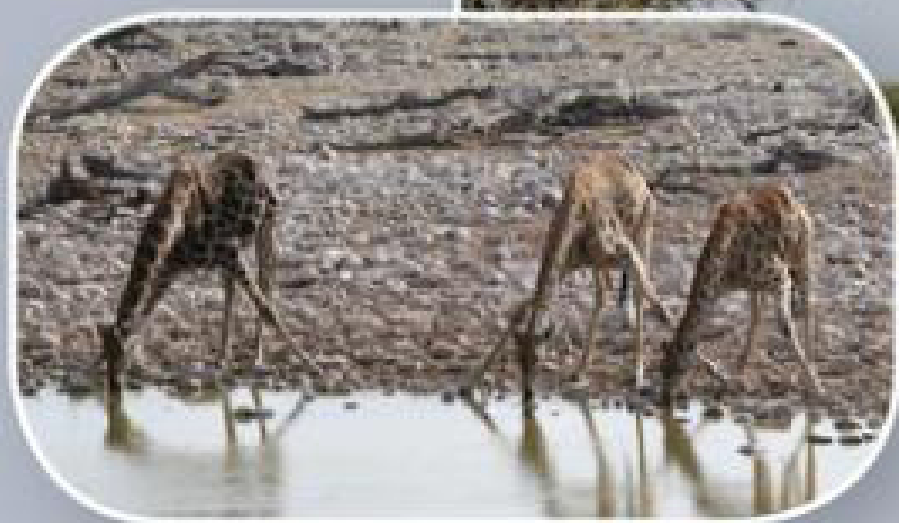
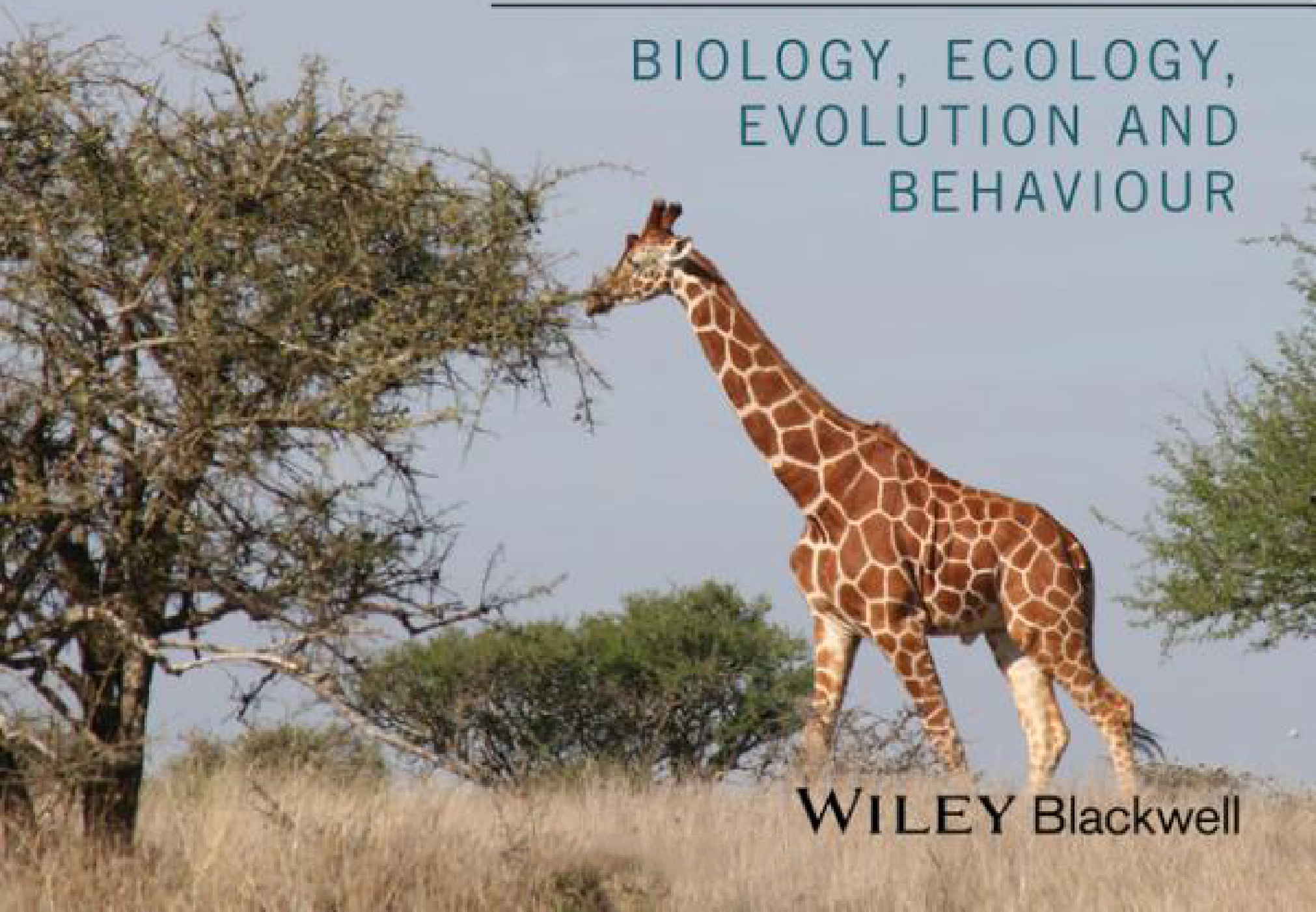


BRYAN SHORROCKS



THE GIRAFFE

BIOLOGY, ECOLOGY,
EVOLUTION AND
BEHAVIOUR



WILEY Blackwell

The Giraffe

The Giraffe

Biology, ecology,
evolution and behaviour

Bryan Shorrocks

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WILEY Blackwell

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Preface

Robert H. MacArthur was an American ecologist at Princeton University who, in the 1960s and early 1970s, made a major impact on many areas of community and population ecology. His emphasis on hypothesis testing helped change ecology from a primarily descriptive field into an experimental field, and drove the development of theoretical ecology. When he wrote his final book, *Geographical Ecology* (1972), he began the introduction with these words:

To do science is to search for repeated patterns, not simply to accumulate facts.

This present book is about the giraffe, but I hope it is not simply a collection of facts. Of course, there are many facts about giraffes in the book, but I have also attempted to look for patterns. And sometimes this has involved reanalysing older data and using data from other species. There are two main reasons for the latter. First, some areas of giraffe biology are poorly documented. Therefore looking at other African browsers, or even other ungulates, might provide an insight into what giraffes are doing, and suggest research areas that require more attention. Second, even if we have the data for giraffes, it is essential to examine what other African browsers/ungulates are doing in order to see if there is in fact a general pattern.

Many enthusiasts who write about giraffes frequently say that this 'piece of biology is unique to the giraffe'. But here lies a danger. If we only look at giraffes and see everything they do as unique to them, then we will always search for answers by looking only at giraffes. For example, giraffes are frequently said to have a unique fast gait in which the legs on the same side of the body move forward together. The 'unique' is not true. This type of gait is called a

pacing gait and, it should be stressed, is not unique to the giraffe, being found in the okapi (*Okapia johnstoni*), camel (*Camelus dromedarius*), llama (*Lama glama*), topi (*Damaliscus lunatus jimela*), kongoni (*Alcephalus buselaphus*), wildebeest (*Connochaetes taurinus*), hyaena (*Crocuta crocuta*) and some canids, all with sloping backs. Look for patterns first, and then within these general patterns look again at giraffes and how they might differ.

Of course, patterns can be misinterpreted, particularly if several quite different causes can produce the same pattern. Researchers must consider all options as an explanation and try and eliminate those for which evidence is lacking. Naturally, conservationists are frequently involved in non-scientific discussions, often involving local 'feelings' about animals and their livestock and crops, but when collecting data and drawing conclusions they must always use the 'tried and tested' protocols of the scientific method.

I would like to thank several people who have provided permissions, thoughts, photographs and encouragement for my work on giraffes. These include: Fred Bercovitch, Rachel Brand, Kerry Carter, Mike Chase, Isobelle Ciofolo, John Doherty, Jack Lennon, Zoe Muller, Mordecai Ogada, Russell Seymour and Robert Sutcliffe. In addition, I thank Dan Rubenstein for discussions, at the Mpala Research Centre in Kenya, on his zebra stripe patterns that gave me the idea for the giraffe codes in Chapter 8. I thank Roger Butlin for discussions about species and DNA, and I thank Craig Hilton-Taylor, Head of the IUCN Red List Unit, for permission to quote extensively from IUCN publications and their website. I thank Darren Croft for introducing me to 'social

networking ideas' and to Paul Ward for reintroducing me to Africa. Finally, I thank the staff at the Mpala Research Centre in Laikipia, Kenya, and Etosha National Park, Namibia, for all their kind help during my stays there.

Most of my work has been centred in Kenya, where I also took MSc students for many years. I thank all the staff and drivers at Concorde

Safaris, in Nairobi, for being so helpful during over 20 years of visits to their country, and providing me with vehicles. I thank the Kenyan Ministry of Education, Science and Technology for providing me with research permits.

Bryan Shorrocks
January 2016

CHAPTER 1

Introduction to the giraffe

In the prehistoric rocky landscape of the Sahara, native people drew pictures of this amazing animal, and in the Egyptian Bronze Age it decorated the tombs of kings. It may even have been the god the Egyptians called 'Set' (Spinage 1968a). In ancient Greece and Rome it was called the 'camelopard', in East Africa today it is *twiga*, and in the English language we now call it 'giraffe'. The name 'giraffe' has its earliest known origins in the Arabic word *zarafa* (*zarāfah*) (زرافة), perhaps from some African language. The name can be translated as 'fast walker' (Kingdon 1997), although some linguistic authorities believe it stems from a source meaning an 'assemblage of animals'. Clearly, the Greeks took this latter view. They contributed part of its scientific name, *camelopardalis*, which literally describes a camel's body wearing a leopard's coat. The Italian form *giraffa* arose in the 1590s and the modern English form developed around 1600 from the French *girafe*. The old and the new now combine to form the giraffe's scientific name, *Giraffa camelopardalis*, although interestingly, the form 'kameelperd' survives in Afrikaans.

In one form or another, giraffes have been around for a very long time. And so has *Homo sapiens*. The interaction between giraffes and humans starts way back in prehistory, and rock art (paintings and engravings) is found all over Africa from Morocco, Algeria and Libya in the north, through Ethiopia, Somalia, Kenya and Tanzania in the east, to Botswana, Zimbabwe,

Namibia and Mozambique in the south (Le Quellec 1993, 2004; Muzzolini 1995). Wherever, in fact, there has been savannah. However, the most extensive and remarkable rock art is found in areas of the Sahara (Coulson & Campbell 2001). Today these are found in remote, inhospitable regions of the desert, so arid that any form of sustained human or animal existence is untenable today. They document prehistoric cultures that apparently thrived in these regions, hunting wild animals and herding domesticated cattle, that have subsequently vanished, leaving little trace of their presence or of the richness of their cultures.

The Sahara has not always been the desert it is today. Over the last 2 million years, it has fluctuated several times between even greater aridity and plentiful rain. Where there are now dry gullies, rivers once flowed. In what are now empty sandy plains, there were lakes surrounded by grasslands and trees, rather like the savannahs of sub-Saharan Africa today. The earliest rock art, much of which represents large wild animals such as giraffe, hippo, elephant, rhinoceros and the extinct long-horned buffalo (*Buffalus antiquus*), is believed to have been created by hunter-gatherers more than 7000 years ago and possibly as early as 10,000 BP (before present).

The Wadi al-Hayat is one of three wadis (dry rivers where the underground water is near enough to the surface to support vegetation and to be accessed through wells) in the modern

region of the Fezzan, situated in south-west Libya. Since about 7000 years ago, possibly earlier, human groups living in the wadi, or perhaps using it periodically, were creating rock engravings of the animals found in their savannah environment. These animals seem to have been chosen deliberately, and presumably had great cultural value and meaning. Precisely what they symbolised to these Stone Age people, and the message that they conveyed, is of course not known for certain. However, they may have been created to give early hunters mastery over their prey. Of course, these early hunters may well have just enjoyed painting and engraving the animals they saw around them. What is noticeable in these prehistoric depictions of, for example, giraffes is the artists' familiarity with their subject. They knew these animals, their graceful bodies and how they moved. In contrast, later medieval depictions are a poor reflection of the real animal, presumably because the artists had never seen a giraffe.

The first significant collection of prehistoric and historic engravings was identified in the Wadi al-Hayat in 2000 and 2002, during the Fazzan Archaeological Project, directed by Professor David Mattingly. These preliminary studies indicated that this was an exciting area to explore further (Mattingly 2003), and after a systematic survey of over 80 km of the wadi, over 900 engraved rocks and several thousand individual carved images have been recorded. Interestingly, many of the paintings and engravings of giraffe show what appear to be human hunters, nets (often called plate nets) and ropes attached to neck collars (Fig. 1.1). Other sites in Libya include Wadi Methkandoush and Karkur-Talh which have pictures of elephants, hippos, giraffes, cattle, crocodiles and birds. In Karkur-Talh, the only large African animal represented is the giraffe. The absence of elephants and rhinoceros seems to indicate that these engravings are younger than the earliest ones in the central Saharan massifs. Most of the engravings are small, 30–50 cm; there is a single example of a giraffe exceeding 1 metre in dimension. Frequently the animals (giraffe and ostrich) are



Fig. 1.1 Line drawing of rock art from the Fezzan, Libya. Notice the leash around the neck of one of the giraffes.

shown tethered, probably caught in some kind of a trap, or held at the neck by a leash.

In the heart of the Sahara, in what is now Niger, lies the Tenere Desert. Tenere means 'where there is nothing'. It is a barren desert landscape stretching for thousands of miles, but this part of the Sahara lay across an ancient caravan route. For over two millennia the Tuareg operated this trans-Saharan caravan trade route, connecting the great cities on the southern edge of the Sahara, via five desert trade routes, to the northern coast of Africa. Here in the heart of Niger lies Dabous, home to one of the finest examples of ancient rock art in the world, two life-size giraffes carved in stone, possibly at least 8000 years old (Dupuy 1988). They adorn an outcrop of rock and, curiously, the carvings cannot be seen from the ground, but only by climbing onto the outcrop. What is also interesting is that the rock surface used, the stone canvas if you like, had been prepared beforehand for the carvings. There are two giraffes, one large male in front of a smaller female, engraved side by side on the sandstone's surface. The larger of the two is over 18 feet tall (5.40 m), combining several techniques including



Fig. 1.2 The Niger giraffes. Reproduced by kind permission of Rudy A. Photography: www.rudyaphotography.com/.

scraping, smoothing and deep engraving of the outlines (Fig. 1.2). This giraffe has a leash on its neck, perhaps implying some level of taming the animals.

Whatever the reasons for these prehistoric depictions of giraffes, what is certain is that they have had a significant place in these African prehistoric cultures for thousands of years, perhaps even being kept as ‘pets’ or ‘status symbols’. Yet despite this, giraffes are hardly mentioned in African folklore today. Only the Tugen (Kamasia) tribe of Kenya retains the giraffe’s image in the face of their god Mda (Spinage 1968a). Intriguingly, the Tugen are a Kalenjin people and they believe that although their ancestors’ aboriginal home was in Kenya, they migrated to Misiri or Egypt, where they stayed for thousands of years, and then migrated back again to Kenya. It is to Egypt that we now turn for images of giraffe.

The early Egyptians used images and symbols of giraffes quite frequently. In predynastic times (before about 3050 BC), the Egyptian climate was much less arid than it is today. Large regions of Egypt were covered in savannah and would have been home to herds of grazing ungulates, including giraffes. In southern Egypt, the Naqada culture began to expand along the Nile by about 4000 BC and manufactured a diverse selection of material goods, which included combs. Figure 1.3 shows an early ivory comb, ca.3900–3500 BC, what is called the Naqada I and early Naqada II periods, with the handle of the comb depicted as a giraffe. More detailed is the giraffe on a carved schist palette, again from Naqada (Fig. 1.4). These cosmetic palettes, of middle to late predynastic Egypt, were thought to have been used to grind and apply ingredients for facial or body cosmetics. Later they became commemorative, ornamental and possibly ceremonial. Many of

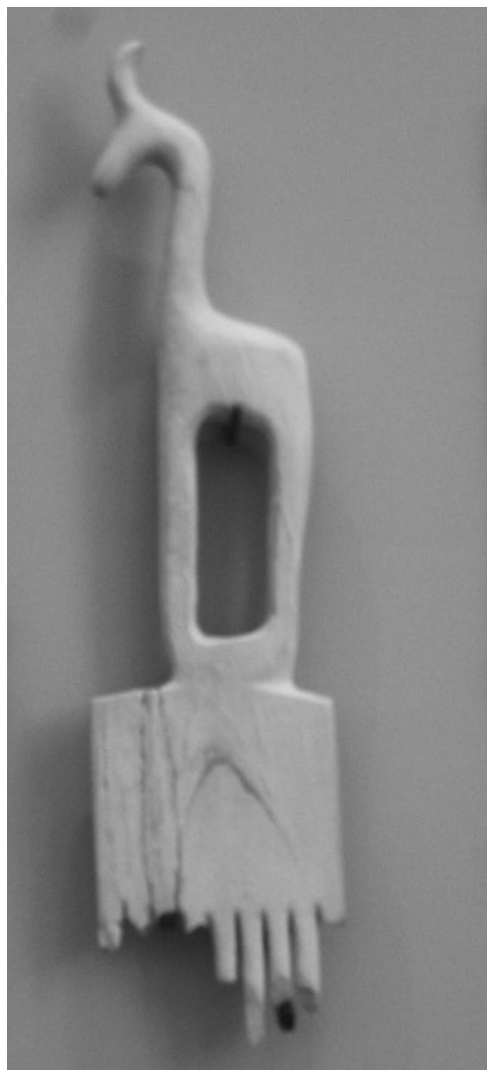


Fig. 1.3 Ivory giraffe comb from Naqada graves. Ashmolean Museum, Oxford. Photograph by Jo Shorrocks.

the palettes (like Fig. 1.4) were found at Hierakonpolis, a centre of power in predynastic Upper Egypt. After the gradual unification of the country (from around 3100 BC), the palettes ceased to be included in tomb assemblages.

We next see giraffes in hunting scenes from the pyramid complex of King Unas (2375–2345 BC), at Saqqara. Unas was the last of the kings of

the Fifth Dynasty. A covered causeway (720 m long) links Unas's mortuary temple to his valley temple and is decorated with high-quality reliefs depicting a range of colourful hunting scenes showing giraffes, lions and leopards. Although many people believe this was the end of the Golden Age of the Old Kingdom, it is interesting to note that the artists were still ignorant of some biological facts (Spinage 1968a). Among the giraffes, stags, bears, leopards, hares and hedgehogs is a maned lion giving birth!

By the time the New Kingdom made its appearance (1500–1350 BC), a change had occurred in the way giraffes were portrayed. In the Old Kingdom, giraffes are seen in hunting scenes, suggesting they were part of the rich savannah fauna of Egypt at that time. By the New Kingdom, they tend to be exotic animals, coming from afar, perhaps indicating that the giraffe had, by this time, disappeared from the lower reaches of the Nile. We know that Egypt had trading connections with regions further south. Queen Hatshepsut, who reigned between 1501 and 1480 BC, sent a trading voyage south, to Punt (Somalia and the Red Sea coast). A report of that five-ship expedition survives on reliefs in 'The Punt Colonnade' in Hatshepsut's mortuary temple at Deir el-Bahri, located on the west bank of the Nile, opposite the city of Thebes (present-day Luxor). Upon its return, the expedition brought back ivory, silver, gold, myrrh trees and the skins of giraffes, leopards and cheetahs which were worn by temple priests. One relief shows the Land of Punt and the Puntine people, who were black Africans. Donkeys are depicted as the method of transporting goods, and white dogs guard the people's houses. Birds, monkeys, leopards and hippopotamus are seen, as well as giraffes; typical African animals depicted as living in Punt. This was by no means the only expedition to southern lands and giraffes are often seen in Egyptian wall paintings of this period. In the tomb of Huy, viceroy of Nubia during the reign of Tutankhamen (1347–1336 BC) we see Nubians carrying offerings, among them a giraffe.



