunruhe*, using them to study the role of magnetism and cues from constellations in the night sky on bird orientation. Similar approaches using a variety of more advanced recording tools continue to be used today to study songbird orientation. Measurements of *Zugunruhe* have also played a valuable role in comparative studies of migration, as birds from different populations with different migratory paths and destinations show differing patterns of *Zugunruhe* intensity (hours per night) and duration (number of nights) that correspond to how long their migrations last under natural conditions.

12.3.2 Biological clocks for migration timing

Birds have internal biological clocks that help them monitor both the time of day and the time of year. Birds can sense the time of day via these internal clocks in the absence of light cues, such as the position of the sun. They similarly have internal biological calendars that tell them about the progression of the seasons even in the absence of a seasonal cue such as a change in day length. Important aspects of these clocks are controlled by changes in hormone levels (Chapter 7).

The time-sense of birds has been investigated using experiments in which wild birds are brought into captivity and kept under artificial conditions where seasonal cues—such as changing temperatures or changing day length—can be manipulated by the researchers. Studies that artificially manipulate the internal calendars of birds take a very long time, and the Max Planck Institute for Ornithology in southern Germany has been one of the few institutions in the world able to sustain lengthy investigations of this fascinating aspect of bird biology. Work there has concentrated on small migrant songbirds such as the Garden Warbler (*Sylvia borin*) and European Blackcap (*Sylvia atricapilla*). The birds used in these experiments often were taken into captivity as young chicks and hand-raised, and lived their lives in individual cages. To eliminate their ability to measure seasonality by any environmental cue, the temperature and light–dark cycles in their cages were kept constant.

Garden Warblers and Blackcaps monitored for up to 10 years showed persistent seasonal cycles in molt, the size of their internal reproductive organs, and *Zugunruhe*, even in the absence of external cues about the changing seasons. Surprisingly, however, the complete annual cycle in these birds is not exactly 12 months, but instead is several months shorter. In contrast, the few similar studies of migratory shorebirds showed that these birds have internal cycles of about 14 months.

Under natural conditions, all of these birds use cues from their environment to help calibrate their internal calendars and thereby keep them in synch with the changing seasons. The most important synchronizing cue (or *Zeitgeber*) from the environment is the **photoperiod**. Birds are sensitive to the relative length of night and day, and the way that this ratio of light and dark changes with the seasons is an important cue for resetting their biological clocks (Chapter 7). Experiments with captive birds have shown that changing their photoperiod alone can cause them to dramatically recalibrate their annual calendar. For example, by manipulating the schedule of lights in their enclosures, European Starlings (*Sturnus vulgaris*) can be induced to have complete annual cycles of breeding and molting activity that are as short as 2 months (Gwinner 1986) (Fig. 12.19).

When birds migrate long distances, they rapidly traverse locations with very different photoperiods, and we still do not fully understand how they are able to synchronize their

***Zugunruhe*:** a German term for the nocturnal restlessness that caged migratory birds exhibit when they are ready to migrate.

Photoperiod: the amount of a 24-hour day in which birds are exposed to light; or the relative lengths of light and dark periods of the day.

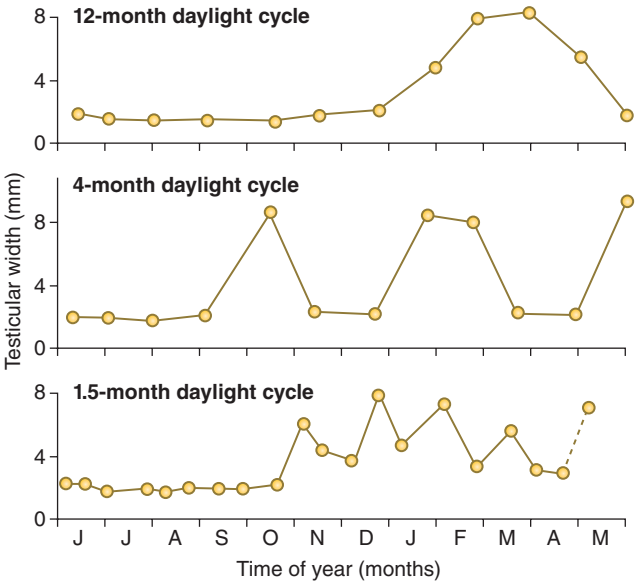


Fig. 12.19 Physiological effect of photoperiod change. The testes of male European Starlings (*Sturnus vulgaris*) enlarge during the breeding season and shrink during the non-breeding season. Photoperiod, or the amount of light each day, serves as a cue for the time of year. The top graph shows the testis size—an indicator of breeding condition—of a starling kept under a normal 12-month daylight cycle. Males kept under artificial daylight cycles that change more rapidly (middle graph) synchronize their annual rhythms to match these faster "years." Even at a cycle length of 1.5 months (bottom graph), the birds eventually adjust their gonad cycles to such short "annual" periods. (From Gwinner 1981, 1986. Reproduced with permission from Springer Science + Business Media.)

internal rhythms with these changing external cues from the environment. For instance, in Sanderlings (*Calidris alba*), individuals originating from the same breeding population may winter over a great range of latitudes (Fig. 12.20). A Sanderling spending the non-breeding season near the equator must respond to very different day-length cues than a bird wintering near the southern tips of South America or Africa, yet all of these birds time their northward migrations to arrive on the breeding grounds in the Arctic at the same time. Depending on where they spend the non-breeding season, different Sanderlings must initiate the migratory flight north in spring under conditions that can vary from lengthening days (the normal condition in the north temperate zone) to very small changes in day length (in the tropics) to shortening day length (if the bird is spending the northern winter in the southern hemisphere).

Although their internal clock tells birds when to start heading off on a migratory journey, this message can be overridden, at least for a short while, if the bird is not yet in appropriate migratory condition or if environmental conditions are not conducive to migration. Birds preparing to embark on a migratory voyage must integrate a great amount of information, and they can be thought of as running through a preflight checklist prior to departure. For example, when White Storks (*Ciconia ciconia*) and Honey Buzzards (*Pernis apivorus*) are leaving their breeding sites to initiate their fall migration, their day of departure is triggered by short periods of locally deteriorating conditions (Shamoun-Baranes et al. 2006).

12.4 Orientation and navigation

Whenever a bird sets out on a journey, be it a short foraging trip or a migration flight to the other side of the planet, it runs the risk of losing its way. The ability of birds to find their way to precise locations on the earth's surface after very long journeys must rank as one of the most fascinating aspects of avian biology. Scientists have been investigating the ways that birds achieve this feat for many decades (Box 12.04). One important question has been whether birds are capable of true **navigation**, estimating their absolute position and planning a route accordingly, or merely **orientation**, being able to judge compass directions accurately.

This distinction between navigation and orientation raises some interesting parallels in the history of human path finding. Only recently have humans been able to fix easily their absolute location on earth, using technologies like the Global Positioning System (GPS) (Box 12.01). Before GPS, human navigation involved the use of sunrise and sunset times and relied on accurate clocks and maps. Before the invention of accurate clocks, humans were limited to orientation based on celestial cues or long-distance cues such as the movement of a needle in a magnetic compass, the directions of sea currents, or the flights of shore-bound birds. As we shall see, there are many similarities in how both birds and humans have found their way.

12.4.1 Magnetic perception of birds

Birds are able to sense the earth's magnetic field in multiple ways, one of which involves cells in the upper layers of the bill that contain magnetite, a magnetic mineral (Chapter 7). The strength of earth's magnetic field varies a great deal at both the global scale (being strongest at the poles and weakest at the equator) and on a regional scale

Navigation: the ability to determine an absolute geographic location in two dimensions.

Orientation: the ability to determine bearings and directionality.

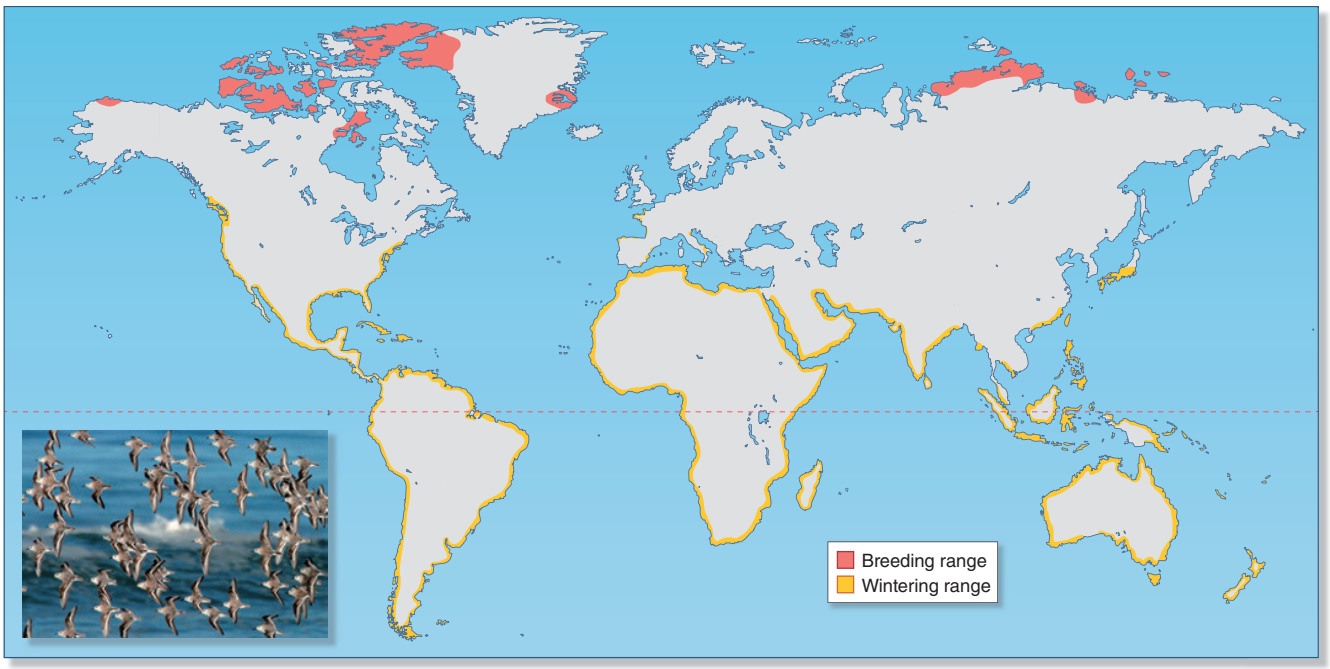


Fig. 12.20 Latitude and photoperiod. All Sanderlings (*Calidris alba*) breed in the high Arctic (red), but different individuals overwinter along various coasts worldwide (yellow), both north and south of the equator. To time their migrations correctly, birds must tune their internal clocks to different photoperiods, depending on latitude. (Map courtesy of www.xeno-canto.org. Adapted from BirdLife International and NatureServe 2011. Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA. Photograph by Eteri Maisuradze. CC-BY-SA 2.5.)

Box 12.04 Devices for the study of orientation

Bird migration takes place outside, far away from laboratories and their scientific devices for taking measurements. Researchers trying to understand how birds orient and schedule their movements therefore have needed to design innovative devices to test ideas about avian orientation and homing. One of the most serviceable platforms for these devices has been the homing pigeon (a domestic variety of the Rock Pigeon, *Columba livia*). Although the homing pigeon is not a migratory bird, it has a strong ability to find its way back to its home loft after being released elsewhere. These birds are useful for free-flying studies of orientation behavior because they are easy to train and keep in captivity, and they are large enough to carry many devices used by researchers to test hypotheses about their orientation ability.

Some such devices remove or alter one of the potential cues that a pigeon might use to orient its flight back to its loft. To shift the pigeons' perception of the earth's magnetic field, researchers developed miniature battery-operated Helmholtz coils to alter the magnetic field around the birds' heads (Walcott and Green 1974). To disrupt information from geographic landmarks, pigeons have been fitted with frosted eyeglasses that allow them to see patterns of light (so they can avoid crashing into things) but that prevent them from being able to recognize more distant landmarks (Schlichte and Schmidt-Koenig 1971). Other researchers temporarily disrupted the pigeons' sense of smell by spraying zinc sulfate into the birds' nostrils, thereby preventing the pigeons from using olfactory information while orienting (Benvenuti and Gagliardo 1996; Gagliardo et al. 2013).

(depending on the composition of the local bedrock, sediment thickness, and so forth). Thus, with experience, birds can potentially gather a great deal of positional information from the strength of the magnetic fields that they encounter. For example, male and female Ruffs (*Philomachus pugnax*), long-distance migrant shorebirds of the Eurasian Arctic, apparently gather and store geomagnetic information in different ways: when there are larger geomagnetic disturbances during the period of their first southward fall migration, males are displaced from their routes more than females are (Rakhimberdiev et al. 2014).

The other magnetic sense in birds involves a compass-like ability to detect direction in the earth's magnetic field. Experiments had long suggested that birds' eyes are involved in this aspect of their direction finding, even in the absence of visual cues. Experiments have shown that light at the blue and turquoise end of the spectrum interacts with a pigment called cryptochrome in the avian retina. Light excites one of the electrons in a cryptochrome molecule, and the molecule and its associated neuron somehow are able to detect the effect of the magnetic field on the quantum-mechanic spins of these solo electrons before they return to their stable paired state. Thus, these cryptochromes may be able to produce a visual pattern in the retina that allows birds to "see" direction akin to a magnetic compass (Wiltschko and Wiltschko 2009).

12.4.2 Solar cues and the circadian clock

The sun is a changeable indicator of direction: at noon it is directly overhead, in the morning to the east, and in the afternoon to the west. Birds, like humans, need to know the time of day to make good use of solar position as an indicator of direction. Some early experiments on solar orientation by Gustav Kramer in Germany used large mirrors to shift the apparent location of the sun, but most subsequent research instead has involved shifting the birds' biological clock. When a domestic homing pigeon (*Columba livia*) is kept for a few days in a room where the photoperiod is artificially shifted by 6 hours and then released to fly back to its loft, it will orient by the sun but fly in the wrong direction. For example, if the pigeon is kept in a photoperiod that is 6 hours fast and is released at 6:00 a.m., the bird will think it actually is noon, and orient by the sun as if that were the case (Fig. 12.21). In the southern hemisphere, where the noon sun is to the north, clock-shifted pigeons make the same sensible mistake, of the opposite direction, when released. Similar clock-shifting experiments have been conducted, with similar results, on a great variety of bird species, including chickadees in the USA and various warblers and robins in Europe. Such studies have shown that some birds use solar orientation even for short daily movements; for example, some jays and nutcrackers use solar cues for spatial direction when returning to the locations where they previously cached food (Wiltschko et al. 1999).

We have already seen that some frequencies of light interact in interesting ways with the geomagnetic sense of birds, and there is additional evidence that birds can perceive the polarization of light in the sky, but how birds use this ability to orient themselves remains uncertain. For birds that can see patterns in the polarization of light in the sky, these patterns shift through the day in ways that likely accent and augment the information derived from solar position alone. Experimental work has shown that birds use polarized light cues close to the horizon to recalibrate their magnetic compass at sunrise and sunset (Muheim et al. 2006b).

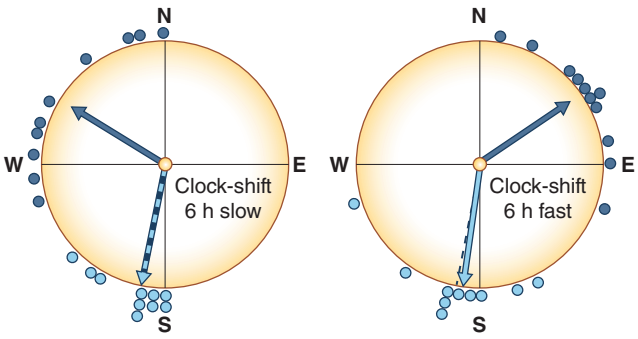


Fig. 12.21 Sun position as a navigational cue. These plots show the orientation of homing pigeons (*Columba livia*) released north of their loft, to which they were trying to return. Birds kept under normal daylight conditions correctly fly south (light blue circles), whereas birds kept under artificial lighting conditions (with daylight shifted ± 6 hours) instead fly in the direction that would be correct (based on the position of the sun) during the clock-shifted time of day (dark blue circles). (From Wiltschko and Wiltschko 2009. Reproduced with permission from American Ornithologists' Union.)

12.4.3 Celestial navigation

Birds are also able to use celestial cues from the night sky to orient their migratory journeys. In experiments with captive-reared Indigo Buntings (*Passerina cyanea*) exposed to planetarium skies with either natural or artificial patterns of nocturnal star movement, Emlen (1970) showed that birds do not memorize a map of the stars, but rather use the apparent rotation of the stars in the sky to determine direction. From watching the sky over several nights, birds can determine the location of the poles in the sky around which the other stars seem to move. This orientation cue is one of the most important that nocturnal migrants use during long-distance migrations.

12.4.4 Other orientation guides

There is much debate about the extent to which birds use their sense of smell (Chapter 7) to find their way, but there is little doubt that tubenosed seabirds effectively use the odors of their colony to trace their way back to the colony and even to their home burrows, and it seems likely that other birds with a keen sense of smell (such as some vultures) likely can acquire olfactory information that could be valuable in finding their way.

Another extraordinary sensory ability of some birds (including domestic pigeons, the species in which this ability has been best studied) is the detection of sound at frequencies as low as 0.05 Hertz, a frequency far below the

range of human hearing. Sound at these extremely long wavelengths can travel enormous distances, potentially giving birds information about the direction of distant ocean shores and mountain ranges, or about the approach of distant storms. Accordingly, there is some evidence that homing pigeons using this ability can be seriously disoriented by the intense sonic booms produced by large supersonic aircraft (Hagstrum 2000).

12.4.5 Displacement experiments

Recall that orientation involves having a sense of direction, whereas navigation involves knowing the specific point on the earth where you are located. Experiments in which birds are displaced from their original location and then tracked have consistently suggested that they may be capable of true navigation, at least for parts of their journeys. Over many decades, ornithologists have captured birds on their breeding or wintering territories and moved them far from these sites. Diverse birds, ranging from sparrows to shearwaters and storks to starlings, have returned successfully to their point of origin, often after periods short enough to suggest an almost straight-line return.

How can these avian travelers achieve such precise feats, especially when they are moved to locations that neither they nor any of their recent ancestors have ever visited? The birds displaced by these experiments may not know precisely where they are; they may sense only some gradient of position and know to travel up that gradient. For instance, they may sense something about the magnetic field or infrasound landscape that gives them a reliable indicator of the direction they should proceed to get home.

An interesting nuance in the results of these displacement experiments is that experienced migrants usually do better in finding their way back home than do first-time travelers. In displaced White-crowned Sparrows (*Zonotrichia leucophrys*), for example, seasoned breeders from the Pacific coast began correcting for their displacement to the opposite side of North America as soon as they were released there, whereas first-time migrants continued their journeys in what would have been the correct orientation had they still been on the Pacific coast (Thorup et al. 2007). This pattern is consistent with studies of homing pigeons showing that experienced birds are better at considering multiple orientation cues.

12.4.6 Multiple and sometimes conflicting orientation cues

Birds clearly use many kinds of sensory information to guide their journeys. They must manage all this information and handle situations in which these cues are in conflict with one another. As birds get older and gain experience, they generally get better at understanding the situations in which a given sensory mode is most likely to be reliable or unreliable. For example, if a homing pigeon is released on an overcast day when the sun's position is not clear, it seems natural that the pigeon would shift to its magnetic compass to find its way. Studies of how birds resolve conflicts between celestial cues and shifted magnetic cues indicate that birds sometimes weigh the available information differently, depending on whether they are migrating or not (Muheim et al. 2006a). Thus, these birds are often able to discern which orientation cues are most reliable in different settings and at different scales of travel.

12.5 Migration physiology

One of the remarkable aspects of avian migration is that tiny birds can make such extended journeys under their own power. They can accomplish these feats of migration because they are efficient flying machines.

12.5.1 Fat: the fuel of avian migration

Birds are the only terrestrial organisms (other than humans using machines) that can repeatedly make round trips of many tens of thousands of kilometers. Although flapping flight is hard work, it is unrivaled in its efficacy at covering distance. The energy used by a bird engaged in flapping flight is about eight or nine times greater than the energy that same bird would expend while sleeping (the resting metabolic rate). To achieve these high levels of physical activity, birds need efficient systems for supplying fuel and oxygen to the muscles, and for removing carbon dioxide.

As covered in more detail in Chapter 7, migrating birds use fat as their primary energy source; given the much higher energy density of fat, this adaptation may have preequipped migrant birds with a means of storing sufficient fuel for very long flights. Birds employ special enzymes to mobilize fat out of their fat cells, special transporter proteins to carry the fat through the blood stream, and special enzymes to get the fats into the muscle cells and finally deliver them to the mitochondria, where fats are oxidized to fuel the muscle's work.

Most birds therefore prepare for migration by storing large amounts of fat within their bodies, some of it just under the skin. Bird-banders working with migratory songbirds often take fat scores: if one softly blows apart the breast feathers on a passerine in migratory condition, the cream-colored subcutaneous fat that builds up in the open triangle below the neck (the furcula) is easily visible. As birds grow fatter, so does the extent of this creamy layer under the skin. Birds deposit fat in the abdominal cavity last. Geese and shorebirds that are ready for takeoff on very long-distance flights can be recognized by their bulging abdomens, loaded with the fat needed to fuel their forthcoming journey.



Fig. 12.22 Fat storage for migration. The Blackpoll Warbler (*Setophaga striata*) on the right has stored enough fat (the white visible through the exposed skin of its breast) for a non-stop flight across the Atlantic Ocean, while the Yellow-rumped Warbler (*Setophaga coronata*) on the left needs to store much less fat for a short journey down the coast of North America. (Photograph by Rebecca L. Holberton.)

Migrating birds preparing to depart on long flights can get very fat indeed. Migrating Blackpoll Warblers (*Setophaga striata*) preparing to depart on a non-stop transoceanic flight from the coast of Maine (USA) to the north coast of South America routinely double their mass in fat before departure (Fig. 12.22). Just before they depart on a flight to South America, some Wilson's Phalaropes (*Phalaropus tricolor*) staging at Mono Lake, California (USA) load up with so much fat that they are unable to fly until after a brief period of weight loss (Jehl 1997). Bar-tailed Godwits (*Limosa lapponica*) on the rich intertidal mudflats of southwestern Alaska accumulate similar proportions of fat before their trans-Pacific journey of more than 11,000 kilometers to New Zealand (Piersma and Gill 1998). Although the fattened godwits still manage to take off, they require a long running start more characteristic of heavy birds such as swans.

Fat storage does not come cheaply. In fact, because fat is so energetically dense, birds that are in the process of adding stores of fat must lengthen their foraging days and double or triple their normal daily food intake. For intake rates to increase so much, the size and capacity of the food-processing organs, the stomach and the intestine, must increase temporarily as well. The surface area of the intestinal wall and the levels of enzymes that help transport nutrients across this wall into the blood stream go up. As a true biochemical factory, the liver transforms sugars and proteins into the appropriate fats for transport to fat cells. The livers of migrants at the peak of their pre-migratory foraging activity may be two or three times larger than during the rest of the year.

The physiological demands of migrants change suddenly when they stop their pre-migratory foraging and set out on long-distance flights. Godwits and similar trans-oceanic terrestrial migrants are able to store relatively enormous amounts of fat in part because all the organs that can be dispensed with during flight, especially the gut and the liver, start to shrink during the last days before migration.

12.5.2 Migration and weather

Weather conditions are important for a migrating bird: clouds and fog can obscure orientation cues like the position of the sun and stars, rain can make flight and thermoregulation more difficult, and high temperatures can influence a bird's water balance. Of all weather variables, wind has the biggest effect on migratory performance. If the wind is blowing in the right direction, it can help a bird save time or energy, but if it is blowing the wrong way, it can blow a bird far off course, cost the bird energy needed for it to stay on course, or cost it days of lost flight time while it waits for better conditions. Helpful wind assistance can double the flight distance of a bird. However, many migrants will make little progress if they are faced with contrary headwinds close to their own flight speeds. Thus, a bird's decision about how to respond to weather conditions during migration can affect many of the risks involved in these avian journeys. For a bird making a short flight over land, these risks may not be particularly life threatening; however, for a small bird like a Northern Wheatear (*Oenanthe oenanthe*) that must fly thousands of kilometers over the northern Atlantic Ocean, taking off in the wrong weather conditions can be a matter of life or death.

Migrating birds generally depart from staging and stopover sites on days with favorable winds. Experiments with migrant European Robins (*Erithacus rubecula*) show that the winds overhead are one of the most important influences on the decision to resume migration (Dänhardt and Lindström 2001; Bulyuk and Tsvey 2013). Alternatively, birds may decide to stop migrating temporarily because of bad weather. However, waiting for good weather or stopping because of bad weather costs time and energy. To make the right choices, birds must weigh different and changing costs and priorities during their journeys.

Broad regional weather conditions also can influence migration routes, because spatial patterns in pressure systems can act as a barrier to migration or create a migratory corridor of beneficial winds. For example, the routes that Eleonora's Falcons (*Falco eleonorae*) use to cross the Mozambique Channel are influenced by the location of low-pressure systems (Mellone et al. 2011). The trans-oceanic routes and timing of migration in Cory's Shearwaters (*Calonectris diomedea*) are shaped by large-scale wind patterns, resulting in longer but more cost-effective paths (Felicísimo et al. 2008).

Soaring birds—including many vultures, eagles, large hawks, buzzards, storks, and pelicans—use winds and other air currents in a distinctive way (Chapter 5). Adroitly exploiting atmospheric dynamics enables them to migrate thousands of kilometers while expending very little of their own energy. Instead, they take advantage of rising air currents to gain altitude and then glide slowly down along their migratory route. By climbing and gliding, a soaring migrant can very efficiently cover several hundred kilometers each day. The thermal convection that creates rising air currents happens only during the day and rarely occurs over open water. These restrictions influence the routes that these birds take, as soaring birds often make long detours to avoid flying over large water bodies such as the Mediterranean Sea or the Gulf of Mexico.

12.5.3 Migratory fallouts and mortality during migration

Although birds have extraordinary capacities to traverse huge distances, at times crossing inhospitable environments or traveling through adverse weather conditions, they sometimes misjudge the weather conditions they encounter during their migration. Birds may have to stop migrating suddenly to wait out difficult conditions, backtrack to previously visited locations, or make an unplanned stop to search for food and replenish their energy reserves. When the situation grows extreme and migratory birds are completely exhausted with no options to rest or replenish their energy, they die.

Migratory fallouts are rare occasions when great numbers of migrating birds suddenly land in the same location, too exhausted to continue. Small birds are particularly susceptible to such events, especially during adverse wind conditions when they are blown off course or are stopped by strong headwinds. For example, during periods of adverse wind conditions, tens of thousands of songbirds—including Common Redstarts (*Phoenicurus phoenicurus*), Northern Wheatears (*Oenanthe oenanthe*), European Pied Flycatchers (*Ficedula hypoleuca*), and Garden Warblers—have sometimes appeared suddenly on a small stretch of coast in eastern England (Davis 1966). The most extreme events often occur during water crossings, and similar fallouts occur along the coast of the Gulf of Mexico when northbound migrants in spring encounter strong cold fronts coming from the north with winds directly opposite to the migrants' flight direction (Gauthreaux 1999).

Migratory fallouts: situations in which very large numbers of migrating birds are forced to land in a small area by adverse winds or other challenging weather conditions.

Vagrants: birds that move far beyond the normal range of their species.

The fallouts renowned among birders involve great numbers of living birds, but fallout conditions also cause great mortality among the exhausted migrants. Only rarely is this mortality observable, as many migrants perish while migrating over water when they are unable to reach land. On April 8, 1993, a tornado off the coast of Louisiana resulted in the death of 40,000 birds of 45 species (Wiedenfeld and Wiedenfeld 1993), and hurricanes can have a region-wide impact on populations of migrants birds such as Chimney Swifts (*Chaetura pelagica*) (Dionne et al. 2008). Mass mortality events also have been observed during extremely cold weather just after arrival at, or just before departure from, breeding areas. Aerial insectivores such as swallows and martins are particularly prone to great losses when temperatures are so cold that insects stop flying. Certain areas along a migration route may be particularly dangerous because of difficult weather conditions. One such area is the vast Sahara desert, crossed by millions of migrants traveling from Europe and Asia to sub-Saharan Africa and back. The combination of dust storms, strong winds, and limited resources if birds are delayed or blown off-course can result in very hazardous situations for migrants. On a less dramatic scale, individual migrants may also go far off course and end up far from their species' normal range; these birds are termed **vagrants** (Box 12.05). Although finding vagrants is exciting for birders, most of these off-course birds are not likely to return successfully to their breeding grounds.

Mortality during migration may be caused by many factors other than inclement weather, including collisions with man-made structures, predation, disease, and habitat loss. A study of Common Chaffinches (*Fringilla coelebs*) and Bramblings (*Fringilla montifringilla*) estimated that 10% of the migratory populations of these species is killed by raptors during fall migrations (Lindström 1989). Predation pressure may be such a risk to migrants that it can influence their timing of migration. For example, because of their early southward movements, adult Western Sandpipers (*Calidris mauri*) precede migratory Peregrine Falcons by almost 1 month, and they complete their annual molt quickly on the non-breeding grounds before the falcons arrive there. Thus, they stay ahead of falcon predation risk during the most risky period when their flight ability is limited. Juvenile Western Sandpipers migrate later, but they too avoid being exposed to falcons while molting because they do not molt at all during their first winter (Lank et al. 2003).

As these examples show, migration may be a period of heightened risk for almost all migratory birds. For Black-throated Blue Warblers (*Setophaga caerulescens*) that breed in New Hampshire (USA) and overwinter in Jamaica, mortality rates are 15 times higher during migration than

Box 12.05 Vagrants, birding, and ornithology

Much of what we know about the distributions and population status of birds is derived from data collected by amateur birders. For many people, one of the most intriguing aspects of birding is vagrancy, the rare occurrence of a bird far outside its normal range. Birds exhibit vagrancy for a variety of reasons. For example, powerful storms like hurricanes and typhoons often carry with them a wake of birds that are transported far outside their normal range by the winds of the storm. Thus a tropical, pelagic seabird like the Sooty Tern (*Onychoprion fuscatus*) can end up in Colorado, in the center of North America.

Yet such storm-displaced birds actually represent a minority of the vagrants that are found by birders. Most vagrants are not simply blown off-course, as they appear in odd places without any environmental perturbation that might have forced them off their path. Instead, these vagrants often started off in the wrong direction early in their migration and then continued to follow that path to end up far from other members of their species. One of the most common of such errors involves a major deviation in migratory orientation—some birds appear to have all their migratory machinery intact, except that their orientation is either a mirror-image or a 180° flip of the normal direction of migration (Fig. 12.B5.01).

Another type of migratory error that produces vagrants, termed overshoot, is a mistake not of orientation, but of the length of the migration. For example, birds that would normally stop migrating at lower latitudes may appear many hundreds of kilometers further north in spring, in habitats unlike anything that others in their population occupy further south. This seems to explain why it is that Pallid Swifts (*Apus pallidus*) sometimes occur as spring vagrants in the UK when the rest of these migrants have already stopped at their normal breeding grounds in Spain and Portugal.

For species that migrate in social flocks, vagrants that join the wrong group can follow the flock to the wrong destination. This process—termed group entrainment—occurs in social species like migratory geese and cranes. In these birds, young birds seldom show up as vagrants, as their first migration is generally in a family group that includes some more experienced birds. But adults, especially failed breeders, may wander from their group and find themselves away from familiar surroundings and familiar companions. Still attracted to groups, they may associate with a group of another species and migrate with those birds to non-breeding grounds far from their normal range. Group entrainment seems likely to explain, for example, why the rare Barnacle Goose (*Branta leucopsis*) almost always appears as a vagrant in North America in a flock of Canada Geese (*Branta canadensis*) (Fig. 12.B5.02).



Fig. 12.B5.01 Vagrancy. The Yellow-Green Vireo (*Vireo flavoviridis*) breeds in Central America and Mexico (red) and typically migrates south (purple) to overwinter in South America (blue). However, vagrants of this species are seen every year as far north as northern California (USA) during the fall migration period (orange dots), when breeding birds should typically be flying south. Vagrant individuals are often first-year birds and the distance they have traveled from their breeding grounds is similar—with a 180° shift in direction—to the distances more experienced adults travel when migrating to South America. (© Cornell Lab of Ornithology. Photograph by Gary Nunn.)

Vagrants sometimes represent pioneers of expanding range boundaries. Expanding populations of animals often include some long-distance dispersers in the vanguard, and the first individual of a species to occur hundreds or thousands of kilometers ahead of an expanding front is often followed by colonization by the expanding population 5 or 10 years later. Even though this sort of vagrant may be far outside its normal range, most of these birds are still very competent migrants and arrived at

Continued

their odd locations because, in some sense, they intended to do so.

A final pattern is that a very high proportion of vagrants are detected at "vagrant traps," hotspots for birders that are usually either along a coast or in an oasis of some kind of favorable habitat in an otherwise inhospitable region. These locations concentrate vagrants because migrating birds—especially those that have been flying for many hours overnight—assess their situation as the first rays of light start dawning over the landscape beneath them. If a terrestrial bird then finds itself far out over water or desert flats, it is very likely to fly toward the shelter of the nearest good patch of habitat that it can see, before setting down for a day of rest and refueling. Thus vagrant traps are points of attraction that concentrate vagrants from large surrounding areas.



Fig. 12.B5.02 Vagrancy via group entrainment. This Barnacle Goose (*Branta leucopsis*) (arrow) has joined a flock of Canada Geese (*Branta canadensis*). (Photograph by Katherine C. Davis.)

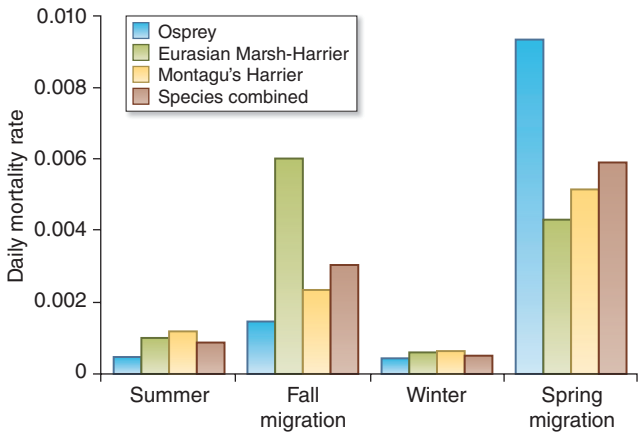


Fig. 12.23 High mortality during raptor migration. This graph depicts the mortality rate for three species of raptors—Montagu's Harrier (*Circus pygargus*), Eurasian Marsh-Harrier (*Circus aeruginosus*), and Osprey (*Pandion haliaetus*)—that annually migrate between Europe and Africa. Mortality is greatest during migration, as opposed to summer or winter when movements are much more localized. (From Klaassen et al. 2014. Reproduced with permission from John Wiley and Sons.)

during stationary breeding and non-breeding periods (Sillett and Holmes 2002). Similarly, a study of the mortality rates of satellite-tagged raptors moving between Europe and Africa (Klaassen et al. 2014) found that their daily mortality risk is substantially higher during migration (Fig. 12.23). In contrast, studies on seasonal survival in Red Knots indicate that hardly any mortality occurs during the long migrations to and from the high arctic breeding grounds (Leyrer et al. 2013; Rakhimberdiev et al. 2015).

12.6 Dispersal

There are two general types of dispersal movements made by birds. **Breeding dispersal** occurs between consecutive breeding seasons when a bird that previously has bred in one location moves to a new breeding location. By contrast, **natal dispersal**—the first dispersal in any bird's life—is the movement between the site where a bird is fledged and the site where it first attempts to breed as an adult.

12.6.1 Breeding dispersal and philopatry

Studying dispersal is difficult because it is usually hard to determine the fates of birds that disappear from a study site: did they die, or did they disperse to a new location? Despite this ambiguity, studies of breeding dispersal indicate that long-distance dispersal is uncommon in most bird species, and instead that most breeding dispersal involves movements of only a short distance. For example, fewer than a third of adult Black Kites (*Milvus migrans*) in southern Spain switch territories after they have begun breeding.

Breeding dispersal: the movement of an individual bird in successive years among different breeding locations.

Natal dispersal: the movement between the site where a bird was fledged and the site where it first attempts to breed as an adult.

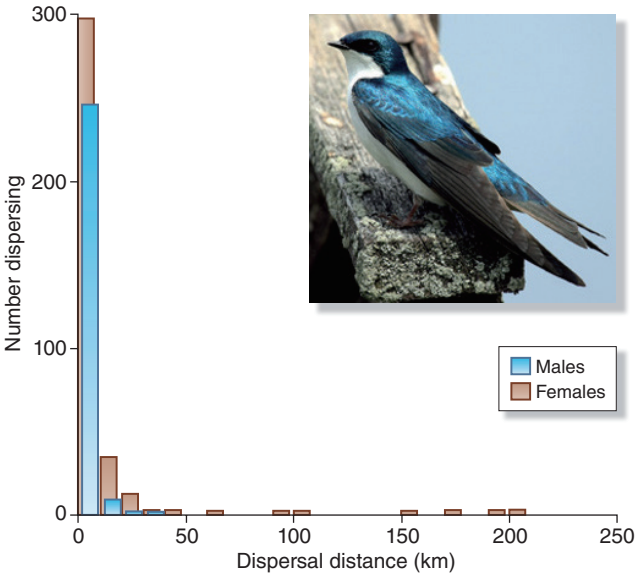


Fig. 12.24 Natal dispersal distances of Tree Swallows (*Tachycineta bicolor*). In this study, more than half the birds moved only a few kilometers between the site in eastern North America where they were hatched and the site where they later bred as adults. Females (red) tended to move a bit farther than males (blue), and a few birds of both sexes dispersed over much longer distances. (From Winkler et al. 2005. Reproduced with permission from John Wiley and Sons. Photograph by Tim Lenz.)

As in many bird species, female kites are more likely than males to move among breeding sites as adults, and members of both sexes are more likely to disperse after nest failure or the death of a mate (Forero et al. 1999). Similarly, Tree Swallows (*Tachycineta bicolor*) in upstate New York (USA) are unlikely to change their breeding sites in successive years by more than a few hundred meters: in one study, only 4% of male and 14% of female breeders were seen to disperse during their lifetimes. Those that dispersed generally moved a short distance, and the number of birds dispersing fell off exponentially with distance from the previous site (Winkler et al. 2004)

12.6.2 Patterns in natal dispersal

Several generalizations can be made about the natal dispersal of birds. First, natal dispersal is much more common than breeding dispersal. Indeed, very few birds have fledging young that do not disperse from the natal territory before breeding. Second, the distances involved in natal dispersal are usually far greater than in breeding dispersal. For example, Black-tailed Godwits (*Limosa limosa*) dispersing in the dairy farmlands of the Netherlands moved on average 2 kilometers during natal dispersal, but only 200 meters during breeding dispersal (Kentie et al. 2014). Similarly, Bobolinks (*Dolichonyx oryzivorus*) dispersing among grassland patches in Vermont (USA), moved an average of 1522 meters during natal dispersal but only 370 meters during breeding dispersal (Fajardo et al. 2009). Third, as in breeding dispersal, females generally are more likely to disperse, and they tend to disperse longer distances than males. For example, in Tree Swallows in upstate New York, females dispersed on average 8.38 kilometers and males only 2.44 kilometers from their natal site (Fig. 12.24) (Winkler et al. 2005).

Almost all data on natal dispersal distances show skewed distributions with long right-hand tails, suggesting that most birds disperse short distances but a few move much farther. Some of this pattern, especially for studies with small study areas, may simply reflect the impossibility of detecting dispersal events that take the dispersers very long distances away from the natal site. However, even when studies include the entire species' range, the pattern seems to be the same: most birds disperse to breeding sites that are not very far from their natal site, with only a relatively small proportion of birds undertaking natal dispersal over much longer distances.

12.6.3 Dispersal and colonization

Dispersal is what drives the expansion of a species' geographic distribution into new areas. This often occurs very slowly over hundreds or thousands of years, but we have also witnessed many examples of explosive expansions in which birds spread very rapidly into areas where they formerly did not occur (Box 12.06). In most such situations, the early colonists that first make it to a new breeding site stay there; it is their offspring that continue dispersing into unoccupied regions.

This process of colonization and dispersal has been particularly well studied in Western Bluebirds (*Sialia mexicana*), a small thrush that breeds in cavities and artificial nest boxes throughout much of western North America. Like many cavity-adopting species, the availability of nesting sites is often a limiting factor for bluebird populations. Before the arrival of humans and human-made cavities, this species had to rely on clusters of natural cavities, which usually resulted from woodpecker excavations in trees damaged by small forest fires. Therefore, Western Bluebird breeding habitat was patchy and relatively ephemeral, and the ability to colonize new areas by natal dispersal was an important part of their natural history. At present, nesting cavities for Western Bluebirds are becoming more common through the provision of artificial nest boxes and an increase in forest fires, and the species' range is expanding rapidly (Fig. 12.25).

Male Western Bluebirds exhibit a set of different behaviors depending on whether they are dispersers moving into a new habitat, or instead natally philopatric, breeding near the nest where they were themselves hatched. Males that show an aggressive, non-cooperative set of behaviors tend to disperse farther, and these males are the ones that tend to

Box 12.06 Cattle Egrets: vagrancy, dispersal, and range expansion

Most invasive bird species have been introduced by humans, but this sort of artificial dispersal is not the only way for a species to dramatically increase its geographic range: some birds can undergo extraordinary natural dispersals and establish themselves in regions far outside their historic native lands. Few birds have been more successful in expanding their range than the Cattle Egret (*Bubulcus ibis*). Native to Africa and parts of Asia, the African Cattle Egret subspecies (*B. i. ibis*) crossed the Atlantic of its own accord sometime in the 1930s and established a breeding population in Brazil. Then, over the subsequent four decades, it spread rapidly throughout most of the Americas and the Caribbean islands (Crosby 1972). The Asian subspecies (*B. i. coromandus*) has also expanded its range in roughly the same timeframe, moving since the 1940s from Southeast Asia through the Malay Archipelago and into Australia and New Zealand (Maddock and Geering 1994). Today Cattle Egrets are widespread in most temperate and tropical regions throughout the world (Fig. 12.B6.01).

Why has the Cattle Egret been so successful in colonizing so many new areas? Its ability to survive a journey across oceans is certainly part of the story, but other bird species have made such journeys and failed to establish new breeding populations. The strengths of Cattle Egrets include this species' flexible range of breeding habitats (Arendt 1988) and their ability to take advantage of a widespread food source—the prey disturbed by domestic cattle. While foraging, Cattle Egrets usually associate with livestock (and sometimes even with humans or tractors), which flush prey for them. Thus, Cattle Egrets have been able to prosper in the many places where humans now raise livestock.

The most important additional factor in the Cattle Egret's success, however, is probably their tendency to move large distances after the breeding season. The phenomenon of long-distance wandering in Cattle Egrets suggests that their arrival in South America, New Zealand, and other distant locations was not from individuals being blown off-course, but rather the expression of an exceptionally well-developed dispersal tendency. For example, Browder (1973) reports that Cattle Egrets had been spotted in South America multiple times in the decades before their successful establishment. Many Cattle Egrets of all ages wander after breeding, but some, especially juveniles, disperse great distances to form new colonies (Maddock and Geering 1994), with some individuals moving several thousand kilometers.

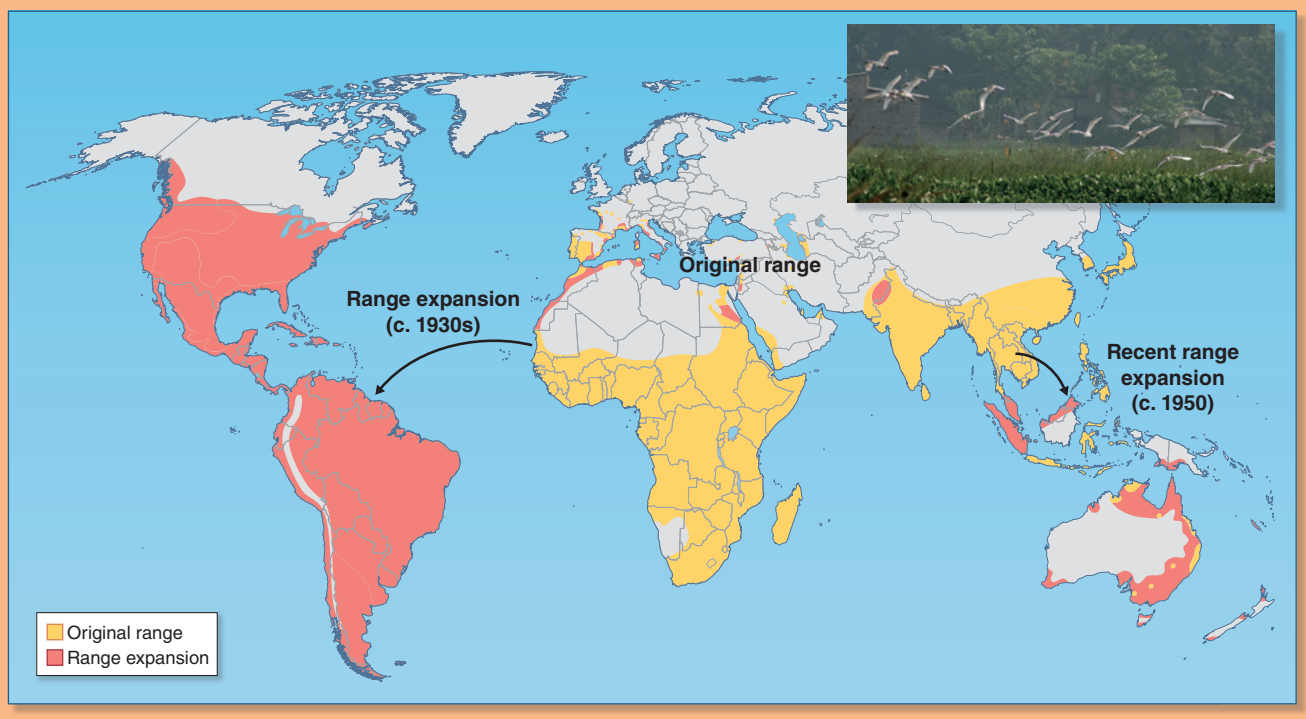


Fig. 12.B6.01 Natural range expansion. Originally native to Africa and parts of Asia, the Cattle Egret (*Bubulcus ibis*) has spread nearly worldwide during the past century. (Cephas, https://commons.wikimedia.org/wiki/File:Bubulcus_map.svg. CC-BY-SA 3.0. Photograph by J. M. Garg, https://commons.wikimedia.org/wiki/File:Cattle_Egret_I2m_IMG_5478.jpg. CC-BY-SA 3.0.)

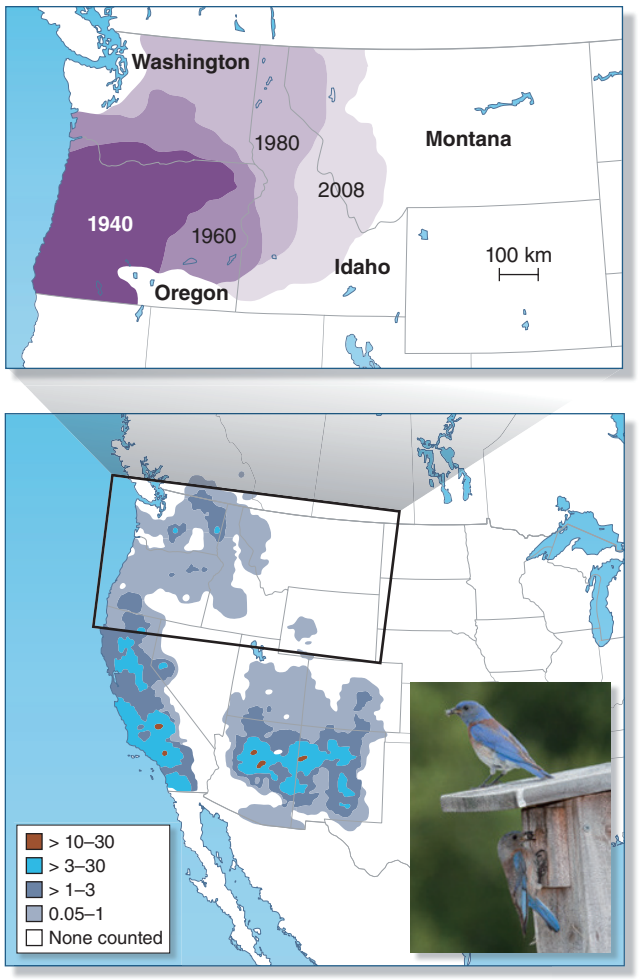


Fig. 12.25 Breeding range expansion. Western Bluebirds (*Sialia mexicana*) of North America continue to spread eastward into higher elevations where artificial nest boxes provide new breeding sites. Darker colors on the lower map indicate larger population sizes. The top panel shows how this species has expanded its range in four northwestern US states from 1940 to 2008. (From Duckworth 2009. Reproduced with permission from the Royal Society. Adapted from Sauer et al. 2008. Photograph by Marlin Harms.)

colonize new areas. Their aggressiveness helps them during colonization by allowing them to win out in competition with the closely related Mountain Bluebird (*Sialia currucoides*). In places away from the range edge where Western Bluebirds are more abundant, these birds breed cooperatively, and philopatric males benefit from being more social and less aggressive because their tolerance of allowing previously fledged offspring to remain on their territory provides them with a source of helpers to assist in future breeding attempts. Each kind of male—aggressive colonists and more tolerant cooperators—has a higher fitness in its respective setting (Duckworth 2009; Duckworth and Kruuk 2009).

Rapid biological expansions are often portrayed on a map as steady enlargements of a species' range, with the edges expanding in a uniform fashion. However, as invasive European Starlings (*Sturnus vulgaris*), House Finches (*Carpodacus mexicanus*), and Collared Doves (*Streptopelia decaocto*) expanded their ranges across the USA, small "propagule" or "bridgehead" populations were founded by birds that dispersed far from the main range boundary of the species. After additional time, the population filled in behind the propagules.

When a species is introduced to a new area or initiates its own natural invasion of an area, it may begin to experience very different selection pressures on its movements than it did in its historic range. For example, although they are poor dispersers in their native range, Common Mynahs (*Acridotheres tristis*) are invasive and expanding in southern Africa, Australia, and elsewhere (Fig. 12.26). The invasion causes spatial sorting in the population whereby individuals that disperse farther accumulate at the front of the expanding range. These longer range dispersers produce more long-distance dispersers, and a positive feedback can thus be created in which the advancing front of a species' range accelerates as it spreads across new territory. Thus, because longer dispersal is beneficial when a species is expanding into favorable habitat, invading populations of a species may show a much greater propensity to disperse than populations of the same species in their original range (Berthouly-Salazar et al. 2012).

12.6.4 Prospecting for new breeding sites

Birds make specific decisions about which habitats to live in, breed in, and move through. They base these decisions on many different factors, such as vegetation type and structure, food availability, and the abundance of predators. The habitat they prefer may vary by their own age or the season. For example, simply because it survived to fledging, a bird knows that the territory on which it was raised was suitable for breeding, and experienced breeders also have information about specific locations from their own past breeding attempts. Many birds use this kind of personal information to inform their choice of a breeding site. Birds can gain additional cues about the quality of different sites by observing the breeding success or habitat occupancy of other birds. Dispersing individuals therefore may base decisions about where to settle the following year on observations of their neighbors. These observations may be indirect, such as witnessing parental activity around a nest (a cue used by Collared Flycatchers, *Ficedula albicollis*) (Pärt and Doligez 2003), the song rates of males (which is correlated with breeding success in Black-throated Blue Warblers, *Setophaga caerulescens*) (Betts et al. 2008), or direct examination of the contents of other birds' nests (as documented in Spotless Starlings, *Sturnus unicolor*) (Parejo et al. 2008).

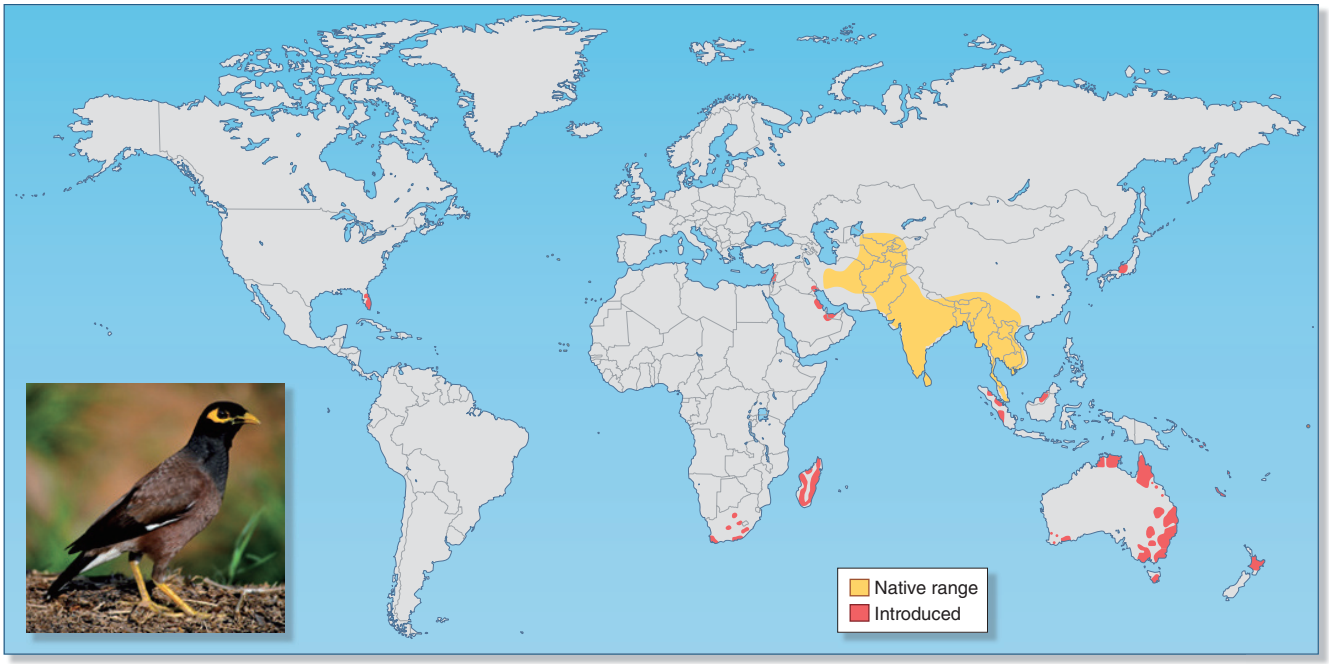


Fig. 12.26 Range expansion in non-native species. The Common Mynah (*Acridotheres tristis*) is a poor disperser in its native range (yellow), but tends to disperse much more readily in locations where it has been introduced (red). (Biatch, https://commons.wikimedia.org/wiki/File:Common_Mynah_distribution_map.png. Photograph by T. G. Santosh, https://commons.wikimedia.org/wiki/File:Indian_Myna.JPG. CC-BY-SA 3.0.)

Birds breeding in colonies can easily gather information from their neighbors. Black-legged Kittiwakes (*Rissa tridactyla*) whose nests were experimentally caused to fail were much more likely to return to the same area the next year if their neighbors had been successful (Boulinier et al. 2008). Similarly, the performance of other breeders in a colony of Lesser Kestrels (*Falco naumanni*) was found to be more important in settlement decisions than the number of kestrels present (Calabuig et al. 2008). Gathering of information by non-breeders (and breeders who have failed early in the season) also occurs in species that breed in looser aggregations.

Prospecting non-breeders are fairly common in many species, but this behavior has been particularly well studied in the Collared Flycatcher of northern Europe. Prospecting flycatchers are attracted by conspicuous parental feeding and vigilance activity (both of which are predictors of fledging success) during the mid-nestling phase. Although prospecting males seemed to be interested primarily in the quality of potential future territories and ignored the quality of individuals living on them, female flycatchers searched for generally high-quality areas that contained territories held by high-quality males (Doligez et al. 2004b). Prospecting Collared Flycatchers tended to return the following year to breed close to the sites they had investigated most frequently (Doligez et al. 2004a).

Some birds, such as Eastern Kingbirds (*Tyrannus tyrannus*) in eastern North America, prospect late in the season after breeding is mostly completed (Redmond et al. 2009). Many other birds that move extensively in the post-fledging period may be prospecting for information, but in most species it is very difficult to track moving fledglings to their eventual breeding sites the following year, and demonstrate that the place they chose for breeding was one that they explored during the previous summer.

12.6.5 Dispersal and genetic connections among populations

Dispersal also is a key factor in determining how populations are connected genetically through time and space. As discussed in more detail in Chapters 13 and 15, a **metapopulation** is a collection of distinct subpopulations connected by dispersal. The amount of dispersal among these subpopulations has important implications for the numbers of birds they each support, their persistence

Metapopulation: an array of spatially separated populations of the same species that are at least partly connected by the dispersal of individuals among them.

through time, and their potential to diverge genetically from one another. In a practical context, the pattern of dispersal of individual birds among subpopulations often has very important consequences for the conservation and management of those subpopulations.

Some avian populations—particularly those in the temperate zone—are extremely well mixed via the natal and breeding dispersal of birds each year. This causes the genetic variation in these species to be fairly homogeneous over large expanses of their range. For example, the Red-winged Blackbird (*Agelaius phoeniceus*) has a very broad breeding distribution across North America, yet notably little genetic variation among its many subpopulations (Ball et al. 1988). Similarly, American White Pelicans (*Pelecanus erythrorhynchos*) show continent-wide mixing across North America because of their long-distance dispersal tendencies, an artifact of the ephemeral nature of their colony sites in shallow lakes that fluctuate dramatically in availability from year to year (Reudink et al. 2011). In contrast, many tropical birds are highly sedentary, and populations of tropical birds that are separated into discrete subpopulations are often genetically distinct. This pattern suggests that temperate zone bird populations are often far more interconnected by dispersal than are tropical populations.

12.6.6 Methods for measuring dispersal

Because dispersal is important but hard to study, many creative methods have been developed to determine which birds disperse and where they go. One of the earliest methods used to study dispersal was to recapture breeding birds that were banded (usually as nestlings, thus natal dispersers) some distance from their site of original banding. Dispersal is then measured simply as the straight line distance between these points.

The vast scale of many avian dispersal movements is the greatest challenge when tracking banded birds. Even on small and intensively monitored study areas, researchers can fail to find and capture some dispersing birds that are breeding there. Small study areas also have the problem of not being large enough to include many of the birds that disperse beyond their edges over intermediate and long distances. Most study areas thus produce estimates of dispersal distances that have a sampling bias against longer dispersal movements.

The movements of birds can sometimes be inferred indirectly. For example, when feathers are being grown, they incorporate the stable isotopes of various elements—including hydrogen and carbon—that are derived from the food, water, and air at that site. Since these isotope ratios vary geographically, it is sometimes possible to use the ratios found in a feather to infer where the bird was when that feather was growing. As technological innovations make it increasingly possible to outfit birds with small tracking devices that last for months or years, it is becoming more feasible to track their dispersal directly (Box 12.01).

12.7 Evolution of avian movement patterns

The tremendous variation in the ways that birds move across the seasons and throughout their lives is the result of past evolutionary forces that selected for individuals whose movements gave them the best opportunities to survive and reproduce (Box 12.07). One theory on the evolution of migration is that it may have occurred through an extension of less extreme annual movements in search of food or breeding opportunities. What at one time might have been a simple short-distance movement to and from seasonal feeding grounds could have become exaggerated as the seasonality of the birds' environments became more variable or more extreme.

However, it is important to remember that earth has had changing environments throughout its history. One extreme example of environmental change is the recent melting of the glaciers that receded from the northern hemisphere only about 15,000 years ago. Those vast sheets of ice were only the latest in a long cycle of more than 20 Pleistocene glacial cycles that ebbed and flowed over the past 2.5 million years. Migrant birds can be seen as having adapted their patterns of movement to the new opportunities and habitats that receding glaciers left behind. Northern migrants today are the descendants of birds that have been adapting to such changing environments for many millions of years. One can imagine that, with every cycle of Pleistocene glaciation, the migrants retreated to more southern breeding localities and made shorter migrations while the ice ruled the north. Then, when the ice receded, the migrants retained their powers of movement and moved north to take advantage of renewed breeding opportunities there.

It is clear that birds like the warblers, thrushes, and flycatchers that migrate every year to breeding sites all across the northern hemisphere have not evolved this power of migration during the past few thousand years. Instead, they are descendants of avian groups with long and repeated histories of migration. Indeed, a recent study of the evolution of migration in the New World warblers indicates that the earliest-diverged members of this diverse group already were long-distance migrants (Winger et al. 2012), and it appears likely that the ancestral ability to migrate may be a shared trait of all birds, if not all vertebrates (Piersma et al. 2005).

Box 12.07 Migratory dropouts and long-distance colonization by Barn Swallows

One enduring enigma in migration biology is why birds often move away from overwintering locations that also seem highly suitable for breeding. If conditions are good year round at non-breeding sites, why not forgo the risks of migration and stay there to breed?

This kind of change in migration behavior is rare, but it does occur occasionally when populations of birds "drop out" of the migration cycle to become breeding residents in places where they formerly occurred only during the non-breeding season. For example, several species of swallows breed only in North America but spend the winter in far southern South America, undertaking long intercontinental journeys twice a year as part of their annual cycle. In 1980, ornithologists in Argentina discovered six pairs of Barn Swallows (*Hirundo rustica*) nesting under a bridge in Buenos Aires Province (Martínez 1983), the first time that this species was known to breed in South America. These breeding dropouts from the migratory Barn Swallow population had somehow been able to skip their northward migration and shift their breeding season by 6 months to match the South American seasons.

This South American Barn Swallow breeding population has continued to grow over the subsequent decades, and genetic studies suggest that it has been continuously augmented by birds born there as well as by new dropouts from the migratory population (Billerman et al. 2011). Dropout breeders have been seen in a few other swallow species with similarly long migratory paths—including a few House Martins (*Delichon urbicum*) from Eurasia that have bred in South Africa and Cliff Swallows (*Petrochelidon pyrrhonota*) from North America that have attempted to breed in Argentina—but only the Argentina Barn Swallows appear to have founded a lasting breeding population. Over evolutionary timescales, however, even fairly rare events can accumulate, and this dropout phenomenon helps explain why there are many sedentary bird populations—particularly on islands—that are most closely related to migratory populations elsewhere.

12.7.1 How does migration evolve?

The imprint of past evolutionary forces is clearly evident in the present-day migrations of many birds (Box 12.08). One remarkable example is seen in the migration paths of the Northern Wheatear (*Oenanthe oenanthe*), a small songbird that breeds over a broad range of latitudes, from the temperate zone to the high Arctic, but always in habitats of sparse vegetation. This species was originally found in Eurasia, but as the northern ice sheets receded after the Last Glacial Maximum, wheatear populations from Siberia spread eastward to colonize Alaska, and wheatears from Europe moved westward across Greenland to breed in the Canadian high Arctic. Amazingly, all of these wheatears that now breed on either side of North America still retrace their ancestral migratory paths to winter in sub-Saharan Africa. Wheatears in arctic Alaska leave in the fall on a westward track for a migration of many thousands of kilometers to non-breeding areas in East Africa, and those in the Canadian high Arctic head east in the fall for the long journey to West Africa. Using tiny geolocators to track individual wheatears, researchers have confirmed that birds breeding in Alaska migrate through Asia to reach eastern Africa, traveling some 14,500 kilometers (Bairlein et al. 2012), the longest distance recorded for a migratory songbird (Fig. 12.27). The routes that birds breeding in eastern Canada take are less well studied, although early observations from birds resting on ships (Snow 1953) and banding data suggest that wheatears from Greenland and Iceland cross several thousand kilometers of open ocean to reach the UK or Europe and then continue south to Africa (Delingat et al. 2008).

The evolutionary results of past movements are sometimes evident over even longer timeframes. For example, the Galápagos Hawk (*Buteo galapagoensis*) is the only raptor endemic to the Galápagos Archipelago. Since most raptors avoid flying over long stretches of open water, how did the ancestors of these birds come to colonize these remote islands that are 1000 kilometers from the South American continent? It turns out that the Galápagos Hawk is an evolutionary offshoot of the Swainson's Hawk (*Buteo swainsoni*), a species that today breeds in northern North America and then migrates, often in large flocks, to the grasslands of southern South America. Genetic evidence for the evolutionary split between the Galápagos and Swainson's Hawks suggests that their ancestors were undertaking this same migration about 300,000 years ago, when a flock of migrating hawks went off-course and ended up in the Galápagos to become the founding population of the species we now know as the Galápagos Hawk (Bollmer et al. 2006; Hull et al. 2008).

12.7.2 Migration and ongoing environmental change

Earth's climate has always been constantly changing, but we are presently in a period of unusually rapid environmental change caused by human activities (Chapter 15).

Box 12.08 Migratory origins: in the tropics or temperate zones?

Most long-distance bird migration occurs between breeding areas located in temperate, highly seasonal environments and non-breeding areas closer to the equator. A longstanding debate about the evolutionary origins of bird migration has centered around which of these regions—the high-latitude breeding areas versus lower latitude non-breeding areas—represents the ancestral home of the non-migratory precursors of these travelling birds (Fig. 12.B8.01). One hypothesis contends that migratory species are descended from tropical, sedentary ancestors, and that migration evolved as these species shifted their breeding grounds from the tropics to the temperate zone. This possibility is often referred to as the "southern home" hypothesis. In contrast, the "northern home" hypothesis contends that migratory species evolved migration by shifting their non-breeding ranges from ancestral high latitudes towards the tropics. These scenarios and their various extensions have been discussed and debated for over a century, but they have proven difficult to test because it is hard to reconstruct evolutionary changes in migration.

Benjamin Winger and colleagues (2014) conducted a novel test of the northern versus southern home hypotheses based on a closely related group of approximately 800 species of songbirds, one that includes a large portion of the migratory species in the western hemisphere: all New World warblers, cardinals and buntings, sparrows, blackbirds, orioles, and tanagers. They developed a model that used the evolutionary tree for these many species to predict the ancestry of their seasonal migrations between North America and the tropics. Rather than examining the phylogenetic history of migration as a behavior by itself, the model instead reconstructed changes in the breeding and non-breeding distributions of these birds throughout their evolutionary history, and used these geographic shifts to infer the changes in migration that must have accompanied them.

These comparisons show clearly that long-distance migration evolved many times in this group as various species shifted their non-breeding range to lower latitudes. In contrast, it was less common for species to evolve migration via shifts of their breeding range out of the tropics. Additionally, the study revealed that many groups of sedentary, tropical species are descended from migratory ancestors that lost migration and stayed in the tropics, a result corroborated in other recent studies (Winger et al. 2012; Rolland et al. 2014). At least in this one large group of birds, these comparisons contradict the southern home hypothesis and suggest that migration evolved most commonly in birds that originally were found in the north.

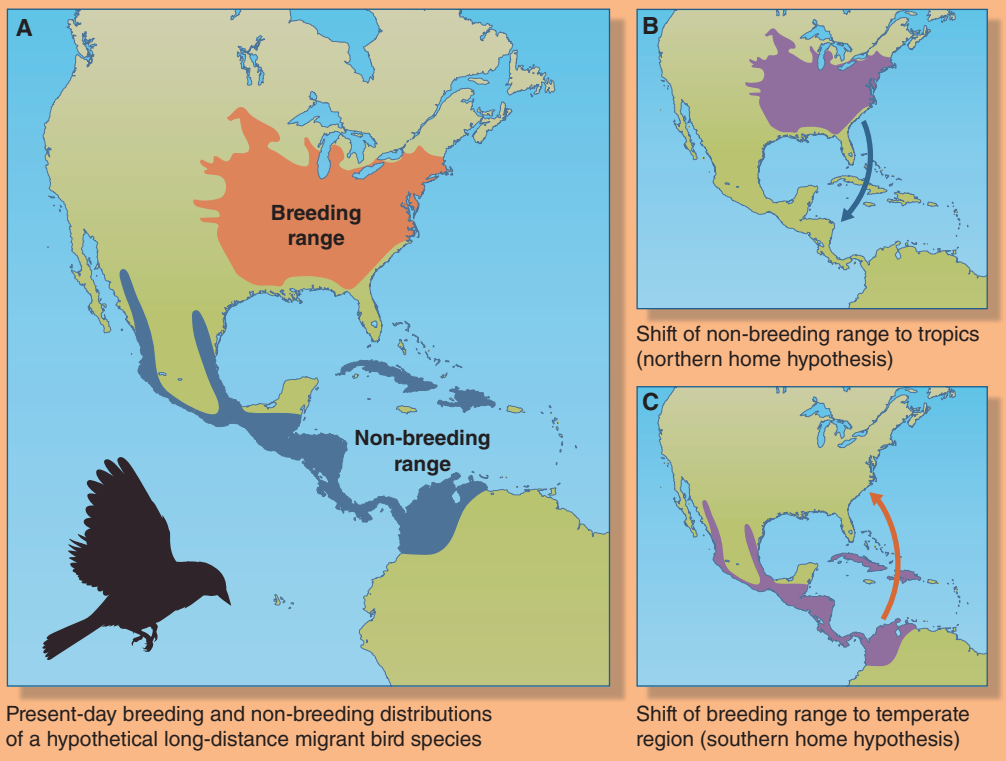


Fig. 12.B8.01 Evolution of migratory ranges. (A) Long-distance migration in present-day temperate zone species might have evolved in two ways. (B) In the "northern home" hypothesis, a population formerly resident in the north evolved migration south to take advantage of richer resources in the non-breeding season. (C) In the "southern home" hypothesis, a population formerly resident in the south evolved migration north to take advantage of richer resources for breeding. (Courtesy of Ben Winger.)



Fig. 12.27 Retracing ancestral migratory paths. Northern Wheatears (*Oenanthe oenanthe*) have recently expanded into the North American Arctic (orange dots) from both the east and west. Wheatears breeding in Alaska migrate over Asia to reach Africa, while individuals breeding in northeastern Canada migrate to Africa via Greenland and Europe. (Adapted from Bairlein et al. 2012. Reproduced with permission from the Royal Society.)

Global temperatures are increasing at an unprecedented rate; as a result, plants are leafing and flowering earlier, insects are emerging on accelerated seasonal schedules, and birds are arriving back from their non-breeding grounds sooner than before. One potential problem faced by migratory birds is that different organisms are responding to climate change at different rates, resulting in the potential for ecological mismatch between migratory birds and the foods that they eat (Both et al. 2009) (Fig. 12.28).

Each species of bird has evolved to breed during a time of the year when they can expect enough food to raise their young. In some cases, environmental changes are disrupting this relationship between the timing of breeding and the available food supply. The best studied example of such ecological mismatch is in the European Pied Flycatcher (*Ficedula hypoleuca*) of northern Europe. Even though these flycatchers have responded to climate change by starting to breed earlier in the year, the key insects with which they feed their chicks have advanced their calendars even more, as the insects are responding to rapidly advancing local conditions that the flycatchers, in their sub-Saharan non-breeding areas, do not experience.

It was long thought that these flycatchers were constrained in moving their time of breeding forward because they time their migration based on their internal biological clocks, which are keyed not to short-term environmental cues but rather to day length. However, it now seems that the birds' migratory clocks can be adjusted physiologically, meaning that they do not need to wait for various genetic variants to be sifted by natural selection. The photoperiods that young birds experience in the nest before making their first fall migration appear to calibrate their clocks to the earlier setting required by the advancing seasons in the north (Both 2010). It turns out that the birds are arriving in

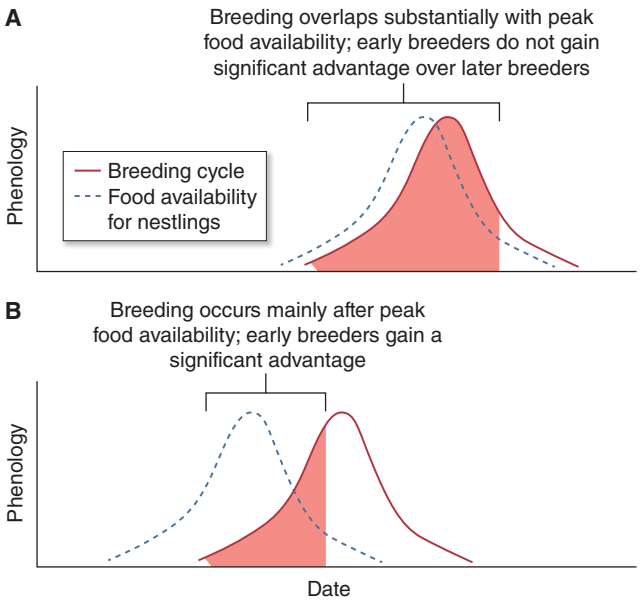


Fig. 12.28 Ecological mismatch caused by changing seasonality. (A) Many migratory birds have evolved to synchronize their breeding timing (solid red curve) with the period of greatest food availability for their offspring (dotted blue curve) so that they can breed successfully (shaded red area represents frequency of successful breeders). (B) If environmental conditions shift such that peak food availability occurs earlier than peak breeding, early breeders will raise the most offspring sucessfully, but much of the population will breed too late to provide optimal levels of food to their young. (From Both et al. 2009. Reproduced with permission from John Wiley and Sons.)

northern Europe later than the spring flush of insects not because their clocks are telling them to leave Africa at a later date, but because they are being held up by poor conditions while migrating through southern Europe, where

spring is not advancing at the same pace as it is in northern Europe. This example highlights the general point that migration is both a powerful way for birds to respond to environmental variation and a trait that renders them vulnerable when conditions deteriorate at any point along their annual journey.

Visit birdbiology.org for many online resources on the topics covered in this chapter.

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Chapter 13 Ecology of Bird Populations

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Many of us are used to seeing a songbird foraging near our home, and if we spend some time watching closely in the spring, we may even find its nest. What may not be so obvious on first glance are the other birds of this species that live nearby and how they all interact with each other. All these birds considered together—the individuals of a species living in a particular place at a point in time—are termed a **population**, and as a collective group, populations have attributes that transcend those of the individual birds. Population size is the most obvious of these group attributes. Bird populations also change: in some years there may be many birds of a given species around, but in other years it may be difficult to find even one individual. This variation leads to questions such as: How do we track and measure differences in bird populations? And why do most bird populations vary in size in the first place?

Population size is important because knowing how many individuals are out there is a first step toward understanding population trends, that is, whether populations are declining, increasing, stable through time, or fluctuating cyclically from year to year. Other important attributes of populations include their age structure (the proportion of the population made up of juveniles versus adult birds and the ages of those adults), sex ratio (the ratio of males to females), fecundity (the number of offspring per female produced each year), and survivorship (the proportion of birds that survives from one year to the next).

Considered in concert, these features describe the **demography** of a population, a term referring to the various factors that determine its size and composition. These types of data may seem easy to gather, but in practice years of detailed study are needed to describe the demographics of a wild bird species accurately, and decades of work may be necessary in order to understand how or why the demography of a population varies across space and time. Even then, the factors affecting the distribution and abundance of populations are usually complex—including both environmental or **abiotic factors** such as

Population: in ornithology, a group of interbreeding birds of the same species that live in the same place at the same time.

Demography: the statistical study of vital rates within a population, especially age-specific birth rates, death rates, and dispersal patterns.

Abiotic factors: features of the environment that result from non-living physical attributes such as temperature, topography, rainfall, altitude, etc.

Opposite: Bird populations can be vast or small. This image shows a mere subset of an impressively large Black-browed Albatross (*Thalassarche melanophris*) breeding population. (Photograph by Geoff Edwards.)

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rainfall and temperature, and **biotic factors** such as the availability of food and presence of competitors and predators.

13.1 Avian population ecology

Describing the demography of a population provides a foundation for understanding where birds are and why their populations vary as they do. At one level, bird distributions are clearly related to habitat preferences. For example, the Kirtland's Warbler (*Setophaga kirtlandii*) (Fig. 13.01A) of North America breeds only in recently burned jack-pine forests where the young trees are less than about 3 meters high, and consequently it is not surprising that these warblers have a very restricted breeding distribution in central and northern Michigan (USA). Conversely, the closely related Yellow-rumped Warbler (*Setophaga coronata*) (Fig. 13.01B) breeds in a wide range of both coniferous and deciduous forests and is common throughout northern and western North America. Two other closely related species with greatly differing ranges are the Eleonora's Falcon (*Falco eleonorae*) (Fig. 13.01C), a relatively rare and threatened

Biotic factors: features of the environment that result from living organisms, such as the presence or absence of competitors, predators, prey, etc.

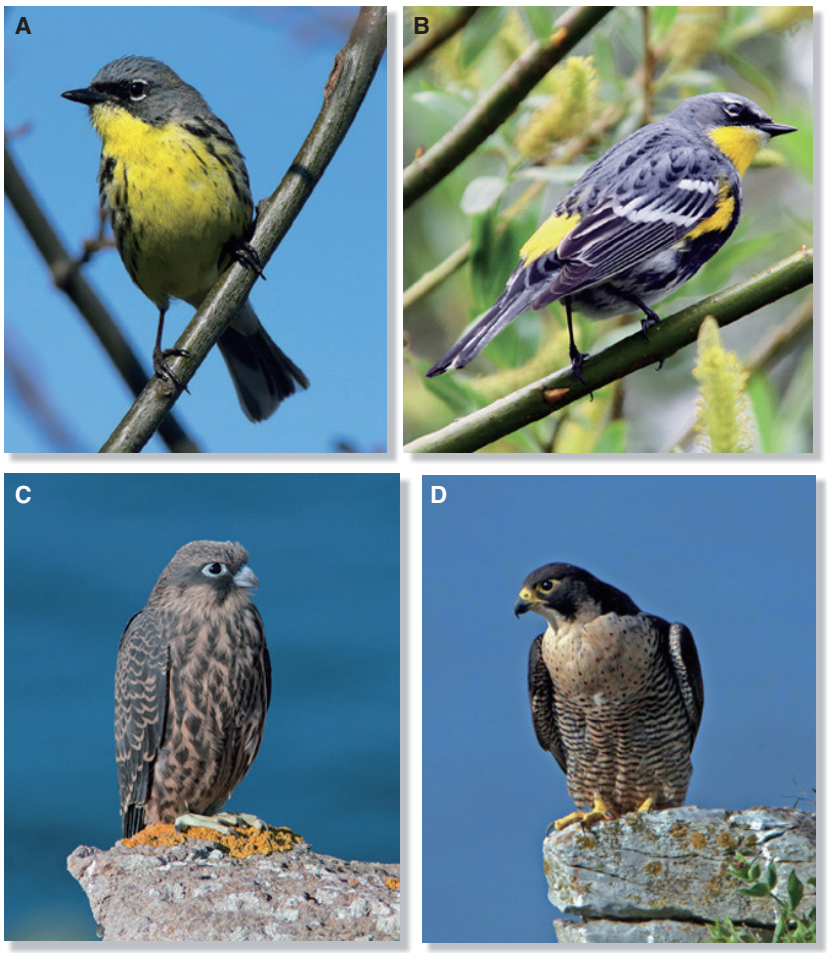


Fig. 13.01 Close relatives with distinct habitat preferences. (A) Kirtland's Warbler (*Setophaga kirtlandii*) is a habitat specialist that breeds only in dense young jack-pine forest in a small region of North America, while its close relative (B) the Yellow-rumped Warbler (*Setophaga coronata*) is a generalist species found throughout much of North and Central America. (C) Similarly, Eleonora's Falcon (*Falco eleonorae*) breeds principally on Mediterranean islands, whereas various subspecies of (D) the Peregrine Falcon (*Falco peregrinus*) can be found throughout most of world in a diversity of habitats. (Photographs by: A, Ryan J. Sanderson; B, Mary Ann Durkin; C, Marco Crivellari; D, Peter Walkden.)

species whose breeding range is restricted to islands in the Mediterranean, and the Peregrine Falcon (*Falco peregrinus*) (Fig. 13.01D), a species that is geographically widespread and found on every continent except Antarctica.

Why are there such dramatic differences in these birds' distributions? Are Yellow-rumped Warblers better competitors than Kirtland's Warblers, forcing the latter into only one restricted type of habitat? Are Peregrine Falcons so widespread because they can prey successfully on a wide range of bird species, whereas Eleonora's Falcons for some reason can only catch migrating songbirds passing through the Mediterranean on their way to Africa? Perhaps Peregrine Falcons simply are better dispersers than Eleonora's Falcons, or perhaps the peregrines' willingness to nest on buildings and hunt in cities, where Rock Pigeons (*Columba livia*) often make up a high proportion of their diet, has allowed them to succeed in many areas where other falcons have not. Although we may not be able to answer fully the fundamental question of why these species have such different distributions, we can measure many of the ways their populations differ and evaluate some of the broader implications of these differences.

Given the wide range of factors that can influence the size of bird populations, how do we know which of these factors determine whether a population is increasing or decreasing? This is one of the most difficult questions in the field of population ecology and typically comes down to the question of timescale (it may be easy to determine whether there are more birds in a particular population this year than last year, but much more difficult to determine whether this represents a long-term trend) and ultimately to the issue of what regulates population size. Ecologists divide the possible regulators into two general groups: **density-independent factors** that are unrelated to population size, and **density-dependent factors** that are sensitive to the number of individuals present in the population. Density-independent factors include events such as storms that can kill a large fraction of a population but whose effects are unrelated to the number of individuals composing the population. Density-dependent factors include anything whose effects are determined, at least in part, by the number of individuals present. For example, the relative availability of food and territories to which young might disperse are two of the many factors often influenced by the number of competing individuals.

Of particular interest to ornithologists through the years has been the extent to which social behavior may regulate populations. For example, territoriality—a common behavior through which birds exclude other individuals of the same (and occasionally other) species from a particular patch of real estate—can limit the number of individuals breeding in the population and thus influence the population's reproductive rate.

13.2 Changes in populations over time and space

The complex ways in which populations vary, not only in time (for example, across seasons), but also among different locations, make the study of population biology both exciting and challenging. Populations of some species appear to fluctuate in numbers cyclically, varying from abundant to rare, often tracking a key food resource. For example, Barn Owls (*Tyto alba*) in Scotland track the densities of field voles—a rodent well known for exhibiting cyclic population fluctuations—that form their primary prey (Taylor 1994). Likewise, Long-tailed Jaegers (*Stercorarius longicaudus*) that breed in the Arctic have boom years when brown lemmings—another rodent prone to dramatic population cycles—are abundant, and decline in years when lemmings are rare (Pitelka et al. 1955). Another well-studied example of cyclic bird populations include the Galápagos finches of Isla Daphne (Chapter 3), where these birds vary in number in response to cycles of rainfall and drought that influence their food supply of seeds.

In cases like these owls, jaegers, and finches, the causes of population cycles in birds can be clear, but in other species the causes of population cycles are more difficult to determine. Several species of grouse—including Red Grouse (*Lagopus lagopus*) in Scotland and Rock Ptarmigan (*Lagopus muta*) in Iceland and elsewhere—exhibit population cycles varying in duration from 3 to 10 years (Fig. 13.02). The causes of these cycles may include interactions with parasites, predators, and food, as well as abiotic factors such as weather (Moss and Watson 2001). In fact, virtually all avian populations vary in size through time for reasons that are rarely easy to determine. Such fluctuations can be worrisome when bird populations drop to such low numbers that a population or species may go extinct (Chapter 15).

Although some bird populations are small and have a limited geographic range, others extend over large areas and may consist of many smaller subpopulations that are only partly connected to each other by means of dispersal.

Density-independent factors: any environmental factor that limits the size of a population that is not dependent on the number of individuals in that population.

Density-dependent factors: any environmental factor that limits the size of a population whose effect or intensity varies based on the number of individuals in the population.

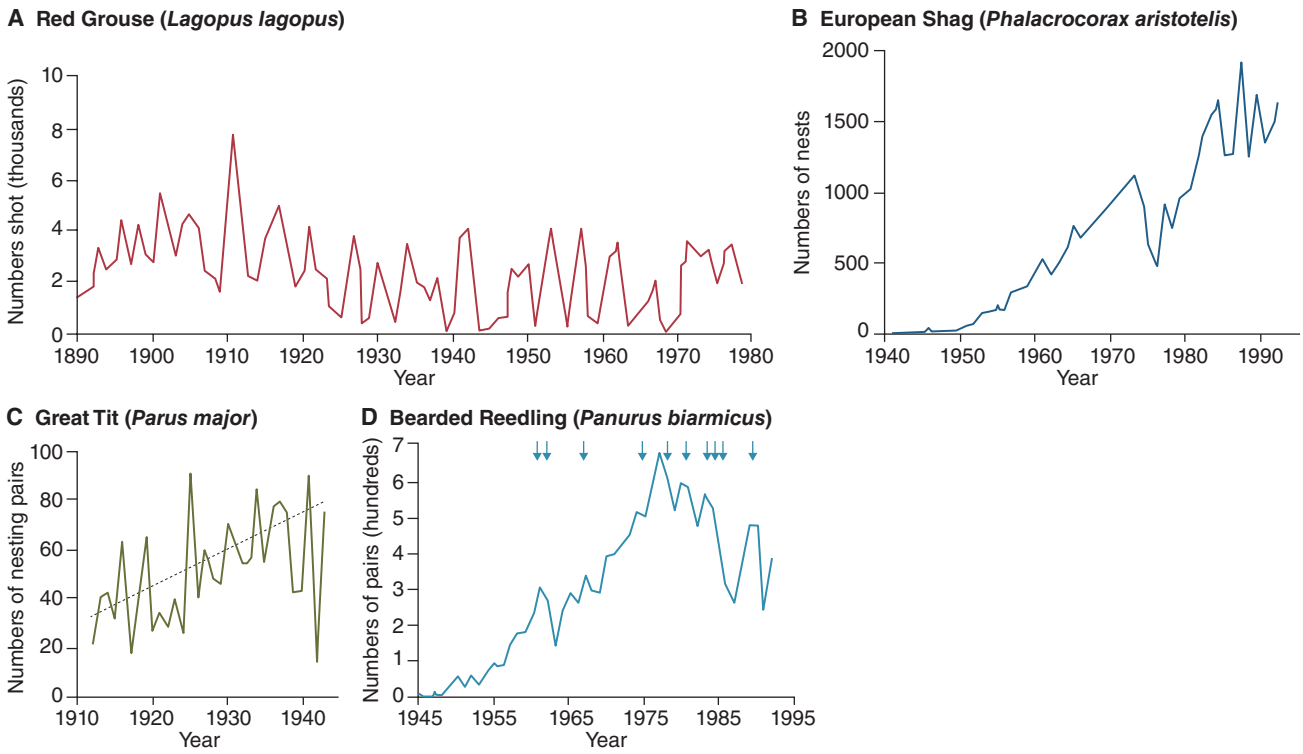


Fig. 13.02 Population trends vary in space and time. Examples include: (A) cyclic fluctuations in population numbers in Red Grouse (*Lagopus lagopus*), (B) a long-term population increase in European Shags (*Phalacrocorax aristotelis*), (C) irregular annual fluctuations despite a general long-term population increase (dashed line) in Great Tits (*Parus major*), and (D) variability in population numbers driven in part by cold winters (indicated by arrows) in Bearded Reedlings (*Panurus biarmicus*). (From Newton 1998. Reproduced with permission from Elsevier.)

Such interconnected **metapopulations** may rescue each other from extinction as long as dispersal is sufficiently common and the population trends of the different areas are sufficiently different. To the extent that population trends in one area are decoupled from those in other areas—that is, when **spatial synchrony** among populations is low—knowledge of the demography of one population provides little help in understanding trends in other populations of the same species. Metapopulation subdivision is not always a good thing: in many cases bird populations are unlikely to persist in areas that have become too subdivided or fragmented by other kinds of habitats, an almost ubiquitous phenomenon in the modern world (Chapter 15).

Metapopulation: an array of spatially separated populations of the same species that are at least partly connected by the dispersal of individuals among them.

Spatial synchrony: the tendency for the size or density of spatially disjunct populations to be correlated through time. Spatial synchrony within a larger metapopulation occurs when the subpopulations grow or shrink in size at the same times.

13.3 Censusing bird populations

How do we know what birds are out there and how many of them there are? Has anyone counted, or even seen, them all? It will not surprise you that the answer is no: although there are a few dedicated birders who have seen a large proportion of the 10,000 or so living species of birds, no one has come close to counting more than a tiny fraction of the estimated 100 billion individual birds that live on earth at any one time. How then do we know which avian populations are healthy and increasing, and which are declining and in need of conservation attention?

The answer depends on the bird species and its location. In many remote places we do not know even what species are present, much less how many individuals of each species there are. In such areas inventories of species must be generated (which can still, even today, involve finding and

describing bird species previously unknown to science), after which more detailed inventories can be done to estimate the numbers and status of particular species.

Researchers use standardized methods for censusing birds, the most common of which are **point counts**, in which an observer standing in a specific location records all the individual birds seen or heard within a circle (often within a circle of a specific radius), and **transect counts**, in which an observer walking a transect of a specific distance records all the birds seen or heard. Such methods must be used carefully, ideally adjusting values for differing detectability among bird species, habitats, and even the time of day. For example, there might be equal numbers of hawks and owls in a particular forest plot, but a census conducted during the day would probably count more of the actively hunting hawks than the less detectible roosting owls. Such techniques can provide valuable information regarding the status of bird populations (Box 13.01).

Although bird census data can be used to determine how many individuals of a particular species there are in a specific locality, they are more commonly used to estimate general population trends. Even these estimates, however, may involve some tricky statistical work and are not necessarily simple to interpret. Consider, for example, North American neotropical migrant landbirds, species that breed in North America but winter in Central or South America (the New World tropics). As early as 1978, researchers began reporting notable declines in neotropical migrants that breed in eastern North America. Chandler Robbins and co-workers (1989) used Breeding Bird Survey data to infer that these declines were particularly strong among species that winter in forested habitats. They concluded that tropical deforestation was having a more direct impact on such migrants than the loss and fragmentation of forest habitats in the breeding grounds in North America.

Many confounding influences can affect these types of conclusions, however, and subsequent analyses have suggested that other factors are also likely to be causing problems for migratory North American songbirds. Katrin Böhning-Gaese et al. (1993), for example, focused on insectivorous songbirds and found that the main declining species were those with low, open nests subject to parasitism by Brown-headed Cowbirds (*Molothrus ater*), from which they concluded that predation and brood parasitism taking place on their North American breeding grounds were more important to the observed declines than tropical deforestation. Marc-André Villard and Brian Maurer (1996) found considerable geographic and temporal variation in the populations of two species of migratory warblers, thus indicating that the trends reported by earlier studies might not be general. Meanwhile, Fran James et al. (1996), analyzing the same Breeding Bird Survey data used by Robbins et al. (1989), concluded that there was no evidence for the general recent decline in migratory wood warbler populations in eastern and central North America originally suggested by these latter authors. Subsequent analyses have indicated that Breeding Bird Surveys are indeed counting fewer numbers of many neotropical migrants, but the causes remain elusive and controversial. Bridget Stutchbury (2007), for example, suggests that the main cause of recent declines is environmental contaminants, particularly pesticides. Others remain skeptical, even pointing out the possibility that the apparent declines are an artifact of increased ambient noise reducing the detectability of birds during surveys.

This is not to say that all reported trends are controversial or that it is impossible to measure population trends of birds accurately. Doing so is rarely easy, however, and it is generally even harder to determine the specific causes of demographic trends. Later in this chapter we discuss several examples in which population size is correlated with a specific ecological or environmental factor, evidence that is consistent with the hypothesis that the factor in question is driving changes in population size of the species. However, only rarely have such factors been tested experimentally and there usually are alternative explanations remaining to be examined.

13.4 Avian demography

Although determining size and population trends is frequently a goal of bird studies, there is also much to be learned from understanding patterns of reproduction and survivorship; that is, by quantifying the demography of a population. Here we discuss several basic facets of avian demography and a few of the ways they can offer important insights into avian population dynamics.

13.4.1 Age structure

Populations consist of individuals, and, with rare exceptions, every one of those individuals can be characterized as being of a particular age and sex. Considered as a whole, each population therefore has an **age structure** and a **sex ratio**.

Point count: a popular census method for birds in which an observer notes the birds seen or heard from a stationary point over a standard period of time.

Transect count: a bird census technique in which an observer moves along a path—the transect—and notes all the birds seen or heard.

Age structure: the statistical distribution of the ages of all the individuals in a population.

Sex ratio: the ratio of males to females in a population.

Box 13.01 Censusing birds and worldwide avian monitoring

Birds play a crucial role as environmental indicators, in part because they are relative easy to identify and census. Although it may be satisfying to imagine counting all the birds in an area, it is often more practical to census only a representative section of the area of interest. Point counts and line transects are the census methods used most widely by ornithologists, during which observers record all birds seen or heard at a particular site (or set of sites) for a predetermined time, often between 2 and 20 minutes. Typically, observers will also estimate the distance the bird is from either the observer (point counts) or transect (line transects), which then allows them to estimate the density of the birds detected on a species-by-species basis by controlling for differences in detectability among species.

More generally, estimates of the size and demographic trends of many bird populations can be determined from the observations of thousands of dedicated amateurs and recreational birders who spend time in the field and diligently record their observations in various national databases. In the USA, sources of distributional data and population size include the National Audubon Society's Christmas Bird Counts, the US Geological Survey's Breeding Bird Surveys (Fig. 13.B1.01), Cornell University's eBird and Project FeederWatch, and the various Breeding Bird Atlases compiled for individual states. In the UK, the British Trust for Ornithology in conjunction with the Royal Society for the Protection of Birds and the Joint Nature Conservation Committee produce an annual breeding bird survey that summarizes population changes and other notable findings from surveys conducted each year. Recently, some of these community efforts—particularly eBird—have expanded around the globe, and as data accumulate, we are likely to gain a much better understanding of bird populations worldwide.

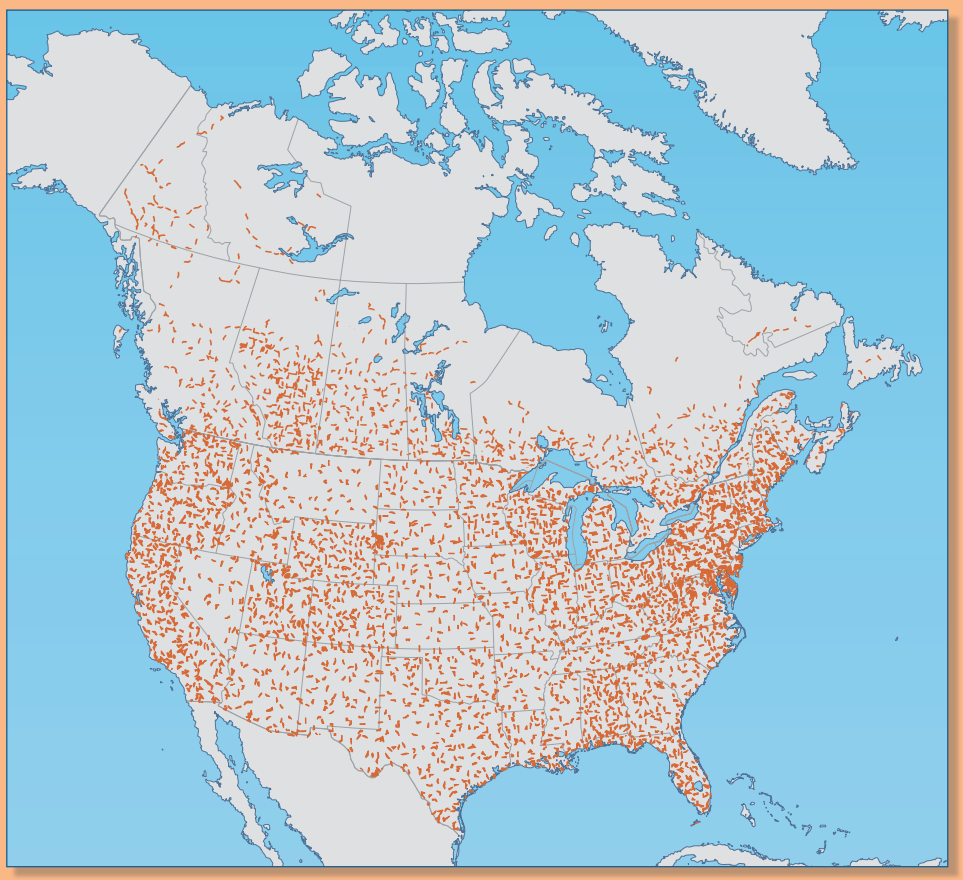


Fig. 13.B1.01 North American Breeding Bird Survey transects. This survey, ongoing since 1966, follows transects along a 24.5-mile (40-kilometer) route. Beginning just before sunrise, observers stop at 0.5-mile intervals and record all birds seen or heard within a 0.25-mile radius during a 3-minute period. Surveys are conducted annually at the height of the avian breeding season. (Courtesy of Environment Canada 2014 and US Geological Survey.)

Datasets from these and other similar citizen science programs are often the best sources of information on the general population trends of individual species, particularly those species with geographic ranges covering a large area. Such data can even be used to estimate total numbers of individuals, as has been done by the group Partners in Flight for North American birds and for birds in the UK (Newson et al. 2008). These estimates suggest that are approximately 5 billion breeding landbirds in North America, representing about 5% of the birds in the world. For individual species, there are an estimated 310 million American Robins (*Turdus migratorius*) in North America, and an estimated 10 million Eurasian Blackbirds (*Turdus merula*) and 8.3 million European Robins (*Erithacus rubecula*) in the UK.

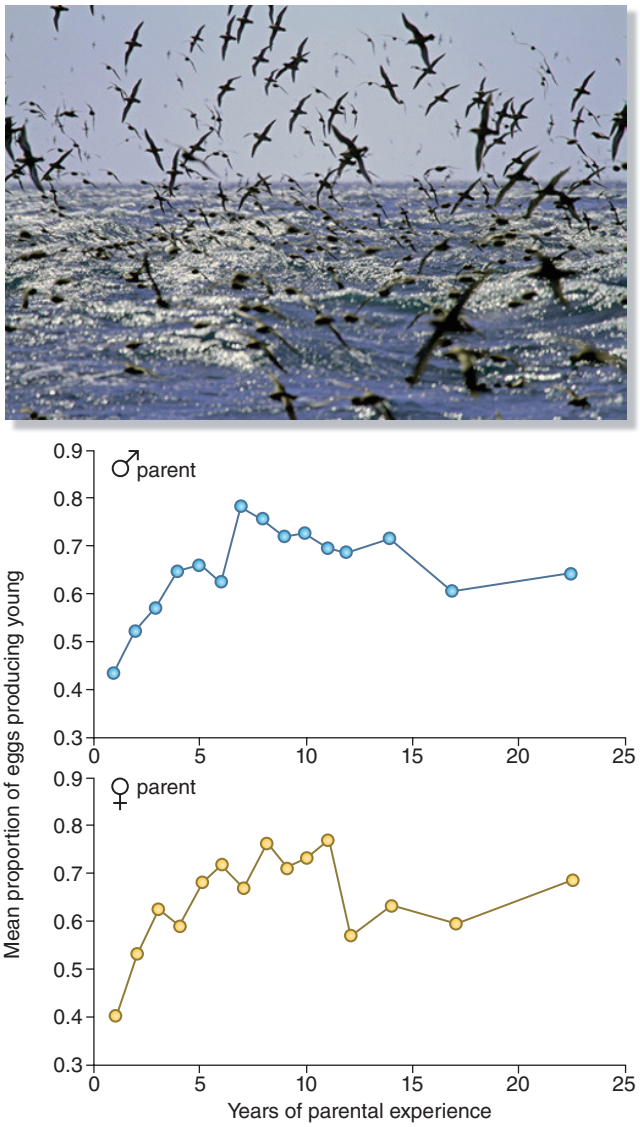


Fig. 13.03 Age-related reproductive success. The proportion of Short-tailed Shearwater (*Ardenna tenuirostris*) eggs that successfully produce fledged young in relation to the breeding experience of their male (blue) and female (yellow) parents. Note that in both sexes, relatively inexperienced parents have lower reproductive success than older parents. (From Wooller et al. 1990. Reproduced with permission from John Wiley and Sons. Photograph by Jim McLean.)

Variations in age structure are important to many populations because young birds are often less likely to successfully attract a mate, defend a territory, or eventually raise young (Fig. 13.03). Such age-related differences are common—although their precise causes usually vary from species to species—and can have effects that are more subtle than simply reduced breeding success. In Bullock's Orioles (*Icterus bullockii*) of western North America, for

example, young males are generally female-like in plumage, a fairly common phenomenon known as **delayed plumage maturation**, and usually achieve full adult male plumage when they are 2 years old. In a study of this species, David Richardson and Terry Burke (1999) found no difference in clutch size or number of offspring fledged from the nests attended by older males versus males breeding in their first adult year. However, 71% of the nests of the young males contained young that had been sired by another (usually older) male in the population, whereas only 32% of adult males had such **extra-pair young** in their nests (Chapter 9).

Birds in their first year of life typically have lower survivorship than adults, and birds breeding for the first time often have reduced clutch size and are less successful in the number of young they raise than older birds. These differences can result in seasonal differences in age structure; in Northern Bobwhite (*Colinus virginianus*) and California Quail (*Callipepla californica*) of North America, for example, the ratio of first-year to adult birds drops from over 9:1 in fall to less than 4:1 by the following spring. Although such age-related differences in survival are common, the causes of such differences are not necessarily obvious. Consider the Yellow-eyed Juncos (*Junco phaeonotus*) in the Chiricahua Mountains of southeastern Arizona (USA), among which only 11% of nestlings survive to their first spring, whereas annual survivorship of adults is nearly 50%. Fledglings are particularly susceptible to predation, whereas slightly older, more independent juveniles are often unable to obtain enough food and consequently lose weight and eventually starve to death (Sullivan 1989). It would seem logical to assume that food limitation is the ultimate cause of these differences, but behavioral evidence indicates that both these effects instead are the result of young birds being incompetent both in avoiding predators and finding enough to eat. Basically, their youthful naïveté and relatively poor judgment place them at high risk until such time—if they are lucky enough to survive—that they gain more experience.

Delayed plumage maturation: the delayed acquisition of adult plumage (usually by males) by birds that are otherwise sexually mature and capable of reproduction.

Extra-pair young: in a bird species with male–female social pair bonds, offspring that are sired by a male that is not the female's social mate.

Senescence: a decline with age in physical, physiological, and/or reproductive performance, or an increase with age in the probability of death.

13.4.2 Aging and senescence

In many birds, annual survival often appears to be more or less constant once individuals have matured, at least for several years. Survivorship tends to be a life history trait (that is, a character affecting the demography of an organism) that is size dependent. Many birds live up to three times longer than mammals of the same size, a result that is particularly surprising given the higher metabolic rate of birds (Holmes and Austad 1995). A long-lived 20-gram house mouse, for example, will at best live to the age of 4 years, whereas a 13-gram White-browed Scrubwren (*Sericornis frontalis*) in coastal Australia has been known to live 17 years (Møller 2008), and a 10-gram Black-capped Chickadee (*Poecile atricapillus*) in North America has been recorded living more than 12 years (Blumstein and Møller 2008).

Many large seabirds are especially long-lived, in some cases surviving longer than the working lifespan of the ornithologists who study them. Albatrosses and fulmars, for example, have been known to live more than 50 years, and based on their survival rates it is possible that there are a few 100-year-old birds out there at any one time. Such impressive longevity among birds is a topic of considerable interest among scientists trying to understand the evolution of aging (Box 13.02).

Do birds eventually get so old that they are less likely to breed and survive than younger individuals? This is the definition of **senescence**, a decline with age in these key life history characteristics. Senescence is not easily detected in the wild, because so few individuals live long enough to show signs of old age. Instead, nearly all wild birds die from predation or other non-age-related causes. However, numerous field studies now have lasted long enough to provide good evidence for such age-related declines in birds. For example, Florida Scrub-Jays (*Aphelocoma coerulescens*) can live to be at least 15 years old, and analyses indicate that the probability of mortality increases from around 15% per year for 2-year-old birds to more than 25% per year for birds 9 years old or older (MacDonald et al. 1996). In Eurasian Sparrowhawks (*Accipiter nisus*) in Scotland, long-term study indicates not only an increase in survival and reproductive success early in life but also a significant decrease—senescence—as birds age, with survival increasing from 49% in first-year females to 66% in 4-year-old birds, and then declining to 28% in 9-year-old birds (Newton and Rothery 1997) (Fig. 13.04A). Similarly, annual production of young increased from an average of 0.3 by first-year females to 3.34 by 5-year-old birds, and then declined to 1.8 by 9-year-old individuals (Fig. 13.04B). Clearly age has important consequences for both survival and reproduction in bird populations.

As usual, understanding such trends involves both long-term study and close attention to the underlying natural history of each bird species, particularly any inherent

Box 13.02 Avian longevity

It is often difficult to determine the age of a wild bird, beyond recognizing relatively young individuals on the basis of their plumage, eye color, or other traits (Chapters 4 and 6). Consequently, most longevity records of birds come from studies of banded birds, or in some cases from captive individuals kept as pets or in zoos. Particularly long-lived birds include flamingos, parrots, petrels, and shearwaters, with mean maximum lifespans of over 30 years, while a few individual albatross are known to be well over 50 years old. Among passerine birds, crows and magpies have been known to live more than 17 years, whereas birds like flycatchers and wood warblers have shorter maximum lifespans.

Of greater interest to the study of aging, however, are the factors that correlate with longevity. A comprehensive analysis of lifespan among a wide range of birds (Fig. 13.B2.01) found that body size, diet, sociality, and whether or not the species lives on an island were factors explaining much of the interspecific variation in longevity (Wasser and Sherman 2010). Large, herbivorous, social island dwellers are longer lived than smaller, asocial birds that are either carnivorous or omnivorous and which live on the mainland. In general, these results are consistent with evolutionary theories of senescence: when individuals can expect to live longer, there will be selection to postpone physical deterioration so as to take advantage of their greater potential lifespan, and thus senescence will take place relatively later.

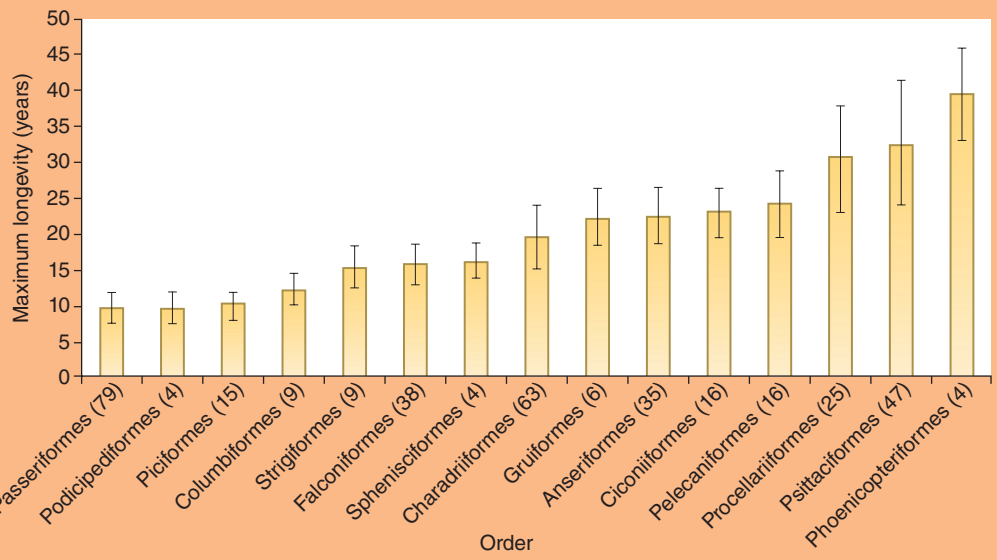


Fig. 13.B2.01 Longevity in wild birds. Mean (±SD) maximum longevity across 15 orders of birds based on banding recoveries in wild populations. (From Wasser and Sherman 2010. Reproduced with permission from John Wiley and Sons.)

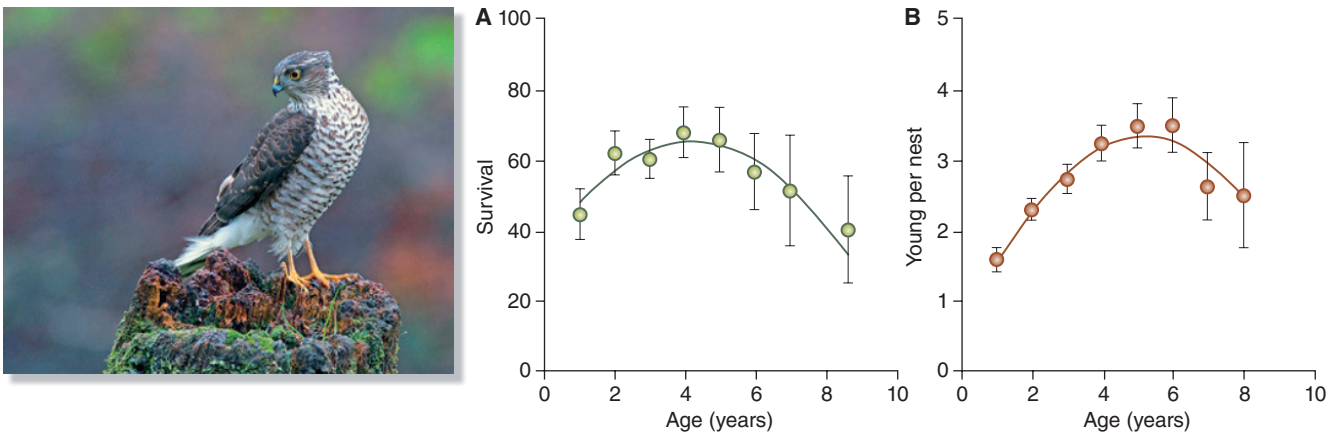


Fig. 13.04 Senescence and aging. The late-age decline in (A) survival and (B) reproduction is an indication that Eurasian Sparrowhawks (*Accipiter nisus*) undergo senescence. (From Newton and Rothery 1997. Reproduced with permission from Ecological Society of America. Photograph by Mark Molloy.)

differences in quality among individuals. In the case of the Florida Scrub-Jays, for example, when analyses were run using all the birds in the population, no evidence of increasing age-related mortality was found, but this result was misleading because lower quality individuals are both overrepresented among younger age classes and more likely to die. As a result, the pattern of increasing mortality demonstrating senescence is apparent only when comparing birds of similar quality as they get older. Similar challenges are encountered in all studies of this phenomenon in wild birds.

13.4.3 Sex ratio evolution

Sex in birds is determined chromosomally (Chapter 7), as it is in humans and other mammals. Consequently, it is not easy for environmental factors to influence the sex of young birds (unlike crocodilians and some turtles, in which the sex of developing young is determined by the temperature at which the eggs develop). Unlike mammals, female birds are the **heterogametic sex**; that is, female birds have two different sex chromosomes (Z and W), and male birds have two copies of the Z chromosome. By choosing which type of chromosome fertilizes their eggs, some female birds may be able to adjust the sex ratio of the eggs they lay.

There are two levels at which such sex ratio manipulation can be considered: at the overall population level, and from the perspective of a particular breeding adult. At the population level, we can ask under what conditions, if any, is it advantageous for the sex ratio of the population to be other than 1:1 (that is, to have unequal numbers of males and females)? For that matter, why should it be 1:1 to begin with?

This fundamental question was solved by the British population ecologist Sir Ronald Fisher (1930), who pointed out the deceptively simple fact that, because all individuals in sexual species (including all birds and mammals) have one mother and one father, the average fitness (or benefit) of producing a male is exactly equal, on average, to that of producing a female. Although this statement may seem obvious in retrospect, it is not a trivial realization. Take, for example, a polygynous species such as the Andean Cock-of-the-rock (*Rupicola peruvianus*) in which only a small proportion of males mate successfully with females (Chapter 9). Would it not make sense for a female Andean Cock-of-the-rock to produce mostly female offspring, nearly all of which would be likely to mate successfully and eventually reproduce, than for her to produce male offspring, the vast majority of which probably will never sire any offspring?

The answer is no: although only a small fraction of males will eventually sire young, those few males that do succeed will be wildly successful and have high fitness exactly compensating for the lower proportion of male birds successfully breeding. In other words, although the variance in reproductive success across individuals may be very different for males and females, the mean fitness of males is always precisely equal to the mean fitness of females, because every offspring is the product of one father and one mother. Therefore, unless something strange is going on, the sex ratio of eggs laid by all bird species, whether they are monogamous, polygynous, or polyandrous (Chapter 9), should be close to 1:1.

What Fisher actually hypothesized is that, because the average fitness of producing a male is equal to that of producing a female, the amount of resources expended on producing the two sexes should be equal across the population, an assertion known as Fisher's principle. To include all relevant expenditures, this principle usually is stated in terms of **parental effort** or **parental investment**. Thus, Fisher's principle asserts that the amount of effort expended on producing males in the population should equal that expended on producing females. Fisher's principle predicts an even sex ratio in the population as long as the cost of producing a male is equal to that of producing a female, and it remains the most widely accepted explanation of why most populations of birds and mammals have a sex ratio that is close to parity.

The second level at which sex ratio manipulation can be considered is that of the individual bird. In some situations, the amount of effort a breeding parent should expend on individual male offspring is not the same as that expended on individual female offspring. For example, consider a sexually dimorphic species such as the Harris's Hawk (*Parabuteo unicinctus*), which lives in open habitats throughout the southwestern USA and much of Central and South America. As with most other raptors, female Harris's Hawks are larger than males. This size difference is evident even during the nestling stage and presumably requires the parents to provide more food to a growing female nestling than to a male nestling. Because each male offspring therefore "costs" less than each female offspring, Fisher's principle predicts that the sex ratio of young at the end of the period of parental care—that is, the Fisherian sex ratio—should be male biased. This prediction turns out to be true: at 30 days of age, 57% of 262 nestlings from 125 nests of Harris's

Heterogametic sex: in animals with genetic sex determination, the sex that has two different sex chromosomes. In birds, females have heterogametic sex chromosomes (Z and W) whereas males are homogametic (Z and Z).

Parental effort or parental investment: any expenditure of time or energy by a parent bird that benefits their current offspring at the cost of the parent's own future survival or reproduction.

Hawks were males, a ratio significantly different from parity (Bednarz and Hayden 1991).

Sexual dimorphism is not the only factor that may affect the cost of raising a male as compared with a female. In Common Grackles (*Quiscalus quiscula*) of North America, for example, males are substantially larger than females and the death of nestlings prior to fledging—known as **brood reduction**—tends to favor the smaller females, particularly among large broods. Thus the amount of effort expended on raising a male to the end of parental care is greater, on average, than the amount of effort expended on raising a female, both because males are larger and because a higher proportion of male nestlings die before fledging, resulting in what effectively amounts to wasted parental effort. In accordance with Fisher's principle, the sex ratio of fledgling Common Grackles is biased significantly toward females, the sex that costs less (per nestling) to produce (Howe 1977).

Still other factors can come into play to influence sex ratios. If relatives of one sex (such as brothers or sisters) compete more among themselves (for resources or mates) than with members of the other sex, a situation known as local resource (or local mate) competition, this competition effectively devalues them and leads to a predicted bias in the Fisherian sex ratio toward the non-competing sex. Conversely, if relatives of one sex cooperate and help each other more than do the relatives of the other sex, this cooperation theoretically can result in local resource enhancement whereby the value of that sex is amplified. In this case the Fisherian sex ratio will be biased toward the more cooperative sex.

One potential example of local resource enhancement occurs in cooperatively breeding birds (Chapter 9) in which helpers at the nest tend to be primarily of one sex (usually males). Assuming that such helpers increase the number of young fledged by their parents, it has been proposed that they are "repaying" their parents and thus in effect are reducing the initial cost of raising them. This repayment principle predicts that the sex ratio of offspring should be biased toward that of the more helpful sex. Current evidence for this hypothesis is mixed; in fact, the helpers may be competing with parents for resources and mating opportunities as well as repaying them by helping to feed their offspring. Despite these complications, Fisher's principle is important because it offers a theoretical explanation of why the global sex ratio of a population of birds should be 1:1, and makes it clear that any instance in which the observed sex ratio deviates significantly from parity demands an explanation.

Sex ratio evolution also can take place at the individual level rather than throughout the population as a whole. That is, although the overall sex ratio of the population may be equal, it still may be advantageous for individual birds to produce young of one sex or the other to take advantage of local environmental or social conditions. Such **facultative sex ratio manipulation** is now believed to occur in a fair number of birds, although there are many remaining mysteries about the precise factors involved (Box 13.03).

The most common situation that might influence the facultative sex ratio of avian broods is the condition of the parents, an effect known as the **Trivers–Willard hypothesis** after the paper first proposing it (Trivers and Willard 1973). It assumes that males in good condition are more likely to be chosen by females as mates and that there is a correlation between female condition and that of the offspring they produce, so that females in good condition raise high-quality offspring. Then, in species in which only a few males breed successfully, it would benefit females in particularly good condition to lay male eggs, because those high-quality mothers would be more likely to produce the rare high-quality male offspring that eventually go on to be successful at mating. Meanwhile, females in poor condition would do relatively better by laying female eggs, because most of their female young are likely to have opportunities to mate even if they are in relatively poorer condition. In contrast, if these poor-condition mothers produced sons, their lower quality sons would face tough odds in the already intense struggle among males for dominance in mating. Such benefits could accrue to females even though the overall, or global, sex ratio of the population remains at parity.

This effect has been demonstrated experimentally in a population of Lesser Black-backed Gulls (*Larus fuscus*) on Walney Island (UK), in which egg laying is costly to females (Nager et al. 1999). As the condition of a female gull declines, the eggs she lays get smaller, and the probability that such smaller, low-quality eggs will survive and fledge is reduced. Accordingly, as a breeding female gull lays additional eggs, the more likely they are to contain a female embryo. When laying female gulls are provided with extra

Brood reduction: a behavior in which during a time of limited food or other resources, a nesting bird directly or indirectly allows one or more of their eggs or nestlings to die, thereby reallocating their available resources to the remaining offspring.

Facultative sex ratio manipulation: the still somewhat mysterious ability of some female birds to change the sex ratio of the eggs that they lay, in response to varying social or environmental conditions.

Trivers–Willard hypothesis: the idea that females should produce offspring of the higher investment sex when the females are in good condition, and offspring of the lower investment sex when the females are in poor condition.

Box 13.03 Sex ratio variation in birds: a continuing enigma

DNA assays can now be used to determine the sex of birds in which it is not otherwise readily apparent, including newly hatched nestlings. A result has been a striking number of studies reporting that female birds can modify the sex ratio of their offspring in response to a variety of factors, ranging from the attractiveness of their male mate, to territory quality, to the laying order of eggs within a clutch. Nonetheless, the question of whether sex ratio variation in wild birds occurs at all, much less whether it is common, remains a source of debate among ornithologists.

There are several reasons for this. First, many factors could affect parental investment, and thus (via Fisher's principle) the expected sex ratio. Given that we do not necessarily know what factors are important for a particular female, it is often difficult to predict the sex ratio we expect to find beforehand.

Consider the Western Bluebird (*Sialia mexicana*), a species common in western North America and in oak woodlands of the southwestern USA and Mexico (Koenig and Dickinson 1996). Male offspring are slightly larger than female offspring, leading to an expected sex ratio bias toward females due to Fisher's principle. On the other hand, male offspring sometimes act as helpers on their natal territory while female offspring do not, leading to an expected sex ratio bias toward males due to the repayment effect. Then again, males are more philopatric than females and thus it is expected that there is greater local resource competition among males than females, leading to an expected sex ratio bias toward females.

The observed sex ratio in this bluebird population was 51.9% males, which is not statistically different from 1:1, despite a sample of some 2000 nestlings from over 500 broods. Whether this result supports all three factors as having important influences on the global sex ratio whose effects cancel each other out, or whether it supports none of them as being important, is not easy to determine. More recent work, however, indicates that female bluebirds can adjust the sex ratio of their broods depending on the frequency of helpers in the population, which, being male offspring, are indicative of there being poor prospects for sons successfully obtaining a breeding position in the population (Fig. 13.B3.01). Thus, local resource competition does appear to influence the sex ratio bias made by individual female bluebirds.

Convincing findings supporting sex ratio manipulation at the individual level have also been reported for a variety of other birds, perhaps the most dramatic being extreme runs of single-sex chicks (up to 20 males in a row) produced by captive Eclectus Parrots (*Eclectus roratus*) (Heinsohn et al. 1997).

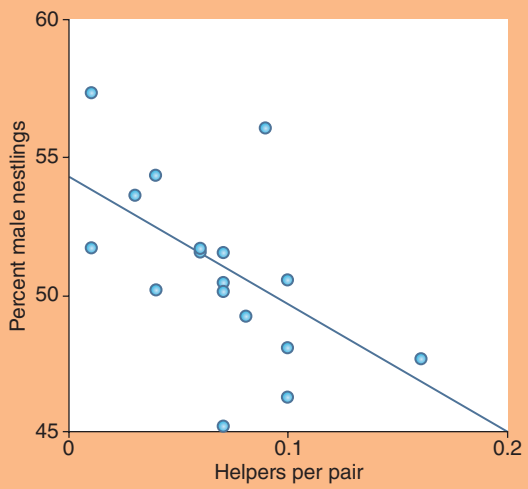


Fig. 13.B3.01 Nest helpers and brood sex ratio among Western Bluebirds (*Sialia mexicana*). Every point on this graph represents a different year; in years when there are more male helpers, an indication of high local competition for breeding opportunities, females bias the sex ratio of their broods toward females, which do not act as helpers in this species. (From Dickinson 2004. Reproduced with permission from Elsevier.)

food, however, the survival of male eggs remains high instead of declining with laying order. As a result, the sex ratio of eggs laid by non-supplemented females, whose condition declines as they lay more eggs, becomes more and more female biased, whereas that of supplemented females—those that remain in good condition—stays constant (Fig. 13.05).

One particularly intriguing hypothesis about sex ratios is the idea that female birds might vary the sex of their offspring depending on the attractiveness of their mate. The underlying idea is that if a female happens to have an especially attractive mate, it would benefit her to lay male eggs, because her male offspring also are likely to inherit those traits and be highly preferred by females. Conversely, if she mates with an unattractive male, it might benefit her to produce female offspring instead. Several studies have found correlations between sex ratio and male traits that are known or potentially known to be preferred by females, including a famous aviary study by Nancy Burley (1981) on Zebra Finches (*Taeniopygia guttata*). Female finches mated to males wearing leg bands in colors known to be particularly attractive to females laid more male eggs, whereas females mated to males wearing unattractive bands tended to lay more female eggs. Similar results from

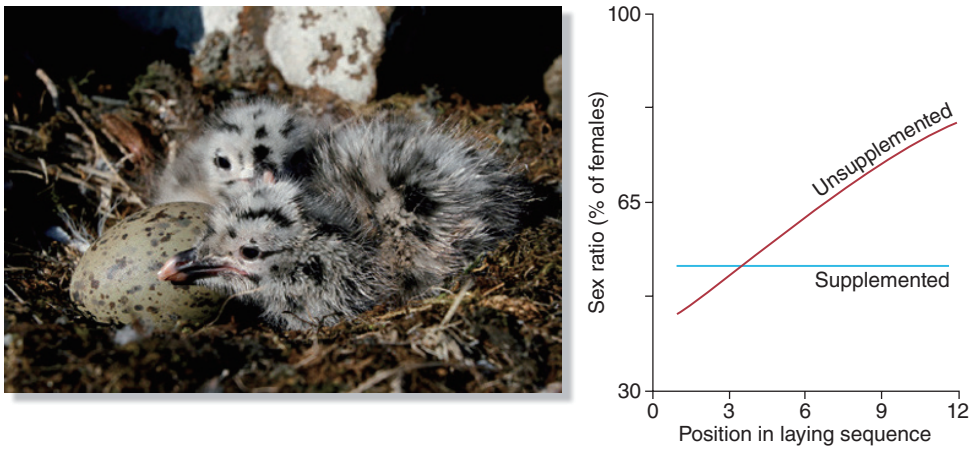


Fig. 13.05 Sex ratio variation and female condition. When researchers remove an egg from the nests of Lesser Black-backed Gulls (*Larus fuscus*), females expend energy to lay a replacement egg. In an experiment, some females were given supplemental food while laying a replacement egg. Unsupplemented females laid eggs that were increasingly likely to contain female offspring, a pattern not seen in the eggs of females provided with extra food. (From Nager et al. 1999. © 1999 National Academy of Sciences, USA. Photograph by Elma Rún Benediktsdóttir.)

wild bird populations include a study of Collared Flycatchers (*Ficedula albicollis*) on the Swedish island of Gotland in which females mated to males with large white patches on their foreheads—a trait found in males that provide more paternal care—produced more males (Ellegren et al. 1996) (Fig. 13.06). Likewise, in Eurasian Blue Tits (*Cyanistes caeruleus*) nesting in Gotland, males with particularly strong ultraviolet (UV) reflectance in their plumage both survive better and are preferred by females, and females mated to males with high UV pigmentation go on to produce male-biased broods.

Sex ratio variation is an active area of current research in avian biology, partly because researchers can now determine the sex of adults and nestlings using a simple DNA-based test. These methods allow ornithologists to explore many contexts in which bird populations, or the offspring of a particular female, may deviate from a 1:1 sex ratio. It now appears that these deviations may be common in wild birds, but we do not fully understand how all the variables that potentially influence sex ratio variation interact (Box 13.03). Nor do we understand how individual females accomplish the feat of sex ratio manipulation in the process of egg laying, because the physiological mechanisms that allow them to determine whether a given egg gets two Z chromosomes of a Z/W pair remain to be discovered.

13.5 Life history evolution

13.5.1 General life history theory

Much of avian population ecology focuses on what are known to ecologists as **life history traits**. Although the term "life history" is sometimes used as a synonym for the complete natural history of a bird, in a scientific context the term "life history trait" is much more specific, referring to those attributes most closely associated with survival and reproduction. In other words, they are the fundamental aspects of a bird's life that determine its evolutionary fitness.

The most obvious avian life history traits include features such as **clutch size**, egg size, number of clutches per season, age at first reproduction, and patterns of survivorship. Other traits that influence a bird's life history include duration of incubation, hatching patterns (whether eggs in a clutch hatch synchronously or asynchronously), duration of the nestling period, growth rate of nestlings, duration of time fledglings are dependent on parents, residency status (whether individuals are permanent residents in an area or migrate elsewhere in the non-breeding season), and dispersal patterns (how far birds move from where they are born, the age at which they move, and whether males disperse farther or more frequently than females).

Several factors should be kept in mind when considering the evolution of life history traits. First, because no two birds are the same—each individual is genetically unique—there

Life history traits: any of the fundamental traits that directly influence an individual bird's survival and reproduction. Examples include lifespan, age at first reproduction, and the number and size of offspring produced per year.

Clutch size: the number of eggs laid by a female bird in a single nesting attempt (a single clutch).

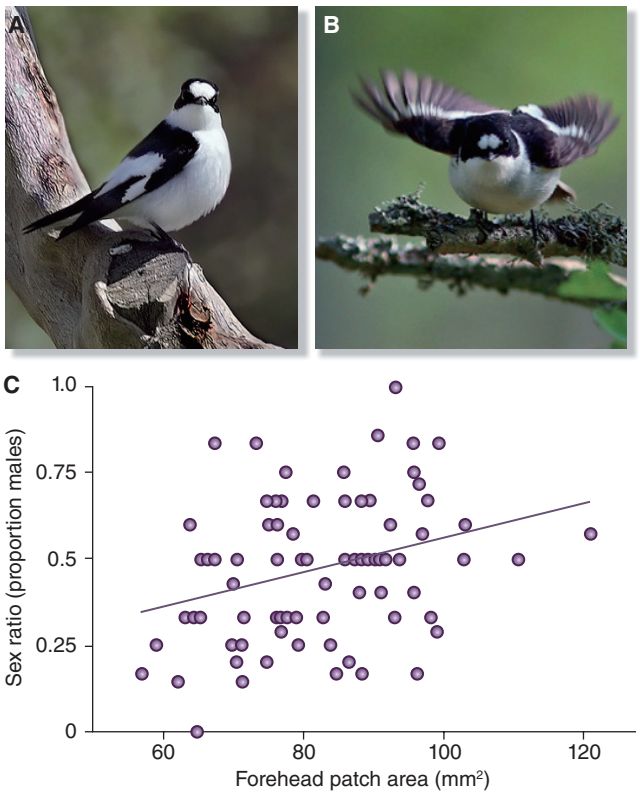


Fig. 13.06 Sex ratio and male quality. Female Collared Flycatchers (*Ficedula albicollis*) prefer (A) males with larger forehead patches (a badge of quality) over (B) males with smaller patches. (C) Females produce a higher proportion of male offspring per brood when the father has a larger forehead patch. (Photographs by: A, Soner Sabirli; B, Stefan Johansson. C, from Ellegren et al. 1996. © 1996 National Academy of Sciences, USA.)

is variability within avian populations in most life history characters.

Second, environments also differ, both from place to place and from year to year, thus ensuring that even if there were a single life history variant that was optimal in a particular place at a particular time, that variant might not be similarly optimal in the territory next door or in the same territory in the following year, much less at more distant locations or several years in the future when the next generation of birds is ready to breed. Taken together, such genetic and environmental variability ensures that there is never such a thing as a perfectly adapted genotype or individual. Instead, with conditions constantly changing, different individuals with varying genetic makeups—each expressing a distinct set of life history characters—are likely to be more successful at different times. As a result, a mix of genetic variants persists within the population, rather than a single dominant variant emerging to the exclusion of all others.

Third, nearly all life history traits vary systematically with body size; that is, they show **allometric scaling**. For example, larger birds lay larger eggs (Fig. 13.07A), but not proportionately so: measured as a percentage of body mass, small birds lay relatively larger eggs than do large birds (Lack 1968) (Fig. 13.07B). Other life history traits exhibiting similar types of allometric relationships include total clutch weight, brain weight, incubation period, age at first breeding, and maximum lifespan. Although it is not particularly surprising that such variables scale with size, the cause of these patterns is not obvious. For example, is lifespan limited by some physiological character, such as metabolic rate or the number of times the heart beats before it finally gives up? Metabolic rate scales inversely with body size—small birds have faster metabolic rates and faster heart beat rates than larger birds—so this hypothesis is plausible. However, it turns out that, after controlling for body size, there is no relationship between metabolic rate and reproductive rate in birds, indicating that differences in metabolic rate are not driving life history variation in birds independent of body size (Trevelyan et al. 1990). Regardless of the root cause of the relationship between body size and life history traits, the ubiquitous allometric scaling observed in such characters means that one always must account for differences in body size when trying to interpret variation in almost any life history character, particularly when comparing different bird species.

Fourth, small changes in a species' life history parameters can have large effects on fitness. The classic example was articulated by Lamont Cole in the 1950s and 1960s who pointed out that, all other things being equal, the increase in fitness achieved by an annual species (one that lives a single year and then dies, as do many plants) switching to being a perennial and living forever is the same as the fitness gain achieved by the same organism dying after 1 year but increasing the number of offspring it produces in that year (litter size) by just a single individual! There are a few real-world complications with this comparison (for example, it assumes that all perennial parents and their offspring are immortal), but the point is simple: a seemingly trivial change in demography, such as a small increase in a bird's clutch size, can have a large overall effect on its fitness.

Fifth, life history characters are invariably interrelated, often in ways that involve trade-offs among them. The reproductive strategy of a population—that is, the combination of all the life history characters that involve reproduction—is a compromise that, in the words of the ornithologist Robert Ricklefs (1977), is "maintained in a balance between the benefits of reproductive effort

Allometric scaling: changes in the magnitude of a trait that are related to, but not directly proportional to, changes in the magnitude of related traits.

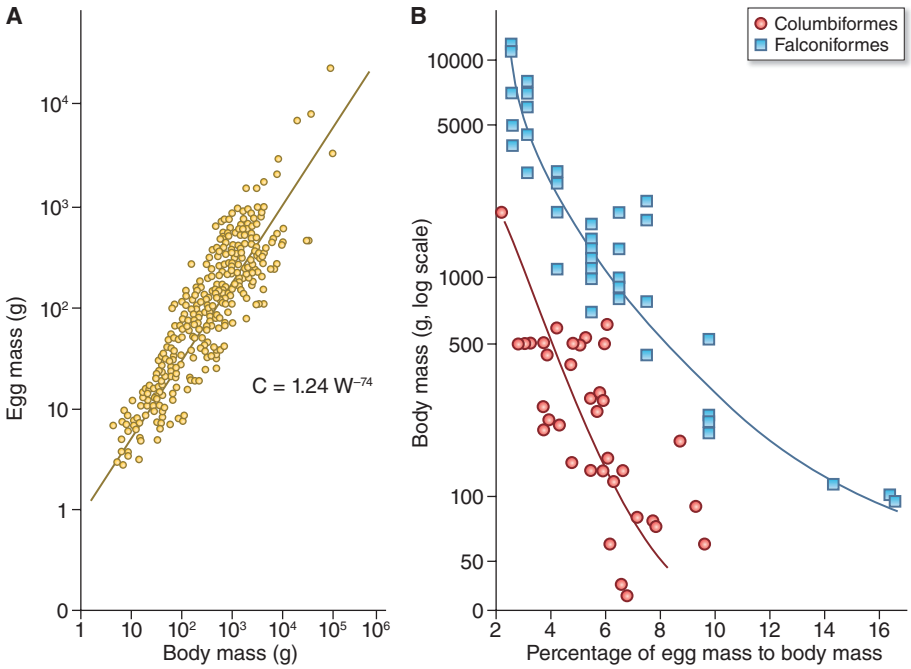


Fig. 13.07 Body mass and egg size. These graphs show the allometric relationship between (A) egg weight and body mass across many bird species, and (B) egg mass as a proportion of body size in raptors (blue) and doves (red). (A, from Blueweiss et al. 1978. Reproduced with permission from Springer Science + Business Media. B, adapted from Lack 1968. Reproduced with permission from Taylor and Francis Books.)

expressed as increased fecundity and the costs of reproductive effort expressed as increased adult mortality." In other words, putting more effort into producing or raising young may increase your reproduction, but only at a cost somewhere else. Put too much investment into reproduction at any one point in time, and the resulting decline in your physical condition means that you are more likely to be picked off by a predator or to die during a winter storm when food is scarce.

Such trade-offs can be observed both across species (Fig. 13.08) and within populations. For example, one study manipulated the brood size of Black-legged Kittiwakes (*Rissa tridactyla*) in northern Norway, where these seabirds usually attempt to raise two chicks (Jacobsen et al. 1995). The researchers either added a chick or removed a chick, resulting in broods ranging from one to three. Chick weight and fledging success were lower in the enlarged broods, and in the end no parents successfully raised all three young to fledging. Nonetheless, females that attempted to raise the enlarged broods were less likely to survive to the next breeding season, indicating that the higher effort they had to devote to these additional chicks came at a clear cost to the mother's longer term survival (Fig. 13.09).

One conclusion from this study is that Black-legged Kittiwakes have optimized their clutch size and the number of young they raise; that is, they raise the most young they can without compromising their subsequent survivorship. Another conclusion we can draw, however, is that there is a trade-off between the effort birds put into reproduction

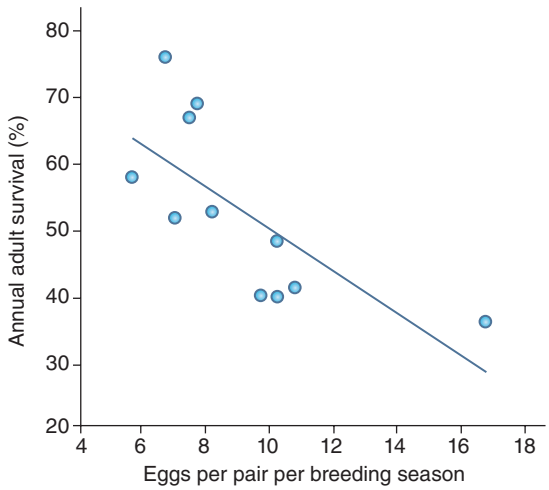


Fig. 13.08 Fertility versus survival. Fertility and annual survival rate are inversely related across 11 species in the genus *Parus*. Species with lower survival tend to lay more eggs per season. (From Dhondt 2001. Reproduced with permission from Ardea.)

and their survival prospects, and thus altering one variable will affect the other. This example represents a whole class of life history trade-offs between current reproduction (that is, the number of young produced at the moment) and future reproduction (young that can be produced in the future). Other traditional examples of life history traits that frequently, if not invariably, trade-off against each other

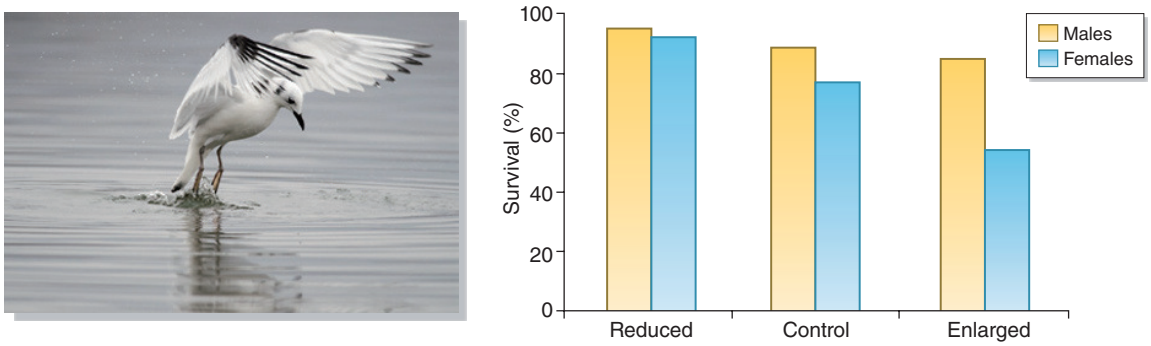


Fig. 13.09 Parental survival and clutch size. The survival of adult Black-legged Kittiwakes (*Rissa tridactyla*) is influenced by breeding clutch size, but differently in the two sexes. In pairs where clutch sizes were experimentally enlarged, females (blue) had significant reduction in survival, whereas males (gold) did not. (From Jacobsen et al. 1995. Reproduced with permission from Ecological Society of America. Photograph by Martin Balog.)

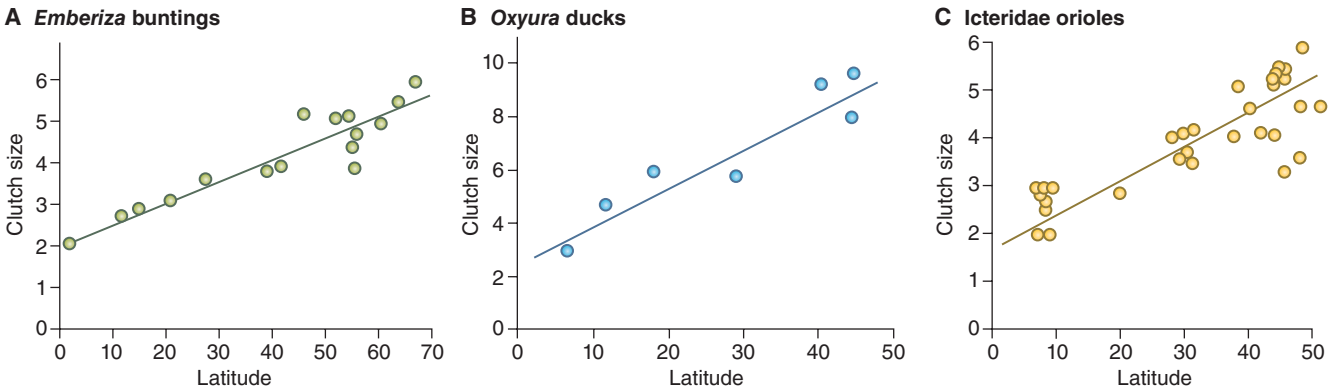


Fig. 13.10 Latitudinal gradients in avian clutch size. In these and many other northern hemisphere groups, species that live at higher latitudes tend to lay larger clutches. (From Cody 1966. Reproduced with permission from John Wiley and Sons.)

include offspring size versus offspring number, and growth versus reproduction.

There is an even more intuitive reason why reproduction and survivorship, as well as other life history characters, must be interrelated. Life history characters, taken together, generate the overall growth rate of a bird population, which can be negative, positive, or neither (that is, a "stable" population with a growth rate of zero). The growth rate of many populations often varies considerably from year to year. Over the long term, however, it must be zero (or very close to zero), for the simple reason that if the growth rate is significantly less than zero over the long term, the population eventually will go extinct, and if the long-term growth rate is greater than zero, the world eventually will be overrun with the species. Bird species do go extinct, so growth rates do sometimes go negative and stay there; alternatively, some bird species do increase their range, their numbers, or both. In general, however, most avian populations are fairly stable, at least when considered over a long period of time and a large geographic area.

Because the growth rate of a population is a function of its reproductive rate and survivorship, changing one of these parameters assures that the other will change as well, at least in the long term. A classic example involves variation in clutch size, which increases with latitude in many taxa of birds (Fig. 13.10), an effect recently confirmed by an exhaustive global analysis of 5290 bird species (Jetz et al. 2008). Other things being equal, this larger clutch size suggests that the reproductive rate of more northern populations is greater than that of more southern populations. It therefore follows that the survivorship of adults must be generally lower in more northern populations. Interspecifically, this assumption is true, because the survival of tropical species is (in general) far greater than that of temperate and arctic species. For example, the estimated annual adult survival rates of forest passerines in Trinidad average 65% per year, compared with 53% per year for comparably sized North American passerines, and 52% per year for European passerines (Johnston et al. 1997).

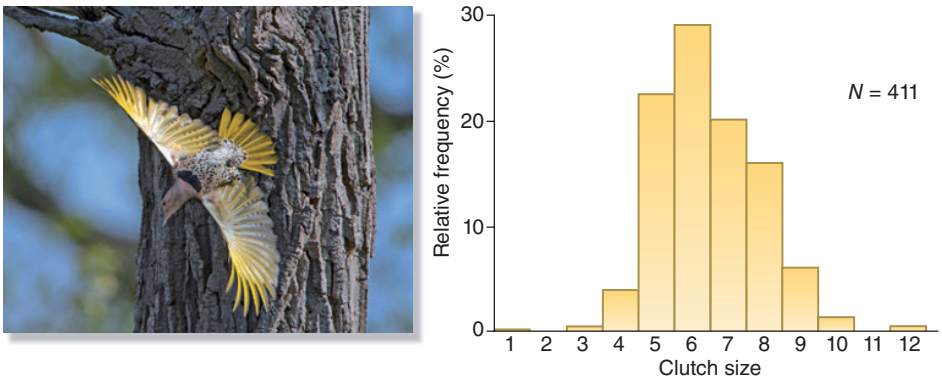


Fig. 13.11 Variation in clutch size. The mean clutch size for Northern Flickers (*Colaptes auratus*) is 6.5, but it varies considerably, from three to 12 eggs. (From Koenig 1984. Reproduced with permission from American Ornithologists' Union. Photograph by Tom Muir.)

13.5.2 Evolution of clutch size

Among avian life history traits, clutch size stands out as a subject of particularly intense study by ornithologists, perhaps because it is so easily measured. Two of the more perplexing questions about clutch size variation in birds are whether birds lay the number of eggs that leads to the most surviving offspring, and whether there is a trade-off between clutch size and survivorship. Although we are unlikely to solve these problems entirely—after all, they have been challenging ornithologists for more than half a century—the great body of research on clutch size variation highlights many features of life history studies in general.

Like most interesting questions in avian ecology, the evolution of clutch size can be addressed at many levels, each of which tells us something unique about this seemingly simple life history trait. First, the question can be addressed by making comparisons among species (interspecifically), among populations within a species (intraspecifically), or among individuals within a population. Although some hypotheses may be the same across all three of these levels, there is no guarantee that the causes of the patterns observed at one level will be important at any other level.

Second, we can address the question at both proximate and ultimate levels of analysis (Chapter 9). Specifically, we might want to examine the proximate development of egg follicles in females to understand what hormones regulate the number that develop at any one point in time. At the ultimate level of analysis, there are likely to be traces of the evolutionary history of the species involved, that is, their phylogeny. After all, it may not make much sense to study the evolution of clutch size in the Giant Hummingbird (*Patagona gigas*), which has the widest latitudinal range of any hummingbird—from slightly north of the equator in Ecuador to 45° south latitude in Aysén Province, Chile—but which like all other species of hummingbirds never lays more than two eggs. Yet one might legitimately ask why hummingbirds in general lay at most two eggs, given that many other types of small birds have much larger clutch sizes.

Although addressing the question of clutch size at any of these levels is valid, here we are concerned primarily with yet a different level: that of the **adaptive value** of clutch size. Although numerous scientists have spent a great deal of time thinking about this problem, none has contributed more than the British ornithologist David Lack, who studied the problem extensively in the 1940s and 1950s. Lack's central premise was that the clutch size of birds is determined primarily by the maximum number of young for which the parents can find sufficient food. Is there support for Lack's hypothesis? And if not, what are the alternatives?

One way to study the evolution of clutch size is to examine differences in clutch size and see whether the observed differences can be explained by Lack's hypothesis. First, consider a single species such as the Northern Flicker (*Colaptes auratus*) of North America. The mean clutch size of this species is 6.5, but clutches range in size from 3 to 12 (Koenig 1984) (Fig. 13.11). What is the explanation for such variation?

We can begin by making a list of the obvious possibilities. One is that all female flickers are laying as many eggs as they can raise profitably to fledging, but variation in quality among individuals makes some females more productive than others. For example, young, inexperienced flickers might get less food and be able to feed only a small number of nestlings, whereas older, higher quality individuals may forage more efficiently and be able to feed more young. A second possibility is that the differences are caused by annual variation in environmental conditions, perhaps differences in rainfall or food supply, so that birds breeding in good years lay larger clutches, and birds breeding in poor

Adaptive value: the contribution of a trait to an individual's ability to survive and reproduce.

years lay smaller clutches. A third hypothesis is that much of the variation is geographic, and the variation in clutch size is related to broader changes in the environment, such as there being more food for flickers in the northern part of their range. Similarly, because spring days are longer in the north, flickers at high latitudes may have more time to find food for their growing young and thus lay larger clutches.

These various possibilities are not mutually exclusive; all could be (and in fact are) true in some populations of birds. However, quantifying the first two requires detailed data on individuals taken over many years, while the third can be examined relatively easily by putting together data on clutch size from egg sets found in museum collections (Box 13.04). Based on data from such collections, it is clear that latitudinal gradients in clutch size are common and exist in many northern hemisphere birds, where clutch size tends to increase as one goes north, and also in the southern hemisphere, where the pattern is reversed and clutch size increases as one goes south. Why might this be true?

Lack's original hypothesis explaining this pattern was quite simple, based on the observation that breeding season day length is shortest in the topics and longest at the poles. Diurnal birds breeding at high latitudes therefore have relatively more time each day to forage and find food for their young, allowing them to support larger clutches. So, at one level, Lack proposed that clutch size should be directly related to day length; at another level, he proposed that the primary factor determining clutch size is the amount of food birds are able to acquire and feed their young.

Although this hypothesis is appealing, it has some problems. For one, if clutch size were simply a function of the ability of parents to feed young, then we would predict that birds with biparental care—species in which both males and females feed offspring—would have twice the clutch size of species in which only females feed young, and that cooperative breeders—species that live in social groups with helpers that further assist in feeding young (Chapter 9)—would have even larger clutches. Alas, such is not the case, as was recognized many years ago by the Finnish ornithologist Lars von Haartman (1954), who compared polygynous species with only female parental care and closely related monogamous species with biparental care. He found that although the monogamous species do tend to have slightly larger clutches, the difference is far from the predicted doubling of clutch size over that of the polygynous species. Similarly, in normally monogamous species such as European Pied Flycatchers (*Ficedula hypoleuca*) in Europe and House Wrens (*Troglodytes aedon*) in North America, females that are widowed or abandoned by their mates and thus raising young on their own are often able to compensate for the work that otherwise would be provided by their mates and raise normal-sized broods successfully. Indeed, birds in general are able to compensate for larger broods by feeding them more frequently, often without apparent difficulty.

There are other reasons to question the generality of Lack's hypothesis regarding avian clutch size. Birds on islands generally lay smaller clutches than their counterparts on the nearby mainland, although day length in the two areas does not differ. In many birds there are differences in clutch size correlated with elevation, another factor unrelated to day length. Cavity-nesting species such as woodpeckers typically lay larger clutches than those of similarly sized open-nesting species breeding nearby. Further, some species such as the European Pied Flycatchers exhibit little or no geographic variation in clutch size, and species in some avian groups (such as pigeons and doves, hummingbirds, and a few others) all tend to lay the same number of eggs regardless of where they breed.

These observations do not totally discount the importance of day length, and certainly not the importance of food, but clearly day length and food are not the only factors that need to be considered. One additional possibility is that conditions during the non-breeding season, rather than just during the period when the birds are breeding, might influence clutch size. This notion is currently of particular interest due to technological advances allowing workers to match breeding birds to particular winter ranges and, in some cases, habitats (Chapter 12). It shifts the focus from considering the food supply only during the breeding season—Lack's hypothesis—to the total amount of available food relative to the number of birds in the population competing to catch that food and feed their young. It is plausible to hypothesize that in general, many bird populations are limited not by food during the breeding season, when there is so much extra food around that the birds can raise young, but rather by food available during the non-breeding season, when conditions are more challenging. Under this scenario, we might predict that clutch size will increase with the seasonality of a particular site—that is, when there is a large difference between resources available during the breeding season and those available during the non-breeding season (Fig. 13.12).

This hypothesis that clutch size is related to seasonality and year-round resources was first proposed by Phillip Ashmole, a British seabird biologist, and has gained support in studies of various groups of birds (Fig. 13.13) and within the ranges of particular species. Such studies have included a comparison involving data on more than 5000 species in which seasonality was found to be an important predictor of avian clutch size on a global scale (Jetz et al. 2008). For example, seasonal fluctuations in resources are correlated with clutch size in Northern Flickers (*Colaptes auratus*), and in this species there is a strong inverse correlation between clutch size and winter productivity, but not between clutch size and breeding season productivity, nor between clutch size and a site's total annual productivity (Koenig 1984).

Based on these various results, we can conclude that Lack, with some modifications, was on the right track—relative food availability has a strong influence on clutch size. Is it the

Box 13.04 Oölogy: the study of birds' eggs

Although no longer a common pursuit even by professional ornithologists, oölogy—the collecting of and study of eggs—was a popular pastime in the latter part of the nineteenth and early twentieth centuries, during which time thousands of egg sets were collected and preserved, often by private individuals. Like other activities destructive of wild bird populations, egg collecting was largely eliminated by changing attitudes and the passing of laws restricting the possession and hunting of most wild birds and their nests or eggs. In fact, current laws in many countries make it illegal to possess wild birds' eggs, even those collected prior to the passing of the various acts restricting such activities. As a result, despite occasional offenses, the hobby of egg collecting has been replaced by birding, bird photography, and other far less harmful activities.

So what has happened to all those egg sets collected in the heyday of oölogy? Most are now housed in natural history museums around the world, the largest of which are the British Museum of Natural History (approximately 250,000 clutches of eggs) and the Western Foundation of Vertebrate Zoology in Camarillo, California (USA) (approximately 225,000 clutches). These collections remain useful for a variety of scientific investigations, perhaps the most famous of which was the discovery of eggshell thinning in Peregrine Falcons (*Falco peregrinus*) (Fig. 13.B4.01), first discovered in Britain by Derek Ratcliffe (1967) and attributed to contamination of the birds by DDE, a metabolite of the pesticide DDT (dichlorodiphenyltrichloroethane). This work was instrumental in banning the use of DDT in the USA in 1972 and for agricultural purposes worldwide by the Stockholm Convention on Persistent Organic Pollutants of 2001.

The role that egg collections played in understanding that pesticides were decimating birds of prey around the world is an excellent example of how basic research—in this case natural history information on birds' eggs—can turn out to be important for addressing problems that are not recognized until long after the relevant specimens are collected.

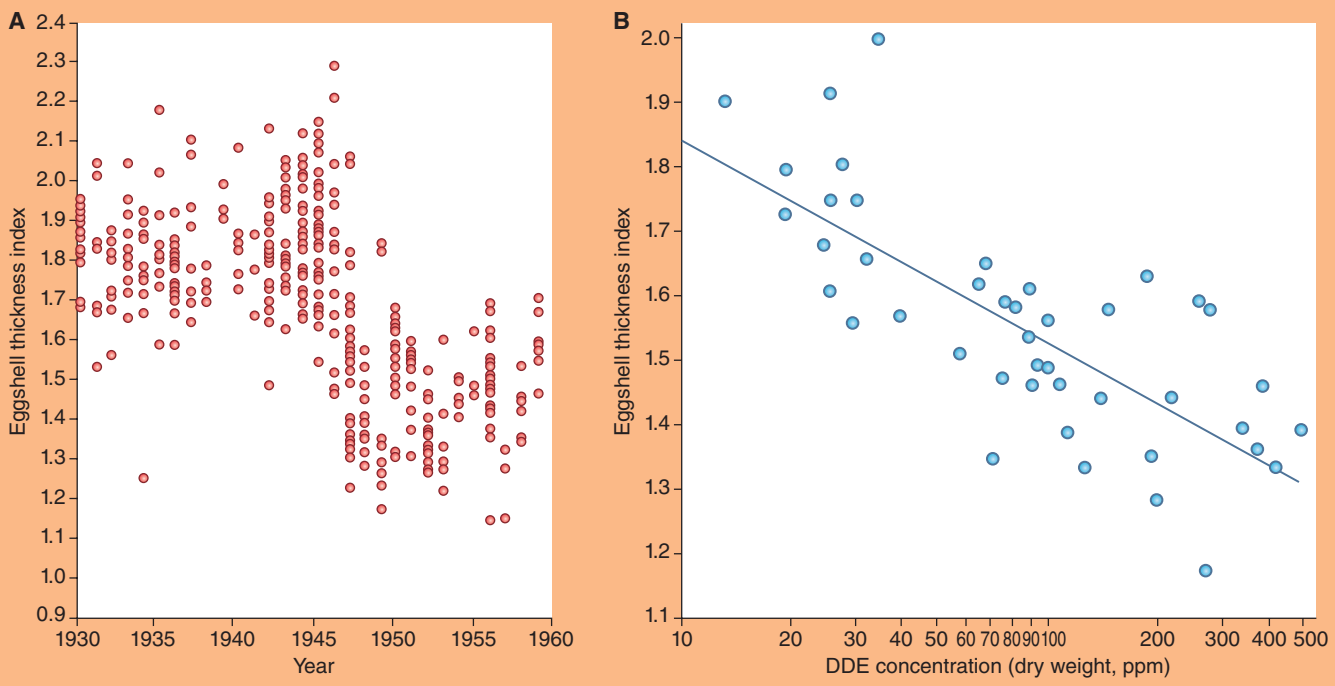


Fig. 13.B4.01 Effects of DDT on Peregrine Falcons (*Falco peregrinus*). (A) Changes in relative shell thickness of Peregrine Falcon eggs in Great Britain through time; note the sharp decline starting in late 1940s when DDT was first widely used during the second half of World War II. (B) Eggshell thickness also declines with higher levels of DDE (a by-product of metabolized DDT). (A, from Ratcliffe 1967. Reproduced with permission from Macmillan Publishers Ltd. B, from Cade et al. 1971. Reproduced with permission from AAAS.)

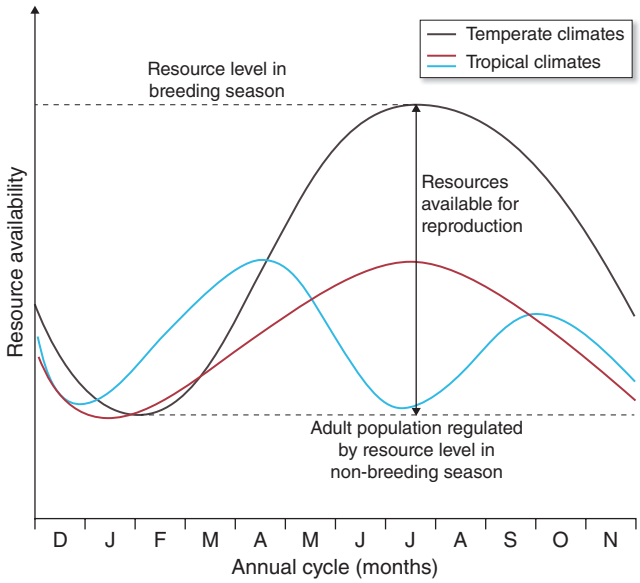


Fig. 13.12 A schematic depiction of Ashmole's hypothesis. Assuming that populations of adult birds are regulated by the resources available to them in the non-breeding season, any additional useable resources during the breeding season may drive difference in clutch size. For example, in many temperate climates (black curve), the difference between non-breeding and breeding season resource levels is large, thereby allowing for large clutches. In tropical latitudes with varying patterns of seasonality (red and blue curves), resources often do not differ as much between seasons, and clutch sizes are therefore smaller. (Adapted from Ricklefs 1980. Reproduced with permission from American Ornithologists' Union.)

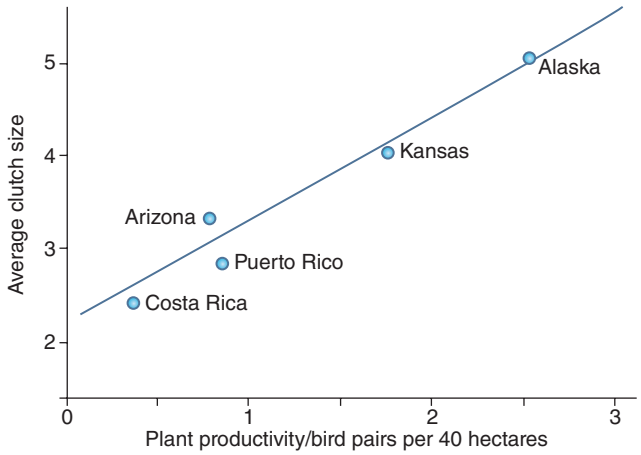


Fig. 13.13 Clutch size, habitat productivity, and bird density. A test of Ashmole's hypothesis in five bird communities shows that mean clutch size increases with the ratio of landscape productivity to population density. Productivity is indexed by maximum actual evapotranspiration—a measure of water availability. (From Ricklefs 1980. Reproduced with permission from American Ornithologists' Union.)

only factor affecting clutch size? Unsurprisingly, the answer is clearly no.

Consider predation. Many bird species lay one egg per day but start to incubate only at the end of their egg-laying period, so that increases in clutch size extend the time during which the clutch is left unguarded and vulnerable to predators. One might predict that species subject to higher rates of predation might lay smaller clutches to shorten the time that their eggs are vulnerable to predators. Potentially even more important is a hypothesis proposed by Costa Rican ornithologist Alexander Skutch (1949) that having more young in the nest requires more feeding visits by the parents. This greater number of trips to and from the nest might then increase the likelihood of the nest being located by predators. Accordingly, birds nesting in high predation environments might lay small clutches, not because they have trouble finding food for their young but rather to limit the probability that their nest will be found and destroyed by a predator. Skutch's hypothesis has been tested by Tom Martin et al. (2000), who monitored thousands of nests in the forests of Arizona (USA) and compared their fates with those of nests in subtropical Argentina, where clutch sizes of passerine birds are smaller and more comparable with those of species in the humid tropics. These comparisons supported both of the main predictions of Skutch's hypothesis: birds with increased parental activity suffered greater predation costs, and species that experienced greater nest predation visited their nests at lower rates (Fig. 13.14).

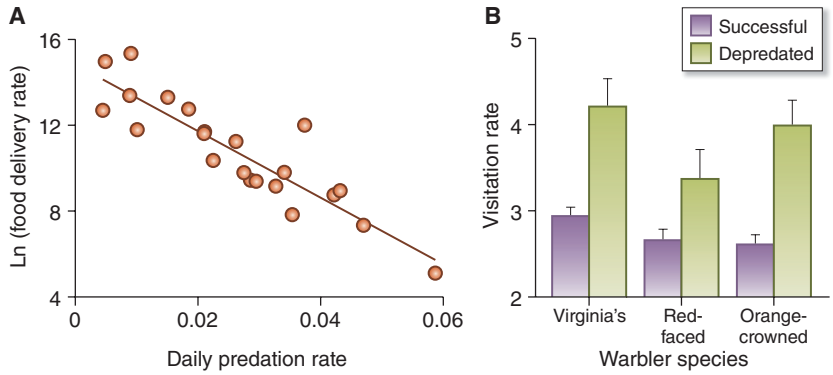


Fig. 13.14 Predation rate correlates with provisioning rate. (A) Daily predation and provisioning rates in 21 species of birds in Arizona (USA) demonstrate a negative correlation between visits and predation. One interpretation is that nests visited more often by parent birds are more likely to attract the attention of nest predators. (B) Support for Skutch's hypothesis also comes from data showing that provisioning rates were higher at nests that were ultimately depredated in Virginia's Warblers (*Oreothlypis virginiae*), Red-faced Warblers (*Cardellina rubrifrons*), and Orange-crowned Warblers (*Oreothlypis celata*). (From Martin et al. 2000. Reproduced with permission from AAAS.)

13.5.3 More life history basics

The trade-offs inherent in life history evolution are often thought to push species into one of two opposing directions: one in which they produce many offspring and have low survivorship, and the other in which they produce few offspring and have high survivorship. Ecologists often refer to evolution favoring one or the other of these extremes as ***r* selection** and ***K* selection**, respectively, borrowing from a foundational population dynamics equation in which *r* symbolizes the growth rate of the population and *K* represents the carrying capacity of the environment. Looked at in this way, species such as tits and chickadees are *r* selected: they reproduce quickly and live only a few years at most. In contrast, large species such as albatrosses and condors may live for many decades but have a clutch size of one, and even experienced breeders often may forego reproduction for a year after successfully fledging a chick. Unsurprisingly, the majority of bird species fall somewhere between these extremes.

***r* and *K* selection:** ecological terms for the ends of a continuum between extreme investment in reproduction at the cost of long-term survival (*r* selection), and extreme investment in survival at the cost of high fecundity (*K* selection).

Life table: an actuarial table that describes the probability of death at each age, and which sometimes also includes the expected reproductive output at each age.

Reproductive value: the expected reproduction of an individual from their current age onward, given that they have survived to their current age.

How do we put this information together to visualize the demography of a population? Data on survivorship and reproduction often are used to generate a **life table**. Life tables for birds are analogous to the actuarial tables used to set life insurance premiums for humans in that they incorporate statistical knowledge of how age influences the probability of survival (and, in the case of life tables, reproduction). Life tables provide researchers with the mathematical tools needed to calculate the relative number of offspring produced by birds of different age classes, that is, the **reproductive value** of each age class. These inferences then can be combined across age classes to estimate the overall growth rate of the population.

Populations have other important features besides their fecundity and survivorship. In particular, many, if not most, populations are partially connected to other populations of the same species by dispersal into (immigration) or out of (emigration) the population (Chapter 12). We will consider the demographic effects of these movements later; for now the important point is that the overall growth rate of a population is a function of the individuals added via fecundity + immigration and those lost via mortality + emigration. Any one of these four factors can play an important role in regulating a population and in determining its spatial distribution.

13.6 Ecological niches

Once again, consider a songbird foraging in your yard. If you are in North America, you might be watching an American Robin (*Turdus migratorius*), which has a range extending over almost the entire continent, although the more northern populations are migratory. If you are in Europe or northern Asia, you might be observing a European Robin (*Erithacus rubecula*), which has a range

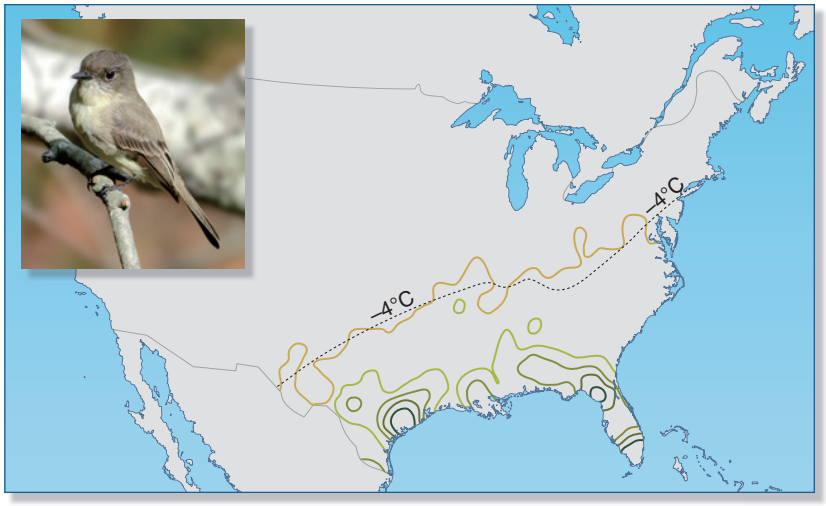


Fig. 13.15 Climate and distribution. This map shows the winter distribution and abundance of the Eastern Phoebe (*Sayornis phoebe*). Its northern range limit is correlated with the –4 °C isotherm (dotted black line) for the mean minimum January temperature in North America. (From Root 1988b. Reproduced with permission from John Wiley and Sons. Photograph by Laura Meyers.)

that extends through Eurasia east to western Siberia, south to North Africa, and as far west as the Azores. European Robins are largely resident, although again many northern populations, particularly in Russia and Scandinavia, migrate south in the winter. On both continents, robins are one of the most common and widespread species, in contrast to the Varied Thrush (*Ixoreus naevius*), a relative of the American Robin that is restricted to the west coast of North America, or Moussier's Redstart (*Phoenicurus moussieri*), a relative of the European Robin that is mainly found in North Africa. Such dramatic variation in the distribution and abundance of different birds is ubiquitous: consider the contrast between the Black-billed Magpie (*Pica hudsonia*), a species that occurs across most of western North America, and its close relative the Yellow-billed Magpie (*Pica nuttalli*), which is limited to a small area of central California (USA). Another such comparison is the Eurasian Green Woodpecker (*Picus viridis*), resident throughout most of Europe and parts of the Middle East, and Levaillant's Woodpecker (*Picus vaillantii*), which is found only in Portuguese oak woodlands and in Tunisia, Algeria, and Morocco. What determines why some species have large geographic distributions and others do not?

Perhaps the best way to approach this question is by focusing on the concept of the **ecological niche** (Chapter 14). The niche concept, which dates back to ideas proposed by North American ornithologist Joseph Grinnell (1917), focuses on the ecological and environmental conditions within which a species successfully exists. When applied to bird distributions, the niche concept brings together information about the species' abundance, physiology, behavior, and habitat preferences in a way that can help infer their relative effects on a species' distribution and abundance. By definition, every species is unique, and thus no two species have exactly the same ecological niche or exactly the same geographic distribution. Although it is often easy to find an example of a single factor, either biotic (such as competition with another species) or abiotic (such as snowfall or temperature), that appears to limit a local population at a particular point in time, it is far more challenging to determine the factors that actually limit a species over a long period of time and over a large geographic region. For example, Terry Root (1988a, 1988b) analyzed the distributional boundaries of wintering North American birds. She was able to show that the northern range limits of many species are associated with minimum temperatures and thus apparently are limited by the energy needed to survive in regions with colder ambient conditions (Fig. 13.15). As intuitively pleasing as this conclusion may be, it accounts for only one edge of the winter range of these species, and Root had less success determining the factors forming other range boundaries.

Although a species' ecological niche is an important concept, it is also inherently observational; after all, the ecological niche of a species is defined by where it occurs. A relatively new approach called **ecological (or environmental) niche modeling** takes data from where a species is known to occur and uses it to predict places where the environment is suitable for the species to be present. This approach allows researchers to predict the larger geographic distribution of a species, potentially directing searches to discover new populations of rare birds. It also

Ecological niche: the set of biotic and abiotic conditions that allow a species to occur; sometimes also used in the sense of the role of an organism within its ecosystem or environment.

Ecological (or environmental) niche modeling: a method for predicting the overall distribution of a species based on the environmental conditions at points where the species is known to occur.

Box 13.05 Avian introductions

Birds have been transported and introduced by humans to areas outside their native range for hundreds and possibly thousands of years. Through the eighteenth and nineteenth centuries, such introductions were frequently done with the aim of establishing what were considered beneficial or desirable species in new settlements for hunting, biocontrol, or purely aesthetic reasons. In one famous example, the American Acclimatization Society, founded in 1871, had the goal of introducing all the bird species mentioned in Shakespeare's plays into the USA. Their efforts included releasing the European Starling (*Sturnus vulgaris*) in New York City's Central Park in 1890 and 1891. Only recently have the downsides of such introductions been recognized, leading to much greater restrictions and control of introductions of avian exotics.