Fig. 1.4 Carved schist cosmetic palette, showing a nice giraffe at the bottom. Late predynastic (Nagada Iic/d or IIIa) from the main deposit at Hierakonpolis. Ashmolean Museum, Oxford. Photograph by Jo Shorrocks.

Rekhmire was Vizier of Egypt during the reign of Tuthmose III (1479–1425 BC) and therefore in charge of much of the day-to-day administration in Egypt. His tomb, in the Valley of the Nobles, is one of the largest and most decorated tombs among all of the Theban nobles' tombs, full of beautiful paintings of daily life. One painting, with five sections, one above the other, shows the tribute brought from Punt and the Mediterranean Islands. In one frame, Nubians or Kushites are bringing various animals – giraffes, leopards, baboons, monkeys, cattle and dogs as well as ostrich eggs and feathers (Fig. 1.5). The

last giraffe picture of dynastic Egypt is on a wall of the temple of Rameses II (the Great), at Beit el-Wali in Nubia (Fig. 1.6). In the bottom scene, the pharaoh receives leopard skins, giraffe tails, giraffes, monkeys, leopards, cattle, antelopes, gazelles, lions, ostrich feathers and eggs, ebony, ivory, fans, bowls, shields made of animal hides, and gold.

What purpose did these giraffes and giraffe products have? Were they tokens of regard, pets or simply exotic curiosities from a foreign land? Certainly animal skins were worn by priests in the temples and giraffe tails were used as fly

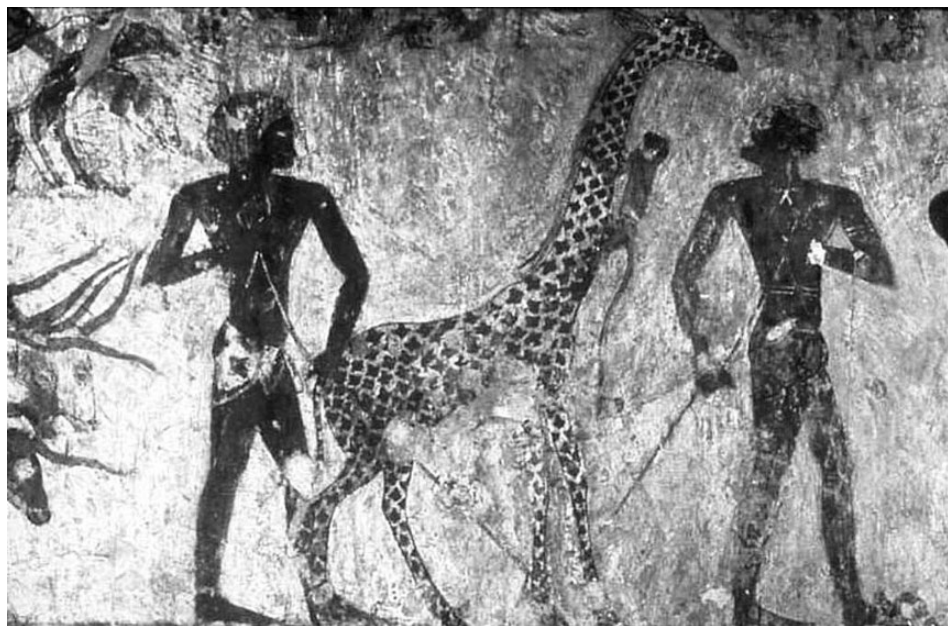


Fig. 1.5 Tomb of Rekhmire about 1504–1540 BC. Photograph by kind permission of Nile Sun Hotels & Cruises, Egypt.

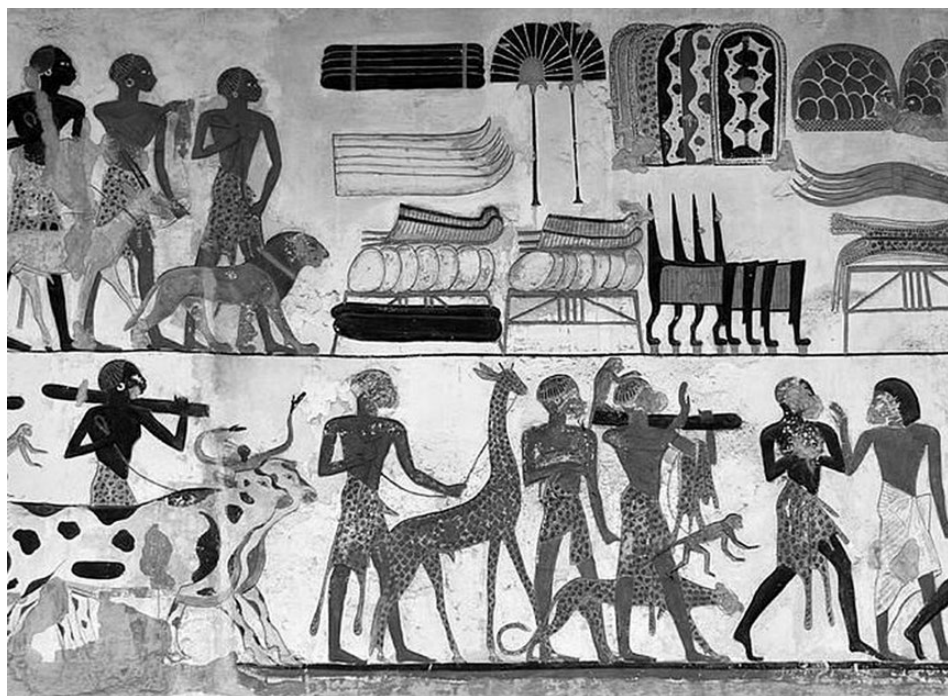


Fig. 1.6 Wall painting in temple of Beit el-Wali, which Rameses II constructed in Nubia.

whisks (they are still today). Some exotic animals were kept as pets and there is a suggestion that giraffes were 'tamed' and kept on leashes. However, there were Egyptian zoos or menageries. Queen Hatshepsut acquired baboons when she had myrrh saplings brought to Egypt from the Horn of Africa, which presumably would have been kept somewhere, but no records exist. Among the animals imported from Punt were rhinos, giraffes, leopards, monkeys and more familiar species like cattle and hounds. There was a zoo at Per-Ramesses, the capital Rameses II built in the eastern Delta, containing, according to the bones found, large animals. Lions, elephants and possibly giraffes were among the animals kept.

What is likely is that the perception of giraffes changed over the 3000 years of Egyptian civilisation. In predynastic and Old Kingdom times, giraffes were undoubtedly hunted locally, probably for their skins and tails. By New Kingdom times, they had disappeared from Lower Egypt and were now exotics, brought as tributary gifts by Nubians and Kushites. However, what is clear is that to the Egyptians giraffes were real beasts. In contrast, the Greeks saw them as almost mythical, a product of the union of a camel and a leopard, and so named them camelopards. They heard rumours of this strange animal but never saw one. After the time of Alexander the Great (356–323 BC), the Ptolemy's ruled Egypt and a Greek scholar, named Athenaeus, described a celebration of the feast of Dionysus in which several animals were paraded through the streets of Alexandria ... ostriches, hartebeest, elephants, oryx, leopards, lynxes, lions, cheetahs, a rhinoceros and a giraffe. In 104 BC another Greek scholar, Agatharchides of Cnidus, gave us the first written description of a giraffe in his book, *On the Erythraean Sea*, on the races and animals to the west of the Red Sea (Burstein 1989).

Among the troglodytes lives also an animal which the Greeks call Camelopardalis, a composite names which describes the double nature of this quadruped. It has the

varied coat of a leopard, the shape of a camel and is of a size beyond measure. Its neck is long enough for it to browse in the tops of trees.

The next notable appearance of a giraffe is the one brought from Alexandria by Julius Caesar in 46 BC, at the end of the civil war (Healey 1991, from Pliny). Some people believe it may even have been a present from Cleopatra, who later followed it to Rome. It was the first giraffe to be seen in Europe. Caesar's return to Rome, and the end of the civil war, were celebrated with five separate triumphs. Caesar exhibited his giraffe at the games in the Circus Maximus, Rome's chariot racing stadium and mass entertainment venue. Apparently there were contests in 'a kind of hunting-theatre of wood ...' (Carter 1996, from Appian; Cary 1914, from Dio). Like the Greeks, the giraffe appeared to the Romans to be part camel and part leopard, and was referred to as the camelopard (Kent 1938, from Varro; Healey 1991, from Pliny). Curiously, Pliny also calls it an *ovis ferae* or wild sheep. Sadly, many of the Roman recordings of giraffes are of their killings in the Circus or Coliseum. Commodus, in the second century AD, slaughtered a giraffe and rhinoceroses, as well as five hippopotamuses and two elephants, in 2 days (Cary 1914, from Dio). Dio may even have witnessed the event. In AD 248, Philip the Arab (Roman Emperor from AD 244 to 249) celebrated the millennium of Rome's founding with the display in the Circus Maximus of 10 giraffes, elephants, tigers, lions, leopards, hippopotamuses and a rhinoceros (*Historia Augusta*, 33). This was probably the largest number of live giraffes ever brought together in Europe, although Aurelian (Roman Emperor from AD 270 to 275) is said to have marked his triumph over Zenobia, queen of Palmyra, in AD 274 with a presentation of giraffes (*Historia Augusta*, 33).

In 1996, some mosaics were uncovered during a highway construction in the modern Israeli town of Lod, not far from Tel Aviv. Lod was ancient Lydda, which was destroyed by the Romans in AD 66 during the Jewish War. Refounded by Hadrian as Diospolis, Lydda was

awarded the rank of a Roman colony under Septimius Severus in AD 200. It remained in Roman hands until becoming a Christian city and eventually succumbing to Arab conquerors in AD 636. The large rooms in which the mosaics were found probably belonged to a private house and served as a series of reception or audience halls where visitors were met and entertained. The main panel, measuring 13 square feet and set in the centre of one of the floors, is divided into a series of smaller squares and triangles by an interlocking cable pattern, in which various birds, fish and mammals are depicted. These surround a larger octagonal space populated by a lion and lioness, an elephant, a giraffe, a rhinoceros, a tiger and a wild bull. The depiction of an elephant, giraffe and rhinoceros would have been very 'exotic' in a place such as the Roman colony of Lydda. On this coastal plain of ancient Palestine, such savannah animals would have been quite unfamiliar. In fact, the giraffe is rarely depicted in ancient art, which makes its appearance in the Lod mosaic all the more remarkable. The only other two that I know of include the head of a giraffe on an elaborate Roman marble sarcophagus, dated about AD 190. Here the giraffe appears in a scene depicting a triumphal procession, together with lions, elephants and leopards. Another giraffe appears on a fragmentary late Roman, or early Byzantine, mosaic dated to the fifth century AD.

Following the demise of the Roman Empire, we see little reference to giraffes in western Europe for nearly a thousand years. One exception is the book by the Bishop of Seville, Isidorus Hispalensis (AD 602–636), called *De Natura Rerum*. In natural history books of this time, animals were often arranged in alphabetical order and so chameleon was followed by chamelopard. The good bishop got the two mixed up:

Chamelopardus does not have one colour, but is spotted with a differing pattern like a leopard. Now it is called this because it has the likeness of a camel and a lion. The body of this Camelion changes to the colours which it sees by a very easy conversion, because the size of other animals is

not so easy for conversion. It is called the Camelopard because while it is sprinkled with white spots like a leopard it is however in its neck like a horse, in its feet like an ox, in its head like a camel; Ethiopia produces it.'

With the Arab Conquests (622–750) reference to giraffes moves back to northern Africa and the East. Egypt was conquered in 642, 10 years after the death of the Prophet. In 652 the Emir Sad Ibn Abi Sarh invaded Nubia and in the treaty arrangements arranged for an annual payment of 400 slaves, a number of camels, two elephants and two giraffes. During the reign of the Caliph Al-Mahdi this was reduced to 360 slaves and one giraffe. Amazingly, this tribute was made until 854 when after an abortive Nubian revolt, there is no more mention of tributary giraffes. One of the great Arab writers was Amr Ibn Bahr, or al-Jahiz (773–869), who wrote a Book of Animals (*Kiab al-Hayawan*) in which, once again, many of the bizarre ideas about the origin of the giraffe, from a female camel and a male leopard, were recounted. Interestingly, these early writers all seem to perceive Nubia as the home of the camelopard.

The next people to 'find' the giraffe were the Chinese, in the mid-12th century. In one of the earliest writings, in the book *Su-po-wu-chi*, by Li Shi, we find:

The country Po-pa-li harbors a strange animal called the camel-ox (t'o niu). Its skin is like that of a leopard, its hoof is similar to that of an ox, but the animal is devoid of a hump. Its neck is nine feet long and its body is over ten feet high.

Po-pa-li is thought to be the coast of Somalia (Laufer 1928) and the stated length of the giraffe's neck is quite accurate, considering that the writer might not have ever seen a living specimen. The designation 'camel-ox' corresponds exactly to a Persian designation of the giraffe, *ushtur-gaw* (*ushtur*, 'camel' ; *gaw*, 'ox, cow'), mentioned as early as the 10th century by the Arabic writer Masudi. It may therefore be that the description of the giraffe had come to China from Persia. The second reference to the giraffe is made by Chao Ju-kwa in his work

Chufan chi, written in 1225. This author was collector of customs in the port of Ts'uan-chou fu in the province of Fu-kien, where he came in close contact with Arabian merchants and representatives of other foreign nations who then had a thriving commercial exchange with China. From oral information given to him by foreign traders, and from earlier Chinese sources, he compiled his brief book. In his notes on the Berbera or Somali coast of East Africa, he mentions as a native of that country:

a wild animal called tsu-la, which resembles a camel in shape, an ox in size, and is yellow of colour. Its fore legs are five feet long, while its hind feet are only three feet in length. Its head is high and looks upward. Its skin is an inch thick.

The word *tsu-la* used in this text is not Chinese but is of Arabic origin; it is intended to reproduce *zarafa*, the Arabic term for the giraffe. In fact, the ancient Chinese did not see a giraffe until the 15th century, under the Ming dynasty, when it was mistaken for the *ki-lin*, a fabulous mythical creature. This confusion is surprising since the *ki-lin* was said to have the body of a deer, the tail of an ox, a single horn and to be covered in fish scales. It was said to symbolise gentleness, goodness and benevolence. Perhaps this was where the confusion lay with the graceful giraffe. However, the fabulous *ki-lin* of antiquity was reputed to appear only at the time of a virtuous ruler, and this may have had more to do with the 'confusion' with the newly arrived giraffe.

Late in 1486–7, in an attempt to establish better diplomatic relations with Florence against the Ottoman Turks, al-Ashraf Qaitbay, the Mamluke Sultan of Egypt, presented a female giraffe to Lorenzo de' Medici (known as Lorenzo the Magnificent). Lorenzo had read of the spectacular success of Caesar's giraffe, and possibly saw it as a way to cement his reputation in Florence by possessing one. He also realised that he could gain further political influence by passing the animal on, and he promised to send it to Anne of France (Regent of France 1483–1491),

after its stay in Florence. In Florence, the giraffe was an immediate sensation. Although Cosimo de' Medici, Lorenzo's grandfather, had maintained a large zoo, and had previously featured a giant mannequin of a giraffe in the animal entertainments he provided for the citizens of Florence, this was arguably the first time a living example had been seen in the city, and even in the whole of Italy. I say 'arguably' because there are reports that Frederick III of Sicily had been given a giraffe in 1261 by the Sultan of Egypt in exchange for a white bear, and that the Duke of Calabria, Duke of Ferrara and the rulers of Naples all owned giraffes. If these giraffes existed, they certainly did not have the success that Lorenzo's giraffe enjoyed. It was immortalised in paintings by Botticini, Vasari and Bacchiacca, and in frescoes and poetry. The poet Antonio Costanzo described it freely roaming the streets:

I have also seen it raise its head to those onlookers offering to it from their windows, because its head reaches as high as eleven feet, thus seeing it from afar the people think that they are looking at a tower rather than an animal. Ours appears to like the crowd, it is always peaceable and without fear, it even seems to watch with pleasure the people who come to look at it.

Although Anne of France had written reminding Lorenzo of his promise to send the giraffe to her, she was to be disappointed. Lorenzo had built special stables for it, either at the family's villa at Poggio a Caiano or in the Via della Scala in Florence itself, with heating to protect it from the damp Florentine winters. Unfortunately, shortly after its arrival the giraffe broke its neck and died after its head became stuck in the beams of these stables.

A living giraffe was not seen in Europe again until 1827, when Muhammad Ali, the Ottoman viceroy of Egypt, presented a giraffe to both Charles X of France and George IV of the United Kingdom and, 2 years later, to the Hapsburg Emperor Franz II of Austria. Indeed, it had been 340 years since Anne of France had written to Lorenzo de' Medici, beseeching him to keep a promise to send his own giraffe to her, 'for this

is the beast of the world that I have the greatest desire to see'. The 1827 giraffes were diplomatic gifts intended to mollify public sentiment at the treatment of the Greeks during their war of independence, and they caused a sensation in art and fashion in *la mode à la girafe*. However, they did not prevent a combined British, French and Russian naval force from decisively defeating the Ottoman Turks a few months later at the Battle of Navarino (20 October 1827), in what was to be the last engagement fought with sailing ships. Two of the Egyptian giraffes were siblings and upon arrival in Cairo, the French and English consuls drew lots for them, with the French winning by far the better draw, as later events transpired, since the smallest sibling was awarded to George IV. Sadly this fragile individual, lashed to the back of a camel when it could no longer walk, was injured during its journey and its legs crippled. The animal arrived in England and was tended in a building in the grounds of Windsor Castle, out of public view. Requiring the aid of a special harness to stand, within 2 years the wretched creature weakened and died. It was painted, in late 1827, by the animal painter Jacques-Laurent Agasse, who tactfully omitted the pulley and harness. The giraffe sent to Vienna also suffered during its transport by camel, an injury no doubt aggravated by walking from Trieste to Vienna, where it succumbed to disease within ten months.

The giraffe presented to Charles X was more fortunate, travelling by ship to France with every comfort. She was allocated her own cabin steward, a groom from the French Consulate, and cared for by native keepers from the Sudan, all of them charged with attending to her every whim. As with the English giraffe, three cows accompanied her on her voyage to supply her daily 6 gallons of milk, and she arrived in the port of Marseilles in a healthy and thriving condition. Upon noting how the fashionable 'mademoiselle' spurned plain water, her keepers devised a menu to suit her appetite, which was observed to favour milk and barley. After debarkation, a hole having been cut in the upper deck to allow her

head to poke through, this pampered giraffe walked in royal livery, cheered by boisterous crowds, the 550 miles from Marseilles to Paris. Here she was presented to Charles X and ate rose petals from his hand. The giraffe was kept in one of the hexagonal wings of the Rotonde de la Menagerie, the world's first civil zoo, in the grounds of the Jardin des Plantes, where she was seen by over 600,000 visitors in the first 6 months alone. The giraffe started a 'giraffemania' in the art world: *à la girafe* furniture, wallpaper, porcelain and even soap, decorated with a giraffe pattern, were produced. As Étienne Geoffroy Saint-Hilaire, who had accompanied the giraffe from Marseilles to Paris, wrote, her new home, with its parquet flooring and straw matting on the walls, was 'truly the boudoir of a little lady'. There, much to the chagrin of the United Kingdom, the animal lived quietly for another 18 years, her influence on fashion and the interest of the public gradually waning. She died in 1845 and her corpse was stuffed and sent to the museum at La Rochelle. Here, some 168 years after her death, she still has an ability to cause surprise and wonder, when unsuspecting visitors round the stairway and encounter Mademoiselle Zarafa peering impassively down from the half-landing where she stands. An entertaining account of the French giraffe, and the surrounding historical events, is given by Allin (1998).