Introduced species are typically released in small numbers, making these founding populations especially prone to extinction. Analyses have shown that introduction effort alone has a big effect—that is, species where more individuals are released during multiple introduction attempts have a higher probability of successful establishment than do species for which only a few individuals were released on a single occasion (Duncan et al. 2003). Nonetheless, other factors are also important. For example, despite the introduction of over half a million Common Quail (*Coturnix coturnix*) between 1875 and 1958, this species has yet to become established in North America. Factors that influence the success of invasions include climate matching—the similarity between the climate and physical environment at the locations of introduction and the species' native range—and niche breadth—the idea that species with wide geographic ranges and broad tolerances to begin with are more likely to be successful when introduced to new locations.

Although deliberate transport is by far the most common source of avian introductions, a few are apparently the result of natural processes. For example, the Cattle Egret (*Bubulcus ibis*), originally from southern Europe and Africa, was first sighted in South America in 1877, and has since spread as far north as Canada (Chapter 12). Such range expansions blur the distinction between exotic and natural avian invasions.

allows us to make predictions about invasions of species; that is, how far an expanding bird population might spread across a continent before it reaches its environmental limits. It can further be used to make predictions about how species' distributions will respond to various scenarios of future climate change (Peterson and Vieglais 2001; Peterson 2003).

Consider, for example, the problem of invasions of species. Exotic, invasive species are responsible for vast economic and environmental damage, making this problem one of considerable importance worldwide. Where did all these exotic species come from? Some have been introduced inadvertently, but many have been released deliberately over the course of the last 500 years (and in some cases even earlier) (Box 13.05). Why did the European Starlings (*Sturnus vulgaris*) that were released in New York City's Central Park in the 1890s succeed and become invasive, whereas the populations of Sky Larks (*Alauda arvensis*), European Robins (*Erithacus rubecula*), and Common Chaffinches (*Fringilla coelebs*) that were introduced into North America at that time all died out?

One goal of ecological niche modeling is to predict the behavior of invasions. This prediction is done by first characterizing the existing known distribution of a species (Fig. 13.16A), modeling its ecological niche (Fig. 13.16B), and then projecting the results back into geographic space to predict both the species' natural range (Fig. 13.16C) and where it might be expected to be successful within an introduced range (Fig. 13.16D). One drawback of this approach is that it focuses solely on the ecological appropriateness of the new landscape, whereas invasions can succeed or fail based on many other factors, including colonization opportunity (Box 13.05), avoidance of demographic problems associated with small population size early in its establishment, and interactions with predators, parasites, and competitors.

A second key application of ecological niche modeling has been to predict changes in species' distributions as a function of climate change. For example, distribution models for Mexican birds (Peterson et al. 2002) suggest that more than 40% of the species in many local communities will change over the next 50 years. The ecological effects of such drastic community reorganization clearly could be significant.

13.7 Limiting factors for bird populations

Many factors may limit the numbers and distributions of different bird species. These include abiotic factors like weather, as discussed previously, as well as biotic factors like food, nest sites, predation, and parasites and pathogens.

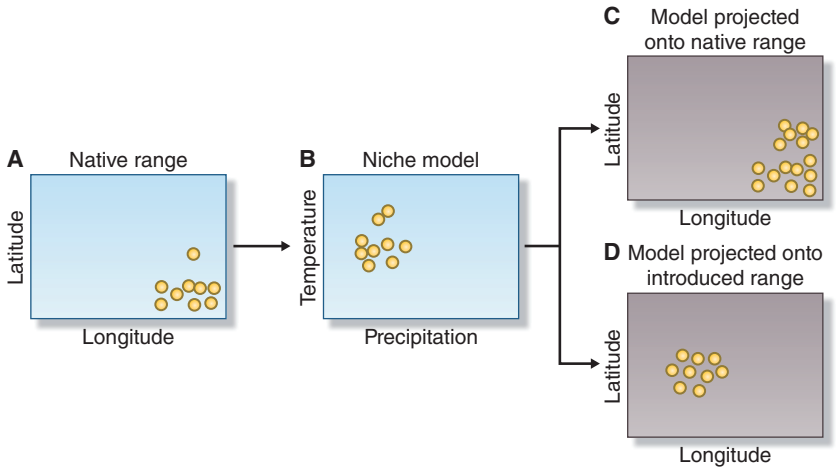


Fig. 13.16 Modeling changes in species distributions. (A–D) A simplified example of the ecological niche modeling process, which predicts the distribution of a species both in its native geographic range and in a newly invaded area. (Adapted from Peterson 2003.)

13.7.1 Food as a limitation

Food supply clearly has an important effect on the demography and distribution of most bird populations, but in many cases the evidence for this effect is indirect. For example, many resident temperate bird species buffer the effects of food shortage in seasonal environments by storing energy in the form of body fat (Fig. 13.17A). Other birds store actual food items for later consumption (Chapter 8), and these caching birds provide intriguing examples of the influence of food on population demography of these species. The Acorn Woodpecker (*Melanerpes formicivorus*) of western North America and Central America, for example, stores acorns, often by the thousands, in individual holes drilled in special trees known as granaries (Fig. 13.17B). The reproductive success and winter survivorship of Acorn Woodpeckers at study sites in California are both highly dependent on the prior year's acorn crop, which varies widely from year to year (Fig. 13.18A). Indeed, in good acorn years, these birds will breed even in the fall (Koenig and Stahl 2007), whereas in poor acorn years the social structure of this highly social species breaks down and many birds abandon their

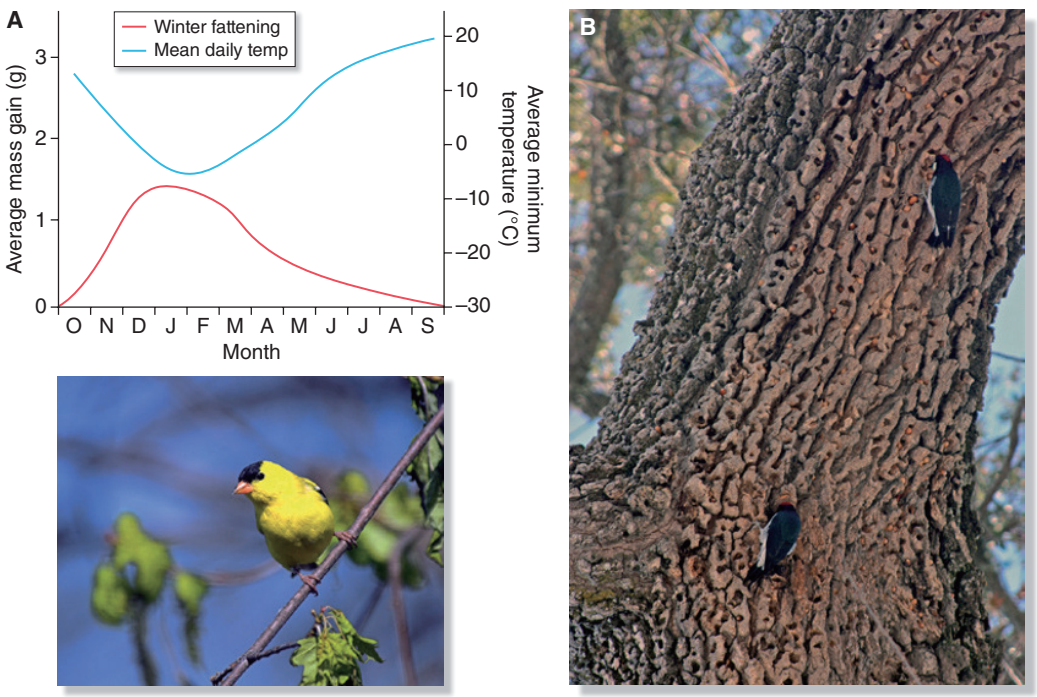


Fig. 13.17 Two kinds of energy storage. (A) Winter fattening (red) is inversely correlated with mean daily temperature (blue) in American Goldfinches (*Spinus tristis*). (B) Acorn Woodpeckers (*Melanerpes formicivorus*) store acorns in granary tree holes. (A, adapted from Dawson and Marsh 1986; photograph by Patricia Ferguson. B, photograph by Devra Cooper.)

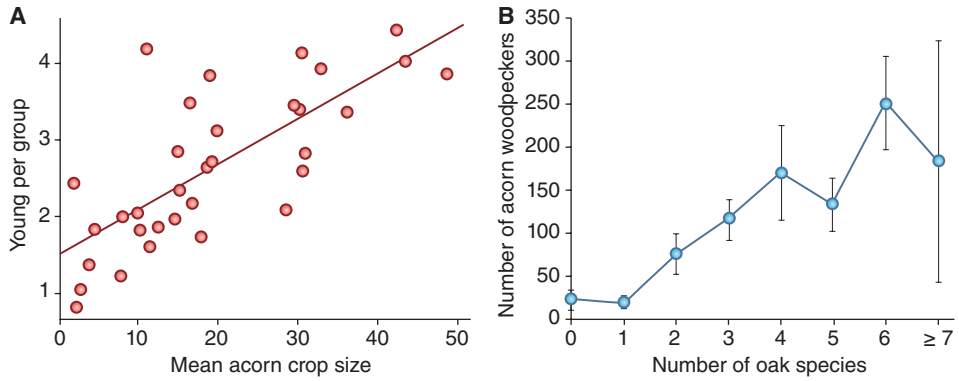


Fig. 13.18 Reproduction and food supply in Acorn Woodpeckers (*Melanerpes formicivorus*). (A) There is a positive relationship between the fall acorn crop and fledgling success the next spring. (B) Acorn Woodpecker density increases with oak species diversity. (A, courtesy of Walter D. Koenig. B, adapted from Koenig and Haydock 1999. Reproduced with permission from John Wiley and Sons.)

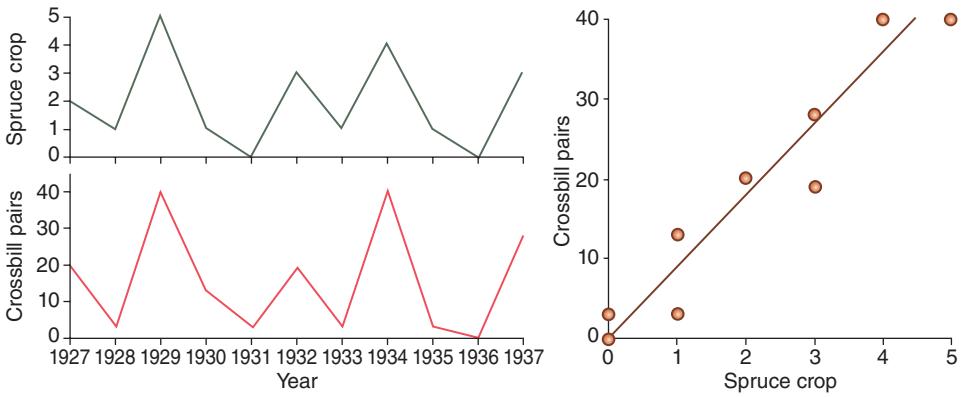


Fig. 13.19 Population cycles and food supply. Red Crossbill (*Loxia curvirostra*) population sizes strongly track their principal cone crop, the Norway spruce. (From Newton 1998. Reproduced with permission from Elsevier.)

territories (Hannon et al. 1987). As a consequence of their dependence on the highly variable and unpredictable acorn crop, Acorn Woodpeckers along the Pacific coast of North America are limited in their geographic distribution not only by the range of oaks, but also by the species diversity or richness of oaks, being generally found only in areas where at least two species of oaks co-occur and thus the probability of a complete acorn crop failure is reduced (Fig. 13.18B).

Other good examples of species for which the food supply is clearly related to reproductive success and/or survival include crossbills and several other northern finches, whose success and distribution are closely tied to the seed crops of boreal trees (Fig. 13.19), and raptors, whose populations often fluctuate in direct proportion to their main prey populations. This fluctuation is particularly evident among species such as Long-eared Owls (*Asio otus*), Northern Goshawks (*Accipiter gentilis*), and jaegers that are dependent on cyclic populations of small mammals such as lemmings, voles, and hares.

Other direct evidence for the importance of food comes from experimental studies in which researchers have manipulated the food supply. Many such studies have been performed over the years with varying results, although in general birds that have access to supplemental food do better in at least some, if not all, reproductive parameters. A good example is work by Peter Arcese and Jamie Smith (1988) on a population of Song Sparrows (*Melospiza melodia*) on Mandarte Island in British Columbia (Canada). At one point they provided feeders containing dog food, mealworms, and millet to some of the pairs of sparrows on the island and documented the differences in their breeding behavior compared with non-supplemented pairs. Pairs with supplemental food bred earlier, had larger clutch sizes, made more nesting attempts, had heavier young, and produced more independent offspring than pairs that did not have access to supplemental food (Fig. 13.20). Other studies have focused on the effects of food supply during the winter, which is likely to be a time of food limitation in many populations. A classic study is that of Hans van Balen

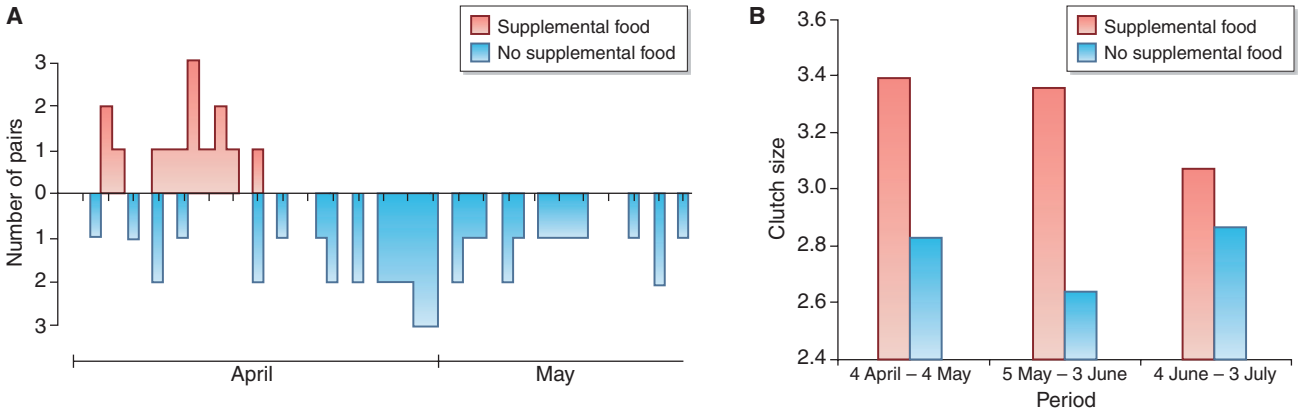


Fig. 13.20 Supplemental food and breeding date. Supplementally fed Song Sparrows (*Melospiza melodia*) (red), compared with non-supplemented control birds (blue), both (A) advanced their laying date and (B) increased their clutch size. (From Arcese and Smith 1988. Reproduced with permission from John Wiley and Sons.)

(1980), who provided supplemental seeds each winter to a population of Great Tits (*Parus major*) in the Netherlands while comparing it with an unsupplemented population a short distance away. The supplemented population increased in density by 40%, demonstrating a strong effect of additional food. However, the difference was observed primarily in years when the primary natural winter food source, the beechnut crop, was poor; in years when the beechnut crop was good, the artificial food had little effect on Great Tit population density (Fig. 13.21).

13.7.2 Nest sites as a limitation

The availability of nest sites can limit some bird populations, particularly in species that do not make their own nests, but instead rely on either natural cavities or old nest holes made previously by excavating species such as woodpeckers. Although in most locations 10% or fewer bird species nest in cavities, the proportion of cavity nesters can be much higher. For example, in the boreal forests of central British Columbia, 32 of 76 (42%) of bird species nest in cavities (Martin and Eadie 1999). Eight of these species are woodpeckers that build their own cavities, whereas the remaining 24 species are either secondary cavity nesters—including ducks and raptors—or species such as nuthatches and chickadees that do not make their own holes but instead enhance existing cavities. Because these latter species are largely dependent on the primary cavity nesters for creating nest sites, there is a positive correlation between these two elements of the community.

In general, the number of usable cavities increases with the age of a forest, which is why leaving snags and large

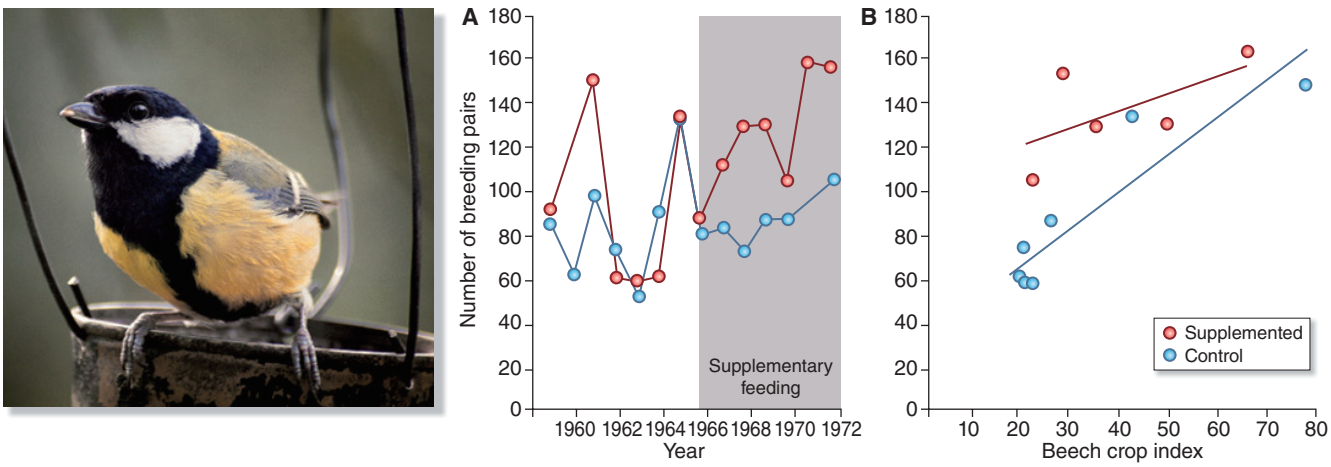


Fig. 13.21 Supplemental food, fecundity, and survival. (A) The number of breeding pairs of Great Tits (*Parus major*) at two sites was similar when no supplemental food was provided in either location, but numbers increased at the supplemented site (red) after additional food was provided there (grey-shaded years). (B) Breeding population size versus the beechnut seed crop index is shown for two sites. (From Newton 1998. Reproduced with permission from Elsevier. Photograph by Dan, http://en.wikipedia.org/wiki/File:Parus_major_-Kew_Gardens,_London,_England-8.jpg. CC-BY-2.0.)

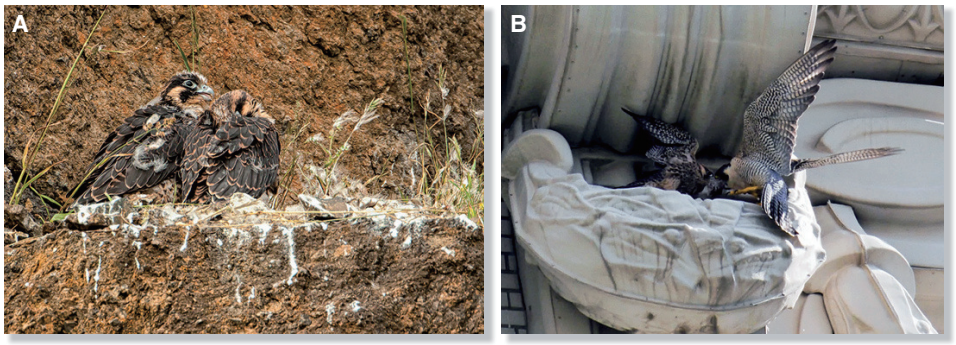


Fig. 13.22 Peregrine Falcons (*Falco peregrinus*) in natural and urban environments. (A) This species nests on steep natural cliffs in the wild. (B) Many individuals have adapted to urbanization by nesting on top of buildings—in this case, a historic landmark in Salt Lake City (USA). (Photographs by: A, Michael Libbe; B, Shelly Spencer.)

trees containing dead limbs can have a beneficial effect on bird community composition and diversity. Potential cavities often do not appear to be limiting in old forest habitats with many dead trees, where only a fraction of apparently suitable cavities may be used by birds in any year. The situation can be quite different in managed forests where snags and large trees are consistently removed; in such sites the addition of artificial nest boxes can greatly increase the breeding densities of cavity-nesting bird species (Brawn and Balda 1988). Indeed, adding artificial nest boxes has been credited with increases in the populations of many cavity-nesting passerines, including Eastern Bluebirds (*Sialia sialis*) in North America, and European Pied Flycatchers (*Ficedula hypoleuca*), Collared Flycatchers (*Ficedula albicollis*), and Common Redstarts (*Phoenicurus phoenicurus*) in Europe, all of which are limited by a shortage of natural cavities in the managed forests found throughout much of their ranges. Such effects are not necessarily limited to nesting density. For example, in some populations of Wood Ducks (*Aix sponsa*) in Missouri (USA), intraspecific brood parasitism is common, and more than 50% of eggs are laid parasitically, resulting in clutches of up to 40 eggs, far more than a normal female's clutch of 11–15 eggs. One cause of this unusually high incidence of nest parasitism is believed to be intense competition for limited nesting cavities, which are found naturally only in old-growth, undisturbed forests (Semel and Sherman 2001).

Although nest-site limitation is particularly evident among many cavity-nesting species, it is also potentially important in species such as swallows, swifts, and some raptors that typically nest on cliffs or other restricted sites. In several notable cases such species have come to accept buildings and other artificial structures in lieu of their relatively rare, naturally occurring, nest sites. Examples include Common House-Martins (*Delichon urbicum*) in Europe, and Barn Swallows (*Hirundo rustica*) throughout the northern hemisphere; both of these species originally nested on cliffs or in caves but are now so closely associated with buildings that it is rare to find them nesting away from human habitation. Purple Martins (*Progne subis*) are another such example, at least in the eastern USA where they frequently nest colonially in artificial structures built specifically with them in mind. A similar shift toward the use of buildings and other man-made structures has occurred among Peregrine Falcons (*Falco peregrinus*), which nest primarily on cliffs (Fig. 13.22A) and other inaccessible sites in the wild, but now, as their populations have recovered, have become relatively common breeders on the tops of large urban buildings (Fig. 13.22B).

Some seabirds and herons may also be limited by competition over the available nesting sites within a breeding colony; experimental studies in which extra nesting habitat was provided resulted in increased numbers of breeding birds. For example, nesting platforms built for the collection of guano off the coast of Namibia between 1930 and 1963 have supported up to 74,000 pairs of Cape Cormorants (*Phalacrocorax capensis*), increasing both their numbers and geographic distribution (Crawford et al. 2007).

13.7.3 Predation as a limitation

Acceptable nesting habitat for colonial species such as cormorants and gulls often involves not only space but also protection from predators, bringing us to our next limiting factor: predation. Although their ability to fly may give birds protection from some predators, there are few places where birds are truly safe, and while nesting many species are especially vulnerable to mammals and snakes. When birds take flight, they leave such predators behind only to become the target of hawks and falcons during the daytime and owls at night. All in all, it is not surprising that the life expectancy of most birds is only a few years at best.

Predation is often an ever-present risk. For example, during a study of shorebirds wintering in Bolinas Lagoon north of San Francisco (USA), more than 5000 shorebirds of at least 13 species were hunted by a panoply of raptors including American Kestrels (*Falco sparverius*), Northern Harriers (*Circus cyaneus*), Cooper's Hawks (*Accipiter cooperii*),

Sharp-shinned Hawks (*Accipiter striatus*), Red-tailed Hawks (*Buteo jamaicensis*), Short-eared Owls (*Asio flammeus*), Long-eared Owls (*Asio otus*), Great Horned Owls (*Bubo virginianus*), and most regularly by a single adult female Merlin (*Falco columbarius*). This one Merlin alone was estimated to have eaten 264 shorebirds during a single winter, and overall the raptors were estimated to have eaten 21% of the Dunlin (*Calidris alpina*) and between 8% and 16% of four other shorebird species (Page and Whitacre 1975).

Conditions are no safer on the breeding grounds. Among tits breeding in the artificial nest boxes set out in Wytham Wood near Oxford (UK), the primary predator is the Eurasian Sparrowhawk (*Accipiter nisus*). At this site, these small raptors kill an estimated 18–34% of young Great Tits (*Parus major*) and 18–27% of young Eurasian Blue Tits (*Cyanistes caeruleus*) each year, with the sparrowhawks significantly reducing tit abundance in the zone of the wood close to their nests (Perrins and Geer 1980).

Predation can have large effects on bird populations. The most obvious examples come from islands where predators have been accidentally or deliberately introduced (Chapter 15). The most common such exotic predators are mammals, including brown and black rats, feral cats, foxes, stoats and other mustelids, and feral pigs, but other species also have had unexpectedly dire effects. For example, feral cats introduce to South Cape Island, New Zealand, exterminated five species of native forest birds. On Socorro Island, Mexico, cats have all but wiped out the endemic Socorro Dove (*Zenaida graysoni*) and Socorro Mockingbird (*Mimus graysoni*). The fact that many islands were nearly or completely predator free until human arrival rendered their birds particularly vulnerable, because many island birds lose their adaptations for avoiding predators.

13.7.4 Nest depredation

One of the most characteristic features of birds is that they build nests and incubate their eggs (Chapter 11). Tied to one spot, not only the eggs but also the adults incubating them are often highly vulnerable to predators. This vulnerability clearly is a strong selective force acting on birds that choose relatively protected nesting sites such as tree cavities, which may be hard to come by but are safer than nests built on the ground or out in the open.

Nest depredation is one of the most important demographic challenges facing many avian populations, with the rate of nest depredation often being at least 50%, and sometimes much higher. In fact, nest depredation typically is so high that it is quantified on a per day basis, both to facilitate comparisons across species and to reduce bias caused by differences in the stage at which nests are first found. Even if the depredation rate is not very high, the cumulative effect over the nesting period can be considerable. For example, in a study investigating the effectiveness of nest protectors placed on trees used by Giant Ibis (*Pseudibis gigantea*) in northern Cambodia (Keo et al. 2009), the survival rates of 24 protected nests were compared with 28 unprotected nests. The daily survival rate for protected nests was 99.85% compared with 99.30% for unprotected nests—a seemingly small difference of only 0.55%. However, given that the ibis nestling period lasts 70 days, these figures multiply across that entire period into a dramatic difference in overall survivorship of 90% for protected nests compared with only 61% for unprotected nests.

13.7.5 Parasites and pathogens as a limitation

Parasites of birds come in a bewildering array of forms, ranging from relatively large organisms such as ticks, fleas, blood-sucking flies, mosquitoes, and helminth worms, to microscopic species of viruses, bacteria, fungi, and protozoa. These latter sometimes qualify as **pathogens** that cause what we typically call a "disease," a clinically abnormal state that may kill or at least compromise an animal's performance. Fortunately, only a relatively small fraction of microscopic organisms cause disease. Those that do, however, can be particularly devastating to bird populations. In many cases pathogens are transmitted through the blood or other fluids by **vectors** such as mosquitoes or ticks. Transmission can also be directly from one individual avian host to another (horizontal transmission), or from parent birds to their offspring (vertical transmission). Infections are often more virulent in populations of birds living at high densities, thus opening the door for density-dependent regulation of population size.

One widespread pathogen of ongoing concern to ornithologists is the West Nile virus, a pathogen that has long been present in the Old World and recently has spread into North America, where it has met with a fauna with little or no natural immunity. West Nile virus is transmitted primarily by mosquitoes, and the primary reservoirs are birds, although it can infect a wide variety of other species from alligators to humans. Since its spread into North America in 1999, individuals of more than 200 bird species are known to have died from West Nile virus infection. Corvids—crows, jays, and magpies—are particularly vulnerable. For example, in the year after West Nile virus reached California, more than half of the Yellow-billed Magpies (*Pica nuttalli*) and American Crows (*Corvus*

Pathogen: any organism or virus that causes disease or illness.

Vector: an organism (usually an insect, tick, or other arthropod) that transmits a pathogen from one kind of host to another.

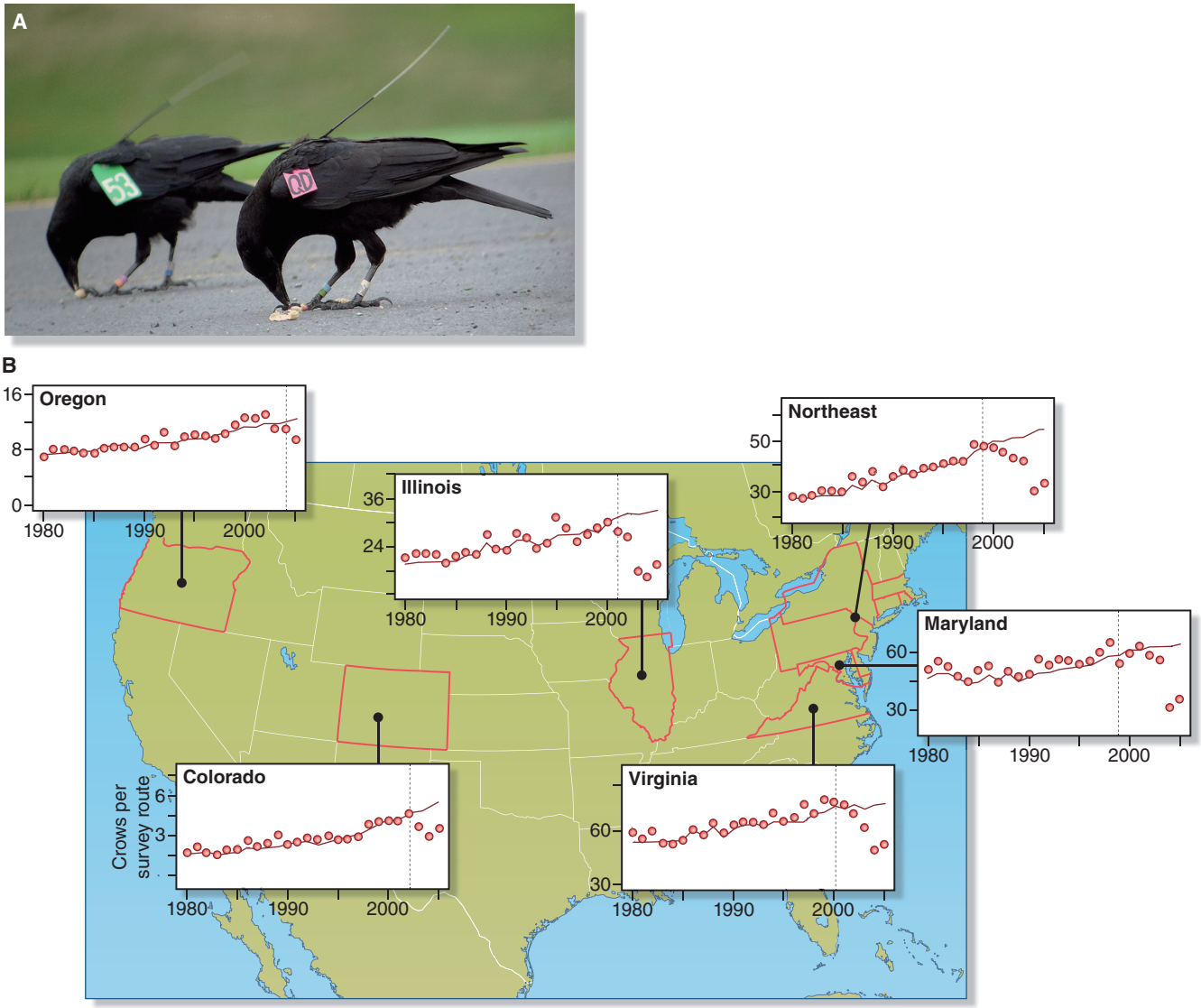


Fig. 13.23 Effects of West Nile virus on populations of American Crows (*Corvus brachyrhynchos*). (A) Monitored crows are tagged for easy identification in the field. (B) Data from surveys conducted in six areas of the USA show a slow increase in crow numbers over many years, with a sudden drop around the more recent advent of West Nile virus infections (dashed vertical lines). (A, photograph by Kevin J. McGowan. B, from LaDeau et al. 2007. Reproduced with permission from Macmillan Publishers Ltd.)

brachyrhynchos) that were found dead had been infected by the pathogen, suggesting that a high proportion of mortality during that period was caused directly by the disease. Indeed, subsequent studies using a variety of datasets have confirmed that West Nile virus caused substantial morality of crows and several other species throughout North America (LaDeau et al. 2007) (Fig. 13.23).

During the West Nile virus outbreak, mortality rates of American Crows throughout the USA depended on factors such as crow density (denser populations of crows were more likely to suffer declines), human population density (crow populations in more urban areas were more likely to decline), timing (populations exposed to the pathogen later in its North American sweep were less likely to suffer declines than those exposed earlier), and species diversity of the avian community (crows in areas of relatively high diversity were less likely to suffer declines) (Koenig et al. 2010). This last relationship, called the **dilution effect**, is of particular interest because it indicates that diverse bird

Dilution effect: the idea that ecological communities with higher species diversity are more resistant to the spread of pathogens, since there are usually fewer individuals of each particular host species in a high-diversity community.

communities dampened West Nile virus transmission and potentially slowed the rate of disease spread, an effect that is of clear potential benefit to other host populations, including humans.

The dramatic effect of West Nile virus on crows is by no means unique. An even more poignant example of how disease can influence bird populations involves the devastating effects of avian malaria, a disease caused by a protozoan (*Plasmodium relictum*), on native Hawaiian landbirds (Chapter 15). Although other bird diseases have been described, many avian pathogens are poorly known, and it is likely that mortality from epidemics plays a much more important demographic role in bird populations than generally is recognized. A rare example of one that was followed carefully from its beginnings is mycoplasmal conjunctivitis (Box 13.06).

13.7.6 Brood parasitism

Many birds are also vulnerable to avian parasites that trick parents into raising young that are not their own (Chapter 14). This strategy turns out to be very successful for some species, which is perhaps not surprising given the high cost of raising young in most birds. Such **brood parasitism** comes in two forms: conspecific (or intraspecific) brood parasitism, sometimes referred to as "dump nesting," in which females choose hosts of their same species in which to lay their eggs, and interspecific brood parasitism (often simply referred to as "brood parasitism"), in which females target hosts of a different species. Conspecific brood parasitism is relatively difficult to detect—after all, the eggs look the same, being from individuals of the same species. Although it is rare in most species, it has been documented in more than 200 species of birds. For some species, however, it is a common nesting behavior; for example, in American Coots (*Fulica americana*) in British Columbia (Canada), 13% of all eggs are laid parasitically, and 41% of pairs are parasitized (Lyon 2003). Even higher frequencies of brood parasitism have been reported in several cavity-nesting ducks, including Common Goldeneyes (*Bucephala clangula*) in southwestern Sweden, where 36% of eggs were laid by parasitic females. Although the fitness consequences of conspecific brood parasitism have not been studied in many species, and its selective basis is controversial (Box 13.07), these female Common Goldeneyes were able to double their reproductive output by combining brood parasitism with normal nesting, a benefit that imposes strong selection for this behavior (Andersson and Åhlund 2001). In colonially breeding Cliff Swallows (*Petrochelidon pyrrhonota*) studied in Nebraska (USA), the percent of nests with parasitic eggs, almost all laid by colony residents living nearby, increases with colony size, becoming as high as 33% (Brown and Bomberger Brown 1996). Not only do female Cliff Swallows lay eggs in neighbors' nests, sometimes they will actually pick up and move eggs they have laid in their own nests to other nests in the colony.

Brood parasitism: any situation in which a female bird lays its eggs in the nest of another individual of the same or different species.

In contrast to conspecific brood parasitism, the demographic effects of interspecific brood parasitism—a phenomenon exhibited by about 1% of bird species worldwide—are relatively well studied (Chapter 14). Brood parasitism has been particularly well investigated in the Common Cuckoo (*Cuculus canorus*) of Eurasia and the Brown-headed Cowbird (*Molothrus ater*) of North America. Female cuckoos often will remove a host egg from a nest at the same time as they lay their own, and young cuckoos exhibit a startling array of adaptations to monopolize their hosts' parental care. Meanwhile, the negative fitness consequences of brood parasitism on hosts ensure that hosts will be selected both to defend against adult cuckoos and to recognize and discriminate against parasitic eggs. Ultimately, either the host becomes so good at recognizing and defending against cuckoos that the cuckoos are forced to shift to a new host or go extinct, or the cuckoo becomes a better mimic and manages to continue to trick hosts into raising their young. Over time, the system may stabilize at equilibrium if a relatively small proportion of nests are parasitized, or it may escalate into an evolutionary arms race as either the hosts or the cuckoos temporarily gain the upper hand.

In contrast to the cuckoos, Brown-headed Cowbirds are generalists, known to parasitize more than 200 species of birds. Within any one avian community, hosts tend either to accept cowbird eggs laid in their nests (accepters), or to recognize and either destroy them or abandon parasitized nests (rejecters). Cowbird parasitism can be high, with as many as 70% of potential host nests being parasitized, particularly in disturbed, fragmented landscapes. High levels of cowbird parasitism are a major factor exacerbating the population declines of several songbirds, including Kirtland's Warblers (*Setophaga kirtlandii*) and Bell's Vireos (*Vireo bellii*) in the USA. Similarly, the Yellow-shouldered Blackbird (*Agelaius xanthomus*) in Puerto Rico is declining as a result of parasitism by the Shiny Cowbird (*Molothrus bonariensis*).

13.8 Population regulation

Given all the factors that can reduce population size, what keeps populations from going extinct? Over the very long term, of course, most populations do go extinct. On an ecological timeframe, however, population numbers tend to be fairly stable, varying within relatively modest limits, with survivorship and reproduction becoming greater when numbers are relatively low, and decreasing when numbers are

Box 13.06 Mycoplasmal conjunctivitis: documentation of an avian epidemic

Mycoplasmal conjunctivitis is an epidemic disease that has been particularly well monitored since its inception. This highly contagious disease is caused by a strain of the poultry pathogen *Mycoplasma gallisepticum* that produces red, severely swollen inner eyelids among House Finches (*Haemorhous mexicanus*) (Fig.13.B6.01A). These birds were introduced in the 1940s into eastern North America. Mycoplasmal conjunctivitis was first detected in birds at backyard feeders in Maryland (USA) in 1994 and, thanks to observations supplied by over 10,000 citizen scientists, the pathogen's rapid spread across eastern North America range was documented in striking detail (Fig. 13.B6.01B).

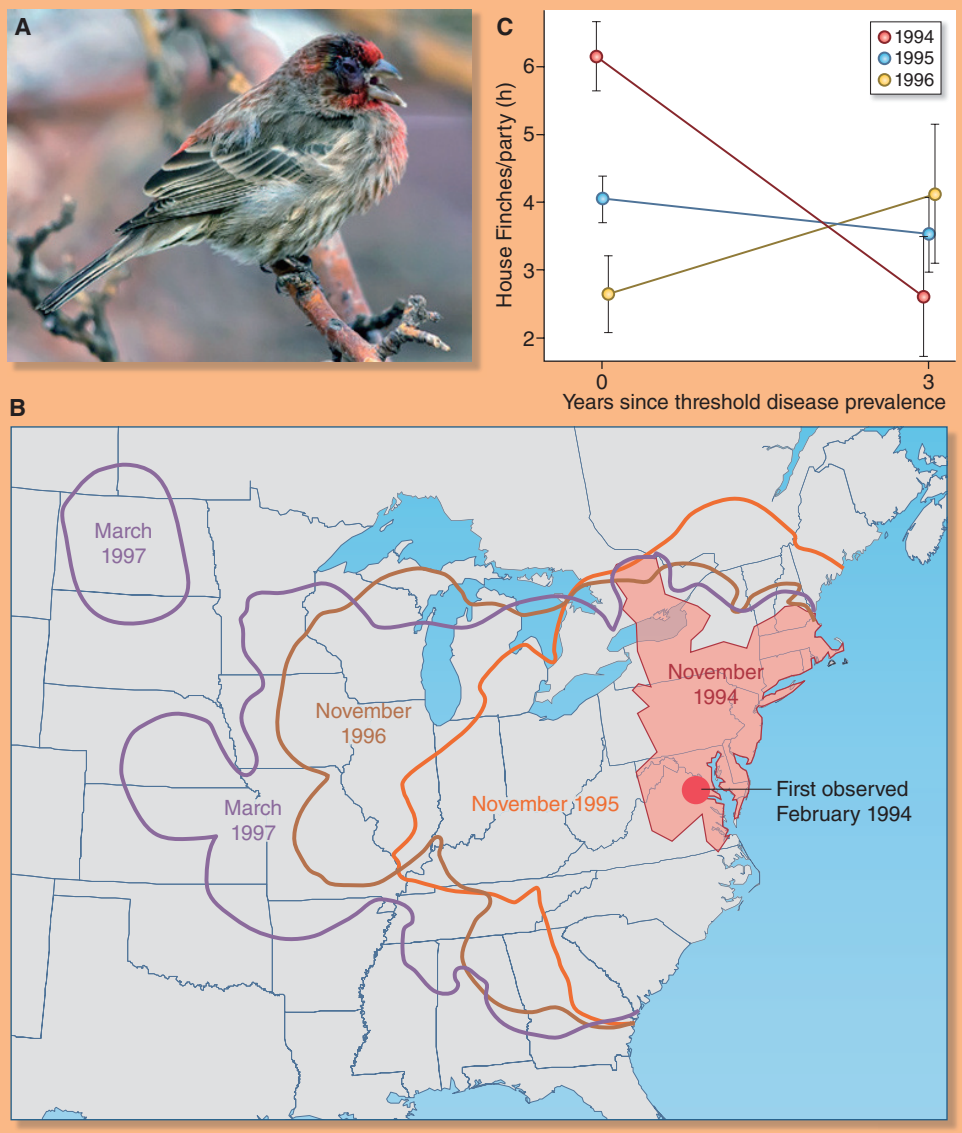


Fig. 13.B6.01 Eye disease in House Finches (*Haemorhous mexicanus*). (A) This diseased male finch has swollen tissues around its eye. (B) Conjunctivitis among House Finches spread quickly in eastern and central North America. (C) Changes in House Finch abundance in the 3 years following the spread of mycoplasmal conjunctivitis into areas where the initial abundance of birds was high (red), medium (blue), and low (yellow). Note that the effects of the disease were density dependent, with the most severe effects occurring in locations where finches were initially most abundant. Consequently, 3 years later, population sizes in all areas were similar regardless of their initial density. (A, photograph by Daniel Arndt. B, courtesy of André A. Dhondt. C, from Hochachka and Dhondt 2000. © 2000 National Academy of Sciences, USA.)

Continued

This disease is estimated to have killed as many as 225 million birds and caused a 60% decline in populations of eastern House Finches (Nolan et al. 1998; Dhondt et al. 2005).

Detailed tracking and experimental studies of the disease have revealed much about how it can affect House Finches and their populations (Dhondt et al. 2005). In particular, the effect of the disease was density dependent: regardless of whether the population had originally been high and stable or small and rapidly increasing, several years after being reached by mycoplasmal conjunctivitis the populations tended to stabilize at similar levels (Fig. 13.B6.01C).

Box 13.07 Conspecific brood parasitism: an evolutionary arms race between parasites and hosts within the same population

Why might some or all females of a species evolve to become brood parasites? One hypothesis is that kin selection (Chapters 3 and 9) might facilitate such parasitism if hosts and parasites are genetically related. Evidence for such relatedness has been found in a Swedish population of Common Goldeneyes (*Bucephala clangula*), where molecular techniques indicate that hosts and parasites are related at about the same average level as first cousins (Andersson and Åhlund 2000). Similarly, conspecific brood parasitism might be favored if the parasitic female mated with the host male—a phenomenon known as quasiparasitism. Quasiparasitism has been reported in about a dozen bird species, but it is almost always rare.

More common—in at least a few species—are the defenses hosts have evolved to reduce parasitism, which include nest guarding, active repulsion of potential parasites, and, if the parasitic eggs can be identified, desertion or ejection of parasitic eggs. These behaviors demonstrate the evolutionary arms race that takes place between parasites and hosts. In an American Coot (*Fulica americana*) population in British Columbia (Canada), for example, females have been shown to identify their own eggs, and they will move parasitic eggs to inferior positions in the nest where they are less likely to hatch (Lyon 2003). Even more strikingly, experiments confirm that female coots use first-hatched chicks as a template from which they learn to recognize their own offspring and subsequently discriminate against later-hatched parasitic chicks in their brood (Shizuka and Lyon 2010) (Fig. 13.B7.01).

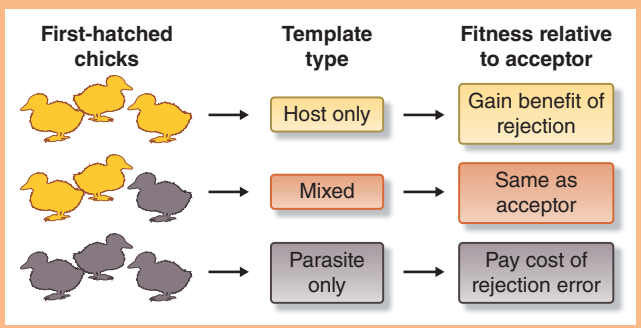


Fig. 13.B7.01 Chick recognition mechanism in American Coots (*Fulica americana*). Experiments show that birds can tell their own chicks (host chicks, yellow) from parasitic chicks (grey) by using the first-hatched chicks to form a template. Thus, if first-hatched chicks are all host chicks, the parent correctly identifies subsequent chicks as either host or parasitic. Most nests (80%) fall into this category. In about 20% of nests, however, both host and parasitic chicks hatch on the first day, and these chicks form a mixed template that prompts parents to accept both host and parasitic chicks. Rarely, only parasitic eggs hatch first, in which case the host will mistakenly accept only parasite chicks and reject their own nestlings. (Adapted from Shizuka and Lyon 2010. Reproduced with permission from Macmillan Publishers Ltd.)

relatively high. Such density dependence is a means by which population regulation can occur, keeping the numbers of individuals within certain bounds. Simultaneously, of course, populations may be affected by density-independent factors such as severe weather that reduce numbers by an amount that is not related to current population size. Only density-dependent factors are capable of regulating population numbers; in contrast, density-independent factors are able to limit populations, but cannot act to regulate them since their effects are by definition independent of population size.

The mechanisms by which population regulation occurs have long been controversial among ecologists and remain a topic of intense research interest. One of the sources of this controversy has been the question of whether some individuals at high densities voluntarily reproduce less so as not to outstrip the available food supply. When considering the entire population, the potential advantage of this type of birth control is clear: if population size becomes too large for the available food supply, all individuals are likely to suffer, and the population may risk extinction. The problem is that, in order for such a system to evolve, selection would have to act at the level of the group rather than on each individual separately. Even when the population as a whole might benefit from lower reproduction, each individual will always benefit, relative to others in the population, by not reducing his or her reproduction,

regardless of the population consequences. In theory, a process termed **group selection** can foster behaviors that provide benefits at the population level, if populations that engage in such behaviors are more successful—that is, go extinct less frequently—than those that do not. In most ecological settings, however, group selection is overpowered by individual selection because of the advantages gained by individuals that ignore the rules and act in their own selfish interests. For this reason, statements about individual birds acting solely "for the good of the species" should always be viewed with great skepticism.

If individuals do not limit their reproduction voluntarily when densities are high, what keeps bird populations from growing indefinitely? The simple answer is that as densities increase, the amount and/or quality of resources available to individuals in the population typically declines. In turn, this lowered availability of resources reduces the reproductive potential of individuals in the population, slowing or ceasing its overall growth.

One factor that is key to limiting reproduction in many bird species is dominance behavior, often in the form of territoriality (Chapter 9). Territoriality comes in a variety of forms, from colonially nesting Double-crested Cormorants (*Phalacrocorax auritus*) that defend only a small area immediately around their nests, to Golden Eagles (*Aquila chrysaetos*) that may defend all-purpose territories used for both nesting and foraging that range in size from 12,000 to 50,000 hectares (Collopy and Edwards 1989). Territoriality of almost all types has the potential both to limit and regulate avian population sizes. Consider Magnolia Warblers (*Setophaga magnolia*) occupying territories in the spring in southern Canada as they return from their wintering grounds in the Caribbean, or Great Reed-Warblers (*Acrocephalus arundinaceus*) returning to a marsh in Romania after wintering in sub-Saharan Africa. The first birds to arrive pick the best sites and defend as much area as they can. As more birds show up, the habitat becomes filled in with territories. Eventually aggression between males starts to reduce the amount of space each male can defend, territory size begins to decrease. At some point, either territory size is reduced to a smaller area that birds can defend most effectively, or the territory holders must devote so much time to territorial defense that holding a territory is no longer profitable. Males arriving after this point are forced to occupy less desirable habitats, or become **floaters** that do not attempt to defend a territory at all (Brown 1969) (Chapter 9). The key point here is that territoriality can regulate population size. Late-arriving territorial migrants settling in poor-quality habitats will be less successful than those settling in high-quality habitats. Moreover, birds arriving later may be forced to settle in territories incapable of supporting successful breeding.

As implied by this scenario, territory size and quality are likely to be related, with territories being smaller (and thus densities greater) in high-quality habitats. This can lead to what Stephen Fretwell and Henry Lucas (1969) dubbed an **ideal-free distribution**, whereby birds in high-quality habitats (where densities are high) have equal reproductive success and fitness as birds in low-quality habitats (where densities are low). Basically, the idea of the model is that birds initially settle in high-quality habitats, but by doing so they decrease each other's expected success, and thus at some point new birds are better off settling in poorer quality habitats, where densities are lower, rather than continuing to pile into the high-quality habitats. The end result is that birds in the different habitats are all expected to have equivalent average success (Fig. 13.24). Generally, it is very hard to demonstrate that differences in bird density and fitness are caused by such differences in the birds' real estate, because in most cases territory quality is notoriously difficult to quantify. One study in which this was achieved was on the Seychelles Warbler (*Acrocephalus sechellensis*), a cooperative breeder that was transplanted to several nearby islands after having gone extinct on all but one island in the Seychelles Island chain. Territory quality was estimated by quantifying the vegetation cover and the insects present in different areas. Initially all birds occupied high-quality territories, later colonizing lower quality territories, and eventually poor-quality territories as the population size increased (Fig. 13.25). In turn, the overall reproductive rate of the population decreased as population density increased and more and more birds were forced to settle on ever more inferior territories (Komdeur et al. 1995). As a second example, Esther Sebastián-González et al. (2010) studied Little Grebes (*Tachybaptus ruficollis*) nesting in irrigation ponds in southeastern Spain, where they were able to estimate pond quality based on various design, size, and vegetation features. During a 2-year study, they found that ponds were occupied by breeding pairs sequentially from best to worst, that high-quality ponds

Group selection: the controversial idea that natural selection can sometimes act collectively via benefits realized by entire groups of organisms, as opposed to the narrower fitness benefits realized by selection acting only on individuals.

Floaters: in largely territorial bird species, individuals that do not hold a territory and instead "float" among territories or less optimal habitats.

Ideal-free distribution: a theoretical model for how birds might distribute themselves over a set of habitat patches, filling in the highest quality patches first and colonizing lower quality patches only when doing so is better than settling in a higher quality but now crowded patch.

supported higher densities of grebe pairs, and that reproductive performance of pairs was unrelated to pond quality, thus supporting all three key predictions of the ideal-free distribution model.

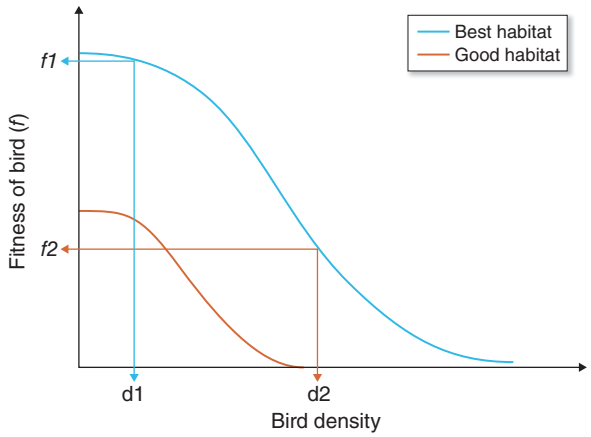


Fig. 13.24 The ideal-free distribution: reproductive fitness correlates with habitat quality. This figure shows habitats of two qualities: the best habitat (blue) and a good habitat of lesser quality (orange). The plot lines represent the average fitness of birds attempting to breed in each habitat. When density in the best habitat is low (d1), all birds are expected to occupy that high-quality habitat and thereby have high fitness (f1). Yet as bird density in the best habitat increases, the average fitness of birds in that habitat decreases as it gets crowded, until birds can be equally successful if they settle in the lower quality, but less crowded, other habitat. (From Fretwell and Lucas 1969. Reproduced with permission from Springer Science + Business Media.)

Increasing densities can limit bird populations even when the birds are not territorial. For example, the increased density of a species might cause higher levels of aggression that decrease foraging efficiency and ultimately the birds' reproductive success (Chapter 8). Whether mediated by territory availability or aggressive behavior, the common theme in these cases is that birds at low densities will, on average, occupy high-quality areas and experience high success, thus tending to increase population size, whereas at high densities birds will occupy lower quality sites, and their success will decrease, eventually leading to population decline. Consider Black-tailed Godwits (*Limosa limosa*) migrating through Britain, where populations have been increasing since the 1970s. Godwits wintering in estuaries with initially low numbers of birds—and thus presumably of low quality—have increased in number considerably more rapidly than those in high-quality estuaries with initially high numbers of birds. Studies have found that the godwits in the low-quality sites have lower foraging success, lower survival, and arrive later on their breeding grounds in Iceland than godwits on high-quality sites where populations have been relatively stable (Gill et al. 2001) (Fig. 13.26). Thus, as the godwit population has increased, a larger proportion of birds are wintering in poor-quality estuaries where they experience conditions that cause them to arrive later on their breeding grounds, a factor that generally results in lower reproductive success and thus provides a mechanism for regulating godwit populations.

One of the more common and most important consequences of territoriality is that some fraction of the male population is unable to obtain a territory, and some

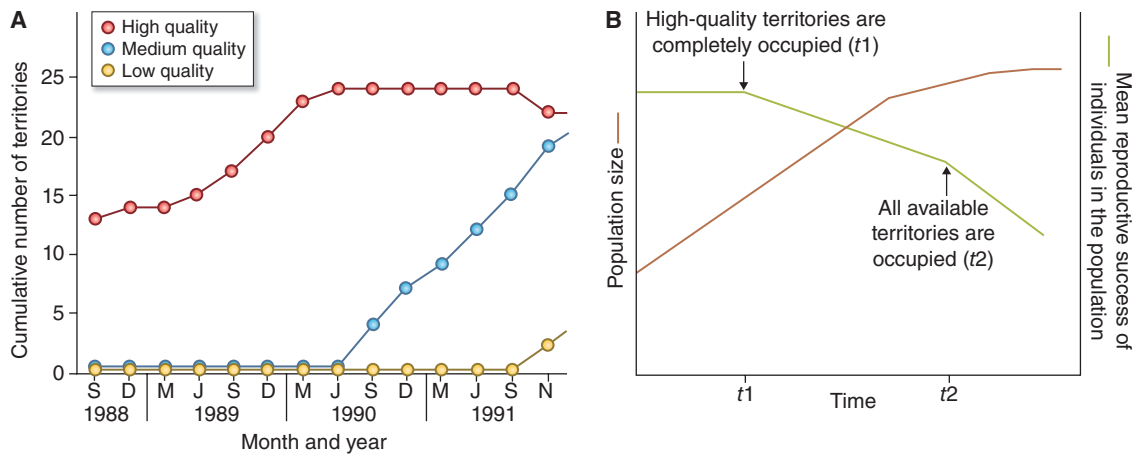


Fig. 13.25 Territorial occupancy and reproductive success. (A) After the reintroduction of Seychelles Warblers (*Acrocephalus sechellensis*) to Aride Island, individuals initially occupied high-quality habitat (red), but eventually dispersed into medium (blue) and low (yellow) quality habitat as competition increased with time. (B) A hypothetical graph shows how territorial occupancy and reproductive success change with time in a new population. Initially, before t1, many high-quality territories are available and individual reproductive success is high. These territories become filled at t1 and individual reproductive success starts to decline as poorer territories are occupied for reproduction (t1 to t2). All available territories are full at t2; the remaining adults are forced to float among territories, and the overall reproductive success of individuals decreases further. (A, from Komdeur et al. 1995. Reproduced with permission from Elsevier. B, © Cornell Lab of Ornithology.)

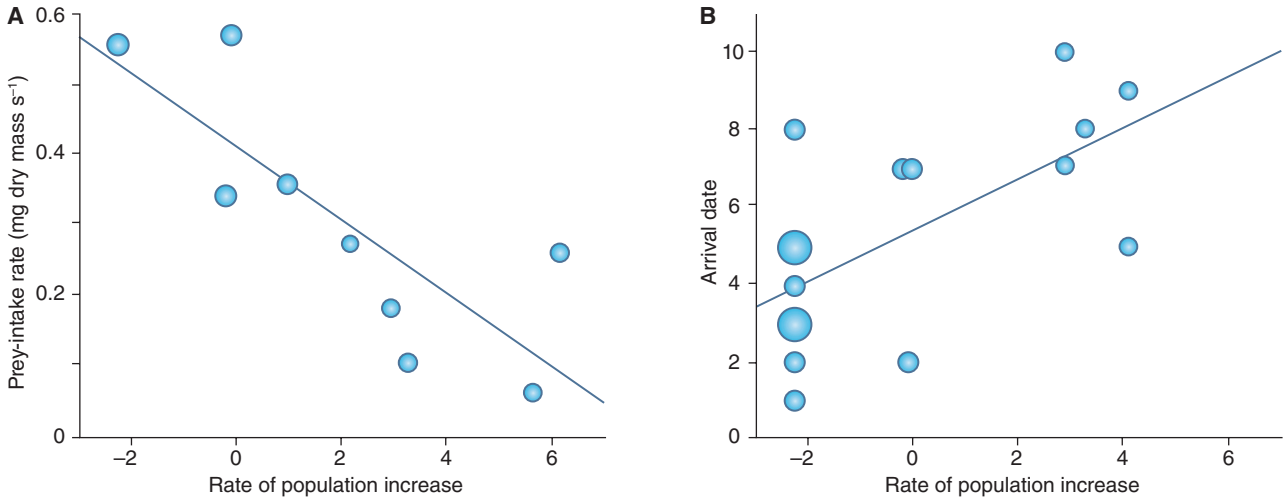


Fig. 13.26 Resource abundance and population growth. (A) As Black-tailed Godwit (*Limosa limosa*) populations increase at wintering sites in Britain, the foraging success (prey intake rate) of individual birds goes down, and (B) their arrival date on the breeding grounds in Iceland gets later. Larger circles represent a higher number of individuals. (From Gill et al. 2001. Reproduced with permission from Macmillan Publishers Ltd.)

fraction of the female population is unable to obtain a mate defending a territory. There are several possible fates for birds in this situation. Under the right circumstances, they may remain in their natal territory as non-breeding helpers, as observed in cooperative breeders (Chapter 9). In other cases, such birds become floaters, an "underworld" of unmated birds lurking on the periphery of the more obvious territorial pairs and waiting for the opportunity to move in should an established breeder die or disappear. Floaters are notoriously difficult to document and study, because they are often less site-specific and almost always are less conspicuous than territory holders. A classic example studied by Susan Smith (1978) is the Rufous-collared Sparrow (*Zonotrichia capensis*) in Costa Rica, where pairs held small territories among which adult, non-territorial floaters lived singly. Floaters did not defend territories, but had home ranges that overlapped with one to four established territories, not all of which were necessarily contiguous (Fig. 13.27). Floaters established their own dominance hierarchies and remained as floaters for as long as a year, in many cases eventually replacing one of the local breeders. Although the behavior of floaters has been studied extensively in relatively few species, their existence has been inferred in many bird populations by experiments in which breeders—usually territorial males—are removed, only to have their newly vacated territories occupied quickly by previously non-territorial males that were present, although often undetected, in the area and clearly on the lookout for such opportunities. More generally, the presence of floaters within a population suggests that the population is subject to density-dependent regulation, because there are more birds present than are able to breed.

Territoriality and other behavioral means of interference are only some of the ways that social behavior can act to limit bird populations. Others include incest avoidance (failing to breed with genetic relatives) and **Allee effects** (Chapter 15), a tendency for populations at low density to have poorer, rather than better, reproductive success (Fig. 13.28); in other words, the process by which small populations may exhibit **inverse density dependence**. Allee effects may occur in any population that is reduced to low numbers, either during a colonization event or later as a result of a population crash. Allee effects may result from a shortage of interactions among conspecifics, a factor that is most likely to be a problem for colonial or other highly social species, but which can occur in any species when densities become so low that mates are hard to find.

Genetic **inbreeding** (Chapter 3) is another potential cause of Allee effects. Reduced fitness stemming from

Allee effect: a disruption of reproductive behavior and/or social structure when population density falls below a threshold level.

Inverse density dependence: a feedback loop in which populations at higher density tend to grow larger, whereas populations that shrink tend to become even smaller over time.

Inbreeding: the offspring resulting from matings between individuals who are more closely related than would be expected by chance within a population.

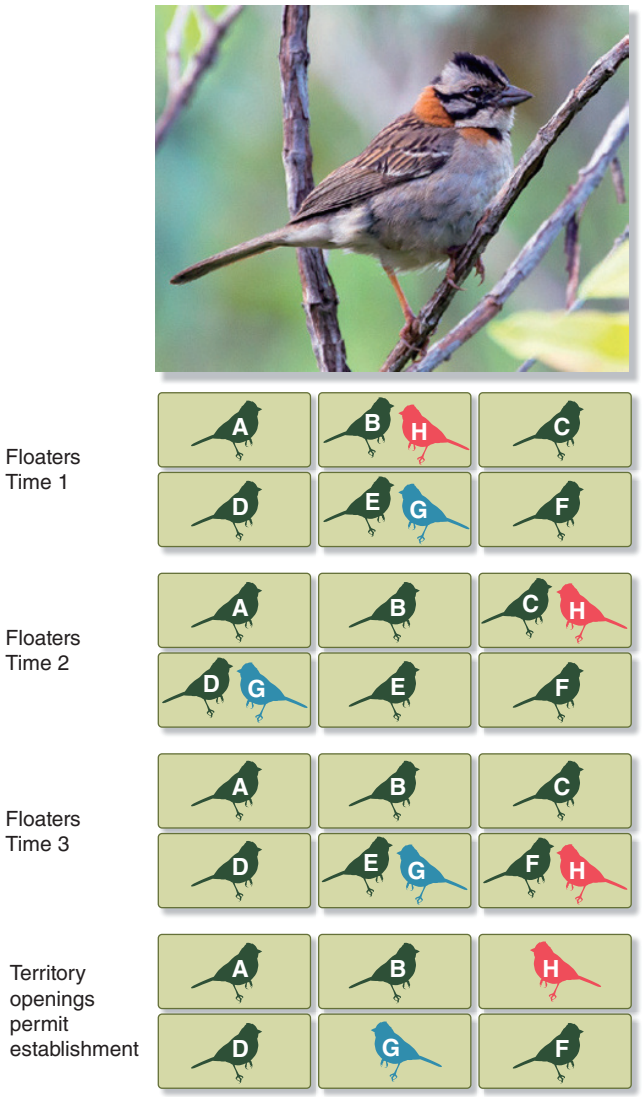


Fig. 13.27 Floaters lack territories. Rufous-collared Sparrow (*Zonotrichia capensis*) floaters move between territories in their home range. In this schematic, two non-territorial individuals (blue G and gold H) transiently float between breeding territories already occupied by males (black A–F) over time. When territories within floater home ranges become available due to death or inadequate defense by the current occupant, floaters move in and defend those territories. (Adapted from Smith 1978. Photograph by Rodrigo Conte.)

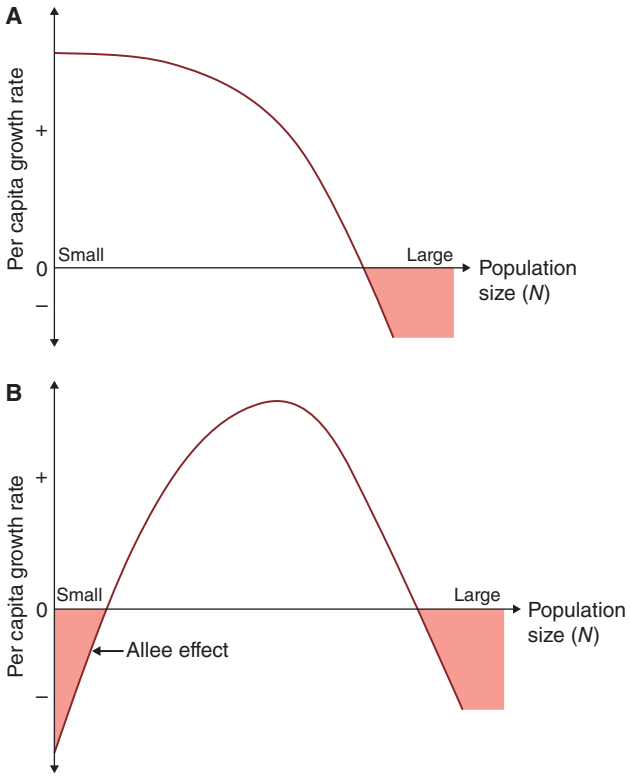


Fig. 13.28 A graphic representation of Allee effects. (A) Once population size reaches its carrying capacity, growth rate decreases. Per capita growth rate of a population is negative above the carrying capacity and positive below. (B) When the Allee effect (arrow) is present, growth rates are also negative when population size is very small. (© Cornell Lab of Ornithology.)

inbreeding is most likely to become an issue in populations that have become so reduced in numbers that mating opportunities are limited to close relatives. Inbreeding and inbreeding avoidance can have adverse effects on population growth of highly social species even when populations are healthy. Negative effects of inbreeding have long been documented in laboratory animals and in humans, where they presumably are the basis for the incest taboos that are widespread in human societies. However, it is recognized now that nearly all birds avoid close inbreeding, usually by sex-biased dispersal (in birds, females usually disperse farther away from their birthplace than males; Chapter 12). In a worst-case scenario when bird populations are reduced to extremely low numbers, however, all potential mates might be close relatives, and thus inbreeding becomes unavoidable. Under these conditions, the reduced fitness of offspring produced from incestuous matings is likely to result in Allee effects working to threaten the population even further.

13.9 Populations through time and space

Few bird populations remain the same size from year to year, or even from season to season. Instead, they fluctuate in size depending on the many factors discussed earlier in this chapter, including environmental conditions, food supply, predators, diseases, and so on. Some of the more intriguing demographic changes involve population cycles—notable and in some cases predictable changes in population size from year to year, with the population rising to high densities

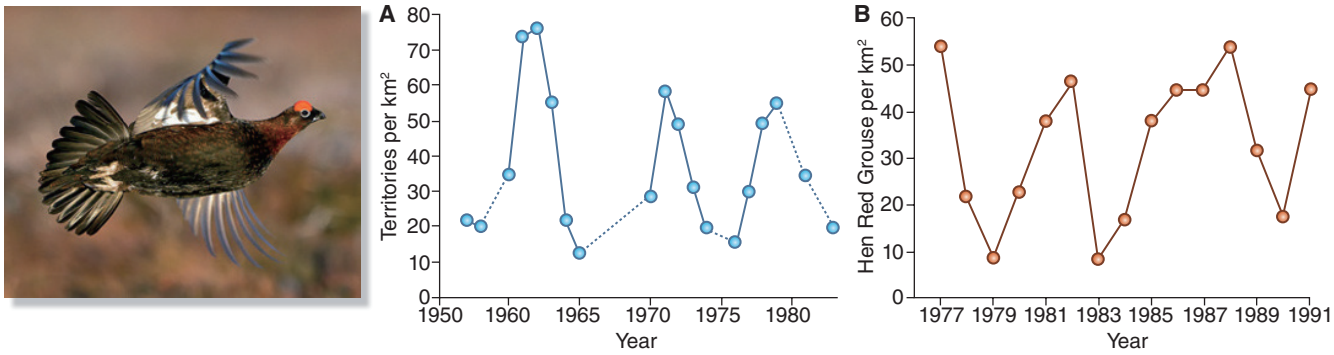


Fig. 13.29 Population cycles in grouse vary over time and space. (A) Willow Ptarmigan (*Lagopus lagopus*) territory densities peak about every 10 years in British Columbia, Canada. (B) Cycles occur in 4–5-year fluctuations in breeding densities of this same species in the UK (where it is known as the Red Grouse). (From Moss and Watson 2001. Reproduced with permission from Elsevier. Photograph by Marcus Conway.)

and then declining to low levels (or even local extinction) on a cycle of several years' duration. One distinctive form of a population cycle is that of **irruptive migration** of wintering species (Chapter 12). Other examples involve more predictable, in some cases equally dramatic, oscillations of breeding population size.

The causes of population cycles can be difficult to determine, and even the cycles themselves can be challenging to detect without data from many years covering multiple oscillations. Some of the best documented cases of bird population cycles are those exhibited by grouse. Grouse population cycles can vary not only from place to place, but also through time. For example, some Red Grouse (*Lagopus lagopus*) populations in Europe exhibit cycles 3–5 years in duration, but others cycle at longer intervals of up to 10 years, and still others fail to cycle at all (Moss and Watson 2001) (Fig. 13.29).

One of the main hypotheses for the cyclic populations of grouse is **prey switching**; that is, generalist predators switch to grouse and other birds when their main prey—usually mice or other rodents—are at low density or otherwise unavailable. Increased predation decreases numbers, first of the grouse and then of the predators, eventually allowing the grouse to recover. Evidence for the importance of such predator–prey interactions is found in numerous species, particularly in boreal and arctic areas where population cycles of small mammals, mainly lemmings and hares, are particularly dramatic and play a key role in their respective communities. Such prey are particularly important to avian predators such as jaegers, Snowy Owls (*Bubo scandiacus*), goshawks, and other raptors, but also affect species such as sandpipers and geese that may serve as alternative food for the raptors, and whose nesting is disrupted by high rodent activity during population peaks. Other factors, such as disease, also may play a role in population cycles. Growth rates of Red Grouse populations, for example, are inversely related to the infection rate of the population by a parasitic nematode worm, so that population crashes occur when the birds have high parasite loads. Peter Hudson et al. (1998) treated birds in four high-density populations in northern England with a veterinary drug that eliminated these parasites and succeeded in averting the population crash that took place in two control populations, demonstrating that the nematodes contributed to the population crash in the untreated grouse populations.

Although environmental factors such as temperature and rainfall can affect populations in various ways, most such effects are not clearly cyclic. A notable exception is the fluctuation associated with large-scale, global climate cycles such as the El Niño Southern Oscillation. In El Niño years, the normally cold and productive waters off the western coast of South America become warm, thereby becoming unsuitable for the anchovies and other fish on which seabirds like Peruvian Boobies (*Sula variegata*), Peruvian Pelicans (*Pelecanus thagus*), and Guanay Cormorants (*Phalacrocorax bougainvillii*) forage. At these times, the vast seabird colonies on the coastal islands of Chile and Peru suffer from massive breeding failures, with most chicks dying of starvation and many adult seabird pairs forgoing nesting entirely. In particularly severe El Niño years, the lack of food can even drive high mortality among the adults of these normally long-lived seabirds. El Niño cycles can have even more wide-ranging effects. For example, long-term studies of Black-throated Blue

Irruptive migrants: birds that occasionally move in large numbers beyond their usual range, usually in response to poor food supplies in their typical habitats.

Prey switching: a behavior in which predators preferentially consume the most abundant type of prey, switching to another prey type when it becomes the most abundant.

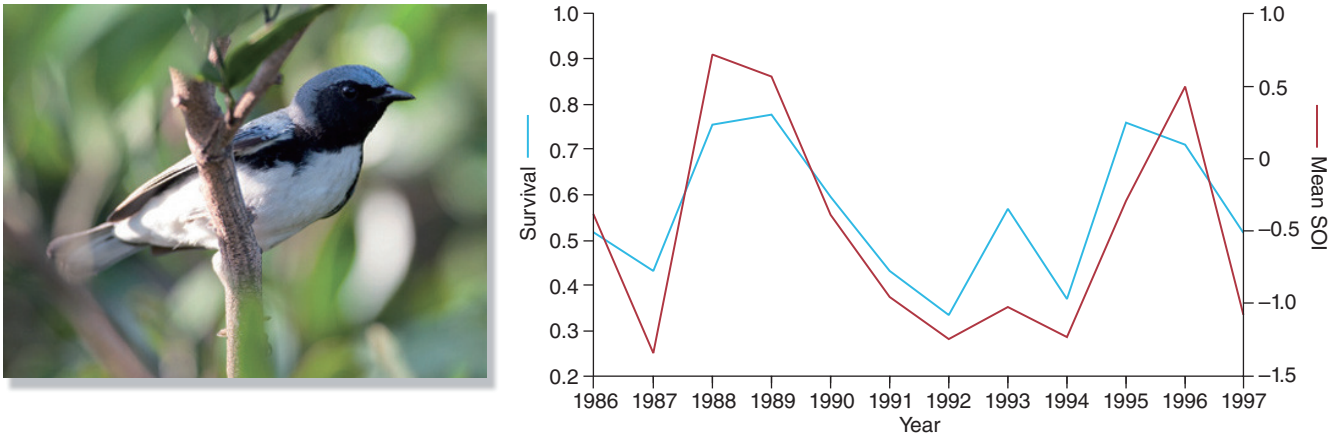


Fig. 13.30 Effects of climate cycles on breeding birds. Black-throated Blue Warblers (*Setophaga caerulescens*) experience higher winter survivorship in Jamaica during years when the Southern Oscillation Index (SOI) is high, which tend to have higher rainfall. (From Sillett et al. 2000. Reproduced with permission from AAAS. Photograph by Christopher Wood.)

Warblers (*Setophaga caerulescens*) on both their breeding grounds in New Hampshire (USA) and their wintering grounds in Jamaica have demonstrated that adult survival and fecundity cycle in relation to the El Niño cycle, being lower in relatively dry El Niño years and higher in wetter La Niña years (Sillett et al. 2000) (Fig. 13.30).

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Chapter 14 Bird Communities

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On a walk through any habitat you might encounter a single chirping songbird, large flocks of a single species, or a vibrant diversity of birds of many species. This extravagant variation in bird diversity naturally leads to questions such as why are there so many bird species in some places and so few in others? How do different assemblages of species interact? Do different groups of birds compete? Do they cooperate? How do birds interact with other aspects of their environment?

There are many definitions of biological **communities** and many approaches to studying them. A typical definition of a biological community is "any group of organisms belonging to a number of different species that co-occur in the same habitat or area and interact through trophic and spatial relationships" (Lincoln et al. 1998). Note that this definition does not include any particular taxonomic limits, and birds are just one component of any group of potentially interacting organisms. However, some biologists argue that the groups we term communities are artificial human constructs (Box 14.01). The term community includes only a subset of the organisms that influence the lives of birds, so the term **species assemblage** is often preferred when referring to only the avian component of a community. Moreover, biological communities are often discussed without the numerous non-biological factors that affect populations, such as climate and other environmental variables. An **ecosystem** is perhaps a more familiar and inclusive term that describes both the collection of species and physical environment in which they interact.

It is often challenging to delineate the most appropriate scale for defining a particular community, because the distributions of individual bird species often change from season to season and from place to place. Furthermore, the

Community: the set of ecologically interacting organisms of different species that occurs in the same location.

Species assemblage: similar to "community," the group of species found in a particular location or habitat.

Ecosystem: the complete set of organisms—the biological community—along with the physical environment in a particular location or region.

Opposite: This tropical African wetland hosts a wide diversity of bird species, which interact with an array of other wildlife as well as each other. The community structure and foraging hierarchies—both within and among bird species—change as the season shifts from wet to dry. (Photograph by Esther J. Horwich.)

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Box 14.01 Defining communities

The scientific view of communities has evolved during the past century, from the proposals of the early and influential plant ecologist Frederick Clements—who viewed communities as discrete entities (super-organisms) comprised of co-adapted species—to a view championed by a later ecologist, Henry Gleason. Gleason proposed that plant species are individualistically distributed along environmental gradients and sometimes form more discrete units of co-occurring species, particularly where there is a sharp environmental gradient (such as a change in soil type).

More recently, research on how species assemblages vary across space and time has tended to reinforce the idea that most so-called "communities" are not cohesive or co-adapted units. True, suites of species sometimes do co-occur in predictable assemblages, particularly if there are sharp discontinuities in the abiotic environment, but rigid attempts to define most communities meet with failure. Complex statistical approaches now are used to define assemblages of species that, to varying degrees, tend to occur together.

number of bird species that occur within an assemblage changes relative to the size of the area that is sampled. Community ecologists therefore usually adopt a pragmatic definition of the community they study that reflects the specific interactions that are of interest to that particular researcher. Despite conflicts in how we formally define a community, we focus in this chapter on the central theme of avian community ecology: the interactions among different bird species.

14.1 Classifying bird species assemblages

Scientists who study plants have been particularly concerned about developing rigorous ways of defining communities, and avian community ecologists often rely upon the classifications developed by botanists, with the proviso that major physiographic features—such as bodies of water—can form the basis for additional types of avian communities.

Biomes are the broadest way of dividing the terrestrial parts of the globe into regions that differ in the prevailing climax vegetation type (such as tropical/subtropical, temperate, dry, and polar/montane, as well as aquatic). Biomes are usually defined by structure rather than species so that similar habitats in two different regions can be grouped together. The major terrestrial biomes, as defined by the World Wildlife Fund's current dataset of 825 global ecoregions, include: flooded grasslands and savannas; coniferous forests; dry broadleaf forests; grasslands, savannas, and shrublands; moist broadleaf forests; broadleaf and mixed forests, deserts and xeric shrublands; Mediterranean forests, woodlands, and scrub; boreal forests/taiga; rock and ice; and tundra. As they overlap with terrestrial ecosystems, lakes and mangroves are included as well. Some of these biome types repeat under broader categories (such as coniferous forests, which occur in both tropical and temperate climates) (Fig. 14.01).

Biome: an ecological community of organisms that occurs across a broad geographic region defined by its location, biogeographic history, and climate.

For example, a characteristically scrubby type of vegetation occurs in areas with climates of cool, moist winters and hot, dry summers. This plant community is dominated by bushy, drought-resistant, aromatic species that are well adapted to survive despite frequent fires. Although it has different names in different places, this Mediterranean scrub biome occurs across the globe, including the west coast of California, USA (where it is termed *chaparral*), coastal Chile (*matorral*), the area surrounding the Mediterranean Sea (*maquis*), the coast of South Africa (*fynbos*), and the southeast coast of Australia (*kwongan*). These distant regions all host structurally similar plant communities, but they are embedded in continents with very different bird species, representing different families and orders. No bird species is found across similar plant communities around the globe; instead, the different birds in these areas often have converged in many aspects of their biology. For example, in a classic comparison of the birds of these habitats in Chile and California, Martin Cody (1974) found that the two areas were very similar both in their overall number of bird species and in the relative abundances of the particular birds that filled different ecological roles, such as foliage gleaners, nectarivores, ground feeders, sallying flycatchers, and so on. Cody went so far as to identify several species that independently evolved such similar ecologies that they could be considered "replacement" species for each other in these two Mediterranean scrub habitats. These comparisons indicate that bird assemblages can converge to become quite similar in ecology when faced with similar environmental conditions.

A different habitat classification system is generally used for mountainous regions, where major climate-driven

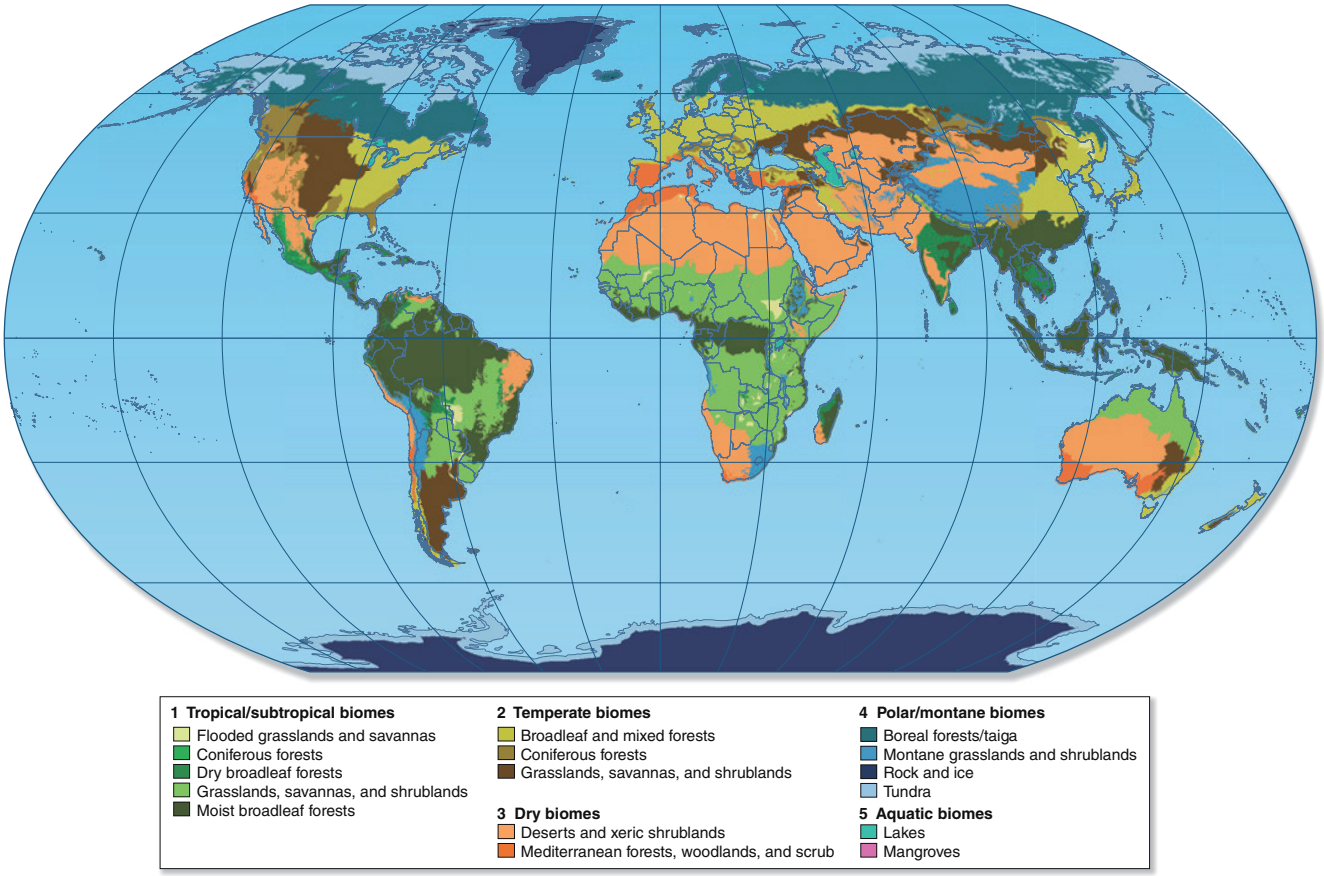


Fig. 14.01 Major biomes of the world. This map depicts the currently recognized terrestrial biomes, based on biodiversity patterns for 825 ecoregions. (© 2012 The Trustees of Columbia University in the City of New York. CC-BY-3.0.)

changes occur over a range of elevations. **Life zones** recognize these transitions of plant and animal species encountered along an elevational gradient. For example, in tropical regions with high rainfall, the life zones you encounter as you travel up a mountain often change from tall tropical forests at low elevations to stunted and moss-covered cloudforests at higher elevations, with treeless habitats at the highest elevations (Fig. 14.02). In some cases, bird communities track these elevational life zones closely, with the bird assemblage changing in composition at **ecotones**, the boundaries between two successive life zone habitats. Elsewhere, bird assemblages may also be sensitive to elevation even in the absence of abrupt changes in habitat types. For example, bird surveys across a range of elevations in the Udzungwa Mountains of Tanzania found that most species fell within one of two distinct assemblages (with a notable switch at 1200 meters) despite apparently similar habitat across the gradient (Romdal and Rahbek 2009) (Fig. 14.03).