Because England did not have a giraffe of its own after 1827, and this was seen as a national disgrace, the new King William IV commissioned a French trader, Monsieur Thibaut, to search for giraffes for England. Thibaut eventually captured eight Nubian giraffes in the Sudan, and four survived the journey to London. So, on 25 May 1836, three males and a female accompanied by their native handlers and Thibaut arrived at the docks in London. The new arrivals made their own procession, of shorter duration than that of *Zarafa* from Marseilles to Paris. A stately 3-hour parade, escorted by Thibaut and the Nubian keepers in native dress, alongside a detachment from the Metropolitan Police, brought them safely to the

Zoological Gardens that evening, where they settled immediately into the new elephant house, their temporary lodgings until their own purpose-built accommodation was completed the following year. Thibaut was paid the enormous sum of £700 for the animals. The lone female, Zaida, gave birth to her first offspring in 1839, and in subsequent years, 17 young were born and these giraffes populated London Zoo until 1881. Following this eventual success (except for the brief period of 1882–1895), London Zoological Gardens has never been without giraffes. The lithographer George Scharf (1788–1860), whose artwork documented events of everyday life in London, recorded the giraffes' arrival in 1836 with an engraving of the four giraffes, their handlers and Monsieur Thibaut. This was immediately followed by the production of John Ridgway's giraffe patterned transfer wares showing the engraving (Fig. 1.7).

The original giraffe house at London Zoo still houses giraffes. It was built between 1837 and 1838 and designed by the architect Decimus Burton and is now a Grade II listed building. Wings were added in 1849–1850. There was bomb damage in 1940 and Franz Stengelhoffen and Colin Wears rebuilt it in 1960–1963.

The first living example of the southern giraffe was imported into Europe in 1895 for London Zoo for a price of £500. It had been captured on the Sabi River in Portuguese territory and brought down to Pretoria, whence it was conveyed to Delagoa Bay and shipped to Southampton.

In 1863 Lorenzo Casanova, a traveller and animal collector, returned from the Egyptian Sudan to Europe with a collection of six giraffes, the first African elephants and many other rare mammals. In 1864 he entered into a contract with the firm of Carl Hagenbeck according to



Fig. 1.7 Plate printed with giraffes and handlers by John Ridgway, ca.1836.

which all animals to be secured on his future expeditions to Africa should be sold to the Hagenbecks. In 1870 the largest consignment of wild animals that ever reached Europe arrived at Trieste, consisting of 14 giraffes, 90 other mammals and 26 ostriches. The giraffes were distributed over the zoological gardens of Vienna, Dresden, Berlin and Hamburg. About that time several itinerant menagerie owners and showmen also began to keep giraffes. Renz, the celebrated circus director, utilised giraffes, antelopes, buffalo and many other creatures for his pantomime 'The Festival of the Queen of Abyssinia'. During the period 1873–1914 the firm of Carl Hagenbeck imported a total of 150 giraffes (called at that time four species, *Giraffa camelopardalis* of Lower Nubia and Abyssinia, *G. capensis* of the Cape territory, *G. hagenbecki* from Gallaland, and *G. tippelskirchi* from German East Africa). The largest specimen imported by Hagenbeck, about 11.5 feet in height, came from the Galla country, and was transmitted to the Zoological Garden of Rome. Prior to 1914, Hagenbeck maintained a station for captive animals, at the foot of Mount Kilimanjaro, where the captured young giraffes moved freely in a larger kraal, after being hunted and lassoed by horsemen. The average price for a young giraffe

before the First World War was about \$1500–2000.

In the United States of America giraffes began arriving towards the end of the 19th century. The Zoological Society of Philadelphia keeps records of all the animals that have arrived at the zoological garden which is the oldest in the United States. The earliest record of giraffes is an entry for 11 August 1874, when five males and one female were purchased. The zoo in Lincoln Park, Chicago, received two giraffes, a male and a female, 2 years old, in October 1913, as a gift from Mrs Mollie Netcher Newberger. The female died in December 1915, the male, in May 1919.

This chapter has been a short introduction to the 'history' of giraffes and their effect on human culture, from the prehistory of North Africa to the art of Victorian England. For a much fuller account, I recommend the old book by Berthold Laufer published in 1928, called *The Giraffe in History and Art*. It is available as a free download on the internet. Of course, this is not the complete history of the giraffe, since its ancestors, and relatives, go back much further in the fossil record. This longer tale, culminating in the subspecies, or species, we presently see in Africa is the subject of the next chapter.

CHAPTER 2

Origins

Introduction

The origin and evolution of the present-day giraffe are not crystal clear, although a credible story, combining fossil evidence and molecular evidence, can certainly be told. A summary would be as follows. Their recent ancestors probably evolved in southern central Europe about 8 million years ago (Mya). These ancestors appear to have arisen from the gelocids (early artiodactyls) that lived in southern Eurasia 20–25 Mya, and it's with these gelocid ancestors that our 'recent' giraffe ancestral tale begins. From this gelocid stock arose the palaeomerycids, and from them the Antilocaprinae (Pronghorns) and two subfamilies of giraffids, the Climacoceratidae and Canthumerycidae. The Climacoceratid line ended with the now extinct massive giraffid *Sivatherium*. The Canthumerycids gave rise to the okapi and giraffes via the intermediate forms of *Giraffokeryx*, *Palaeotragus* sp. (of which the okapi is the extant form), *Samotherium* sp. and *Bohlinia* sp., all of which are now extinct. The *Bohlinia* line entered China and north India, and evolved into typical *Giraffa* species, becoming extinct there about 4 Mya. African *Giraffa* entered that continent, via Ethiopia, about 7 Mya. Here, unaffected by the climate changes occurring to the east and causing the extinction of their Asian counterparts, *Giraffa* radiated into several species, culminating in the evolution of *G. camelopardalis* in East Africa, from where it dispersed to its modern range.

That is the brief tale, but there are many additional facts and informed speculations, and this chapter will look at these in more detail. But first, let me recount some background information about the ancestors of the gelocids, the origin of artiodactyls, and the evolution of mammals in general, that will be useful. Many of you will know this, but for those who don't, or have forgotten, it will set the background.

Modern molecular opinion (Macdonald 2001; Murphy *et al.* 2007), based on both nuclear and mitochondrial genes, now places placental mammals into four groups, or clades: the Euarchontoglires, Laurasiatheria, Xenarthra and Afrotheria. The Euarchontoglires include the primates, insectivores and rodents. Members of the Xenarthra are found entirely in the New World and include such mammals as anteaters, sloths and armadillos. The Afrotheria are interesting. They are entirely African and contain a very diverse group of species which include elephants, hyraxes (conies), the armadillo, golden moles and elephant shrews. Within the Laurasiatheria are the carnivores (e.g. cats, dogs, badgers and otters), ungulates (e.g. giraffes, antelopes, horses and rhinoceroses), whales and dolphins, bats and the enigmatic pangolins. This molecular evidence also supports the monophyletic origins of the Euarchontoglires and Laurasiatheria into a clade known as Boreoeutheria (Springer *et al.* 2004). Each of these four superordinal clades and Boreoeutheria have been verified by the identification of numerous rare genomic changes such

as coding indels (mutations that include both insertions and deletions) and retroposons (reversed transcribed DNA inserted into chromosomes) (de Jong *et al.* 2003; Kriegs *et al.* 2006; Nikaido *et al.* 2003; Nishihara *et al.* 2005, 2006; Poux *et al.* 2002; Thomas *et al.* 2003).

However, the exact details of the root of the placental mammal tree have so far proved to be elusive (Kriegs *et al.* 2006; Murphy *et al.* 2004, 2007; Springer *et al.* 2004), although three hypotheses are currently proposed (Shoshani & McKenna 1998; Waddell *et al.* 1999, 2001). The Exafroplacentalia hypothesis proposes a mammalian clade merging Boreoeutheria (Supraprimates plus Laurasiatheria) and Xenarthra, with Afrotheria as the sister group. The Epitheria hypothesis merges Boreoeutheria and Afrotheria, with Xenarthra as the sister group. The Atlantogenata hypothesis proposes Xenarthra and Afrotheria in one clade. All three hypotheses are supported by molecular data, although analysis of more than 180,000 coding exons (the parts of the gene sequence that are expressed in the protein product) in a multitude of mammals (Murphy *et al.* 2007) supports Atlantogenata, with afrotherians and xenarians forming a monophyletic group. Using nuclear and mitochondrial data, Murphy and colleagues estimated that the split between Afrotheria and Xenarthra occurred about 103 Mya, which intriguingly is consistent with the time estimated for the rifting of South America and Africa, of 100–120 Mya (Hay *et al.* 1999; Smith *et al.* 1994) which separated the ancestors of Xenarthra and Afrotheria respectively. Wildman *et al.* (2007) came to similar conclusions. However, this debate is not over. More recent analysis of transposable element (a DNA sequence that can change its position within the genome) insertions around the time of divergence strongly supports a fourth hypothesis, that of a near-concomitant origin (trifurcation) of the three super-orders of mammals (Churakov *et al.* 2009; Nishihara *et al.* 2009).

There is still uncertainty regarding the phylogenetic tree for extant Laurasiatherians, primarily due to disagreement about the placement of Chiroptera and Perissodactyla. However, recent

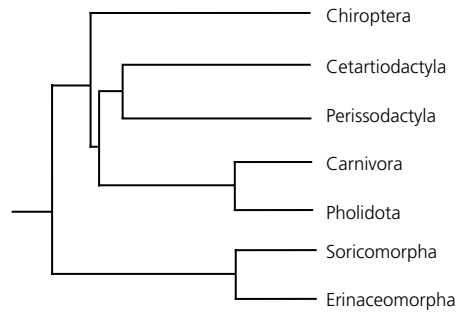


Fig. 2.1 Phylogeny of Laurasiatherian orders showing the timing of splits, based upon various molecular data. Source: adapted from Meredith *et al.* (2011) and Zhou *et al.* (2012).

molecular studies (Meredith *et al.* 2011; Zhou *et al.* 2012) have revealed a possible molecular phylogeny that is also in better agreement with the fossil record than previous molecular studies (Wible *et al.* 2007). I have drawn a simplified, and consensus, version of this phylogenetic tree in Fig. 2.1. The Euarchontoglires and Laurasiatheria are thought to have diverged between 74 and 93 Mya. Next to split off from the lineage leading to the ungulates are thought to be the hedgehogs and shrews (71–86 Mya), followed by the bats (62–71 Mya) and carnivores and pangolins (47–60 Mya), leaving the cetungulate lineage to diversify into the members of the two ungulate assemblages (artiodactyls and perissodactyls) and the whales.

The term ‘ungulate’ is used for those groups of mammals that have hooves. Ungulates dominate present-day terrestrial communities, making up about 80% of mammal species over 50 kg. The great majority of these ungulate species are artiodactyls (about 92%). A hoof consists of a hard or rubbery sole and a hard wall formed by a thick horny nail (keratin) rolled around the tip of the toe. The primitive mammalian limb ended in five such digits, all of which were placed on the ground during locomotion. During the course of evolution, modern ungulates have reduced this basic number of digits and also lengthened and compressed the metapodial bones (the long bones in our hands and feet). Ungulates therefore

walk on tiptoe, rather like a ballerina. In addition, there is restricted movement in the joint surfaces so that the main movement of the limbs is forward and backward, rather than sideways. This 'suite' of ungulate limb characteristics appears to be associated with a terrestrial, herbivorous lifestyle, often in open savannah habitats, in which both fast and sustained galloping locomotion are useful.

Ungulates were traditionally classified into two different groups, the perissodactyls and artiodactyls, depending on whether they had an odd (Greek: *perisso-*) or even (Greek: *artio-*) number of toes (Greek: *dactyla*). In artiodactyls (for example, buffalo, antelopes and giraffe), the axis of the foot passes between digits 3 and 4, while in perissodactyls (for example, zebras, rhinoceroses and horses) it passes through the third middle digit. The number of hooves has been reduced to one pair in the ruminants (for example, the African buffalo, wildebeest and giraffe), although the vestiges of digits 2 and 5 are still present as the false hooves. The early artiodactyls had four hooves (digits 2–5), a condition that persists in pigs and hippos. Whales and hippos are thought to have split from the Cetartiodactyla line about 58 Mya, the camelids about 45 Mya (Cui *et al.* 2007), leaving the ruminant artiodactyls to continue our story of the giraffe. At this point, a small digression about ruminants will be useful, although the specific details of the giraffe digestive system will be left until a later chapter.

Ungulates have evolved two rather different systems for converting cellulose, a major constituent of all plant tissues, into digestible carbohydrates. These two systems are called hindgut fermentation and rumination. In both systems, the conversion from cellulose to digestible carbohydrate is not directly brought about by the ungulate, but by micro-organisms that achieve the breakdown by a process of fermentation. The two systems are closely associated with the two groups, perissodactyls and artiodactyls. The perissodactyls (e.g. zebras and rhinos) are hindgut fermenters while most of the artiodactyls (e.g. giraffes, buffaloes, antelopes and gazelles) are ruminants. In hindgut fermenters,

the food is chewed once, swallowed and then digested in a 'simple' stomach. Only in the caecum (our appendix is a reduced vestige) and colon is the cellulose of the plant cell wall fermented by micro-organisms. More on this topic is found in Chapter 5, but now back to artiodactyls, ruminants and giraffe phylogeny.

The oldest known fossil artiodactyls belong to the family Dichobunidae, and the duiker-like, forest-dwelling *Diacodexis* provide the only complete skeletal remains (Rose 1982). It was a genus that lived in North America, Europe and Asia, and its fossils have been dated to the early Eocene (60–55 Mya). What made these species unique and clearly artiodactyls was their astragalus, a part of the ankle. Their astragalus limited the movement of their foot to the vertical plane, articulating with the tibia above and the cuboid and navicular bones below, and undoubtedly conferring improved running and leaping. Movement would have been assisted by their elongated metapodials, and the transfer of most weight bearing to the third and fourth digits.

Diacodexis also had the archetypical mammalian complement of teeth – incisors (I), canines (C), premolars (P) and molars (M). The dental formula (showing the upper and lower teeth in half the jaw) was $I^{3/3} C^{1/1} P^{4/4} M^{3/3} = 44$. However, the molars were low-crowned (brachydont) teeth and had knob-shaped cusps (bunodont) on their upper surface. By comparison, the dental formula of the giraffe is $I^{0/3} C^{0/1} P^{3/3} M^{3/3} = 32$, and the chewing teeth are high crowned (hypsodont) with low-crowned, crescent-shaped cusps (selenodont). Such teeth differ from human molars, for example, by having their chewing surface not covered with enamel. Instead, layers of enamel, dentine and cementum are all exposed, with cementum in the middle, surrounded by a layer of enamel, then a layer of dentine, all wrapped in a second outer layer of enamel. Such a surface makes the sideways jaw motion of ruminants an effective way to break up tough vegetable matter. Teeth are therefore important in the fossil record. Not only are they frequently the only items to

survive the difficult process of fossilisation, they are also highly correlated with the nature of the diet and therefore the anatomy and physiology of the digestive system. So when we note the primitive nature of *Diacodexis* teeth, we can deduce that these animals were probably omnivorous, and had a simple intestinal tract. The corollary is that their initial evolutionary success lay not in any dietary adaptation, the adaptation most characteristic of modern ruminants, but rather in their improved mobility (Mitchell & Skinner 2003).

In the middle Eocene, the early artiodactyls underwent an extensive adaptive radiation that gave rise to 20 or more families, one of which gave rise to the ruminants (Ruminantia) (Carroll 1988). The earliest fossils showing changes that would lead to ruminants, and ultimately to modern giraffes, are specimens of the hypertragulids. Once again, these were small forest dwellers, probably feeding on a low-fibre, non-abrasive diet rather like their living descendants the tragulids (chevrotains or mouse deer) do today. They lived in what is now North America, Europe and Asia, and the divergence that gave rise to them occurred about 40 Mya. The hypertragulids were characterised like higher ruminants today, but unlike *Diacodexis*, by a fusion between the cuboid and navicular bones of the ankle into the cubonavicular bone. In the forelimb, the radius and ulna were fused proximally as were the tibia and fibula of the hindlimb (proximal is the end nearest the shoulder or hip). In addition, a reduction in digits had begun. The medial metacarpal and metatarsal bones had begun a process of fusion, while the lateral metapodials had reduced in size. This was more apparent in the hindlimb (where only four toes were present) than in the forelimb which retained all five toes.

By about 35 Mya, a cohesive group of ancestral ruminants had emerged from the hypertragulid assemblage. This group was the Leptomerycidae and it comprised about seven species (Heaton & Emry 1996) (Fig. 2.2a). Leptomerycids had an astragalus whose proxi-

mal and distal parts formed a straight line. The magnum (capitate) and trapezoid bones of the wrist had fused rather like the earlier cubonavicular fusion of the ankle. The radius and ulna of the forelimb, and tibia and fibula of the hindlimb, that fused proximally in the hypertragulids had by now fused distally as well. These fusions were accompanied by fusion of the third and fourth metapodials, and further reduction of the lateral ones. These reductions and fusions in the lower parts of the limbs are essential precursors for the later limb elongation that is characteristic of ruminants, especially giraffes, because they provide the strength to support increases in length. Leptomerycids also show another important development. The odontoid process of their second cervical (neck) vertebra is elongated and spout shaped, a change which increases neck stability, allowing it to rotate about its long axis, and heralds the increasing importance of the neck.