In other places, bird species have even more subtle and variable distributions across elevations. **Elevational zonation**, a pattern in which related bird species replace one other at different bands of elevation, is particularly common in tropical regions. This type of distribution pattern helps explain why tropical regions with extensive topography have notably high diversities of birds—and why birders wishing to see the largest number of species within these regions need to divide their time across a range of elevations. In some cases, elevational replacement species meet one another only in a very narrow band that does not correspond with any obvious habitat change. Here, competition and aggression between the species may be the main forces keeping them from overlapping, as seen in a

Life zone: a geographic region (or, in mountains, an elevational band) characterized by a distinct group of animal and plant species.

Ecotone: a transition zone connecting two habitats and the communities of birds and other organisms that occur in them.

Elevational zonation: a pattern in which related bird species replace one other at different bands of elevation along a mountain slope.

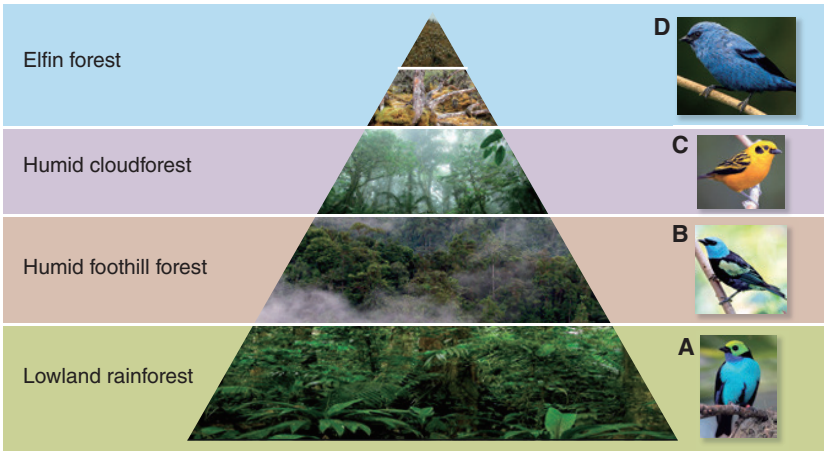


Fig. 14.02 Life zones. In the Ecuadorian Andes, different tanager species occupy distinct habitat- and climate-driven strata along an elevation gradient: (A) Paradise Tanagers (*Tangara chilensis*) in lowland rainforest, (B) Blue-necked Tanagers (*Tangara cyanicollis*) in humid foothill forest, (C) Golden Tanagers (*Tangara arthus*) in humid cloudforest, and (D) Blue-and-black Tanagers (*Tangara vassorii*) in high-elevation elfin forest. (Photographs by: A, Bill Fleites; B, Timothy Wong; C, Peter Hawrylyshyn; D, Francesco Veronesi; pyramid habitats, Alexandra Class Freeman.)

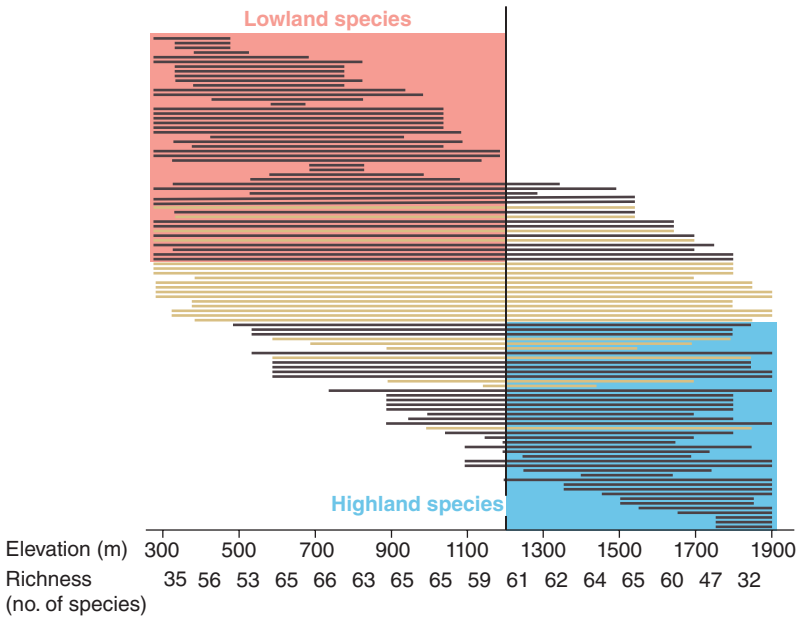


Fig. 14.03 Community assembly shifts along a montane elevational gradient. Each horizontal bar represents a different bird species surveyed on a mountain slope in Tanzania. Bars are ordered by the midpoint of each species' elevational range. Black bars represent species with ranges that occur above or below 1200 meters at least 75% of the time. These species belong to either the highland (blue box) or lowland (red box) community. Black bars represent widespread species that do not distinctly belong to either assembly. Richness (number of species) recorded at each elevation is denoted below. In this case, complex dynamics among species appear to influence community assembly more than do sharp environmental ecotones. (From Romdal and Rahbek 2009. Reproduced with permission from John Wiley and Sons.)

group of thrush species in Costa Rica. Experiments in which researchers played recordings of the songs of these species and then recorded the birds' responses show an intriguing pattern: each species is more aggressive towards the song of the other species at locations nearest their shared elevational boundary, suggesting that aggression plays a direct role in keeping the species separated into distinct elevational zones (Jankowski et al. 2010).

14.2 Ways of describing communities

14.2.1 Species diversity

Scientists and birders alike know that the number of bird species found in a particular habitat or region is a simple but useful number. Species diversity can be looked at in two ways, depending on whether we prioritize just tallying the total number of species present or also consider their relative abundances. If we think of a particular bird species assemblage as a jar of jelly beans, and we want to buy the jar with the most flavors, we could empty the jar completely and simply determine the total number of different kinds. Applied to birds, this count would represent **species richness**, the number of different species present. However, we might find a jar that has a variety of different flavors but a preponderance of lemon-flavored jelly beans; if we grab a handful, the chances of getting more than a couple of types of beans is small, because there are so many yellow ones. The chance of getting the most types of beans in a jar, or bird species in a particular survey, depends both on the total number of different types/species and their pattern of relative abundance. This combination of bird community attributes—the number of species plus their relative abundances—is what most avian ecologists consider when they refer to species diversity.

14.2.2 Patterns of species abundance and estimating species richness

In practice, species richness almost always grows with increased effort on the part of the people searching an area, and with a greater number of individual birds identified. A plot with the number of species detected on the *y*-axis and the number of survey samples or individuals observed on the *x*-axis is known as a **species accumulation curve** (Fig. 14.04). Most species accumulation curves first rise sharply, then rise more gradually, and finally level off at a maximum number known as the asymptote. On one extreme, assemblages with few but common species will reach an asymptotic number of species rapidly. In assemblages with many species, particularly many rare or transient species, the accumulation curve will be long and gradual, and tremendous surveying effort may be needed to reach the asymptote. Because most bird surveys are not complete but instead provide a snapshot of the total number of possible species, a simple comparison of species totals may be very misleading. For example, an equivalent survey effort may produce a similar species total for two assemblages, but in one assemblage all the species present were sampled, whereas in the other only a fraction of the total possible species was detected in the same amount of time. Similarly, if two survey sites differ in the overall abundance of birds of different species, a similar survey effort will result in a higher species list for the habitat that contains more birds. Statistical programs now are available that estimate the asymptotic species richness of an assemblage from different kinds of field surveys.

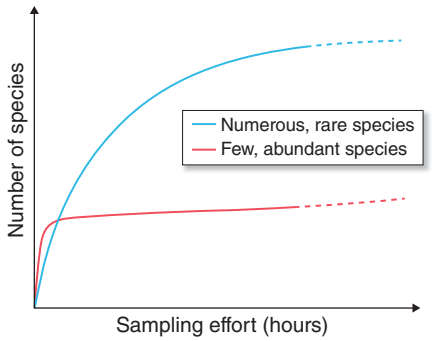


Fig. 14.04 Species accumulation curves. More species are discovered as sampling effort (hours) increases, but discovery rate decreases with increased effort. Researchers can approximate species richness in an area by fitting the start of a species accumulation curve to a mathematical function. For areas with many rare species (blue plot), the curve has a long, gradually increasing tail; this represents the considerable sampling effort necessary to discover most of a region's species. For areas with relatively few and abundant species (red plot), the curve does a better job of rapidly approximating species numbers. (© Cornell Lab of Ornithology.)

Species richness: the number of different species present in a location, ecological community, or region.

Species accumulation curve: a graph that shows the number of species detected on the *y*-axis and the number of survey samples or individuals observed on the *x*-axis.

Species–area plot: usually a graph showing the cumulative number of species detected as the area sampled increases. The resulting relationship is typically a curve, as fewer and fewer new species are detected with increasing area.

14.2.3 Species–area curves

It is a general truism that larger areas contain more bird species. The richness of bird species seen or heard in any survey is therefore always highly dependent on the area surveyed. A graph of the number of species found in a survey versus the area being surveyed is termed a **species–area plot**. Curves based on increasing sampling areas—from a hectare to a square kilometer to 100 square kilometers to thousands of square kilometers—nearly always show a steady increase

in species totals because more habitats are sampled and more local and rare bird species are detected.

Species–area relationships are most clearly visible in archipelagos of islands of different sizes, which share a few nearly universal patterns. First, islands generally have fewer species than areas of similar size on a nearby continent. The number of species on an island also is strongly related to its distance from the mainland (which presumably affects how readily birds can colonize the island) and the size of the island. Avian ecologists have surveyed the number of bird species on most of the world's islands and have found that, in general, the number of species roughly doubles with every 10-fold increase in island area. For example, within the Lesser Antilles Archipelago in the Caribbean, the relatively small island of St. Kitts (168 square kilometers) has 37 resident breeding bird species, whereas the larger nearby island of Guadeloupe (1713 square kilometers) has 72 species (Ricklefs and Bermingham 2008).

The reasons that small islands support fewer bird species than do larger islands are similar to those that cause small areas on a continent to have fewer birds than larger continental areas, with one twist: for many species, the small population size that can be supported on a small island, coupled with the lack of other places to go when local conditions become stressful, leads to higher extinction rates on islands. The **Theory of Island Biogeography** developed by Robert MacArthur and E. O. Wilson (1967) was groundbreaking when it was introduced because it provided an elegantly simple model for predicting the number of species on islands based on an equilibrium between colonization rates (which decline with distance from a source of new species, such as a nearby continent) and extinction rates (which decline with increasing island size, since large islands can support larger bird populations than smaller islands). Under this simple theory, we would expect to see the greatest avian diversity on large islands that are close to a continent or other source of potential colonists, and the lowest diversity on small, remote islets (Fig. 14.05).

Similarly strong relationships between habitat size and bird species richness occur in other settings where either natural or man-made habitat "islands" occur (Chapter 15). For example, a team of ornithologists working in central Panama surveyed the bird species in 18 forest fragments of varying sizes, from 21 to more than 15,000 hectares (Robinson et al. 2004). As expected under the island biogeography theory, they found a strong relationship between forest patch size and bird species richness: the smallest fragment supported only 10 species of forest-dependent birds, whereas the most expansive sites contained more than 150 such species.

Theory of Island Biogeography: a relationship formalized by ecologists Robert MacArthur and E. O. Wilson that describes how the total number of species inhabiting an island or habitat patch results from a balance between the rate at which new species colonize and the rate at which populations of established species become extinct.

Alpha diversity: the count of the number of species present in a single habitat or location.

Beta diversity: the accumulation of species that results as a sampled area includes a greater number of habitats, each with some species found only in that habitat.

14.2.4 Understanding abundance and rarity

Most bird assemblages have a few common (dominant) species and many uncommon to rare species. Assemblages differ considerably in the number of rare species they contain, but, particularly in the tropics, some avian assemblages contain a large number of individually rare species. For example, Peter Pearman (2002) used mist nets to survey the understory bird community on 23 small study plots in the Amazonian forest of Ecuador. Of the 93 total species he captured, only the nine most common birds were found at more than half of the plots, whereas 39 rare species were captured only on one or two plots.

Determining the factors that explain why some species are rare (Fig. 14.06) is both an interesting academic challenge and important for conserving rare species. Reasons that a species might be rare in a particular assemblage include: (1) the site is at the edge of the species' range or the site is in suboptimal habitat, but the species is common elsewhere in suitable locations; (2) the species is large bodied or high on the food chain, and hence few individuals can persist in any one area; (3) the species has specialized habitat requirements; (4) the species has suffered from human activities that have reduced its abundance; (5) the species is at a low point in a long-term population cycle; or (6) the species is globally rare without any identifiable limiting factors.

14.2.5 Three kinds of diversity

Community ecologists have defined three types of diversity that are easily applied to bird assemblages. **Alpha diversity** is the count of the number of species present in a single habitat or location. The alpha diversity of birds is most often assessed using a simple species list, a species diversity index, or a more sophisticated estimate of the number of species present that factors in the amount of effort put into the survey. **Beta diversity** is the additional accumulation of

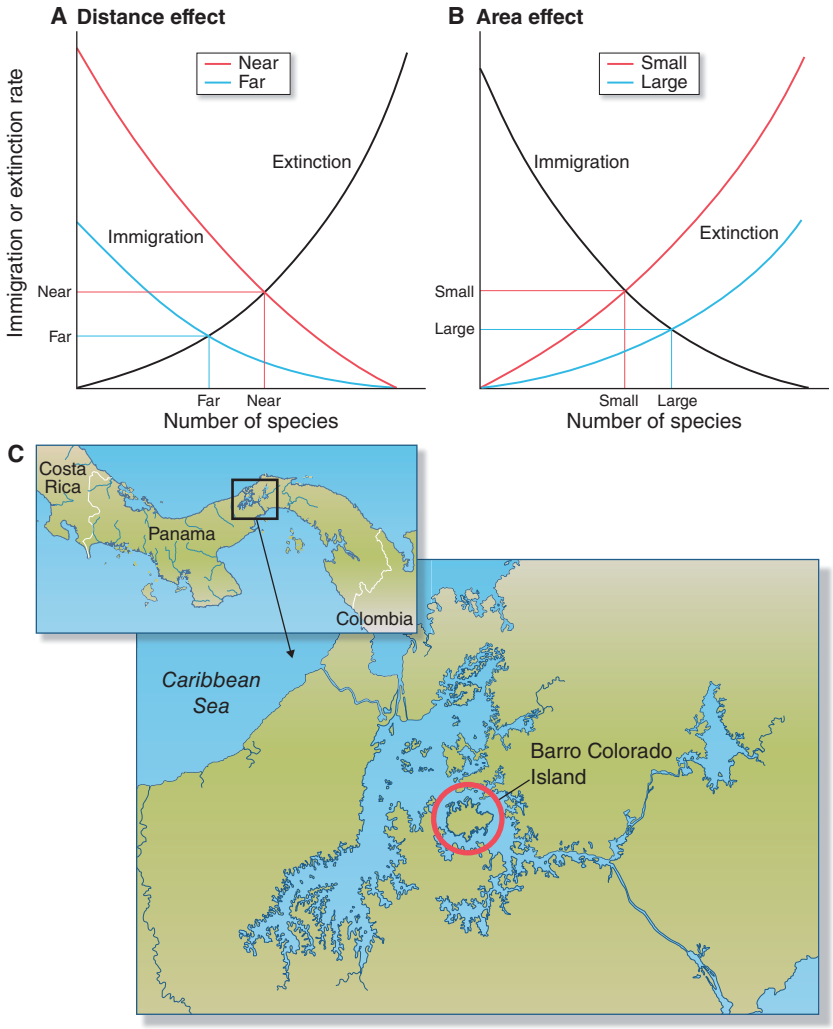


Fig. 14.05 Theory of Island Biogeography. MacArthur and Wilson observed that (A) distance from a source population and (B) area are both good predictors of species richness. (C) Gradual species loss on Barro Colorado Island, an island in the Panama Canal that was first surrounded by rising waters in 1913, provides an opportunity for biologists to test the MacArthur–Wilson model. (A and B, from Simberloff 1974. Reproduced with permission from Annual Reviews. C, courtesy of Smithsonian Tropical Research Institute.)



Fig. 14.06 A notably rare neotropical forest bird. Factors thought to influence the rarity of the Banded Ground-Cuckoo (*Neomorphus radiolosus*) include low fecundity, particular habitat requirements (intact, primary, humid, mid-elevation tropical forest), dependence on large prey, and hunting by humans. Much of its original range has been destroyed via logging and habitat alteration. (Photograph by Glenn Bartley.)

species that occurs across different habitats or sites within a region. The beta diversity of birds is most often estimated using indices that focus on the turnover of species among habitats. **Gamma diversity** is the total number of species within a region, summing together the different birds found at any site or any habitat. It is most commonly based on a simple regional species list.

Patterns of alpha diversity can be explored and compared using standardized censuses focused on single habitat types. For example, small plots of forest in eastern North America generally support 18–23 bird species, whereas similarly sized forest plots in western North America have only 15–16 species. However, the overall abundance of birds on these plots is quite similar. Marshes support few species (averaging 8.5 per site) but have among the highest total abundances, and western riparian woodlands support both a large number of species (21) and the highest overall abundances of birds of all North American habitats.

A return to the comparison of the landbirds of Chile and the California coast (USA) shows how the three types of diversity interact. Although far apart, these two regions are strikingly similar in their physical geography and climate: both are isolated from the rest of their continent by a long range of tall mountains, both have substantial areas of desert, and both have coastal regions with a similar Mediterranean-type climate. The total species lists (gamma diversity) of breeding landbirds in these regions are also very similar, as are the alpha diversities of individual habitats within them. However, the species turnover between habitats is much lower in Chile than in coastal California; that is, individual species in Chile are less habitat-specific, and thus different habitats in that region tend to share more of the same species. Chile's overall diversity is comparable with that of coastal California because Chile's species are more geographically restricted, so there are more subregions with large differences in the composition of their species.

14.3 Patterns of species diversity

Species richness follows some well-documented worldwide patterns often referred to as species **diversity gradients**. Overall, bird species richness decreases markedly with distance from the equator, at higher elevations in mountains, and on smaller and more isolated islands and land masses.

14.3.1 Latitudinal gradients

Overall, bird species richness is much greater in the tropics than in the temperate zone and Arctic (Box 14.02). For example, Colombia holds the record for the country with the greatest number of birds: with nearly 1900 species, it has about twice the number of species as the USA and Canada combined. Likewise, Cameroon has a species list of more than 900 birds, whereas Sweden, a country with a similar land area, has only about 480 (Fig. 14.07).

Box 14.02 Regions with the greatest bird diversities

For many years, a 97-hectare study plot at the Cocha Cashu Biological Station in Peru's Manu National Park held the world record for the highest avian alpha diversity, with a carefully documented list of 319 species (Terborgh et al. 1990) (Fig. 14.B2.01). Recent surveys at a few other sites in Peru and Ecuador show that they likely have similarly high levels of avian richness (Blake and Loiselle 2009; Bass et al. 2010). At a slightly broader scale, species lists approaching 600 birds have been recorded within a few square kilometers in the Tambopata National Reserve in southeastern Peru, and in Yasuní National Park in eastern Ecuador (Bass et al. 2010). Many other unexplored sites in this general region probably host equivalently high, or even higher, diversities of birds.

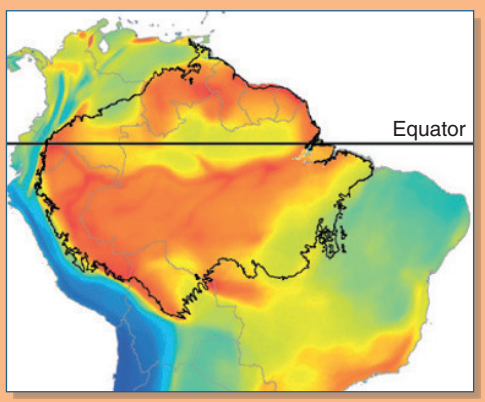


Fig. 14.B2.01 Species richness throughout northern South America. This heat map of avian species richness represents relative species diversity with a color gradient: warmer colors represent more species diversity. The region where the Peruvian Andes meet the lowland Amazon rainforest is thought to support the highest avian species diversity on earth. (From Bass et al. 2010. © 2010 Bass et al. CC-BY-2.5.)

Gamma diversity: the overall species diversity across all the sites and habitats within a broader region.

Diversity gradient: a consistent change in species richness along some environmental gradient.

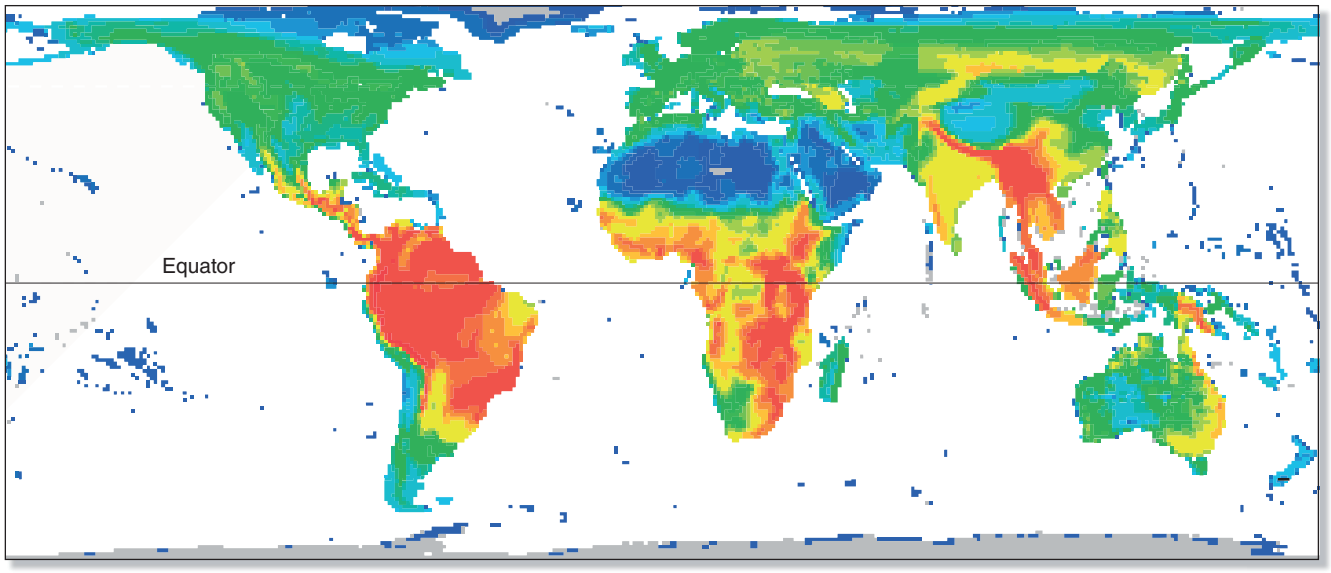


Fig. 14.07 Avian species richness around the world. This heat map depicts bird diversity with a color gradient: warm colors for high richness and cool colors for low (less than 10 species in dark blue areas, around 150 in lime green areas, and over 950 in deep red). (From Orme et al. 2006. © 2006 Orme et al. CC-BY-2.5.)

The general latitudinal gradient in species diversity seen in birds is found in many other groups of organisms, including mammals, trees, and ants (to name a few), but it is not universal. Seabirds, for example, tend to reach their peak diversity at mid-latitudes. Likewise, many shorebirds and other species that thrive in coastal and estuarine habitats tend to reach their breeding season peak diversity in the far north and their peak winter diversity at mid-latitudes. Despite these exceptions, the increase in diversity towards the tropics is dramatic in most avian groups, and particularly pronounced in forested habitats.

Many hypotheses have been advanced to explain the greater species richness in the tropics. These ideas can be divided into two general groups: (1) those that propose long-term evolutionary explanations for how the processes of speciation, extinction, and dispersal generate higher tropical diversities; and (2) those that propose ecological explanations for how tropical habitats can allow more species to coexist at any one time. These explanations are not mutually exclusive, because many of these evolutionary and ecological factors likely act in concert to increase tropical diversity.

Among the evolutionary explanations, one possibility is that tropical environments have been more stable over the past several million years, in comparison with the more dramatic climatic shifts experienced by temperate regions during the glacial cycles of the Pleistocene. This stability of tropical habitats might reduce the extinction rates of the birds in these areas. However, the stability of the tropics is only relative: the tropics, too, have experienced large swings in precipitation and even in temperature. Under cooler, drier conditions, when savanna prevailed in many more tropical areas than it does today, remnant regions of forest (termed Pleistocene **refugia**) remained intact. Because these forested refugia were isolated from one another, they may have allowed many tropical bird populations to start the process of speciation (Chapter 3). The Pleistocene refugia hypothesis was popular for several decades in the late 1900s, but it has fallen somewhat out of favor as the prime driver of high tropical bird diversity, primarily because DNA-based estimates of the ages of tropical birds often show that closely related species began to split long before the Pleistocene.

Some researchers have argued instead that speciation may proceed more rapidly in the tropics, perhaps because the sedentary lifestyle of many tropical birds leads to reduced dispersal and hence reduced gene flow (which tends to work against species formation). Indeed, experiments have shown that many tropical forest species, particularly understory species, are hesitant to cross even the smallest barriers (such as rivers); this tendency also might promote their speciation (Moore et al. 2008). In contrast, some genetic studies have countered this hypothesis by demonstrating that avian speciation sometimes occurs faster in temperate zone groups of birds. Tropical diversity

Refugia: geographic regions that remained relatively unaltered by past changes in climate or other environmental shifts, and which therefore supported populations of organisms that were lost in the surrounding regions.

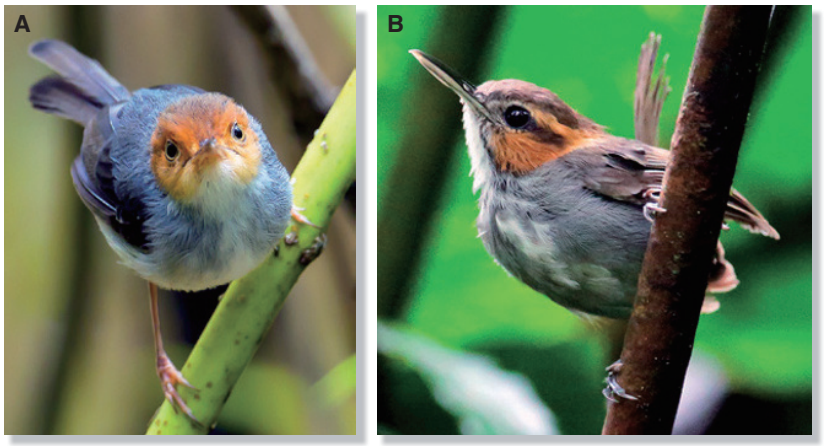


Fig. 14.08 Tropical microhabitat specialists. (A) The Ashy Tailorbird (*Orthotomus ruficeps*) of Southeast Asia and (B) the Tawny-faced Gnatwren (*Microbates cinereiventris*) of the neotropics both occupy dense vine tangles, a microhabitat found commonly in tropical forests. (Photographs by: A, Jason Tan; B, Nicholas Athanas.)

may still be higher if extinction rates are also disproportionally higher in the temperate zone, so that tropical diversity builds up relative to temperate environments where there is more turnover of species over time (Weir and Schluter 2007).

These evolutionary considerations can explain how a greater number of species might occur in a tropical region, but they do not provide insights into how so many species can coexist in a single habitat or at a single site. Several ecological factors in tropical forests seem to contribute to their high local diversities of birds. First, the physical structure of a tropical forest is highly complex. The high diversity of forest tree species contributes to this complexity, but perhaps even more important is the abundance and diversity of epiphytic plants and lianas. Entire groups of bird species specialize on microhabitats that are present only in the tropics, such as the deep vine tangles used by the Ashy Tailorbird (*Orthotomus ruficeps*) in Southeast Asia (Fig. 14.08A) and the Tawny-faced Gnatwren (*Microbates cinereiventris*) in the neotropics (Fig. 14.08B)—the two species look similar but are only distantly related.

More generally, the food resources available in the tropics often allow birds to evolve highly specialized ecologies. For example, many tropical forest plants have fruits that are dispersed and flowers that are pollinated by birds, and in many tropical habitats, fruit and nectar are available throughout the year to specialized avian frugivores and nectarivores. Similarly, the year-round activity of army ants provides a foraging opportunity for another specialized set of birds (Chapter 8).

14.3.2 Habitat change and avian communities

Biological communities change in structure and composition in predictable ways as they develop on newly available land or reform after a major disturbance. For example, at most latitudes, a forested area cleared for agriculture and later abandoned progresses from an old field dominated by grasses and forbs, to a shrub or sapling stage, and finally to a forest. Even at the forest stage, fast-growing but less competitive tree species eventually give way to old-growth species. Many other kinds of disturbance, such as periodic fires, are natural components of ecosystems; some bird species thrive in certain stages of a habitat's successional cycle (Fig. 14.09).

Where human-caused or natural disturbances are common, bird species that rely on mature habitats will be extirpated. Similarly, bird species that thrive in early

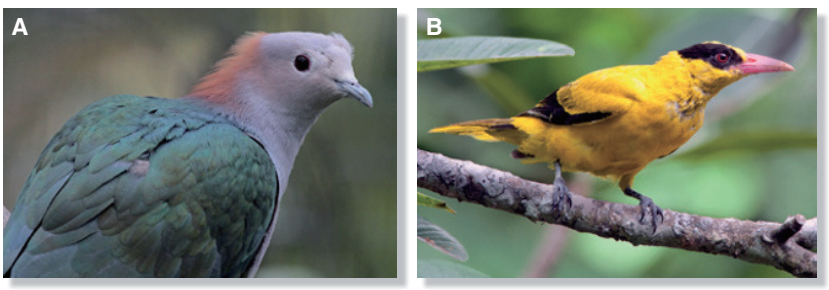


Fig. 14.09 Post-disturbance colonizers. (A) Green Imperial-Pigeons (*Ducula aenea*) and (B) Black-naped Orioles (*Oriolus chinensis*) often colonize regenerating successional habitat on Asian islands where natural disasters—such as volcanic eruptions, floods, and fires—have wiped out most or all existing flora and fauna. (Photographs by: A, Dick Daniels, https://commons.wikimedia.org/wiki/File:Green_Imperial_Pigeon_RWD5n.jpg. CC BY-SA 3.0; B, Mohamad Zahidi.)



Fig. 14.10 An early successional habitat specialist. Kirtland's Warblers (*Setophaga kirtlandii*) require newly regenerating jack-pine forests to breed. Natural forest fires historically kept trees in an early successional stage. However, the Kirtland's Warbler is now endangered, in large part due to the recent suppression of fires in north-central North America. (Photograph by James D. Ownby.)

successional habitats will not occupy the same area once it passes a desired successional stage. For example, the endangered Kirtland's Warbler (*Setophaga kirtlandii*) of North America can breed only in jack-pine stands that are 5–20 years old (Fig. 14.10). This warbler underwent a disastrous decline during a long period of active fire prevention during which its required young pine habitat grew too old to provide good breeding conditions for the warbler. Other bird species that are restricted to flammable habitats likewise rely on fire to regenerate essential resources. For example, surveys across hundreds of points in western conifer forests have shown that in this part of its range, the Black-backed Woodpecker (*Picoides arcticus*) is an extreme fire specialist that very rarely is found far from recently burned stands of timber (Hutto 2008).

14.3.3 Landscape effects on bird diversity

Similar habitats can host different numbers of bird species, depending on factors such as the size and shape of the habitat patch and the nature of the surrounding area. To a large degree, this landscape effect stems from the general species–area curves discussed earlier in this chapter: larger patches support more birds and/or a greater diversity of habitat, and for both reasons they are more likely to contain rare species. Individual bird species also show varying degrees of **area sensitivity**, as they are not able to persist in habitat patches below a certain size. The effects of area sensitivity are apparent in most areas of the world where small habitat remnants hold only a subset of the birds that would be expected to occur there if those patches were instead part of a more continuous block of intact habitat.

Some of the best evidence for how birds respond to habitat reductions comes from experimental studies of fragmentation, such as long-term research in a series of artificial forest fragments near Manaus, Brazil. Starting in 1980, a team of scientists subdivided the previously continuous forest at this site into a series of smaller forest patches ranging in size from 1 to 100 hectares. They then closely monitored the bird communities within each patch. As expected, the smaller patches suffered much greater levels of bird extinction than the larger patches, starting almost immediately after their fragmentation and continuing on through the next several decades (Stouffer et al. 2009).

Fragmentation effects on birds vary in intensity in different regions. Although they generally are severe in tropical forests around the world, they tend to be less of an issue in Eurasian than in North American forests, and less severe in boreal coniferous forest than in deciduous forests. Fragmentation effects are not restricted to forest, and have been documented for a variety of habitats from desert to salt marsh. For example, in a region of southern France where the landscape is a mix of pine forests and savanna patches, grassland specialists such as the Sky Lark (*Alauda arvensis*) and Northern Wheatear (*Oenanthe oenanthe*) show strong declines when their habitat is fragmented, whereas habitat generalist bird species are less affected (Caplat and Fonderflick 2009).

Fragmentation is not always bad for birds, and many habitats are naturally fragmented. Where the avifauna has evolved in a natural habitat mosaic, the effect of human-caused fragmentation may be less drastic. For example, the bird assemblages in cloudforests of Central America and the Andes—which often occur in isolated patches on mountain slopes—are thought to be more resilient to fragmentation than the assemblages of nearby lowland tropical forests.

14.4 The niche: a fundamental unit in community ecology

The **ecological niche** concept was first introduced in the early 1900s by Joseph Grinnell, an influential California ornithologist (Grinnell 1917). It holds that the ecological niche is the ultimate distributional or spatial unit occupied by a species, to which the species is held by limitations such

Area sensitivity: refers to bird species that are found only in habitat patches larger than some critical size.

Ecological niche: the set of biotic and abiotic conditions that allow a species to occur; sometimes also used in the sense of the role of an organism within its ecosystem or environment.

as climate, kind (and amount) of food, nesting sites, and cover. The niche concept became widely used by ecologists, leading to the now famous (but far less poetic) definition that a niche is an "*n*-dimensional hypervolume of viable interactions between organisms and their environments" (Hutchinson 1959).

The ecological niche thus comprises the place where birds live and the resources they use. Biological considerations take the niche concept beyond this simple level of description and imbue it with additional complexity. A bird species might be capable of making a living in a broader range of habitats or of consuming a broader diet were it not for the presence of predators, competitors, and parasites—both avian and non-avian. The complete potential niche, unaffected by these interactions with other species, is referred to as the **fundamental niche**. A bird species' real-world niche that is circumscribed by all its interactions with other species is known as the **realized niche**.

14.4.1 Niche overlap and niche breadth

Niche breadth is a measure of a bird's level of ecological specialization. A species with a narrow niche breadth is a specialist, and one with a broad niche breadth is a generalist. Niche breadth can be measured for a particular resource (for example, diet), and a bird species can be a specialist in one area and a generalist in others. Most commonly, this spectrum is used to describe the variety of foods eaten by a certain bird species (Chapter 8), or the range of habitats in which it occurs. Closely related bird species can differ notably in their level of specialization; for example, the rare Rufous Twistwing (*Cnipodectes superrufus*) of Peru, Bolivia, and Brazil is an extreme habitat specialist that is only found in dense *Guadua* bamboo patches (Fig. 14.11A). In contrast, a close relative, the Brownish Twistwing (*Cnipodectes subbrunneus*), is a habitat generalist common throughout much of Central and South America (Tobias et al. 2008) (Fig. 14.11B).

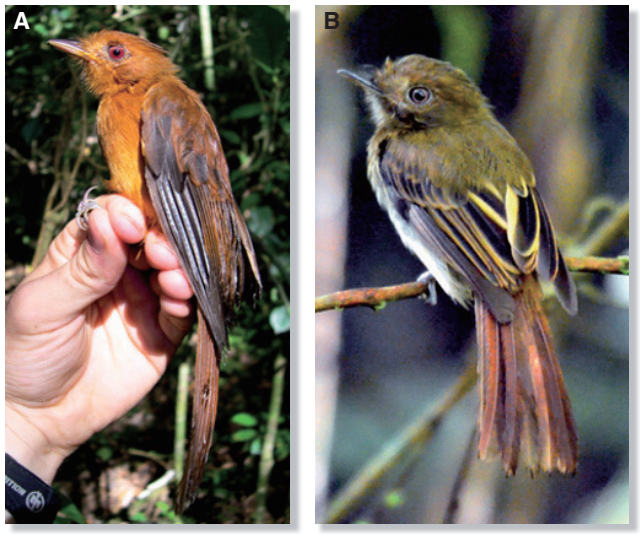


Fig. 14.11 Close relatives can differ in niche breadth. (A) The rare Rufous Twistwing (*Cnipodectes superrufus*) is a habitat specialist restricted to mature bamboo patches, while (B) the closely related Brownish Twistwing (*Cnipodectes subbrunneus*) is a common habitat generalist found across most of Amazonia. (Photographs by: A, Daniel J. Lebbin; B, Yvonne Stevens.)

The specialist/generalist concept does not necessarily account for how readily birds change resource use in response to changed conditions. So the specialist/generalist contrast is related to—but is not the same as—a contrast between plastic and stereotyped behaviors. A behaviorally plastic bird species will readily change its foraging behavior, nest site preference, or some other aspect of its ecology in the face of habitat or climate change, whereas a behaviorally stereotyped species remains relatively constant in its preferences. The Cocos Finch (*Pinaroloxias inornata*) discussed in Chapter 8 is a classic example of a species with highly plastic foraging behavior, in which individual finches adopt a range of foraging behaviors even within the same habitat.

No single niche breadth strategy is intrinsically better than another. Under appropriate conditions, specialist birds may outcompete other species by being very good at what they do. If conditions change, however, a decline in their preferred food item or essential habitat feature may place specialist species at high risk of local or complete extinction. There are many unfortunate examples of specialized birds that have gone extinct following human-caused changes to their environment. For example, the remarkable Huia (*Heteralocha acutirostris*) specialized on digging grubs from decaying trees in old-growth forest; the clearing of most of the New Zealand forest contributed to its extinction in the 1900s (Chapter 8). Last seen in 1927, the Paradise Parakeet (*Psephotus pulcherrimus*) (Fig. 14.12A) of south-central Queensland and northern

Fundamental niche: the full range of environmental conditions and resources a bird could possibly occupy and use without regard to other limiting biological factors such as the presence of competitors, pathogens, or predators.

Realized niche: the subset of its fundamental niche that a species actually occupies.

Niche breadth: the range of resources utilized by a species; a species with wide niche breadth is referred to as an ecological generalist, whereas a species with narrow niche breadth is termed an ecological specialist.

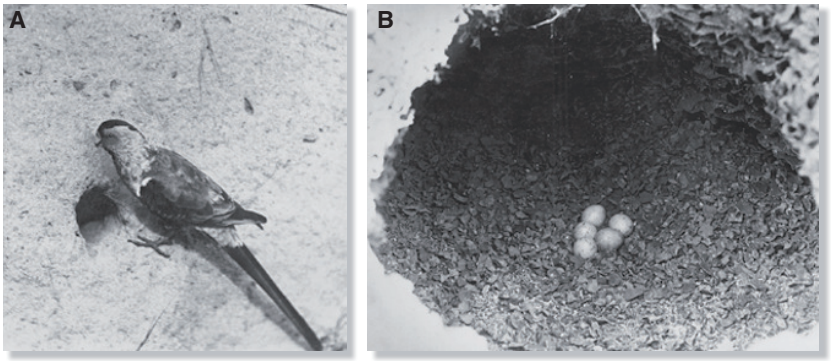


Fig. 14.12 Presumed extinction of an Australian grassland specialist. (A) This is the last known photograph of the extinct Paradise Parakeet (*Psephotus pulcherrimus*), taken in the wild at Burnett River, Queensland in 1922. The individual is perched at (B) its nest entrance located in a hollowed-out termite mound, a very specialized substrate. Humans are largely to blame for destroying its breeding habitat. (Photographs by Cyril Henry H. Jerrard, courtesy of the National Library of Australia: A, nla.pic-vn3124459; B, nla.pic-vn3125063.)

New South Wales (Australia) is considered extinct due to its obligate dependence on a specific grassland community and specialized nesting substrate. Human habitat alteration through altered burn regimes, cattle grazing, and agriculture destroyed the wild grasses that provided the species' principal food (grass seed) and altered the landscape such that old termite mounds (necessary for breeding) were no longer available (Fig.14.12B). Hunting for the colorful plumes of this species exacerbated the population decline.

Generalists are "jacks of all trades and masters of none." However, the ability to move readily between habitats and consume a wide variety of foods allows generalists to persist under conditions where specialists perish. Habitats with a greater number of relatively constant resources will tend to support more specialists than habitats with fewer resources that fluctuate markedly in their availability. Some of the most impressive avian generalists are urban invasive species such as the Rock Pigeon (*Columba livia*), House Sparrow (*Passer domesticus*), and European Starling (*Sturnus vulgaris*), which have all spread around the world and now occur in thousands of cities with highly variable climates and food resources.

The degree to which two species share resources (as compared with their total potential resource use) is known as their **niche overlap**. Species that have high niche overlap are likely to compete for similar resources (Box 14.03). This pattern of partially overlapping niches occurs, for example, on mudflats where several different shorebird species forage together (Fig. 14.13). In these instances, the dominant species often occupies a niche that is wholly contained within the niche of the subordinate species. For example, in western North America, the nesting habitat of the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) is wholly contained within the preferred nesting habitat of the Red-winged Blackbird (*Agelaius phoeniceus*) (Fig. 14.14). In places where both species occur, the Yellow-headed Blackbird dominates the Red-winged Blackbird, excluding it from the best nesting sites: cattail marshes with standing water. The male Yellow-headed Blackbirds, perhaps because of their larger size (80 versus 64 grams), are able to dominate and exclude both sexes of the other species (Orians and Willson 1964).

In competition for resource exploitation, the impact that one species has on another is strongly related to their niche overlap. However, developing a standardized way of estimating niche overlap between species has vexed avian ecologists for decades. Birds seldom compete over resources along a single, easily described range (such as prey size or foraging height). Instead, they can share or differentiate the resources they use by a huge variety of variables, including habitat, vegetation level, microhabitat searched, plant type preferred, prey type preferred, prey size, and many more. These variables often are referred to as **niche axes**. Examined from this perspective, niche overlap is a measure of similarity along one or many of the possible axes. Researchers most commonly calculate niche overlaps using statistical approaches that incorporate many variables at once, as in the comparison of the foraging niches of three penguin species on Ardley Island in Antarctica (Wilson 2010) (Fig. 14.15). Careful tracking of foraging penguins showed that although the three species feed on similar prey, they generally do so at different times and places, and hence their niche overlap in time and space is surprisingly low: they forage together in ways that might lead to direct competition less than 10% of the time.

Niche overlap: the extent to which two species use the same resources or occur in the same habitats or locations.

Niche axes: particular components of the environment that influence whether a species is present or absent, or how it interacts with members of the same or other species.

Box 14.03 Shorebird niches on a tidal mudflat

In many places, mudflats attract high densities of a dozen or more shorebird species. These concentrations of shorebirds bring out the spotting scopes of inquisitive birders who peer intently at the length of the birds' legs and the shapes of their bills. How is it possible that so many birds of so many species can forage successfully in the same habitat?

Among the diverse array of shorebird species concentrating along estuarine shorelines, a closer examination shows a remarkable diversity of feeding adaptations (Chapter 8) involving differences in behavior, sensory modalities, and morphology. These differences are combined with habitat separation—some species prefer mudflats, others prefer beaches, still others concentrate in shallow water in impoundments and tidal pools—so that each species has a distinct niche. Body size is particularly important in determining where particular shorebirds forage and what foods they consume.

Along with body size, leg length differs profoundly among shorebirds, determining more than any other feature where in the intertidal zone a shorebird can forage. Short legs allow efficient and rapid movement on mud or sand, and are found in many of the sandpipers and plovers that hunt for prey on solid surfaces. Long legs allow species to wade into water: the longer its legs, the deeper a bird can forage. Along with leg length, bill length affects how deeply into the water or mud a bird can probe. In general, bill length and leg length are correlated: surface foragers (such as plovers) who use visual cues have the shortest bills, whereas wading shorebirds (dowitchers, curlews, and godwits), who use probing techniques, have longer bills. Probing shorebirds locate their prey tactilely, aided by a sensory organ near the bill tip, and often have long, downturned or upturned bills. Curved bills allow flexibility in probing burrows made by shrimp, crabs, and shellfish, and increase the overall volume of mud, sand, or water sampled. These and other morphological and behavioral differences allow shorebirds to forage on different prey resources within the same beach or mudflat (Chapter 8).

Although a long history of competition has shaped these species' specializations on different food items and places in the tidal gradient, a number of fairly similar species often forage side by side. Has limiting similarity been suspended in these birds, or do they differ in subtle ways? The answer to both questions probably is "yes." A number of studies have shown that seemingly similar shorebird species (such as several species of "peeps," small sandpipers in the genus *Calidris*) differ subtly in where they search for prey.

Migrating shorebirds often form ephemeral congregations at abundant resources, situations in which interspecific competition may not be sufficiently strong to keep any shorebird in the area from joining the others at the water's edge. A food source that is in such ample supply that it does not limit the number of birds or species using it is termed "super-abundant." Just how super-abundant or limiting tidal invertebrates are is a continuing area of research for shorebird ecologists.



Fig. 14.13 Niche overlap and resource competition. Ruddy Turnstones (*Arenaria interpres*; red arrow), Sanderlings (*Calidris alba*; yellow arrow), and Semipalmated Sandpipers (*Calidris pusilla*; black arrow) actively hunt for insects, crustaceans, and worms on the same crowded Peruvian shoreline. Each species has a slightly different foraging morphology and behavior, reducing their competition for resources. (Photograph by Eveling Tavera Fernández.)

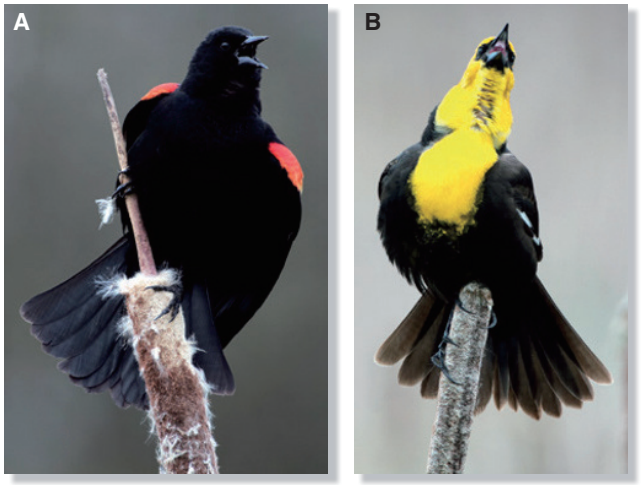


Fig. 14.14 Competitive dominance in overlapping niches. Where their ranges overlap, (A) Red-winged Blackbirds (*Agelaius phoeniceus*) are outcompeted for nesting habitat by (B) Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), which are larger and more aggressive. (Photographs by Richard Cameron.)

14.4.2 Competitive exclusion and limiting similarity

The **competitive exclusion principle**, which holds that no two species can occupy identical niches indefinitely without one going extinct, is an important extension of the niche concept. This principle has had many proponents since the beginning of the twentieth century, but California ornithologist Joseph Grinnell proclaimed it succinctly in 1917: "It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche requirements."

The competitive exclusion principle did not initially lead to especially productive insights into avian ecology, for two reasons. First, for birds and other mobile organisms with complex life histories, the important components of the niche must be measured at the particular time of year when the population is most limited. Additionally, the degree to which populations experience limitation or regulation (Chapter 13) varies from year to year in response to fluctuations in climate, food supply, and predator populations. Accordingly, some ecologists believe that competition may be important only rarely, when conditions are particularly bleak. Second, observant ornithologists are almost always able to detect some ecological difference between two bird species, and the question then becomes how similar two species really must be to violate this principle. Nonetheless, in the decades following the introduction of the competitive exclusion principle, many field studies focused on the

Competitive exclusion principle: the proposition that two species requiring exactly the same set of resources will compete intensely and therefore will not be able to coexist in the same locations.

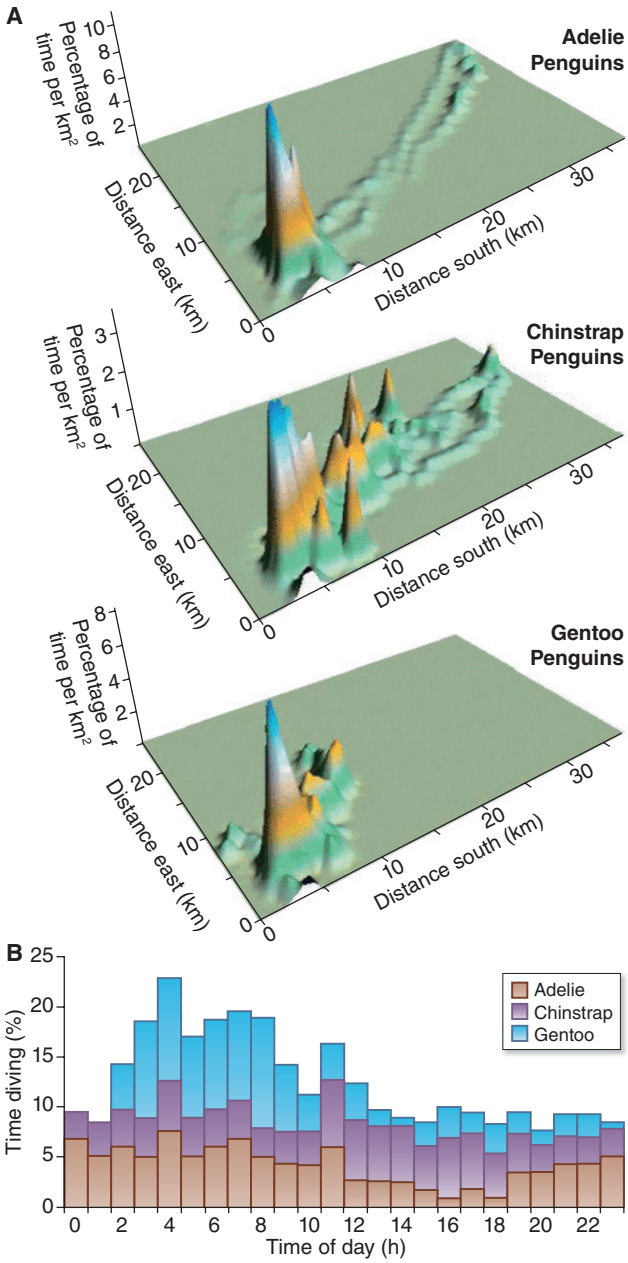


Fig. 14.15 Foraging niche overlap. Although Adelie (*Pygoscelis adeliae*), Chinstrap (*Pygoscelis antarcticus*), and Gentoo (*Pygoscelis papua*) Penguins hunt similar prey, they partition foraging effort in space and time to decrease resource competition. (A) These maps illustrate the relative time spent foraging (diving) per location for each species. All three breed on Ardley Island, located at point 5, 5. (B) This graph demonstrates that each species has a different diving strategy based on time of day. (From Wilson 2010. Reproduced with permission from John Wiley and Sons.)

patterns of niche differentiation in coexisting bird species, and this work generated many interesting insights into just how crudely or finely birds divide up their habitats and resources.

The competitive exclusion principle focuses on competitive interactions between species in its definition of a species' ecological niche. Another approach is to define the niche in terms of the critical aspects of the bird's environment by examining which of the many possible environmental factors seem to define a species' distribution and abundance across a number of different habitats. For example, Fran James and her colleagues carefully analyzed the distribution and density of Wood Thrushes (*Hylocichla mustelina*) on study plots distributed over a large portion of the species' breeding range in eastern North America (James et al. 1984). The researchers were able to identify common features of the niches that supported the highest densities of Wood Thrushes, including a low density of understory shrubs, a tall tree canopy, and a well-developed layer of leaf litter on the forest floor.

14.4.3 Ecological guilds

Groups of birds with similar niches are known to ecologists as **guilds**, a concept developed by Richard Root (1967) as part of his studies of the Blue-gray Gnatcatcher (*Polioptila caerulea*) in a Californian oak woodland. Root wanted to compare that species' foraging ecology with the foraging behavior of other local birds that might be its potential competitors. Previous studies of avian competitors had generally focused on birds within the same taxonomic family, but Root reasoned that more distantly related birds may compete over their use of the same resources. Borrowing the concept of the trade guild (organizations of craftsmen doing the same job), he defined an ecological guild as a group of species that share the same basic foraging strategies and resources. At Root's California study sites, various species of wood warblers and vireos—distantly related groups of small, foliage-gleaning birds—were grouped together with the gnatcatcher in a "foliage-gleaning" guild of insectivores.

The guild idea has since been broadened to include other aspects of habitat use, such as nest sites. For example, the hole-nesting guild in a well-studied primeval forest in Poland comprised 31 bird species, of which nine species (mostly woodpeckers) excavated their own cavities and the remaining species adopted pre-existing cavities (Wesołowski 2007). One benefit of defining guilds in this way is that studies of ecological interactions can be undertaken for a logically selected subset of species within an entire assemblage. For example, a complete guild approach to the study of canopy foliage-gleaning birds in a North American spruce forest would not be arbitrarily restricted to a single genus of wood warblers (as in Box 14.04), but also would include local species of kinglets, vireos, and chickadees. Divvying up species into guilds also provides researchers with a quick assessment of overall diversity, abundance, and biomass of the birds consuming different food resources. Habitats can be characterized by their dominant guilds as well: forests are often dominated by foliage-gleaning birds, whereas grasslands are likely to host many ground-foraging granivores.

14.5 Interspecific competition

Interspecific competition occurs when individuals of two or more bird species simultaneously use a resource—such as food or nest sites—that are in short supply. Competition can occur when one species simply is better at obtaining the resource and thereby reduces the availability of the resource below the level that can sustain the less proficient species. Ecologists refer to this process as **exploitation competition**. In contrast, **interference competition** occurs when one species interferes with the ability of other species to gain access to a critical resource, usually through aggression and dominance.

14.5.1 Exploitation competition

Through efficient resource use, one bird species may reduce the abundance of a resource to a level that is too low to support a less efficient species. However, if the species have different specializations, each may be able to concentrate on and competitively exclude potential competitors from a particular set of resources.

Flower nectar is one type of food that is particularly susceptible to exploitation competition when the first bird to visit a flower takes most of the nectar and leaves little for later visitors (Box 14.05). Nectar is relatively easy to measure in real flowers and to provide experimentally using artificial feeders. Researchers have taken advantage of

Guild: a group of species that use components of their habitat or resources in a similar way; for example the "insectivore guild" or the "hole-nesting guild" of a woodland habitat.

Interspecific competition: this occurs when birds of different species compete for the same resources.

Exploitation competition: competition among species that results from indirect interactions, usually when both or all species require the same set of limited resources such as food or nest sites.

Interference competition: competition among individuals or species in which they interact directly—often via aggression—over access to the same resources.

Box 14.04 Boreal forest songbird communities

Spending a summer day in a boreal forest in northeastern North America is an exciting birding experience, because up to eight species of colorful wood warblers can be seen foraging vigorously for insects in the needle clusters of the spruce and fir trees that dominate conifer stands. As a graduate student, the pioneering community ecologist Robert MacArthur asked: Does the presence of so many ecologically similar birds in the same place, often even in the same trees, violate the competitive exclusion principle? This principle holds that two species cannot occupy the same niche in the same place. He focused his studies on five species of the genus *Setophaga* under the assumption that, with their close evolutionary history and similar morphology, species in the same genus are more likely to experience mutual effects of competition for food resources (MacArthur 1958).

By quantifying the details of foraging behavior and location, MacArthur was able to demonstrate that, even in this extreme case of "species packing," subtle but consistent differences minimized overlap in the locations within trees where warblers searched for prey. In particular, by dividing trees into height strata, and branches into zones of distance from the trunk, he was able to delineate each species' preferred foraging site (Fig. 14.B4.01). Although foraging zones overlapped, each species nonetheless preferred a different part of the tree for foraging.

MacArthur also recognized that the presence of so many species could not be explained entirely by this fine-scale partitioning of foraging sites and subtle differences in search behavior. For example, two species—the Cape May Warbler (*Setophaga tigrina*) and the Bay-breasted Warbler (*Setophaga castanea*)—were not present every year in his primary study area. These species were known to be strongly associated with outbreaks of a major defoliating insect, the spruce budworm. These "budworm species" recruit to outbreak areas in large numbers and often lay very large clutches to take advantage of the feeding bonanza. In contrast, populations of other species of *Setophaga* may decline in the face of the budworm outbreaks. MacArthur invoked the concept of "fugitive species" as a mechanism for increasing local diversity, noting that these species move from site to site to take advantage of a temporally available habitat or food source.

MacArthur's study was one of the first detailed investigations into resource partitioning among ecologically similar birds. In the decades that followed, many studies of other groups of ecologically similar species adopted his approach of careful analysis of foraging behavior. For example, Douglass Morse continued to explore the wood warblers of Maine, where he found that the foraging locations of males and females usually differ, often by as much as the foraging locations of separate warbler species

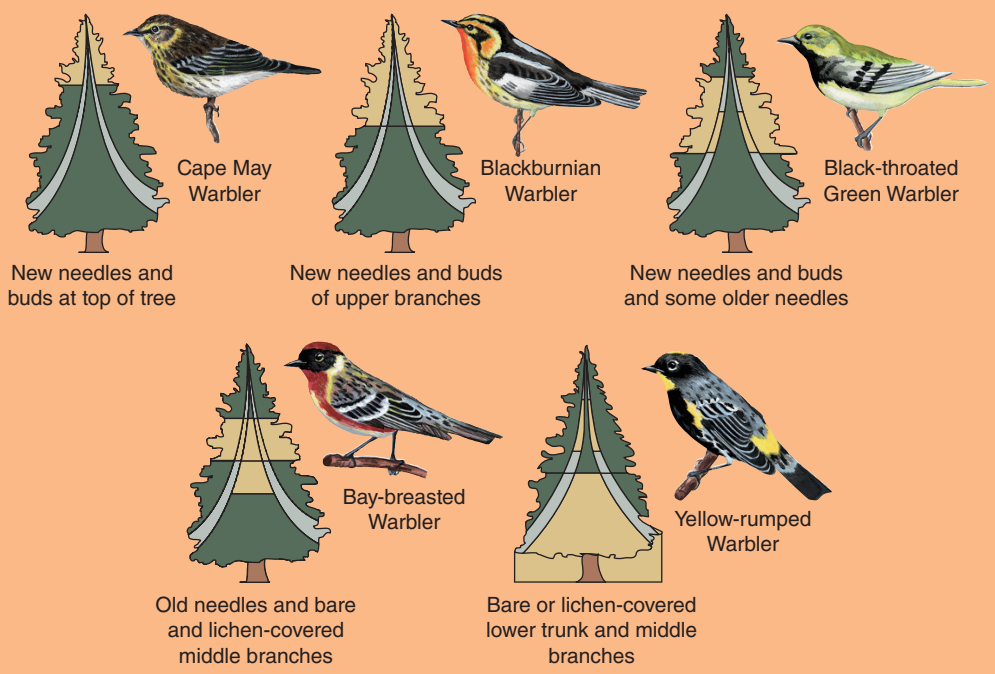


Fig. 14.B4.01 Niche partitioning in North American warblers. Each warbler illustrated here spends about 50% of its foraging time in a species-specific area of a conifer tree (orange shading). During the remaining time, foraging niches of each species partially overlap. (From Enger et al. 2011. Reproduced with permission from McGraw-Hill.)

Continued

(Morse 1989). This difference probably is related to the role that each sex plays in reproduction, with males busily maintaining territories and females foraging closer to the nest. Second, Morse demonstrated that aggression and interference competition was important in determining where birds foraged, and he documented a predictable dominance hierarchy among the species. Finally, and perhaps most importantly for the competition hypotheses, he studied the warbler assemblages on several small islands that contained only a few of the species present on the nearby mainland. These comparisons showed that the warbler species shifted and expanded their foraging zones when behaviorally dominant competitors were absent.

Box 14.05 Battle of the bills: interspecific strife in hummingbirds

Hummingbirds are universally captivating. They have such a distinct way of life that, despite their high energy demands, competition with other birds is minimal. However, nectar is a rich, renewable, and patchily distributed resource, and competitive strife between hummingbirds, both within and among species, is rampant.

Nestled in the foothills of the Cordillera de Tilarán in Costa Rica, the community of Monte Verde is surrounded by tropical pasture and abuts a large cloudforest reserve. This mosaic of habitats makes it a famous destination for birders, and its diversity of hummingbirds is a star attraction. Shaped by millions of years of coevolution with the high diversity of flowering plants, and honed by intense competition, each of the 13 core hummingbird species of second-growth successional habitats has developed a unique strategy for cornering its share of the readily depleted nectar resource. Mobility, aggression, and morphological specialization—particularly evident in diverse bill shapes—combine to form a mosaic of feeding strategies that allow coexistence (Fig. 14.B5.01). Ornithologists have described six different strategies: high-reward trapliners that cover long distances at high speed; low-reward trapliners; territorialists that defend flower patches; large, marauding territory parasites; smaller, sneaky filching species; and generalists that move among many flower types.

To a large degree, these hummingbird strategies correspond to flower types. Characterizing floral characteristics, dispersion, and the amount of nectar produced, researchers have identified five flower types with different foraging strategies:

1. Dispersed rich flowers, such as isolated *Heliconia* flowers, which often have a long, tubular shape that favors long-billed hummingbirds and excludes most insects. These favor the high-reward traplining species, such as hermit hummingbirds, with their long, curved beaks.
2. Clumped rich flowers, which tend to grow in areas of disturbance.
3. Dispersed "moderate" flowers with long floral tubes and a moderate amount of nectar, visited by low-reward traplining species with shorter bills.
4. Clumped moderate flowers, which are defended by territorial species that must fend off the territorial parasite species.
5. "Insect flowers" with short corollas that offer small nectar rewards (or produce nectar primarily at night for bats and moths) that are visited occasionally by short-billed, low-reward trapliners and generalist species.

This complex and diverse assemblage shows a complex pattern of exploitative and interference competition and is driven by the coevolution of flower structure, display, and seasonality, on one hand, and hummingbird behavior and morphology on the other.

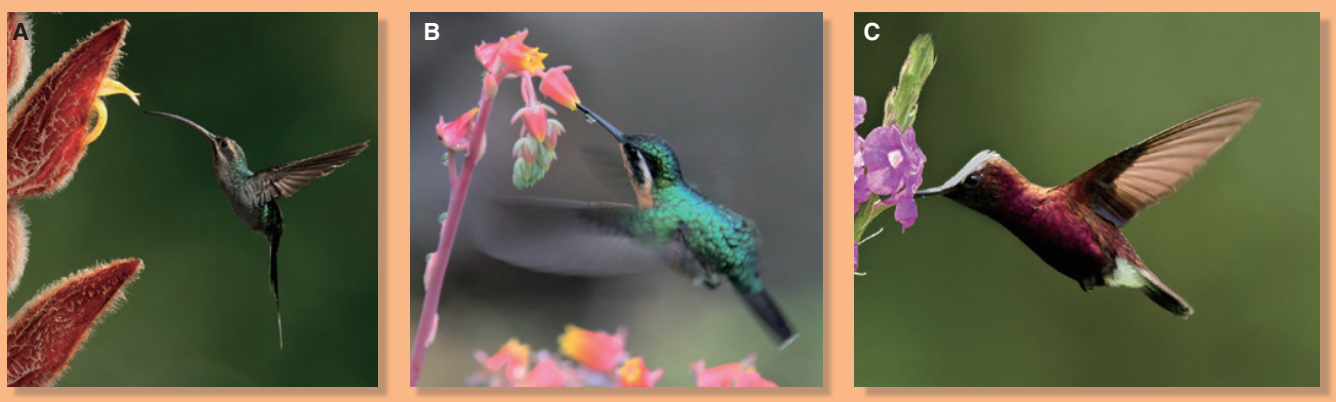


Fig. 14.B5.01 Bill morphology matches foraging preference. (A) Hummingbirds that are equipped with long, decurved bills—such as this Green Hermit (*Phaethornis guy*)—forage for nectar in *Heliconia* flowers; this seamless match is a prime example of coevolution. (B) White-throated Mountain-gems (*Lampornis castaneoventris*) and other species with medium-length, slightly decurved bills prefer flowers with a similar shape. (C) Hummingbirds with short and straight bills, like the Snowcap (*Microchera albocoronata*), typically prefer small, shallow flowers. (Photographs by: A, Steven Metildi; B, Kevin Watson; C, Christopher Jiménez Cordoba.)

these attributes to explore how nectivorous birds such as hummingbirds and sunbirds respond to exploitation competition. For example, Long-tailed Hermits (*Phaethornis superciliosus*) in Costa Rica change their foraging strategy depending on the level of exploitation competition: when competitors are few, individual hermits visit particular flowers at long intervals, thereby allowing the flowers to replenish their nectar. In contrast, when competing hummingbirds are more of a threat, the hermits visit the flowers much more often to increase their access to new nectar (Gill 1988).

Exploitation competition may involve other kinds of animals with similar resource requirements. For example, researchers working in Sicily (Italy) found that breeding Eurasian Blue Tits (*Cyanistes caeruleus*) compete with a small rodent, the common dormouse, for ownership of artificial nest boxes. Particularly in places where boxes were rare, tit breeding success was low in years when dormice were abundant, and vice versa: the dormice did badly in years when tits were abundant (Sarà et al. 2005), because each nest box could be used by only one breeding animal at a time. In the Negev desert of Israel, several species of seed-eating gerbils (small rodents) compete with Crested Larks (*Galerida cristata*) for seeds. Although the gerbils are more efficient than the larks at finding and eating seeds, the larks can coexist with these small mammals because their ability to fly allows them to cover a larger area of sandy habitat to find ephemeral patches of seeds uncovered by the wind (Garb et al. 2000).

14.5.2 Interference competition

When more than one species occurs in an aggregation feeding on the same type of food, the dominant species may gain access to the best food or feeding site by displacing subordinate species. This type of interaction often can be witnessed at a bird feeder, where dominant (usually larger) species can supplant subordinate species from a pile of seeds or a suet ball. The interaction may be subtle, with the subordinate leaving just before the dominant arrives, but the lack of overt fighting probably is an adaptive response by the subordinate to avoid unnecessary injury.

Contrary to what you might expect, dominants do not always try to get first access to a feeder. After a predator (or in the case of a human disturbance, a potential predator) disturbs a feeder, subordinates may return first. In this case, the dominant is ultimately assured of access to the best feeding site but uses the subordinate to "test the waters" for further danger. The subordinate takes the risk to gain access it otherwise would not have when the dominant species is at the feeder.

Interference competition at bird feeders has been particularly well studied in European locations where several species of tits occur. These tit species usually differ conspicuously in their ranks in an interspecific dominance hierarchy (Chapter 9), with some species able to displace others from preferred feeding sites. In one such study site in the mountains of Spain, researchers provided the five local tit species with peanut-filled feeders hung at either safe locations (near dense vegetation with potential hiding places for tits) or dangerous locations (exposed sites with no nearby refuge from predators) in the forest (Carrascal and Alonso 2006). The most dominant species, the Great Tit (*Parus major*), used only the safe feeders; the most subordinate species, the Long-tailed Tit (*Aegithalos caudatus*), most frequently used the unsafe feeders. Interference competition among these species explains this pattern, with the more dominant tit species displacing the less dominant species from the best foraging sites.

In birds, some of the most extreme cases of behavioral dominance of one species over another involve **interspecific territoriality**. As in the much more common intraspecific territoriality (Chapters 9 and 13), interspecific territoriality involves the active defense of a specific place. The area defended by one species against another can vary from a large plot of land to a single food plant, and the number of excluded species can range from one to many.

The defense of patches of habitat usually occurs between related species. With no strong divergence in foraging behavior or nest ecology, the species may not be able to persist except though excluding the other species from the entire area. Such interactions tend to be found in habitats with relatively simple structure (grasslands, marshes, or shrubby second growth) or when the species involved are closely tied to a specific stratum within a more diverse habitat (such as ground or bark foragers) (Orians and Willson 1964). Usually there is some habitat segregation, and interspecific territories are defended at the border between habitats. For example, the various species of North American *Empidonax* flycatchers are extremely similar in morphology and behavior, often bedeviling birders trying to identify them. Although most *Empidonax* species have distinct ranges and habitat preferences, some species defend interspecific territories where their preferred habitats come together. For example, the Dusky Flycatcher (*Empidonax oberholseri*) occurs in mixed coniferous woodland in the mountains of California, and the Gray Flycatcher (*Empidonax wrightii*) prefers scrubbier habitats with only scattered trees characteristic of the Great Basin of western North America. At habitat edges, however, the two exceedingly similar species exclude each other from their territories (Johnson 1966).

Interspecific territoriality may play an important role in enforcing sharp distributional boundaries. Among the more than 300 species of birds that occupy vegetation along the Manu River in the Peruvian Amazon, from shoreline pioneer

Interspecific territoriality: aggressive, territorial behavior directed by individuals of one species against members of other species.

Box 14.06 Field studies of a tropical bird community

The first step in understanding the factors that control species diversity and abundance in any assemblage of birds is to develop an accurate estimate of assemblage composition. Interesting questions about assemblages start with data obtained from well-designed censuses, but developing accurate census techniques continues to be a daunting challenge. Nowhere is this difficulty more apparent than in the moist tropical forest habitats that support the world's most diverse avian assemblages.

Surveying and censusing birds has proven so difficult that comprehensive species-diversity data are available for only a few tropical sites worldwide. Problems that bedevil tropical forest bird censuses include those that are common to any avian census: Can all the birds be detected reliably? Does the presence of a bird indicate its residency, or is it a dispersing bird or a transient? Is the study plot representative of a particular habitat, and is it large enough to include the complete assemblage, especially the rarest, most wide-ranging, or most patchily distributed species? How many replicate surveys are necessary to detect all birds?

Censusing problems are compounded in tropical forests because their diverse avifauna demands a high level of technical skill in detection and identification. In some of the most diverse regions, birders still are struggling to catalogue all the vocalizations for many rare species. The difficulty is exacerbated by the rarity and patchy distribution of many species. For example, tropical forest avifauna generally shows sharp patterns of vertical stratification, with many canopy species never descending below the outer shell of vegetation of the tallest trees. Furthermore, aside from the diversity of nocturnal birds, a number of tropical forest birds, such as woodcreepers and tinamous, vocalize only for short periods of time before dawn or at dusk. The social systems of tropical forest birds are also extremely diverse, so simple territory mapping of singing birds, the standard operating procedure for censusing temperate zone forests, is not easily applied. For example, in many species of tropical birds, both males and females sing, but in some cases males and females move through the territory separately, so detailed studies of birds with transmitters is required to determine the pair status of seemingly separated birds. Other tropical forest birds are extremely quiet and can be detected only at very short ranges. Lekking species (Chapter 9) offer yet another challenge: although they are conspicuous, simply counting the number of males at a lek may not reflect the number of nesting females, because the sex ratio can be far from 1:1. Birds that follow ant swarms often have overlapping territories, so a number of pairs from a single species can be found at the swarm at any one time. Wide-ranging species that move in flocks, such as many parrots, provide another set of unique surveying problems.

The Cocha Cashu Field Station in the Manu National Park of Peru lies at the extreme eastern edge of the Amazon Basin near the base of the Andes. At this ultra-diverse site, a team of tropical ornithologists undertook one of the most comprehensive efforts to fully describe a tropical forest bird community (Terborgh et al. 1990). The core of their project was spot-mapping territorial birds from an extensive trail system. This survey was assisted by the presence of a large number of previously color-banded birds, which helped to sort out different territories. In addition, the research team used special techniques, including flock following, radio-tracking, and intensive transects, to detect and track many of the species that are difficult to census using standard techniques.

The result of this huge amount of labor was a solid estimate of the number of regular breeding species (295) and additional visitors (74). Besides this astounding level of alpha diversity, they found high levels of beta diversity, with other nearby habitats (such as riverine successional habitat) having many bird species not found on the main study plot. The species richness of this small Amazonian forest plot was up to 10 times greater than in similarly sized plots in temperate forests. However, the total abundance of birds was similar to that found in temperate forests, because each tropical bird species generally is far less common than its temperate zone counterparts. In addition, many tropical species occur sporadically or patchily in small numbers.

Despite the similar abundance, the total estimated biomass of birds at Cocha Cashu was five times higher than is typical of the temperate zone, because the tropical forest supports many more species of large birds, such as currasows, tinamous, and raptors. Needless to say, the Amazonian assemblage was also far more ecologically diverse. A typical temperate zone forest supports primarily small, insectivorous birds during the breeding season, whereas more than 60% of the avian biomass in the Cocha Cashu assemblage comprised terrestrial granivores and large canopy frugivores, guilds that are poorly represented in the world's temperate forests.

scrub communities to primary forest (Box 14.06), Scott Robinson and John Terborgh (1995) found 20 pairs in which related species were divided strikingly between early and late successional habitats. Using song playbacks, they showed that often the larger species approached the playback aggressively, but the smaller species shied away. The pairs of species showing these dominance-related behaviors had the lowest distributional overlap, suggesting

that interspecific territoriality allowed the dominant larger species to control the more productive habitat.

As discussed earlier in this chapter, interspecific resource defense is particularly prevalent among flower-feeding birds: defending the energy-rich and renewable nectar resource against all potential competitors often may be worth the energy cost it entails for the territory-holding bird. Fruiting plants also may be defended against birds of other species, although this behavior is less common. In the highlands of Papua New Guinea, Thane Pratt (1984) monitored the interactions of all birds visiting several species of fruiting trees and found that birds in four different families (a bird-of-paradise, a cuckoo, a pigeon, and a wattlebird) each attempted to drive off all competitors from its respective tree. In North America, the Northern Mockingbird (*Mimus polyglottos*) similarly may attempt to dominate dogwood and other fruiting trees in the fall and winter (Moore 1978). Although most interactions are with neighboring mockingbirds, the birds aggressively chase away other birds too. Mockingbirds are largely successful in excluding individual birds, but they generally fail when confronting large flocks of American Robins (*Turdus migratorius*) or Cedar Waxwings (*Bombycilla cedrorum*).

Interspecific site defense by birds can have large ecological consequences that go far beyond the birds themselves. For example, some Australian woodlots suffer from a syndrome known as "Bell Miner-associated damage." The highly aggressive Bell Miners (*Manorina melanophrys*) defend eucalyptus trees infested with a small, plant-sucking insect known as a psyllid. The psyllids excrete a sugary liquid that hardens into "lerp," a rock-candy-like layer. The Bell Miners feed on lerp and chase away a host of smaller insect-eating birds, thus allowing the psyllids to achieve a great abundance, sometimes to the point that they kill the trees on which they feed (Loyn et al. 1983).

Some cases of extreme interspecific aggression defy the simple dichotomy between interspecific territoriality and resource defense. For example, in snow-melt lakes in the foothills of the southern Andes in Argentina, Flying Steamer-Ducks (*Tachyeres patachonicus*) attack and occasionally kill a wide variety of ducks and other aquatic birds (Nuechterlein and Storer 1985). These lakes are relatively unproductive, so this interspecific aggression may reserve precious food for the aggressive steamer-ducks. An alternative possibility is that the aggressive behavior is a way for a feisty male duck to show off to females.

14.6 Evidence for interspecific competition

The importance of interspecific competition in shaping species assemblages remains a hotly debated issue in ecology. Simply finding overlap between two species in the type of food they eat or the habitat they use does not automatically mean that the species are competing with one another. To detect competition, researchers must show that the resources are limited and that the activities of one species reduce the fitness of individuals of another species. Although documenting these outcomes might seem straightforward, it can be challenging to do in field studies. For example, resource competition might be strong when two species first occur together but then declines as the species evolve differences in foraging behavior or other traits. Ecologists sometimes refer to these evolved differences in resource use as "the ghost of competition past," a phrase that captures the idea that some of the ecological and behavioral differences we see today among species might be the result of former competitive interactions that no longer are occurring.

Even present-day competition can be surprisingly challenging to document. Interference competition would seem the easiest to demonstrate, because aggression, dominance, and territoriality between species often can be readily observed. Even in these cases, however, the long-term effects on individuals and populations need to be measured carefully, because not all aggression is really competition in the ecological or evolutionary sense of the term.

14.6.1 Density compensation and ecological release

If interspecific competition is an important ecological force, then anything that reduces the abundance or diversity of a competing species should increase resources for the remaining species. **Density inflation** occurs when one species increases in number when its competitors are absent. This phenomenon often is particularly striking on islands that are dominated by a few—but very common—bird species. For example, the island of Bermuda, located in the Atlantic Ocean 960 kilometers from the coast of eastern USA, has been colonized by several North American bird species. Three of those species—the Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), and White-eyed Vireo (*Vireo griseus*)—comprise more than 80% of the individual birds found on Bermuda. The densities of each of these species are substantially higher than in similar habitats on the mainland. For example, cardinal densities on the island range from 62–67 birds per 40-hectare plot, whereas similar areas on the continent have only 3–35 cardinals (Crowell 1962).

Density inflation: a pattern in which a species increases in abundance in locations where competitor species are not found.



Fig. 14.16 Ecological release. On the island of Trinidad, the Barred Antshrike (*Thamnophilus doliatus*) must forage in less-preferred habitat (second-growth scrub) due to fierce competition for large insect prey. However, many of these competitors do not occur on the nearby island of Tobago, where the Barred Antshrike is "released" from competition and forages in a wider array of habitats. (Photograph by William H. Atwood, Jr.)

Although reduced competition for food resources is a common explanation for density inflation, other factors can cause or contribute to this phenomenon. Nest predation often is lower on islands, so birds living there may produce more young (George 1987). In addition, islands provide a natural barrier to dispersal, so that surplus birds may not be able to move to other sites as their population on an island increases beyond normal levels. This phenomenon, known as the "fence effect," was first discovered in experiments with meadow voles (*Microtus* species), where the simple act of fencing off an area contributed to a tremendous increase in vole populations. It is likely that the same effect applies to birds, especially those with populations trapped on small, remote islands.

Under certain circumstances, the high populations of a few species of island birds can increase total bird density to the levels found in equivalent mainland habitats, a phenomenon known as **density compensation**. The degree to which a low-diversity island fauna reaches full density compensation depends upon how similar the island's habitats are to the original mainland source habitat for the colonizing species and on the diversity of island species: the more species there are, the greater is the overall degree of compensation (MacArthur et al. 1972). In some situations, overcompensation in bird numbers can occur when larger species are underrepresented on the island and the smaller species therefore have proportionately more resources. Density compensation can be striking on islands where the few birds present have extraordinarily high densities. For example, the Bananaquit (*Coereba flaveola*) is an uncommon resident of tropical habitats throughout much of Central and South America. In contrast, it often is the most abundant bird on islands in the West Indies, especially on small islands that have few other songbird species (Cox and Ricklefs 1977).

In the absence of competing species, birds may widen their habitat use and increase their population size, a pattern termed **ecological release**. For example, the Barred Antshrike (*Thamnophilus doliatus*)—a 30-gram bird with a long, hooked bill (Fig. 14.16) and a penchant for eating katydids and other large insects—is restricted to second-growth scrub on Trinidad, where it is part of a diverse insectivore guild. However, this species occupies a much broader array of habitats on the nearby island of Tobago, which lacks many of the other Trinidadian insectivores (Keeler-Wolf 1986). Ecological release can involve a broadening of foraging niches as well as an expansion in occupied habitats. For example, a team of researchers compared the foraging behavior of a variety of white-eyes (*Zosterops* species) in high-diversity faunas on Australia and New Zealand and on low-diversity islands nearby (Scott et al. 2003). The island white-eye populations consistently showed a much greater range of feeding behaviors, indicating that in the absence of competitors on those islands they used a broader range of food resources.

14.6.2 Character displacement

As we have seen, if two species are similar in their requirements for a limiting resource, theory suggests that one of two things should occur: either one species will go extinct (at least locally), or one species will diverge in its requirements and in its behavioral and morphological features to adapt to the new resources. This latter process is termed **character displacement** and it leads to the prediction that two similar species should show the greatest morphological

Density compensation: an extreme form of density inflation in which the total number of individual birds in a setting with low species diversity (such as an island) equals the number of individuals in an analogous setting with high species diversity (such as a nearby continent); for this to occur, one or more species must be extremely abundant in the low-diversity habitat.

Ecological release: a situation in which the absence of competitors allows a species to occupy an expanded niche compared with locations in which the competitors are present.

Character displacement: a situation in which two competing species are more dissimilar in places where they both occur, compared with locations where only one species is present.

divergence where their ranges overlap, and should be more similar to one another where they occur alone (Brown and Wilson 1956).

Clear-cut examples of character displacement in birds are surprisingly rare, perhaps because of the great challenges of documenting a subtle set of changes that occurred in the past. Observing the evolution of character displacement between two ecologically similar bird species is even more unusual. For decades, scientists hypothesized that the number of species of Darwin's finches that could co-occur on a single island in the Galápagos was governed by limiting similarity, so that two species with similar bills could not co-occur. Peter Grant and Rosemary Grant (2006) had the exceptional opportunity to document the process of character displacement over a 22-year period when the Large Ground-Finch (*Geospiza magnirostris*) invaded a small island already occupied by the Medium Ground-Finch (*Geospiza fortis*) (Chapter 3). The bill size of the Medium Ground-Finch species declined after the arrival of the larger species, especially during droughts when the birds depleted most of the available food and the larger finches were able to outcompete the smaller birds in seeking large seeds. Selective pressure favored Medium Ground-Finches with smaller bills, which could survive by eating smaller seeds. This study illustrates how competition and natural selection can shape traits such as bill size over even short periods of time.

14.6.3 Community structure, competition, and assembly rules

Avian community ecologists have long been interested in how competition and other interspecific interactions influence the composition of bird assemblages. In a classic paper, ecologist G. Evelyn Hutchinson argued that limiting similarity is important in structuring animal assemblages, and that many show corresponding patterns of morphological diversity (Hutchinson 1959). He focused on the diets of species that could be positioned along a size gradient of prey items, in which each species eats prey in only part of the overall size range. In these situations, one often finds a series of increasingly large animals that differ from one another in size ratios of around 1.1 to 1.3. In birds, this pattern has been applied to bill-length ratios in flycatchers feeding on different-sized insects and in kingfishers feeding on different-sized fish (Fig. 14.17). This regular spacing of birds along a size gradient is indirect evidence that the species in these assemblages are constrained by limiting similarity.

Of course, most birds and their prey do not differ along one simple size gradient, so an examination of size ratios does not allow an ecologist to determine whether an entire bird assembly is structured by competition. In a series of bird studies on the Bismarck Archipelago in the southwest Pacific, Jared Diamond proposed that the species assemblage on any specific island (which is always a subset of the

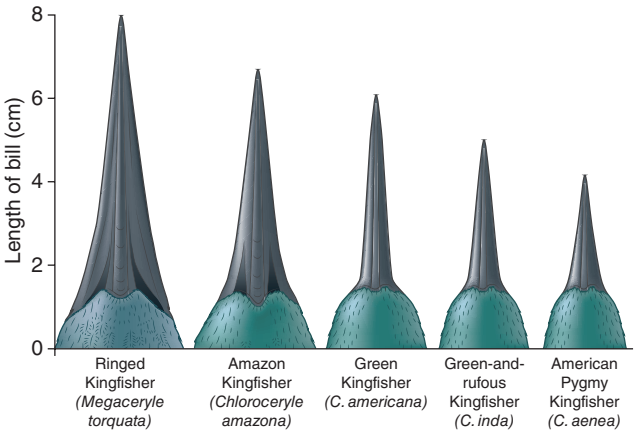


Fig. 14.17 Kingfisher bill-length ratios demonstrate limiting similarity. As overall body size decreases, these morphologically similar kingfisher species show a remarkable stepwise difference in bill lengths. Each bill proportionally corresponds to the size of the fish its owner can catch, handle, and consume. (© Cornell Lab of Ornithology.)

bird species found across an island group) is determined largely by competitive interactions (Diamond 1975; Sanderson et al. 2009). Diamond formulated these interactions into a set of **assembly rules**. These rules have been hotly debated among ecologists because demonstrating patterns that conform to them is statistically very tricky. The most important (and contentious) of these rules is what Diamond aptly termed a "checkerboard" distribution pattern, in which each island hosts only one of several ecologically similar birds (Fig. 14.18). Diamond suggested that these checkerboards arise from the presence of limiting similarity: certain combinations of species will not occur because of their inability to coexist.