From these adaptations, we can speculate that the evolutionary pressures favouring particular characters were probably changing. The early development of the first artiodactyls, and then the hypertragulids, was dominated by adaptations that improved locomotion. After the hypertragulids, changes occurred that improved feeding (the teeth changed), and this change is associated with a dramatic change in the Earth's climate. In the first 10 My of artiodactyl evolution, the ambient temperature was hot and precipitation high. These conditions lasted until separation of the Pangean landmass initiated a fall in temperature. Australia separated from Antarctica, and Greenland from Norway. Separation initiated cooling by establishing cold sea currents between the separating masses, the Antarctic icecap developed and sea levels fell (Janis 1993). The rate of cooling was accelerated by the Asia-India collision that occurred about 40 Mya, throwing up the Alps and Himalayas (Janis 1993) and producing the Tibetan plateau (Raymo & Ruddiman 1992), events that rearranged airflow currents and effectively divided the world's climate into

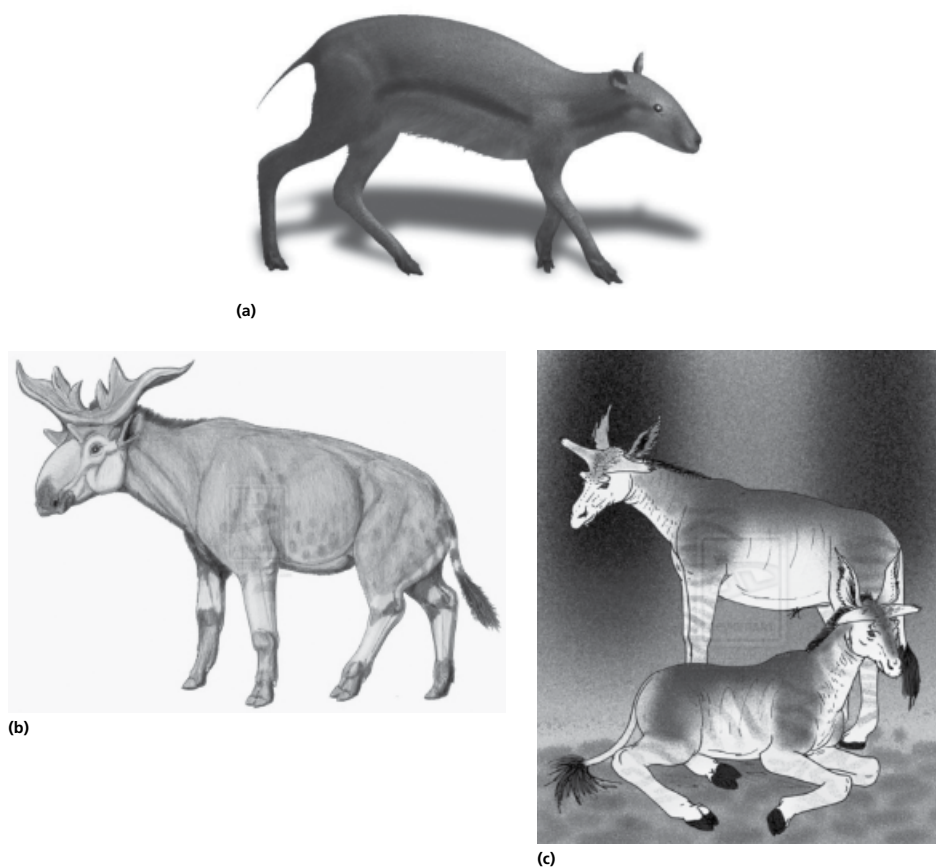


Fig. 2.2 Ruminant ancestors of the giraffe. (a) *Leptomeryx evansi*. (b) *Sivatherium*. (c) *Injanatherium*. Source: DeviantArt website, with kind permission from Ntamura, DiBbg and avancna.

north and south. A more arid world was a consequence, and it resulted in the shrinking of forests and the expansion of savannah-woodlands. Towards the end of the Oligocene, it is possible to recognise new characters in artiodactyls that had survived this climate change. The family of fossil artiodactyls that arose out of the Leptomerycidae and showed these characters was the Gelocidae. Gelocids appear in the fossil record of 25 Mya and are a key group in the evolution of the pecoran ruminant families, of which the Giraffidae are one. The Pecora include all the extant members of the Ruminantia, except the chevroteins. The latter lack horns

and have a less developed system of stomachs than the pecorans, who are sometimes called the 'higher ruminants'.

Gelocidae

Gelocids lived in southern Eurasia around what are now the Black and Caspian Seas, both remnants of what was then the inland Paratethys Sea. A typical fossil species is *Gelocus communis*, said to be the 'first fully progressive artiodactyl' (Carroll 1988). *Gelocus* is characterised by increased selenodonty of molar cusps, showing its high reliance on tough plant material for its food, and suggesting that gastrointestinal

adaptations to herbivory had become a major evolutionary pressure. *Gelocus* also had elongated principal metapodials and a compact and parallel-sided astragulus, which illustrate the increasing role of speed and agility in the lives of artiodactyls. It must have looked and functioned much like a modern-day gazelle. From the gelocid genetic pool came all of our modern pecoran ruminants: the Cervidae (Old World deer), Bovidae (buffaloes, antelopes, gazelles, sheep, goats, musk ox and cattle), Giraffidae (okapis and giraffes), Antilocapridae (pronghorn antelopes) and Moschidae (musk deer). The appearance of distinct families of pecoran ruminants in the Miocene fossil record occurred at about 18–21 Mya, which means that they probably started evolving from their ancestral stock much earlier. Analysis of the evolution of the cytochrome *b* gene (Irwin *et al.* 1991), DNA sequence analysis (Allard *et al.* 1992; Kraus & Miyamoto 1991), and known rates of mutation suggest that in fact, this pecoran radiation occurred over a 5-My period between 28 and 23 Mya.

The pecorans are a diverse group, all of which have an advanced ruminating stomach. They all display cranial appendages (except for two genera: *Hydropotes* and *Moschus*), but this characteristic has evolved independently among the different pecoran families. All five of the pecoran ruminant families are accepted as monophyletic, but the inter-relationships within the Pecora are still controversial. Different analyses have arrived at different relationships between the five modern pecoran families. This may well be the result of the rapid diversification in the early Miocene already referred to, and it is compounded by parallel evolution within the groups (e.g. the evolution of cranial appendages and the loss of upper canines).

Gentry and Hooker (1988) suggested that a subfamily of the Gelocidae, the Palaeomerycidae, were the ruminant ancestral stock. This idea was further developed by Matthew (1929) and Colbert (1935a) and refined by Stirton (1944), who also suggested that the palaeomerycids

were the ancestral stock. In a later analysis, Gentry (1994) revised this proposal and suggested that the ancestral gelocid from which both deer and the palaeomerycids arose was *Dremotherium*, and that the bovids and giraffids were closely related and arose from an ancestral grouping that included the genus *Teruelia* (the giraffid ancestor) and *Walangia* (the bovid ancestor). A third suggestion is that pecorans arose from both the gelocid and palaeomerycid assemblages, because the ancestors of Giraffidae appear in the fossil record after the appearance of the cervids, at about the time of the bovid radiation of 18 Mya (Allard *et al.* 1992; Gentry 1994). This temporal association suggested to Gentry (1994) that giraffids arose from, and are closely related to, the bovids. Finally, Mitchell and Skinner (2003) suggest that giraffids share a common origin with cervids and not with bovids. They say that anatomical evidence for this conclusion lies in the similarities of their teeth, which differ markedly from those of ancestral bovids, and by giraffe hair slope patterns, which are more similar to those of cervids than of other ungulates (Kidd 1900). Ridewood (1901) also reported that the hairs of giraffes and okapis are similar and differ from those of antelopes. They also quote biochemical evidence. Analysis of cytochrome *b* gene evolution (Irwin *et al.* 1991), pancreatic ribonuclease primary structure (Beintema *et al.* 1979), DNA sequence analysis (Allard *et al.* 1992; Kraus & Miyamoto 1991) and K-casein gene phylogeny (Cronin *et al.* 1996) all show that giraffids are more closely related to cervids than they are to bovids. However, the most complete, modern analysis is that of Hernandez Fernandez and Vrba (2005), who combined estimates of ruminant relationships into a single phylogenetic supertree using matrix representation with parsimony (MRP). This approach combines phylogenetic information from different types of studies that otherwise could not be analysed simultaneously (Bininda-Emonds *et al.* 2002; Sanderson *et al.* 1998). Supertree methods resemble meta-analysis, which provides a quan-

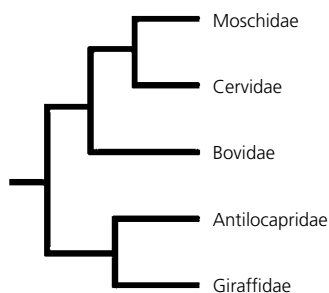


Fig. 2.3 Pecoran ruminant phylogenetic tree. Source: adapted from Hernandez-Fernandez & Vrba (2005).

titative synthesis of all available data (Mann 1990). In their analysis, they used all 197 species of extant and recently extinct ruminants, combining fossil, morphological, ethological and molecular information. A simplified version of their results is shown in Fig. 2.3. This clearly places the bovids and cervids together and the antilocaprids with the giraffids.

So it appears that Stirton's 1944 refinement was essentially correct. The Palaeomerycidae were the origin of New World deer (the Antilocapridae) and the Giraffidae via two sub-families, the Dromomerycinae and the Palaeomerycinae. Dromomerycids evolved into the New World deer, and made their way to temperate North America to survive there as pronghorn antelopes. The Palaeomerycinae were the origin of the Giraffidae. It is possible that the Palaeomerycine *Teruelia*, a hornless gelocid about the size of a small gazelle, the only fossil form of which has been found in Spain (Agusti & Moya Sola 1991), was the earliest ancestral giraffid. If so, from Teruelian stock two families of giraffids arose: the Climacoceratidae and the Canthumerycidae.

Climacoceratidae

One of the most important and so far the most primitive known climacoceratid is *Climacoceras africanus*, first described by MacInnes (1936) from fossils found at Koboko Island in Lake Victoria. MacInnes called it the 'fossil deer' of Africa, saying it was the size of a roe deer,

Capreolus capreolus, but it was in fact a giraffid, but not on the lineage to *Giraffa*.

This climacocerid must have been remarkably successful. It is said they lived in large herds (Hendey 1982) and were widespread throughout Africa. Fossils of other climacoceratid species have been found at Fort Ternan in Kenya (*C. gentryi*) (Gentry 1970), estimated age 14 Mya (Churcher 1970), at Arrisdrift in Namibia (Hendey 1978), dated about 17 Mya (Gentry 1994), and at Nyakach, Kenya, dated to 15 Mya (Thomas 1984). The Arrisdrift climacoceratid was about 20% larger than either the Koboko or Fort Ternan species. It lived in a forested riverine habitat and could have been a regional variant isolated from its eastern and northern African relatives by the southern African river systems (Hendey 1978). The other animals measured about 1.5 m in height and had large ossicones resembling antlers. *Climacoceras africanus* had ossicones resembling tall thorn-covered plant stems, while the ossicones of *C. gentryi* resembled thorny crescents. All species have characteristics that link them to giraffids generally and their sister group the Canthumerycidae specifically. However, although having features that indicate their closeness to giraffes, they are not on the lineage that leads to modern giraffes. It is more likely that *Climacoceras* gave rise to a sister group of giraffes, the Sivatheriinae.

Sivatheres (from the Hindu god Shiva – meaning 'Shiva's beast') were as big as elephants, massive and heavily built, short-legged, short-necked, with large and ornamented horns (ossicones) (Fig. 2.2b). They ranged throughout Africa to southern Asia (mostly India). The African species may have become extinct as recently as 6000 years ago, as depictions that greatly resemble sivatheres are known from ancient rock paintings in the Sahara desert (Colbert 1936). Tooth structure and tooth wear show that *S. hendeyi* (a southern African species) was brachyodont and probably a bulk grazer/browser (Franz-Odenaal & Solounias 2004). Their centre of origin was Asia in the early Miocene, and they evolved via *Prolibytherium magnieri* into two successful species.

The first was *Sivatherium giganteum*, the terminal Asian form, which became extinct in the early Pleistocene, and *S. maurusium*, which was widespread in Africa. *Sivatherium maurusium* was originally described as *Libytherium*, and this explains the name *Prolibytherium*, the ancestor of *Libytherium*.

Canthumerycidae

The earliest known giraffine ancestor is *Canthumeryx sirtensis* (originally *Zarafa zelteni*). It was discovered near Gebel Zelten escarpment, in Libya, an area that is now desert but at the time that *Canthumeryx* lived was flourishing savannah (see Chapter 1). The fossil fauna of Gebel Zelten appears to have a date range of 15–25 Mya (Gentry 1994; Hamilton 1973). Drake *et al.* (1988) suggest a date of 17.8 Mya for the origin of *Canthumeryx*, using a molecular clock, informed by cytochrome *b* and kappa casein gene sequences.

Canthumeryx was a medium-sized, slender antelope about the same size as a fallow deer (*Duma duma*) (Hamilton 1973, 1978). Importantly, it had the characteristic bilobed giraffoid lower canines. Hamilton (1978) suggests that this feature would facilitate the stripping of foliage from browse. Its limbs were about 85–100 cm long, and its shoulder height could therefore have been about 1.5 m. It had simple, unbranched horns that projected horizontally to the side of the head. Like its gelocid ancestor, it seems to have been very similar to a lightly built, medium-sized, slender-limbed gazelle.

Related and later species have been discovered throughout the Middle East, in Iraq and Saudi Arabia and Greece, and these species existed 15–18 Mya. These include *Injanatherium* (Fig. 2.2c), which flourished in the mid-Miocene in Saudi Arabia and in the late Miocene in Iraq (Morales *et al.* 1987), and *Georgiomeryx* from Greece (De Bonis *et al.* 1997). *Georgiomeryx* was a direct descendant of *Canthumeryx*, had flattened supraorbital horns, and its fossils have been dated to 15–16 Mya (De Bonis *et al.* 1997). Significantly, *Injanatherium* had two pairs of

horns and the distribution of its fossils suggests that it occupied a more easterly part of the southern European biome, while *Georgiomeryx* had migrated more westwards.

While *Canthumeryx* and its relations clearly are at the base of the *Giraffa* line, they existed 10–15 My before the first appearance of the genus *Giraffa* and clearly did not have a giraffe-like shape. They also appear to have become extinct towards the early middle Miocene, about 14 or 15 Mya. The 7–8 My gap between the Canthumerycidae and the appearance of the first undoubted giraffes is filled by the Palaeotraginae.

Palaeotraginae

The Palaeotraginae arose in the mid-Miocene, African-Arabian fauna, from an ancestral canthumerycid stock. The date of this radiation is variously estimated at 12–17 Mya by DNA analysis (Allard *et al.* 1992; Hassanin & Douzery 1999). The Palaeotraginae contains three genera: *Giraffokelyx*, *Palaeotragus* and *Samotherium*.

In giraffe evolution, *Giraffokeryx* (keryx=herald) is a key species. Firstly, it has all the attributes of a giraffe ancestor. Second, its features straddle its Palaeomerycine antecedents and the Palaeotraginae assemblage that seems to have arisen from them. *Giraffokeryx* was first identified by Pilgrim (1911) from a number of teeth and mandibles found in the Chinji deposits of Pakistan, a deposit variously dated to 11–16 Mya (Matthew 1929; Simons *et al.* 1971) (Palaeobiology database: <https://paleobiodb.org/#/>). Fossil remains have also been found in India, Nepal, Russia and again in Pakistan (Bhatti *et al.* 2012). It was a medium-sized member of the Giraffidae distinguished by its two pairs of horns (ossicones). However, reconstructions of it differ. Colbert (1935a) concluded that it had an elongated neck and drew it as a small giraffe. Savage and Long (1986) show it looking more like an okapi, but still with an elongated neck. This resemblance to the 'living fossil' okapi (Colbert 1938; Joleaud 1937) might in fact be quite accurate. Both these authors

believe that the okapi is a persistent, little changed palaeotragine that has survived by occupying a forest refuge niche unchallenged by other species.

Palaeotragus sp. were medium-sized giraffids with slightly elongated legs and neck. The skull was elongated and broadened, especially between the horns (Forsyth Major 1891), but apparently it did not have the sinuses of later *Giraffa*. Their geographic range appears to have been immense since they have been found from East Africa (Churcher 1970) to Mongolia (Colbert 1936). Churcher (1970) described the earliest fossils recovered from a deposit dated at 14 Mya (Retallack *et al.* 1990) in eastern Kenya, and named it *Palaeotragus primaevus*. At the Kenyan site, near Lake Victoria, this species was so common that it could be described from 243 specimens. It had gracile long limbs, and its dental formula was $I^{0/3} C^{0/1} P^{3/3} M^{3/3} = 32$ which is the same as *Giraffa*. Although the lower canine was bilobed, the teeth were primitive, slim and brachydont. The shape of its muzzle was similar to that of the okapi and giraffe (Solounias & Moelleken 1993), and its teeth show microwear patterns of pits and scratches, similar to those found in modern giraffes (Cerling *et al.* 1997). It therefore appears to have depended almost completely on browse for food and water (Cerling *et al.* 1991, 1997). Churcher (1970), following the assumptions of the time, regarded *P. primaevus* as an offshoot of the Asian palaeotragine stock that had reached Africa by migrating across the Suez isthmus as sea levels fell between 23 and 16 Mya. However, both Hamilton (1978) and Gentry (1994) regard *P. primaevus* as being close to or identical to *Giraffokeryx punjabiensis* and this linkage provides the continuum between *Giraffokeryx*, which was becoming extinct, and the palaeotragine assemblage that filled the niche created.

The subsequent discovery of numerous other palaeotragine fossils led Heintz (1975) to suggest that palaeotragines migrated from a north African centre of origin, sometime before 12 Mya, into eastern Eurasia (Mongolia), cen-

tral Europe (Greece, Turkey, Crimea, Iraq), western Europe (Spain, Portugal), Africa and India, but not temperate northern Europe. The fossil records described by Crusafont-Pairo (1952) in Spain, Arambourg (1963) in North Africa, Heintz (1975) in North Africa and Greece, Churcher (1970) in East Africa, Pilgrim (1911), Matthew (1929), Bohlin (1926, 1935) and Colbert (1935b) in the Pakistan Siwalik deposit, Pilgrim (1934) and Colbert (1936) in Mongolia, and Ciric and Thenius (1959) in Yugoslavia all support this hypothesis. Eurasian paleotragines did not have *Giraffa*-like morphology and are thought to be completely unrelated to *Giraffa* (Gentry 1994). They probably form an independent lineage and assemblage of animals that are a sister group to the paleotragines that ultimately produced modern giraffes. In Africa, two *Palaeotragus* sp. are thought to have existed: *P. primaevus*/*Giraffokeryx* and *P. germaini*. The latter species was a paleotragine first described by Arambourg (1959) and known from Moroccan, Algerian and Tunisian fossil deposits of the late Miocene and is therefore a later species than *P. primaevus* (*Giraffokeryx*). It was of large size and resembled *Giraffa* in its elongated neck and limbs. The evolutionary line of these species could therefore be *Canthumeryx* > *Injanatherium* > *Giraffokeryx* > *P. primaevus* > *P. germaini*. The propensity to generate *Giraffa*-like features can be seen even more in the third palaeotragine genus, *Samotherium* (beast of Samos).

Samotheres differ from *Palaeotragus* sp. by being much larger and having longer faces with a typical giraffe profile (Churcher 1978). Their ossicones were supraorbital and therefore further forward than they are in giraffes. The skull roof was broad and inflated by 'pneumatic cavities' (Forsyth Major 1891). Such cranial sinuses are characteristic of living giraffes and enable the skull to be large without adding weight, an important prerequisite if you have a long neck. Their teeth are hypsodont, as they are in giraffes, but in other ways resemble those of *Palaeotragus*, showing the close relationship

between them (Hamilton 1978). *Palaeotragus* sp. appear to have become extinct around 9–10 Mya. Samotheres then became the dominant palaeotragines (5–9 Mya) (Churcher 1970; Gentry 1994), probably occupying the ecological niche left vacant by the extinction of *Palaeotragus* species. Although several samotheres ‘species’ have been described, they are likely to be geographical variations or subspecies. Present-day giraffes, like all species, show a degree of intraspecies variation, and this is frequently overlooked by the describers of fossil material. Just three species seem to be sufficiently distinct to warrant separation. These are *S. africanum*, *S. boissieri*, from the Greek island of Samos (= *S. sinense* = *S. tafeli*, from China) and *S. neumayri* (that resembles *S. sinense* (Hamilton 1978)), an early Pliocene form from Iraq and China (Churcher 1970).

The Eurasian samotheres do not appear to have left any descendants and did not really have the morphology that makes them a strong candidate for the ancestors of *Giraffa*. However, *S. africanum* did have the required morphology, although its origins are less clear than those of the Eurasian species. A likely origin of *S. africanum* is *Palaeotragus germaini*. Harris (1987b) noted that the skeleton of *P. germaini* had the same dimensions as that of *S. africanum* and differed only in that *S. africanum* had larger ossicones. He concluded that *P. germaini* was *S. africanum* or at least a recent antecedent. *S. africanum* fossils have been recovered from Algeria, Tunisia and Egypt, and possibly Kenya (Churcher 1970). Mitchell and Skinner (2003) conclude that its giraffe-like features, and chronological age, make it a logical antecedent of the *Giraffa* lineage.

A fossil that could have evolved from *S. africanum* was *Bohlinia attica*. It had appropriate, progressive, giraffe-like morphology and could therefore be regarded as the immediate ancestor of giraffes. The earliest discovered fossils of *Bohlinia* were so similar to both extant and fossil giraffes that they were initially classified as *Giraffa attica* by Gaudry and Lartet (Forsyth

Major 1891). Bohlin (1926) gave a more complete description, from fossils found in Pikermi in Greece, about 100 miles south west of Athens. These Pikermi fossil deposits are estimated to be 7–9 My old (Agusti *et al.* 1999), so the chronology of *Bohlinia* means that it occupies the right time-frame for an immediate ancestor of *Giraffa*. Bohlin in fact called it *Orasius* (derived from a corruption of the Latinised form *Oraflus* for giraffe), but both Matthew (1929) and Simpson (1945) suggested that it be called *Bohlinia*. In fact, the position of *Bohlinia* as an intermediate form between its palaeotragine-samotheres ancestors and *Giraffa* is confirmed by the many traits that it has in common with *Giraffa*. It has long legs and a long neck, similar ossicones, the characteristic bilobed lower canine, and selenodont molars with rugose (ridged) enamel. Harris (1976c) also remarked that although it was smaller than early African *Giraffa* (e.g. *G. gracilis*), *Bohlinia* resembled them closely. From an examination of ‘adult’ fossils in the Athens Museum, it appears that there were two size classes, suggesting sexual dimorphism (Roussiakis & Iliopoulos 2004). Over the next few million years, it is suggested that *Bohlinia* gave rise to a series of ‘rapid’ adaptive radiations, which finally led to the emergence of the genus *Giraffa* (Mitchell & Skinner 2003).

If *Bohlinia* was the *Giraffa* ancestor, then its descendants must have migrated to India in the late Miocene or early Pliocene, the time when the first *Giraffa* species, *G. priscilla*, appeared. However, the fossil remains of this species amount to only three molar teeth and a fragment of mandible (Pilgrim 1911). No postcranial skeleton is known. A second Asian species was *G. punjabiensis* which, according to Harris (1991), is the oldest known and unmistakable *Giraffa*. It is dated to approximately 7 Mya or the late middle Pliocene. *G. punjabiensis* had features similar to those of *Bohlinia* but is regarded as being an advanced form closely related to modern giraffes (Harris 1976c) and generically distinct from *Bohlinia*, especially with respect to its brachydont, less selenodont but rugose

molars. It was smaller than the early African *Giraffa* and was probably the ancestor of the later Asian *Giraffa*. It was extinct by the end of the Pliocene. The descendent of *G. punjabiensis* and the climax of the Indo-Asian line was *G. sivalensis*. It was first described by Falconer and Cautley (1843–1844), and lived in the early Pleistocene (Churcher 1978). In body size it was larger than extant giraffes and its teeth, although larger than those of *G. punjabiensis*, were smaller than those of extant giraffes. It was extinct by the mid-Pleistocene.

It seems likely that a later radiation from *Bohlinia*, probably by a south-westerly migration into Ethiopia and southwards, produced at least five described African ‘species’ (*G. gracilis*, *G. pygmaea*, *G. stillei*, *G. jumae* and *G. camelopardalis*), of which only one has survived.

The African lineage

It seems clear that Africa provided very suitable habitats for a ‘giraffe’ niche. *Giraffa* anatomy, physiology and behaviour fitted the ‘savannah biome’ well. Unfortunately, the phylogenetic sequence within Africa is confused. However, to make any sense of the existing data, it must be assumed that the history of *Giraffa* in Africa started about 7 Mya with an arrival in Ethiopia across the Arabian–African land bridge. This conclusion is rendered necessary by the presence of a *Giraffa* in a fossil deposit in the northern Kenya Rift Valley, dated to 7.0–5.4 Mya (Pickford 1975). This ancestor may have been a derivative of one of the Asian *Giraffa*, in particular the contemporary *G. punjabiensis*, that entered Africa by migration. Kurten (1957), for example, showed that ‘an unchecked spread of some 1000 km in a century would seem a moderate estimate for most larger mammals’; thus, both the chronology and the time scale required for such a migration are right. Mitchell and Skinner (2003) consider that the absence of a suitable migratory route makes it unlikely. Moreover, they point out that the anatomy of

G. punjabiensis is different and more advanced than that of African *Giraffa*, and in fact Churcher (1978) regarded *G. punjabiensis* as similar but not in the same lineage.

Giraffa gracilis

Because migration of an Asian form seemed unlikely, Mitchell and Skinner (2003) suggest that the alternative solution is that the African *Giraffa* arose from Pliocene *Bohlinia*. The Pliocene biome (named after the fossil site at Pikermi in Greece) reached its peak about 8 Mya, in the Mediterranean, at which time the climate was dry. Constructing a lineage on this basis, Mitchell and Skinner (2003) believe that the earliest African species of *Giraffa* was *G. gracilis*, which has at various times been synonymised with *G. stillei* and *G. pygmaea*. *Giraffa gracilis* was a late Miocene to early Pleistocene species with a range restricted to East Africa (Hamilton 1978; Harris 1976c). It is abundant in the Laetoli deposits of Kenya dated at 5–2 Mya (Harris 1987a), at East Rudolph (Harris 1976b) another Pliocene/Pleistocene site, the Serengeti (Harris 1976c) and at Olduvai (Leakey 1965), but not with any certainty in other parts of Africa. Although the dimensions of its fossils vary, some examples of *G. gracilis* suggest that it was of comparable proportions to *G. camelopardalis*, although probably half the size (Arambourg 1947; Harris 1987a). It was larger than *G. pygmaea* and *Bohlinia* (Harris 1976c), but more lightly built than either *G. camelopardalis* or *G. jumae*.

In fact, the status of the three smaller ‘species’ is unclear. An Ethiopian (Omo) fossil form, identified by Arambourg (1947) and called *G. stillei*, came from a fossil deposit of Pliocene/Pleistocene age and known to be 3.8–1.8 My old (Harris 1976c). However, Harris (1976c) argued that *G. gracilis* and *G. stillei* are in fact the same species. Except for more rugose enamel and possibly the smaller size of *G. stillei*, the two cannot be separated on the fossil evidence. An even smaller ‘species’ is *G. pygmaea*, which is a rare Pleistocene form at least at Lake Rudolph (Harris 1976b, c).

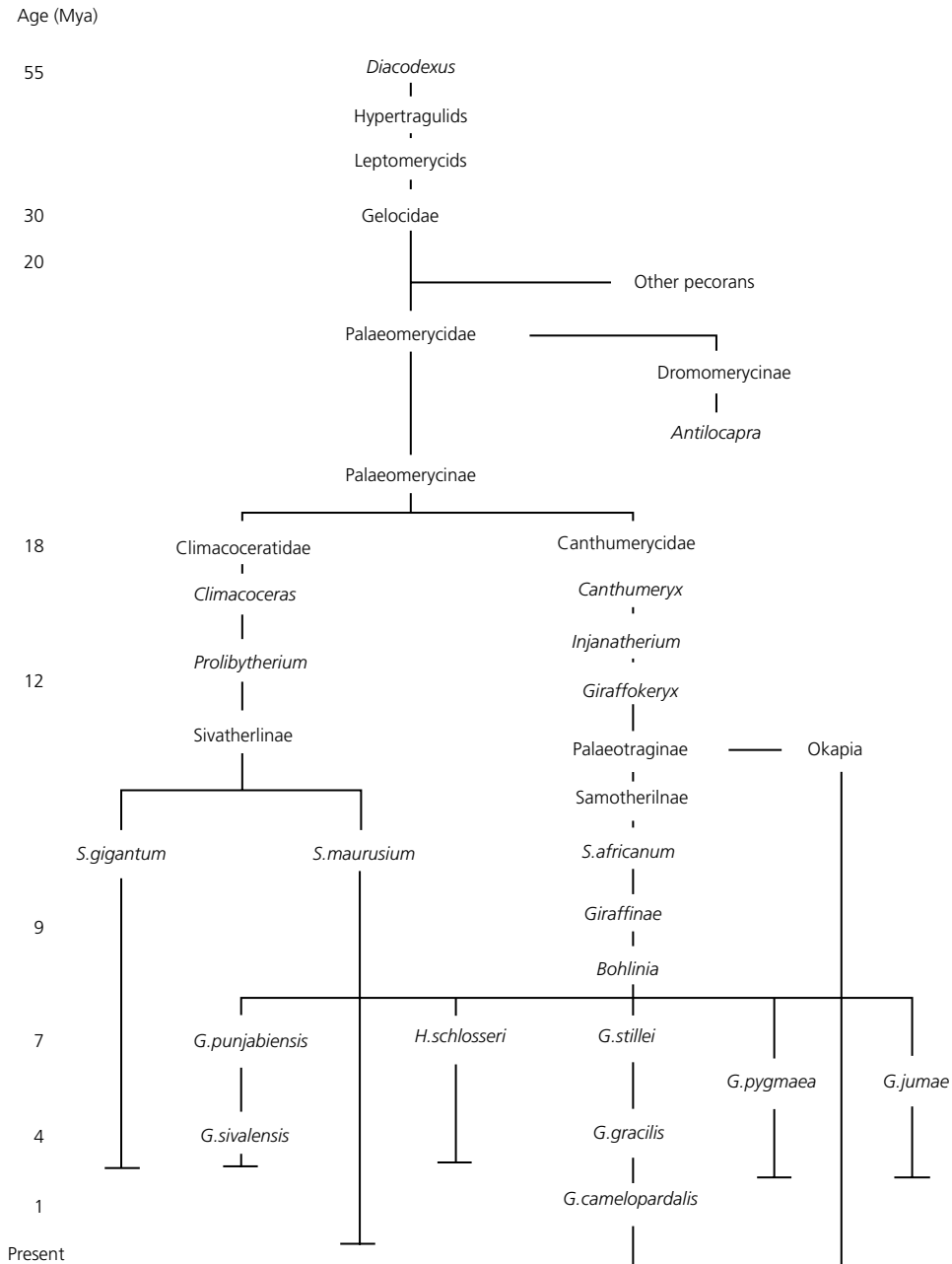


Fig. 2.4 A possible phylogeny of giraffes. Source: adapted from Mitchell & Skinner (2003). Reproduced with permission of Taylor & Francis.

Harris implied that Arambourg's Omo specimen of 3.5 Mya could in fact be *G. pygmaea*. Confusingly, he at first thought all three species the same (Harris 1987a) but later separated *G. pygmaea* from the other two (Harris 1991). Mitchell and Skinner (2003) suggest that *G. stillei* may have been ancestral to *G. gracilis* and that *G. pygmaea* was a contemporary, smaller 'variant', perhaps a subspecies. Harris's (1991) suggestion, based on Pellew's (1983b) analyses of giraffe feeding ecology, is that *G. pygmaea* was a valley bottom, riverine woodland 'variant', while *G. gracilis* (and presumably *G. stillei*) was a ridge top *Acacia* woodland feeder.

Of all the African *Giraffa*, the age of *G. jumae* is most uncertain. It could be as old as 6.5 My (Pickford 1975). Churcher (1978), summarising information known at the time, said it was present in East and South Africa from the late Miocene to mid-Pleistocene. Hendey (1982) and Harris (1976a, 1991) agree that it was found at the Langebaanweg fossil deposit, in the far south of South Africa, around 4.5 Mya. These fossil deposits were formed towards the end of the Mediterranean (Messinian) salinity crisis as the polar icecaps receded (Hendey 1981), and dated to 6.6–5.2 Mya (Hsiu *et al.* 1977). The area affected would have included North Africa, and *G. jumae* may have reached the Langebaanweg during this crisis, and perhaps even as a consequence of it.

Leakey (1965) described its morphology on the basis of a skull and other fragments obtained from Rawi Gully, southwestern Kenya. A second specimen found in 1963 was described by Leakey in 1970, and he concluded *G. jumae* was more heavily built than *G. camelopardalis* (Leakey 1970). Both *G. jumae* and *G. gracilis* appear to have become extinct about 1 Mya, the

time that *G. camelopardalis* makes its appearance in the fossil record. Indisputable *G. camelopardalis* fossils occur for the first time at 1 Mya at West Turkana in East Africa (Harris 1991). Mitchell and Skinner (2003) suggest that this 'simultaneous' disappearance of two species, in favour of one, has several possible explanations. Harris (1987a) suggested that *G. jumae* could have evolved into *G. camelopardalis*, mainly by a reduction in its size. Alternatively, an increase in size of *G. gracilis* would have achieved the same outcome. As *G. gracilis* has a more similar morphology to *G. camelopardalis* (Harris 1976c), *G. gracilis* might be considered the better option as an ancestor. The changing climate between 8 and 6 Mya (Cerling *et al.* 1998), that had induced the development of grasslands and made the African woodland savannah a habitat ideal for giraffes, could have restricted the feeding niches on which the three then extant *Giraffa* depended. Finally, if *G. jumae* was no more than a variant, as suggested by Harris, then *G. camelopardalis* could also be a successful product of interbreeding between *G. jumae* and *G. gracilis*. Of the evolutionary possibilities, the best conclusion is that *G. camelopardalis* is derived from *G. gracilis* rather than *G. jumae*. A possible phylogeny of it is shown in Fig. 2.4.

Giraffes evidently found the African environment congenial and *G. camelopardalis* was clearly found in prehistoric and historic time from the north to the south of the continent. Lydekker (1904), who reported the results of 20 years of arduous data collection, that had the aim of classifying *G. camelopardalis* by variations in skin markings, ossicones and geographical distributions, was able to distinguish 11 subspecies. This modern distribution of the only extant giraffe species is the subject of the next chapter.

CHAPTER 3

Present distribution and geographical races

We know that the giraffe has been recorded in Africa from prehistoric times because of the rock paintings and engravings that are found from Morocco, Algeria and Libya in the north, through Ethiopia, Somalia, Kenya and Tanzania in the east, to Botswana, Zimbabwe, Namibia and Mozambique in the south (see Chapter 1). However, the first formal observation of extant giraffes in Africa was made on 28 November 1663, by Pieter van Meerhoff (Godeem Olsbergen 1951) about 120 miles south of the Orange River in Namaqualand (an arid region of Namibia and South Africa, extending along the west coast for 970 km). Following this, at the close of the 17th century an English scientist, John Ray, produced a systematic dictionary in which he placed the giraffe in the genus *Cervus*, along with deer, sheep, goat and others (Spinage 1968a). In the early to mid 1700s, taxonomic classification became the thrust of scientific research, encouraged by Carl Linnaeus's publication of his binomial system in *Systema Naturae* in 1735, and its definitive 10th edition of 1758 (Linnaeus 1758). Unfortunately, Linnaeus followed Ray's classification and placed the giraffe in the genus *Cervus*, as he thought it was related to the deer family because of its antler-like horns, naming it *Cervus camelopardalis*. This was in many ways strange because even Ray had been uncertain of the giraffe's taxonomic position: 'The Camelopard seems to be a unique animal, called Giraffa by more recent writers'. In 1762 the French zoologist Mathurin Jacques

Brisson placed it in the new genus *Giraffa*. He thought that the horns were permanent, and this difference merited its placement in its own genus (Brisson 1762). However, neither Brisson nor Linnaeus had ever seen a giraffe. In 1761 Captain Hendrik Hop, a former officer in the Stellenbosch Cavalry, led an expedition into Namaqualand. On 5 October, just north of the Orange River, they saw their first giraffes. A female was killed and a young one captured. Of the dead female he says:

The height from hoof to head was seventeen feet, and the proportion of body length to height was as one to two and a half. Moreover on account of this shortness of body in comparison with its other members and because of its extraordinary movements, it is unthinkable that this animal can be employed for any useful purpose.

Five days later the young giraffe died, and on 16 October they shot another giraffe, a male.

In 1764, the skin of the young animal and a rough sketch were sent by the Governor of the Cape Colony, Ryk Tulbagh, to Professor Allamand of Leiden University, Holland. From the skin and the sketch, Allamand made a drawing that was published in Buffon's *Histoire Naturelle* (Fig. 3.1a). In 1769, Captain Philip Carteret took a copy of the drawing to England where it was published by the Royal Society of London, and this drawing became the image that entered the encyclopaedias of natural history emerging at that time (Fig. 3.1b). In 1780, more skins, drawings, skeletons and notes were sent to Holland by Colonel Robert



(a)



(c)



(b)

Fig. 3.1 Early drawings of giraffe. (a) Allamand's giraffe from Buffon's *Histoire Naturelle* of 1770. (b) Captain Carteret's drawing of the Cape giraffe, 1769. (c) William Paterson's giraffe from *Narrative of Four Journeys into the Country of the Hottentots and Caffraria*, 1789. Source: adapted from Spinage (1968a).

Jacob Gordon, and were taken to England by Lieutenant William Paterson (1789). Other specimens were sent to France by François Le Vaillant, and to England by William Burchell.

Although the specimens sent to England were largely ignored, Paterson did provide what is regarded as the first really good picture of a giraffe (Spinage 1968a). It was the frontispiece

of his *Narrative of Four Journeys into the Country of the Hottentots and Caffraria 1777–1779* (Fig. 3.1c).

Following in the footsteps of Lieutenant Paterson in the Cape was the French naturalist François Le Vaillant. During his second journey (1783–1785) to the banks of the same Orange River, he recounts how he encountered a full-grown giraffe, hunted it and killed it. Later he performed some on-the-road taxidermy (Le Vaillant 1795).

I commenced my chace at sun-rise, in hopes of finding some kind of game to furnish us with food. After walking some hours, on turning a hill we perceived seven giraffes, which my dogs instantly attacked. Six took flight together; the seventh, intercepted by my dogs, fled a different way.

... I had scarce turned the hillock, when I perceived him surrounded by the dogs, and endeavouring by forcible kicks to drive them off. I had only the trouble to alight, and brought him to the ground with a single shot. Delighted with my victory, I returned to call my people, that the animal might be skinned and cut to pieces. While I was looking for them, I saw Klaas Baster, who with eagerness made signs to me, which at first I did not understand. Looking, however, towards the spot to which he pointed, I perceived with surprise a giraffe standing under a large ebony tree, and assailed by my dogs. Supposing it to be another, I ran towards it; but it was the one I had just before shot, which had in reality recovered its feet; but the moment I was preparing at it a second time, it dropped down dead.

Le Vaillant sent the stuffed giraffe to Louis XVI. Unfortunately, this gave the impression that he was a royal lackey, and on his return to Paris he was imprisoned, only escaping execution by the timely death of Robespierre.

Although these southern specimens were the first to be examined by European naturalists, live specimens were not seriously examined until the early 19th century. These came from North Africa. The French zoologist Étienne Geoffroy Saint-Hilaire, following his study of Le Vaillant's southern specimen in the Paris Museum, and observation of the living northern giraffe in the collection of King Charles X (Allin 1998) (see Chapter 1), decided that the 'northern' and 'southern' forms represented

different species. Although he never published a formal paper on the topic, it is notably that the Paris Museum labelled the two forms with different specific names, *senmaarensis* and *capensis*. This view was probably endorsed by Richard Owen (1841) when he examined the skulls of Cape and Nubian giraffes. He pointed out certain characters in the cranium of the Cape giraffe as distinguishing it from the Nubian giraffe, and seems to recognise the validity of the two 'species'. This was also the view of Swainson (1835) who quoted the observations of Eduard Ruppel:

... while the Camelopardalis antiquorum Sw., or the northern giraffe, has recently been detected by Mr. Ruppel, whose elaborate observations have enabled us to characterise it as a distinct species from the giraffe of Southern Africa (C. australis Sw.).