Whenever an ecological pattern such as checkerboard distribution is proposed, it is important to determine through statistical analysis if the pattern differs from what one might see if species distributed randomly from the source pool without selective pressure. In any real set of species assemblages, there always will be combinations of species that do not occur simply because of chance. The random model of species composition is referred to as the "null hypothesis" for community structure. Searching for patterns that cannot be generated from a null hypothesis has been a major activity of community ecologists for the past few decades. For example, much of the debate over checkerboard patterns has centered on the best ways to test whether such patterns differ from what might be expected

Assembly rules: the hypothesis that competition among species creates possible and impossible combinations of particular species within biological communities.

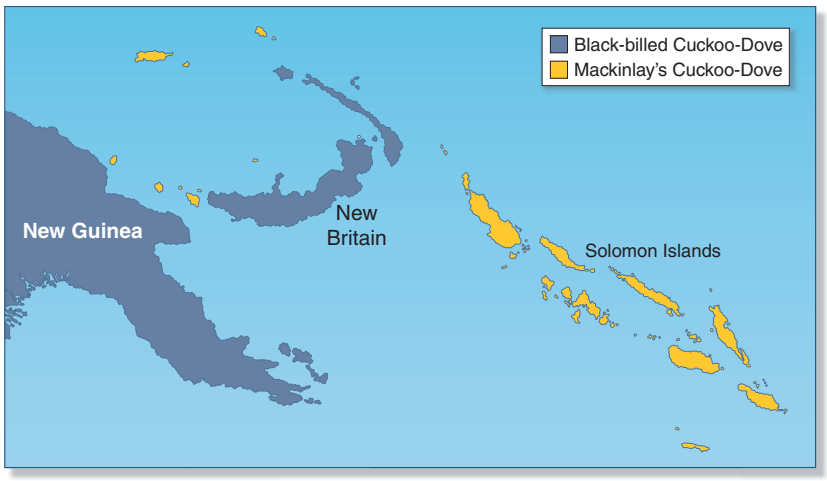


Fig. 14.18 Checkerboard pattern of species distributions. The Black-billed Cuckoo-Dove (*Macropygia nigrirostris*) and Mackinlay's Cuckoo-Dove (*Macropygia mackinlayi*) require similar resources and segregate spatially. Though both species occur in the Bismarck Archipelago, each island has only a single species: *M. mackinlayi* (gold) occupies small and/or remote islands, while *M. nigrirostris* (blue) occupies larger islands (New Britain and New Ireland). In the Solomon Islands, however, where *M. nigrirostris* is absent, *M. mackinlayi* occurs on all islands, regardless of size. (From Mayr and Diamond 2001. Reproduced with permission from Oxford University Press, USA.)

by chance if competition plays no role in influencing which species can co-occur on the same island.

Studies of other avian assemblages also have found that species occur in non-random patterns. In North America, the massive glaciers that receded at the end of the Pleistocene (about 18,000 years ago) left behind landscapes dotted with small ponds and lakes. These areas, including the prairie potholes and the Canadian Shield regions of subarctic boreal forest, often are referred to as the "duck factories of North America" because of the abundance of waterfowl that breed in these wetlands. Most ducks are readily divided into two foraging guilds (Chapter 8): dabbling ducks that feed in shallow water for insects and submerged vegetation, and diving ducks that plunge into deeper water for invertebrates and fish. In a single region of subarctic ponds, in theory, as many as a half-dozen dabbling duck species could co-occur during the breeding season, but in fact only a few dabbling species generally breed along any single body of water. Ecologists have used the combinations of ducks breeding on a series of ponds to test the hypothesis that competition determines which combinations of species occur (Toft et al. 1982; Gurd 2008). Combinations comprising duck species that have a similar breeding schedule or habitat preference were less likely to occur than would be expected by chance, suggesting that competition has a role in determining duck community structure.

14.6.4 Phylogenies and the history of communities

Recent advances in phylogeny analysis (Chapter 2) provide tools for comparing how assemblages form and allow a different kind of test of the role of competition and other forces. In these studies, real assemblages are often compared with computer-generated random assemblages to see if the real assemblages contain birds that are more closely or distantly related than one would find by chance. For example, armed with a phylogeny of hummingbirds, Catherine Graham and her colleagues (2009) calculated the average relatedness of species at different sites across Ecuador. They found that in the lowland tropics, species were less related than would be expected by chance, but the opposite was true for highland assemblages. They inferred that competitive exclusion of close relatives is important in the lowlands, whereas "ecological filtering" selects for particular clades of hummingbirds adapted to the more climatically challenged environment in the highlands (Box 14.07). Continent-wide comparisons of breeding assemblages of North American wood warblers similarly show that closely related species tend to occur together less often than expected by random chance (Lovette and Hochachka 2006).

14.6.5 Competition experiments in birds

As with the birds of the Bismarck Archipelago in Papua New Guinea and dabbling ducks in prairie potholes, the effects of competition on patterns of avian niche displacement, expansion, and contraction most often are inferred from natural patterns and correlations. However, a controlled experiment is the gold standard for establishing any form of causation in science. For example, a researcher might infer character displacement when she finds that the foraging ecology of two species varies more in the areas where they occur together. However, every site can have numerous uncontrolled (and sometimes unsuspected) ecological differences that influence patterns in unknown ways.

Box 14.07 Ecological filtering and community relatedness

Phylogenetic studies use community composition and evolutionary relationships to infer different processes of community assembly. For example, consider Fig. 14.B7.01. Suppose that two local communities (Y and Z) each have four species of a regionally represented phylogeny (orange dots). Though these communities have the same number of species, they differ in their phylogenetic relatedness. This measure is referred to as the net relatedness index (NRI). Species in phylogenetically clustered communities (Y) have a high NRI and are thought to have divergent traits that have permitted coexistence. In contrast, communities that display dispersed phylogenetic relationships (Z) have a low NRI and consist of distantly related species, suggesting strong interspecific competition limiting the coexistence of similar species. In other words, when closely related species occur in the same region, they must differ enough from one another to limit competition.

Ecuadorian hummingbird species provide a real-life example of this concept. Overall, 71% of hummingbird communities show positive NRIs, which suggests that phylogenetic clustering is more common than predicted by chance. Among many hummingbird communities, the NRI increases with higher elevations (Fig. 14.B7.02). This implies that the environment likely serves as a filter for specific suites of characteristics common in more related species. Many mid-elevation and most lowland humid forest communities have low NRIs, as their species are often phylogenetically overdispersed. However, some specific habitat types appear to predict higher NRIs than others throughout Ecuador.

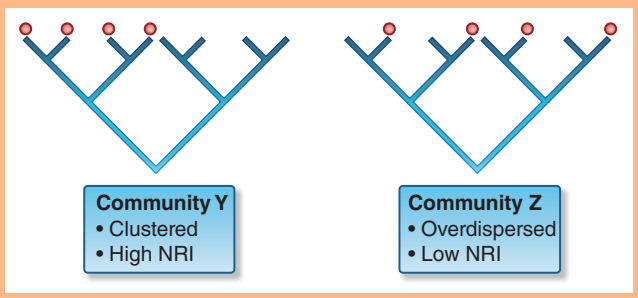


Fig. 14.B7.01 Comparison of the net relatedness index (NRI) in two communities. Imagine a community has four species (orange dots). These species are highly "clustered" in community Y, which means they are close relatives. In community Z, the species are instead "overdispersed," or less closely related to one another. Therefore, community Y has a higher NRI than community Z. (© Cornell Lab of Ornithology.)

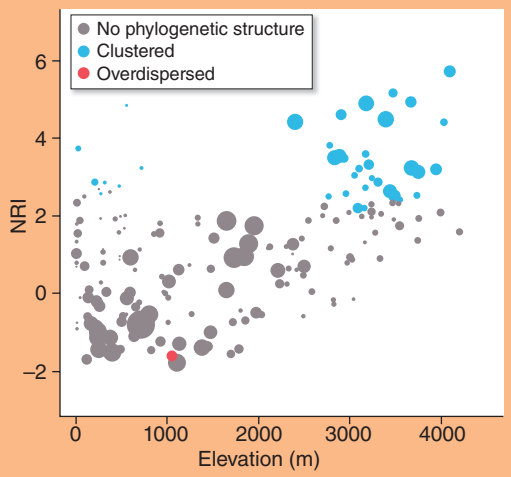


Fig. 14.B7.02 Net relatedness index (NRI) plotted against elevational distribution for Ecuadorian hummingbirds. Circle size denotes the relative number of species in a community. Blue circles represent communities with more closely related species than predicted, grey circles represent communities with expected relatedness, and red circles represent communities with more distantly related species than expected. Species tend to be more related in higher elevation communities. (From Graham et al. 2009. Reproduced with permission from National Academy of Sciences, USA.)

Carefully designed and executed experiments eliminate confounding variables and provide a more definitive evaluation of the competition hypothesis.

Although it might sound ruthless, the most obvious experimental manipulation for testing the effects of competition is to remove a potential competitor and then track any subsequent niche shift, increase in survival, or change in reproductive output (fitness effects) in the remaining bird species. Such manipulations often are very difficult to accomplish in practice, so relatively few experimental removal studies have been conducted in avian assemblages. In the forests of Scandinavia, two species of tits, the Willow Tit (*Poecile montanus*) and the Coal Tit (*Periparus ater*), form winter flocks with the Goldcrest (*Regulus regulus*). The Coal Tit and Goldcrest restrict their search for insects to the outer branches of conifers, and the Willow Tit explores the larger, inner branches. On islands where the Willow Tit is absent, the Coal Tit shifts its foraging to include both the outer and inner portions of the trees. This observation suggested that either exploitative competition (perhaps Willow Tits are better at foraging in the inner branches and make it unprofitable for Coal Tits

to shift) or interference competition (perhaps Willow Tits are dominant to Coal Tits) restricts the Coal Tits to the outer branches when both species are present. To test this idea, Rauno Alatalo and his co-workers successfully captured and removed Willow Tits at the beginning of the winter from mainland sites and carefully measured the foraging behavior of the remaining Coal Tits (Alatalo et al. 1985). They found that, just as on islands lacking Willow Tits, the Coal Tits shifted to forage towards the trees' centers in the absence of Willow Tits. This study was one of the first to demonstrate clearly the role of competition in shaping a songbird species' foraging niche.

Although field experiments that add or remove species are logistically difficult, researchers sometimes can measure the effects of competition by taking advantage of so-called "natural experiments" in which species change in abundance for other reasons. For example, ornithologists already working on the island of Hawaii monitored native bird populations before, during, and after a dramatic population increase in an introduced species, the Japanese White-eye (*Zosterops japonicus*), which became ultra-abundant at some study sites around the year 2000 (Freed and Cann 2009). As the white-eye population increased, the native Hawaiian honeycreepers suffered, declining both in overall numbers and in the body condition of the remaining individuals, with juvenile honeycreepers doing particularly poorly. These native birds showed no such decline at nearby study sites where Japanese White-eyes remained uncommon. White-eyes are successful generalist feeders, so it seems likely that food resources became limiting for honeycreepers when they had to compete with large numbers of white-eyes. White-eyes suffered less from the reduced food because they moved more freely to and from disturbed habitats outside the forest and, as generalists, had greater diet flexibility.

Although community ecologists have focused primarily on competition over food, other limiting resources also can cause intense interspecific strife. Competition for the best nest sites can occur between species that build their own nests as well as among cavity-nesting species. For example, Orange-crowned Warblers (*Oreothlypis celata*) and Virginia's Warblers (*Oreothlypis virginiae*) often breed at the same sites in the southwestern USA. The experimental removal of Virginia's Warblers did not affect where Orange-crowned Warblers nested, but it did result in lower losses to nest predation, presumably because the reduced overall density of warbler nests attracted fewer nest predators to the area (Martin and Martin 2001). In contrast, the removal of Orange-crowned Warblers led Virginia's Warblers to shift their nest sites to those previously used by Orange-crowned Warblers, allowing them both to feed nestlings at a higher rate and to suffer less nest predation. Here too, competition was asymmetrical, with the Orange-crowned Warblers dominating Virginia's Warblers and maintaining access to better sites.

14.6.6 Competition between birds and other animals

Ecological guilds can include animals of various kinds. For example, the nectar-feeding guild in a tropical forest in southern Mexico includes many hummingbirds; other nectivorous birds such as the Bananaquit (*Coereba flaveola*), Red-legged Honeycreeper (*Cyanerpes cyaneus*), and migratory Chestnut-sided Warbler (*Setophaga pensylvanica*); various species of nectar-feeding bats; a medium-sized nectar-feeding mammal called a Kinkajou; and hundreds of species of bees, flies, and other nectar-feeding insects. Although these various animals have preferences for certain types of flowers, they are all potential competitors for nectar resources.

Competition between birds and other animals can take many forms. Examples noted earlier in this chapter included desert birds that compete for seeds with small mammals, and tits that compete for nest boxes with dormice. Of course, humans probably are the greatest looming source of competition for many bird species. For example, the fisheries of the world's oceans have been diminished dramatically by human exploitation, and this reduction in food supply often has unfortunate consequences for seabirds. At times, however, the impact of heavy human fishing on seabird populations is the reverse of that expected (Tasker et al. 2000). Most seabirds depend on small fish, and human fisheries can act as predators on small fish, or, alternatively, as hyper-predators on larger predatory fish. Thus, depending upon the situation, humans can deplete the prey base for seabirds, or can remove the competitors for that prey base. Some increases in seabirds in the northeastern Atlantic may have occurred as large predatory fish populations have been fished to near exhaustion, allowing population increases in the smaller fish species these birds depend upon. In contrast, fisheries off the California coast (USA) and the west coast of Mexico have greatly depleted populations of sardines, anchovies, and rockfish, whose loss correlates with declines of pelicans and other coastal seabirds (Anderson et al. 1982; Field et al. 2010).

Birds and humans may compete locally for even smaller prey. A local industry of digging and collecting worms for fish bait from the mudflats of the Bay of Fundy in eastern Canada probably has caused a decline in the Semipalmated Sandpipers (*Calidris pusilla*) that depend upon a high abundance of these invertebrates to fuel the last leg of their migration to the high Arctic (Shepherd and Boates 1999). In this case, the interaction between humans and sandpipers involves exploitation competition: human harvesting of invertebrates directly depleted the food resources used by birds. More commonly, shorebirds around the world face interference competition with humans who use intertidal areas, because the simple presence of people may keep birds away from the best foraging areas or cause them to have lower foraging rates.

14.7 Interspecific commensalism

Commensalism occurs when one species derives a benefit from another species without affecting the species with which it is associating. For example, the disturbance caused by a foraging bird may make unused prey available to other species. Wilson's Phalaropes (*Phalaropus tricolor*) follow Northern Shovelers (*Anas clypeata*) and feed voraciously on the tiny insect larvae flushed out of the sediment by the ducks' spatulate bills as they plow the mud at the bottom of shallow ponds (Siegfried and Batt 1972). In many parts of the world, Cattle Egrets (*Bubulcus ibis*) associate with large herbivores, taking prey flushed by the passage of those animals. For similar reasons, Double-toothed Kites (*Harpagus bidentatus*) and White Hawks (*Pseudastur albicollis*) follow troops of monkeys through the canopies of Central and South American forests, capturing flying insects that are flushed by those primates (Heymann 1992; Zhang and Wang 2000). Although commensal associations between mammals and raptors are most common in the wet tropics, they also occur elsewhere; for example, in the Namib Desert of Namibia, a subspecies of the Rock Kestrel (*Falco tinnunculus rupicolus*) follows large groups of baboons as they move through open areas, taking advantage of the locusts flushed by the baboons (King and Cowlishaw 2009).

Birds also may take advantage of the sentinel or mobbing behavior of other species to reduce predation on their nests. For example, birds in many parts of the world nest near other species that are more effective mobbers of predators. Red-breasted Geese (*Branta ruficollis*) may set their colonies near the nests of Peregrine Falcons (*Falco peregrinus*) and Snowy Owls (*Bubo scandiacus*), and thus gain protection against prowling arctic foxes (Quinn et al. 2003). Birds take their protection where they can get it, and some habitually nest near colonies of stinging wasps or bees, or in trees that are occupied by aggressive ant colonies. Some birds have highly specialized nesting-site requirements that take advantage of insect defense, as shown in a study conducted in central Panama where 80% of Song Wren (*Cyphorhinus phaeocephalus*) nests were placed in acacia trees containing defensive ant colonies, although those trees were relatively rare at the study site (Robinson et al. 2000). Likewise, in Ghana, pairs of Red-cheeked Cordonbleus (*Uraeginthus bengalus*) tend to nest close to active wasp nests, where they gain a two-fold increase in nesting success over pairs not nesting near wasps (Beier and Tungbani 2006). In an impressive experiment conducted in Costa Rica, Frank Joyce moved nests of a highly aggressive wasp to trees where Rufous-naped Wrens (*Campylorhynchus rufinucha*) were nesting (Joyce 1993). The wasps' presence greatly lowered the risk of the wren nests being depredated, explaining why the wrens often naturally choose nest sites near these wasps.

Commensalism: an ecological relationship involving two species, in which one species benefits without influencing the other species either positively or negatively.

Mutualism: an ecological relationship involving multiple individuals or species in which all parties benefit in some way from the other.

14.8 Mutualisms

Win–win situations in which two or more species receive benefits from their association are termed **mutualisms**. One of the most famous—but probably fictional—avian mutualisms involves the Greater Honeyguide (*Indicator indicator*) of Africa and a mammal, the honey badger or ratel. Honeyguides are said to use a special vocalization to lead ratels to wild beehives; when the ratels break open a hive with their strong legs and claws, the birds are able to feast on the exposed brood and eggs. Although ratels do sometimes break into beehives, there is no solid evidence that they ever follow honeyguides (Dean et al. 1990). It does appear true, however, that honeyguides lead human foragers to beehives and reap the mutualistic benefits (Isack and Reyer 1989) (Fig. 14.19).



Fig. 14.19 A legendary bird and human mutualism. In Zambia, Greater Honeyguides (*Indicator indicator*) are rumored to lead human honey hunters to beehives. Here, researcher Orlando Yassene holds one of these putatively resourceful birds. (Photograph by Claire Spottiswoode.)

14.8.1 Mixed-species flocks

It is common for different bird species to occur together in mixed-species assemblages (Chapter 8). Sometimes these assemblages are simply the result of the species being attracted to the same food source, such as a fruiting tree, a tidal mudflat, a bird feeder, or a safe roosting site. Sometimes, however, birds of different species move together in integrated groups. This phenomenon of **mixed-species flocks** reaches its apex of complexity in forests.

Forest mixed-species flocks can consist of 2 to as many as 40–50 species in some tropical regions (Box 14.08). Most species in these mixed flocks occur in singletons, pairs, or small family groups. Often these species continue to maintain intraspecific territories while participating in the mixed flock. Wandering individuals of rare species may move through the habitat, joining the local mixed-species flock as they pass through unfamiliar areas. At the right season, migrating birds may also join the local mixed-species flock, a phenomenon useful to birdwatchers wishing to locate rare visitors. Although mixed-species flocks are most frequent in the non-breeding season in the temperate zone, they often occur year round in tropical forests. A forest in the neotropics may even have two such flock systems, one in the understory comprised of antshrikes, antwrens, woodcreepers, and ovenbirds, and another (with a larger group territory) in the canopy dominated by tanagers and flycatchers (Chapter 8).

Mixed-species flocks often consist of at least one **nuclear species**. These species are usually gregarious, noisy, and conspicuous. North American birders are familiar with the flocks that form around chickadees and titmice, and often hunt for these birds in the hope of finding the other species that follow this noisy core group. In other settings, playback studies have shown that flock-joining birds are attracted to the vocalizations of nuclear species. In Sri Lanka, for example, flocks form around a noisy core of Orange-billed Babblers (*Turdoides rufescens*) and Greater Racket-tailed Drongos (*Dicrurus paradiseus*). To help recruit birds into their mixed flock, drongos even learn to mimic the vocalizations of the other flock species (Goodale and Kotagama 2006).

A flocking system can form when the costs of joining (such as competition and interference) are outweighed by the advantages. For forest birds, the potential advantages of joining a flock are myriad, including having other individuals to flush prey and locate good foraging sites. Some species take advantage of the success of subordinate species in the mixed flock by practicing kleptoparasitism (stealing large prey). However, there is good evidence that the greatest advantage of joining a flock is that birds can utilize the predator alarm system of other individuals. Further, when the species that join together in a mixed flock are foraging specialists with distinctly different niches, the costs that accrue via competition over food are less than the costs of joining a single-species flock comprised of individuals with similar or identical ecological needs.

14.8.2 Heterospecific attraction

Birds may use the presence of other species as a shortcut in searching for high-quality breeding sites, rich foraging areas, or safe resting areas. The process of cueing in on the presence of other species is termed **heterospecific attraction**. For example, boreal forests at northern latitudes around the globe support millions of breeding songbirds, the majority of which are migratory. When the migrants return north in May or June, they find the forests occupied by one to four species of resident chickadees or tits already well into their nesting cycles. Ecologists have long wondered about the interaction of the resident and migratory songbirds, because they all depend upon foliage insects to fuel their breeding efforts. By providing or removing nest boxes, researchers in northern Finland manipulated the densities of resident tits and found that more migrants of other species settled on study plots with higher numbers of breeding tits (Thomson et al. 2003). Studies at unmanipulated sites elsewhere have shown that migrants that settle at sites with a higher tit density initiate nesting earlier and fledge more young than those nesting where tits are scarce (Forsman et al. 2002). In this context, heterospecific attraction appears to function primarily where tit densities are low because of harsh winter conditions; the resident tits tend to find and occupy the most food-rich sites, and their presence thereby provides a reliable clue for migrants searching for suitable breeding habitat.

14.9 Parasitism

Interspecific **parasitism** occurs when one species benefits at the expense of another species through the taking of a critical resource. When people consider parasitism, they

Mixed-species flocks: flocks of birds that contain individuals of more than one species.

Nuclear species: refers to the one or more species within a mixed-species flock that are central to its formation and cohesiveness.

Heterospecific attraction: a behavior in which individuals of one bird species use the presence of individuals of another species as an indicator of the quality of a habitat patch in which to forage or breed.

Parasitisim: an ecological interaction involving two species in which one species benefits and one species is harmed.

Box 14.08 Two tropical foraging guilds: ant followers and mixed-species flocks

First-time visitors to tropical forests often anticipate a wonderland of bizarrely colored birds crowding the trees all around them, and are disheartened when they find themselves trudging along muddy paths, peering intently into endless walls of green vegetation, listening to the drone of cicadas, and wondering where all those fancy birds might be. Luckily, these long periods of avian inactivity are punctuated by encounters with tropical understory flocks that can be populated by as many as 30–40 bird species and are characterized by intense activity.

Diverse bird flocks in the tropical forest understory come in two general varieties, with different behaviors and largely non-overlapping species lists: mixed-species flocks (which occur in most tropical forests worldwide) and ant-following associations (which are most evident in Central and South American forests). These two concentrations of bird activity provide some of the most exciting tropical birding opportunities and illustrate very different sorts of interspecific interactions, particularly in competition for food.

We think of the tropics as insect-ridden, but the type of insects preferred by birds—particularly the insects that birds need to raise young—are harder to find than one might think. In a temperate forest, caterpillars are the most sought-after prey items by most breeding birds. The growing season is short and intense, and many caterpillars invest heavily in rapid growth and little in defenses against predation. In contrast, in tropical forests, katydids, roaches, and other large insects are often the most sought-after prey (Chapter 8). Besides being mobile and often well defended with spiny appendages and biting mouthparts, these insects typically hide by day and are active primarily during the warm nights. This pattern of activity makes them surprisingly hard for birds to find.

One strategy that some tropical birds use to locate prey is to follow massive swarms of certain species of army ants that move through the forest leaf litter and low vegetation (Chapter 8) (Fig. 14.B8.01). Army ants are not the threat to human life and limb that has been portrayed in some Hollywood movies, but they are a danger to multitudes of



Fig. 14.B8.01 Following army ants as a foraging strategy. The following species are among those typically found in close association with army-ant swarms, which flush up prey: (A) the Ocellated Antbird (*Phaenostictus mcleannani*), (B) the White-chinned Woodcreeper (*Dendrocincla merula*), (C) the Bicolored Antbird (*Gymnopithys bicolor*), (D) the Hairy-crested Antbird (*Rhegmatorhina melanosticta*), (E) the Blue-lored Antbird (*Myrmeciza immaculata*), and (F) the Black-spotted Bare-eye (*Phlegopsis nigromaculata*). The Ocellated Antbird is entirely dependent on a particular species of voracious forest army ant (*Eciton burchellii*), which it follows to find food; these other species forage both with and without the help of army ants. (Photographs by: A, Jim Burns; B, Joseph Tobias; C, Matt Deres, https://en.wikipedia.org/wiki/File:Gymnopithys-leucaspis-001_edit2.jpg. CC-BY-3.0; D, Thiago Orsi Laranjeiras; E, Pia Öberg; F, Bertie Allison.)

Continued

small inhabitants of the tropical forest floor. As the moving wave of ants flushes out hiding insects, birds wait for the insects to fly out or crawl up the trunks of saplings as they try to escape the ants but become prey for the birds. The widely distributed neotropical army ant *Eciton burchellii* provides a perfect target for specialization by birds that make a living following the mass movements of ants, because this ant species is active during the day, during both rainy and dry seasons.

Finding an ant swarm is surprisingly easy once one knows how to search, because they are signaled by the vocalizations of specialized ant-following bird species. Observing birds at a swarm is a lesson in activity, aggression, and dominance as the birds chase, supplant, and repeatedly vocalize at one another. The best positions around the front of the swarm are dominated by a few so-called "professional" ant-following species, which may include a few of the thrush-sized birds with curious blue "eye make-up" appropriately named antbirds, various species of woodcreepers, and (for a really lucky birder), the roadrunner-sized ground cuckoos (*Neomorphus* species). These species spend most or all of their time following the swarm. Many other species—various tanagers, warblers, and other antbirds and woodcreepers—visit the swarm opportunistically as it passes through their territories.

Although birds at ant swarms are clearly aggressive, we need additional evidence to prove that the participation of birds in ant swarms is, in the long run, limited by competition. In the 25-year period after the large and dominant Ocellated Antbird (*Phaenostictus mcleannani*) went extinct on Barro Colorado Island, the smaller subordinate Spotted Antbird (*Hylophylax naevioides*) increased greatly in abundance because of a sharp increase both in its attendance at ant swarms and in its feeding success at the swarms (Touchton and Smith 2011).

Understory flocks can be larger and even more diverse than ant-following aggregations (Fig. 14.B8.02). Such flocks often spend large parts of the day foraging quietly in dense, viney vegetation, and, therefore, can be surprisingly easy to overlook. Periods of quiet foraging are interrupted occasionally as core or "nuclear" flock species rush to a territorial boundary for lengthy and noisy boundary interactions with members of a neighboring flock. Such flocks have a certain kaleidoscopic quality, because their size and



Fig. 14.B8.02 Diverse mixed-species foraging flock. This illustration depicts the taxonomic diversity typical of a mixed-species flock in the neotropics: woodpeckers, trogons, antbirds, ovenbirds, woodcreepers, New World flycatchers, manakins, vireos, gnatcatchers, tanagers, and blackbirds. Each species has its own set of foraging substrates, behaviors, and prey. (Illustration by Karl Mokross.)

composition changes continuously throughout the day as a flock attracts a host of species that drop in and follow for short periods of time. The core flock often is remarkably constant, with some species playing unique roles in flock dynamics. For example, in Amazonian flocks, species of *Thamnomanes* antshrikes act as flock sentinels, giving loud alarm calls when they detect a threat such as a passing forest falcon.

Generally, however, aggression in mixed-species flocks is remarkably low. Rather than jostle for a few good feeding sites, each bird species in a mixed-species flock specializes in searching a particular microhabitat. As described in more detail in Chapter 8, some species feed entirely by searching the fallen, dead leaves of canopy trees caught in understory vegetation. These leaves form protective tubes in which nocturnally active spiders, katydids, and roaches seek refuge. Other species probe bromeliads and other epiphytes, or the tiny tunnels made by leaf-mining insects on leaf surfaces, or dead twigs. Some species have special ways of flushing certain types of insects; others have a unique method of flying to attack insects from a distance. Most species have a special routine in the forest they search, hour after hour, day after day, in their own unique manner. By joining a mixed group, a bird gains the advantages of flocking, such as more eyes to detect predators, yet the mixed-species composition inherently reduces the probability that another bird with a similar niche will find the prey first.

Although these associations among understory birds have been used to illustrate different forms of avian competition, each also involves other biological interactions. For example, the ant-following birds are technically parasites of army ants (Wrege at al. 2005). By systematically scaring off antbirds from swarms and comparing the foraging success of ants with and without birds present, researchers determined that such birds remove more than one-fourth of the prey that otherwise would be consumed by the ants they follow.

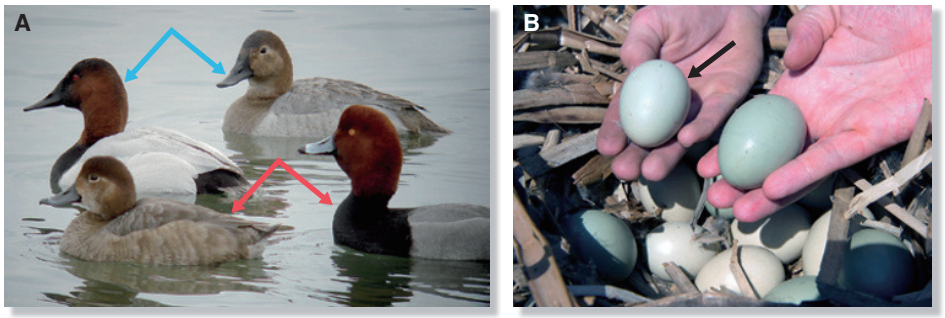


Fig. 14.20 Nest parasitism. (A) Canvasbacks (*Aythya valisineria*; blue arrows, female on right) and Redheads (*Aythya americana*; red arrows, female on left) look very similar and are often observed together. (B) Female Redheads often parasitize Canvasback nests, a behavior often identified via egg size differences; Redheads lay smaller eggs (black arrow) within Canvasback clutches. (Photographs by: A, Jay McGowan; B, Fred Greenslade.)

generally think of microbes, worms, and insects: organisms that may cause disease. Birds likewise provide a home for many kinds of internal and external parasites, ranging from microscopic malaria-causing pathogens within their blood cells to large, blood-sucking flies that live between feathers. However, birds also can parasitize other birds in two distinct ways. In **brood parasitism**, a female lays eggs in the nest of another bird of the same or a different species. In kleptoparasitism, a bird steals prey items from another bird, thus parasitizing the successful hunting of the subordinate.

Brood parasitism: any situation in which a female bird lays its eggs in the nest of another individual of the same or different species.

14.9.1 Brood parasites

Females of many bird species occasionally lay eggs in the nests of conspecifics in addition to laying eggs in their own nests (Chapter 13). A few of these species also may lay eggs in the nests of other species; for example, Redheads (*Aythya americana*) often parasitize Canvasbacks (*Aythya valisineria*), a related duck species (Sorenson 1997) (Fig. 14.20). One lifestyle stands in stark contrast to the prodigious care that most birds provide to their young: obligate brood parasitism. This form of parasitism, in which females lay all their eggs in the nests of other species, is very rare; only about 1% of the world's bird species exhibit this trait. However, it has arisen independently at least six times in the evolution of birds (Box 14.09).

Brood parasites have developed a variety of adaptations to help them deceive and exploit their hosts. Among their most important behavioral attributes are their cryptic

Box 14.09 The six groups of obligate brood parasites

While some species employ the brood parasitism strategy occasionally (mainly by dropping some eggs in other birds' nests while also maintaining their own), there are six groups of birds that do this exclusively. These birds do not build nests and have particularly advanced adaptations to trick host parents and/or sabotage host nestlings.

1. The Black-headed Duck (*Heteronetta atricapilla*) (Fig. 14.B9.01) parasitizes other duck species, ibises, gulls, and coots. Ducklings of this species are remarkably precocial, leaving their host parents within 2 days to care for themselves without assistance.
2. Honeyguides (family Indicatoridae) (Fig. 14.B9.02) are obligate parasites on Old World warblers, barbets, and other cavity-nesting species.
3. Old World cuckoos (family Cuculidae, subfamily Cuculinae), consisting of over 50 species, parasitize a broad range of hosts, from pipits and warblers to honeyeaters and magpies. Even as nestlings, cuckoos are often much larger than their hosts (Fig. 14.B9.03).



Fig. 14.B9.01 Brood parasitism in Black-headed Ducks (*Heteronetta atricapilla*). (A) The female Black-headed Duck (on left, in this pair) parasitizes many host species, including (B) the Red-gartered Coot (*Fulica armillata*). (C) A Black-headed Duck egg (arrow) in the nest of a host. (Photographs by: A, Cláudio Dias Timm; B, John Sutherland; C, Daniel Martínez Piña.)



Fig. 14.B9.02 Greater Honeyguide (*Indicator indicator*). All honeyguide species are obligate brood parasites. (Photograph by Frans Vandewalle.)



Fig. 14.B9.03 Size disparity in parasite and host. Even though this parasitic Common Cuckoo (*Cuculus canorus*) nestling is at least double its size, this Eurasian Reed-Warbler (*Acrocephalus scirpaceus*) continues to feed it. (Photograph by Per Harald Olsen, https://en.wikipedia.org/wiki/File:Reed_warbler_cuckoo.jpg. CC-BY-SA 3.0.)

4. Neomorphine cuckoos (family Cuculidae, subfamily Neomorphinae) (Fig. 14.B9.04) are more related to other non-parasitic New World cuckoos than to the parasitic cuckoos of the Old World. Thus, obligate brood parasitism must have arisen separately in New and Old World cuckoos. There are three brood parasites in this subfamily.
5. The Parasitic Weaver (*Anomalospiza imberbis*), indigobirds, and whydahs (all family Viduidae) are closely related to the Old World finch family Estrildidae, which contains their primary hosts. All estrildid nestlings have amazingly diverse and detailed mouth markings that young whydahs and indigobirds have evolved to mimic to a remarkable degree.
6. Cowbirds (family Icteridae, genus *Molothrus*) (Fig. 14.B9.05) are the most prevalent brood parasites in the western hemisphere. A host generalist, the Brown-headed Cowbird (*Molothrus ater*) successfully parasitizes at least 140 different bird species (Lowther 1993).



Fig. 14.B9.04 Pheasant Cuckoo (*Dromococcyx phasianellus*). One of three parasitic New World cuckoo species. (Photograph by Justin Khalifa.)



Fig. 14.B9.05 Giant Cowbird (*Molothrus oryzivorus*). This species parasitizes oropendola and cacique nests. (Photograph by Flavio Guglielmino.)

movements. Females in search of host nests can be extremely difficult to follow. Not only do female brood parasites find host nests without being detected, they often monitor the activity of a large number of potential host nests simultaneously, waiting to lay an egg at the time that it is least likely to be detected. For example, the Common Cuckoo (*Cuculus canorus*) often lays in the afternoon, when the host is likely to be away, instead of at dawn as is more typical in birds. In many Old World cuckoos, pairs work together: the males fly conspicuously up to the nest and sing, attracting aggressive chases by the host pair, while the female cuckoo stealthily lays her egg in the host nest.

The Common Cuckoo parasitizes a wide variety of Old World warblers, buntings, wagtails, and pipits. Common Cuckoo eggs reflect a spectacular adaptation in which they mimic distinct host species' eggs. The cuckoo eggs vary dramatically and often closely resemble those of the most common host in the area that each cuckoo parasitizes (Fig. 14.21). Genetic studies suggest that these egg types are inherited via the mother, and that female cuckoos are extraordinarily good at choosing the appropriate host nest in which to lay (Gibbs et al. 2000). It is not yet clear how the females know which hosts to choose or how this ability evolved.

Many characteristics of brood parasites set them apart from other birds. The young of most brood parasites have very short incubation periods and rapid growth rates for their size, helping them outcompete the host nestlings (Fig. 14.22). Some species, however, leave little to chance. Young honeyguides and cuckoos employ various means of killing and ejecting the host nestlings from the nest. At hatching, young honeyguides are blind and naked, and both



Fig. 14.21 Parasitic cuckoo versus host eggshell variation. Female Common Cuckoos (*Cuculus canorus*) produce eggs that look strikingly similar to their host species (arrows point to the cuckoo eggs in each host nest). Spot pattern and background color are the most important characteristics to mimic. (Photographs by: A, Csaba Moskát; B, Tomáš Grim.)



Fig. 14.22 Brood parasite advantage. If a Brown-headed Cowbird (*Molothrus ater*) egg is accepted by its host (any of over 220 species in North America), the nestling will typically hatch earlier, grow faster, and beg louder than the hosts' own offspring—all traits that increase its chances of survival. This large, begging cowbird nestling has succeeded in a Wood Thrush (*Hylocichla mustelina*) nest. (Photograph by Kelly Colgan Azar.)

of their jaws bear a hook on the tip, a modification of the egg tooth found on the upper beak of most newly hatched birds (Fig. 14.23). In the nest, they either bite the host's young until the young die and the host removes them, or they push and shove the host's young, ejecting them one by one from the nest. Young cuckoos, within 10–12 hours of hatching, can push away any small object that lies between the shoulders of their sensitive backs, be it an acorn, an egg, or another young bird (Fig. 14.24). In this way they quickly eliminate all other eggs or young. Not surprisingly, females of these parasites usually lay only one egg in each host nest.

14.9.2 Kleptoparasitism

Kleptoparasitism occurs when one bird steals food from another (Chapter 8). Kleptoparasitism can be obligatory—that is, the kleptoparasite depends on stolen prey to survive (at least for part of the year). Or it can be facultative—that is, prey is stolen as the opportunity arises, but such theft is not a mandatory part of the bird's life. Facultative kleptoparasitism is widespread. For example, when watching gulls along a beach or at a landfill in most parts of the world, it is common to witness a particularly large and popular item of food be stolen and re-stolen several times before one gull finds refuge long enough to consume it. Kleptoparasitism is also seen in mixed-species flocks of smaller birds, when one bird captures a large prey item only to have it taken away by a more dominant individual.

14.10 Predation

Birds interact with other organisms by preying upon them and becoming prey themselves. Beyond the direct impact of predation on bird populations (Chapter 13), the threat of predation affects how birds use their habitat by creating a so-called "landscape of fear." For example, depending on their strategies for predator avoidance, different sparrow species feeding at seed piles are willing to feed at different distances from the safety of shrubbery. Shorebirds likewise may join concentrations rather than feed in areas with less competition because flocking reduces the probability of a successful attack by a falcon. Thus, the degree to which different birds are willing to take risks is a strong determinant of their resource use.

One other important aspect of risk taking is the way that birds respond to novelty, such as new foods, new habitats, or new habitat features. Some birds seek out novelty (neophilia), but most are averse to new situations. Try placing a new, conspicuous object next to your bird feeder and watch the response. Although new foods or new objects are not inherently more dangerous, they have the potential to be so. The tendency to shy away from novelty varies among

Kleptoparasitism: a parasitic interaction in which one bird steals prey or food from the individual who originally obtained it.

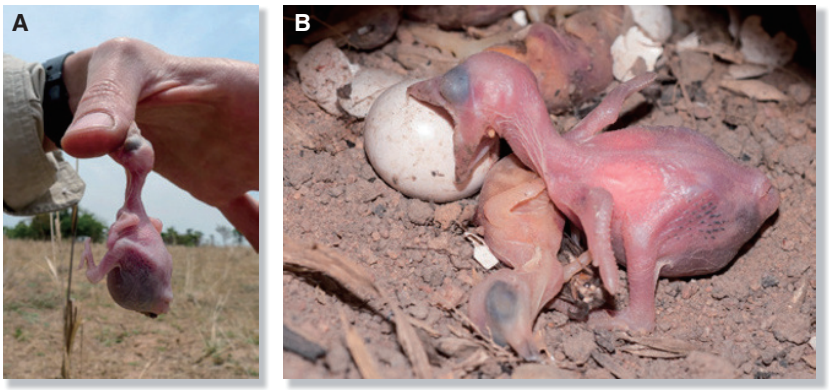


Fig. 14.23 Adaptations for killing host nestlings. (A) Greater Honeyguide (*Indicator indicator*) nestlings hatch with razor-sharp "bill-teeth," giving them amazing grip strength. (B) As brood parasites, Greater Honeyguide nestlings use these bill-teeth as weapons, puncturing host eggs and killing host nestlings to gain maximum resources for themselves. (Photographs by Claire Spottiswoode.)



Fig. 14.24 Brood parasite chick eliminating competition. Hours after hatching, a parasitic African Cuckoo (*Cuculus gularis*) nestling pushes the last of its host species' eggs out of the nest. (Photograph by Claire Spottiswoode.)

species. Laboratory experiments show that the more specialized species of warblers and sparrows are also more neophobic (Greenberg 1990); their neophobia might make them less prone to shift to new food resources and is a psychological component of their niche. Species that live in danger of poisoning or hunting by humans also are highly neophobic. In this case, neophobia protects them from the unpredictable dangers that the presence of humans poses. Neophobia, therefore, can be an indirect effect of different predator environments.

Although few good avian examples exist, predation can alter the competitive relationship of species within an assemblage. To the degree that predators reduce the population level of all potentially competing species, predation can maintain populations below their carrying capacity and thus allow greater species diversity. This effect is particularly true if predation is density dependent (Chapter 13), so that the most common species of prey are taken preferentially. Likewise, if predation is most intense on larger species, then their removal may allow the ecological release of populations of smaller species that share the same resources. Human predation (hunting) often follows this pattern, and it has been hypothesized that the relatively high abundance of small-bodied bird species on islands is partially the result of humans eating most large island-dwelling bird species to extinction, thus allowing the smaller birds to prosper.

14.11 Food chains and food webs

Understanding entire ecosystems is daunting, so ecologists sometimes approach the task by focusing on a few key processes such as the cycling of nutrients and energy flow. The trophic, or "feeding," structure of an ecosystem is based on a **food chain**, the sequence in which organisms feed upon other organisms. A simple food chain in a field, for example, might start with the grass: grasshoppers eat grass, larks eat grasshoppers, and kites eat larks. Even in the simplest ecosystems, the various food chains are usually so complex and interconnected that the trophic structure is

Food chain: a hierarchy in which organisms in a location or ecosystem are organized into levels based on their feeding relationships, with primary producers (usually plants) on the lowest level and top predators on the highest level.

best described as a food web. One can simplify the web somewhat by grouping organisms into categories based on their position in the food chain.

The ultimate source of energy for all animals, including birds, is the sun. Plants capture energy from the sun and introduce it into the food chain by using it to make foods that can be eaten by animals. Because of this role as food "makers," plants are called producers. Bird and other animals that directly eat plants—herbivores—are called primary consumers. Animals that eat primary consumers are carnivores (meat-eaters) and are called secondary consumers. Carnivores that eat secondary consumers are called tertiary consumers, and so forth. Many birds have varied diets and thus occupy more than one position within a food chain. Those that eat both plants and animals are called omnivores, and they may act as both primary and secondary consumers.

Birds occupy food chain levels above that of producers. Most birds that are primary consumers are granivores (seed-eaters), frugivores (fruit-eaters), or nectivores (nectar-feeders), but some birds feed directly on green plant parts such as leaves, shoots, buds, and stems (Chapter 8). Although there are many avian herbivores, most bird species are secondary or tertiary consumers. For example, most of the bird families of the world include species that feed primarily on insects or other small invertebrates.

Despite being conspicuous components of most ecosystems, birds only rarely form major links in the overall flow of energy within the environment. For example, detailed studies of energy flow through terrestrial forest food chains have shown that less than 1% of the energy produced by plants moves upward via birds (Holmes and Sturges 1975). This total energy consumption by birds is notably small in comparison with that of other less conspicuous animals, such as insects and other invertebrates. Nonetheless, birds are important conduits of energy flow in some situations. For example, in polar regions, endothermy has allowed birds to become more energetically dominant members of the ecological community. On remote islands, accessible to birds because they can fly, birds have taken over niches usually filled by other animals. For example, some birds on remote islands—such as the extinct moas of New Zealand and the elephant birds of Madagascar—evolved traits such as a massive body size more typical of mammals. In such ecosystems, the importance of birds in the energy flow is greater because they fill more links in the food chain.

14.12 Communities within birds

Like a nested set of Russian dolls, communities live within communities. Bird assemblages exist within larger communities of plants and animals and, in turn, are host to assemblages of microbial organisms that live on their feathers, on their eggshells, within their nests, and inside their digestive tracts. Microbes affect the fitness of birds in many ways, and the compositions of microbial assemblages are determined to a great degree by environmental interactions. The study of avian microbial assemblages is in its infancy, particularly for wild birds. Unlike birds themselves, avian microbes cannot be surveyed with binoculars or detected by vocalizations; the seemingly simple act of determining the components of a microbial assemblage requires genetic survey techniques.

Highly diverse assemblages can be found in the avian gut (Kohl 2012). Although some of the microbes are carried over from the egg, the assemblage develops primarily in young birds through contact with parental saliva, the nest, and food items. Diversity develops over time, and the composition becomes more stable at adulthood. Composition is determined in part by the genetics of an individual bird, but is overwhelmingly responsive to the immediate environment, particularly that of the nest (and associated parents). For example, one study of tits in Europe found, by cross-fostering nestlings in different nests, that the particular nest determined microbial assemblage far more than genetic relatedness or even species (Lucas and Heeb 2005). This individual variation is important because studies on domestic fowl show that gut microbes play important roles in nutrition, immune function, and development, and thus almost certainly affect the fitness of each individual.

In addition to the gut, microbes also live in great numbers on the feathers of birds. It is thought that birds pick up most of these microbes from the surrounding environment and that they vary over time, particularly with molt. These assemblages have been studied as potential geographic markers for bird travel. Thus far, descriptions of these microbes, achieved through painstaking amplification and sequencing of DNA, have documented that there is much variation among individuals within a species, between tropical and temperate passerines, between migratory birds and residents from the same collection sites, and among birds of different ages (Bisson et al. 2007, 2009).

One group, however, has received a great deal of attention in the last decade: feather-eating bacteria. At least 20 species of bacteria are capable of breaking down the keratin of hair or feathers (Gunderson 2008). Much of what we see as general "feather wear" may result from the activities of these keratin-feeding microbes (Fig. 14.25). Counteradaptations by birds include feather pigments such as melanin that help resist bacterial degradation (Burtt and Ichida 2004) and mutualistic relationships with helpful bacteria that live in birds' uropygial glands, which birds then spread onto their feathers when preening (Ruiz-Rodríguez et al. 2009).

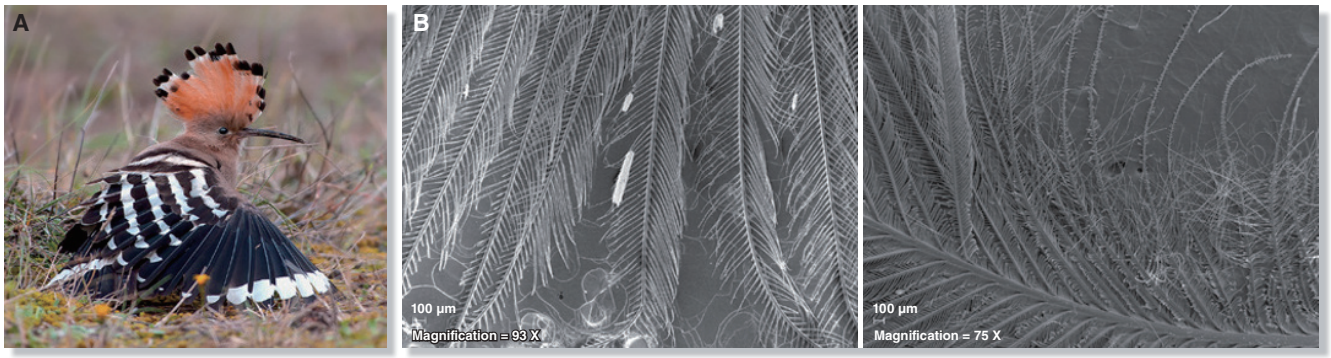


Fig. 14.25 Symbiotic bacteria may prevent feather degradation. (A) Eurasian Hoopoes (*Upupa epops*), like most birds, preen by spreading uropygial gland oils over their feathers. These oils contain helpful bacteria that protect feathers from keratin-eating bacteria. Without these probiotic oils, harmful bacteria can completely consume a feather's barbules within the span of 16 days. (B) Scanning electron microscope photos demonstrate medium (left) and advanced (right) levels of feather barb degradation. (Photographs by: A, Nick Holland; B, Magdalena Ruiz-Rodríguez.)

14.13 Top-down effects, trophic cascades, and ecological services

When predation largely determines the abundance of a species, this control is referred to as a **top-down effect**. In contrast, **bottom-up effects** occur when the abundance of a species is determined primarily by its supply of food. To see these concepts applied, we can ask: With all the extant herbivorous animals today, why is the world as green as it is? Why do herbivores not eat most or all of what is produced by plants? A bottom-up argument holds that moving up a food chain is climbing a food pyramid, with decreasing amounts of energy transferred towards the apex. The abundance of photosynthetic plants is determined primarily by access to nutrients, water, and sunshine, with herbivores and their predators playing a decreasingly important role in ecosystem energetics as you move up the food web. A contrasting top-down argument holds that predators keep herbivores in check by consuming many of them. In the latter part of the last century, the relative importance of these two processes was debated fiercely. As with most strongly argued dichotomies in ecology, the answer to the question—top down or bottom up?—is that both can be important, depending on the situation.

14.13.1 Trophic cascades

One manifestation of top-down effects, **trophic cascades**, occurs when a predator reduces the abundance or otherwise affects the feeding patterns of its prey, creating a cascading effect down the food web. The topic of trophic cascades has caught the attention of ecologists and conservation biologists because it speaks to the functional significance of individual species. Ecosystems harbor **keystone species** (often top predators) whose presence is particularly important in determining overall community structure beyond their apparent abundance. One well-documented trophic cascade involving birds occurs in remnant patches of native chaparral habitat in and around the city of San Diego, California (USA) (Crooks and Soulé 1999). Some of these habitat patches still support populations of coyotes, a top mammalian predator, but other patches are too small or too isolated to host them. Where coyotes are present, they are the keystone species that greatly reduces the density of

Top-down effect: in ecology, a situation in which the amount of predation or consumption by organisms at the top of the food chain has large effects on lower components of the ecosystem.

Bottom-up effect: in ecology, a situation when the abundance of a consumer or predator—or important parts of the ecosystem overall—is determined primarily by the degree of primary production at the bottom of the food chain.

Trophic cascade: a situation in which predators high in a food chain exert top-down effects that ramify through the food chain levels to influence the abundance of species that the predators do not eat directly.

Keystone species: a species that has a disproportionately large effect on its habitat, biological community, or ecosystem. Named after the top block of stone—the keystone—in an arch that is essential for holding the other stones in place.

smaller mammalian carnivores such as foxes, opossums, and domestic cats. In contrast, these medium-sized predators (especially cats) are abundant in patches where coyotes no longer occur. Because coyotes rarely prey upon birds but most of the smaller carnivores commonly do, the interplay between the mammalian predators has cascading effects on the birds: native songbirds are far more diverse in the fragments that support coyotes.

Birds also are impacted by trophic cascades involving herbivorous mammals that degrade avian breeding habitats. For example, across North America the loss of top mammalian predators has caused populations of deer, elk, and moose to increase greatly. Intensive browsing by these large herbivores often causes vegetation changes that negatively impact bird populations. In the Yellowstone region of the western USA, migratory songbirds are less common or absent from streamside habitats where moose are particularly abundant (Berger et al. 2001). Similar patterns occur in the Haida Gwaii Archipelago off the coast of British Columbia (Canada), where deer are present on some but not all of the islands. The islands with deer have greatly reduced understory vegetation and, in turn, support markedly lower populations of birds (Allombert et al. 2005).

14.13.2 Ecological services

As covered in more detail in Chapter 15, birds provide many kinds of **ecosystem services**. For example, the ability of insectivorous birds to reduce the number of detrimental insects that attack crops or other economically important plants is touted as an important ecological service. However, as noted, birds usually are responsible for only a small fraction of the energy flow through an ecosystem. Is predation by birds ever high enough to reduce insect populations enough to benefit plants and the people growing them?

Researchers have addressed this question experimentally by using netting to exclude birds from plants and comparing insect abundance, herbivore damage, and plant growth with control plants that lack netting and thus are available to foraging birds. It turns out that the impact of birds on insects varies greatly among sites, seasons, habitat types, and plant types, but birds often do have a detectable effect. For example, experiments on patches of grassland in southeast Arizona (USA) showed that birds reduced grasshopper density and thereby reduced herbivory (Bock et al. 1992). Considered in concert, the general pattern across many such bird-exclosure studies is that birds often reduce populations of herbivorous insects in ways that benefit plants (Mäntylä et al. 2011).

Ecosystem services: the collection of beneficial effects of ecosystems that provide substantial and ongoing economic value to human societies.

This ecological service by insectivorous birds can have economic impacts for humans. Similar exclosure experiments in tropical forests, cacao (chocolate) plantations, and shade coffee farms have shown that birds can limit insect abundance, particularly during the winter (tropical dry season) when migrants are present (Greenberg et al. 2000; Van Bael et al. 2008). In some coffee plantations, for example, birds reduce the population of coffeeberry borers, a small but devastating beetle pest that bores into coffee beans while they are still in the fruit (Kellermann et al. 2008). Birds may therefore save coffee farmers thousands of dollars of lost production. These results confirm the belief held by many small-scale farmers raising crops throughout the tropics: birds reduce insect pests.

Other ecological services by birds include pollination by nectivores and seed dispersal by frugivores. If these birds are lost from an area, their ecological function leaves with them. For example, large frugivorous birds such as hornbills in Asia and Africa and toucans in the neotropics are essential seed dispersers for many tropical trees. These birds often eat a fleshy fruit, process it in their crop, and later regurgitate the still-viable seed. When these large birds are extirpated by hunting, the trees drop their fruit directly below their canopy, where they are exposed to animals that eat the seeds rather than disperse them (Sekercioglu 2006). This ecological service is pervasive in places such as the Atlantic rainforest of eastern Brazil, where more than 30% of the native tree species depend on birds for seed dispersal (da Silva and Tabarelli 2000).

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Chapter 15 Bird Conservation

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Until the mid-1800s, travelers in the springtime woods of eastern North America would marvel as multitudes of large, long-tailed doves swirled into dark clouds overhead during the spring migration. Millions of beating wings resonated like strong winds through pine boughs while the immense horde streamed northward. The passage of such a flock might continue all day, with straggler flocks following thereafter for weeks.

The Passenger Pigeon (*Ectopistes migratorius*) was then almost certainly the most abundant bird on earth (Fig. 15.01). Accounts of their numbers written between 1630 and 1880 read like science fiction (Schorger 1955). John James Audubon wrote of a flock passing for three successive days near Louisville, Kentucky (USA) in 1813, stating that "the light of the noonday sun was obscured as by an eclipse." He estimated the mile-wide flock to contain a minimum of 1.1 billion birds. Alexander Wilson, often called the father of North American ornithology, considered his own 1806 estimate of a single flock—2,230,272,000 birds—to be well below its actual number.

How many Passenger Pigeons existed across the entire range of the species? Nobody knows for sure, but the number may have been 5 billion or more. For perspective, only one wild bird species in the world today, the Red-billed Quelea (*Quelea quelea*) of sub-Saharan Africa, likely reaches 1 billion individuals. Yet by 1914 the Passenger Pigeon was extinct, just 100 years after Audubon and his contemporaries wondered at its incredible abundance. Accounts of Passenger Pigeons provide deeply moving glimpses of a world that was very different from today, yet existed only a few generations ago. This contrast reminds us of the astonishing changes caused by humans across the world's landscapes and across bird populations.

No doubt exists about why Passenger Pigeons disappeared. As for so many other species, this gregarious dove was extinguished by the deadly one-two-three punch that already had become a signature of human expansion across the world: (1) uncontrolled exploitation (in this case, hunting for food); (2) advances in technology that aided exploitation as numbers decreased (firearms and railroads); and (3) large-scale alteration of the landscape for agriculture and human settlement (clearing of mature, seed-producing oak and beech forests).

Many contemporary accounts of Passenger Pigeon nesting colonies emphasized the frenzied slaughter of the birds by hunters more than the natural wonder of the birds themselves. Even at the last large colony documented—in 1878 near Petoskey, Michigan (USA)—300 tons of Passenger Pigeons killed by professional market hunters were shipped by railroad to restaurants in Chicago,

Opposite: The critically endangered Spoon-billed Sandpiper (*Calidris pygmea*). With just 100 known breeding pairs, two factors contribute to this species' decline: the elimination of important refueling grounds during a long migration, particularly in the Yellow Sea intertidal region, and subsistence hunting of shorebirds in their coastal wintering ground in Southeast Asia. (Photograph by Gerrit Vyn.)

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Fig. 15.01 Passenger Pigeons (*Ectopistes migratorius*). At the time of the European settlement of North America, this species was considered to be the most abundant bird on earth. Audubon reported a flock estimated to contain over 1 billion individuals. Flocks once migrated across eastern North America, settling to breed in huge colonies where they found bounties of tree-nuts (such as acorns, chestnuts, and beechnuts). (Illustration by N. John Schmitt.)

New York, and Boston. Because the species nested in dense colonies and nestlings were easy and delicious prey, a colony's entire reproductive output could be wiped out during a single season. Last-ditch efforts to avert the Passenger Pigeon's extinction in the 1890s through publicity and legal protection came too late: Martha, the world's last individual Passenger Pigeon, died at the Cincinnati Zoo (USA) on September 1, 1914.

Preserved as a specimen at the National Museum of Natural History in Washington, DC, Martha invites reflection on humans' relationship with the earth. She died just as the global conservation movement was being born. This new movement would go on to establish the revolutionary laws, organizations, and actions that serve to protect birds and other emblems of wildness today.

15.1 History of bird conservation

The roots of bird conservation lie in the many past tragedies of overexploitation that are exemplified by the Passenger Pigeon. The earliest bird protection laws were efforts to curb overuse of hunted species. Laws establishing hunting seasons and regulations for particular groups of birds, such as upland game birds, were passed in the early 1700s in North America. Likewise, in both Britain and Newfoundland (now Canada), some of the first laws protecting birds were passed in 1775 to stem the exploitation of the Great Auk (*Pinguinus impennis*). In response to an already staggering level of market hunting in eastern North America, the state of New York passed legislation in 1791 to restrict hunting seasons for Heath Hen (*Tympanuchus cupido cupido*), and Massachusetts (USA) passed an Act to Protect Useful Birds in 1818. As early as the mid-1800s Michigan passed several laws attempting to limit the hunting of Passenger Pigeons, although they were weakly enforced.

New Zealand enacted its first law to protect native birds with the Wild Birds Protection Act of 1864 (earlier misguided regulations had instead protected introduced bird species). Shortly thereafter, the UK passed the Sea Birds Preservation Act of 1869, which restricted shooting and egg collecting during the breeding season. This act was followed by a series of Wild Birds Protection Acts in the UK between 1880 and 1896 that prohibited harvesting outside of certain seasons and taking the eggs of wild birds. These initial legislative efforts proved insufficient to curtail the loss of certain species but did fuel a more organized and widespread conservation movement.

Commercial plume hunting in the late 1800s was a turning point for early bird conservation. At this time, feathers (and sometimes entire birds) were considered fashionable adornments on women's hats (Fig. 15.02). Gaudiest were the plumes of several herons, such as the Great Egret (*Ardea alba*) and Snowy Egret (*Egretta thula*),



Fig. 15.02 Feathers as fashion accessories. The widespread use of feathers—and sometimes entire birds—as fashion accessories (A) led to the near extinction of some populations of egrets and other charismatic birds, thereby sparking some of the earliest bird conservation movements such as these early supporters of the Royal Society for the Protection of Birds in the United Kingdom (B). (Photographs courtesy of the Royal Society for the Protection of Birds.)

which bred in large rookeries. By the 1890s, the scale and biological effects of commercial plume hunting rivaled the wholesale slaughter of Passenger Pigeons two decades earlier. In North America, concern over plume hunting and the decline of birds led, in part, to the founding of the American Ornithologists' Union (AOU) in 1883, along with its influential Bird Protection Committee. In 1886 a charter committee member, George Bird Grinnell, established the Audubon Society dedicated to the protection of birds. In 1889 in the UK, the Royal Society for the Protection of Birds (RSPB) was similarly created in response to the feather trade; today the RSPB is one of the world's largest conservation organizations.

Despite laws regulating the commercial harvest of certain birds, widespread hunting and trading continued largely unchecked around the world until the early 1900s, when activists began focusing on trade rather than harvest. Catapulted by the social activism of local Audubon societies, the US government passed the landmark Lacey Act, which banned interstate shipments of birds killed in violation of any state or local law. Revisions to this act ultimately gave rise to the Migratory Bird Treaty Act in 1918, which implemented elements of the International Migratory Bird Convention Act signed in 1916 by Great Britain, Canada, and the USA. Later, other international treaties were incorporated into the act, including the Migratory Bird and Game Mammal Treaty with Mexico (1936), and the Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere (1940). International treaties that protect birds continued to be ratified around the world throughout the twentieth century; among the most important were the African Convention on the Conservation of Nature and Natural Resources (1968) and the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (1995).

Expanding the targets of conservation beyond the regulation of hunting and trade, major efforts to conserve birds by protecting their habitats came in the late 1800s and early 1900s. Preserves were created in many countries around the globe; in the late 1800s, for example, several New Zealand islands were named as sanctuaries for native birds such as the Kakapo (*Strigops habroptila*) and Kiwi (*Apteryx* species).

This period also saw the birth of broader, organized systems of protected areas. Partly in response to the plume trade, Theodore Roosevelt designated the first federal refuge in 1903 at Pelican Island, Florida, thereby launching the National Wildlife Refuge System within the USA. Not long afterward, Mexico's first wildlife refuge was established at Isla Guadalupe. The National Park concept remains a foundation of habitat conservation around the globe. In the USA, after establishment of the first National Park in Yellowstone (1872), a trove of other areas received similar protection through the newly created system of National Forests, National Parks, and National Monuments. Australia followed (1879), then Canada (1885), and New Zealand (1887). Today nearly 100 countries boast internationally recognized national parks. Among the most recent is Afghanistan, which created its first national park, Band-e-Amir, in 2009.

Habitat protection remains among the most important elements in bird conservation and involves every level of society. In addition to government-led efforts, a variety of non-governmental organizations promote protection and management of habitats for birds. An increasing number of places around the world are officially recognized for their international importance to birds. The Ramsar List of Wetlands of International Importance and the UNESCO World Heritage List are two examples of multinational conventions that have identified places of global importance

for conservation. BirdLife International now recognizes more than 11,000 Important Bird Areas (IBAs) around the globe, although legal recognition and protection of these areas vary widely among countries.

Bird conservation in the twentieth century was shaped profoundly by the public's increasing awareness of environmental problems and growing sense of collective responsibility for environmental protection. In an influential collection of essays titled *A Sand County Almanac,* Aldo Leopold (1949) established both a philosophical and a practical framework for treating the natural landscape as a long-term resource to be used carefully and held in safekeeping for future generations. Leopold introduced the concept of the "land ethic," whereby natural resources are seen to warrant the level of ethical consideration typically given to humans and human culture. A few decades later, the book *Silent Spring* by Rachel Carson (1962) exposed the devastating environmental effects of pesticides, which later were confirmed to be the cause of drastic declines in Peregrine Falcons (*Falco peregrinus*) and other raptors (Chapter 13).

In the 1970s, growing environmental concerns spawned the landmark legislation and international treaties that today provide strong legal mechanisms for bird protection. In 1973, the USA enacted its most far-reaching piece of environmental legislation, the Endangered Species Act (ESA). For the first time, individual species were legally recognized as possessing intrinsic value and rights to protection under law, regardless of how trivial or irrelevant any species might seem to human society. In 1972 the United Nations Conference on the Human Environment helped frame environmental policies and global treaties that eventually led to the Kyoto Protocol for greenhouse gas emissions. Conservation legislation in the European Union also continues to be shaped by milestone legislation that occurred in the 1970s, when the Birds Directive (1979) established a framework for conserving all birds throughout the European Union, banned activities that directly threaten birds, required that hunting be managed sustainably, eliminated nonselective and large-scale killing, and closely regulated the trade of live and dead birds.

Today, the most important global treaty for bird protection is the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), drafted in 1973 by the World Conservation Union (now the International Union for the Conservation of Nature and Natural Resources, IUCN). This international agreement, to which 175 countries now voluntarily subscribe, binds participating parties to monitor, regulate, or prohibit the international import and export of species deemed in need of global protection. The legal framework for enforcement within each participating country is provided by domestic laws. The heart of CITES lies in three appendices constituting the list of species for which international trade is restricted. Appendix I includes the most endangered species (including for example all macaws, many other parrots, and a few falcons), for which all commercial trade is strictly prohibited and special import/export permits are required for scientific transport. Appendix II lists species that are not in immediate danger of extinction but that could become so in the absence of regulation (for example, all parrots, hawks, and falcons not in Appendix I). Species may be added to or removed from Appendices I and II, or moved between them, only via discussion and vote at periodic CITES conferences. Appendix III lists species added by individual countries that, for any reason, request international assistance in regulating their trade. Without doubt, the international protection afforded by being listed as a CITES species has prevented many birds species from going extinct: until the loss of the last wild Spix's Macaw (*Cyanopsitta spixii*) in 2000 (Fig. 15.03), not a single bird species regulated by CITES had become extinct in the wild as a result of international trade.



Fig. 15.03 CITES regulations help preserve wild birds. One of the main benefits of CITES regulations is to ban the import and export of protected bird species. The Spix's Macaw (*Cyanopsitta spixii*) is one of the few CITES-protected bird species that has been extirpated in the wild owing to the captive bird trade. Hope remains that regulated captive breeding of this species will allow its future reintroduction into its former range. (Photograph by Alain Breyer.)

15.2 Conservation biology

As the disciplines of ecology, population biology, evolutionary biology, animal behavior, and genetics matured during the twentieth century, scientists also began to study the human-generated threats and biological attributes that were causing many species around the world to decline and go extinct. Gradually, these disciplines coalesced into

efforts to derive solutions to conservation problems, giving rise to the applied science now known as conservation biology. Today the field of conservation biology continues to grow in its number of practicing professionals, in the breadth and scope of its research, and in the global importance of its contributions to conservation issues.

Applied sciences like conservation biology generally combine basic principles of several fields to solve everyday problems and to accomplish specific, real-world tasks. Just as engineers use mathematics, physics, and chemistry to design bridges or fuel-efficient automobiles, conservation biologists employ basic biological disciplines in the effort to stabilize ecosystems and restore wild populations. Conservation biologists often face grim realities of impending disaster, and they work within ecological systems that differ vastly from one another and contain hundreds or even thousands of species that are engaged in myriad physical and biological interactions. The complexity of interactions among natural populations and the relative youth of the sciences engaged to understand them help explain why so many bird species went extinct between the sixteenth and twenty-first centuries, before humans could fully recognize the underlying problems and work to ameliorate the threats.

Successful bird conservation involves five integrated steps: (1) understanding the native functions and fluctuations characterizing bird populations, species, and ecological communities; (2) determining whether and how these natural conditions have been, or could be, perturbed by human impacts; (3) projecting how the desired conditions could be restored; (4) taking action for protection and management; and (5) measuring the consequences of alternative management scenarios. Understanding the decline of a bird population requires knowing basic facts about the species' evolutionary history, its degree of habitat specialization, and what regulates its populations. At the most basic level, all population declines fundamentally reflect changes in birth rates, death rates, and the area of available habitat, or combinations of these three parameters. The task of conservation biology is to pinpoint what has changed for the worse and to devise strategies for eliminating or mitigating those changes.

15.3 Recent avian extinctions

Bird species have been evolving and going extinct throughout their existence (Chapter 2). These past origins and disappearances have been driven by naturally occurring, long-term processes across the earth's surface. Continents split apart and came together. Volcanic islands arose from the sea and then eroded away. Earth's climate fluctuated between hot and cold, wet and dry. Such slow but enormous events made the extinction of species a natural feature of evolutionary change, as local environments shifted and species of different regions encountered and competed with one another. In fact, it is estimated that 99% of all bird species that have ever lived on earth are now extinct. So, why should we be concerned about bird species becoming extinct today?

The answer is simple: the wave of extinction currently underway is occurring at a pace and scale fully comparable to the five greatest extinction episodes in the earth's history, but this sixth **mass extinction** is directly caused by human activities across the globe. The physical and biological changes humans have caused on earth are so profound and widespread that a new expression—the **Anthropocene**—has been coined to describe this epoch in geological terms (Ellis 2011; Steffen et al. 2011). The worldwide spread of modern *Homo sapiens* has resulted in the extinction of about 8000 species of landbirds, according to recent estimates based on fossil deposits (Martin and Steadman 1999). Most biologists agree that human-caused extinctions now rival those associated with the events that extinguished the dinosaurs about 65 million years ago (Chapter 2). Such enormous ecological impact is outside the bounds of natural processes and therefore should be a matter of intense concern for all people who care about the natural environment.

15.3.1 Avian extinctions in the Anthropocene

On an evolutionary timescale, modern humans have spread across the globe only very recently from our origins in Africa, but we have had enormous impacts on birds everywhere we have colonized. A great wave of extinctions in Australia, for example, coincided with the arrival of humans on that continent about 50,000 years ago, apparently resulting in part from vastly increased fire frequency (Miller et al. 2005). Similar extinction patterns occurred near the time of human colonization on every land mass on earth except Africa. We cleared forests, replaced grasslands with crops, built towns, drained marshes, filled swamplands, irrigated dry areas, and suppressed natural fire in some places and increased its frequency in others. Everywhere we went, we hunted birds for food, clothing, and ornamentation. In each newly colonized area we

Mass extinction: in earth history, the *extinction* of an exceptionally large proportion of species within a relatively short period of time.

Anthropocene: the current geological age, marked by human activity having become a dominant influence on the earth's climate and environments.

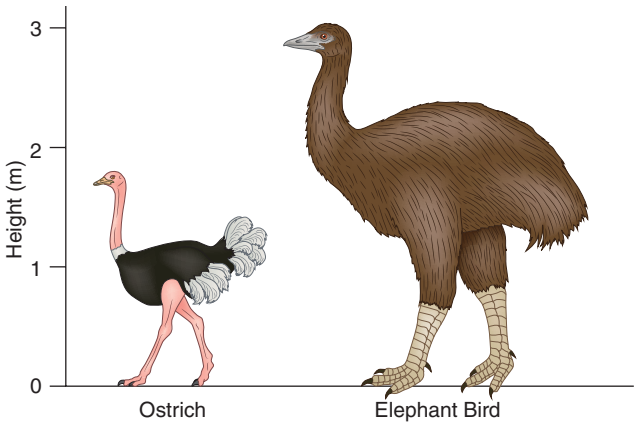


Fig. 15.04 The extinct Elephant Bird (*Aepyornis maximus*) of Madagascar. This was the largest known bird in history, and it briefly coexisted with humans: Elephant Bird remains have been found with traces of human butchery and many eggshells have been found in archaeological fire pits. Single eggs could feed entire human families, and this may be one reason this species went extinct around 1000 years ago—eggs would have been the most vulnerable stage of an Elephant Bird's life. An Elephant Bird (right) is shown next to an Ostrich (*Struthio camelus*) (left) for scale. (© Cornell Lab of Ornithology.)

encountered birds that had evolved no defenses against our evermore advanced hunting techniques and our steadily increasing numbers. On remote islands filled with uniquely adapted species, we introduced new avian diseases and new predators. On the continents we did the reverse, systematically destroying the largest predators—wolves, bears, and big cats—and thereby releasing cascades of herbivores and middle-sized predators that altered ecosystems in numerous ways (Prugh et al. 2009). Everywhere, we introduced domesticated herbivores into habitats that had evolved without them. By steadily making the world more accommodating for ourselves, we profoundly altered every natural system we encountered. The effects on birds have been devastating.

Humans began documenting the world's birds in modern scientific terms—with written records, paintings, and preserved specimens—around AD 1500. By that time, tropical islands the world over already had been ravaged, resulting in the loss of many hundreds of bird species now known only from a few bones or descriptions by early explorers. Many birds on predator-free islands had lost the need for flight, resulting in the evolutionary reduction of their wings. Included among the pre AD 1500 extinctions are some of the most unusual and spectacular birds ever to have evolved, including the 400-kilogram Elephant Bird (*Aepyornis maximus*) on Madagascar (the largest modern bird known) (Fig. 15.04), at least 10 species of moas in New Zealand (Chapter 2), flightless ibises on Hawaii, flightless owls on Caribbean islands, flightless pigeons on Indian Ocean islands, and probably thousands of other island-dwelling bird species, including numerous flightless rails, worldwide.

Humans began populating North and South America less than 20,000 years ago and reached the Caribbean Islands around 6500 years ago. These earliest Native Americans spread rapidly across the hemisphere, introducing wholly new ecological forces that coincided with a spectacularly swift and catastrophic disappearance of animals. Most dramatic was the nearly complete extinction of the New World **megafauna**, a varied assemblage of large mammals that included horses, camels, giant sloths, mammoths and mastodons, glyptodonts, gomphotheres, saber-toothed cats, and many others. Why such a large and diverse animal fauna disappeared so suddenly between 12,000 and 8000 years ago remains hotly debated. The tight coincidence between human arrival and the disappearance of the megafauna strongly suggests that humans were a primary cause, perhaps setting in motion a cascade of extinctions compounded by rapid habitat changes, disappearance of keystone species, direct predation by humans, and human-borne diseases to which the native fauna had no immunity.

Extinction of the western hemisphere megafauna included dozens of species of birds as well as mammals. The most spectacular of these birds included many species of scavengers that lived on the carcasses of large mammals, as African vultures do today. These extinct vultures, condors, and teratorns (giant, soaring scavengers apparently only distantly related to vultures) included some of the largest flying birds ever to have lived. They once occurred throughout the western hemisphere and dwarfed today's raptors (Fig. 15.05).

Until a few thousand years ago the Caribbean Islands also harbored remarkably diverse assemblages of now-vanished landbirds, including crows, large flightless owls, numerous macaws, giant parakeets, and nightjars. Bones of these species are found at human archaeological sites dating back only 3000–4000 years (Pregill et al. 1994). Just as they did later across the islands of the Pacific, humans caused a steady disappearance of birds in these fragile tropical islands, both by cutting down the forests and by killing and eating the birds directly. Today, only a small fraction of the original bird fauna persists in the Caribbean, and many of these—including parrots, doves, nightjars, woodpeckers, thrashers, and orioles—are among the most seriously threatened in the world.

Megafauna: continental assemblages of exceptionally large-bodied mammals and birds, most of which (except in Africa) became extinct as humans spread across the world's continents and islands.

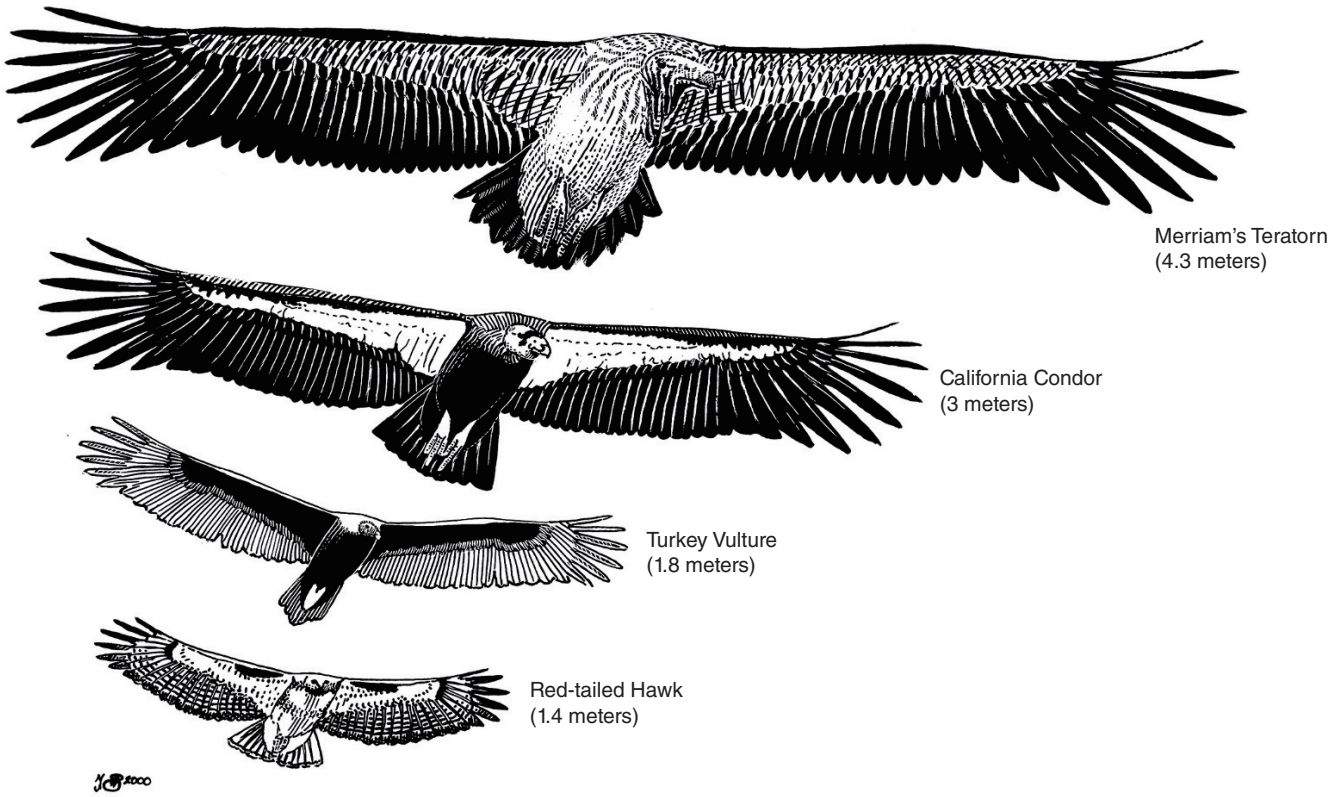


Fig. 15.05 Wingspan of Merriam's Teratorn (*Teratornis merriami*) compared with living raptors. Similar to modern vultures, the teratorn group (now extinct) scavenged carcasses in open landscapes. However, when the prehistoric megafauna that composed the teratorn diet went extinct around 10,000 years ago, teratorns soon followed. Here, the wingspan of Merriam's Teratorn is compared with the wingspans of some modern raptors and vultures (three bottom species). (Illustration by N. John Schmitt.)

15.3.2 Historical extinctions on oceanic islands

As of 2014, the IUCN Red List for birds tallied 130 bird species known to have gone extinct since AD 1500, plus four species classified as "extinct in the wild." The 198 additional species classified as Critically Endangered include many that have not been sighted in recent decades and which also may be extinct. These modern extinctions demonstrate much about the impacts of humans on the world's birds. The most obvious pattern is that all but a handful of extinct species were restricted to oceanic islands where the earlier absence of humans and other mammals had left birds especially vulnerable to predation and habitat change.

Flightless birds were especially easy prey for humans and their domesticated cats. For example, on Mauritius Island in the Indian Ocean, sailors drove the naïvely fearless Dodos (*Raphus cucullatus*) (Fig. 15.06) aboard their ships to serve as food for ensuing weeks at sea. The species was last observed in 1662, and not a single whole specimen has been preserved. A close relative of the Dodo, the Rodrigues Solitaire (*Pezophaps solitaria*), met a similar fate. On another nearby island lived a large and poorly documented bird once called the Reunion "Solitaire" (*Threskiornis solitarius*); recently uncovered bones show that this extinct bird was not related to the Dodo but rather was an ibis (Mourer-Cauviré et al. 1995). In the North Atlantic, sailors feasted on the abundant Great Auk (*Pinguinus impennis)* (Fig. 15.07A), and fishermen even chopped them up to use as bait; the last Great Auk was killed in 1844. In the Bering Sea, Pallas's Cormorant (*Phalacrocorax perspicillatus*) (Fig. 15.07B), the largest member of its family, vanished at about the same time, and for similar reasons as the whaling industry expanded across the North Pacific. In the islands of the South Pacific, numerous species disappeared as introduced mammals spread among the islands. Notable among the dozens of species lost from Pacific islands were several species of New Zealand wren (suborder Acanthisitti), an ancient and enigmatic lineage of tiny insectivorous songbirds that had included three flightless species (Fig. 15.08).

The full list of modern extinctions is dominated by rails, parrots, pigeons, and Hawaiian honeycreepers (Box 15.01). This highly non-random taxonomy of avian extinction is largely a consequence of the propensity for certain bird groups to colonize oceanic islands and evolve into unique—and vulnerable—island endemics.

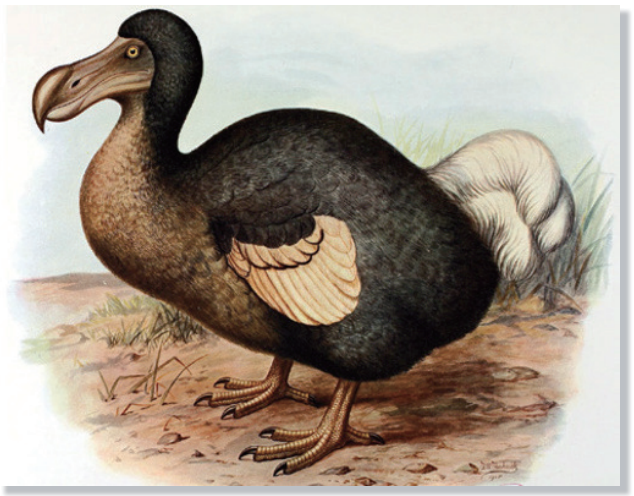


Fig. 15.06 Dodo (*Raphus cucullatus*). This flightless inhabitant of Mauritius Island was an easy target for hungry sailors and the introduced pigs, cats, and rats they left behind. Dodos, along with now-extinct native tortoises, may have dispersed and enabled the hard-shelled seeds of several trees to germinate, as their digestive tracts scoured the hard seed exteriors. Introduced tortoises are now employed to help conserve native tree species in place of these extinct species. (Artwork by Frederick William Frohawk, from Rothschild 1907, public domain.)

15.3.3 Historical extinctions on continents

Continents largely have been spared the massive wave of recent avian extinctions that have occurred on islands, although this trend may be reversing (Butchart et al. 2006b). Avian extinctions are so rare on continents that it is possible to list them all here.

North America has lost the most bird species among continental land masses, with at least three and probably five or six species disappearing since 1850. The Labrador Duck (*Camptorhynchus labradorius*) apparently bred on rocky islands off the Gulf of St. Lawrence, where it was exposed to plume hunting, egg robbing, and introduced mammalian predators. The last Labrador Ducks were shot in the 1870s, just as Passenger Pigeons (*Ectopistes migratorius*) were becoming history's most spectacular example of overexploitation. The Carolina Parakeet (*Conuropsis carolinensis*) declined rapidly throughout the 1800s because of forest clearing and hunting (Fig. 15.09). By 1890 only the most remote forests of central Florida harbored a few parakeets; small flocks were seen through 1915, but reliable reports ceased in the early 1920s. Immense flocks of Eskimo Curlews (*Numenius borealis*) migrated north through the Great Plains in spring and then southeastward in fall across eastern Canada and the Atlantic Ocean to winter in Patagonia. During spring migration curlews depended on prairie insects, especially in areas recovering after wildfires or bison trampling. By the late 1800s such critical habitat patches were virtually eliminated by agricultural conversion, suppression of wildfire, and annihilation of the great bison herds. Some accounts suggest that migrating Eskimo Curlews relied on enormous swarms of Rocky Mountain

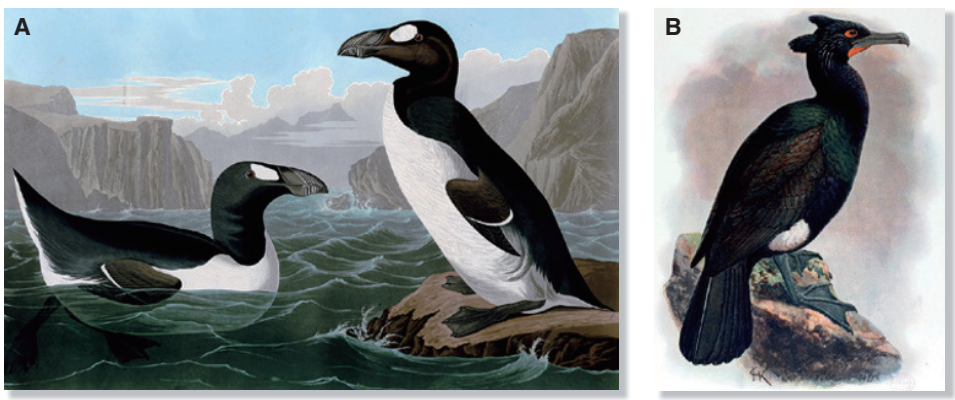


Fig. 15.07 Extinct seabirds. (A) Prehistoric Great Auk (*Pinguinus impennis*) bones, recovered from middens and caves in much of northwest Europe, suggest that they were heavily hunted long before sailors and fisheries destroyed populations off northeastern North America starting in the 1700s. The Great Auk was extinct by 1844. (B) Pallas's Cormorant (*Phalacrocorax perspicillatus*), the largest species of cormorant ever known, met a similar fate. Whalers and fur trappers began overhunting populations off the northeastern Russian coast and Rocky Islands around 1750. The species became extinct about 100 years later. (Artwork by: A, John James Audubon, from Audubon 1827–38, public domain; B, John Gerrard Keulemans, from Rothschild 1907, public domain.)