However, other people disagreed. Ogilby (1837), using characteristics he felt important for the 'œconomy' of ruminants (such as the presence of horns, the form of the upper lip and the presence of interdigital pores), saw no difference between *C. aethiopicus* (northern) and *C. capensis* (southern). Similarly, Carl Jakob Sundevall (1842), a Swedish zoologist, considered the several specimens he examined as simply variations of the same species, saying that 'The only differences seem to arise from climate'. He noticed that the Cape giraffe had longer hairs, probably because of the cold climate. However, in the same year, René Lesson (1842), a French surgeon and naturalist, disagreed with Sundevall and agreed with Geoffroy Saint-Hilaire that there were two species which he called *Camelopardalis giraffa* (from the north) and *C. capensis* (from the south) (Dagg & Foster 1982). Of course, in the mid 19th century specimens of giraffe were still rather limited, which may have contributed to this division among 19th-century naturalists as to whether there was one or two species of extant giraffe. However, even as Africa was opened up by hunters and explorers, and skins became more available, the taxonomic position still remained uncertain. In fact, even at the turn of the century, de Winston (1897)

reviewed the taxonomic status of the giraffe, and considered the lack of available specimens to be 'the reason for the nomenclature of the two species being left in a very unsettled state'. He suggested the following reason:

That so few specimens of this extraordinary animal find their way to this country (meaning the UK) is no doubt due to the value set upon the hides in the countries where they are obtained, by the natives for making shields and by the settlers for 'sjamboks', or whips, the skin of the neck of a bull giraffe standing second only to Hippopotamus hide in value.

Although de Winston uses 'forms' and 'species' almost interchangeably throughout his paper, he does finally describe them as two species, and one subspecies, under the headings of *Giraffa camelopardalis*, *G. c. reticulatus* and *G. capensis*, from the 'northern', 'eastern' and 'southern' areas of Africa. He also cites a personal communication from Arthur Henry Neumann (hunter, soldier and explorer) who noted that the two 'forms' (southern and northern) were not geographically separated, yet had no intermediate forms. '... and therefore both must be given full specific rank.' The situation was further confused because certainly the so-called northern species was not always the same entity. For example, the situation was potentially confused by de Winston's use of a 'northern' specimen from Somalia, rather than from Sennar (Senaar), on the Blue Nile in Sudan (where Charles X's giraffe came from, and the type locality for the species). The de Winston specimen appears to have been what we now call the reticulated giraffe, since Thomas (1894) remarks that the pelage spots were 'large, sharply defined, and only separated from each other by narrow pale lines'. Later Thomas (1901) suggested that the reticulated giraffe should be recognised as a distinct species, since he found no evidence of intermediate forms between it and neighbouring northern forms. He further suggested that this northern form connected, through intermediate populations, into the southern form, making the southern form a subspecies. Thomas (1901) also recognised two

species, but they were different from those previously proposed by the Saint-Hilaire, Owen and Swainson set of commentators.

The foundation of our present giraffe classification was finally laid down by Richard Lydekker (1904) of the British Museum. Not able to identify any of the Museum specimens with previously named forms, *stricto sensu*, he decided that a complete revision of the giraffe group was necessary. Using drawings, photographs, skins and live animals, and noting variations in skin markings, ossicones and geographical distributions, he recognised two species: the netted giraffe *Giraffa reticulata* (Somalia) and the blotched giraffe *Giraffa camelopardalis*. The latter species he divided into 10 subspecies: *G. c. typica* (Nubian giraffe, Ethiopia), *G. c. antiquorum* (Kordofan giraffe, Sudan), *G. c. peralta* (Nigerian giraffe, Nigeria), *G. c. cottoni* (South Lado giraffe, Uganda), *G. c. tippelskirchi* (Kilimanjaro giraffe, western Kenya), *G. c. rothschildi* (Baringo giraffe, eastern Kenya), *G. c. congoensis* (Congo), *G. c. angolensis* (Angola), *G. c. wardi* (northern Transvaal, South Africa) and *G. c. capensis* (Cape giraffe, South Africa) (Fig. 3.2a) (Seymour 2001). Lydekker (1911) later named two more subspecies. He proposed another form of the blotched giraffe, which he named *G. c. thornicrofti* (Thornicroft's giraffe, Zambia) and he split his reticulated species into two subspecies; the original reticulated giraffe became the subspecies *G. r. reticulata* and a new one, *G. r. nigrescens*, was proposed. Although Lydekker's classification was based largely on pelage patterns plus dubious ossicone variation, and his geographical ranges were restricted and sometimes incorrect, his work was based on 20 years of arduous and unrepeatable data collection, and his ideas still form the basis of our modern classification.

In 1939, Ingo Krumbeigel examined Lydekker's (1904 and 1911) subspecies more adequately by using larger sample sizes. He based his classification on the pelage pattern of the giraffe, using many skins and a great number of photographs. He ignored pelage colour, since this changes with age, and with death and treatment of the skin

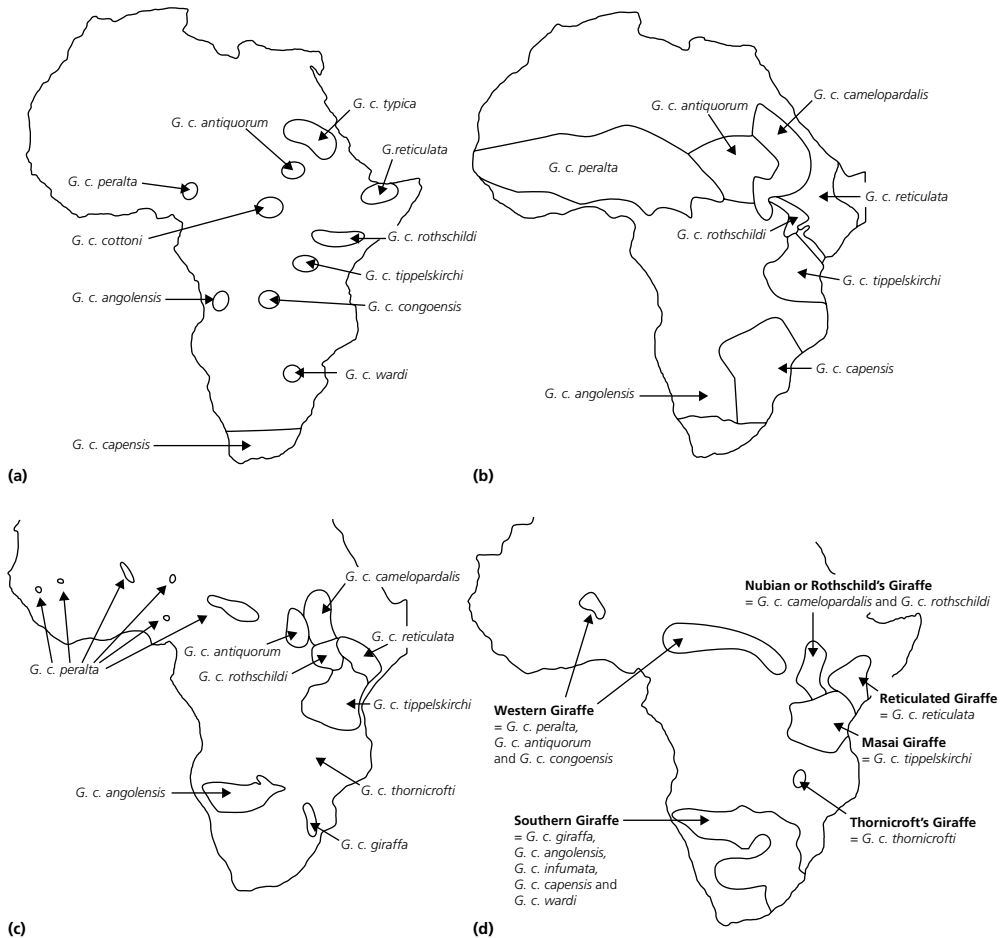


Fig. 3.2 Historical subspecies ranges proposed by various authors. (a) After Lydekker 1904, (b) after Krumbeigel 1939, (c) after Dagg 1971, (d) after East 1998. Source: Seymour (2001). Reproduced by kind permission Russell Seymour.

(but also because his photographs were black and white). Notably, he did not use the pattern of 'blotches' on the face and head, which he found too variable, even though Lydekker had used this as one of his main criteria. Krumbeigel's analysis resulted in two changes. Firstly, he only recognised one species of giraffe, with two subspecies. However, within these two subspecies, many of Lydekker's subspecific names can be recognised as 'infrasubspecies'. These 'infrasubspecies' were given a fourth Latinised name by Krumbeigel. Secondly, he extended Lydekker's subspecies ranges and consequently

presents a more realistic range map in his monograph (Fig. 3.2b) (Seymour 2001). This appears to have remained the basis for contemporary range maps. Since 'infrasubspecies' are not consistent with the International Commission on Zoological Nomenclature (ICZN) (1999) protocol, they usually 'revert' to the more traditional subspecies names in the literature. Out of Lydekker's 11 species/subspecies, Krumbeigel retained eight, although their indicated distributions on his map are more widespread, and sometimes quite different in geographical location to those of Lydekker.

In the 1960s, several biologists modified this giraffe classification. These were Dagg (1962b, 1968), Haltenorth (1962) and Ansell (1968). Ansell's classification was largely based on those of Dagg and Haltenorth. Dagg (1971) later updated her classification and until recently was the authority most frequently consulted for the status of giraffe taxonomy. The result of this 'decade' of modification was summarised by Dagg in 1971 (Fig. 3.2c) (Seymour 2001) and endorsed by Dagg and Foster (1976). They recognise one species, with nine subspecies (as did Ansell 1968), with *Giraffa camelopardalis camelopardalis* as the nominate subspecies. In zoological nomenclature, when a species is split into subspecies, the originally described population is retained as the 'nominate subspecies', which repeats the same name as the species. The list (I will call this 'Dagg&Foster76') is as follows, along with the original naming authorities, and the commonly accepted name in bold. Also included (in brackets) are what are regarded as previous names for the same subspecies (synonyms).

- *G. c. camelopardalis* Linnaeus 1758 **Nubian** (*bituigum* Duvernoy, *aethiopica* Ogilby and *typica* Bryden).
- *G. c. antiquorum* Jardine 1835 **Kordofan** (*senariensis* Trouessart and *congoensis* Lydekker).
- *G. c. peralta* Thomas 1898 **West African**.
- *G. c. reticulata* de Winton 1899 **Reticulated** (*hagenbecki* Knottnerus-Meyer, *nigrescens* Lydekker and *australis* Rhoads).
- *G. c. rothschildi* Lydekker 1903 **Rothschild's** (*cottoni* Lydekker).
- *G. c. tippelskirchi* Matschie 1898 **Masai** (*schillingi* Matschie).
- *G. c. thornicrofti* Lydekker 1911 **Thornicroft's**.
- *G. c. angolensis* Lydekker 1903 **Angolan** (*infumata* Noack).
- *G. c. giraffa* Schreber 1784 **Cape** (*capensis* Lesson, *australis* Swainson and *wardi* Lydekker).

At this juncture it is important to point out that none of these authors actually examined specimens or undertook an extensive alpha

taxonomic¹ analysis in order to reassess the validity of these giraffe subspecies. In fact, Ansell (1971) later stated that his list of subspecies 'should be regarded as provisional'. Prophetically, the range described by Ansell for *G. c. rothschildi* (and, as a result, those of *G. c. reticulata* and *G. c. tippelskirchi*) was derived from Dagg's (1968) range map and is incorrect. It was later corrected by Dagg (1971). However, as Seymour (2001) has so rightly pointed out, these subspecies appear to be based on personal preference and this list of nine subspecies owes as much to the opinion of previous authors as to rigorous taxonomic appraisal. Nonetheless, these nine subspecies have become the 'accepted list' and are, for example, the nine given by the Giraffe Conservation Foundation (GCF), and the International Union for Conservation of Nature (IUCN) International Giraffe Working Group (IGWG 2012).

However, not all more recent authors agree on the status of this list. Kingdon (1979, 1997, 2004) lists only eight subspecies and his proposed list differed in three ways:

- the subspecies *antiquorum* was discarded, as all populations inhabiting the Sahelian zone, from Senegal to Sudan, were included in the subspecies *peralta*
- the woodland populations from Cameroon to Uganda were put in the subspecies *congoensis*
- possible hybrid populations were described in Cameroon between *congoensis* and *peralta*, and in Kenya between *congoensis* and *reticulata*.

As a consequence, *rothschildi* was not regarded by Kingdon as a valid subspecies. Intriguingly, in his *Pocket Guide to African Mammals* (Kingdon 2004), he anticipates to some degree the conclusions of later genetic studies and places these

¹The traditional term 'taxonomy' was originally used for what is now called alpha taxonomy, which deals mostly with species and subspecies, both fossil or extant. Relationships between higher ranking taxa are mostly the area of beta taxonomy, more commonly called systematics.

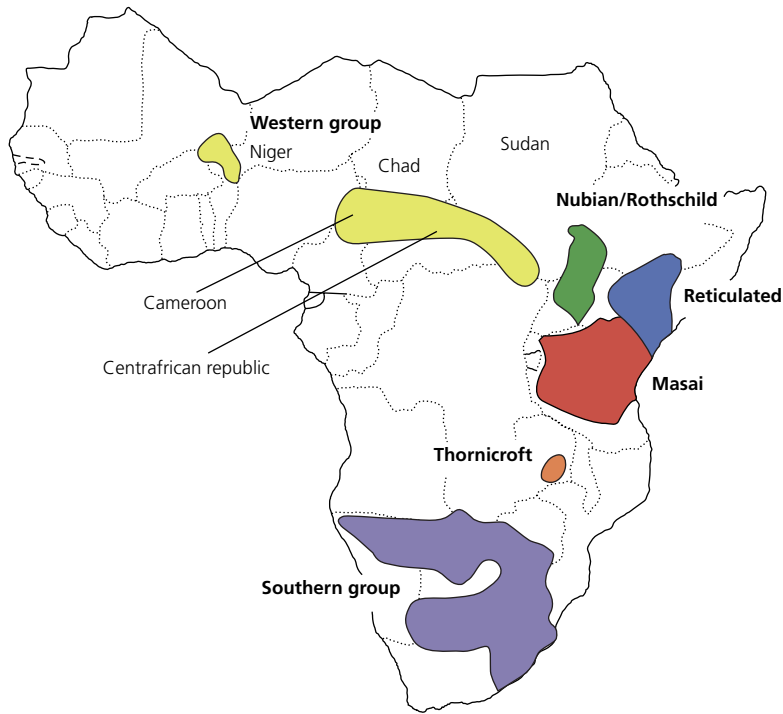
eight subspecies into four 'population groups': a 'Somali arid' group containing *camelopardalis* and *reticulata*, a 'Saharan group' containing only *peralta*, a 'Northern Savannah group' containing *congoensis* and *rothschildi*, and a 'Southern Savannah group' containing *tippelskirchi*, *thornicrofti*, *angolensis* and *giraffa*.

Rod East (1999), in the IUCN *African Antelope Database*, in which the giraffe and okapi were included, suggested only six 'subgroups', combining some of the traditional nine in the list of 'Dagg&Foster76' (Fig. 3.2d). These six were (1) the '**western giraffe group**' (*G. c. peralta* + *G. c. antiquorum*), (2) the '**Nubian giraffe group**' (*G. c. camelopardalis* + *G. c. rothschildi*), (3) the '**reticulated giraffe**' (*G. c. reticulata*), (4) the '**Masai giraffe**' (*G. c. tippelskirchi*), (5) '**Thornicroft's giraffe**' (*G. c. thornicrofti*) and (6) the '**southern giraffe group**' (*G. c. giraffa* + *G. c. angolensis*). Referring to the Dagg71 list, East says that 'Considerable uncertainty surrounds the validity and geographical limits of most of the described subspecies ...', he thought due to the lack of geographical barriers between supposed subspecies. However, he does acknowledge that his groupings are also '... arbitrary, like other treatments of giraffe subspecies'. Grubb (2005) also recognised six 'subspecies'. However, these were different to those of East. Grubb (2005) groups the western giraffe (*G. c. peralta*) in with *G. c. camelopardalis*, while East had included Rothschild's giraffe with the nominate subspecies. Six years later, Grubb increased the list once again (Groves & Grubb 2011), to eight. What's more, they are all classified as species, not subspecies. The list Grubb proposed was (1) **Angolan giraffe** (*Giraffa angolensis*), (2) **Kordofan giraffe** (*Giraffa antiquorum*), (3) **Nubian or Rothschild's giraffe** (*Giraffa camelopardalis*), (4) **Cape giraffe** (*Giraffa giraffa*), (5) **West African giraffe** (*Giraffa peralta*), (6) **reticulated giraffe** (*Giraffa reticulata*), (7) **Luangwa giraffe** (*Giraffa thornicrofti*), (8) **Masai giraffe** (*Giraffa tippelskirchi*).

Apart from the change in taxonomic level, the only difference between the 'Dagg&Foster76' list and this recent one is the inclusion of Rothchild's giraffe with the Nubian giraffe,

retaining East's idea on this taxonomic grouping, and changing the common name of *Giraffa thornicrofti*. One of the reasons for this recent increase in giraffe groups (interestingly, a virtual revival of 'Dagg&Foster76'), plus their frequent elevation to species rank, may be the newer 'molecular genetic' studies that are being carried out. For example, the recent book *Ungulate Taxonomy* (Groves & Grubb 2011) has changed the classification of hoofed mammals quite dramatically. Whereas traditional species lists relied on the 'Biological Species Concept' (which differentiates species on the basis of reproductive isolation, that is, a lack of interbreeding in the wild), Groves and Grubb use the 'Phylogenetic Species Concept', which separates species on the basis of heritable, usually molecular characteristics, that are consistently different between taxa. This approach tends to increase the number of species and reduce the number of subspecies, since any populations that can be differentiated on their molecular fingerprint are listed as separate species and those which cannot be so distinguished are grouped as a single taxon. Using this criterion, however, it must be pointed out that our species, *Homo sapiens*, would be reclassified as several new species. Nonetheless, we should now consider what these genetic results suggest, and what they add to our giraffe taxonomy story.

The first molecular survey of the subspecies of giraffe was by Hassanin *et al.* (2007). Their study material came from just 23 giraffe specimens, representing seven of the nine subspecies of *G. camelopardalis* in the list of Dagg and Foster (1976). Thornicroft's giraffe (*thornicrofti*) from Zambia and the Nubian giraffe (*G. c. camelopardalis*) from eastern Sudan and western Eritrea were not sampled. Some of their samples were taken directly from the wild, but 13 were taken from individual giraffes in zoos whose subspecies origin was known. Their analysis was based on a mitochondrial DNA (mtDNA) fragment of 1765 nucleotides (nt), which covered the complete cytochrome *b* gene, three transferRNA (tRNA) genes (codons for glutamic acid, threonine and



(a)

Fig. 3.3 (a) The map of East (1999) shown with the colour scheme of Hassanin (2007). (b) Phylogenetic tree of the 12 giraffe haplotypes. The tree was constructed with a Maximum Parsimony method. At the end of the terminal branches, the coloured circle matches the subspecies group in (a). Hassanin *et al.* suggest including the four haplotypes highlighted in orange in the subspecies *antiquorum*. Source: Hassanin *et al.* (2007). Reproduced with permission of Elsevier. (See insert for colour representation of the figure.)

proline) and the 5' region of the control region. In their approach, they appear to have been greatly influenced by the IUCN groupings of East (1999), since their 'colour scheme' of results matches their coloured map of East's suggested groupings (Fig. 3.3a). They identified a total of 12 mitochondrial haplotypes among the 23 samples (a haplotype is a collection of identical sequences likely to share common ancestry). They used four methods of phylogenetic tree reconstruction, all of which show that *G. camelopardalis* is a monophyletic species² (Fig. 3.3b).

²Strictly speaking, monophyly can only be inferred given an outgroup and also possible ingroups. Probably it is not an issue for giraffe since okapi is clearly distinct and there is no other possible ingroup.

The 12 haplotypes can be classified into three distinct lineages: (1) northern giraffe, comprising the subspecies *peralta*, *antiquorum*, *rothschildi* and *reticulata*, (2) Angolan giraffe, and (3) a south-eastern group, composed of the subspecies *giraffa* and *tippelskirchi*. In this regard, they shadow the previous suggestion by Kingdon (2004). The three groups of giraffe haplotypes are supported by high values of robustness and several molecular signatures diagnose each group.

Perhaps the most extensive genetic survey is that of Brown *et al.* (2007). Like that of Hassanin *et al.* (2007), their results also suggest the existence of geographic subdivisions in mitochondrial DNA sequences and microsatellite allele frequencies, which map onto giraffe subspecific geographic ranges. Brown *et al.* propose the

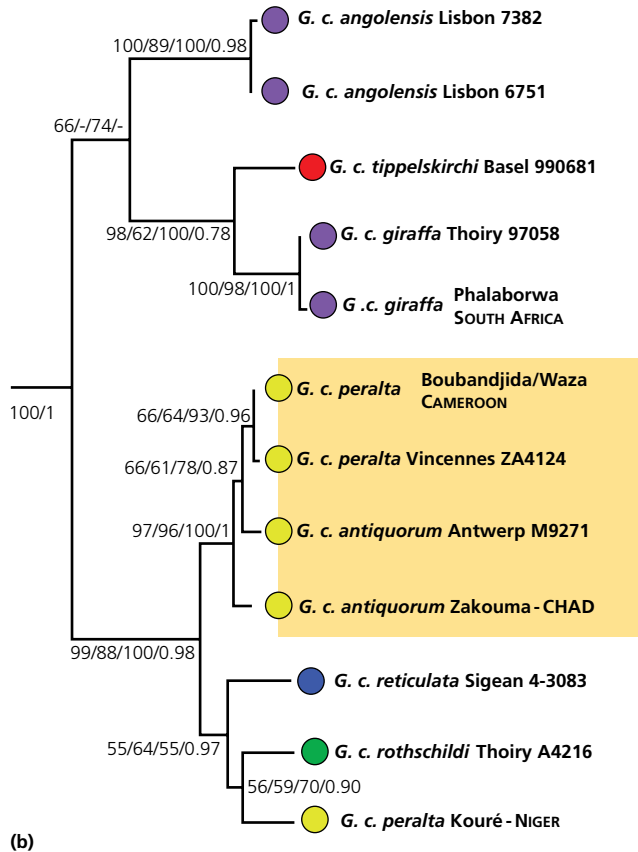


Fig. 3.3 (Continued)

existence of at least six full species of giraffe in Africa, and possibly as many as 11 species. Certainly their mitochondrial DNA sequence analyses suggest between five and seven geographically defined clades (a clade, from the Greek *klados* or branch, is a monophyletic group consisting of an ancestor and all its descendants). This DNA data (Fig. 3.4 top) is consistent with the fact that the earliest fossil remains of *G. camelopardalis* have been found in East Africa. A neighbour-joining analysis of shared genetic differences revealed that giraffe genotypes were strongly clustered into subspecific groups (Fig. 3.4 bottom). These results suggest that the divergence times between the seven giraffe clades ranged from 0.13–0.37 Mya between Masai and South African clades, to 0.54–1.62

Mya between the southern clade (Masai, Angolan and South African giraffes) and the northern clade (West African, Rothschild's and reticulated giraffes). Divergence values for the northern giraffe grouping were intermediate, with West African and Rothschild's giraffes diverging about 0.16–0.46 Mya, and these two species splitting from ancestors of reticulated giraffes about 0.18–0.54 Mya. These dates argue for a mid to late Pleistocene radiation of these giraffes, a time of intense climatic change in sub-Saharan Africa. Of course, while this study demonstrates an identifiable genetic structure among giraffe populations, which Brown *et al.* (2007) claim is a species-level differentiation, such distinction depends wholly on the species concept used (see earlier in this chapter).

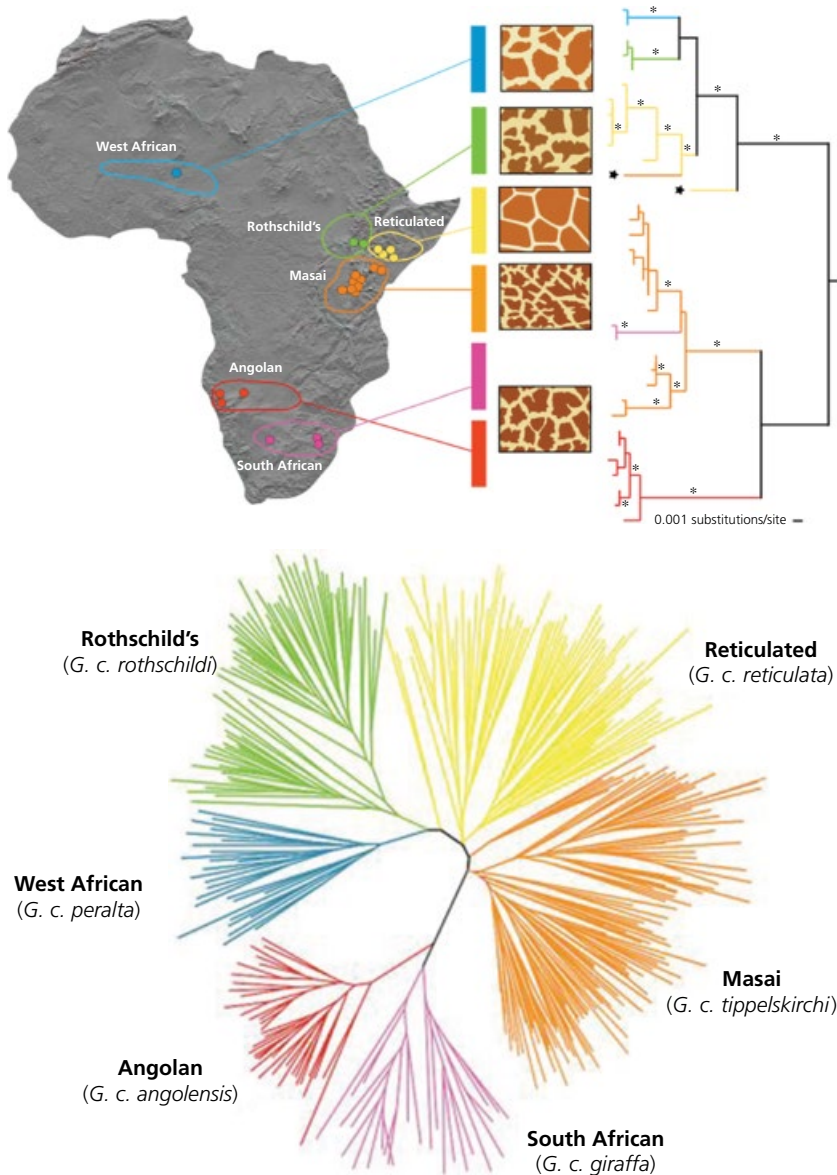


Fig. 3.4 Genetic subdivision in the giraffe. (Top) Approximate geographic ranges, pelage patterns and phylogenetic relationships between subspecies based on mtDNA sequences. Colour-coded dots on the map are sampling localities. The phylogenetic tree is a maximum likelihood phylogram based on 1707 nucleotides of mtDNA sequence from 266 giraffes. Asterisks along branches correspond to node-support values of >90% bootstrap support. Stars at branch tips identify paraphyletic haplotypes found in Masai and reticulated giraffes. Key: red, Angolan giraffe, *G. c. angolensis*; blue, West African giraffe, *G. c. peralta*; green, Rothschild's giraffe, *G. c. rothschildi*; yellow, reticulated giraffe, *G. c. reticulata*; orange, Masai giraffe, *G. c. tippelskirchi*; pink, South African giraffe, *G. c. giraffa*. (Bottom) Genetic subdivision in the giraffe based on microsatellite alleles. Neighbour-joining network of allele-sharing distances (Ds) based on 14 microsatellite loci typed in 381 giraffes. Colours are coded as in the top figure. Source: Brown *et al.* (2007). (See insert for colour representation of the figure.)

Interestingly, although also invoking six taxa, the conclusions of Brown *et al.* (2007) differ from those of both East (1999) and Grubb (2005).

Other recent genetic studies include that of Brenneman *et al.* (2009), Fennessy *et al.* (2013) and Bock *et al.* (2014) and look at the isolation of giraffe populations in two areas. The former study showed that the endemic giraffes of northern Namibia demonstrate a unique genetic architecture quite unlike giraffes studied in other regions of Africa to date, and with a very low genetic diversity. The next study examined 34 Thornicroft's giraffe, *G. camelopardalis thornicrofti*, in Zambia's South Luangwa National Park and the adjacent Lupande Game Management Area, and seven individuals from northern Botswana, using skin biopsy darting. A blood sample from the okapi (*Okapia johnstoni*) was collected from a zoo individual (Basel, Switzerland) to give the phylogenetic analysis a direction as the closest outgroup to the giraffe. Again, the cytochrome *b* gene was analysed. Figure 3.5 shows their results, along with other cytochrome *b* data for giraffe. The sequences within the *G. c. thornicrofti* were identical for the cytochrome *b* gene and control region sequences (red dots in Fig. 3.5), suggesting they are a monophyletic group.

The final study of Bock *et al.* (2014) presents an analysis of mitochondrial cytochrome *b* (cytb) and partial control region (CR) sequences for eight of the nine currently described giraffe subspecies. Their sampling focused on geographic regions that had not been analysed before, especially in southern Africa (Namibia and Botswana), but also central Africa's Democratic Republic of Congo (Garamba National Park). The most obvious pattern is a north–south split, with the southern subspecies Angolan giraffe, South African giraffe, and Masai/Thornicroft's giraffe being separated from the northern subspecies Kordofan giraffe, reticulated giraffe, Rothschild's giraffe and West African giraffe. This more recent molecular data

set, using a molecular clock³ analysis with BEAST (Bayesian Evolutionary Analysis Sampling Trees) software, estimates slightly different divergence times for giraffe subspecies clades. These authors estimate that the northern and southern clades diverged about 2.0 Mya. This was followed by the divergence of a mtDNA clade containing the Angolan, South African and Masai/Thornicroft's giraffe about 1.4 Mya. A northern clade, which included the Kordofan, reticulated, Rothschild's and West African giraffe, diverged about 0.8 Mya. Intriguingly, nine individuals that were thought to be one subspecies (Brown *et al.* 2007) showed genotypes consistent with another subspecies. In addition, 46 individuals sampled as 'Angolan giraffe' from northern Botswana and northeastern Namibia were grouped with the 'South African giraffe' from the Khamab Kalahari Reserve in South Africa. These areas therefore contain mtDNA haplotypes of the South African giraffe subspecies and not of the Angolan giraffe. However, there was a considerable amount of variation within subspecies.

As a final note on these recent molecular studies, let me just say a few words. They place more reliance on mtDNA than perhaps is the case nowadays, as evidence accumulates for the impact of selection on mtDNA patterns. The number of nuclear loci is perhaps low by more recent standards, but adequate to detect population structure. The inferences about reproductive isolation are less well supported, I suspect. It is possible for boundaries formed on secondary

³Since its proposal in the 1960s, the molecular clock has become an essential tool in many areas of evolutionary biology. The molecular clock hypothesis states that DNA and protein sequences evolve at a rate that is relatively constant over time and among different organisms. A direct consequence of this constancy is that the genetic difference between any two species, or subspecies, is proportional to the time since these subspecies last shared a common ancestor. Therefore, if the molecular clock hypothesis is true, it provides an extremely useful method for estimating evolutionary time-scales.

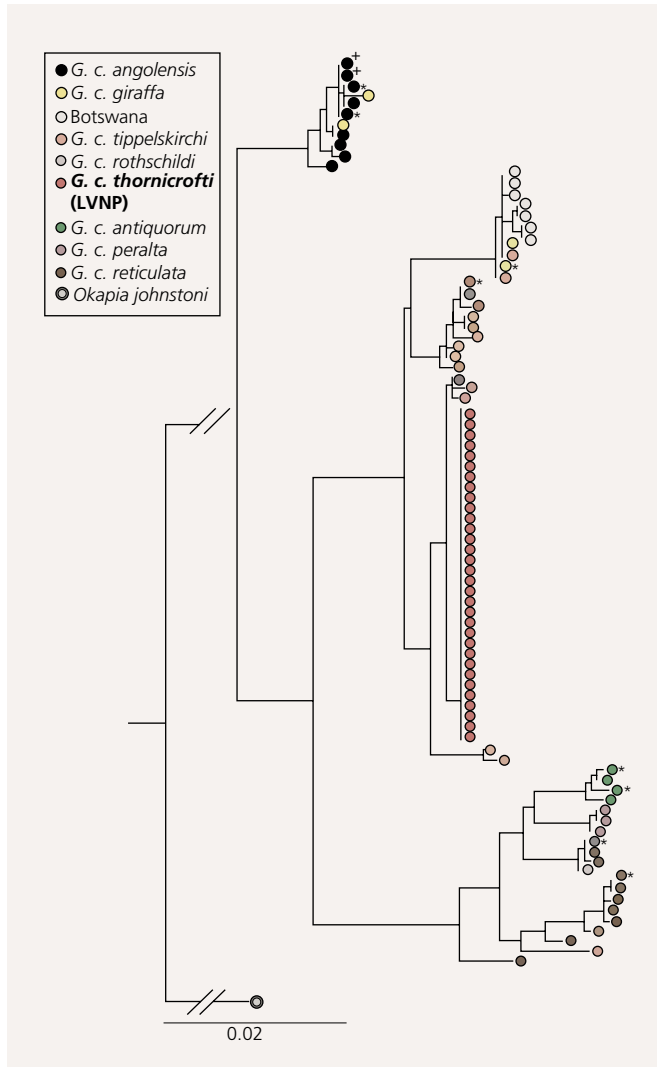


Fig. 3.5 ML phylogram of the concatenated mtDNA sequences. The circles indicate individuals and the colour the respective population or geographical origin. A star (*) denotes zoo individuals, while a plus (+) indicates an individual with a population designation but no geographical origin. Source: Fennessy *et al.* (2013). Reproduced with permission of John Wiley & Sons. (See insert for colour representation of the figure.)

contact to be trapped by small features of the environment that are hard to detect. Transitions in multiple markers (phenotypic and genetic) are brought together by secondary contact and this coincidence can decay rather slowly unless traits or genes are under directional selection (which tends to advance one trait or allele into

the other population). This is true for neutral markers and it takes only a small amount of selection against hybrids (or against animals that cross into the 'wrong' habitat) to greatly increase the stability and keep the transition sharp. Although there are clearly genetically distinct groups present, the genetic distinctiveness may

reflect past spatial isolation rather than current reproductive isolation, which could only be assessed by detailed analysis in contact zones.

So how many species or subspecies of giraffe are there at the present time? Brown *et al.* (2007) suggest between six and 11 and the studies discussed above show clearly that there is substantial genetic divergence between many geographical populations. Whether we finally call these species or subspecies will depend, as Seymour (2001) has pointed out, on our view of 'species'.

From a taxonomic perspective none of these recent studies do anything to further the classification of giraffe populations as they contain no diagnoses or descriptions of the purported taxa nor any of the required taxonomic discussion.

As pointed out earlier in this chapter, the review of ungulate taxonomy by Groves and Grubb (2011) includes eight full species of giraffe, placed into northern and southern groups, though not all of the taxa have full diagnoses and descriptions. Their review does include examination of specimens, though their sample sizes are small for certain taxa, and they find significant overlap in their analyses. Although their recognition of eight taxa is based on novel analyses of morphology and pelage characters, it is also largely based on the genetic results of Brown *et al.* (2007) and Hassanin *et al.* (2007). Their decision to elevate all taxa to species level reflects a philosophical switch, not accepted by all taxonomists or biologists. The current situation is therefore that there are nine taxonomic groupings of extant giraffe. These are probably subspecies, but some may eventually be regarded as species (Dagg 2014; Fennessy 2012; Tutchings 2013; Shorrocks & Bates 2015) (Fig. 3.6).

I end this chapter by briefly describing these currently recognised nine subspecies of giraffe. Estimated numbers and conservation are discussed further in Chapter 9. The old Giraffe Conservation Foundation (GCF) has produced Giraffe Conservation Status reports in the past. At present, it is unclear if they will in the future.

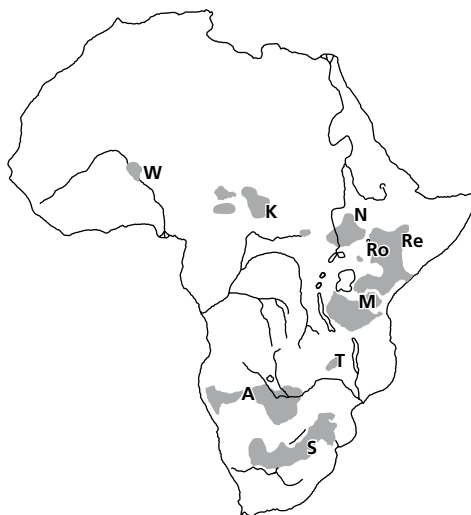


Fig. 3.6 The nine subspecies of *Giraffa camelopardalis*: West African giraffe (W) (*G. c. peralta*), Kordofan giraffe (K) (*G. c. antiquorum*), Nubian giraffe (N) (*G. c. camelopardalis*), Rothschild's giraffe (Ro) (*G. c. rothschildi*), reticulated giraffe (Re) (*G. c. reticulatus*), Masai giraffe (M) (*G. c. tippeskirchi*), Thornicroft's giraffe (T) (*G. c. thornicrofti*), southern, or Cape, giraffe (S) (*G. c. giraffa*), and the Angolan, or smokey, giraffe (A) (*G. c. angolensis*). Source: Shorrocks & Bates 2015.

Their new website is www.giraffeconservation.org. Status reports can be found on the IUCN website at <http://dx.doi.org/10.2305/IUCN.UK.2010-2.RLTS.T9194A12968471.en>.