Fig. 15.08 Bush Wren (*Xenicus longipes*). Once widespread across New Zealand, populations crashed by the early twentieth century owing to introduced mammalian predators. Small numbers of a distinct subspecies persisted into the 1960s, but the final attempt to relocate them to a predator-free island failed in 1972. (Artwork by John Gerrard Keulemans, from Buller 1888, public domain.)

grasshoppers, which also mysteriously went extinct around 1900 (Lockwood and DeBrey 1990). A few Eskimo Curlews were collected in South America through the early 1920s, and the last documented occurrence was a single bird photographed near Galveston, Texas in 1962.

Hopes are now dim for the continued survival of two specialized denizens of the forests and bottomlands of southeastern North America, the Ivory-billed Woodpecker (*Campephilus principalis*) and Bachman's Warbler (*Vermivora bachmanii*). Ivory-billed Woodpeckers lived in the treetops of old-growth pine and bottomland hardwood forests, foraging on beetle larvae by chipping the bark from large, dying trees. These great forests experienced wildfires, floods, hurricane damage, and destruction by massive wintering colonies of Passenger Pigeons, thereby providing copious dead and dying wood, the critical resource for this powerful woodpecker. By the early 1900s the old-growth forests had been logged, fires were being suppressed, and remnant Ivory-billed Woodpeckers were being collected as specimens whenever spotted. No Ivory-billed Woodpecker nest has been found in North America since the 1930s, and the last photographic record from Cuba was in 1956. Credible reports did persist, however, and an intriguing series of encounters in 2004/2005 (Fitzpatrick et al. 2005) spawned a multi-year, range-wide search involving hundreds of participants. Nevertheless, no indisputable evidence exists that the species survives today. Bachman's Warblers preferred dense forest openings and cane thickets, perhaps favoring habitats regenerating after hurricanes. The species declined as forests were converted to farmlands, and the rich floodplains were channelized and drained. Bachman's Warbler experienced double jeopardy because its sole wintering grounds (Cuba and the Isle of Youth) also underwent rapid habitat conversion into sugar cane plantations. The last confirmed Bachman's Warbler was a singing male that returned to the same location in South Carolina for three successive breeding seasons in 1958, 1959, and 1960.

Box 15.01 Modern avian extinctions

This box lists those avian groups with significantly more recently extinct species ("Extinct," "Extinct in the Wild," and "Possibly Extinct") than expected by chance. The extinction number for rails (Rallidae) is probably a great underestimate, as many island populations of rails became recently extinct before they were described formally by scientists.

Family	No. species	No. extinct	% extinct
Acanthisittidae (New Zealand wrens)	7	5	71%
Drepanidinae (Hawaiian honeycreepers)	34	16	47%
Casuariidae (Cassowaries and emus)	5	2	40%
Callaeidae (New Zealand wattled crows)	5	2	40%
Upupidae (hoopoes)	3	1	33%
Rallidae (rails)	156	23+	15+%
Podicipedidae (grebes)	22	3	14%
Ardeidae (herons)	67	4	6%
Psittacidae (parrots)	374	20	5%
Columbidae (pigeons)	320	15	5%
Sturnidae (starlings)	114	5	4%
Anatidae (ducks, geese, swans)	164	7	4%

Modified from Butchart et al. 2006a.



Fig. 15.09 Carolina Parakeets (*Conuropsis carolinensis*). The Carolina Parakeet was the only species of parrot native to the USA and Canada. Though the precise reasons for its extinction remain unknown, extensive hunting, deforestation, and disease are all implicated as potential factors. (Watercolor by Francis Lee Jaques, courtesy of Madelyn Morey.)



Fig. 15.10 Imperial Woodpeckers (*Campephilus imperialis*). Now extinct, this was the world's largest woodpecker. The species depended on large tracts of mid-montane pine-oak forests in western Mexico. Before the mid-twentieth century, small social groups were seen foraging on dead trees, although the species was poorly known. The last confirmed birds were observed before logging operations destroyed much of their preferred habitat; hunting and harvesting young were additional factors leading to their extinction. (Illustration by N. John Schmitt.)

Avian diversity reaches its global peak in Central and South America, but together these continental land masses are known to have lost only five bird species: one resulting from habitat destruction, one from illegal trade, and three from degradation of local wetland ecosystems. The colossal-sized Imperial Woodpecker (*Campephilus imperialis*) (a close relative of the Ivory-billed Woodpecker) occupied old-growth pine forests of the Cordillera Occidental in western Mexico until these forests were obliterated by logging (Fig. 15.10). The species has not been documented since 1956. The Colombian Grebe (*Podiceps andinus*) was endemic to a wetland system near Bogotá (especially Lake Tota). Systematic drainage, increased concentration of pollutants, dramatically altered aquatic vegetation, and introduced rainbow trout combined to cause a grebe population collapse in the mid-twentieth century, and the last individuals were seen in 1977. The flightless Atitlan Grebe (*Podilymbus gigas*), endemic to Lake Atitlan, Guatemala, met a similar fate during the same time period, apparently accelerated by competition for food from introduced bass. The Slender-billed Grackle (*Quiscalus palustris*) was endemic to marshlands in a tiny area of central Mexico which over hundreds of years have been systematically ditched and drained for agricultural uses and urban development. The last free-flying Spix's Macaw (*Cyanopsitta spixii*) disappeared from southeastern Brazil in 2000 (Fig. 15.03). Its decline throughout the twentieth century began with widespread clearing of its forest habitat but was hastened by persistent capturing for illegal trade. Fortunately, this spectacular species persists in captivity, providing hope that someday it can be successfully reintroduced into its native habitat.

Remarkably, the continental mainlands of Europe, Asia, Africa, and Australia appear to have lost only two bird species among them during recorded history. The mysterious, non-migratory Pink-headed Duck (*Rhodonessa caryophyllacea*) was always rare across the marshlands of the Indian subcontinent (Fig. 15.11). Wetland drainage throughout its limited range hastened its disappearance. Although occasional unsubstantiated reports continue, reliable sightings ceased after 1935. The colorful Paradise Parakeet (*Psephotus pulcherrimus*) (Chapter 14) once was common in grassy woodlands within a limited range in northeastern Australia but began declining rapidly near the end of the nineteenth century as a result of land clearing, overgrazing, hunting, and predation by introduced mammals. The bird was believed to be extinct for a time and then was rediscovered, but the last confirmed sighting was in 1927. Similarly, the mysterious, nocturnal Night Parrot

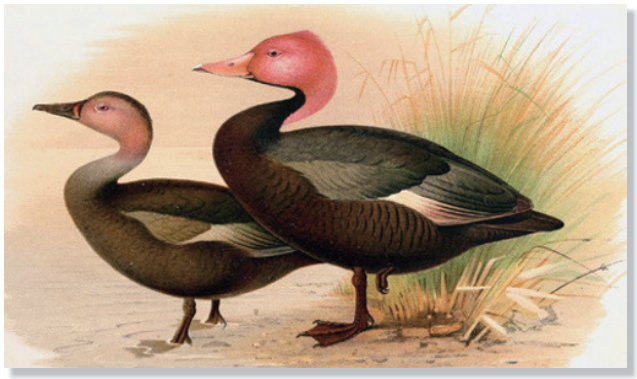


Fig. 15.11 Pink-headed Duck (*Rhodonessa caryophyllacea*). Always considered rare, this species was native to India, Bangladesh, and Myanmar; the last confirmed sighting was in 1935. (Artwork by Henrik Grönvold, from Wall 1908, public domain.)



Fig. 15.12 Night Parrot (*Pezoporus occidentalis*). This is an extremely rare, nocturnal parrot that inhabits grasslands and swamps of western Queensland (Australia), feeding mainly on grass seed. Its population status remains a mystery, but a few live birds have been observed recently. (Photograph by Peter W. Lindenburg.)

(*Pezoporus occidentalis*) of Australia has been reported only a few times in recent decades, and has long hovered around the list of modern avian extinctions. Recent evidence suggests the existence of at least a tiny population in western Queensland (Fig. 15.12).

15.4 Causes of avian population declines

Except through cataclysmic geological events, extinctions do not happen overnight. Instead, species decline from forces acting over time—from just years in exceptional cases, as with naïve or flightless island birds faced with introduced predators, to decades or longer when the cause is slow conversion of essential habitat. Bird populations are extremely sensitive to changes in the composition, function, and stability of their natural communities and ecosystems. Devising conservation solutions requires first identifying the forces that are causing the declines, most of which fall into two interacting categories: extrinsically imposed stressors or threats (nowadays mostly brought about by humans) and intrinsic biological attributes that provide evolutionary advantages under natural conditions but can make a species vulnerable as environmental conditions change.

15.4.1 Demography, habitat, and life histories

All populations fluctuate year to year, but average numbers can remain stable over time because average birth rates and death rates are balanced. As covered in more detail in Chapter 13, the scientific study of birth rates and death rates, called **demography**, plays an enormous role in conservation biology. Age-specific birth rates and death rates specify, for individuals at each age, their average number of offspring produced and their probability of dying. Age-specific death rates compound to produce a schedule of **survivorship**, the probability of being alive at a given age. Population stability over any given time period requires that, on average, the total accumulated reproductive output from all age classes matches the number of deaths occurring during that same period. Therefore, understanding the factors that affect birth rates and death rates is essential in conservation research.

The word **habitat** also holds a crucial place in conservation biology and refers to the comprehensive range of physical, biological, and geographic conditions required by individuals of a given population in order to survive and/or reproduce. As discussed later, bird species vary considerably in their tolerance limits for environmental conditions. Conservation biologists devote enormous effort to

Demography: the statistical study of vital rates within a population, especially age-specific birth rates, death rates, and dispersal patterns.

Survivorship: in a demographic life table, the probability of being alive at a given age.

Habitat: the comprehensive range of physical, biological, and geographic conditions required by individuals of a given population to survive and/or reproduce.

understanding in detail the extent and nature of these habitat tolerances. Conservation practitioners devote similarly huge efforts to ensuring that sufficient habitat area exists and is properly managed.

All bird populations have an evolutionary history. In adapting to the range of environmental conditions characterizing its habitat, every population evolves numerous **life history traits** that provide survival and reproductive advantages within that habitat (Chapter 13). For birds, some of the most important variables relevant to conservation are the period of nest dependency, period of juvenile dependency, age at first breeding, mating system, age-specific clutch size, reproductive lifespan, and dispersal/migration pattern. Understanding long-term changes in population numbers requires identifying how environmental changes interact with these life history attributes to cause changes in birth rate, death rate, and distribution of suitable habitat, or a combination of these factors.

15.4.2 Habitat specialization and the six forms of rarity

Outright habitat loss obviously leads to population decline for any species that depends on that habitat, but not all species are affected equally. Certain species are more vulnerable than others when native habitats disappear. Rare species generally are more vulnerable than common ones, but what exactly does "rare" mean? Most species thought of as naturally rare actually are (or once were) reasonably common in one or a few localized areas and may have very specific habitat requirements. Protecting their local geographic centers or special habitats may be sufficient to ensure these species' survival, but if these primary centers of occurrence have been destroyed, then protecting such species is extremely challenging. Identifying the nature of a target species' rarity is a critical step in designing its protection and recovery.

Three features of a species' distribution affect its vulnerability: its overall geographic distribution (range size); the overall numbers of the species within its range (population density); and the spectrum of habitats in which the species can live and breed (habitat specificity). Deborah Rabinowitz et al. (1986) categorized British plants according to these three variables to produce a simple framework for identifying seven different forms of rarity, six of which are relevant to birds (Fig. 15.13). Below we describe these six forms of rarity and give examples of endangered birds that fit each category:

Life history traits: any of the fundamental traits that directly influence an individual bird's survival and reproduction. Examples include lifespan, age at first reproduction, and number and size of offspring produced per year.

Habitat specialization		Generalist		Specialist	
Local abundance		High	Low	High	Low
Geographic range	Large	N/A	1	2	3
	Small	4	N/A	5	**6**

Fig. 15.13 Six forms of rarity in birds. Geographic distribution (large or small), local abundance (high or low), and habitat specialization (generalist or specialist) are all factors that influence vulnerability. Species in category 6—which are highly specialized with small populations and a narrowly local range—typically have the greatest risk of extinction. (From Rabinowitz 1981. Reproduced with permission from John Wiley and Sons.)



Fig. 15.14 Crowned Hawk-Eagle (*Stephanoaetus coronatus*). As one of the largest and most powerful eagles of Africa, the Crowned Hawk-Eagle is a species of increasing concern because of habitat destruction, hunting, and trapping. Although this species is a widespread, generalist predator, its population density is low even in patches of preferred habitat, which makes it vulnerable. (Photograph by Peter R. Steward.)

Rarity form 1: Widely distributed, small local populations with broad habitat tolerance

Most continental raptors fit this category, which explains why few other than the very largest eagles appear on endangered lists. Being at the top of the food chain, hawks and owls generally have large home ranges and consequently low population densities. The Crowned Hawk-Eagle (*Stephanoaetus coronatus*) (Fig. 15.14) of sub-Saharan Africa is the second largest eagle on that continent and recently was moved to a higher risk category by the IUCN because, although the bird occurs across a wide range of forested habitats, its populations suffer persecution from local farmers. The Lesser Kestrel (*Falco naumanni*) breeds in a variety of open habitats across Europe and Asia, and winters broadly across Africa. Once listed as Vulnerable



Fig. 15.15 Red-cockaded Woodpecker (*Picoides borealis*). An endemic of the southeastern USA, this species is locally common, but highly specialized on long-leaf pine forests that depend on frequent burn cycles to remain healthy. As primary cavity excavators, Red-cockaded Woodpeckers provide a service to numerous other secondary cavity-nesting species. (Photograph by Juli Wells.)

because intensifying agriculture and pesticide use caused sharp declines across its entire breeding range, the species has rebounded since 2000 and recently was reclassified as Least Concern (BirdLife International 2016a).

Rarity form 2: Widely distributed, large local populations with narrowly specialized habitat requirements

Numerous declining bird species fit this category as humans reduce and fragment populations of once-widespread ecological specialists. Red-cockaded Woodpeckers (*Picoides borealis*) originally were common in old-growth pine savannas across the entire southeastern USA (Fig. 15.15). This cooperative-breeding woodpecker nests in cavities excavated high on the trunks of living pines and protects its nests from predation by snakes and small mammals by drilling tiny "resin-wells" into the surrounding bark, producing a barrier of sticky pine pitch. Red-cockaded Woodpeckers nest almost exclusively in mature long-leaf pine stands in which fungus renders the center of certain trunks soft enough to hollow out. They also require an open, grassy understory and gradually disappear from pine forests that are not burned regularly. Therefore, populations persist today only in well-managed locations where mature pine stands remain uncut and are burned every 2–3 years.



Fig. 15.16 Piping Plovers (*Charadrius melodus*). A recently hatched Piping Plover nestling is guarded by its parent. This species exists only in small, local populations. It prefers to nest in sparsely vegetated sandy beaches, making it vulnerable to coastal development, introduced predators, and rising sea levels related to climate change. (Photograph by Brendan Toews Photography.)

Oilbirds (*Steatornis caripensis*) are found broadly across the tropical forested regions of northern South America, but they are locally common only at their widely scattered breeding colonies. These nocturnal birds have a highly specialized breeding habitat, as they nest only within large, dark caves (Chapter 12).

Rarity form 3: Widely distributed, small local populations with narrowly specialized habitat requirements

Small population size combined with habitat specialization render species in this category vulnerable despite their broad geographic ranges. Piping Plovers (*Charadrius melodus*) (Fig. 15.16) breed on barren sandy beaches from central Canada and the Great Lakes east to the Atlantic coast of North America, but even the largest of these beaches rarely harbors more than two or three pairs. Its narrow habitat tolerance places the species directly in competition with humans, who also love sandy beaches. Consequently, Piping Plovers always will be vulnerable simply because of insufficient breeding habitat free of human disturbance, and the species now depends on active protection of nest sites by humans. A recent analysis suggests that this species will be particularly vulnerable to rising sea levels and storm surges resulting from climate change (Seavey et al. 2011). The endangered White-headed Duck (*Oxyura leucocephala*) (Chapter 3) breeds in scattered populations across Europe and western Asia on small, semipermanent or temporary lakes that have extensive areas of shallow water with fringes of dense emergent vegetation and pondweeds. Numbers have plummeted because of wetland

draining, pollution, and hybridization with Ruddy Ducks (*Oxyura jamaicensis*) introduced from North America (Muñoz-Fuentes et al. 2007) (Chapter 3).

Rarity form 4: Small geographic range, large local populations with broad habitat tolerance

This form of rarity is often seen in bird species that are restricted to islands, where they may have small global population sizes despite being common within their restricted range. For example, the Gray Trembler (*Cinclocerthia gutturalis*), an odd member of the mockingbird family that gets its name from its habit of quivering its body and tail while singing, is found only on the islands of Martinique and St. Lucia in the Lesser Antilles (Fig. 15.17). The global range of the Gray Trembler is therefore small, but within those islands the species is relatively common across a range of habitat types, from lowland dry scrub to high-elevation tropical forest.



Fig. 15.17 Gray Trembler (*Cinclocerthia gutturalis*). Island species like the Gray Trembler may be quite common in their native range and occupy a variety of habitats, but they are vulnerable because their global range is small. (Photograph by Ed Schneider.)

Rarity form 5: Small geographic range, large local populations with narrowly specialized habitat requirements

This category probably contains the largest proportion of at-risk bird species around the world. Most geographically restricted species, even those with narrow habitat tolerances, can be locally common in places where their specific habitat needs are met. However, they easily become threatened if those habitats are altered. For example, the spectacular Strange-tailed (*Alectrurus risora*) and Cock-tailed (*Alectrurus tricolor*) Tyrants remain locally common within their limited ranges in grasslands of southeastern South America (Fig. 15.18). However, global numbers of both species are plummeting, as are those of many other grassland specialists, because of agricultural conversion and persistent burning of grasslands for livestock foraging (Di Giacomo et al. 2011). All around the world, bird species in this important category of rarity depend on the protection and long-term management of habitat patches within their respective native ranges.

Rarity form 6: Small geographic range, small local populations with narrowly specialized habitat requirements

Species in this category are the world's most vulnerable, because local perturbations or catastrophes can extinguish them immediately. Temperate zone habitats of North America and Eurasia contain few avian examples, because most birds on these large continents have large ranges compared with other, more sedentary and vulnerable groups of organisms such as plants, stream fishes, freshwater mollusks, and cave-dwelling arthropods (Stein et al. 2000). Throughout the world's tropical realms, however—both on



Fig. 15.18 Two at-risk South American flycatchers. Species around the globe are vulnerable to extinction when they are locally common but highly specialized and limited to a small geographic range. (A) The Strange-tailed Tyrant (*Alectrurus risora*) requires tall-grass marsh habitat. (B) Similarly, the Cock-tailed Tyrant (*Alectrurus tricolor*) occurs in limited areas of humid and seasonally dry tall-grassland habitats. Both are threatened by rapid agricultural and grazing habitat conversion. (Photographs by: A, Cláudio Dias Timm; B, Scott Olmstead, https://en.wikipedia.org/wiki/File:Cock-tailed_Tyrant_(Alectrurus_tricolor)_perched.jpg. CC-BY-SA 2.0.)

islands and on continents—many ecologically specialized and locally endemic birds also have naturally low population densities. Such species are vulnerable to every threat discussed in this chapter. Examples include numerous island-endemic species of hawks, owls, and nightjars, such as the Mauritius Kestrel (*Falco punctatus*), Seychelles Scops-Owl (*Otus insularis*), and Puerto Rican Nightjar (*Antrostomus noctitherus*). Many bird species similarly occupy tiny ranges on isolated mountain ridges across the world's tropics, and those having low population densities, such as Bannerman's Turaco (*Tauraco bannermani*) (Fig. 15.19) of western Cameroon, are especially at risk as forests are cleared.



Fig. 15.19 Bannerman's Turaco (*Tauraco bannermani*). Among the rarest and most vulnerable species in the world, Bannerman's Turaco is range restricted, locally rare, and highly specialized. Tropical species such as this turaco are particularly at risk because of their dependence on habitats that occur only in a single geographic area, which are easily lost to habitat conversion. (Photograph by Paul Ellis.)

15.5 Major threats to bird populations

The IUCN recognizes 11 categories of threats facing the world's living species (IUCN 2012). These IUCN categories differ widely from one another in how and where they affect birds (Box 15.02). Several of the IUCN categories lump extremely important human-caused threats to birds together under a single designation. For example, direct hunting and killing are lumped together with timber extraction, under the heading "Biological resource use." Here we describe the most important threats causing bird population declines.

Box 15.02 International Union for Conservation of Nature and Natural Resources (IUCN) categories of threats to living species

This box lists IUCN-identified threats and their proportional contributions to the "Endangered" and "Critically Endangered" status of bird species by geographic region. Columns sum to more than 1 because many species face multiple threats.

IUCN threat	Antarctica	Caribbean	Asia	Europe	Africa	Meso-America	South America	Oceania	North America
Residential and commercial development	0	0.21	0.38	0.08	0.14	0.33	0.42	0.15	0.23
Agriculture and aquaculture	0	0.71	0.83	0.42	0.76	0.64	0.83	0.50	0.37
Energy production and mining	0	0.12	0.15	0.17	0.08	0.06	0.20	0.09	0.13
Transportation and service corridors	0	0.06	0.11	0.08	0.14	0.11	0.17	0.07	0.10
Biological resource use	0.55	0.65	0.94	0.58	0.80	0.53	0.68	0.54	0.70
Human intrusions and disturbance	0.18	0.12	0.29	0.25	0.23	0.06	0.04	0.14	0.18
Natural system modifications	0.09	0.21	0.30	0.25	0.33	0.08	0.26	0.19	0.15
Invasive and other problem species and genes	0.55	0.59	0.22	0.42	0.53	0.39	0.23	0.90	0.85
Pollution	0.00	0.12	0.26	0.17	0.15	0.17	0.11	0.05	0.21
Geological events	0.09	0.09	0.02	0.00	0.02	0.08	0.02	0.06	0.07
Climate change and severe weather	0.36	0.50	0.32	0.25	0.44	0.36	0.24	0.56	0.62

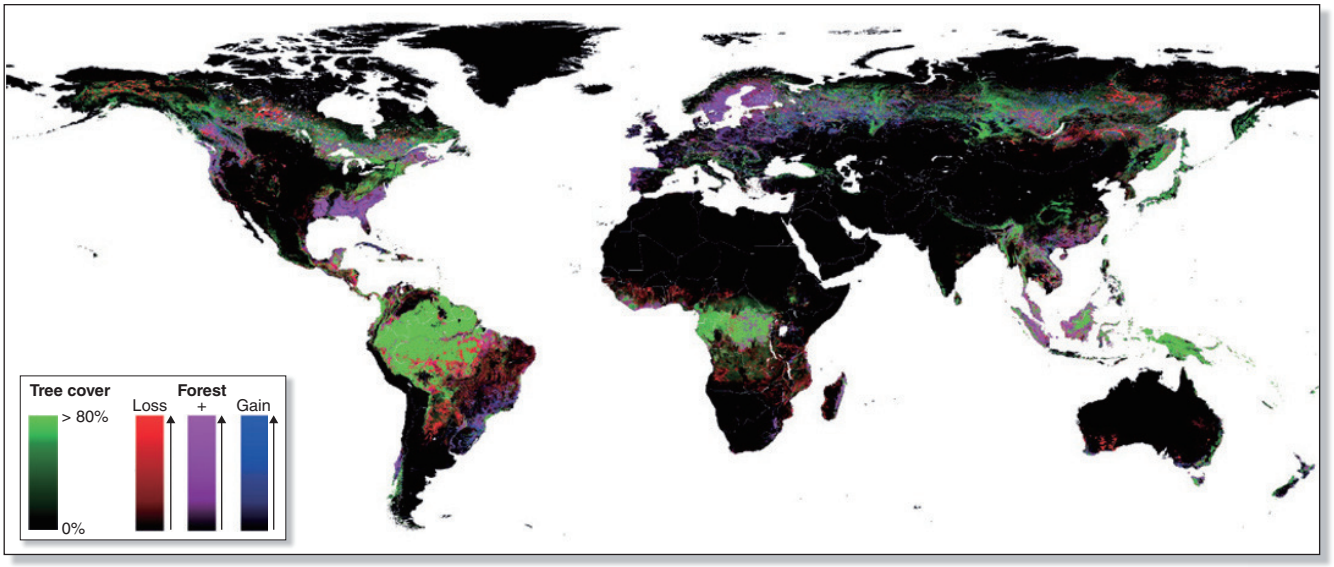


Fig. 15.20 Forest turnover worldwide. Using high-resolution satellite imagery, this map characterizes forest extent (green), gain (blue), loss (red), and both gain and loss (magenta) from 2000 to 2012. During this 12-year study, 2.3 million square kilometers of forest were lost, and 0.8 million square kilometers were gained (through regrowth and planting initiatives). Deforestation in the tropics is of particular conservation concern; the extent of tropical forest at the turn of the twentieth century was twice that of today. (From Hansen et al. 2013. Reproduced with permission from AAAS.)

15.5.1 Habitat loss

The most pervasive cause of avian population declines worldwide is loss of suitable habitat. All birds have unique adaptations that allow them to take advantage of specific and predictable features of their habitat. Humans have continually changed the structure, composition, and distribution of habitats, eliminating some and grossly changing others, but we cannot change the fundamental requirements of the bird species that use these habitats. For example, across North America, Europe, and Asia native prairies and steppes have been converted to grow grain crops or introduced forage grasses, thereby reducing population sizes of the grassland larks, pipits, shrikes, sparrows, and buntings that rely on native grassland habitats. By draining wetlands to create more areas for grazing or cultivation, humans similarly have reduced the total number of ducks, grebes, and shorebirds. Forests have been cleared for timber, agriculture, and livestock; coastlines and shorelines have become centers for residential and commercial development; and native scrubs have been replaced with pines and eucalyptus. All such cases of widespread habitat modification have resulted in dramatic declines among the birds adapted to the orginal habitats.

Worldwide, forest habitat continues to be lost at an unsustainable rate, especially in the tropics, and the loss of forest is a particularly prominent conservation concern (Fig. 15.20). Indonesia, for example, supports the third-largest expanse of tropical forest in the world, at almost 100 million hectares; only the forests of Amazonia and the Congo Basin are larger. A recent report found that Indonesia's rates of forest clearing and conversion to oil palm plantations are accelerating, placing it among the five countries with the highest percentage of primary forest loss (Wich et al. 2011). Indonesia's numerous tropical islands harbor hundreds of locally endemic forest birds, almost all of which are declining as their habitat is converted. On Madagascar a number of birds are similarly poised on the brink of extinction because of the centuries-long conversion of the island's habitats into vast grazing lands and rice paddies. The Madagascar Serpent-Eagle (*Eutriorchis astur*) (Fig. 15.21), suspected to be extinct since the 1930s, was rediscovered in the early 1990s but exists only as a tiny population in a remote forest tract at the northeastern corner of the island. Owing to the evolutionary uniqueness of the flora and fauna of Madagascar (Chapter 3), considerable international assistance has been focused on helping its government identify the best remaining patches of native habitat and secure them as ecological preserves. Today, however, a tremendous increase in illegal logging threatens to undermine these efforts (Randriamalala and Liu 2010).

Non-forest habitats are mentioned less frequently than forest in most discussions of habitat loss, but many such habitats are also at the highest level of conservation concern. For example, arid habitats in the wheatbelt region of Western Australia, part of which is recognized formally as a National Biodiversity Hotspot, face continued pressure from agriculture and other stressors that threaten its many endemic species. The Brazilian cerrado similarly



Fig. 15.21 Madagascar Serpent-Eagle (*Eutriorchis astur*). This rare eagle persists only because some of its important lowland Madagascar forest habitats have been protected by international conservation efforts. Unfortunately, illegal logging continues throughout Madagascar, leaving this bird's future uncertain. (Photograph by Russell Thorstrom.)

ranks among the 25 global biodiversity hotspots (Myers et al. 2000), and almost 5% of its more than 770 bird species are endemics (Fig. 15.22). Two-thirds of the cerrado's original extent has been converted to agriculture (mainly soybeans) over the past 40 years (Cavalcanti and Joly 2002). Estimates suggest that the cerrado could be gone entirely by 2030, and progressive extinctions of its avifauna will have detrimental effects on the functional ecology of central Brazil (Batalha et al. 2010).

15.5.2 Habitat fragmentation

One of the most widespread patterns in nature is that larger islands hold more species than smaller islands, in part because population size tends to mirror island size, and because small populations tend to go extinct from random fluctuations more easily than large ones. In addition, larger islands contain a greater diversity of habitat types than smaller islands, thereby providing niches for more kinds of species. The importance of this **species–area relationship** (Chapter 14) goes far beyond its explanatory power for biodiversity on islands: virtually all continental habitats around the world now are subdivided into a mosaic of island-like patches.

By converting native forests, grasslands, scrubs, and deserts into patchworks of landscapes designed for our own use, humans create **habitat islands** of different sizes, at differing distances from one another, and separated by different intervening habitats than would occur naturally. Persisting as islands, remnant patches of native habitat can be isolated as thoroughly as if they were surrounded by water. Just as on oceanic islands, habitat islands inevitably begin to lose their bird species.

Loss of species from habitat patches following isolation has been demonstrated by hundreds of studies around the world over the past 50 years. One of the most consistent patterns is that species with the smallest populations disappear first. In Java, for example, after the Bogor Botanical Garden arboretum had been isolated for 50 years, it had lost 75% of the bird species with originally small populations, but the species that were more common largely persisted (Diamond et al. 1987). In Panama, nearly 50% of the original bird community disappeared from the island of Barro Colorado after it was formed by the flooding of Gatun Lake during construction of the Panama Canal (Chapter 14). The birds that disappeared first were those with naturally low population density, such as ground-cuckoos, raptors, and woodpeckers (Willis 1974; Robinson 1999).

Species that require the largest tracts of habitat in order to breed successfully and persist are termed **area-sensitive species**. In eastern North American forests, Wood Thrushes (*Hylocichla mustelina*), Eastern Wood-Pewees (*Contopus virens*), and Red-eyed Vireos (*Vireo olivaceus*) are sensitive only in regard to tracts below about 20 hectares and occur in most tracts above this size. In contrast, species such as Pileated Woodpeckers (*Dryocopus pileatus*) and Worm-eating Warblers (*Helmitheros vermivorum*) require much larger tracts, and their frequency increases steadily with patch size, even above 1000 hectares (Fig. 15.23). Therefore, tracts of considerable size are required to preserve the complete community of woodland bird species.

Grassland birds also exhibit area sensitivity. In agricultural regions, remnant patches of native grassland may form habitat archipelagos amid encroaching oceans of alfalfa, grain crops, or soybeans. As a result, grassland species all over the world are deeply threatened. Species having the lowest population densities are threatened most severely, a problem compounded by the fact that density itself is area sensitive—that is, many grassland birds occur at the highest densities within the largest tracts of good habitat (Ribic et al. 2009). Birds such as stone-curlews and sandgrouse in Europe (Goriup et al. 1991), prairie-chickens and Sprague's Pipits (*Anthus spragueii*) in North America, and seriemas and rheas in South America are failing to persist in any but

Species–area relationship: the nearly universal tendency for larger areas to harbor greater numbers of species; used most often in reference to islands or habitat fragments.

Habitat island: an isolated patch of a given habitat that is surrounded by other, potentially inhospitable, habitats.

Area-sensitive species: species for which probability of occurrence increases with the size of the habitat patch, and hence are usually missing from the smallest patches.

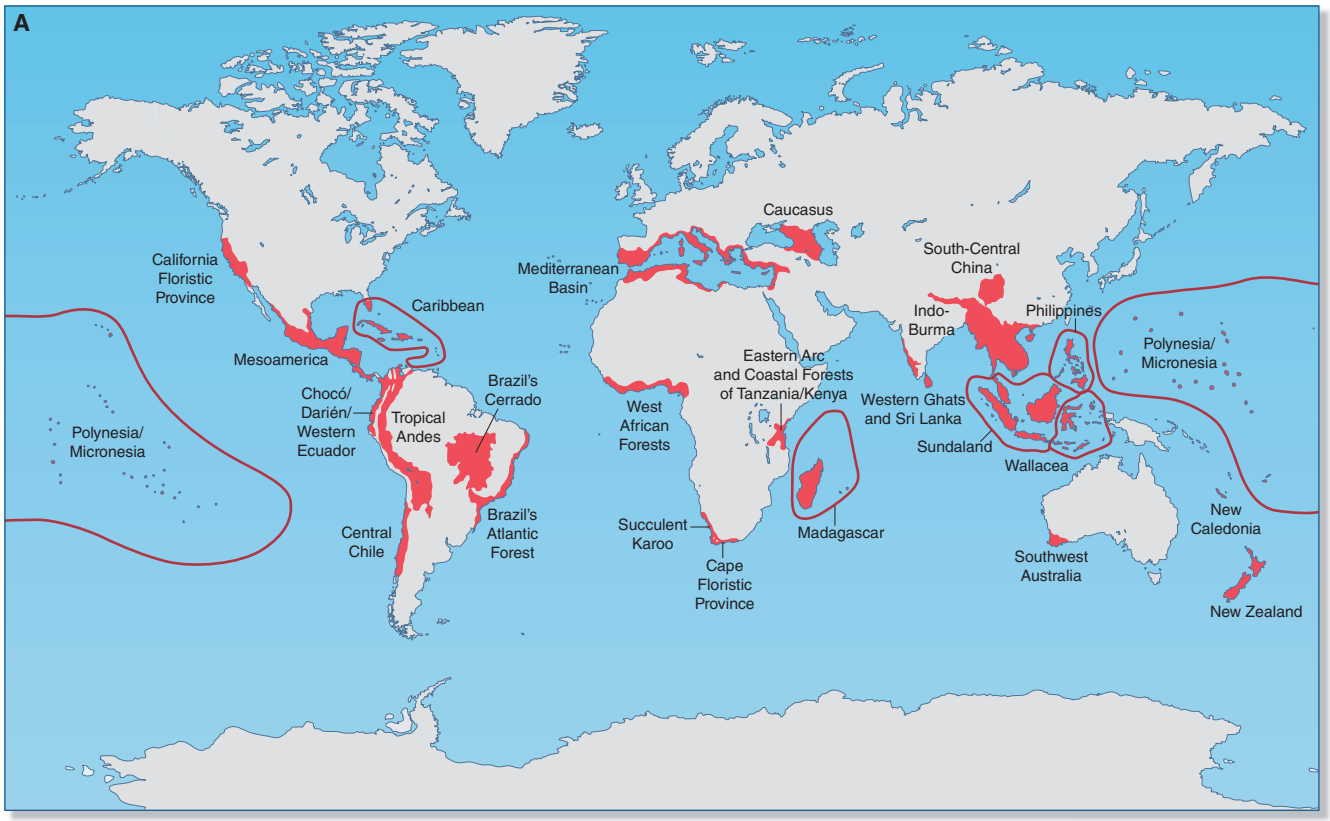




Fig. 15.22 Biodiversity hotspots. (A) Habitats with a large proportion of endemic species—those found nowhere else on earth—are considered the highest priority for conservation action. Saving these hotspot habitats protects species that are at high extinction risk. (B) Many hotspots, including this Brazilian cerrado, are threatened because of agricultural conversion and human encroachment. (A, from Myers et al. 2000. Reproduced with permission from Macmillan Publishers Ltd. B, photograph by Benjamin G. Freeman.)



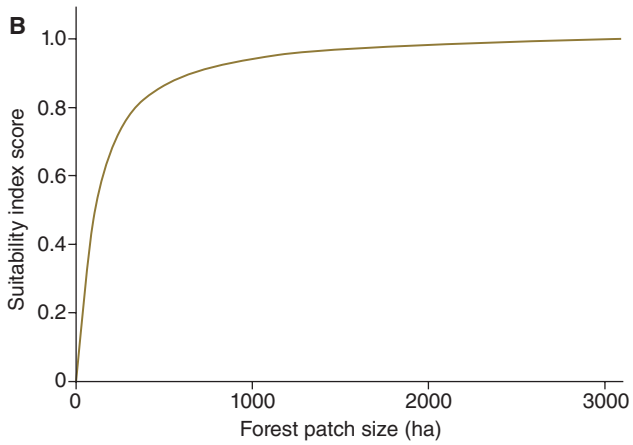


Fig. 15.23 Some species require large forest tracts. (A) The Worm-eating Warbler (*Helmitheros vermivorum*) is one of many species that requires large areas of intact, primary forest to sustain healthy breeding populations. (B) The larger the area, the greater the habitat suitability index for this species. (A, photograph by Andrew Jordan. B, from Tirpak et al. 2009.)



Fig. 15.24 Grassland birds are declining worldwide. This Indian Bustard (*Ardeotis nigriceps*) is one of the many bustards that face extinction due to hunting and habitat destruction. Fewer than 250 individuals of this species remain in the wild. (Photograph by Nitin Vyas.)

the very largest islands of native grassland. Almost all the world's bustards (Fig. 15.24) and other birds of the Asian shrub-steppes are declining, even in areas where they are protected (Bota et al. 2005). Protecting the largest remaining expanses of native grassland has emerged as an urgent global priority for bird conservation.

Compounding problems of habitat fragmentation are **edge effects**, or factors causing habitat near the edge of a patch to be less suitable for survival or reproduction than habitat in the middle. For birds, the most important edge effects are: (1) changes in microclimate (sunlight, temperature, and humidity) near a habitat edge, which can affect plant composition, habitat structure, and prey abundance; (2) introduced plants and animals, which penetrate habitat fragments and alter their characteristics near the edge; (3) increased frequency of habitat disturbance such as fire or wind damage; (4) greater numbers of generalist or edge-using mammalian and avian predators; and (5) elevated brood parasitism, especially by cuckoos (in the Old World) and cowbirds (in the New World). For example, in forest fragments of southern Illinois (USA), 50–100% of songbird nests are parasitized by cowbirds, and 70–99% are destroyed by predators before hatching (Brawn and Robinson 1996). Edge effects are especially pronounced in tropical forests, where they can be the dominant influence affecting community composition in fragmented habitats (Laurance 2008).

Edge effects: the tendency for conditions near the edge of a habitat patch to differ from conditions at the core of the patch, usually owing to different physical conditions (such as light, humidity, or wind), the effects of neighboring habitats, or the presence of competing or predatory species that prefer edges.

15.5.3 Introduced predators

The introduction of new predators into habitats previously lacking them ranks among the most pervasive threats to birds all over the world. Rats, cats, mongooses, stoats, and ferrets are the most widespread and notorious culprits, but the full list is long and even includes reptiles such as monitor lizards and snakes. As noted elsewhere, the problem is especially acute on islands where many native birds evolved flightlessness, have few defensive behaviors against predators, or nest on the ground. Even on continents, however, non-native predators (especially domestic cats) kill millions of birds annually, causing population declines and local extirpations (Loss et al. 2013).

Oceanic islands across the Pacific once provided predator-free breeding places for millions of seabirds comprising dozens of species of petrels and shearwaters, albatrosses, terns, boobies, frigatebirds, tropicbirds, and cormorants. During recent decades, huge populations of invasive rats and cats have caused precipitous population declines, endangerment, and extinction on these islands. On Kiritimati (formerly called Christmas Island), cat eradication measures have failed, and black rats recently arrived. Seabird numbers have dropped by half, and the largest remaining population of the endangered Phoenix Petrel (*Pterodroma alba*) is in grave danger of extinction (BirdLife International 2016b). A comprehensive analysis of seabird–rat interactions worldwide shows that storm-petrels and other burrow-nesting seabirds are by far the most vulnerable, and that gulls and other ground nesters are less so (Jones et al. 2008).

In Madagascar, the introduction of exotic fish into Lake Aloatra is blamed for the loss of the endemic Alaotra Grebe (*Tachybaptus rufolavatus*), which has not been seen since 1985 and was declared extinct in 2010. A similar fate appeared to befall the Madagascar Pochard (*Aythya innotata*), but a tiny population was rediscovered in 2006 on Lake Matsaborimena in northern Madagascar, and a captive-rearing program has been undertaken to restore its numbers.

15.5.4 Direct exploitation

The most blatant cases of human-induced population declines are those in which adults were killed at such a scale that the birth rate of new recruits could not compensate for the death rate imposed by humans. Familiar examples involved killing of adults for food—as for the Dodo (*Raphus cucullatus*), Passenger Pigeon (*Ectopistes migratorius*), and Eskimo Curlew (*Numenius borealis*)—or ornamentation, as for egrets and herons. At least 857 bird species are currently at risk from direct hunting or trapping (IUCN 2012).



Fig. 15.25 Imperial Parrot (*Amazona imperialis*). This species is found only on the island of Dominica in the West Indies. Populations were already in sharp decline from the illegal parrot trade when tropical storms killed many adults in 1979. This event galvanized efforts to more actively guard the species' preferred nesting areas. Populations are now beginning to recover. (Photograph by Mikko Pyhälä.)



Fig. 15.26 Red Siskin (*Spinus cucullatus*). This species is prized in the pet trade because it will breed readily with domestic canaries. A common sight in the grasslands of Venezuela and Colombia during the early twentieth century, it now is endangered, as entire populations have been extirpated by illegal capture. (Photograph by Siskini, http://en.wikipedia.org/wiki/File:Cucullatamachocolombia.jpg.)

During the late twentieth century, global trade in exotic pets introduced a new element to the birth rate–death rate story. Many large tropical parrots became extremely rare in their native ranges because humans were stealing young parrots from their nests. This predation did not change the biological birth rate, because surviving adults continued to produce chicks, but it vastly reduced the effective birth rate, because most chicks were stolen from the wild and smuggled out to foreign countries. In the Lesser Antilles, for example, the illegal sale of Imperial Parrots (*Amazona imperialis*) (Fig. 15.25) reduced the effective birth rate to nearly zero in the mountaintop forests of Dominica. In 1979 the population of this spectacular parrot dropped further to about 50 individuals after a devastating hurricane. In the decades since, organized guarding of parrot nest sites and protection of mountaintop forests across Dominica has allowed offspring once again to recruit into the breeding population, effectively reversing the decline; as of 2008 the Imperial Parrot population had increased to about 350 individuals (Reillo and Durand 2008). Similar actions have greatly reduced the illegal parrot trade throughout the other islands of the Lesser Antilles.

The beautiful, somewhat nomadic Red Siskin (*Spinus cucullatus*) originally was common in open, semiarid areas of northern South America but has fallen to critically low numbers as a result of massive pressure from trappers for global trade (Fig. 15.26). This species has a pleasant song, and captive siskins will mate with domestic canaries to produce highly sought-after rose-colored hybrids. Tiny siskin populations persist in northern Venezuela, where it is among the country's four bird species with the highest priority for conservation (Rodríguez et al. 2004). A recently discovered population in Guyana supplies additional hope, although it too is under pressure from illegal trapping (Robbins et al. 2003).

15.5.5 Chemical toxins and pollution

The publication of Rachel Carson's *Silent Spring* in 1962 alerted the world to the ecological dangers of chemical herbicides and insecticides, and her fears proved well-founded when many raptor species began disappearing from long-occupied habitats all over the world. Declines were especially pronounced for Bald Eagles (*Haliaeetus leucocephalus*), Ospreys (*Pandion haliaetus*), and Peregrine Falcons (*Falco peregrinus*) in the USA and for Eurasian Sparrowhawks (*Accipiter nisus*) in Europe. The primary cause turned out to be reproductive failure from eggs being crushed in the nest. The resulting flurry of studies became some of the most famous in the history of conservation biology. By comparing the fragments of crushed eggs with egg specimens stored in museum collections (Chapter 13), scientists discovered that modern eggshells were up to 30% thinner than normal (Ratcliffe 1967; Hickey and Anderson 1968; Cade et al. 1988). The problem was traced to contamination of adult birds by chlorinated hydrocarbon pesticides, in particular the common organic pesticide DDT (dichlorodiphenyltrichloroethane) and its stable form DDE. At that time, DDT had become one of the most widely used pesticides in the world. Migratory birds of prey were eating birds, mammals, and fish that had been accumulating DDE in their tissue, thereby accumulating even higher concentrations of

Box 15.03 Asian vultures suffer historic declines

Until very recently, five species of vultures (genus *Gyps*) were among the most common of all birds in many areas of southeastern Asia. For example, the White-rumped Vulture (*Gyps bengalensis*) had an estimated population of 40 million individuals in India alone. Once the most abundant large bird of prey in the world, this vulture now is perilously close to extinction, as are related species like the Indian (*Gyps indicus*) (Fig. 15.B3.01) and Slender-billed (*Gyps tenuirostris*) Vultures.

This mysterious and precipitous decline of *Gyps* vultures in southern Asia began in the 1990s, and was first documented in India by biologist Vibhu Prakash of the Bombay Natural History Society. Surveys conducted from 1992 to 2007 found a staggering 99.9% decline in White-rumped Vultures and 96.8% declines for Indian and Slender-billed Vultures. Similarly alarming declines also were seen at the same time in neighboring Pakistan. Heavy mortality and total breeding failure caused such precipitous losses that the situation quickly became one of the most catastrophic avian declines ever recorded. Scientists from around the globe pooled knowledge and resources trying to identify the responsible causes. Sick birds initially were observed with drooped necks and then were found dead in or under trees. Initially, researchers suspected that some type of virulent pathogen had caused a lethal epidemic in these vulture populations: *Gyps* vultures are obligate scavengers and congregate in large numbers while feeding, a behavior that could contribute to the rapid transmission of disease among individuals.

Instead, the problem turned out to have a human cause. In 2004, a joint effort between the Peregrine Fund and the Ornithological Society of Pakistan conclusively identified the agent to be diclofenac, an inexpensive drug widely used in the Indian subcontinent for the veterinary treatment of ailing livestock. Traditionally in these areas, livestock that died of disease or injury was left for scavengers—primarily vultures—to remove. Therefore, vultures were being exposed inadvertently to the drug when they ate animals that had died after being dosed with diclofenac. Clinical trials with *Gyps* vultures showed that even very low concentrations of this drug cause acute renal failure and death.

In response to the toxic impact of diclofenac, India banned its manufacture and veterinary use in 2006. However, despite both the ban and the availability of alternative anti-inflammatory drugs that are not lethal to vultures, diclofenac continues to be distributed and used illegally. Moreover, the low natural birth rate of large vultures makes it difficult for the population to rebound. Vultures are slow to reach sexual maturity, and breeding pairs typically fledge only one chick each year. More ominously, the use of diclofenac is increasing in Africa, and is beginning to have similar impacts on the profoundly important vulture communities on that continent too.



Fig. 15.B3.01 Indian Vulture (*Gyps indicus*). Vultures are indicators of environmental health, and many populations vital to humans for their natural waste management are declining worldwide. This and other endangered vulture species once numbered in the tens of millions, but became endangered through extensive poisoning from diclofenac, a drug used to treat ailing livestock. (Photograph by Ramki Sreenivasan.)

DDE than did species lower in the food chain. Physiological effects on raptors included higher death rates among adults, but the reduced birth rate from eggshell thinning was an even bigger problem. Populations of most northern hemisphere hawks and falcons plummeted in places where DDT use was widespread, but they began to recover almost immediately in places where DDT was banned.

Vast quantities of organic pesticides continue to be used around the world, and their long-term effects on birth rates and death rates among birds remain poorly documented. The toxic insecticide monocrotophos is now banned in the USA, much of Europe, and Australia because of its impact on birds. Highly publicized deaths of nearly 6000 Swainson's Hawks (*Buteo swainsoni*) in Argentina during the late 1990s (Goldstein et al. 1999) brought global attention to its dangers, but monocrotophos remains widely used in many countries.

Vultures are especially susceptible to environmental toxins (Box 15.03). Many factors contributed to the steady decline of California Condors (*Gymnogyps californianus*) throughout the twentieth century, but the chief cause was lead poisoning. Virtually all condors found dead in the wild

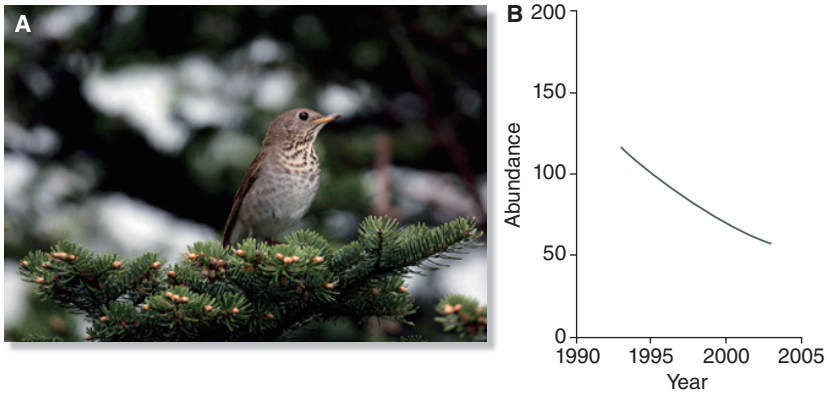


Fig. 15.27 Population decline due to acid rain. (A) Bicknell's Thrush (*Catharus bicknelli*) breeds exclusively in dense spruce-fir thickets in northeastern USA and adjacent Canada. (B) Surveys of the species over the last few decades have revealed strong declines in abundance, particularly in the White Mountains of Vermont. Since their forest habitat remains largely intact, researchers believe these declines are due to acid rain. (A, photograph by Gerard R. Dewaghe. B, from King et al. 2008. Reproduced with permission from Springer Science + Business Media.)

had numerous lead pellets in their crops, and the species is unusually sensitive to elevated levels of lead in its blood. In 1982 all 21 remaining wild condors were captured in order to protect the species from further exposure to environmental lead and to launch a captive-breeding program. Today, lead poisoning continues to be the chief cause of illness and death among free-flying condors, and experts agree that the species' true recovery depends on elimination or substantial reduction of lead in the environment (Finkelstein et al. 2012).

The release of sulfur-containing compounds into the atmosphere as a by-product of coal-fueled power plants and steel manufacturing causes a widespread form of environmental pollution. **Acid rain** is caused by the condensation of water droplets that incorporate atmospheric gases such as hydrogen sulfide in areas downwind of major industrial centers in North America and eastern Europe. The environmental effects of acid rain vary geographically, depending largely on the availability of chemical buffers in the soil such as calcium carbonate from dissolving limestone. In particular, in granitic landscapes that lack buffers, lakes and soils can become acidified, causing zooplankton and mollusks to become scarce. The ensuing ecological chain reaction often culminates in the loss of snail-eating and fish-eating birds such as loons, ducks, and raptors. Acid rain also is correlated with widespread deposition of methylmercury, an extremely toxic form of mercury produced by burning fossil fuels for power generation. The combination of food-chain disruption and mercury accumulation is blamed for dramatic declines in the reproductive success of Common Loons (*Gavia immer*) in both North America and Europe (Burgess and Meyer 2008).

Declines in calcium uptake as a consequence of acid rain deposition have been linked to significantly impaired reproductive success among European songbirds, in part because they cannot obtain enough calcium to produce viable eggs (Graveland 1998). In the northern Appalachian Mountains of the USA, acid rain has caused a 10-fold reduction in land snails, and Bicknell's Thrush (*Catharus bicknelli*) numbers are declining within otherwise intact forest (Lambert et al. 2008) (Fig. 15.27).

Since the late 1800s, environmental pollution from human sewage, manufacturing plants, oil refineries, coal-powered energy plants, and agricultural fertilizers has changed the chemistry of the air, water, and soils throughout the industrialized and agricultural worlds. Pollution reduces prey diversity and alters vegetation structure in lakes, marshes, rivers, and streams, in turn reducing the reproductive success of aquatic birds such as ducks, grebes, bitterns, and loons. Some of the worst effects are caused by **eutrophication**, when excess nutrients in the water allow one or a few species of algae or cyanobacteria to explode and take over the entire system, reducing dissolved oxygen and choking out the native food web.

Acid rain: rainfall that is unnaturally acidic owing to atmospheric pollution.

Eutrophication: a condition caused by excess nutrients (usually from pollution) that stimulates the growth of aquatic plants or blue-green algae in a body of water, resulting in the depletion of dissolved oxygen and cascading negative effects on other aquatic organisms.

15.5.6 Introduced disease

By the time of Captain Cook's arrival in the Hawaiian Islands in 1778, the resident Polynesians already had caused the extinction of numerous large bird species, but about

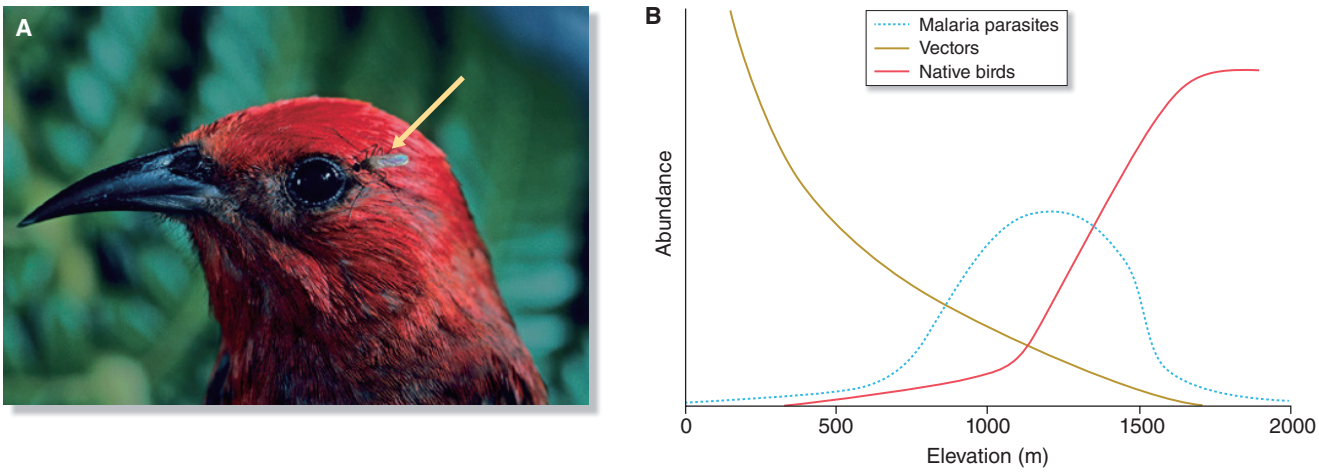


Fig. 15.28 Hawaiian birds and avian malaria. (A) Mosquito vectors (arrow), which transmit avian malaria to birds, are relatively recent introductions to Hawaii. Endemic Hawaiian birds like this Apapane (*Himatione sanguinea*) lack resistance to the disease. (B) Their highland habitat keeps birds isolated from the vectors that prefer warmer, lower elevations. Many lower-elevation endemic birds of Hawaii have gone extinct because of avian malaria and compounding factors including habitat destruction, invasive species, and other diseases. Global warming puts all remaining species at risk as the mosquitoes that transmit malaria are able to move into higher elevations. (A, photograph by Jack Jeffrey Photography. B, from van Riper et al. 1986. Reproduced with permission from the Ecological Society of America.)

70 species of small native birds continued to occupy the forests from sea level to mountaintop. During the second half of the 1800s, a baffling wave of disappearances overtook Hawaiian songbirds, island by island. In 1902, ornithologist H. W. Henshaw described the phenomenon: "large areas of forest, which are yet scarcely touched by the axe save on the edges and except for a few trails, have become almost absolute solitude. One may spend hours in them and not hear the note of a single native bird. Yet a few years ago these areas were abundantly supplied with native birds." Across the entire archipelago, dozens of bird species went extinct almost simultaneously, and throughout the twentieth century additional species steadily met the same fate.

Many factors were responsible for these losses, but the introduction of disease-bearing mosquitoes on Maui in 1826 certainly was the single-most devastating event for Hawaii's bird fauna since the original arrival of humans 1000 years earlier. Avian malaria and avian pox are the two most virulent agents. Both are carried and transmitted by a complex of mosquito species originally brought to Hawaii from Mexico in the water casks of merchant ships. These two diseases occur worldwide among continental birds, which have evolved resistance, and no doubt were carried annually to Hawaii by migratory birds for hundreds of thousands of years. Before the mosquito's introduction, however, no vector existed to transfer these deadly pathogens from resistant migrants to naïve native birds. Consequently, no native Hawaiian bird had evolved resistance to malaria or pox (Fig. 15.28).

As humans began transferring mosquitoes among the Hawaiian Islands, avian death rates soared. Because mosquitoes are scarce in the colder habitats above 1300 meters, a remnant native avifauna could persist above this elevation, but at lower elevations mosquitoes have been impossible to control because they breed in tiny water reservoirs, including tree-fern trunks hollowed out by introduced pigs. In many areas of Hawaii today, 50% of the free-flying mosquitoes below 1000 meters elevation carry avian malaria, an infection rate that is vastly higher than any known in continental sites. In the future, warming climates might expand the elevational range of mosquitoes, slowly eliminating the high-elevation refuges essential to the survival of some Hawaiian bird species. The long-term hope for the few remaining native forest birds is the gradual development of resistance through natural selection, as apparently is underway in the Hawaii Amakihi (*Hemignathus virens*) (Woodworth et al. 2005). The statistics are grim, however: over the Hawaiian Islands as a whole, 17 of the 42 recently living native songbird species already have gone extinct, and most of the remaining species are poised on the brink (Pratt et al. 2009). The most recent to disappear were the Poo-uli (*Melamprosops phaeosoma*) of Maui (the last male died in captivity in 2004), and the Kauai Oo (*Moho braccatus*) (a single, long-lived male in the Alakai Swamp disappeared in 1989) (Fig. 15.29).

15.5.7 Climate change

Direct links are often difficult to document conclusively, but climate change increasingly is implicated as a threat to bird populations around the world. Northward-shifting distributions and progressively earlier spring arrival and nesting dates among northern hemisphere birds are well documented (Thomas and Lennon 1999; Parmesan and Yohe 2003). An ambitious study comparing distributions of California birds across a century has documented numerous

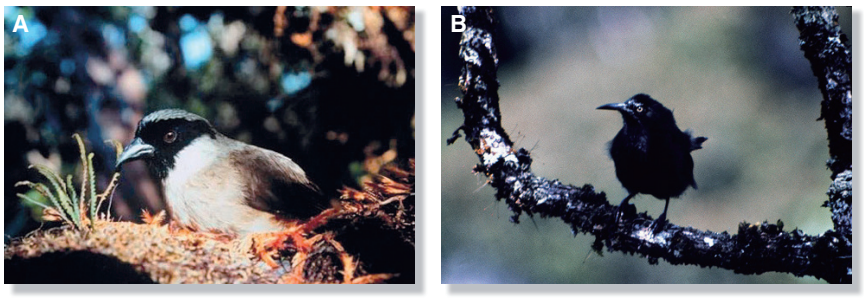


Fig. 15.29 Recent species extinctions in Hawaii. (A) In 2004, Maui lost its last remaining captive Poo-uli (*Melamprosops phaeosoma*). (B) In 1989 the last male Kauai Oo (*Moho braccatus*) was heard in Alakai Swamp singing without a mate to hear him. (Photographs by: A, US Fish and Wildlife Service; B, Robert Shallenberger.)

changes, with almost every species tracking its climatic niche through shifts along elevational or rainfall gradients (Tingley et al. 2009). Some northern hemisphere birds are no longer breeding at the time of maximal food abundance because of failure to keep pace with progressively earlier peaks in arthropod prey. Mismatched migration timing is not always species-wide. Hudsonian Godwits (*Limosa haemastica*), which winter in southern South America and breed in the high Arctic, have arrived progressively earlier near Anchorage, Alaska, where spring has shifted earlier very steadily. Elsewhere, the godwits' arrival is now mistimed in places where spring temperatures are cooler and more variable than in previous decades (Senner 2012). Birds such as the Kittlitz's Murrelet (*Brachyramphus brevirostris*) and Ivory Gull (*Pagophila eburnea*), which breed at the edge of polar and glacial ice, appear to be undergoing especially rapid population declines as climate change alters the distribution and conditions of their specialized habitats.

15.5.8 Stochastic extinction

A major objective of conservation biologists is to reduce the probability that a target species will experience **stochastic extinction**, that is, disappearance resulting from random population fluctuations (Chapter 13). Even the most stable bird populations in nature always fluctuate through time because of year-to-year variation in physical and biological factors such as rainfall, storms, food supply, parasites, disease, and predation. These normal fluctuations in population size are referred to as stochastic variation (Fig. 15.30). Large and widespread populations have great capacity to persist despite this stochastic variation, in part because of their sheer numbers (after all, half of a huge population is still huge) but also because at any one time different parts of the population may be affected by different variables, so numbers may increase in some areas while decreasing in others. Because birds usually can disperse into areas where density is reduced, larger populations are buffered against perturbations, both natural and human generated. For smaller populations, even minor perturbations can cause a population to disappear entirely. For example, on the island

Stochastic extinction: extinction resulting from random changes in population size when the population drifts to zero individuals.

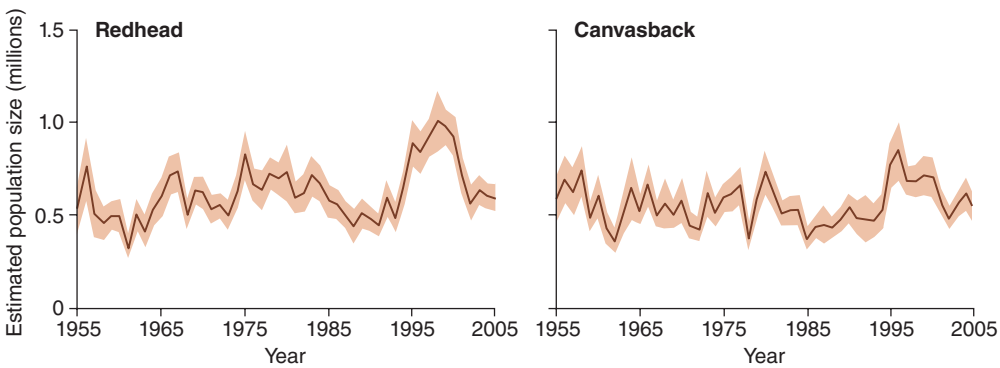


Fig. 15.30 Stochastic variation in population size. Over the years, the size of Redhead (*Aythya americana*) and Canvasback (*Aythya valisineria*) duck breeding populations show the stochastic variation that is normal in healthy populations. Population estimates were calculated using point counts. (From US Fish and Wildlife Service 2012.)

of Hawaii, a small population of the endangered, fruit-eating Ou (*Psittirostra psittacea*) survived until 1984. Unfortunately, in that year the Mauna Loa volcano erupted and, by chance, sent a small lava flow directly through the Ou's forested refuge. The last confirmed sighting of an individual was in 1987: reduced to a tiny population, the Ou had become highly vulnerable and finally succumbed to an isolated, natural, random event.

15.5.9 Tipping points in extinction: Allee effects

The Passenger Pigeon (*Ectopistes migratorius*) went extinct mainly because humans killed them for food in vast numbers while also systematically destroying their breeding and wintering habitats. The final years of the Passenger Pigeon's disappearance, however, still present a biological mystery. The species had become rare over most of its range, but for a decade or more thousands of adults still migrated northward in scattered bands, too few in number to attract market hunters. Why, then, did these scattered individuals not begin to recover, instead of vanishing completely within a few years? The **Allee effect** (named for its discoverer, W. C. Allee) refers to a decline in per capita reproductive success as population density decreases (Chapter 13). Small numbers of pigeons remained after hunting mostly had stopped, but this species was adapted to breed in huge colonies where local predators could feast on young pigeons yet still leave millions of young birds to fledge. Passenger Pigeon numbers may have fallen below a critical threshold required for finding suitable mates and stimulating hormonal pathways required for successful reproduction. Isolated individuals and small flocks instinctively may have searched for large colonies rather than nesting on their own. It is speculated that when the Passenger Pigeon population fell below a critical density, a manifestation of the Allee effect took the species the rest of the way to extinction. Species vary widely in their susceptibility, but strong Allee effects are important to discover. In certain species, falling below a density threshold can accelerate a previously gradual population decline that might be occurring for other reasons, thereby rendering such species more extinction-prone than others.

15.5.10 Multiple stressors

Many bird species are declining because of multiple factors that have compounding effects on both birth and death rates. For example, the extraordinary disappearance of native birds from the Hawaiian islands resulted from combinations of habitat loss, introduced grazing mammals, introduced predatory mammals, introduced diseases and disease-bearing insects, and the spread of exotic vegetation, among other stressors. Many migratory birds experience threats on both their breeding and wintering grounds, as well as in migratory transit. The most extreme examples may be the long-distance migratory shorebirds (Chapter 12). These species breed in high arctic habitats of North America and Asia, where they face habitat degradation and mismatched timing of food resources resulting from climate change. Twice a year, they migrate thousands of kilometers, stopping only at traditional stopover sites on food-rich interior marshes and coastal tidal flats, many of which are being depleted of natural food resources or converted for agricultural and commercial development. They overwinter on the tropical coastlines and grasslands of South America, Africa, Australia, and southeastern Asia, where many are hunted, trapped, and netted for food. Recent, dramatic population crashes among dozens of once-common migratory shorebird species represent one of the most challenging conservation dilemmas facing avian conservation biologists (Fig. 15.31).

15.5.11 Genetics and the extinction vortex

When populations are reduced to very small sizes, they face risks not only from environmental fluctuations and chance perturbations but also from genetic effects. Because close inbreeding increases the chances that offspring will have low genetic diversity, the **incest taboo** is exceptionally strong among birds: individuals typically avoid pairing and breeding with members of their immediate genetic family.

Through many generations of sexual reproduction, genetic mutations and recombination permit the accumulation of vast pools of genetic diversity among bird populations that are relatively large. When a population becomes very small, three related factors cause genetic variation to decline. First, **genetic drift** occurs as a result of chance sampling errors during mating: some genetic variants, beginning with the rarest ones, disappear altogether while others increase in frequency. Second, the occurrence of new genetic variants declines, because fewer individuals exist in which new mutations can appear. Finally, inbreeding occurs more frequently, because breeding adults in a small population are more likely to be related to one another than in a

Allee effect: a disruption of reproductive behavior and/or social structure when population density falls below a threshold level.

Incest taboo: behavioral avoidance of mating with close genetic relatives.

Genetic drift: random changes in genetic diversity in a population over time, often leading to the loss of genetic diversity when populations are small.

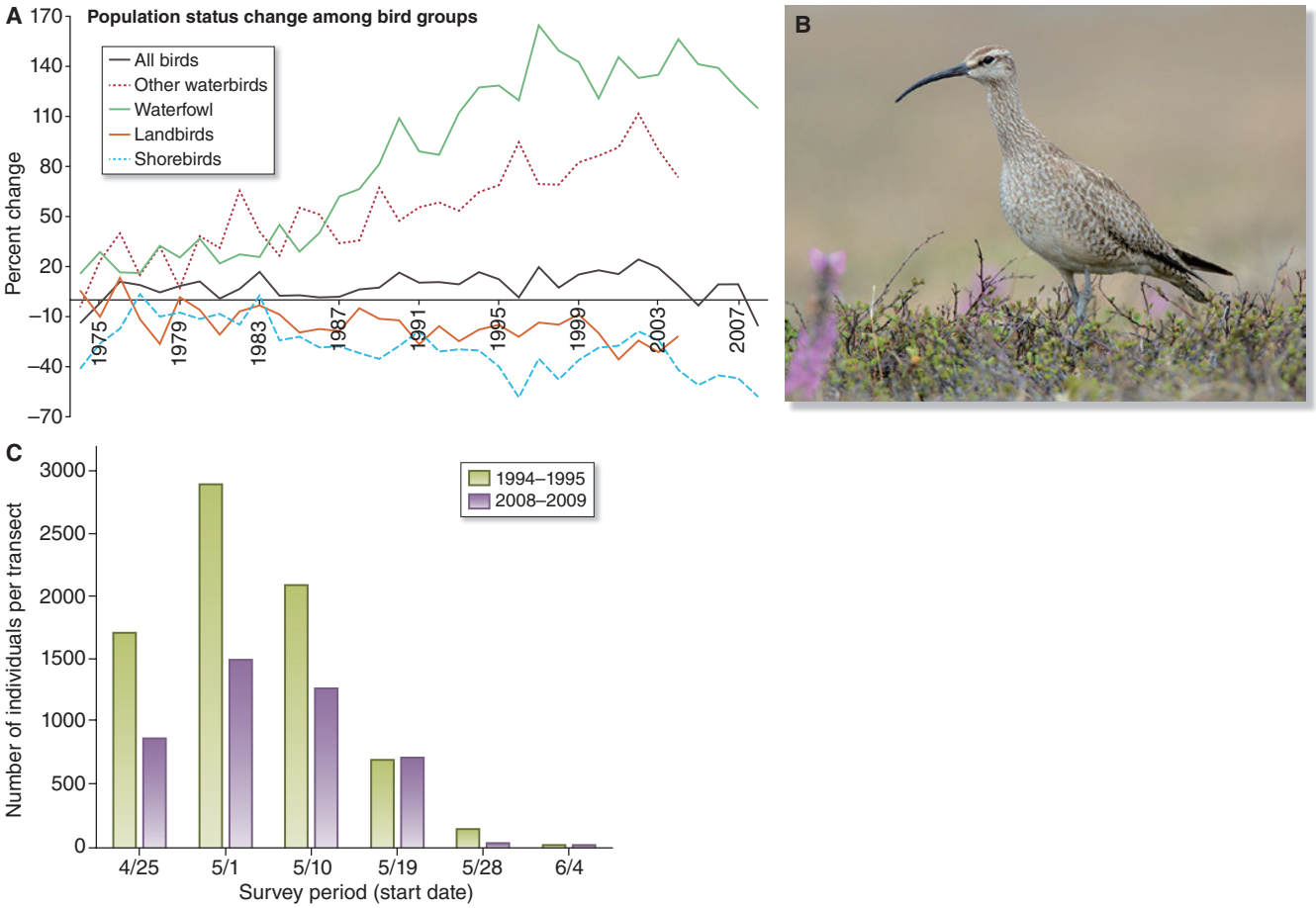


Fig. 15.31 Shorebirds are in worldwide decline. (A) Compared with other bird groups, migratory shorebird populations are declining most severely. (B) The Whimbrel (*Numenius phaeopus*) is one shorebird species facing population declines, although the reasons remain ambiguous. (C) Surveys of Whimbrels conducted along Virginia Beach (USA) transects in the 1990s (green bars) compared with the 2000s (violet bars) show significant declines. (A, adapted from North American Bird Conservation 2012. B, photograph by Gerrit Vyn. C, from Watts and Truitt 2011. Reproduced with permission from the Waterbird Society and authors.)

large one. The resulting **inbreeding depression** is of particular conservation concern when endangered birds have been reduced to tiny population sizes. The Stitchbird (*Notiomystis cincta*), recently discovered to represent its own distinctive family (Notiomystidae), was once common across the vast North Island (New Zealand) but was extirpated everywhere except on small Little Barrier Island. Recent translocations intended to establish several new populations were severely hampered by hatching failure and poor survival associated with inbreeding (Brekke et al. 2010).

Extreme reduction in genetic diversity following a population reduction, known as a **genetic bottleneck**, constrains the population's ability to adapt to changing environmental conditions and progressively lowers average fitness by reducing the birth rate and increasing the death rate. One thing to remember is that not all birds in a population will reproduce successfully during their lifetimes; therefore, the number of individuals passing along their genes is always lower than the total number of individuals alive at any one time. Thus, extremely small populations with even fewer active breeders may be subject to an ever-worsening spiral, known as the **extinction vortex** (Fig. 15.32). As each succeeding generation fails to replace

Inbreeding depression: the reduced survival or reproductive success of offspring produced by the mating of two close relatives.

Genetic bottleneck: a loss of genetic diversity in a population resulting from a period in which few individuals successfully reproduced.

Extinction vortex: a negative feedback loop affecting small populations, in which genetic and demographic factors compound one another and worsen with every successive generation.

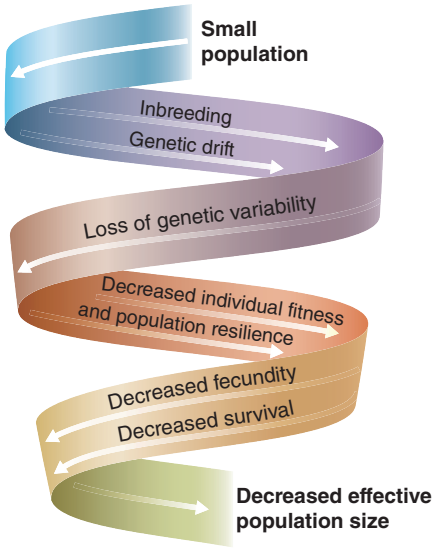


Fig. 15.32 The extinction vortex. Compounding negative effects on population demographics occur more rapidly in small populations, as overall genetic diversity steadily declines. (© Cornell Lab of Ornithology, adapted from Krebs 2008.)

itself fully, more alleles are lost, and the population becomes ever more genetically homogeneous, further lowering reproduction and survival. All these genetic effects are compounded by the ever-worsening demographic risks as the population grows smaller and smaller.

15.6 Avian population increases

Not all environmental changes cause population declines. Across eastern North America, for example, forest-inhabiting birds such as the Northern Cardinal (*Cardinalis cardinalis*), Tufted Titmouse (*Baeolophus bicolor*), and Red-bellied Woodpecker (*Melanerpes carolinus*) have increased and spread northward as humans increased the availability of winter food (sunflower seeds from bird feeders) and shelter (ornamental plantings), and as landscapes once cleared for farmlands have reverted to forest. A century earlier, populations of birds associated with farmlands and successional habitat, such as the Bobolink (*Dolichonyx oryzivorus*), Brown Thrasher (*Toxostoma rufum*), and Eastern Towhee (*Pipilo erythrophthalmus*), surged with the clearing of eastern forests. These open-land birds now are declining in parallel with the increases in tree cover.

Introduced species often undergo major population expansions after long periods of being restricted to a small area, as birth rates and death rates adjust to the new environment. Beginning in the early 1900s, Eurasian Collared-Doves (*Streptopelia decaocto*) suddenly began expanding from their original Mediterranean range, eventually colonizing most of Europe and Asia before being introduced to the Bahamas in the 1970s. From there, the species continued a spectacular expansion across much of North America (Fig. 15.33). This species represents a case in which birth rates have exceeded death rates for a long time across its entire range.

Increases in certain species can have cascading ecological consequences affecting many other species. During the late twentieth century, Snow Goose (*Chen caerulescens*) numbers across arctic Canada began burgeoning, with some populations increasing at the phenomenal rate of 8% per year (US Fish and Wildlife Service 2012). Large-scale farms in the migration and wintering areas of North America provided huge quantities of remnant rice, corn, and other grains left on the ground after harvesting (lowering goose death rates), and adult geese arrived on their breeding grounds in such excellent condition that they could breed earlier and lay larger clutches (increasing goose birth rates). These human-induced environmental changes caused a Snow Goose population explosion. Ironically, this change threatens many other tundra-breeding bird species because of an ecological chain reaction: Snow Geese forage by snipping and tugging up the roots of native tundra vegetation, and their numbers have grown so large that vast areas of once-verdant tundra are being reduced to sterile, hypersaline (extra salty) dirt. Consequently, certain migrant shorebirds such as Hudsonian Godwits (*Limosa haemastica*), Lesser Yellowlegs (*Tringa flavipes*), and American Golden-Plovers (*Pluvialis dominica*) are losing breeding habitat, and their numbers in the affected areas appear to be declining.

15.7 Conservation solutions

Accomplishing lasting conservation in real-world settings is not easy. Conservation is a time-consuming, long-term, often messy effort requiring many steps, most of which are social, political, and economic. Accomplishing the steps necessary both to reverse population declines and to recover the underlying ecosystems almost always requires addressing the human social and economic realities that caused the problems in the first place. Indeed, engaging all stakeholders in the process of accomplishing lasting conservation usually is much harder than identifying and resolving the biological issues. Most aspects of this human element in conservation are outside the scope of this chapter, but it must be recognized that fully integrated conservation solutions are extraordinarily complex undertakings in balancing the needs of both humans and the natural world (Kareiva and Marvier 2011).

Successful conservation depends on good scientific information. This section summarizes how principles of conservation biology are applied in efforts to prioritize, stabilize, restore, and recover declining bird populations



Fig. 15.33 The invasion of Eurasian Collared-Doves (*Streptopelia decaocto*). Over the past several decades, this invasive species has spread from Europe into the Bahamas, through Florida, the USA, and Canada. Currently it is spreading from Mexico into Central America. The maps represent sightings across North America from 1998 to 2013 as logged into the eBird citizen science portal. The probability of detection is higher in areas with darker shades of purple. (Maps © Cornell Lab of Ornithology. Photograph by Horia Varlan, https://en.wikipedia.org/wiki/File:Streptopelia_decaocto_-balcony_-two-8.jpg. CC-BY-2.0.)

around the world. Important steps include: (1) discovering and accurately documenting specific population declines; (2) setting priorities for research and action; (3) understanding the biological underpinnings of the problem; (4) deriving steps that could resolve the problem for the long term; (5) identifying the relevant socioeconomic contexts, opportunities, and constraints; (6) implementing the prescribed steps; (7) measuring the outcomes; and (8) repeating as necessary until desired conditions are achieved and demonstrated to be lasting.

Given these general approaches, no universally effective solutions exist for conservation issues. Countries and cultures may differ in the conservation strategies they regard as being the most useful and successful.

For birds, the most commonly identified problems involve population declines, but resolving every genuine problem is impossible, so prioritization is crucial. Understanding the biological underpinnings of conservation challenges means applying basic principles of genetics, evolutionary biology, life history theory, population biology, community ecology, animal behavior, ecological modeling, and computer simulations to interpret the decline and prescribe steps to reverse it. The necessary steps are as diverse as the myriad reasons for decline and include efforts such as reducing illegal trade and hunting, establishing reserves to protect native habitats and watersheds, controlling introduced mammals, promoting sustainable harvesting of tropical forest resources, and developing ecotourism in and around protected areas as an incentive for local and indigenous people to maintain these habitats in their natural state. Once such steps are undertaken, follow-up monitoring is essential, because the prescribed steps may be incorrect or insufficient, or because environmental conditions and threats might continue to change.

15.7.1 Monitoring populations

Not every population decline represents a problem. For example, dramatic declines in certain forest songbirds on long-term study plots in New Hampshire (USA) between 1969 and 1998 resulted not from ecosystem degradation or alarming demographic imbalances, but rather from steady forest succession following the end of the region's agricultural era. It turns out that other species in this area that use older forests were increasing in number for exactly the same reason, but it took careful analysis of a 30-year dataset to comprehend the reasons for these changes (Holmes and Sherry 2001). This example illustrates a vital ingredient for bird conservation the world over: identifying population declines that warrant conservation attention often depends upon the availability and dispassionate statistical scrutiny of carefully gathered long-term data (Chapter 13).

15.7.2 Setting priorities

Limited resources make it impossible to devote equal attention to every conservation problem in the world. Priority setting is essential. Several different approaches exist by which to compare bird species and/or their habitats in terms of their conservation priority. No one of these approaches is necessarily better than the others, so it pays to consider all of them when evaluating where to invest time, energy, and resources.

Taxonomic distinctiveness

Species that are taxonomically distinct (such as species that are the sole members of their genus, family, or order) have especially high conservation priority, because their disappearance would mean permanent loss of a globally unique evolutionary lineage. An excellent example is the Kagu (*Rhynochetos jubatus*) (Fig. 15.34), a distinctive terrestrial bird restricted to New Caledonia in the southwest Pacific. This species is an ancient evolutionary relict, and its relationship to its closest living relative—the Sunbittern (*Eurypyga helias*) of the American tropics—likely dates to the period when the southern continents were united (Chapter 2). The only member of its family (Rhynochetidae), the Kagu is highly endangered as a consequence of habitat loss and depredation by dogs.

Genetic distinctiveness

The advent of DNA-sequencing technology revolutionized our capacity to detect the previously hidden genetic distinctiveness of local populations, often resulting in their new recognition as fully separate species. In many cases this recognition elevates the conservation priority placed on the newly elevated species, especially when it represents a flagship for a distinctive ecological community. For example, the California Gnatcatcher (*Polioptila californica*), only recently recognized as a full species, instantly galvanized attention, money, conservation planning, and controversy as an indicator species for the coastal sage scrub habitat that is imperiled by explosive human population growth throughout southern California (USA) (Chase et al. 2001).



Fig. 15.34 The Kagu (*Rhynochetos jubatus*) is a taxonomically distinctive species. Losing relictual species like the Kagu, endemic to New Caledonia, means the loss of an entire evolutionary branch on the avian tree of life. (Photograph by Tony Palliser.)

Endemism

Concentrations of locally **endemic** bird species represent regions of extremely high conservation priority, where investment can save multiple species with no other geographic opportunities for protection. Some of the most distinctive and seriously threatened areas of endemism receiving worldwide conservation attention include Madagascar, the Hawaiian Islands, various Indonesian archipelagos, the Atlantic forests of southeastern Brazil, and the fynbos shrublands of the Western Cape of South Africa.

Hotspots

Regions of high overall biological diversity, or **biodiversity hotspots** (Myers et al. 2000) (Fig. 15.22), command high conservation priority because of the sheer number (richness) of species that can benefit from a given unit of investment. Birds are good indicators of overall biodiversity in

Endemic: a species or larger taxonomic group that occurs exclusively in a limited geographic region.

Biodiversity hotspot: a location or region with an exceptionally high number of species.

most terrestrial habitats. Tropical forests rank highest in species richness, but many non-forest hotspots are of particular importance because they have undergone proportionally greater habitat loss than forests have.

Endangerment (vulnerability)

Of all the criteria for prioritizing conservation investment, arguably the most important is the degree to which a species or ecosystem faces the threat of disappearance. Categories of endangerment are defined in all official lists of species at risk, such as the US Endangered Species List and the IUCN Red List, and the very term "Critically Endangered" all but demands global attention for the 147 species currently bearing this rank (BirdLife International 2013).

Indicators, flagships, and umbrellas

Birds are beacons of broader environmental conditions. Many kinds of birds serve particularly well as **indicator species** for ecological communities, because increases or decreases in these species correlate with the health and status of hundreds of other species of animals and plants. California Gnatcatchers were viewed as good indicator species for coastal sage scrub in California (USA) and Baja California (Mexico); hence they were given special significance in a landmark multi-species habitat conservation plan to protect this ecosystem. The Northern Spotted Owl (*Strix occidentalis*) is an indicator species that is especially charismatic to humans; such species are called **flagship species** because they draw our collective attention and attract special resources toward conservation of their habitat. **Umbrella species** are those whose successful conservation would ensure the long-term security of a host of others species or whole ecological communities, by virtue of their special needs. The critically endangered Great Philippine Eagle (*Pithecophaga jefferyi*)—the largest raptor in the Asia–Pacific region—is both flagship and umbrella for the rapidly disappearing, endemic tropical evergreen forests of the Philippine Islands (Fig. 15.35). Because of its large home range size, low population density, and dependence on large mammals as prey, this charismatic eagle requires very large and ecologically intact forest tracts to remain secure in the presence of a growing human population. Ensuring its protection would secure countless other less noticeable species, including many birds.

Ecological role

Some bird species play such pivotal ecological roles that their decline or elimination would have a disproportionate impact on community or ecosystem function. Examples include parrots, pigeons, and hornbills, which disperse seeds and nuts across their respective landscapes, and in so doing provide such a vital service to shrubs and trees that the plants and the birds have coevolved and are now dependent on one another. The loss of intact parrot



Fig. 15.35 Great Philippine Eagle (*Pithecophaga jefferyi*). This species is the world's largest and most endangered eagle. Due to habitat destruction, hunting, and low reproductive rates, its continued survival depends upon nation-wide conservation actions to protect remnant tracts of tropical forest. (Photograph by Kike Arnal © Cornell Lab of Ornithology.)

communities because of capture and illegal international trade (Fig. 15.36) therefore threatens not only the birds but also the long-term health of their forest habitats.

Utilitarian role

The importance of native bird species in the daily lives of humans might not have ranked highly in conservation priority setting until the recent, sudden, and dramatic declines in the vulture community of India and southeastern Asia (Box 15.03). The functional disappearance of an entire scavenger community in a region with the world's highest human densities reminds us of the importance of intact native systems in supplying ecological services to humans. In this case, loss of the native vultures even threatens centuries-old funeral and burial traditions of groups such as the Zoroastrian Parsis. Perhaps the best example of establishing conservation priorities based on the economic

Indicator species: a conspicuous or easily monitored species that is associated with a given habitat and which acts as an early warning signal that the habitat is changing in ways that are likely to affect many other species.

Flagship species: a charismatic species that is typical of a given habitat and is the target of special public and/or conservation attention.

Umbrella species: a species for which successful conservation actions would also help preserve many other species within its biological community.

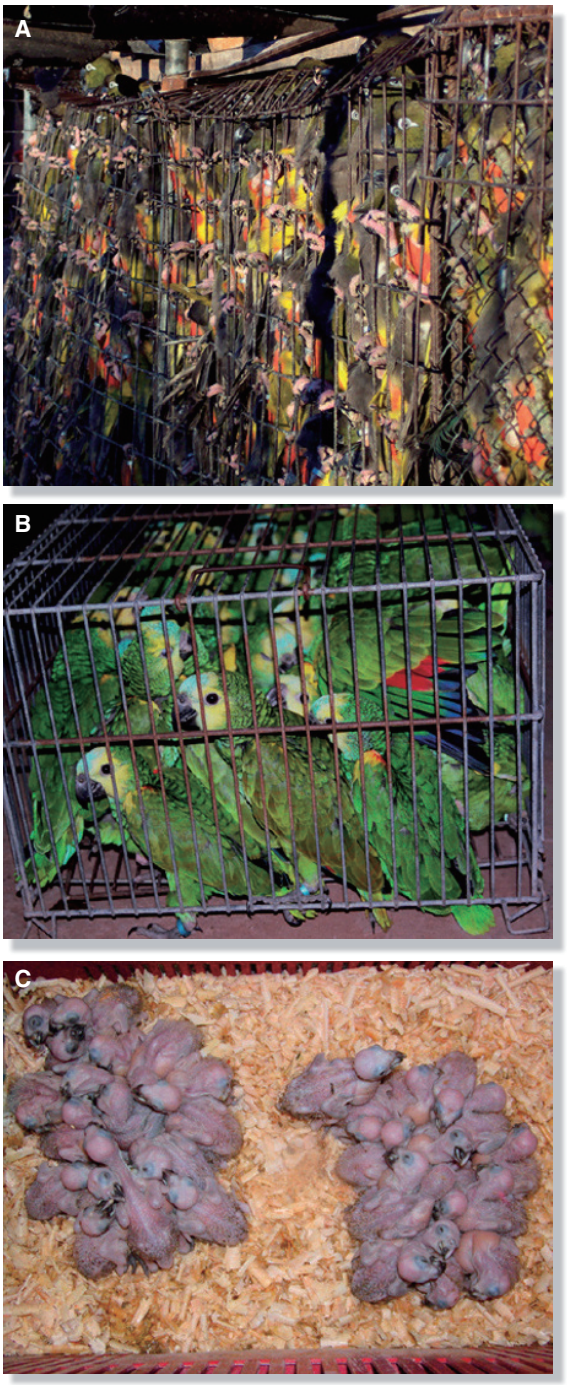


Fig. 15.36 Illegal capture and trade of parrots worldwide. Illegally caught in the wild, (A) Burrowing Parakeets (*Cyanoliseus patagonus*) of Patagonia and (B) Turquoise-fronted Parrots (*Amazona aestiva*) of Brazil—in addition to many other species—are shipped long distances in poor conditions to be sold as pets. (C) These nestlings were confiscated en route after being robbed from their nests. With no way of returning them to their wild nests, these individuals became part of a Brazilian public education program. Most parrots captured illegally either die or enter the worldwide pet trade. (Photographs by: A and B, © World Parrot Trust. All rights reserved; C, Gláucia Seixas, Blue Fronted Amazon Project–Brasil, www.fundacaoneotropica.org.br.)

impact of native birds is the tri-national, public–private partnership represented by the North American Waterfowl Management Plan. This agreement coordinates wetland protection across Canada, the USA, and Mexico to enhance migratory waterfowl. It originally was motivated by the economic impact of sport hunting and more recently was strengthened by the even greater public investment in passive wildlife viewing. Many non-profit organizations raise millions of dollars annually to further the conservation of wildlife habitats based on their economic and cultural importance.

Gap analysis

With the advent of sophisticated computer mapping and geographic information system (GIS) technology, conservation scientists can overlay distribution maps of threatened and endangered species with maps of protected areas. This crucial exercise is known as **gap analysis**, because its goal is to reveal important gaps in landscape protection that leave certain species with few or no refuges under conservation management. Gap analysis provides a useful tool for prioritizing the establishment of new protected areas, from local to global scales.

15.7.3 Population viability analysis and metapopulations

Small populations of virtually any species eventually will become isolated from the rest of their kind. Random population fluctuations, depressed reproduction and survival resulting from edge effects, and unpredictable catastrophic disease or weather events make small populations highly vulnerable to extinction. The general observation that all bird populations naturally fluctuate through time is of particular relevance to their conservation and management, because a central goal of avian conservation programs is to reduce the probability that a bird population will decline to zero—that is, go extinct. A typical (although arbitrary) goal may be to sustain a population that has a 95% chance of persisting over a long period of time, for example 100 years. Such a metric is known as a **minimum viable population** (Shaffer and Samson 1985).

Gap analysis: in conservation, the comparison of maps of species distributions with those of protected areas to identify critical but still unprotected areas that merit additional conservation action.

Minimum viable population: the smallest population size considered likely to allow the species (or population) to avoid extinction for a specified number of years.

How does one estimate the probability of a population going extinct over the course of a century? To provide some precision in measuring population vulnerability, conservation biologists in the 1980s and 1990s developed **population viability analysis (PVA)** as a tool for predicting the likelihood of extinction for populations of different sizes. The PVA is a computer simulation of the trajectory and fate of populations undergoing annual cycles of reproduction, dispersal, and mortality, and represents an exercise that today serves as a cornerstone of conservation biology. The simplest PVAs are single-population models, which simulate numbers through time, based on assumed initial and maximum allowable population sizes, key demographic variables (especially age-specific birth rates and death rates), and the degree and nature of annual variability in these demographic variables. Typically, each run of a PVA model is allowed to proceed until the simulated population either goes extinct or survives to an arbitrary end-point, perhaps 500 or 1000 years in the future. Runs are repeated many times using identical starting population sizes and demographic assumptions to gain an understanding of the range of possible outcomes, and then the process is repeated for different starting population sizes. Typical outputs are various forms of graphic representation of extinction probabilities or mean projected population sizes as a function of both time and starting population size (Fig. 15.37). In most real-world cases, population sizes are limited by the sizes of extant habitat patches, so the PVA is used to set minimum requirements for how big a habitat preserve must be to ensure an acceptably low probability that a target species within it will go extinct over a given time period (often 100 years).

A PVA conducted for Lammergeiers (*Gypaetus barbatus*) shows the value of this method. Lammergeiers were exterminated from the Alps of Europe in the late nineteenth century, but recently have been reintroduced there through the release of captive-bred young birds. By 2006, the reintroduced population had increased to nine breeding pairs. Based on a population viability analysis involving age-specific survival probability and observed fecundity rates, Michael Schaub et al. (2009) showed that the population was likely to increase in the future even if no further captive birds were released. Such information provides data critical for making informed decisions about where to invest future conservation efforts and, in this case, suggested that efforts should be redirected from captive breeding to demographic surveillance of the wild population.

Population viability analysis (PVA): a modeling technique used by conservation biologists to identify the biological and human factors most strongly affecting the long-term survival of a population or species, and to estimate how population persistence varies with population size.

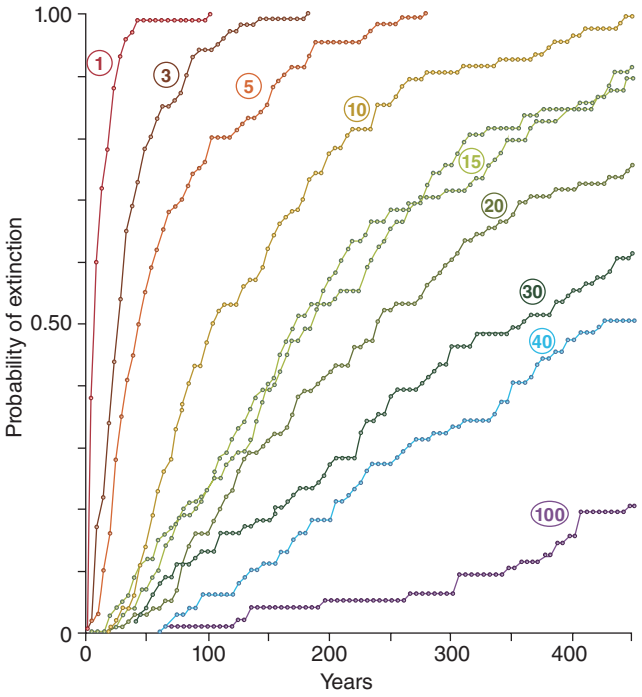


Fig. 15.37 Population viability analysis. Here various starting population sizes (in circles beside each plotline) of the threatened Florida Scrub-Jay (*Aphelocoma coerulescens*) were used in a simulation model to determine extinction probabilities over time, given well-documented demographic information about the species' population biology. In each set of simulations, each population size was repeated for 100 runs, yielding predicted extinction probabilities through time. (From Fitzpatrick et al. 1991. Reproduced with permission from Florida Fish and Wildlife Conservation Commission.)

Today, most PVAs involve complex models that integrate factors such as density dependence, habitat succession cycles, and genetic considerations. Many modern PVAs incorporate advances in which the hypothetical population is modeled as a collection of separately tracked individuals, each having its own lifespan and reproductive history. In the most realistic models, individuals disperse across the simulated landscape according to a set of rules, which themselves are subject to explicit assumptions built into the model. Therefore a common challenge for field studies of target species is to document when and how individuals disperse between birth and breeding.

Of course, even if a bird population goes extinct locally, it does not necessarily mean the end of the line for that species, because nearby conspecific populations potentially could recolonize the empty site through dispersal and thereby "rescue" the population in that habitat patch. Indeed, it is now recognized that one of the most important demographic processes in natural bird populations is the exchange of individuals among relatively discrete subpopulations. A network of populations that

have some level of connectivity via dispersal is termed a **metapopulation**.

The metapopulation concept recognizes that many bird populations in the real world are subdivided into more or less discrete subpopulations, each occupying a patch of suitable habitat within a larger area of poor or wholly unsuitable matrix habitat. Each suitable habitat patch may be large enough to accommodate a potentially independent population of birds, but except in the very largest patches, local extinctions followed by recolonizations still can occur simply because of demographic fluctuations. Metapopulation modeling is especially useful in conservation planning for species that are highly susceptible to local extinction because they breed in naturally patchy or artificially fragmented habitats. For example, the Golden-cheeked Warbler (*Setophaga chrysoparia*) breeds only in the state of Texas (USA) in mature oak-juniper forests, a specialized breeding habitat that has always been naturally patchy. The configuration of appropriate oak-juniper patches further changes over time as individual patches burn in both natural and human-caused fires, becoming poor warbler habitat until they regenerate into mature forest. Metapopulation models for the Golden-cheeked Warbler therefore must take into account factors like the size of oak-juniper habitat patches, their likelihood of persistence as appropriate habitat into the future, the number and reproductive success of the warbler pairs breeding in each patch, and the dispersal of warblers among patches (Alldredge et al. 2004; Horne et al. 2011) (Fig. 15.38).

The related concept of source–sink dynamics recognizes that even within more or less continuous habitat, patches may differ from one another in size, topography, resource abundance, or predator communities, so that factors affecting local population density or growth rate are not necessarily the same from patch to patch. Therefore, bird populations in different patches may differ from one another in overall productivity. In a **source population** more offspring are produced than can be accommodated in that patch, whereas **sink populations** experience high mortality or low reproduction and will not produce enough young to replace dying individuals. Source populations tend to export dispersing birds, which may settle in less productive patches that have vacant space for immigrants to settle. Dispersers also can colonize uninhabited patches that either experienced a local extinction or became newly suitable because of succession, fire, or some other change in habitat.

Even though flying birds have the capability to disperse widely, avian populations often are subdivided by the patchiness of their habitat. This is especially true within modern landscapes where humans have fragmented many habitats that formerly were continuous over large geographic areas. Indeed, metapopulation dynamics may be particularly important in populations of many bird species in areas—from islands to tropical forest fragments—where small patches of habitat support remnant bird populations.

Landscape structure is likely to have a strong effect on the degree of independence or connectivity of different subpopulations in a metapopulation. In many cases connectivity between habitat patches is enhanced if they are linked by **habitat corridors**, or strips of suitable habitat that connect two or more larger patches. Although corridors generally are thought to facilitate the dispersal of individuals from one patch of habitat to another, this idea rarely has been tested. Douglas Levey et al. (2005) used small (approximately 1 hectare) clear-cuts within a matrix of a South Carolina (USA) pine forest to test the importance of corridors to the movement of Eastern Bluebirds (*Sialia sialis*). They tracked the birds in an innovative way, using seeds marked with fluorescent dyes that were easily detected at night to find the remains of seeds eaten and then defecated by the birds. They found that seed dispersal, and thus movement of the birds themselves, was strongly facilitated by the existence of a narrow corridor connecting two of the clear-cuts, primarily because the bluebirds tended to follow habitat edges as they moved through the landscape.

15.7.4 Managing exploitation

Perhaps the most complete recovery of any bird in the world is that of the Wood Duck (*Aix sponsa*), once hunted so extensively across eastern North America that by 1900 ornithologist Joseph Grinnell, editor of *Forest and Stream* magazine, wrote "Being shot at all seasons of the year [Wood Ducks] are becoming very scarce and are likely to be exterminated before long." Instead, this beautiful duck became the first clear beneficiary of regulated hunting. In 1918, the hunting season for Wood Ducks was completely closed. Thanks to its high reproductive rate, by the 1930s the Wood Duck had recovered across much of its former range, and by 1941 its numbers were high enough that hunting was

Metapopulation: an array of spatially separated populations of the same species that are at least partly connected by the dispersal of individuals among them.

Source population: a population in which more offspring are produced than can breed in the original patch, leading some to disperse away to other locations.

Sink population: a population in which reproduction is not sufficient to maintain population size, and which therefore must receive immigrants dispersing from other populations to remain extant.

Habitat corridor: an area of habitat that connects larger patches of that habitat and through which species dependent on that habitat can move.

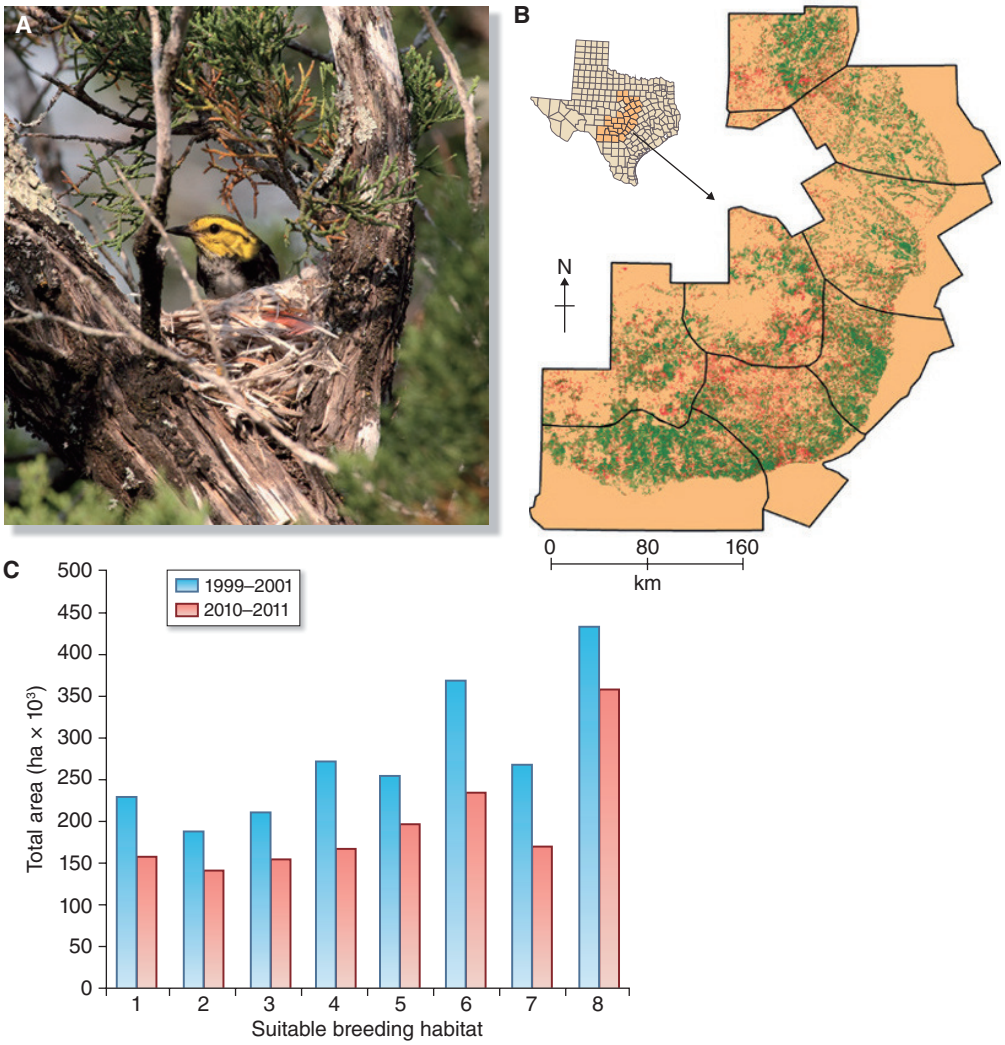


Fig. 15.38 Habitat loss and conservation planning. (A) The Golden-cheeked Warbler (*Setophaga chrysoparia*) is an endangered species that prefers to breed in large patches of mature oak-juniper forest. (B) Habitat alteration from 1999 through 2011, where the areas shown in red no longer support breeding warblers and green indicates areas in which the species has persisted, and (C) the general decline of suitable breeding habitat in eight monitored areas, demonstrates that landscape-scale planning for conservation of remaining suitable habitats is vital. (A, photograph by Gil Eckrich. B and C, from Duarte et al. 2013. CC-BY-SA 3.0.)

permitted broadly again. By the 1960s, population estimates ranged between 1 and 2 million, and during the 1970s and 1980s the Wood Duck began spreading into previously unoccupied areas of the Great Plains, northwestern Canada, and northern Mexico (Hepp and Bellrose 1995).

The early phase of the Wood Duck's recovery depended on complete cessation of hunting as an extra source of mortality for several decades. This ban was followed by careful population monitoring by wildlife personnel and strict management of hunting limits throughout the USA and Canada. One wonders what North America would be like today if the same management strategies had been imposed for Passenger Pigeons (*Ectopistes migratorius*) only a few decades earlier.

15.7.5 Reserve design

Few species can persist if their range is reduced to a single patch of habitat, especially if that patch is small. The key to conserving rare species and vanishing ecological communities is to secure habitat reserve networks that are designed to accomplish long-term protection, ideally by securing multiple local populations and permitting movements among them. Single-population modeling helps us project the minimum size required to reduce within-patch extinctions, and metapopulation modeling can help estimate extinction probabilities for alternative network configurations. Such exercises have produced a series of general rules that guide the ideal design of reserves and reserve

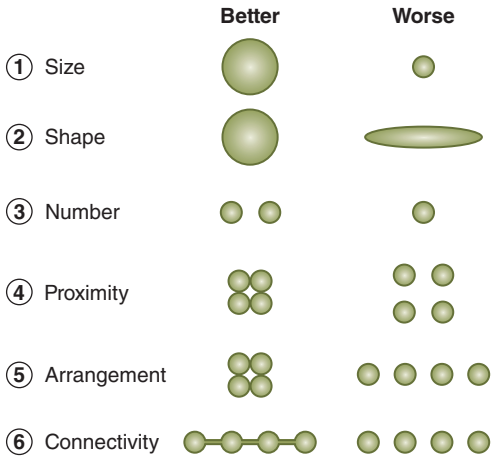


Fig. 15.39 Guidelines for habitat reserve networks. Several widely accepted rules guide the ideal design of reserves and reserve networks, in order to maximize their capacity for preserving target species or regional biodiversity. (From Diamond 1975. Reproduced with permission from Elsevier.)

networks (Fig. 15.39). The following are the most important of these rules:

- Bigger is better, because larger reserves contain larger total population sizes of birds, reducing vulnerability to stochastic extinctions.
- Round or square is better than long and thin, to minimize the proportion of the bird population that is subject to edge effects.
- Create multiple reserves whenever possible to reduce the chances that a catastrophe could wipe out an entire species.
- Ensure at least one large reserve in the network to provide a reliable source of dispersers to recolonize smaller patches after local extinctions.
- Minimize distances among reserves to facilitate local movements of birds among patches and reduce genetic isolation within them.
- Add "stepping stones" and "corridors" between reserves, because these small pieces of habitat often greatly facilitate the movement of birds among reserves, thus allowing a fragmented reserve system to act more as if it were larger and more continuous.
- A two-dimensional landscape configuration is better than a linear one because it promotes opportunities for dispersal and recolonization among all habitat patches.

Protecting networks of habitat reserves by securing and properly managing islands of habitat remains the single most important means for protecting the world's rarest birds and most endangered ecological communities. The Brazilian Atlantic forest, for example, contains one of the highest concentrations of locally endemic birds on earth, but these birds also are among the most endangered because of habitat loss. Comprehensive analysis of remnant patches and protected areas shows that only 11.7% of the original forest remains, and fully 83% of this remainder exists in tracts that are 50 hectares or smaller in size (Ribeiro et al. 2009). Clearly, protecting the largest remaining tracts is essential, and three of these contiguous tracts contain more than 13% of the remaining forest. With more than 40% of the remaining forest located more than 50 kilometers from its nearest protected nature reserve (Fig. 15.40), it is equally crucial to identify and protect the smaller tracts that are the most vital corridors and stepping stones connecting the larger reserves.

15.7.6 Genetic augmentation

Close inbreeding and genetic bottlenecking probably explain why some of the most endangered bird species begin failing to breed successfully as they reach critically low numbers. In the Hawaiian Crow (*Corvus hawaiiensis*), for example, the last few pairs of wild individuals failed to fledge any young between 1991 and 2001, when the last wild pair disappeared (Fig. 15.41). A number of the eggs they produced appeared to be infertile when examined after the breeding season, and the inbreeding hypothesis was reinforced when DNA fingerprinting of the small captive population revealed the survivors to be unusually similar to one another genetically. To maximize successful reproduction within the captive flock, project managers did their best to pair individual crows with mates as genetically dissimilar as possible. Analysis of genetic similarity, plus carefully tracking of the pedigrees of all breeders and their offspring, allows keepers to avoid sib–sib or parent–offspring pairings and also to promote pairings likely to keep the existing genetic diversity from declining further (Hoeck et al. 2015). This pairing is accomplished by keeping a **studbook**, now a standard practice in zoos around the world and one that is especially important in captive-rearing programs involving rare birds. This process has been highly successful for the captive flock of Hawaiian Crows, which grew from only 12 birds in the early 1990s to 114 by 2014.

Human intervention sometimes can relieve genetic bottlenecks within tiny wild populations, thereby avoiding the associated extinction spiral caused by the loss of genetic variability. A dramatic example of **genetic rescue** was seen in an isolated population of Greater Prairie-Chickens (*Tympanuchus cupido*) in southern Illinois (USA) that was declining in the 1980s. By 1993, fewer than 50 individuals

Studbook: the genealogical record of parents and offspring used in captive-breeding programs.

Genetic rescue: the introduction of individuals bearing novel genotypes from elsewhere into a population suffering from low genetic diversity, thereby increasing that diversity.

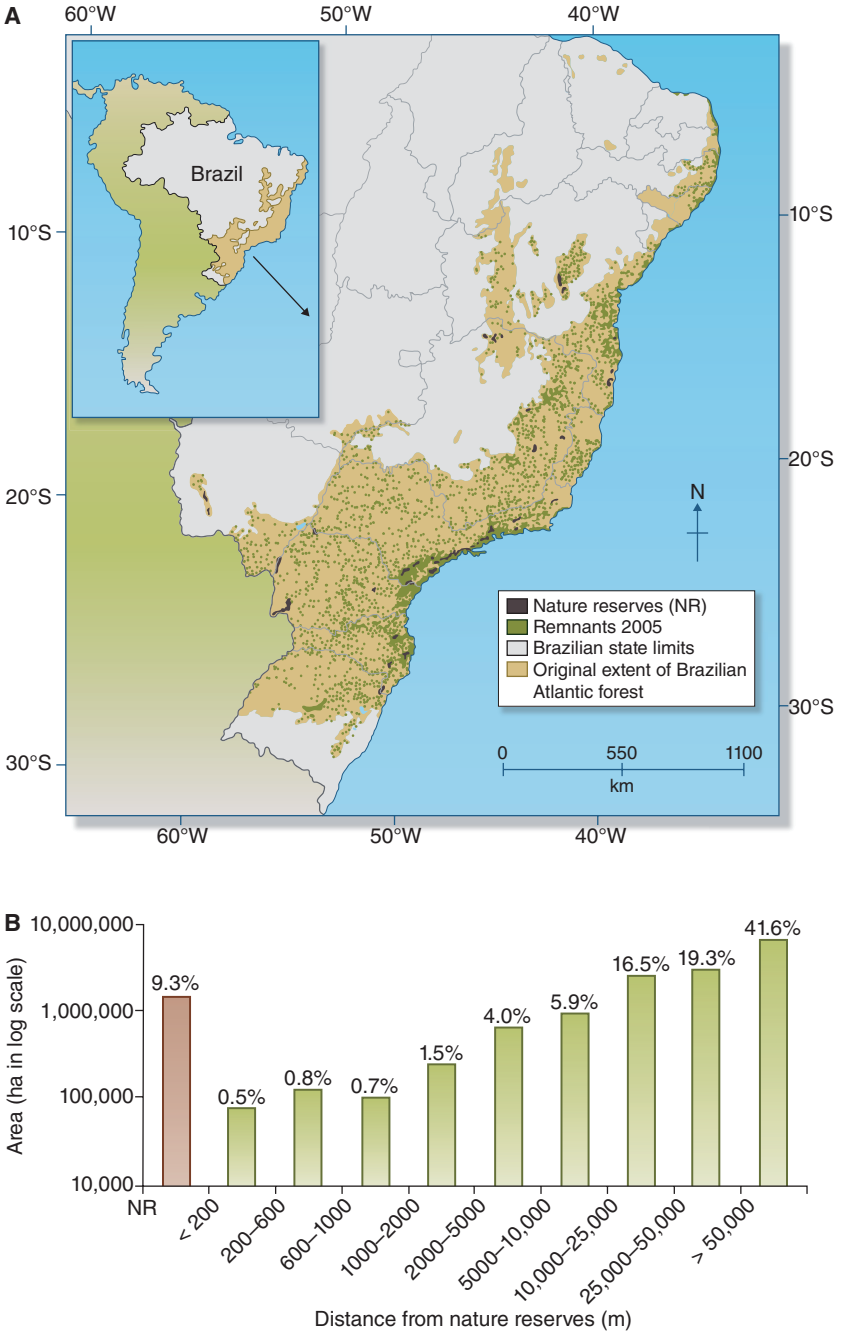


Fig. 15.40 Remnant Brazilian Atlantic forest. (A) Only 11% of the original Brazilian Atlantic forest (tan-shaded area) remains. Nature reserves are shown in black and remnant patches of forest in green. (B) The area (height of bars) and percentage (given above bars) of remnant Atlantic forest patches are shown for distinct classes of distances from nature reserves. Note that over 40% of remnant patches occur more than 50,000 meters from the nearest nature reserve, leaving them isolated and vulnerable to species loss without recolonization. (From Ribeiro et al. 2009. Reproduced with permission from Elsevier.)

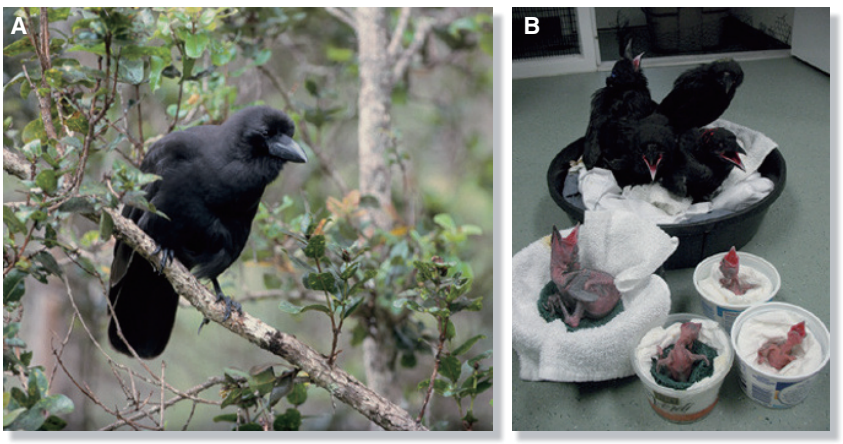


Fig. 15.41 Captive rearing to recover endangered species demands careful genetic record-keeping. (A) The few remaining Hawaiian Crows (*Corvus hawaiiensis*) are part of ongoing captive-breeding programs aimed at eventual reintroduction into the wild. Paired birds must have minimal genetic similarity to reduce infertility of eggs and lethal birth defects in offspring. (B) Successfully hatched young birds are potential breeders for future generations, providing a glimmer of hope for this critically endangered species. (Photographs: A, by Jack Jeffrey Photography; B, courtesy of Zoological Society of San Diego © 2014 DSZG.)

remained, and these possessed only about two-thirds of the genetic diversity found in the larger populations in nearby Nebraska, Kansas, and Minnesota. Only about half of the eggs laid by the Illinois females were hatching, compared with 93% hatchability elsewhere (Westemeier et al. 1991), strongly suggesting inbreeding depression. When birds from other populations were experimentally introduced into the declining population, the hatching rate increased to pre-bottleneck levels (Fig. 15.42), and the population was stabilized (Bouzat et al. 1998).

Maintaining genetic variability in small populations across many generations is a difficult challenge. Recently, in a sobering review, one of the original architects of population viability analysis argued that species management in zoos is failing to achieve this goal for a large proportion of target species (Lacy 2013). On the other hand, captive-rearing programs increasingly are being combined successfully with conservation efforts in the field, effectively blurring the distinction between in situ (field-based) and ex situ (captivity-based) conservation strategies. Some examples of these hybrid efforts are described in the following sections.

15.7.7 Captive rearing and reintroduction

Captive rearing to protect critically endangered animals began early in the twentieth century, with the breeding by European nobility of the last few Pére David's deer (which were extinct in their native China) often cited as the first example. In the UK, the Wildfowl and Wetlands Trust was founded in 1946 to breed endangered waterfowl, and in 1959 a breeding program for a broad array of globally endangered birds and mammals was initiated at the Jersey Zoo, later called the Durrell Wildlife Park. In the 1960s biologists in the USA began collecting the eggs of wild Whooping Cranes (*Grus americana*) to establish a captive-breeding flock in Patuxent, Maryland (Box 15.04), and in 1970 the Peregrine Fund was established to breed, rear, and release Peregrine Falcons (*Falco peregrinus*). Today the conservation practice of captive rearing is widespread and often embraced as an important mission of zoos and aviaries around the world. Broadly speaking, the goals of all such programs are similar: to use modern incubation and husbandry techniques, often supplemented with eggs collected from wild individuals, to increase the overall birth rate and juvenile survival rate of rare birds, resulting in an increasing population of healthy adults. Then, employing strategically designed, species-specific release strategies, to use these captive-reared individuals to establish or augment free-ranging natural populations in appropriate habitat, while still maintaining genetically healthy stocks in captivity.

Dramatic success stories illustrate the conservation value of captive rearing and reintroduction, and some failures illustrate the most important pitfall. By 1972, when DDT and related compounds were banned from widespread use, the Peregrine Falcon had functionally disappeared from most of North America. Using eggs from tundra-breeding subspecies, conservation biologists reared and

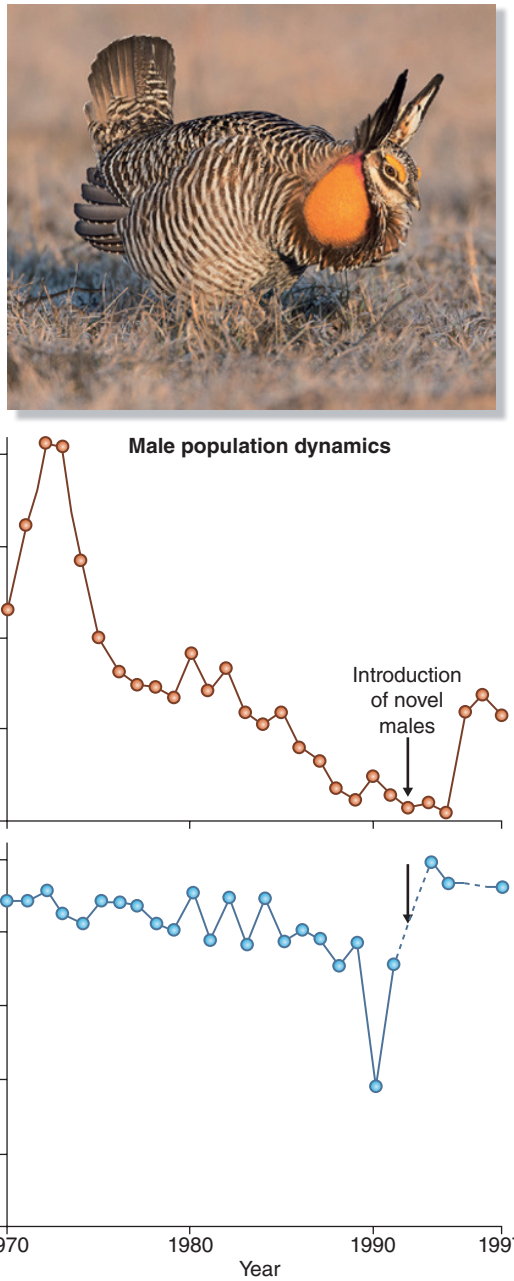


Fig. 15.42 Genetic rescue. (A) By the 1980s, a small isolated population of Greater Prairie-Chickens (*Tympanuchus cupido*) in southern Illinois was declining, and fewer than 50 individuals remained in 1993. Biologists introduced males (indicated by arrows) from larger populations in an attempt to "rescue" the genetic diversity of the population. (B) One sign of a genetic bottleneck is egg-hatching failure, a clear trend in the early 1990s. After genetic rescue, both hatching success and number of breeding males immediately began to increase. (From Westemeier et al. 1998. Reprinted with permission from AAAS. Photograph by Jeff Dyck.)

Box 15.04 Whooping Crane conservation, a hands-on success

Perhaps no bird more dramatically symbolizes intensive species-level conservation than the stately Whooping Crane (*Grus americana*), first for so closely approaching extinction and more recently for the spectacular, human-assisted migration route now characterizing one of its reintroduced populations. Once occurring across most of eastern North America, the species reached its historic low when only 16 individuals wintered along the Texas coast in 1941. Its decline began with market and sport shooting, but was hastened dramatically by draining and agricultural conversion of the American prairies. With a low reproductive rate (only one young is fledged annually, and breeding is delayed until age 5 years), even in fully restored habitat the species would take hundreds of years to recover without human assistance. By 1937 both the Canadian breeding grounds and the Texas wintering grounds had been protected as national parks. Captive breeding began in 1967, and the wild population grew steadily as a consequence of its range-wide protection. Cranes bred well in captivity, as demonstrated early on when a young researcher at Cornell University, George Archibald, personally induced courtship displays by dancing himself (Fig. 15.B4.01). Archibald later established the International Crane Foundation in Baraboo, Wisconsin (USA), a rearing center featuring all 16 species of the world's cranes as international symbols for wetland conservation.

Captive flocks at three locations began providing birds for wild reintroduction by the 1990s. In 1995 a small population intended to be non-migratory was established in the Kissimmee Prairie of central Florida (USA), but this population experienced persistently high predation, mainly from native bobcats and coyotes. Supplementation with captive-reared birds ceased in 2006, the population rapidly shrank from more than 50 to fewer than 20, and its future is in doubt. A non-migratory flock initiated in 2011 in Louisiana is experiencing similar difficulties. However, an unexpected success occurred in 1999 when two Whooping Cranes that had been missing and presumed dead were found nesting in a farmer's field in the Upper Peninsula of Michigan.

In 2001 a group of captive-reared Whooping Crane chicks was imprinted on a white ultralight aircraft in Wisconsin and then led, day after day, on a successful fall migration to central Florida. As hoped, the survivors returned northward the following spring. Similar introductions and training flights now occur annually (Fig. 15.B4.02). The establishment of a permanent migratory eastern flock appears hopeful, because northward-migrating cranes now form pairs, and a few have fledged young cranes into the population. As of 2011, the original western population of Whooping Cranes numbered 279, and the eastern migratory population numbered 112.



Fig. 15.B4.01 George Archibald inducing courtship displays to captive-bred Whooping Cranes (*Grus americana*). Archibald went on to create the International Crane Foundation because many crane species are threatened or endangered owing to the destruction of wetland habitats, pollution, persecution, and agricultural conversion. (Photograph courtesy of International Crane Foundation.)



Fig. 15.B4.02 Ultralight aircraft guiding Whooping Cranes (*Grus americana*) in migration. Training captive-reared cranes to migrate from breeding grounds in Wisconsin to Florida (USA) provides hope that new migratory populations of wild-breeding cranes might be restored. However, the intricacies of breeding behavior continue to hinder the success of this reintroduction effort, as we lack the ability to teach parental behavior to novice captive-bred birds, required to ensure successful breeding. (Photograph courtesy of operationmigration.org.)



Fig. 15.43 Mauritius Kestrel (*Falco punctatus*). This species recovered from the brink of extinction in the mid-1970s thanks to the timely intervention of biologists. Eggs were removed and raised in a captive-breeding program, while parents raised their own replacement clutches in the wild. The population today is healthy and at carrying capacity in remaining forest habitats. (Photograph by Sam Cartwright.)



Fig. 15.44 California Condor (*Gymnogyps californianus*) puppets help rear captive-bred chicks. By using barriers and puppets to minimize imprinting on humans during captive rearing, the San Diego Zoo (USA) has successfully raised and reintroduced captive-bred chicks into the wild. (Photograph courtesy of Zoological Society of San Diego © 2014 SDZG.)

began releasing young falcons from wooden boxes that served as artificial nests, constructed to provide human access from the rear for feeding. Soon, falcons were being hatched successfully from the convenient and predator-free "cliffs" provided by urban skyscrapers across eastern North America (Chapter 13). Eventually, released birds began returning and pairing with one another, establishing new territories and new nest sites. The population recovered steadily, and in 1999, the Peregrine Falcon was removed from the US Endangered Species List. Recent population estimates suggest that the species has achieved or surpassed its pre-1900 numbers.

Similar efforts began in the late 1970s to rescue the critically endangered Mauritius Kestrel (*Falco punctatus*) (Fig. 15.43) on the island where the Dodo (*Raphus cucullatus*) had gone extinct two centuries earlier. Habitat loss and pesticides had reduced this distinctive small falcon to only four individuals by 1974. Biologists removed the first eggs laid in several nests and supplemented the kestrels' diet to promote their ability to lay replacement clutches, effectively doubling the population's birth rate. Young birds were released back into the wild and supplied with food. The population recovered dramatically and currently numbers more than 800 individuals occupying essentially all of the remaining forest habitat on the island. The species' long isolation on a small oceanic island probably explains why inbreeding has not hampered this recovery: deleterious genetic variants were likely already eliminated by the functionally perpetual "bottleneck" imposed by the small size of the island. Other species on Mauritius that appear to have escaped extinction thanks to captive breeding include the Echo Parakeet (*Psittacula eques*) and the Pink Pigeon (*Nesoenas mayeri*).

Following a century-long population collapse and predictions of imminent extinction, all the 21 remaining wild California Condors (*Gymnogyps californianus*) were taken into captivity between 1982 and 1987, thereby launching a successful captive-breeding program. The first captive-bred young hatched in 1988. Nestlings were fed by keepers hidden behind barricades, via hand puppets resembling condor heads to minimize imprinting on humans (Fig. 15.44). Experimental releases using Andean Condors (*Vultur gryphus*) as surrogates allowed biologists to hone techniques for tracking and monitoring released birds by practicing with a biologically similar but less endangered species—female Andean Condors were released into the wild, and later were recaptured and transported back to South America. Captive-bred California Condors were first reintroduced in 1992, and by 2014 the total free-flying population numbered 228 in four separate populations (Fig. 15.45), with an additional 193 in captivity. Despite this success, free-flying condors continue to suffer excessive illness and death, mainly from lead poisoning caused by the ingestion of lead ammunition in mammal carcasses (Church et al. 2006). As a result, individuals throughout the range need to be recaptured regularly for veterinary treatment to remove lead from their systems.

For the California Condor, the original problem still has not been solved, and the population is growing only because of persistent augmentation from the captive-breeding program (Walters et al. 2010). Failing to remedy the original problems can cause captive rearing and reintroduction to fail entirely. Expensive and well-executed efforts during the 1990s to augment the dwindling wild population of Hawaiian Crows (*Corvus hawaiiensis*) with

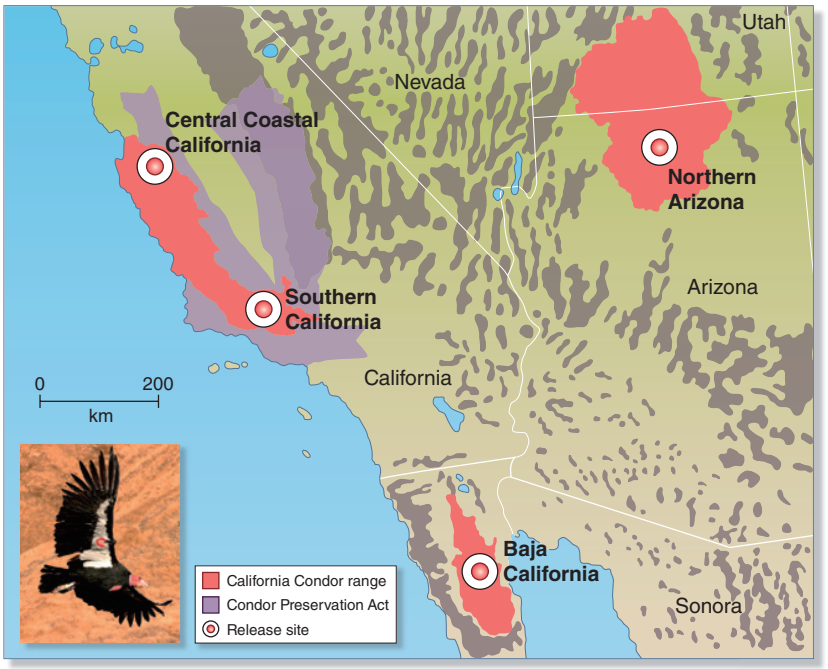


Fig. 15.45 Reintroduction of California Condors (*Gymnogyps californianus*). Although captive-breeding programs have released individuals into the wild successfully, many birds become ill after ingesting meat from animals killed with lead ammunition. (Photograph courtesy of US Fish and Wildlife Service/Pacific Southwest Region.)

young birds raised in captivity failed because the habitat in the mid-elevation Kona forests still suffered from the suite of challenges originally threatening the species. These threats included avian pox, avian malaria, introduced rats and feral cats (and associated toxoplasmosis), a degraded forest understory grazed by feral cattle, and—ironically—predation by the native Hawaiian Hawk (*Buteo solitarius*), itself on the US Endangered Species List but now thriving. Success of a new Hawaiian Crow reintroduction (tentatively scheduled for 2016) will depend upon controlling at least some of the continuing problems in the release zone.

15.7.8 Eliminating introduced mammals

Birds that evolved in the absence of grazing and/or predatory mammals are especially vulnerable to a vicious combination of threats from introduced mammals: habitat degradation from grazing and browsing, reduced nesting success caused by rat predation, and elevated predation on juveniles and adults by everything from rats (Fig. 15.46) and cats to mongooses and pigs (Box 15.05). Beginning in earnest in the 1980s and now rapidly gaining momentum all over the world, the eradication of introduced rats, goats, sheep, pigs, deer, and cattle from oceanic islands has begun to recover some of these unique ecosystems and reverse population declines among their birds. New Zealand is widely recognized as the world leader in rat eradication, having developed and applied a method using bait poisoned with the anticoagulant brodifacoum, which proved to be the most effective eradication agent (Taylor and



Fig. 15.46 Invasive mammalian predators. Numerous invasive predators have caused the decline and extinction of native avifauna. The black rat is infamous the world over for its skill at accessing and eating nestling birds. (Photograph courtesy of Nga Manu Images.)

Thomas 1989, 1993). In recent decades rats have been eliminated on dozens of New Zealand islands. In one of the largest eradication projects ever undertaken, Campbell Island, with an area of 113 square kilometers, was declared rat-free in 2005, 5 years after the project began, and it now supports populations of several endemic New Zealand birds.

Off the coast of Baja California (Mexico), tiny Socorro Island harbors a diverse community of landbirds and breeding seabirds, including a number of endemic species and subspecies. Introduced sheep altered the vegetation composition and structure, leaving every one of the island's

Box 15.05 Conservation milestones on Lord Howe Island

Lord Howe Island is a 10-kilometer-long, crescent-shaped volcanic island located in the Tasmanian Sea between Australia and New Zealand. When discovered by British explorers in 1788, the island supported 15 bird species, nine of which then went extinct over the ensuing 150 years as humans settled the island, cleared the forests, and introduced an assortment of mammals. One bird that remained into the twentieth century was a remarkably tame, flightless rail, the Lord Howe Rail (*Gallirallus sylvestris*) (Fig. 15.B5.01), which had been common and widespread but which was an easy source of food for both transient sailors and permanent settlers. By the 1860s the rail was rare, and its decline continued until the species was poised to become the island's tenth avian extinction. Detailed surveys in the late 1960s revealed fewer than 30 individuals, all restricted to steep, forested ravines atop the island's two mountains. By 1980 only three healthy breeding pairs remained.

The Lord Howe Rail's steady decline presented a conservation mystery, because humans had long since stopped taking them for food. Hypotheses included predation by rats, cats, and even the introduced Tasmanian Masked-Owls (*Tyto novaehollandiae castanops*), which had been brought to the island in the 1930s in an unsuccessful effort to control rats. A now-classic example of careful, conservation-directed ecological research on the few remnant pairs finally revealed that predation on adults by introduced feral pigs was exceeding juvenile recruitment, pointing to inevitable extinction unless humans intervened (Miller and Mullette 1985). In 1980 the three remaining pairs were captured and moved to a new captive-breeding facility on the island, where they thrived and proliferated. Simultaneously, the feral pigs on Lord Howe Island were eradicated completely by the end of 1981. By 1984, 93 Lord Howe Rails had been released back into native habitats on both mountains, and the captive-breeding facility was closed. Today the population of Lord Howe Rails is stable at about 250 birds, which is estimated to be the maximum size sustainable within the available habitat across the island.

Additional eradication projects were undertaken after the success of the Lord Howe Rail recovery program. Goats were eliminated by the mid-1990s; predatory big-headed ants were controlled using chemical baits not attractive to native ants; exotic Mallards (*Anas platyrhynchos*), which had been hybridizing with the native Pacific Black Duck (*Anas superciliosa*), were eliminated. Today, meticulous planning is underway for a broad-based eradication program of rats, as are deliberations about eliminating the Tasmanian Masked-Owl, now threatening many of the island's birds including an endangered subspecies of the Pied Currawong (*Strepera graculina crissalis*). Once the Tasmanian Masked-Owl is removed, plans are to reintroduce the Southern Boobook (*Ninox novaeseelandiae*), an owl that is closely related to the now extinct Lord Howe Boobook (*Ninox novaeseelandiae albaria*).

This impressive suite of restoration efforts has begun paying off for the entire Lord Howe Island ecosystem. Besides the birds, numerous plants and invertebrates are recovering island-wide. Once rats are controlled, plans exist to reintroduce the Lord Howe Island stick insect, one of the largest and arguably the world's most remarkable terrestrial insect. Lord Howe Island has become a worldwide model for restoring island ecosystems.



Fig. 15.B5.01 Lorde Howe Rail (*Gallirallus sylvestris*). Predation by introduced feral pigs led to the dramatic decline of this species in the twentieth century. Successful captive breeding of these rails, accompanied by the extermination of all feral pigs (among other feral animals), remedied the situation. This species now occurs in numbers (approximately 250 birds) assumed to be the maximum carrying capacity of their small remaining habitat. (Photograph by Toby Hudson, http://commons.wikimedia.org/wiki/File:Lord_Howe_Woodhen_3.jpg#mediaviewer/File:Lord_Howe_Woodhen_3.jpg. CC-BY-SA 3.0.)

specialties threatened, critically endangered, or extinct. Removal of sheep by the Mexican navy and replanting of some native shrubs and forbs have steadily improved the habitat, and the critically endangered Socorro Mockingbird (*Mimus graysoni*) appears to be recovering. The Socorro Dove (*Zenaida graysoni*), extinct in the wild since 1972, might be reintroduced if current plans to control the significant feral cat population move forward.



Before management (1998) After management (2005)

Fig. 15.47 East Maui Watershed Preserve and the effects of excluding feral pigs. In order to restore the ecological integrity of forest undergrowth after decades of devastation by feral pigs (left image), this preserve was fenced and the pigs were systematically exterminated. This action was controversial, but it achieved the desired outcome, as understory regrowth occurred in just a few years (right image). Maintaining fenced mammal exclosures and removing invasive exotic plants remain essential management actions for the persistence of rare native plants and birds in this watershed. (Photographs courtesy of The Nature Conservancy of Hawaii.)

Ground-nesting seabirds, so vulnerable to rat depredation on oceanic islands all over the world, now have been shown to respond rapidly to predator removal. On the island of Anacapa, off the coast of southern California (USA), Scripps's Murrelet (*Synthliboramphus scrippsi*) had declined severely for decades because of predation by black rats. During 2001 and 2002 all rats were eradicated via helicopter broadcasts of poison pellets. By 2005, nest-site occupancy, nesting attempts, and hatching rates had increased substantially, and the nest-depredation rate had dropped from 52% to 7% (Whitworth et al. 2005). Predator control (first rats, then cats) has similarly also prevented extinction of Europe's most endangered seabird, Zino's Petrel (*Pterodroma madeira*) of Madeira Island.

On the Hawaiian island of Maui, one of the world's wettest rainforests is the site of at least a partial success story. About 500 critically endangered Maui Parrotbills (*Pseudonestor xanthophrys*) and several thousand Akohekohes (*Palmeria dolei*) persist in ohia forests largely above the elevations of malaria-bearing mosquitoes, where another critically endangered native honeycreeper, the Poo-uli (*Melamprosops phaeosoma*), was first discovered in 1972. Amid the billowy mosses were more than a dozen endangered plants, including spectacular lobelias that had not flowered in decades. Feral pigs were rooting the soil, eating young emerging plants, and reducing overall plant diversity. In part because of the forest's importance in protecting and purifying the watershed for the human population along the coast, a consortium of owners formed the East Maui Watershed Preserve. Their most controversial management decision was to fence the lower boundary of the preserve and eliminate feral pigs by lethal snaring, which produced the desired effects almost instantly (Fig. 15.47). The lobelias are flowering again, and Maui Parrotbills and Akohekohes thrive above them, augmented by a captive-breeding program. Unfortunately, this habitat restoration came too late to save the Poo-uli, as the last individual died in captivity in 2004.

15.7.9 Translocation

Among the most important strategies for rescuing critically endangered species is **translocation**, or moving individuals from one location to another area where threats have been reduced or eliminated. As with predator eradication, the conservation biologists of New Zealand have been global pioneers in using translocation, often coupled with intensive habitat management, to prevent the extinction of extremely rare bird species. Much of lowland New Zealand has been converted into grazing land, which has resulted in the loss of all but the most resilient native species. Furthermore, because the main islands are teeming with introduced rats, cats, ferrets, and stoats, most native landbird species are threatened or endangered. During recent decades, New Zealanders have produced truly dramatic conservation success stories, teaching the rest of the world much about what is possible even in the face of daunting odds.

A particularly compelling conservation success involves the recovery of the Chatham Robin (*Petroica traversi*) (Fig. 15.48), which by 1980 was extinct except for three males and two females, one of which was infertile. All five

Translocation: the human-assisted movement of individuals from one location to another for conservation purposes. It is used most effectively to establish or supplement populations in areas where threats have been reduced or eliminated.



Fig. 15.48 Chatham Robin (*Petroica traversi*). Reduced to five individuals by the mid-1980s, human intervention was the last option for species recovery. This was accomplished by transferring the few remaining individuals to offshore islands that were free of predators and carefully cross-fostering eggs within nests of other small passerines. The population currently has recovered to approximately 250 individuals. (Photograph by Leon Berard.)



Fig. 15.49 Kakapo (*Strigops habroptila*). A large, flightless, nocturnal parrot, this New Zealand endemic was an easy target of introduced feral cats and was nearly extinct by the late 1970s. In 1989, the Kakapo Recovery Plan moved 65 individuals to several small, virtually predator-free islands. With extensive volunteer efforts and successful captive rearing, current populations include 130 monitored individuals. (Photograph by Stephen Jaquiery, Otago Daily Times.)

survivors were translocated to predator-free Mangere Island, and each year the first clutches of the final breeding female (nicknamed "Old Blue") were transferred to be **cross-fostered** by Tomtits (*Petroica macrocephala*). Old Blue re-nested each year, and the population began recovering after she paired with the breeding male, "Old Yellow." All surviving black robins are descended from these two individual birds. Key to this landmark project's success is the ongoing absence of predators on Mangere Island and the larger South East Island, where today the Chatham Robin population numbers more than 200. Although genetic diversity is exceedingly low after this dramatic population bottleneck, the effects of inbreeding depression have not been observed, suggesting that this population has faced several dramatic crashes over evolutionary time, potentially eliminating deleterious recessive alleles.

The charismatic Kakapo (*Strigops habroptila*) (Fig. 15.49), a huge, flightless, nocturnal parrot that roosts and breeds in burrows, was once widespread but is now entirely gone from all three of New Zealand's main islands. With the species at the brink of extinction, it was widely feared that only males still existed, but in 1977 a small population was discovered on Stewart Island, where they were being devoured by cats. In 1989 the historic Kakapo Recovery Plan moved 65 individuals to small, nearly predator-free offshore islands, where any arriving cats, rats, or stoats could be systematically eliminated. Some islands proved unsuitable, but on others the population expanded, aided by intensive care and captive rearing by humans. As of 2014, 130 Kakapo remain.

Cross-fostering: in avian conservation, the practice of using surrogate parents (sometimes of a different species) to raise the young of the species being conserved.

A number of other New Zealand endemics, all highly vulnerable to mammal predation, have been similarly rescued. Notable among these is the Takahe (*Porphyrio mantelli*) (Fig. 15.50), a giant, flightless rail once believed extinct but rediscovered in 1948 and today numbering well over 200. Between 1983 and 1991, Takahe were transferred successfully to four different predator-free islands (Maud, Mana, Kapiti, and Tiritiri Matangi). Importantly, a remnant Takahe population now is expanding within its native range in the Murchison Mountains of South Island in a large preserve where the concerted elimination of red deer and stoats has restored the tussock grass habitat to nearly pristine condition.

Other distinctive New Zealand endemics now being rescued via translocation to predator-free or predator-controlled islands include the Little Spotted Kiwi (*Apteryx owenii*), Saddleback (*Philesturnus carunculatus*), Kokako (*Callaeas cinereus*), and Stitchbird (*Notiomystis cincta*). Especially notable is the Maungatauri Restoration Project on North Island, New Zealand's largest and most ambitious example of "mainland" restoration. Beginning in 2004 and completed in 2006, this 34-square-kilometer forested ancient volcano is now surrounded by a remarkable, 47-kilometer fence designed to prohibit entry by rodents, cats, stoats, brush-tailed possums, and ungulates. Systematic



Fig. 15.50 Takahe (*Porphyrio mantelli*). This large, flightless rail was presumed extinct until a small population was rediscovered in 1948. Similar to other island endemics that are threatened by invasive mammal predators, this species recovered strongly with efforts to eliminate invasive animals, restore native grassland habitat, transfer individuals to several predator-free islands, and monitor populations with intensive radio-tagging. (Photograph by Janice McKenna.)

poisoning, trapping, and hunting of pests began once the fence was closed, and very soon thereafter a number of rare species were rediscovered. A pair of Takahe was introduced in 2006, followed by a series of other rare endemics. The intent is to have a full complement of surviving North Island birds free-flying and reproducing within this landmark project. One of the world's rarest seabirds—the Magenta Petrel (*Pterodroma magentae*) of Chatham Island—has been saved by within-island translocation of chicks prior to fledging to the Sweetwater Secure Breeding Site, a 3-hectare area fenced against predators.

15.7.10 Conservation-reliant species

In 2005, a group of well-known conservation biologists published a landmark paper announcing that a large proportion of today's threatened and endangered species likely will never be able to survive on their own in the absence of human investment of energy, time, and resources (Scott et al. 2005). They further proposed that our twenty-first century definition of "recovery" for endangered species explicitly acknowledges that many are bound to remain **conservation-reliant species** because they will require some form of continuing active management. Their proposal, which met only casual, mostly philosophical, resistance, makes a profound statement about human aspirations for conservation. We must no longer expect or hope that our planet might someday achieve a state in which natural systems persist sustainably, with an essentially complete array of native species, unless we continue to invest actively in their well-being.

Conservation-reliant species: species that will require active, ongoing, and perhaps permanent conservation measures to avoid extinction.

"Conservation-reliant" bird species exist all over the world, with two types now broadly recognized (Goble et al. 2012). Population management-reliant species require continual human intervention for local populations to persist. For example, predator-proof cages and/or human exclosures have become essential for successful breeding of endangered shorebirds such as Black Stilts (*Himantopus novaezelandiae*) in New Zealand, Hooded Plovers (*Thinornis cucullatus*) in Australia, Piping Plovers (*Charadrius melodus*) in eastern North America, and perhaps African Oystercatchers (*Haematopus moquini*) in South Africa. California Condors (*Gymnogyps californianus*) probably always will require capture and chelation therapy to keep lead poisoning from greatly reducing the free-living population. Periodic genetic augmentation from captive populations may be essential for a variety of species.

"Threat management-reliant" species are those capable of persisting as wild populations as long as their habitat is managed to reduce or eliminate otherwise recurring threats. For example, the Palila (*Loxioides bailleui*) and numerous other endangered Hawaiian birds can persist indefinitely on their own, but only if introduced mammals are actively and continuously controlled throughout sufficient areas of habitat (Reed et al. 2012).

15.7.11 Habitat management and restoration

Habitat is the essential requirement for the conservation of any species, community, or ecosystem. Because habitat loss and degradation are the leading causes of avian population declines worldwide, efforts to protect or restore habitat always will be the cornerstones of conservation solutions for most species. As discussed earlier, conservation is accomplished most effectively by protecting large habitat patches, ideally with multiple patches configured across the landscape to promote functional metapopulations for target species. However, simply establishing a habitat patch as a protected area without attending to its long-term management is usually insufficient to ensure successful conservation of its species and natural ecosystem functions. Almost everywhere on earth, habitats experience continuing human influences, either directly (as through exposure to exotic predators such as cats) or indirectly (as through altered water regimes or fire cycles). Therefore, most natural area preserves—even the very largest ones—require



Fig. 15.51 Riparian restoration. The San Pedro River is the last free-flowing (undammed) river of the southwestern USA, providing habitat for over 300 bird species throughout the year. Cattle attracted to water can destroy such habitats (top images), as they compact the soil and overgraze native plants. The Nature Conservancy now owns and manages several portions of this critical habitat corridor, actively keeping cattle out and restoring damaged plant communities (bottom images) essential to birds and numerous other animals. (From Krueper et al. 2003. Reproduced with permission from John Wiley and Sons.)

active habitat management to remain suitable for the species and ecological systems they are designed to protect.

Mimicking natural disturbance is often a vital form of habitat management. Many grassland habitats, for example, support higher species diversity when subjected to periodic disturbances that mimic the passing of a herd of grazing ungulates. Consequently, short-rotation grazing by domestic cattle actually can improve grasslands as a habitat for some birds. On the other hand, cattle tend to loaf and forage near streams, causing erosion of stream banks and degradation of the riparian thickets that are so important for breeding bird communities. Habitat management in grazing lands may require the construction and maintenance of fencing to permit control of stocking rates, to limit exposure periods within each grazing unit, and to reduce or prohibit access of cattle to riparian habitats (Fig. 15.51).

The influence of fire on bird species diversity has become a major focus of conservation research and management experiments in ecosystems around the world. Especially in tropical dry forests, human-caused fires at unnaturally high frequencies degrade forest structure and composition and sometimes eliminate forest altogether. Vast areas of interior Madagascar, for example, once supported dry forests but are now dominated by introduced grass because of purposeful annual burning by humans. The severely endangered Van Dam's Vanga (*Xenopirostris damii*) is among many Madagascar endemics whose dry forest habitat has been reduced to tiny fragments by uncontrolled brush fires. Similar threats face dry-forest endemics in Western Australia, where birds such as the Mallee Emuwren (*Stipiturus mallee*) (Fig. 15.52) are reduced to tiny forest fragments with a dense understory of *Spinifex* vegetation. These areas are extremely vulnerable to fire, and emuwrens strongly favor patches that have not burned in decades (Brown et al. 2009). For such habitats and all their threatened birds, the most crucial form of habitat management is prevention and active suppression of fire. In fact, inappropriate fire-management regimes have been identified as the greatest single threat to Australia's birds after direct habitat destruction (Olsen and Weston 2005). The same may be true for the cerrado and campo bird communities of central Brazil (Cavalcanti and Alves 1997).

On the other hand, a surprising number of the most globally threatened bird species now are understood to



Fig. 15.52 Mallee Emuwren (*Stipiturus mallee*). Although this species strongly prefers habitat that has not burned recently, the scrub they prefer is highly vulnerable to fire. Habitat management that includes frequent burning can have strong negative influences on such species. (Photograph by Colin Cock.)

respond positively to periodic wildfire, and some actually depend on it. Most are tightly associated with plant communities where lightning-caused fires are natural and frequent, and local populations can decline to extinction if fire is suppressed or excluded. Indeed, many post-fire specialists currently may be endangered more by fire suppression than by outright habitat loss. In these cases, successful habitat management requires **prescribed burning** to maintain the ecological conditions under which the species evolved. Florida Scrub-Jays (*Aphelocoma coerulescens*), for example, gradually decline within otherwise optimal scrub oak habitat where fire has been suppressed. Their numbers rebound quickly once fire is reintroduced to their habitat (Fig. 15.53), and recruitment of new breeders reaches its peak in habitat tracts managed by prescribed burning every 5–10 years (Breininger and Oddy 2004).

Many ecosystems around the world are so degraded (from overgrazing, excessive ditching and draining, introduction of exotic plants, intensive logging, and other causes) that they may be unable to recover on their own. Such patches may require habitat restoration in the form of aggressive, often recurring, treatments intended to bring back some or all of the original species, plant and animal community structures, and ecosystem functions.

Restoring freshwater wetlands is a major priority worldwide. Restoration strategies may include fencing out grazing herbivores, filling agricultural drainage ditches, removing dams and diversions, and even using bulldozers to knock down levees and redirect stream flows into former channels. Such actions help restore water levels and riparian habitats, renew seasonal marshes, and bring back annual wet/dry cycles to which herons, migratory shorebirds, and waterfowl are adapted. The largest wetland restoration project in the world involves the massive Everglades watershed in southern Florida (USA), a colossal, multibillion dollar effort to re-establish wetlands and seasonal water flow originating in the central peninsula and extending south to Florida Bay. Until humans ditched and

Prescribed burning: deliberate and carefully planned burning of an area to achieve management goals, usually to maintain the diversity and quality of habitats that evolved with regular fire.

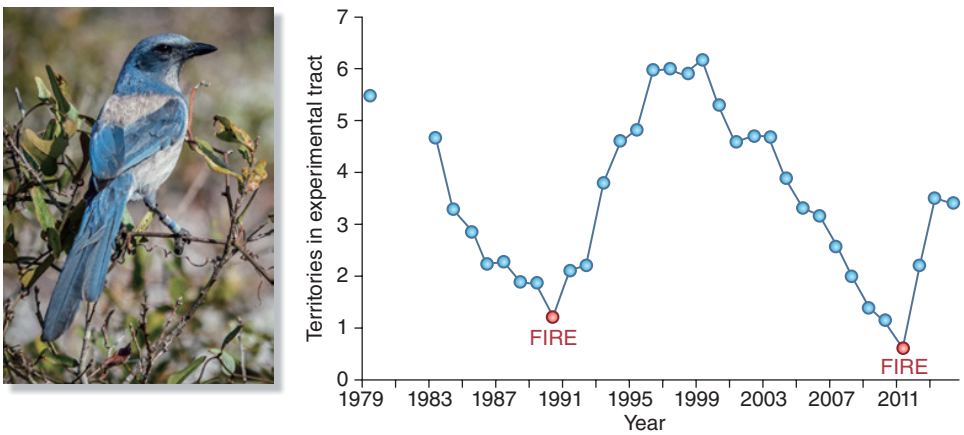


Fig. 15.53 Florida Scrub-Jay (*Aphelocoma coerulescens*). A highly specialized bird of lighting-prone scrub oak habitats, the persistence of this species depends on frequent (every 5–10 years) prescribed or permitted natural burns. This graph shows a dramatic population increase after a prescribed burn at a study site in central Florida (USA), but in the absence of another fire, the population declined again after 10 years. Without such natural fire cycles producing early successional habitat, populations of this species disappear. (From Fitzpatrick and Bowman 2016. Reproduced with permission from Cambridge University Press. Photograph by Jane Luxton Photography.)



Fig. 15.54 Kissimmee River restoration. (A) Channelization of the Kissimmee River in Florida in the 1960s destroyed the ecological values of one of the world's largest river–floodplain–wetland networks. (B) In 1992, the Kissimmee River Restoration project began to restore the ecological role of the original river by backfilling the channel and re-meandering the river. (Photographs courtesy of South Florida Water Management District.)

drained this region during the 1950s and 1960s, annual summer rains produced vast sheet flows covering nearly 30,000 square kilometers of wet prairies and marshlands. Spring dry seasons contracted many of these wet areas, concentrating fish, snakes, and amphibians into shallow pools that supported huge nesting colonies of wading birds such as Wood Storks (*Mycteria americana*), Roseate Spoonbills (*Platalea ajaja*), and various herons, egrets, and ibises. Restoring native biological functions to this system involves purchasing ranches and farmlands from private landowners, securing **conservation easements** from others, bulldozing down massive levees bordering channelized rivers (Fig. 15.54), and constructing huge culverts that allow seasonal flood waters once again to inundate large areas, including lands that have been farmed or grazed for decades. Wetland bird populations will flourish as a result.

Restoration projects in tropical areas of the world teach important lessons. In western Costa Rica, the restoration of bird-rich tropical dry forest habitats is enhanced by actively reducing fire frequency. Habitat management that limited grazing, reduced fire, and controlled nest-parasitic Shiny Cowbirds (*Molothrus bonariensis*) has prevented the likely extinction of the Pale-headed Brush-Finch (*Atlapetes pallidiceps*) in southern Ecuador, which was reduced to 14 pairs in 1994 but now numbers in the hundreds. Forest restoration has helped prevent the extinction of the Rodrigues Warbler (*Acrocephalus rodericanus*) and Rodrigues Fody (*Foudia flavicans*) on the island of Mauritius, the Waldrapp (*Geronticus eremita*) of Morocco, the Grenada Dove (*Leptotila wellsi*) in the Caribbean, and the Cerulean Paradise-flycatcher (*Eutrichomyias rowleyi*) in Indonesia.

In Australia, a widespread region of subtropical forest in northern New South Wales called the "Big Scrub" was largely cleared for agriculture, endangering numerous locally endemic bird species, among them the Black-breasted Buttonquail (*Turnix melanogaster*). Public awareness of the biological importance of this area, combined with active replanting of native plants on both private and public lands, has begun to ameliorate this habitat loss. In other temperate forests of southeastern Australia, bird species of conservation concern, such as the locally threatened Hooded Robin (*Melanodryas cucullata*), were found to be much more numerous in younger forests under restoration than in nearby stands of old growth, perhaps because of the presence of aggressive Noisy Miners (*Manorina melanocephala*) in the old-growth forests (Lindenmayer et al 2012).

15.7.12 Adaptive management

Some of the biggest challenges in conserving birds and their habitats occur because management actions must be taken before full knowledge of the system has been gained. In the long run, therefore, effective ecosystem management requires not only defining a conservation target but also acknowledging the gaps in knowledge about how to achieve it. The best approach is a three-step process known as **adaptive management**. First, specific goals are defined

Conservation easement: a legal agreement in which a landowner permanently limits uses of his or her land in order to protect its conservation value.

Adaptive management: a feature of ecosystem management in which land managers treat management practices as experiments, measure or monitor the results, continue learning about the ecosystem as they proceed, and progressively modify management practices to incorporate new information.

as the desired outcomes of management actions (perhaps to sustain a specified population size or density of an indicator species, or a specified abundance target for a suite of different species). Second, by experimenting with management alternatives and constantly monitoring, evidence about how the target species respond to different management actions is gathered continually. Third, management plans are modified periodically as a consequence of the new information, and the process is repeated. As time goes on, therefore, we adapt management techniques to incorporate new understandings about the system. The approach stresses the importance of "learning as we go" through landscape-scale experiments (for example, different burn regimes, grazing frequencies, water depths, or forest thinning), accompanied by monitoring of key species and processes. Adaptive management demands that managers be ready, willing, and able to modify management techniques as new information comes in. Such an approach can be challenging to carry out, especially by public land-management bureaucracies such as park services, wildlife agencies, forestry divisions, and local governments that are accustomed to operating with fixed and longstanding management formulae. Often, such agencies also lack the funding and scientific infrastructure for designing and conducting experiments and subsequent monitoring. For these reasons, adaptive management represents an important opportunity for public agencies to partner with private conservation groups and research institutions to accomplish the most effective long-term management of their ecological landscapes and conservation of priority species.

15.7.13 Ecosystem management is complicated

During the past half-century, conservation-minded ecologists began recognizing that relationships among native species and communities are complex, have evolved across large landscapes and long timescales, and exist within a complex milieu of human social and economic realities. Because ecological relationships occur at many scales, the protection of a target species (such as an endangered or declining bird) or an assemblage of species (such as a grassland bird community) requires ensuring the continued functioning of a host of ecological processes: fire, periodic flooding, nutrient cycling, plant succession, and seasonal migrations. Such processes may occur unpredictably (for example, damaging storms), or in cycles that may be daily (activity patterns of insectivorous birds and their prey), annual (seasonal flooding of vernal pools), regular multi-year (predator–prey cycles), or irregular multi-year (floods or fires). All these processes, in turn, differ across the landscape and among different ecological regions (Fig. 15.55). For this reason, large-scale conservation efforts break the challenges down into geographically separate, locally tailored planning efforts called ecoregional planning (Box 15.06).

If the human factor could be ignored, the overriding management challenge for preserving native bird species would be to ensure that all the above-mentioned processes continue to function within landscapes of sufficient size so that extinctions would not occur simply because populations were too small. Today, however, meaningful conservation success can be achieved only by recognizing that the human factor does exist. Although human social needs complicate the challenges even further, they must be incorporated into any long-term management solution. Socioeconomic needs can be addressed in the context of conservation planning through a number of tools, including community development via ecotourism, economic incentives for land management, payments for ecosystem services, and education.

Understanding and maintaining the full range of natural processes across landscapes, together with conserving their ecological services and natural resources that meet the human political and cultural communities in which they are nested, has become known as **ecosystem management**. This term is inexact and sometimes controversial, but it acknowledges that human cultures and ecological systems are now inescapably woven together. Birds in their native habitats will not be conserved without embracing a holistic approach that identifies how conservation management strategies engage with, and even serve, the human societies that surround them.

15.8 Value of wild birds

Why should humans care about protecting birds, given how expensive and difficult it is to do so? What are birds worth to society? What values are gained by investing in their protection? Is bird conservation worth the cost?

Such questions can be asked about any aspect of biodiversity, not only birds; yet as in so many other areas of biology, birds provide a popular framework for addressing these wider issues. Practical as well as ethical and spiritual answers exist to these questions, and the subject is worth reviewing here for two reasons. First, questions about the values of biodiversity often are debated in public and political forums but rarely get resolved, because the subject involves not only facts but also experiences and emotions. Second, conservation requires a collective willingness to

Ecosystem management: the holistic management of habitats and landscapes for the simultaneous purposes of biodiversity conservation and human use.

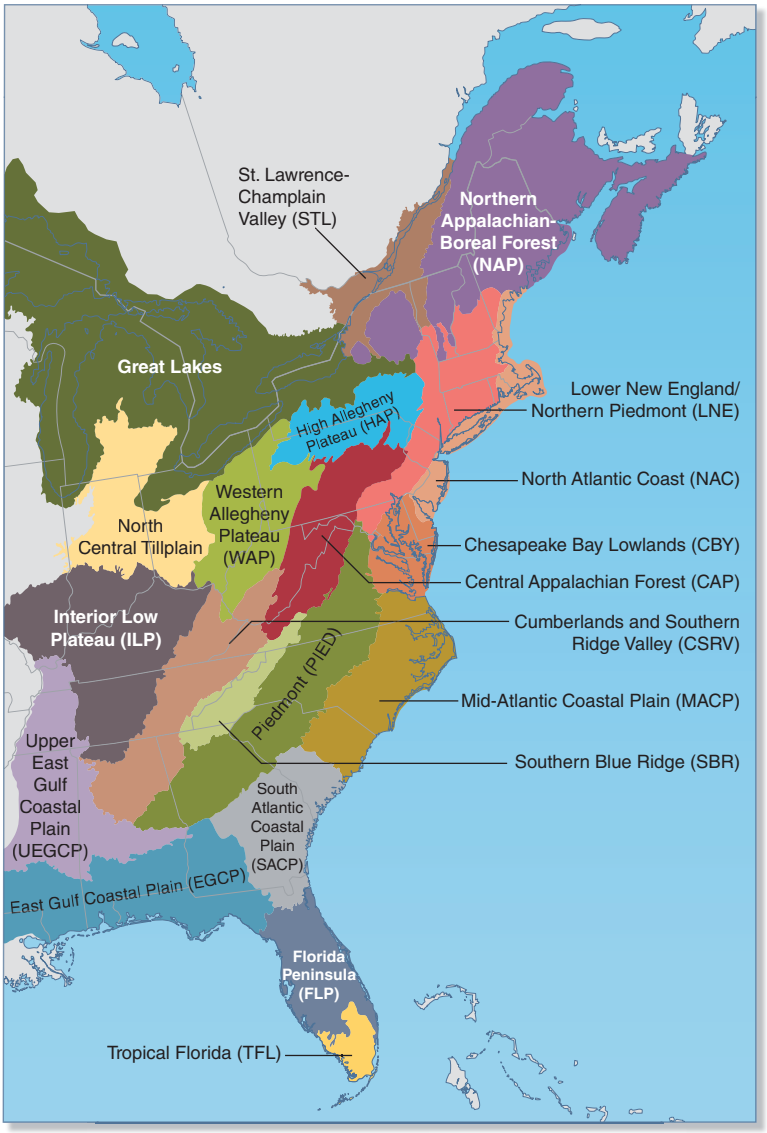


Fig. 15.55 Ecoregional conservation planning. Instead of using political borders to define areas, ecoregional conservation planning uses watersheds, soils, topography, climate, and dominant vegetation formations to delineate different ecosystems across the landscape, as in this ecoregional map of the eastern USA. Conservation plans for each region begin by identifying viable populations of rare species, the best examples of characteristic natural communities, and the list of threats facing these places. The result is a set of priorities for conservation actions in each ecoregion. (From The Nature Conservancy 2015. Reproduced with permission from The Nature Conservancy.)

protect shared resources from experiencing the **tragedy of the commons**; that is, the loss of communally valuable assets as a result of individually selfish behavior.

Tragedy of the commons: a common dilemma in natural resource management, in which benefits to an individual are contrary to the collective benefits of the group, so that individuals are inclined to act selfishly, despite this being to the detriment of everyone. Named after communal grazing lands (the "commons") to which each herder could freely add additional livestock, thereby helping themselves in the short term but ultimately leading to severe overgrazing and the destruction of the commons as a long-term resource for the community.

Appreciating the values of communally shared assets is essential for gauging the community's willingness to invest in their protection.

Values of biodiversity fall into at least four distinct categories: direct, indirect, emotional, and ethical. Direct benefits, such as food, other commercially traded products, and direct economic gains, are the benefits that are most measurable and material. Indirect benefits, such as environmental services, biological indicators, genetic information, and research values, are more diffuse. For many people, the emotional benefits are even more important than the previous two, because birds capture our attention, feed our imagination, stimulate our aesthetic senses, and even populate our spiritual lives. Finally, on ethical grounds, it has been argued that birds, as components of the natural world, possess an intrinsic right to exist, so failing to invest in their protection constitutes a

Box 15.06 Conservation planning at ecoregional scales

To have lasting impact, conservation efforts need to involve prioritization and planning at large ecological and geographic scales that are independent from political units such as townships, counties, states, provinces, or even countries. Biologically distinct ecoregions differ from one another based on annual temperature and rainfall regimes, topography, soil type, plant communities, and watersheds. Many conservation organizations now practice ecoregional planning, developing strategies to preserve whole suites of species and communities typical of each ecoregion. Such planning entails:

- *Mapping ecoregions*. Each biologically meaningful region warrants its own unique plan (Fig. 15.55).
- *Taking inventory*. For each ecoregion, the dominant native plant communities, key indicator species, and important ecological features are identified; detailed maps specify habitat tracts and other natural features where examples of each ecological community remain or could be restored.
- *Prioritizing conservation targets*. For each ecoregion, the rarest, most threatened, or most rapidly declining native species and communities that represent the ecoregion are identified as the elements having the highest priority for monitoring and conservation action.
- *Prioritizing sites*. Sites playing the greatest role in maintaining the integrity and functions of the ecoregion and its indicator species should receive the most attention and resources. Ranking sites can require choosing among conflicting variables such as species diversity, populations of rare species, the landscape role as a corridor or stepping stone, and capacity for long-term management.
- *Setting goals*. Long-term biological and population goals are established for indicator species and communities (such as minimum or average population size, total area occupied, minimum sizes of intact habitat blocks, and stabilized population trajectory).
- *Identifying threats*. Certain threats are so destructive that their elimination is mandatory to achieve conservation objectives, so planning must identify actions to reduce the impacts of these threats.
- *Identifying stakeholders*. Honestly identifying the human social and economic contexts prevailing within the ecoregion leads to forthright engagement, working partnerships, and compromises with all relevant social, cultural, governmental, and industry stakeholders. Communication, education, and outreach are crucial for engaging new human sectors into conservation efforts.
- *Specifying actions*. Steps may include land protection (such as outright acquisition, easements, voluntary agreements, or mitigation banks), management protocols, community or political action (such as local ordinances, public referendums, or public policy discussions), public campaigns, and education.
- *Monitoring results*. Adaptive management requires long-term monitoring of indicator species and communities to measure success and, if necessary, change management courses. Changes can occur over long timescales and unpredictable intervals; hence monitoring must be sustained. Resources must be committed to the monitoring process, including coordination among relevant agencies, conservation and research organizations, and committed volunteers.

selfish and short-sighted violation of the moral imperative that we share to preserve the natural world.

15.8.1 Direct benefits

Many humans all over the world still harvest wild birds for food. In many regions this tradition damages bird populations and is illegal, but the practice continues. On the other hand, dozens of species of game birds, including ducks, grouse, quail, tinamous, cranes, and rails, and upland shorebirds, such as woodcocks and snipe, are legally regulated for sport and subsistence hunting in various countries. Hunting regulations are usually intended to ensure the long-term sustainability of these bird populations, and the practice generates huge economic value. In the USA, for example, expenditures related to equipment and trips for waterfowl hunting produced a total economic output of $2.3 billion in 2006 (Carver 2008). In addition, taxes on ammunition used by duck hunters, augmented by private charitable giving, have resulted in the protection of more than 40.5 million hectares of wetland and adjacent upland habitat for the benefit of game birds, especially ducks and geese. Such protection efforts simultaneously provide habitat for non-game bird species, as well as for thousands of other species of plants and animals.

In southeastern Asia, nests of the White-nest Swiftlet (*Aerodramus fuciphagus*), which are made of hardened saliva, are such a favored human food that these birds are encouraged to nest in artificial houses to facilitate the harvest, and the taking of nests from natural caves is tightly controlled (Chapter 11). Elsewhere, down feathers from wild geese and ducks have been used for centuries as insulation and cushioning in pillows and blankets. Nitrogen-rich guano from cormorants and boobies also still is harvested from tropical oceanic islands around the world for the production of agricultural fertilizer.

Recreational bird watching is among the most rapidly growing outdoor pastimes in the world. During 2006 in the USA, about 48 million people participated in bird watching, spent $36 billion in travel and equipment, and generated $82 billion in total industry output (Carver 2009). The global ecotourism market is even larger, and it is beginning to provide strong local incentives for the conservation of natural ecosystems. For example, an economic analysis of ecotourism in one region of Amazonian Peru concluded that ecotourism and conservation concessions, as a replacement for logging concessions, are justified on narrow economic grounds alone (Kirkby et al. 2010). In this sense, bird conservation can be viewed as essential in maintaining an important and rapidly expanding economic influence in the world.

15.8.2 Indirect benefits: ecosystem services

Birds provide crucial **ecosystem services** in maintaining healthy and diverse ecological systems and processes throughout the world. For example, by eating or caching fruits, seeds, and nuts, birds provide an environmental courier service promoting dispersal, gene flow, and colonization opportunities for thousands of species of plants in all kinds of forests and shrublands. Indeed, these interactions have been instrumental in the very evolution of sugar- and nutrient-laden fruits and seeds. In western North America and in Eurasia, numerous pine species have coevolved with birds such as the Pinyon Jay (*Gymnorhinus cyanocephalus*), Clark's Nutcracker (*Nucifraga columbiana*), and Eurasian Nutcracker (*Nucifraga caryocatactes*) to produce large seeds that are dispersed and cached by these corvids.

By creating nest holes in dead trees, cacti, river banks, and even flat prairie ground, birds such as woodpeckers, bee-eaters, kingfishers, swallows, and even terrestrial owls create cavities that last for decades, providing shelter and breeding places for whole communities of insects, mammals, reptiles, and other birds. Because birds are mid-level and top-level predators in the food chains of almost every ecosystem in the world, they influence the evolution of mimicry in butterflies, cryptic coloration in insects, schooling behavior in fishes, and sentinel behavior in social birds and mammals.

Birds serve human economic interests by controlling insect populations. In Salt Lake City, Utah (USA) a gold statue of two California Gulls (*Larus californicus*) celebrates the role played by this gull in devouring huge swarms of crickets that threatened to destroy the crops of early farmers. Both migrant and resident songbirds maintain the health and condition of the world's forests by consuming untold billions of leaf-eating insect larvae, and many bird populations respond rapidly to regional outbreaks of damaging insect pests such as gypsy moths, tent caterpillars, and spruce budworms (Holmes et al. 1979). Other ecological services provided by birds include the scavenging of animal carcasses by vultures, caracaras, crows, and gulls, and the pollination of flowering plants by hummingbirds, sunbirds, and honeyeaters.

Ecosystem services: the collection of beneficial effects of ecosystems that provide substantial and ongoing economic value to human societies.



Fig. 15.56 The "canary in the coal mine." This expression originated from the practice of bringing domesticated canaries (*Serinus canaria*) into active underground coal mines. Since toxic methane gas affects these birds faster than it does humans, the canaries were used as biological indicators of this invisible risk to the miners. Today many wild bird species serve as sensitive indicators of changing environmental conditions. (Photograph courtesy of the Queensland Mines Rescue Service.)

The idiomatic expression "canary in the coal mine" symbolizes one of the most important services provided to humans by birds. Until recently, coal miners around the world descended into their risky underground workplaces carrying caged canaries (*Serinus canaria*) (Fig. 15.56), to which miners paid close attention. Deadly methane gas is odorless, but a gasping or dying canary warned miners to escape before accumulating gas threatened them with the same fate. Today we understand that birds can reveal environmental changes and dangers in far more diverse ways. Their position atop natural food chains makes hawks, eagles, and falcons highly susceptible to accumulations of environmental poisons, as experienced by the Peregrine Falcon (*Falco peregrinus*) in the 1960s. Cadmium poisoning of White-tailed Ptarmigan (*Lagopus leucura*) in the Rocky Mountains of western North America revealed the lethal impacts of heavy metals in mining areas worldwide (Larison et al. 2000). Population declines of birds occupying freshwater habitats signal problems stemming from poor water quality or invasive species. In a wide variety of habitats around the world, ecologically specialized birds,

as well as other animals, can serve as indicator species that allow us to evaluate the success of habitat management and restoration efforts.

15.8.3 Indirect benefits: genetic information and scientific study

A major reason for protecting the world's biodiversity is that we are only beginning to explore the wonderful storehouses of genetic information represented by wild organisms. Information contained in the DNA of every individual bird has survived millions of years of evolutionary challenges. All these complex evolutionary stories still are largely untold, and some could be directly useful to humans. For example, we possess at best only a rudimentary understanding of the genetic bases for disease resistance, protein synthesis, detoxification of natural compounds, complex behavior patterns, neural pathways, and many other natural functions of organisms. Every time we allow an organism to go extinct, we lose potential information about its history, evolutionary potential, and capacity for helping us lead our own lives more fully.

As subjects of scientific research all over the world, birds continue to teach us how nature works. They are mostly diurnal and are relatively easy to observe. They occur in virtually every habitat on land and sea. They are extremely diverse, both socially and structurally. They migrate from pole to pole and from mountaintop to valley bottom. They exhibit remarkable feats of both short-term problem solving and long-term memory. They are environmentally sensitive, and their birth rates and death rates reveal much about the world around them. For all these reasons and more, birds provide raw materials for never-ending scientific inquiry into virtually all aspects of the living world.

Many of the foundational discoveries in the modern science of biology have involved birds. Charles Darwin and Alfred Russel Wallace used birds to derive the theory of evolution by natural selection. By studying closely related bird species on islands in the South Pacific, Ernst Mayr deduced how allopatric speciation gives rise to new species (Chapter 2). David Lack developed time-tested principles of life history theory based on birds (Chapter 13). Using birds on islands as principal examples, Robert MacArthur and Edward O. Wilson and their followers derived groundbreaking principles of ecology, island biogeography, population biology, and community structure (Chapter 14). Konrad Lorenz and Niko Tinbergen won Nobel prizes for their studies of bird behavior (Chapter 9). The most successful game-management theories in the world were derived from studies of birds. Modern studies of environmental toxicology and wildlife disease often focus on birds as bio-indicators. The biology of migration, navigation, and homing behavior, and the neurophysiology of memory are all illuminated through studies of birds both within and outside of the laboratory (Chapters 7 and 12). Many key principles of social evolution and animal communication stem from research on birds (Chapter 9). Accordingly, hundreds of scientific journals now regularly publish technical research on bird biology.

15.8.4 Emotional benefits

Rachel Carson chose the title *Silent Spring* for her landmark 1962 book that called attention to the explosion of global threats from pesticides and pollution and helped launch the modern environmental movement. Carson intended this title to shock the public world into contemplating a landscape so impoverished as to lack bird songs in the spring—she chose it because she appreciated the power of bird song for all of us.

By representing beauty in nature, by providing spiritual and even religious experiences for millions of humans, birds deliver emotional enjoyment to people all over the world. It is impossible to estimate the collective value of our pleasure in seeing migratory bird flocks, hearing the chorus of bird songs in a forest, watching gulls wheel at the seashore, enjoying the kaleidoscope of gaudy birds at a feeder, or admiring an astoundingly nimble hummingbird at a flower. The true monetary value of these and countless other encounters with birds cannot be known, but without doubt they contribute enormously to the flood of pleasures that humans derive from nature. Moreover, these very pleasures increasingly are demonstrated to have remarkable physical and psychological healing power (Buzzell and Chalquist 2009; Selhub and Logan 2012). This connection is reflected further in the symbolic bird names we give ourselves—from New Zealander "kiwis" to sport teams like the "Pittsburgh Penguins" and "Baltimore Orioles" to innumerable school mascots.

15.8.5 Ethical considerations

In progressively dominating the earth, humans have demonstrated phenomenal (and ever-increasing) power to destroy life. It frequently is argued, on both theological and secular grounds, that humans have a moral obligation to protect the natural and evolutionary heritage of the earth, including all of its species, not just the ones that provide us economic value. In this view, all non-human life forms such as birds have intrinsic value by virtue of their unique evolutionary histories, their modern ecological roles, their structural and behavioral complexity, and their aesthetic beauty, even if they have no "purpose." Every bird, like the entirety of nature—arising over 3 billion years of evolutionary history—can be viewed as a work of natural art every bit as exquisitely complex, mysterious, and beautiful as the cathedrals, paintings, literature, and poetry of humankind, if not more so. For anyone holding such a view of nature



Fig. 15.57 Bird-friendly yards are easy and effective. All available outdoor spaces can be transformed from ecological wastelands into diverse, wildlife-friendly habitat. For instance, this yard in Ohio (USA) started out with little plant and structural diversity (left image) and was transformed into a rich habitat for birds (right image) with dense shrubs, birdbaths, feeders, and a diversity of native plant species. (Photographs courtesy of www.backyardhabitat.info.)

and its birds, it is especially easy and important to answer the question "Why should we save them?"

15.9 What each of us can do

Most conservation projects require the involvement of many people working together, including communities, public agencies, research groups, land-management specialists, not-for-profit organizations, education programs, fund-raising efforts, and even political initiatives. Besides participating actively in any of these activities, individual citizens also can contribute on their own towards keeping common birds common and keeping rare birds from going extinct. Birds and biological diversity exist everywhere, and their long-term protection depends just as much on managing millions of small places across the landscape as it does on establishing and managing large parks and preserves. Every little bit helps.

15.9.1 Backyard conservation

Every piece of outdoor space, from city parks and suburban backyards to rural farmlands and forests, can serve as habitat that helps conserve birds. The elements that birds need to survive—shelter, nesting habitat, food, and water—can be maintained in all kinds of backyards, schoolyards, and parks (Fig. 15.57). As is true for natural ecosystems, managed landscapes will support more bird species if they have a varied habitat structure, including grassy open spaces; gardens interspersed with boulders, ferns, and shrubs; and trees of different species and heights. Crucial to any bird-friendly yard is dense shrubbery to provide both nesting habitat and protection from predators for a wide variety of songbirds. Trees attract both year-round residents and migratory songbirds. Water helps, even if supplied by a simple birdbath placed near protective shrubbery. Pesticides and lawn chemicals should not be used, because they reduce both insect and plant diversity, and some are even directly harmful or fatal to birds.

Healthy forests are filled with dead and dying trunks and limbs. It is important to fight the common tendency to remove these elements. Allowing dead limbs and trees to remain in place whenever possible makes a yard much more attractive to a wide variety of bird species. In addition to being essential for woodpeckers, dead and dying wood provides important foraging habitat for many songbirds, nesting habitat for even more species, and vital perch sites for raptors, shrikes, and countless songbirds that sally after flying insects.

Domestic cats should remain indoors at all times (Fig. 15.58). This precaution is especially important during the spring and summer, when recently fledged and naïve juvenile birds are most vulnerable to predation. A recent, comprehensive review suggests that, in the USA alone, about 2.4 billion birds are killed annually by free-roaming house cats (Loss et al. 2013). Therefore, "cats indoors" must be a year-round rule for anybody seriously committed to bird conservation.

15.9.2 Citizen science

Population monitoring is essential for bird conservation, because it provides data for detecting population declines, setting priorities, and measuring the success of management practices. However, public agencies and professional scientists alone cannot possibly monitor every species, habitat preserve, and important bird area, even though doing so at both local and continental scales is essential for detecting changes and planning action. In short, monitoring is crucial, but the task seems impossibly enormous. This dilemma increasingly is being resolved by the extraordinary

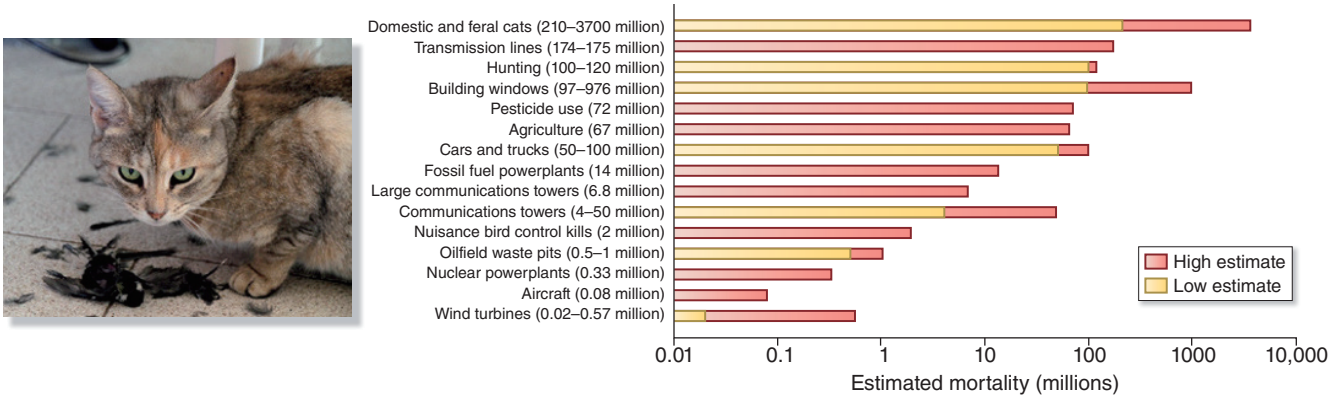


Fig. 15.58 Cats and bird mortality. Domestic and feral cats are the leading source of human-caused avian mortality in the USA, and this is probably true in many other places as well. Studies have shown that regardless of the use of bells, claw removal, and other forms of cat control, cats remain effective bird killers if permitted to roam free. The only way to protect avian wildlife from cats is to keep all domestic cats indoors. (Data from Nigelj, http://en.wikipedia.org/wiki/File:Bird_mortality.svg#file. CC-BY-SA 3.0. Photograph by Egisto Mannini.)

rise of **citizen science** as a tool for environmental research. Bird watchers and ornithologists have led the way in the explosion of citizen science, and bird-monitoring projects involving volunteers are being carried out all over the world. Through involvement in these projects, legions of amateur bird enthusiasts now contribute crucial information of direct relevance to conservation while simultaneously having fun and enriching their lives. In recent years the most accessible, powerful, and informative global citizen science project involving birds is eBird (http://ebird.org), an internet-based global database managed by the Cornell Lab of Ornithology (Sullivan et al. 2014). Tens of thousands of eBird participants from around the world now regularly submit checklists that specify species, numbers, location, date, time of day, and minutes of effort during the observation period. We invite you to join us in this endeavor.

Detailed statistical analysis of citizen science data has long been an accepted method for determining both local and range-wide population trends. Citizen science data also provide the basis for bird atlases that document the distribution of birds throughout states and countries. Recent advances in machine learning and high-performance computing, combined with data-intensive citizen science projects such as eBird, have yielded spectacularly fine-scale modeling of bird distributions and movements (Fig. 15.59). Contributing observations to any citizen science project that connects to a globally available database is one of the easiest and most important ways that an individual can contribute to bird conservation.

Citizen science: scientific endeavors in which members of the public are core participants in collecting data and/or interpreting results.

15.9.3 Adopting a place

Sustaining bird populations and biodiversity so that future generations can enjoy them requires the recognition that humans now manage the earth. Whether or not we like this complicated role, we are stewards of the world's species and natural systems. Doing a good job will require widespread cultural adoption of conservation ethics into our morally and spiritually driven prescriptions for human behavior. Adoption of this land ethic means that each individual must strive to allow natural systems and species to coexist with us within our human-dominated world. A powerful route to this long-term result is for individuals to choose a favorite outdoor place and actively invest in its well-being. Our important places need not be large, spectacular, or rare, because keeping common birds common must go hand-in-hand with rescuing the endangered ones. Besides, many of the big, spectacular places, such as national parks and wildlife refuges, already are equipped for long-term conservation, and it is the smaller local places that need our help.

Individuals can contribute to conservation by personally committing to a local park, schoolyard, recreation area, commercial woodlot, beachfront dune, or grounds of a corporate headquarters. Becoming familiar with the ownership, management plans, and real-world challenges of a place can reveal numerous opportunities for personal contributions, such as volunteer work, teacher training, or fund raising. Encouraging owners to examine management plans that favor native birds often reveals simple changes that can have positive impacts on bird populations, such as planting native shrubs, lengthening mowing cycles, altering drainage regimes, or removing invasive plants. Financial investments, especially endowments for land management, improve the chances that favorable management practices will continue indefinitely.

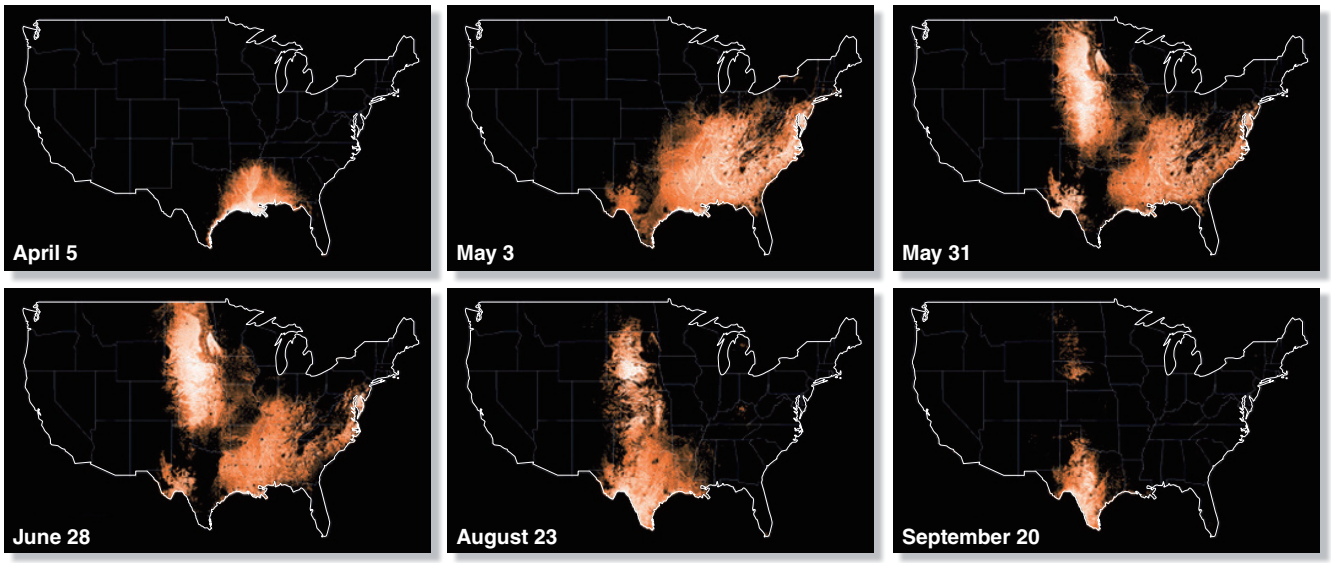


Fig. 15.59 Citizen science brings bird distributions to life. These spectacularly fine-scale maps show the seasonal distribution of Orchard Orioles (*Icterus spurius*) across eastern North America. Data were provided via hundreds of thousands of citizen scientist records from free eBird software, which permits people to record their bird observations worldwide. These maps use eBird data to generate probabilistic models, predicting the likelihood that a species will be present at a given date and location (white, high probability of observing; deep orange, low probability). Such maps are expanding our understanding of animal movements by providing precise information at continental scales at relatively low cost. (© Cornell Lab of Ornithology.)

BirdLife International's Important Bird Areas (IBAs) program recognizes more than 11,000 specific sites that play unusually important roles for birds in 200 different countries and territories around the world (Fig. 15.60). Through input from birders and scientists, specialists within participating countries have identified these as key sites for conservation because they harbor notable numbers of threatened species, represent concentrations of endemic or ecologically specialized species, or support unusually large numbers of migratory or colonial species. Recognition of these sites promotes both public and private investment in their long-term protection, management, and monitoring. At any scale, an important feature of every IBA is its capacity to attract conservation action from public agencies and to motivate private individuals to invest their own time and energy in its future through vigilance, grassroots activism, and advocacy.

15.9.4 Vigilance, grassroots activism, and advocacy

Every individual can help promote bird conservation by exercising vigilance (such as noticing and reporting violations of wetlands or endangered species laws), political activism in elections (such as supporting public referendums that support the conservation of open space and biodiversity), and advocacy (such as working to convince local planning or zoning authorities to adopt open space provisions or to monitor key local indicator species). Advocacy that promotes long-term protection of key parcels of land will always be a backbone of conservation action, but public advocacy about laws, policies, and industrial practices may be equally important in protecting the welfare of bird populations. Examples include advocating against recreational uses of lead in fishing and hunting, against certain pesticides that kill non-target species, for the use of streamers by the long-line fishing industry (these greatly reduce seabird bycatch), and for legal restrictions on siting and lighting of communication towers and wind turbines. Local and regional conservation organizations often produce excellent information on these and many other issues for which individual advocacy can make a real difference.

15.9.5 Consumer choices

Some consumer products support conservation. An excellent example is shade-grown coffee, which is grown in the shaded understory of managed forests that provide other forest products (such as fruits and firewood), reduce erosion, and support a wide diversity of birds. In Central and South America, millions of migratory birds, including some rapidly declining species such as the Cerulean Warbler (*Setophaga cerulea*), prefer shade-coffee plantations. Moreover, shade-coffee areas represent most of the remaining forest cover in some countries, such as El Salvador. Worldwide, shade-coffee ground is being rapidly converted to less ecologically

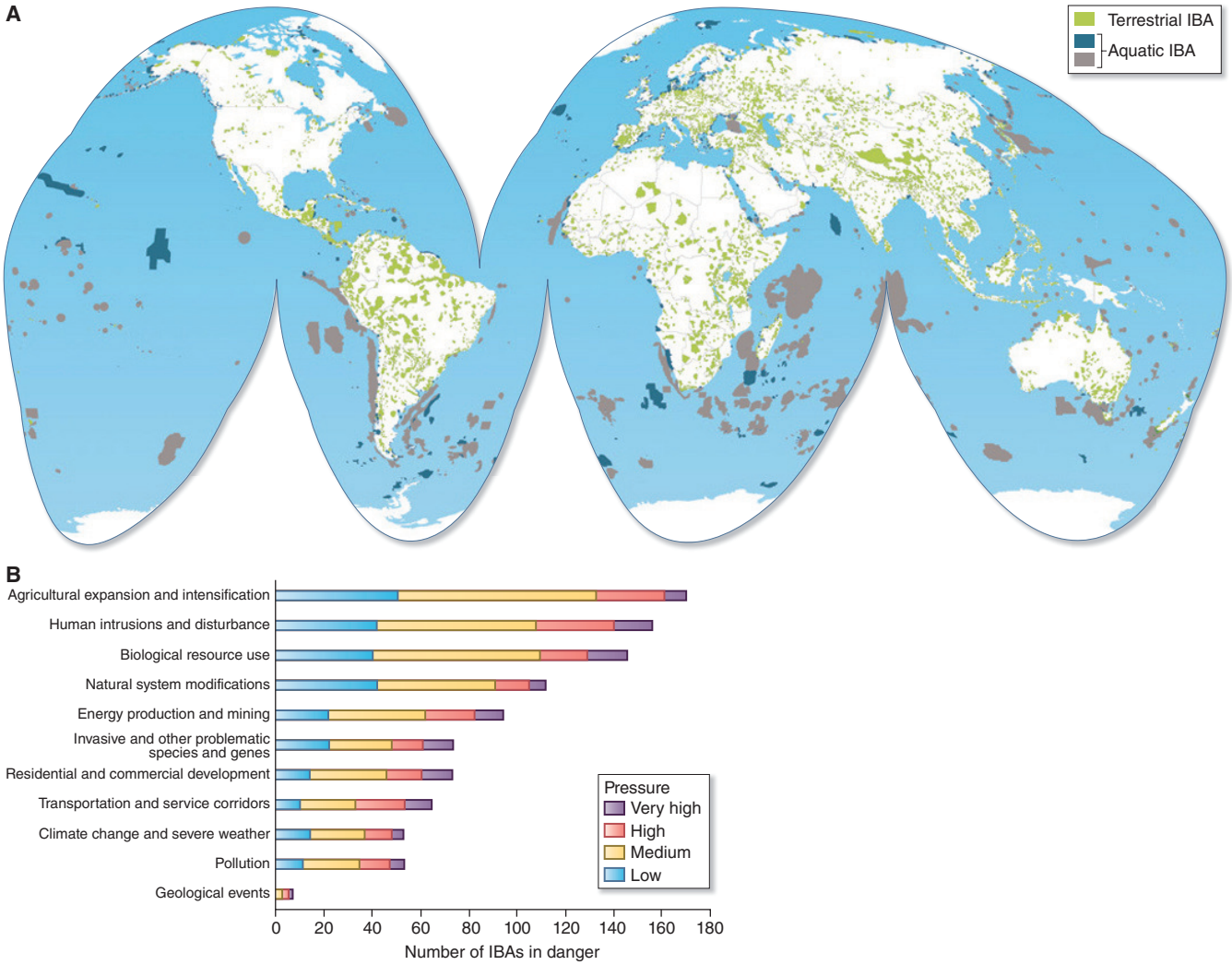


Fig. 15.60 BirdLife International's Important Bird Areas (IBAs). This program identifies key habitat areas for protecting birds and bird populations around the world. (A) IBAs are recognized worldwide in both terrestrial (green) and marine (brown and dark blue) habitats. By identifying the world's most important bird conservation areas we can help to promote investments to conserve, manage, and monitor them. (B) Types of disturbances that endanger IBAs, ranked by number and risk level. (Case study 80 (A) and case study 545 (B) from www.birdlife.org. Courtesy of Birdlife International.)

valuable habitats, such as sun-coffee plantations in which coffee is grown as an intensively managed monoculture. In response, conservation-minded groups have created a market and certification standards for shade-grown coffee. Similarly, in both South America and in southeastern Asia and Indonesia, spectacularly diverse native rainforests are being replaced by single-species oil-palm plantations. Production of "certified sustainable palm oil" more than tripled between 2009 and 2011, reaching 4.8 million tons.

15.9.6 Environmental education

Promoting and participating in local environmental education helps broaden the community of people who grasp the importance of conserving birds and biodiversity. Half of the world's human population now live in cities, and the proportion will increase to 70% by 2050 (Cohen 2003). This trend, combined with the sweeping popularity of digital entertainment, means that fewer and fewer of the world's citizens will grow up in direct contact with nature. Because humans are more likely to protect what they understand and love, all possible forms of environmental education—via books, media, museums, nature centers, and classroom curricula—will be even more crucial in the future than they are today.

Every individual motivated to protect birds and habitats can help pass that passion on to others in his or her community. Thousands of interpretive nature centers, museums, and zoos rely on volunteers to help provide interpretation and hands-on experiences for their visitors.

Classroom teachers often seek local experts to assist with environmental material, both in the classroom and on field trips. Outstanding supplementary materials for environmental education are now available for elementary and middle-school teachers. Donating such materials to schools—and volunteering to help teach them—can help the next generation learn about saving birds, wildlife, and habitats.

15.9.7 Birding with youngsters

Most people who are passionate about birds and conservation can identify the mentors who helped spark their initial interest in the natural world, sometimes even with just a single event or outing during childhood. Conservation will endure only if each generation contributes, and one of the best ways to help the next generation embrace the need to conserve birds and habitat is to share one's own knowledge and passion with today's children. Lifelong passions can begin as a consequence of remarkably simple experiences. The singular thrill of seeing a beautiful bird, or studying a complex display, through binoculars or a telescope can be just such an experience for a young person (Fig. 15.61). Seeing birds in real life and being taught how to use optics and field guides can open a child's mind to a lifelong appreciation of diversity and beauty in nature. This appreciation is the all-important first step on the pathway toward commitment to conserving such wonderful things.

15.9.8 Contribute to conservation organizations

Not-for-profit organizations (also known as non-governmental organizations, or NGOs) play vital roles in the conservation of birds and biodiversity all around the world. These charitable institutions depend upon gifts and bequests from the public, and in many countries such gifts can provide tax advantages to the donor. Most conservation organizations are staffed by mission-driven, hard-working individuals who earn only modest salaries and operate via four principal sources of revenue: charitable gifts, membership dues, and bequests from the public; grants from private or publicly funded foundations; contracts with public agencies or industry to carry out specific projects; and proceeds from permanently invested endowments.

The best NGOs have clear mission statements describing what they do and why they do it. Programs remain tightly focused to these missions and typically are described succinctly in an annual report providing the potential contributor an excellent way to learn about and compare different organizations. Discretionary resources such as public gifts help support essential operating costs, such as salaries for management, development, and clerical staff, building or rental costs, utilities, travel, computer hardware and software, and communications.

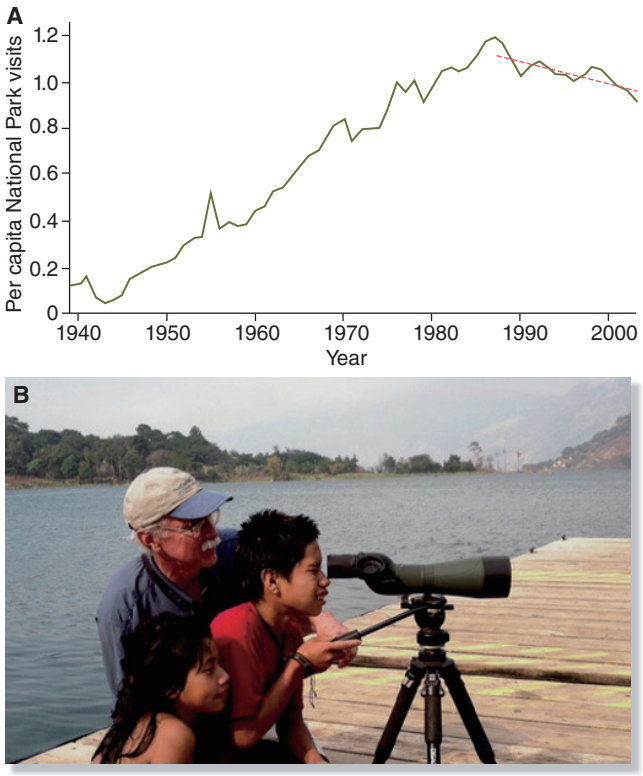


Fig. 15.61 Promoting environmental ethics, continued respect, and responsibility. Respect and continued conservation interest will only occur if today's concerned citizens transmit their knowledge and values to tomorrow's citizens. (A) Fewer and fewer people are going outside, visiting natural parks, and permitting their children to experience nature. This graph shows that visitation rates to national parks in the USA have steadily declined in the last two decades. (B) Showing children the beauty of a bird in its natural setting is a wonderful, easy way to share environmental values with future generations. (A, from Pergams and Zaradic 2006. Reproduced with permission from Elsevier. B, photograph by Molly Fitzpatrick.)

Hundreds of conservation-oriented NGOs exist around the world, and their roles in accomplishing conservation vary widely. Local land trusts, country-wide organizations, and a select few, large, international NGOs specialize in land acquisition or land management via conservation easements, often leveraging their own resources by forming partnerships with governmental agencies on public land. Many NGOs have strong programs in environmental education, delivered through publications, websites, citizen science projects, teacher-training workshops, and interpretive nature centers. Some organizations concentrate on advocacy, strategically lobbying local, state, and federal legislators to influence public policy, public investment, or environmental regulations. Still others devote substantial resources to legal research and environmental litigation. Finally, many conservation organizations invest in scientific research to advance understanding in conservation biology, some by developing strong partnerships with

research universities or natural history museums. All these roles are vital, because the challenges facing the natural world are far too great to be met solely by governments or by any organization acting in isolation. Therefore, contributing financially to conservation NGOs constitutes one of the most tangible ways in which an individual can participate in the process.

15.9.9 Never give up

The idea of personally investing in protecting birds and conserving nature may be new to some readers of this *Handbook*, while others may have been passionately involved since childhood. For both groups, the most important message of all is to do what you can, persist at it, and never give up. It is essential never to resign oneself to the notion that conservation battles cannot be won.

To be sure, many environmental losses caused by humans are now irreversible. We cannot bring back the Dodo (*Raphus cucullatus*), Elephant Bird (*Aepyornis maximus*), or moas. Sightings of Labrador Ducks (*Camptorhynchus labradorius*) and Kona Grosbeaks (*Chloridops kona*) ended forever more than a century ago. The Pink-headed Duck (*Rhodonessa caryophyllacea*) appears to be gone from Asia, and the Slender-billed Curlew (*Numenius tenuirostris*) may be lost from Europe, thus joining its North American cousin, the Eskimo Curlew (*Numenius borealis*), as testaments to overexploitation. Most sobering of all, despite abundances that defied imagination, Passenger Pigeons (*Ectopistes migratorius*) remain only as museum specimens and as a history lesson. All these species still call to us, but only about the immorality and immortality of our mistakes in allowing them to disappear.

Today, however, we have unprecedented capacity for learning and for change. If we retain the resolve to do so, we have the knowledge and ability to repair ecosystems, even ones damaged for centuries by cultures less aware than our own about the values that such places provide. We have more power than ever before to model the trajectories of populations and ecosystems and to predict with remarkable precision the ecological consequences of our actions before we commit to them. Instantaneous global communication has spawned revolutions, but it also provides the imperative to convince new generations of humans in every culture—the next managers of the earth—to avoid committing the mistakes made by our forebears. A growing list of conservation success stories proves that we really do have the power to bring bird species back from the very brink of extinction. In short, humans have extraordinary power to rescue and retain nature simply by deciding that we value other species, that we can protect natural systems if we put our minds to it, and that we can improve our behavior as managers of the earth.

It is by no means too late to imagine that human societies can coexist peacefully and gainfully with flourishing and intact natural systems. Such a day, however, will not be achieved without effort. We must put our collective minds to the task. Fortunately, enjoying and learning from birds will always be part of the process.

Visit birdbiology.org for many online resources on the topics covered in this chapter.

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Glossary

Abiotic factors: features of the environment that result from non-living physical attributes such as temperature, topography, rainfall, altitude, etc.

Acclimatization: changes in a bird's physiology after it has been in a new environment for several days or weeks that allow it to function better in the new conditions.

Acid rain: rainfall that is unnaturally acidic owing to atmospheric pollution.

Adaptation: any heritable trait in an individual that has evolved by past natural selection to make birds with the trait more successful at survival and reproduction. All kinds of traits—from subtle aspects of internal physiology to complicated avian behaviors—are potentially adaptations.

Adaptive (or acquired) immunity: components of the immune system that become tailored to respond to previously encountered pathogens, usually involving antibodies that recognize and attack specific antigens on those pathogens.

Adaptive management: a feature of ecosystem management in which land managers treat management practices as experiments, measure or monitor the results, continue learning about the ecosystem as they proceed, and progressively modify management practices to incorporate new information.

Adaptive radiation: evolutionary radiations that are exceptional in having quickly evolved many species from a common ancestor, in response to natural selection that causes these species to differ from one another in their use of their environment.

Adaptive value: the contribution of a trait to an individual's ability to survive and reproduce.

Aerodynamic power: for birds, the total power required to match the various forms of drag and thereby maintain flight.

Afterfeather: a second, smaller feather that grows from the shaft of a larger contour feather.

Age structure: the statistical distribution of the ages of all the individuals in a population.

Air sacs: found only in birds, thin-walled, transparent sacs extending from the mesobronchi or the lungs to different regions of the body; they act as bellows to bring air into the body and store it until expiration.

Airfoil: a suitably shaped object—such as an airplane wing or bird wing—that creates lift when placed in a current of flowing air.

Albumen: commonly known as "egg white," the clear regions of a freshly laid egg that are comprised primarily of water and protein.

Allantois: a membrane inside the egg that forms a sac into which the developing embryo shunts all the metabolic wastes that cannot evaporate through the shell (such as uric acid).

Allee effect: a disruption of reproductive behavior and/or social structure when population density falls below a threshold level.

Allometric scaling: changes in the magnitude of a trait that are related to, but not directly proportional to, changes in the magnitude of related traits.

Allopatric: populations that occur in separate regions with no geographic overlap.

Alpha diversity: the count of the number of species present in a single habitat or location.

Alternate plumage: the plumage that results from a partial molt of the basic plumage before breeding.

Altitudinal migration: seasonal migration up or down mountain slopes.

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Altricial: the condition of young birds that hatch relatively undeveloped and in many cases naked or with sparse down; such helpless young require complete parental care.

Alula: the small "thumb" of a bird's wing that bears three to five small, asymmetrical flight feathers.

Amino acids: a class of organic compounds that are the chief components of proteins.

Angle of attack: in a flying bird, the angle between the main surface of the wing and the oncoming airstream.

Anthropocene: the current geological age, marked by human activity having become a dominant influence on the earth's climate and environments.

Antibody: a blood protein able to attach to an infectious pathogen, thereby guiding other components of the adaptive immune system to attack that pathogen.

Aposematic coloration: often known as "warning colors," conspicuous patterns or colors that signal to potential predators that an organism is potentially toxic or dangerous.

Apteria: regions of bare or less-feathered skin between the feather tracts.

Archosaurs: a large group of reptiles that includes the non-avian dinosaurs, pterosaurs, crocodiles, and birds.

Area-sensitive species: species for which probability of occurrence increases with the size of the habitat patch, and hence are usually missing from the smallest patches.

Area sensitivity: refers to bird species that are found only in habitat patches larger than some critical size.

Artificial selection: the evolutionary process analogous to natural selection that results when humans are the selective agent that determines which individuals are allowed to reproduce; often this occurs when humans selectively breed individuals for desirable traits.

Aspect ratio: the ratio of an object's length to its width. In birds, it refers to the shape of the wing: birds with higher aspect ratios generally have more pointed wings.

Assembly rules: the hypothesis that competition among species creates possible and impossible combinations of particular species within biological communities.

Asynchronous hatching: a pattern of hatching in which the eggs within a clutch hatch over a period of many days, rather than on or near the same day, resulting in a brood of chicks of different ages and sizes.

Austral migration: refers to seasonal migration in the southern hemisphere, in which birds typically move north in the fall and south in the spring.

Barbicels (or hooklets): tiny hooks on the barbules that allow them to attach to adjacent barbules, thereby forming the flat surface of a feather vane.

Barbs: the regular, parallel fibers that extend from each side of the rachis to form the feather vane.

Barbules: Branchlets off the barbs of a feather that hook together with adjacent barbules.

Basal metabolic rate: the rate of heat production by a bird that is in a non-active state of rest, not digesting, and within thermoneutral environmental temperatures; a measure of the energy required for basic physiological processes alone.

Basic plumage: the plumage that a bird wears for the longest period within the year, between molts to another plumage.

Beak: a bird's upper and lower jaws, including the external covering. In current ornithological usage, synonymous with bill.

Behavioral isolation: a form of reproductive isolation involving incompatibilities in behavior that prevent the interbreeding of two populations. These can include behaviors involved in recognizing members of the same species, specialized courtship displays, or any other behaviors necessary for successful mating.

Beta diversity: the accumulation of species that results as a sampled area includes a greater number of habitats, each with some species found only in that habitat.

Bill: a bird's upper and lower jaws, including the external covering. In current ornithological usage, synonymous with beak.

Binomial name: a naming system in biology in which each species is assigned a unique name consisting of two parts, the name of the genus and the name of the species, as in the scientific name of the House Sparrow: *Passer domesticus*.

Biodiversity hotspot: a location or region with an exceptionally high number of species.

Biogeographic realms: a traditional classification of the earth's terrestrial regions that groups them by their broadly similar faunas, floras, and evolutionary histories.

Biological species concept: a classic species concept that is still widely used in ornithology; it places the greatest emphasis on whether or not the members of two populations retain the ability to interbreed.

Biome: an ecological community of organisms that occurs across a broad geographic region defined by its location, biogeographic history, and climate.

Biotic factors: features of the environment that result from living organisms, such as the presence or absence of competitors, predators, prey, etc.

Blastoderm: a flattened disk of dividing cells that lies on the upper surface of the yolk in the first stages of the developing avian embryo.

Body down: down feathers that lie under the contour feathers in many adult birds.

Bottom-up effect: in ecology, a situation when the abundance of a consumer or predator—or important parts of the ecosystem overall—is determined primarily by the degree of primary production at the bottom of the food chain.

Branches: the lines on a phylogeny that trace the pathway of evolutionary lineages through time.

Breeding dispersal: the movement of an individual bird in successive years among different breeding locations.

Bristles: specialized contour feathers in which the rachis is stiffened and lacks barbs.

Broad-front migration: a pattern in which the migrating individuals of a species are spread across a wide area rather than concentrated into narrower flyways.

Brood parasite: a female bird that lays its eggs in the nest of another individual of the same or different species.

Brood parasitism: any situation in which a female bird lays its eggs in the nest of another individual of the same or different species.

Brood patch: a patch of skin on the breast and belly of a bird that has lost its feathers and has become swollen and vascularized to increase the efficiency of heat transfer to the eggs.

Brood reduction: a behavior in which during a time of limited food or other resources, a nesting bird directly or indirectly allows one or more of their eggs or nestlings to die, thereby reallocating their available resources to the remaining offspring.

Brooding: sitting on hatched young, or sheltering them under the body or wings, to keep them warm and/or protect them from sun, rain, or predators.

Burrow nest: a cavity nest in the ground that is longer than it is high; usually accessed by an entrance tunnel.

Caching: the behavior of storing food in an often hidden location (a "cache") for later retrieval and consumption.

Caeca: in the digestive tract of birds, side pouches that open into the large intestine or rectum.

Calamus: the hollow lower portion of the feather shaft that lacks vanes.

Call: an avian vocalization that is shorter and simpler than a typical song.

Camber: the curvature of the wing as seen through a cross-section; highly cambered wings are more arched and therefore the upper and lower surfaces are less symmetrical.

Carina: a mid-ventral ridge of bone that projects outward from the sternum and provides an attachment site for the flight muscles. Synonymous with keel.

Carotenoids: pigments obtained by birds through their diet that often produce bright yellow, orange, or red colors.

Cavity adopter: a bird that does not construct its own nest cavity, but rather uses cavities created by other animals or by forces such as decay or erosion.

Cavity nest: a nest located in an empty space within a larger substrate, such as the cavities excavated by woodpeckers or the nest boxes provided by humans.

Cere: a leathery band of skin covering the base of the bill in some birds, into which the nostrils open.

Chalazae: the gelatinous, stringy coils of albumen that surround and protect the egg yolk and that suspend it in the middle of the egg.

Character: in avian systematics, any heritable trait that can be compared among different groups of birds.

Character displacement: a situation in which two competing species are more dissimilar in places where they both occur, compared with locations where only one species is present.

Chorioallantoic membrane: the membrane that forms during embryonic development from the fusion of the chorion and allantois. As it grows to cover the entire surface of the eggshell, inside the inner shell membrane, its rich blood capillaries allow the embryo to exchange oxygen and carbon dioxide through the pores of the eggshell.

Chorion: the membrane inside the egg that surrounds the entire avian embryo and the other three extra-embryonic membranes (the allantois, amnion, and yolk sac).

Citizen science: scientific endeavors in which members of the public are core participants in collecting data and/or interpreting results.

Clade: a synonym for a monophyletic group, referring therefore to any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

Classification: in an evolutionary context, the process by which scientists name organisms and assign them into larger group based on their evolutionary relatedness.

Cloaca: the common opening of the digestive, excretory, and reproductive systems at the lower end of the avian digestive tract.

Cloacal phallus: the copulatory organ of male ratites and waterfowl, an elongated, spiral, ridged structure that erects during copulation. Sperm travel along its surface to reach the cloaca of the female.

Clutch: a complete set of eggs laid in an uninterrupted series, during a single nesting period, by one female bird.

Clutch size: the number of eggs laid by a female bird in a single nesting attempt (a single clutch).

Coevolution: an evolutionary interaction between two (or more) species in which both species evolve adaptations in response to the other.

Commensalism: an ecological relationship involving two species, in which one species benefits without influencing the other species either positively or negatively.

Community: the set of ecologically interacting organisms of different species that occurs in the same location.

Competitive exclusion principle: the proposition that two species requiring exactly the same set of resources will compete intensely and therefore will not be able to coexist in the same locations.

Conservation easement: a legal agreement in which a landowner permanently limits uses of his or her land in order to protect its conservation value.

Conservation-reliant species: species that will require active, ongoing, and perhaps permanent conservation measures to avoid extinction.

Contour feathers: the feathers that make up the exterior surface of a bird, including the wings and tail.

Cooperative breeding: a breeding system in which adults other than the social breeding pair aid in rearing the offspring.

Copulation-solicitation display: a stereotyped posture adopted by female birds that indicates their readiness to copulate.

Countercurrent heat exchange: in birds, the direct exchange of heat between warm outgoing blood (such as that traveling to the feet in arteries) to adjacent returning cold blood (such as that returning from the feet in veins) that helps retain heat within the body.

Countershading: a pattern of coloration in which a bird is darker on top than below.

Courtship feeding: a behavior in which one member of a pair (usually the male) presents his potential partner with food during courtship or before mating. The food item is sometimes termed a "nuptial gift" and this behavior is an important part of pair bonding in some bird species.

Coverts: the smaller, overlapping feathers that overlie the bases of the flight feathers of the wing and tail.

Creche: a group of the still-dependent young of two or more breeding females, attended by one or more adults.

Crepuscular: refers to organisms that are most active near dawn and dusk.

Crop: an enlargement of the lower esophagus that stores food in some groups of birds.

Crop milk: a nutritious, milk-like substance produced by pigeons and doves from cells sloughed from the lining of their crop.

Cross-fostering: in avian conservation, the practice of using surrogate parents (sometimes of a different species) to raise the young of the species being conserved.

Crown group: a special type of monophyletic group (i.e., clade) that includes all organisms descended from the last common ancestor of all *living* members of a larger clade.

Crypsis: patterning or coloration that allows a bird to remain concealed by blending into its environment.

Cup nest: as the name implies, a nest in the shape of a cup that is at least half as deep as it is wide.

Delayed plumage maturation: the delayed acquisition of adult plumage (usually by males) by birds that are otherwise sexually mature and capable of reproduction.

Demography: the statistical study of vital rates within a population, especially age-specific birth rates, death rates, and dispersal patterns.

Density compensation: an extreme form of density inflation in which the total number of individual birds in a setting with low species diversity (such as an island) equals the number of individuals in an analogous setting with high species diversity (such as a nearby continent); for this to occur, one or more species must be extremely abundant in the low-diversity habitat.

Density-dependent diversification: the somewhat controversial concept of a feedback loop in which speciation within a group slows down over time as the number of species increases, since the presence of existing species blocks opportunities for new species to arise.

Density-dependent factors: any environmental factor that limits the size of a population whose effect or intensity varies based on the number of individuals in the population.

Density-independent factors: any environmental factor that limits the size of a population that is not dependent on the number of individuals in that population.

Density inflation: a pattern in which a species increases in abundance in locations where competitor species are not found.

Determinate layer: a bird species that will not lay additional eggs if any are removed from a clutch during the laying period.

Dialects: in birds, regional variants of the songs of a particular species.

Dilution effect: the idea that ecological communities with higher species diversity are more resistant to the spread of pathogens, since there are usually fewer individuals of each particular host species in a high-diversity community.

Direct benefits: the tangible benefits that a mate derives directly from their partner, such as food, access to a good territory, protection from predators, or a high-quality nest site.

Direct fitness: the fitness an individual bird gains through its own production of offspring; direct fitness is usually measured via a bird's lifetime reproductive success.

Dispersal: the movement of an individual bird from one breeding site to another.

Disruptive coloration: a type of camouflaging coloration in which patches, streaks, or other bold patterns help break up and distract from the overall shape of the bird.

Diversity gradient: a consistent change in species richness along some environmental gradient.

Divorce: occurs when members of a socially mated pair of birds cease being pair bonded, often to re-pair with different individuals.

DNA sequence: the precise order of the nucleotides in a region of the DNA molecule.

Domed nest: a cup nest with an overhead dome that helps conceal the eggs and nestlings.

Dominance hierarchy: a ranking of social status among members of a group.

Down feathers: soft, fluffy feathers that typically lack a rachis.

Drag: a force on a moving object that opposes the direction of travel of the object through a fluid (such as air). Induced drag comes from accelerating air to produce lift; pressure and friction drag are due to air colliding with and moving past the object.

Duets: coordinated songs performed simultaneously by two individuals, usually a mated pair of birds.

Dynamic pressure: the pressure of a flowing fluid, or of movement through a fluid such as air or water. You feel dynamic pressure when wind blows against your face.

Dynamic soaring: a type of flight in which birds use the gradient in wind speed that exists over the surface of the ocean to travel long distances without expending much of their own energy: the bird glides down the gradient at an angle, then turns and rises abruptly into the wind, using its momentum to gain height quickly. It then turns and glides down again, crossing the waves in large zig-zags. Dynamic soaring is used most by albatrosses and other large pelagic birds.

Eclipse plumage: the set of dull-colored feathers worn briefly after the breeding season in adult birds such as ducks.

Ecological (or environmental) niche modeling: a method for predicting the overall distribution of a species based on the environmental conditions at points where the species is known to occur.

Ecological niche: the set of biotic and abiotic conditions that allow a species to occur; sometimes also used in the sense of the role of an organism within its ecosystem or environment.

Ecological release: a situation in which the absence of competitors allows a species to occupy an expanded niche compared to locations in which the competitors are present.

Ecological speciation: the evolution of reproductive isolation between populations as a result of divergent natural selection in their different locations or environments.

Ecosystem: the complete set of organisms—the biological community—along with the physical environment in a particular location or region.

Ecosystem management: the holistic management of habitats and landscapes for the simultaneous purposes of biodiversity conservation and human use.

Ecosystem services: the collection of beneficial effects of ecosystems that provide substantial and ongoing economic value to human societies.

Ecotone: a transition zone connecting two habitats and the communities of birds and other organisms that occur in them.

Ectoparasites: parasites such as flies, ticks, lice, and mites that inhabit the exterior of a host's body.

Edge effects: the tendency for conditions near the edge of a habitat patch to differ from conditions at the core of the patch, usually owing to different physical conditions (such as light, humidity, or wind), the effects of neighboring habitats, or the presence of competing or predatory species that prefer edges.

Egg tooth: a short, pointed structure on the tip of the beak that develops in avian embryos shortly before hatching, and which the hatching bird uses to break through the eggshell.

Electrolytes: dissolved inorganic salts that carry either positive or negative charges.

Elevational zonation: a pattern in which related bird species replace one other at different bands of elevation along a mountain slope.

Endemic: a species or larger taxonomic group that occurs exclusively in a limited geographic region.

Endothermic homeotherm: an organism able to use metabolic heat production to keep its internal body temperature within a restricted temperature range despite conditions in the surrounding environment.

Eutrophication: a condition caused by excess nutrients (usually from pollution) that stimulates the growth of aquatic plants or blue-green algae in a body of water, resulting in the depletion of dissolved oxygen and cascading negative effects on other aquatic organisms.

Evaporative cooling: the loss of heat via the energy required to evaporate water.

Evolutionarily stable strategy: an equilibrium strategy or behavior that, once established in a population, cannot be displaced by selection for an alternative strategy that gives individuals higher fitness.

Exploded lek: a loose aggregation of males that engage in competitive mating displays toward visiting females; exploded leks are more spread out in space than are classic leks.

Exploitation competition: competition among species that results from indirect interactions, usually when both or all species require the same set of limited resources such as food or nest sites.

Extinction vortex: a negative feedback loop affecting small populations, in which genetic and demographic factors compound one another and worsen with every successive generation.

Extra-pair copulation: matings between two members of a population who are not pair bonded, usually when each is socially pair bonded to a different mate.

Extra-pair fertilization: the fertilization of eggs resulting from matings between two members of a population who are not pair bonded.

Extra-pair young: in a bird species with male–female social pair bonds, offspring that are sired by a male that is not the female's social mate.

Facultative migration: a pattern in which the timing and distance of migration changes from year to year in response to varying environmental conditions.

Facultative sex ratio manipulation: the still somewhat mysterious ability of some female birds to change the sex ratio of the eggs that they lay, in response to varying social or environmental conditions.

Fault bars: transverse regions on a mature feather with slightly different coloring or texture that correspond to different stressful days of feather growth.

Feather follicle: a small, epidermis-lined pit in the skin of a bird from which a feather grows and to which it remains attached.

Fecal sac: a tough, flexible bag enclosing the feces of most passerine nestlings that allows the parents to remove these wastes from the nest area.

Female defense polygyny: a mating system in which one male is the predominant mate for multiple females, through defending that group of females against other males.

Fertility insurance: mating with multiple males to help ensure that at least one partner is sexually fertile.

Field metabolic rate: the rate of heat production by a bird that is engaging in a natural daily routine of activities; a measure of the total energy required for physiological maintenance, movement, digestion, heating and cooling, etc.

Filoplumes: hair-like feathers having a rachis but few or no barbs.

Fitness: the relative success of an individual—compared with other individuals in their population—in passing along their own genes to later generations.

Flagship species: a charismatic species that is typical of a given habitat and is the target of special public and/or conservation attention.

Flight feathers: the feathers that form the wings (remiges) and tail (rectrices).

Floaters: in largely territorial bird species, individuals that do not hold a territory and instead "float" among territories or less optimal habitats.

Flush–pursuit foraging: a foraging strategy in which birds first scare prey (usually insects) out of hiding and then chase and capture them.

Flyways: general routes used by large numbers of migrants of many species.

Food chain: a hierarchy in which organisms in a location or ecosystem are organized into levels based on their feeding relationships, with primary producers (usually plants) on the lowest level and top predators on the highest level.

Foraging guild: a group of species in a community that use similar foraging behaviors and/or which feed on a generally similar type of food resource.

Founder event: the loss of genetic variation that occurs when a new population is established by a very small number of individuals immigrating from a much larger source population.

Functional response: in the context of avian foraging behavior, the graphical relationship between varying food or prey density and its consumption rate by a foraging bird.

Fundamental niche: the full range of environmental conditions and resources a bird could possibly occupy and use without regard to other limiting biological factors such as the presence of competitors, pathogens, or predators.

Furcula: a V-shaped bone of the pectoral girdle in birds, formed by the fusion of the right and left clavicles with a small interclavical bone. Commonly called the "wishbone."

Game theory: mathematical cost–benefit models of alternative behavioral strategies involving conflict versus cooperation.

Gamma diversity: the overall species diversity across all the sites and habitats within a broader region.

Gap analysis: in conservation, the comparison of maps of species distributions with those of protected areas to identify critical but still unprotected areas that merit additional conservation action.

Gape flanges: brightly colored enlargements around the base of the bill in nestlings of species in which parents feed the chicks.

Gape size: size of the mouth opening through which food items must pass.

Generalist: an organism that is able to use a wide range of some type of resource; for example, birds with generalist diets eat many different kinds of foods.

Genetic benefits: benefits of mate choice that stem from the high-quality genetic variants inherited by offspring of partners that choose genetically high-quality mates.

Genetic bottleneck: a loss of genetic diversity in a population resulting from a period in which few individuals successfully reproduced.

Genetic drift: random changes in genetic diversity in a population over time, often leading to the loss of genetic diversity when populations are small.

Genetic monogamy: a mating system in which a female mates with only one male.

Genetic rescue: the introduction of individuals bearing novel genotypes from elsewhere into a population suffering from low genetic diversity, thereby increasing that diversity.

Genome: the complete set of genetic material—DNA—within an individual bird.

Geographic isolation: a barrier to interbreeding between two populations that arises from them being separated in space, often with some kind of geographic barrier to movement between them.

Geophagy: the consumption of soil, clay, or sand.

Germinal spot: the site on the egg yolk where the embryo will develop; it sits atop a cylinder of light-colored yolk that runs from the yolk's core to its surface.

Ghost lineages: an evolutionary lineage that is inferred from a phylogeny, but for which no fossil evidence has been found.

Gizzard: the muscular lower part of the avian two-part stomach that grinds and softens food, often with the aid of stones held within the gizzard.

Glide angle: the angle at which a gliding bird descends through the air.

Gliding flight: unpowered flight, as in birds that are flying without flapping their wings.

Globular nest: a spherical dome nest with a top that completely encloses the nest, usually entered through a hole on one side.

Gondwana: the name of the ancient southern supercontinent of 180–600 million years ago that included most of present-day Africa, Antarctica, Australia, India, Madagascar, New Zealand, and South America.

Good genes benefits: the fitness advantage that individuals (usually females) gain by selecting mates on the basis of the genetic qualities that they will pass on to their mutual offspring.

Good genes hypothesis: the idea that individuals choose mates based on an assessment of their potential genetic contribution to their mutual offspring, either directly by demonstrating components of the mate's fitness or indirectly by being able to survive and compete despite exaggerated sexual ornaments.

Great American Interchange: the exchange of animals that commenced about 3 million years ago when a land bridge first connected the previously isolated continents of North and South America.

Group selection: the controversial idea that natural selection can sometimes act collectively via benefits realized by entire groups of organisms, as opposed to the narrower fitness benefits realized by selection acting only on individuals.

Guild: a group of species that use components of their habitat or resources in a similar way; for example the "insectivore guild" or the "hole-nesting guild" of a woodland habitat.

Gular fluttering: a behavior of opening the bill wide and vibrating the thin gular membranes of the throat in order to dissipate heat via evaporative cooling.

Habitat: the comprehensive range of physical, biological, and geographic conditions required by individuals of a given population to survive and/or reproduce.

Habitat corridor: an area of habitat that connects larger patches of that habitat and through which species dependent on that habitat can move.

Habitat island: an isolated patch of a given habitat that is surrounded by other, potentially inhospitable, habitats.

Habitat isolation: a barrier to interbreeding between two populations that arises from them being found in different habitats, even if otherwise they are in close proximity.

Hamilton's Rule: the formula that describes when an individual should forgo its own reproduction and instead help its relative reproduce. One formulation of this idea suggests helping should be favored when $rB > C$, where r is the genetic relatedness of the individual and its breeding relative, B is the additional number of offspring this helping behavior will add to the relative's reproductive success, and C is the cost to the helper in the form of offspring that they cannot produce themselves if they invest instead in helping their relative.

Handicap principle: the hypothesis that females of some species have evolved mating preferences for males who display very costly and exaggerated ornaments or behaviors, since these costs ensure that only particularly high-quality males can afford these so-called handicaps.

Heritability: the proportion of the variation in a trait that is due to underlying genetic variation.

Heterogametic sex: in animals with genetic sex determination, the sex that has two different sex chromosomes. In birds, females have heterogametic sex chromosomes (Z and W) whereas males are homogametic (Z and Z).

Heterospecific attraction: a behavior in which individuals of one bird species use the presence of individuals of another species as an indicator of the quality of a habitat patch in which to forage or breed.

Homeostasis: the ability to maintain relatively constant physiological conditions within the body.

Homeotherm: an organism that maintains its internal body temperature at a constant or nearly constant level regardless of environmental conditions.

Hormones: chemicals produced by organs or tissues that are conveyed through the circulatory system to act on target tissues located at a distance from their source.

Hybrid index: a number derived from measuring a series of traits or genes that describes the proportion of a hybrid individual's ancestors that belonged to each parental species.

Hybrid zone: a geographic area where two species (or distinct populations) come into contact and hybridize.

Hyperphagia: rapid feeding, as often exhibited by birds putting on pre-migratory fat.

Hyperthermia: internal body temperatures higher than typical.

Ideal-free distribution: a theoretical model for how birds might distribute themselves over a set of habitat patches, filling in the highest quality patches first and colonizing lower quality patches only when doing so is better than settling in a higher quality but now crowded patch.

Immune system: the organs, tissues, cells, and antibodies that differentiate self from non-self and which act in concert to neutralize potentially pathogenic organisms or substances.

Immunocompetence: an individual bird's ability to mount a functioning immune response after exposure to a pathogen or antigen.

Immunology: the study of the immune system.

Inbreeding: the offspring resulting from matings between individuals who are more closely related than would be expected by chance within a population.

Inbreeding depression: the reduced survival or reproductive success of offspring produced by the mating of two close relatives.

Incest taboo: behavioral avoidance of mating with close genetic relatives.

Incubation: the behaviors by which parent birds keep their eggs within the temperature range for proper embryonic development.

Incubation period: the number of days from the start of regular incubation of the eggs until hatching.

Indeterminate layer: a bird species that will lay additional replacement eggs if any are removed from its clutch during the laying period.

Indicator species: a conspicuous or easily monitored species that is associated with a given habitat and which acts as an early warning signal that the habitat is changing in ways that are likely to affect many other species.

Indirect fitness: the component of an individual's fitness that results not from their own reproduction, but rather by the aid they give to relatives that then enhances their relative's reproductive success.

Innate immunity: components of the immune system that are standard responses to a potential pathogen, not arising from or requiring previous exposure to that pathogen.

Interference competition: competition among individuals or species in which they interact directly—often via aggression—over access to the same resources.

Intermittent flight: a common flight style among small and medium-sized birds that consists of flapping phases interspersed with flexed-wing bounds or extended-wing glides.

Intersexual selection: a subset of sexual selection, one involving the reproductive success of individuals that depends on the actions of the opposite sex. In birds, intersexual selection often (but not always) involves mate choice by females who are selecting among potential male mates.

Interspecific competition: this occurs when birds of different species compete for the same resources.

Interspecific territoriality: aggressive, territorial behavior directed by individuals of one species against members of other species.

Intrasexual selection: a subset of sexual selection, one involving the reproductive success of individuals that depends on competition with members of the same sex. In birds, intrasexual selection often (but not always) involves competition among males over access to females.

Inverse density dependence: a feedback loop in which populations at higher density tend to grow larger, whereas populations that shrink tend to become even smaller over time.

Irruptive migrants: birds that occasionally move in large numbers beyond their usual range, usually in response to poor food supplies in their typical habitats.

Keel: a mid-ventral ridge of bone that projects outward from the sternum and provides an attachment site for the pectoral flight muscles. Synonymous with carina.

Keratin: a stiff protein that forms scales, claws, and feathers.

Key innovation: a newly evolved trait that allows a lineage to take advantage of new ecological opportunities, and which results over time in that lineage diversifying into multiple species that are specialized for those new ecological niches.

Keystone species: a species that has a disproportionately large effect on its habitat, biological community, or ecosystem. Named after the top block of stone—the keystone—in an arch that is essential for holding the other stones in place.

Kidneys: organs that maintain water and electrolyte balance and filter the blood of metabolic wastes, thereby producing urine.

Kin selection: natural selection arising through indirect fitness, via the reproduction of relatives that are aided by an individual.

Kleptoparasitism: a parasitic interaction in which one bird steals prey or food from the individual who originally obtained it.

Landbridge islands: islands that were formerly part of the nearby mainland, and which often retain some of the birds and other organisms from that earlier period, that were created by a rise in the level of the ocean. In contrast, oceanic islands rose directly out of the sea, and all land organisms on them had to have arrived by overwater colonization.

Latitudinal diversity gradient: the general rule that in most groups of organisms, species diversity is greatest in the tropics and steadily decreases towards the earth's polar regions.

Leapfrog migration: a pattern in which the individuals at the extreme of the breeding distribution migrate farthest, in the process traveling past birds that breed and winter in intermediate locations.

Lek: an aggregation of males that engage in competitive mating displays towards visiting females.

Lek paradox: a theoretical conundrum where, in a population in which all females mate only with the rare highest quality males, all offspring will inherit the traits that make those males so attractive, and hence over a few generations there will be little genetic variation among males in those important traits.

Lévy flight: a pattern of movement based on mathematical models that generates a mix of short random movements and occasional longer movements.

Life history traits: any of the fundamental traits that directly influence an individual bird's survival and reproduction. Examples include lifespan, age at first reproduction, and the number and size of offspring produced per year.

Life table: an actuarial table that describes the probability of death at each age, and which sometimes also includes the expected reproductive output at each age.

Life zone: a geographic region (or, in mountains, an elevational band) characterized by a distinct group of animal and plant species.

Lift: the force acting on a moving airfoil (such as a bird's wing) perpendicular to the direction of airflow.

Local movements: the non-migratory movements involved in the daily activities of birds.

Lumping: informal term for changes in classification that involve merging into one species two or more taxa that were previously each considered to be a separate species.

Mandible: in birds, usually refers to the lower half of the beak; the lower jaw.

Maniraptora: a group that includes birds and their closest relatives within the theropod dinosaurs.

Mass extinction: in earth history, the *extinction* of an exceptionally large proportion of species within a relatively short period of time.

Matched countersinging: a behavior in which rival males respond to one another's songs, with both males matching different song types one after another.

Mate guarding: a behavior in which a male attends closely to his mate during her fertile period to help ensure that she does not mate with other males.

Mating system: the pattern in which matings are distributed among males and females within a population, sometimes but not always involving longer term social bonds.

Maxilla: in birds, refers to the upper half of the beak; the upper jaw.

Maximum range speed: the flight speed that maximizes the distance traveled for a given amount of energy.

Mechanical isolation: a barrier to interbreeding between two populations that arises from an incompatibility between the male genitalia of one species and the female genitalia of the other species.

Megafauna: continental assemblages of exceptionally large-bodied mammals and birds, most of which (except in Africa) became extinct as humans spread across the world's continents and islands.

Melanins: pigments, manufactured within cells, that generally produce a range of earthy colors in various shades of black, brown, gray, reddish brown, and pale yellow.

Metabolic rate: the rate of energy production (often measured as heat production) in an organism.

Metabolism: all chemical processes that take place in the cells and tissues of the body, including those involved in energy use and heat production.

Metapopulation: an array of spatially separated populations of the same species that are at least partly connected by the dispersal of individuals among them.

Migration: the regular, seasonal movement of individuals away from, and back to, the breeding grounds.

Migratory connectivity: the degree to which individuals breeding in a particular region migrate to the same overwintering region.

Migratory divides: locations where two populations of the same species with different migratory orientations meet and potentially interbreed.

Migratory fallouts: situations in which very large numbers of migrating birds are forced to land in a small area by adverse winds or other challenging weather conditions.

Minimum power speed: the flight speed that maximizes time in the air for a given amount of energy.

Minimum viable population: the smallest population size considered likely to allow the species (or population) to avoid extinction for a specified number of years.

Mitochondrial DNA (or mtDNA): in birds, the DNA that is found not in the cell nucleus, but rather in the cell's mitochondria, a structure involved in generating energy within the cell. Mitochondrial DNA is passed down only from mother birds to their offspring.

Mixed-species flocks: flocks of birds that contain individuals of more than one species.

Mobbing: behavior in which a number of birds (sometimes of different species) swoop and dash at a potential predator, often while broadcasting loud calls to alert and potentially recruit other birds into the mobbing flock.

Molecular clock: the idea that DNA changes accumulate at a relatively steady rate, and that the genetic differences among organisms can therefore be used to estimate the time in the past when they started to diverge from one another.

Molting: the process of shedding some or all of the feather coat and replacing it with newly grown feathers.

Monomorphic: describes species in which males and females are similar in outward appearance.

Monophyletic group: in evolutionary terms, any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

Motion parallax: a depth cue that results from the motion of the observer, as objects that are closer move farther across the visual field than do objects that are more distant.

Mound nest: a nest comprised of a pile of material, usually with a chamber in the middle for the eggs.

Mutualism: an ecological relationship involving multiple individuals or species in which all parties benefit in some way from the other.

Nares: the two openings of the nasal cavity located in the upper beak, usually near its base. Singular: naris.

Natal dispersal: the movement between the site where a bird was fledged and the site where it first attempts to breed as an adult.

Natal down: the down feathers that cover the body of a hatchling bird.

Natural selection: an evolutionary process in which the higher survival and reproduction of individuals with favorable inherited traits causes those traits to increase in the population over time.

Navigation: the ability to determine an absolute geographic location in two dimensions.

Neognaths: one of the two groups of living birds, containing all living birds except the ratites.

Nephrons: structures within the kidney that filter wastes from the blood to produce urine.

Niche axes: particular components of the environment that influence whether a species is present or absent, or how it interacts with members of the same or other species.

Niche breadth: the range of resources utilized by a species; a species with wide niche breadth is referred to as an ecological generalist, whereas a species with narrow niche breadth is termed an ecological specialist.

Niche overlap: the extent to which two species use the same resources or occur in the same habitats or locations.

Nictitating membrane: the "third eyelid" of birds, a thin, translucent fold of skin that sweeps across the eye.

Nidicolous: the condition of chicks that stay in the nest for long periods after hatching.

Nidifugous: the condition of chicks that leave the nest soon after hatching.

Nodes: the points on a phylogeny where branches separate, usually representing points where an ancestral lineage splits into two or more descendant lineages.

Nomadic: refers to birds that move irregularly, rather than in a predictable migration, usually in response to highly variable food resources or other environmental variation.

Nuclear species: refers to the one or more species within a mixed-species flock that are central to its formation and cohesiveness.

Nucleotides: the basic molecular building blocks of DNA and RNA.

Obligate migration: a pattern in which individuals migrate to the same areas on the same schedule every year.

Open-ended learners: songbirds that remain able to learn new songs throughout all or most of their lives.

Optimal Foraging Theory: models of foraging behavior in which it is assumed that animals maximize their food intake while minimizing the overall costs of obtaining it, such as energy and time devoted to searching, capturing, and processing.

Orientation: the ability to determine bearings and directionality.

Ornament: any physical trait that has been exaggerated for social display by sexual selection; usually refers to conspicuous traits involved in mate attraction.

Oscillogram: a graphic representation of a recorded sound (like a bird song) where sound intensity (loudness) is plotted against time.

Oscine passerines: the "true songbirds," one of the two groups within the order Passeriformes, the most diverse avian order.

Osmosis: the movement of water or another solvent through a semipermeable membrane into a region of higher solute concentration, tending thereby to equalize the concentrations of solutes between the two sides of the membrane.

Ossification: the hardening or calcification of soft tissue (such as cartilage or tendon) into bone or a bone-like material.

Pair bond: the social bond between a mated pair (usually a male and female) in a socially monogamous species, usually lasting for one breeding attempt or longer.

Paleognaths: one of the two groups of living birds, containing all ratites as well as the extinct elephantbirds and moas.

Parasitisim: an ecological interaction involving two species in which one species benefits and one species is harmed.

Parasympathetic system: the part of the autonomic nervous system that acts on smooth muscle to reduce the heart rate and regulate physiology under non-stressful conditions.

Parental effort or parental investment: any expenditure of time or energy by a parent bird that benefits their current offspring at the cost of the parent's own future survival or reproduction.

Partial migration: a pattern in which some individuals within a population or species are migrants and others are non-migratory residents.

Passive stability: when applied to flying birds, components of the bird's aerodynamic structures that cause the bird to return to an original flight posture when it is disrupted by an outside force (such as wind) without flapping or other active movements.

Pathogen: any organism or virus that causes disease or illness.

Pectinate claw: a modification of the side of the middle toe claw into a comb-like, serrated edge used for preening.

Pennaceous: describes that portion of the vane that is relatively flat and has a defined shape.

Phagocytic cell: a cell that engulfs and absorbs potential pathogens, waste compounds, or other foreign bodies.

Philopatry: the tendency to return to the same location in successive years.

Photoperiod: the amount of a 24-hour day in which birds are exposed to light; or the relative lengths of light and dark periods of the day.

Phylogenetic species concept: a species concept that focuses on the history of a related set of organisms, in which a species is usually defined as the smallest group descended from a common ancestor that shares some kind of distinguishing feature that separates them from other such groups.

Phylogeny (or phylogenetic tree): a diagram that depicts the evolutionary relationships connecting a set of organisms.

Phylogeography: the scientific study of the evolutionary relationships of populations and species across space, usually as inferred from genetic information.

Pin feathers: developing feathers that are still surrounded by a feather sheath.

Pipped: the condition of an egg that is approaching hatching, in which the embryo within has punctured the first small hole through the shell.

Platform nest: a nest consisting of a shallow depression on the top of a mound of nest material.

Plumage: refers either to a bird's entire feather coat, or to the set of feathers produced by a particular partial or complete molt.

Plumulaceous: describes that portion of the vane for which the loose, fluffy barbs are not structured into flat vanes.

Pneumatic: describes bones that are filled with air spaces and may contain air sacs; nearly all the bones of most birds are pneumatic.

Pneumatized: filled with small air cells.

Point count: a popular census method for birds in which an observer notes the birds seen or heard from a stationary point over a standard period of time.

Polyandrous mating system: a mating system in which one female mates with multiple males.

Population: in ornithology, a group of interbreeding birds of the same species that live in the same place at the same time.

Population connectivity: the degree to which two breeding populations are connected by dispersal and gene flow.

Population viability analysis (PVA): a modeling technique used by conservation biologists to identify the biological and human factors most strongly affecting the long-term survival of a population or species, and to estimate how population persistence varies with population size.

Powder down: specialized down feathers that grow continuously and disintegrate at their tips to produce a fine powder.

Precocial: the condition of chicks that are already well feathered with down when they hatch, with substantial powers of thermoregulation and locomotion, and a considerable degree of independence from the parents for feeding.

Preening: feather maintenance behavior in which a bird tends to its feathers with its bill.

Prescribed burning: deliberate and carefully planned burning of an area to achieve management goals, usually to maintain the diversity and quality of habitats that evolved with regular fire.

Prey switching: a behavior in which predators preferentially consume the most abundant type of prey, switching to another prey type when it becomes the most abundant.

Primaries: the flight feathers of the outer wing that are attached to the manus.

Principle of allocation: the assumption of a trade-off in energy and other resources, such that those devoted to one aspect of life history (such as survival) thereby become unavailable for others (such as reproduction).

Proprioceptive: nerve stimuli that give information on the position and movement of the body or parts of the body.

Proteins: complex molecules composed of strings of amino acids; proteins are the main building blocks of birds and other organisms and also act as enzymes in the chemical reactions within a bird's cells and tissues.

Proximate questions: in biology, questions that pertain to immediate, internal, and/or mechanistic processes, often addressing "how" the process is produced by physiological, behavioral, or other means.

Pterylae: feather tracts, the areas of a bird's skin to which feathers are attached.

Pterylosis: the pattern and location of the feather tracts on a bird's skin.

Pygostyle: the tail bone of birds, formed by the fusion of the final several caudal vertebrae; it provides an attachment site for the flight feathers of the tail.

***r* and *K* selection:** ecological terms for the ends of a continuum between extreme investment in reproduction at the cost of long-term survival (*r* selection), and extreme investment in survival at the cost of high fecundity (*K* selection).

Rachis: the portion of the feather shaft distal to the calamus; it is often relatively solid and supports the vanes, when present.

Ramus: the central shaft of a feather barb (from which barbules extend).

Range disjunction: a pattern of geographic distribution in which two or more occupied areas are separated by substantial intervening areas where the species is not found.

Ratite: a group of mostly large and flightless birds that includes ostriches, kiwis, rheas, cassowaries, emus, and tinamous, as well as the recently extinct moas and elephantbirds.

Realized niche: the subset of its fundamental niche that a species actually occupies.

Rectrices: flight feathers that originate from the tail bones and form the tail surfaces/airfoil.

Reflex: a relatively simple, rapid, and stereotyped response to a stimulus; it may be either automatic or learned.

Refugia: geographic regions that remained relatively unaltered by past changes in climate or other environmental shifts, and which therefore supported populations of organisms that were lost in the surrounding regions.

Regional heterothermy: the ability to maintain core body temperature while allowing the temperature of the extremities to deviate from the core temperature.

Reinforcement: a situation in which natural selection fosters the divergence of two hybridizing populations, either by selecting against hybrid offspring directly or by favoring individuals that choose members of their own population as mates.

Remiges: flight feathers that originate from the wing bones and form the wing surfaces/airfoil.

Reproductive isolation: a mating incompatibility that occurs when some kind of behavioral, physiological, or genetic barrier prevents successful interbreeding among individuals from two different populations even where they occur together.

Reproductive retaliation: a behavior in which one member of a pair provides less parental care in situations where the offspring in the nest may not be their own and/or when their mate also provides less care.

Reproductive skew: refers to the degree to which reproduction is limited to only a few adults in the population (high skew) or is more equal among all adults in the population (low skew).

Reproductive success: the number of viable offspring produced by an individual over their lifetime.

Reproductive value: the expected reproduction of an individual from their current age onward, given that they have survived to their current age.

Residents: birds that remain in the same area year round.

Resource defense polygyny: a mating system in which one male is the predominant mate for multiple females, through defending against other males a high-quality territory or other valuable resource that attracts a group of breeding females.

Retort nest: a globular nest with an entrance tunnel.

Reverse sexual dimorphism: a situation in which the sex that is usually smaller or less ornamented is the larger or more conspicuous sex in a particular species. In birds, sexual selection is usually stronger on males, so reverse sexual dimorphism refers to species where females are the flashier sex.

Rhamphotheca: the outer covering (sheath) of the beak.

Rhynchokinesis: the ability of some birds to independently move or open the upper tip of a long bill, most often seen in birds that feed by probing in soil or mud.

Rictal bristles: stiff, hair-like feathers projecting from the base of the beak in some birds.

Runaway sexual selection: a hypothesis for how extremely exaggerated ornaments or behaviors might evolve, via a feedback loop that involves females choosing males with the extremes of that trait, the resulting generations of male offspring having more and more elaborate variants of the trait, and the resulting female offspring having ever stronger preference for males with the trait.

Salt glands: paired glands that extract and excrete excess salt from the blood; most conspicuous in marine birds, especially the "tubenosed" seabirds.

Scrape nest: a shallow depression created for use as a nest; scrapes usually contain little or no nest material.

Search image: a general idea or cognitive representation of an object or prey type being sought; if a bird has a search image for a particular type of prey, it is able to find that prey more easily than it can find prey for which it lacks a search image.

Secondaries: the flight feathers of the inner wing that are attached to the ulna.

Senescence: a decline with age in physical, physiological, and/or reproductive performance, or an increase with age in the probability of death.

Sensitive period: the period of time during a songbird's neural development when it is able to learn songs after hearing a tutor.

Sequential polyandry: a mating system in which one female mates with multiple males within a breeding season, but with only one male during each successive nesting attempt.

Sex ratio: the ratio of males to females in a population.

Sexual dimorphism: a situation in which males and females of the same species differ in aspects of their size, color, or form.

Sexual selection: a special form of natural selection that involves the differential reproductive success of individuals that arises specifically from competition over mating opportunities; this can involve direct competition with members of the same sex or competition to attract members of the opposite sex.

Sexy son hypothesis: the idea that breeding females can achieve higher fitness by mating with particularly attractive males because their sons are thereby more likely to inherit those attractive traits and be reproductively successful themselves.

Shaft: the stiff, central spine of a feather from which the vanes, if present, extend.

Sheath: the temporary tube-like covering that surrounds a growing feather.

Sink population: a population in which reproduction is not sufficient to maintain population size, and which therefore must receive immigrants dispersing from other populations to remain extant.

Sister taxa: two groups (often but not always two species) that are each other's closest evolutionary relatives.

Slope soaring: a type of soaring in which a bird derives lift from the air currents that are deflected upward when wind strikes a hill or ridge, or from rising eddies created when wind spills over a cliff.

Social mate: the individual with which a bird has a pair bond.

Social monogamy: in birds, a mating system in which one female forms a lasting pair bond with one male, though she may also copulate with other males.

Song: an often loud and sometimes complex vocalization used to attract mates or compete with members of the same sex.

Source population: a population in which more offspring are produced than can breed in the original patch, leading some to disperse away to other locations.

Spatial synchrony: the tendency for the size or density of spatially disjunct populations to be correlated through time. Spatial synchrony within a larger metapopulation occurs when the subpopulations grow or shrink in size at the same times.

Specialist: an organism that uses only a narrow range of some type of resource; for example, birds with specialized diets eat only one or a few kinds of food.

Speciation: the evolutionary process by which one ancestor lineage splits into two or more descendant species.

Species: the basic unit of biological classification for birds. Criteria for defining bird species vary, but they generally group into a single species the individuals and populations with very similar traits, a history of recently shared ancestors, and the continued ability to fully interbreed.

Species accumulation curve: a graph that shows the number of species detected on the *y*-axis and the number of survey samples or individuals observed on the *x*-axis.

Species–area plot: usually a graph showing the cumulative number of species detected as the area sampled increases. The resulting relationship is typically a curve, as fewer and fewer new species are detected with increasing area.

Species–area relationship: the nearly universal tendency for larger areas to harbor greater numbers of species; used most often in reference to islands or habitat fragments.

Species assemblage: similar to "community," the group of species found in a particular location or habitat.

Species concept: the precise sets of criteria that systematists use when deciding whether two populations are members of the same species, or two separate species. Different species concepts tend to emphasize different such criteria, sometimes leading to disagreements about classification.

Species richness: the number of different species present in a location, ecological community, or region.

Spectrogram: a graphic representation of a recorded sound (like a bird song) that includes information on both frequency and loudness, usually by plotting frequency against time and indicating intensity by shading or colors.

Sperm competition: in birds, a form of intrasexual selection that arises after more than one male has copulated with the same female, and therefore the sperm of multiple males are in competition to fertilize an egg within the female's reproductive tract.

Splitting: informal term for changes in classification that involve separating into different species populations that were previously considered to be part of a single species.

Staging areas: locations where migrating birds fuel up just before, or in a pause during, migration.

Steppingstone dispersal: the dispersal that proceeds by a series of colonizations, one after another, across a chain of islands or among habitat patches.

Sternum: the breastbone; it provides an attachment site for the ribs and pectoral muscles. In all flying birds except tinamous, the sternum has a keel (carina).

Stochastic extinction: extinction resulting from random changes in population size when the population drifts to zero individuals.

Stopover sites: locations where migrating birds take a short break to rest, eat and drink for maintenance, and/or await favorable migratory conditions.

Stress response: in avian endocrinology, the rise and fall in hormone levels (particularly corticosterone) during and after a bird is exposed to some kind of stressor.

Studbook: the genealogical record of parents and offspring used in captive-breeding programs.

Suboscine passerines: the group within the order Passeriformes in which song learning is rare or absent.

Subsong: the quiet practice songs made by young birds that are just learning how to sing.

Subspecies: in birds, a distinct population or group of populations within a more widespread species that is distinguishable from other subspecies on the basis of one or more diagnostic traits.

Supertramp species: a term applied to bird species that are particularly good at dispersing long distances and at colonizing newly created habitats.

Survivorship: in a demographic life table, the probability of being alive at a given age.

Suture zone: the somewhat controversial idea that broad-scale changes in past habitats have affected many species in similar ways and thereby created locations where multiple hybrid zones overlap.

Sympathetic system: the part of the autonomic nervous system that functions under conditions of stress, preparing the body for "flight or fight."

Sympatric speciation: the speciation that occurs even when the two diverging populations breed in the same locations and therefore have the possibility of intermixing within each generation.

Sympatry: refers to organisms or groups of organisms that occur in the same place.

Synsacrum: the segment of the vertebral column of birds that is formed by the fusion of some thoracic vertebrae with all of the lumbar and sacral vertebrae and the first several caudal vertebrae.

Syrinx: the primary sound-producing organ of birds, located at the point where the trachea divides to form the two bronchi.

Temporal (or allochronic) speciation: an unusual form of speciation in which the two diverging populations occur in the same location, but diverge because they reproduce at different times of the year.

Territoriality: a behavior in which an individual defends an area against other individuals.

Theory of Island Biogeography: a relationship formalized by ecologists Robert MacArthur and E. O. Wilson that describes how the total number of species inhabiting an island or habitat patch results from a balance between the rate at which new species colonize and the rate at which populations of established species become extinct.

Thermal neutral zone: the range of ambient temperatures over which a bird does not require additional metabolic energy for the heating or cooling of its body.

Thermal soaring: a type of soaring in which birds use rising air thermals—rising columns of warm air—to gain height.

Thermoregulation: the active ability of an organism to modulate its internal body temperature.

Thoracic cage: the rib cage; in birds it consists of the ribs connected to the thoracic vertebrae above and to the sternum below.

Thrust: in a bird, the portion of the force generated by the flapping wings that propels the bird forward.

Top-down effect: in ecology, a situation in which the amount of predation or consumption by organisms at the top of the food chain has large effects on lower components of the ecosystem.

Torpor: a resting state in which the body temperature drops, metabolic processes slow, and reactions to external stimuli are slow or lacking.

Total fitness: the sum of direct fitness via the individual's own reproduction plus their indirect fitness via their relative's reproduction. Sometimes also termed "absolute fitness."

Tragedy of the commons: a common dilemma in natural resource management, in which benefits to an individual are contrary to the collective benefits of the group, so that individuals are inclined to act selfishly, despite this being to the detriment of everyone. Named after communal grazing lands (the "commons") to which each herder could freely add additional livestock, thereby helping themselves in the short term but ultimately leading to severe overgrazing and the destruction of the commons as a long-term resource for the community.

Transect count: a bird census technique in which an observer moves along a path—the transect—and notes all the birds seen or heard.

Translocation: the human-assisted movement of individuals from one location to another for conservation purposes. It is used most effectively to establish or supplement populations in areas where threats have been reduced or eliminated.

Traplining: foraging movements in which a bird rotates through a set of discrete food sources; most often applied to individual hummingbirds that visit a set flower patches in an established and repeated sequence, allowing the time in between for the flowers to replenish their nectar.

Trivers–Willard hypothesis: the idea that females should produce offspring of the higher investment sex when the females are in good condition, and offspring of the lower investment sex when the females are in poor condition.

Trophic cascade: a situation in which predators high in a food chain exert top-down effects that ramify through the food chain levels to influence the abundance of species that the predators do not eat directly.

Tubenoses: birds in the order Procellariiformes—including albatrosses, shearwaters, fulmars, petrels, and storm-petrels—all of which have tube-shaped nares.

Ultimate questions: in biology, questions that pertain to long-term evolutionary processes, often addressing "why" a particular trait arose within a species or higher taxonomic group.

Umbrella species: a species for which successful conservation actions would also help preserve many other species within its biological community.

Uric acid: the less toxic molecule to which the liver of birds coverts the highly toxic nitrogenous waste products of protein metabolism.

Uropygial gland: a gland near the upper base of the tail that secretes oils that a bird distributes across its feathers via preening.

Vagrants: birds that move far beyond the normal range of their species.

Vanes: the broad, usually flat, surfaces that extend from the shaft of contour and flight feathers; the vanes are formed by interlocking barbs.

Vector: an organism (usually an insect, tick, or other arthropod) that transmits a pathogen from one kind of host to another.

Vestigial: describes a structure with little current apparent function that is thought to be present solely because it derives from a structure that was functional in an ancestor.

Vicariance: the subdivision of a species' originally large distribution into smaller and separated geographic fragments via some new geographic barrier or the fragmentation of the species' originally widespread habitat.

Vicariant speciation: speciation that results over time after populations that become divided by new barriers have diverged from one another.

Vitelline membrane: the transparent membrane that surrounds the yolk.

Vocal signals: vocalizations that influence the behavior of other individuals.

Wing loading: the ratio of body weight to wing area; wing loading is a measure of how much load each unit area of wing must carry when a bird is in flight.

Wingspan: the distance between the tips of the fully extended wings of a living bird.

***Zugunruhe*:** a German term for the nocturnal restlessness that caged migratory birds exhibit when they are ready to migrate.

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