- *G. c. angolensis*. The Angolan or smokey giraffe (Fig. 3.7a). It is no longer found in Angola, but reputed to be found across Namibia (10,000) (Fennessy *et al.* 2003), southwestern Zambia (>50), Botswana (6500) and possibly into western Zimbabwe. It is therefore estimated that in 2012 there were about 17,000 remaining in the wild. In 1998 the estimate was much the same, although in the 14-year period Namibia and Botswana have swapped their numbers. ISIS (the International Species Information System, based on zoological data information) records indicate that only about 20 individuals are kept in zoos. The Angolan giraffe is relatively light in colour (hence the name 'smokey')

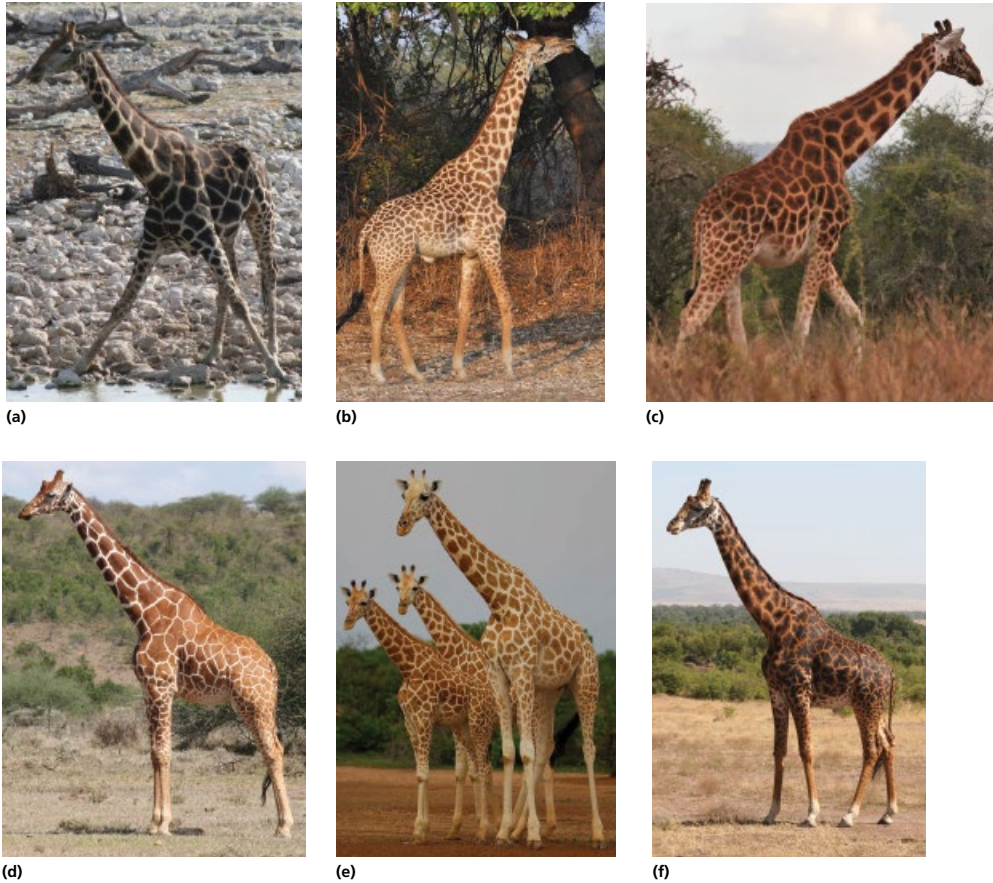


Fig. 3.7 Six giraffe (sub)species. (a) *G. c. angolensis*, Etosha National Park (NP), Namibia, (b) *G. c. thornicrofti*, South Luangwa NP, Zambia, (c) *G. c. rothschildi*, Nakuru NP, Kenya, (d) *G. c. reticulata*, Laikipia, Kenya, (e) *G. c. peralta*, Niger, and (f) *G. c. tippelskirchi*, Kenya. Photographs (a), (c), (d) and (f) by Jo Shorrocks, (b) by Fred Bercovitch and (e) by Jean-Patrick Suraud (kindly provided by Isabelle Ciofolo). (See insert for colour representation of the figure.)

with large uneven, notched spots covering the entire leg. **Status: increasing.**

- *G. c. antiquorum*. The Kordofan giraffe's range includes some of the most hostile areas in Africa: southern Chad (unknown), the Central African Republic (162), northern Cameroon (unknown) and northern Democratic Republic of Congo (DCR) (75). In the DCR they are restricted to the Garamba National Park and adjacent hunting reserves (Marais *et al.* 2012). 'Large giraffe herds' have been seen from the air in southern Sudan, but it has been impossible to determine their

specific identity. The estimated 400 giraffe in the Sudan might be the Kordofan, Nubian or Rothschild, so we are unsure about the precise numbers of these three subspecies. Also, the Cameroon populations were formerly assumed to be *G. c. peralta*, but Hassanin *et al.* (2007) cast doubt on this. This research resulted in giraffes from zoos all across Europe, which were initially thought to be *G. c. peralta*, being reclassified as *G. c. antiquorum*. As a result, ISIS records indicate that today there are in the region of 65 individuals kept in zoos. The Kordofan's spots are pale

and irregular with a covering that includes their inner legs. **Status: stable/decreasing.**

- *G. c. camelopardalis*. Commonly known as the Nubian giraffe, this is also the nominate species. Numbers are now estimated at fewer than 250 individuals (depending on the identity of the Sudan individuals). Its home range covers western Ethiopia (150) and maybe eastern Sudan (unknown numbers, see Kordofan entry above), areas recently ravaged by civil war, and therefore exact information regarding its small fragmented populations is extremely difficult to ascertain. There are almost no Nubian giraffes in captivity, though there is likely a small pure-bred population in the United Arab Emirates, at the Al Ain Zoo. The distinctive coat of the Nubian giraffe has large, normally four-sided, chestnut brown spots set against a slightly off-white background. It has no markings on the inside of its legs or at all below the knees.

Status: decreasing.

- *G. c. giraffa*. The South African, or Cape, giraffe ranges east to west through northern South Africa (8000), southern Botswana (?) and southern Zimbabwe (?), with limited reintroductions into Mozambique (<50), Senegal (50) and Swaziland (25). There are concerns that reintroductions of South African and Angolan giraffes into the same populations have probably resulted in hybrid individuals. There are less than 12,000 left in the wild and according to ISIS only approximately 45 individuals in zoos. The South African giraffe's pattern extends all the way down the leg and is made up of blotchy, star-shaped spots set against a more tan-coloured than cream or white background. **Status: stable/increasing.**
- *G. c. peralta*. The West African, or Nigerian, giraffe (Fig. 3.7e) survives in an isolated pocket of fewer than 250 individuals just south east of Niger's capital city Niamey (Suraud 2006, 2008, 2009; Suraud & Gay 2010). Protected by the Niger government, this is possibly the world's rarest giraffe

subspecies and in 2008 was listed on the IUCN Red List as 'endangered' (Fennessy & Brown 2008). The West African giraffe is strikingly light in appearance with tan-coloured, rectangular spots set amongst thick creamy lines.

Status: decreasing.

- *G. c. reticulata*. Best known as the reticulated giraffe (Fig. 3.7d) though sometimes also called the Somali giraffe on account of its former home range of southern Somalia (?), southern Ethiopia (<25) down into northeastern Kenya (5000). It is estimated therefore that fewer than 5000 remain in the wild (from an estimated 28,000 as recently as the late 1990s). Interestingly, based on figures provided by ISIS, the reticulated giraffe is one of the more common captive giraffes with approximately 450 kept in zoos across the world. It is understandable why this is so. Arguably it has the most attractive pelage of any giraffe, with the brownish-orange coat patches clearly defined by a network of thick and often extremely white lines. **Status: stable/decreasing.**
- *G. c. rothschildi*. The Rothschild's giraffe, sometimes called the Baringo or Ugandan giraffe (Fig. 3.7c), ranges through Uganda (350) and west-central/central Kenya (350), and possibly into southern Sudan (?; see Kordofan above). With fewer than 700 individuals remaining in the wild, in 2010 the Rothschild's giraffe was listed on the IUCN Red List as 'endangered' and of high conservation importance (Fennessy & Brown 2010). Efforts in 2011 to reintroduce individuals back into the Lake Baringo area have proved successful. ISIS reports more than 450 individuals in captivity. The Rothschild's giraffe has large, dark rectangular spots or blotches set irregularly against a cream-coloured background, though the legs are noticeably white and are not patterned. **Status: stable/decreasing.**
- *G. c. thornicrofti*. The Thornicroft's giraffe (Fig. 3.7b) (rarely referred to as the Rhodesian giraffe) survives as an entirely isolated population restricted to eastern Zambia's South

Luangwa Valley (see Fennessy *et al.* 2013). Estimates indicate there are fewer than 750 remaining in this isolated pocket, and according to ISIS there are none kept in captivity. The Thornicroft's giraffe has large dark, ragged leaf-shaped spots that continue down the length of the leg, set against a cream-coloured background. **Status: decreasing.**

- *G. c. tippelskirchi*. The Masai (Fig. 3.7f) (occasionally known as the Kilimanjaro) giraffe ranges across central and southern Kenya (12,000) and south into Tanzania (28,000), with populations also translocated into

Rwanda (<100). This may be the most numerous of the subspecies with an estimated 40,000 remaining in the wild. However, recent reports of significant poaching would suggest it is likely to be significantly less. ISIS records indicate approximately 100 individuals kept in zoos. Though all (sub)species can become extremely dark in colour, especially the males, the Masai giraffe is noticeably darker than the rest. It has large, distinctive, dark brown, vine leaf-shaped, jagged spots interspersed by creamy-brown irregular lines. **Status: decreasing.**

CHAPTER 4

Anatomy

This chapter will look at the skin, skeleton, muscles and movement of the giraffe. The giraffe is a large animal. In fact, it is the tallest living terrestrial animal, although only the ninth heaviest terrestrial animal, behind the hippopotamus, three elephant species and four rhinoceros species.

Surprisingly, the records for height and weight given by a selection of authors in my African library vary somewhat (Apps 1996; Bush 2003; Dagg 2014; Estes 1991a; Kingdon 1979, 1997, 2004; Skinner & Smithers 1990; Stuart & Stuart 1997a,b; Tutchings *et al.* 2013). This may be because authors are quoting local subspecies or geographical differences. For example, Apps (1996) gives the average height for giraffe from Botswana as 3 m (male) and 2.74 m (female), but for the low veldt of South Africa as 3.3 m (male) and 2.8 m (female). Of course, the number of individuals measured is frequently small and whether these differences are statistically significant is another matter. Conflating all the above authors, we arrive at a weight range of 970–1950 kg for males and 450–1200 kg for females. Average weight seems to be around 1200 kg (males) and 800 kg (females). Similarly, height range is 3.9–5.5 m for males and 3.5–4.7 m for females. Average height is around 5.5 m for males and 4.3 m for females. Of course, adult giraffes are not easy to weigh in the field. In this regard, the analysis by Hall-Martin (1977) is interesting and very relevant. Fifty seven giraffe were dissected and

weighed in pieces, in the field. The giraffes came from a culling programme in the eastern Transvaal Lowveld of South Africa. There is usually a good relationship between weight and volume in animals, where the volume is expressed as $\text{length} \times \text{girth}^2$ (McCulloch & Talbot 1965; Rideout & Worthen 1975) and this relationship was examined for the 57 giraffe. Correlations were very good. For body weight (kg) and $\text{length} \times \text{girth}^2$, $r^2 = 0.993$ for males, 0.977 for females and 0.990 for both sexes combined. Length included head and tail and chest girth was caudal to front legs. This relationship suggests a practical way of measuring giraffe weight without dissection, or trying to weigh the whole animal.

The skin

In adult giraffes, the head is approximately 2 m above the heart (Mitchell & Skinner 1993). This gravitational challenge poses a serious problem for the maintenance of sufficient blood circulation to the brain (Goetz *et al.* 1960; Mitchell *et al.* 2006; van Citters *et al.* 1969), since an insufficient blood supply could result in fainting. In addition, the long legs of the giraffe mean that its heart is approximately 2 m above the ground (Howard 1977), providing a second gravitational challenge to the returning blood supply, via the veins, from the legs. If the removal of tissue fluid does not function correctly and there is a

build-up, this can cause swelling around the lower legs known as oedema. A number of oedema-preventing mechanisms have been suggested, including thick walls and small lumens of the neck and leg blood vessels, variable venous pressures, capillary membranes with low permeability, a prominent lymphatic system and unidirectional valves in the veins (Hargens *et al.* 1987; Pedley 1987; Mitchell & Skinner 2004). However, the skin of the giraffe is also believed to contribute to oedema inhibition because of its 'tightness' in the legs (Hargens *et al.* 1987; Lillywhite 1996; Pedley 1987; Pedley *et al.* 1996). However, Mitchell and Skinner (2004) concluded that the average thickness of the skin in the head, neck and legs was largely uniform, and that the thickest skin was found in the body. They did notice that the skin was typically collagenous, making it inflexible, and they suggest that this inflexibility allowed the skin to provide resistance against high blood pressure. The skin is heavily pigmented, but similar to other mammals with regard to its histological structure (Dimond & Montagna 1975).

Another function of thick skin in other large mammals has been that of forming 'armour' for protection against predators or during aggression from conspecifics (Jarman 1972, 1989) and this factor is used to explain the thickness of the skin in the rhinoceros (Shadwick *et al.* 1992). Since male giraffes show intraspecific combat (Coe 1967; Simmons & Scheepers 1996), it may be that variations in the thickness of the skin are related to both physical protection and haemodynamics. Sathar *et al.* (2010) took skin samples from two young and one adult male giraffes. In one of the younger giraffes, one-half of the skin was analysed from which approximately 170 sites were measured. In the other young and adult giraffes, spot tests were undertaken to confirm the pattern observed in the fully analysed individual. The skin was found to vary substantially in thickness across the body (Fig. 4.1), with a very thin epidermis, a thicker superficial dermis and a very thick deep dermis, with substantive densities of elastic fibres in the

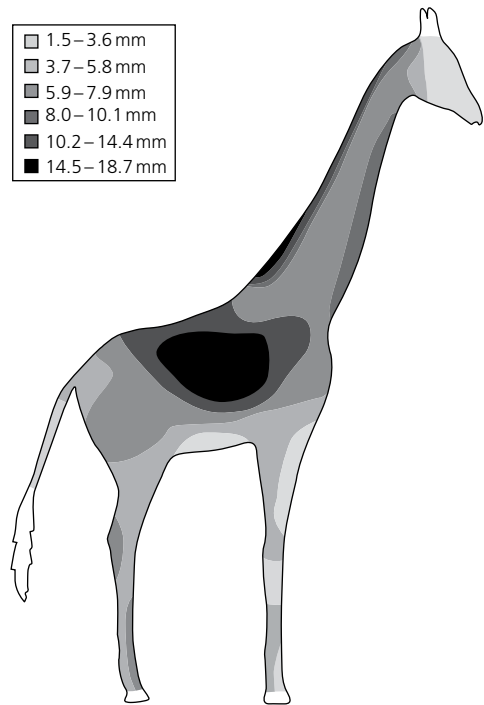


Fig. 4.1 Smoothed maps of entire skin thickness based on measurements done macroscopically with sliding callipers. Source: adapted from Sathar *et al.* (2010). Reproduced with permission from John Wiley & Sons.

superficial dermis. Each region of the body displayed a high or very high density of collagen fibres, indicating that collagen fibres formed the dominant feature of the dermal tissue as noted previously (Dimond & Montagna 1975; Mitchell & Skinner 2004). The authors conclude that the skin in the neck and legs shows a morphology that may assist in cardiovascular regulation of blood flow to and from the head and legs (see later), and the skin of the trunk and anterior neck has the possibility of functioning in a protective role.

The pelage of giraffe is well known, quite variable between subspecies and has already been briefly mentioned in Chapter 3. If species are able to travel large distances, and are distributed across semi-continuous habitat, gene flow can prevent, or slow down, genetic differentiation

and therefore speciation (Shorrocks 1978). Adult giraffes frequently range over several hundred square kilometres and are capable of long distance movements of 50–300 km (see Chapter 8). In addition, they live in loosely constructed social groups with large home range sizes, from 5 km² to 992 km² (Le Pendu & Ciofolo 1999; van der Jeugd & Prins 2000) (see Chapter 8). However, giraffes not only show geographic variation in pelage colouration and pattern (Seymour 2001), but also variations in ossicone number (Lydekker 1904; Singer & Boné 1960; Spinage 1968b) and mitochondrial DNA variation (Brown *et al.* 2007) (see Chapter 3) that map onto subspecies geographic ranges. This suite of traits suggests a degree of distinct population differentiation.

Of course, the past African habitat of giraffes has almost certainly not been continuous (de Menocal 1995, 2004; Kingdon 1989; Kingdon *et al.* 2013; Stokes *et al.* 1998), and gene flow may have been reduced sufficiently in the past to allow natural selection to establish the present subspecies with their different pelage patterns. If so, what are the possible adaptive reasons for, firstly, the unique giraffe coat colour and, secondly, the subspecies differences that are seen? The answer to both questions is probably visual. However, Kingdon (1989) did note that because the *peralta* subspecies is the lightest coloured and lives in the hottest and driest habitats, a thermoregulation explanation might be made. This 'role' for the dark patches in giraffe skin has also been made by Ackerman (1976) and Mitchell and Skinner (2004). In this case, the dark patches of the skin are thought to act as heat loss areas enabled by vasodilatation of the blood vessels beneath the dark patch skin surface. Clear experimental evidence of this is, however, lacking.

Several people (Kingdon 1989; Trouessart 1908) have suggested camouflage as the answer to the first question, although others find this explanation quite absurd (Roosevelt & Heller 1914) since the giraffe's size and shape are so obvious. Of course, an adult giraffe in a rather

open savannah habitat can stand out. However, in *Acacia* woodland/scrub savannah of Kenya, I have often not spotted a group of giraffe until getting quite close to them. And it is the young giraffe, that are often left in hiding by the mother (Bercovitch & Berry 2015a), that are most vulnerable to predation. About half fail to survive their first year of life (Bercovitch & Berry 2010a; Dagg 2014). Kingdon (1989) makes an interesting and believable case for camouflage. He points out that many species of forest-dwelling herbivores pass through a cryptically coloured stage while they are young and often retain the pattern into adulthood. The resemblance between their 'blobs and stripes' is interesting since bovids, chevrotains, pigs, tapirs and some neotropical rodents must have evolved these patterns independently. This suggests that these 'patchy' patterns really work as camouflage. Assuming modern giraffes evolved from a smaller ancestor such as *G. gracilis* or *G. pygmaea* (see Chapter 2), the progression towards greater height and dryer habitats (after about 6–8 My) could have put greater demands on the system of camouflage that protected the young. Perhaps, Kingdon suggests, ancestral spots extended and joined.

With regard to the more specific question of why different giraffe subspecies have different patterns, Brown *et al.* (2007) put forward the following suggestion. Given that communication among giraffes is primarily visual (Dagg & Foster 1982) (although ultrasound has also been suggested, see Chapter 5) and given marked subspecific variation in pelage pattern, assortative mating by pelage type could occur, and be important in maintaining coadapted gene complexes suited to specific local environments. For example, sexual imprinting, in which early exposure to conspecifics influences mate choice later in life (Kendrick *et al.* 1998; Laland 1994; Owens 1999; Verzijden *et al.* 2005), can promote and maintain differences between populations that have diverged while separated because of habitat fragmentation, reinforcing and maintaining differences upon

secondary contact. Giraffe calves are likely to be in close contact with only their mothers and other members of the local crèche until they are several months old (Bercovitch & Berry 2015; Pratt & Anderson 1979). Individual giraffes might therefore develop pelage-specific mate preferences, even in regions of overlap between subspecies. In zoological garden settings, visual barriers to interbreeding might not be maintained if calves are exposed to multiple pelage types. These interesting ideas need to be investigated.

The literature on giraffe hair is rather eclectic. Some early work (Beddard 1906; Broman 1938) noted that two 3-month-old giraffe embryos had no hair, one of 4 months had hair on its face and tail and one of 8 months had hair over most of its body, but of a uniform colour. Also at this time, the arrangement and direction of whorls of giraffe hairs, in embryos and adults, intrigued a number of authors (Kidd 1900, 1903; Rothschild & Neuville 1911), believing it supported the Lamarckian idea of acquired characters. This was a reflection of the wisdom of the time accepted by many natural historians, but has been decisively rejected by modern genetics (Bowler 2003; Mayr 1997). Giraffe hair, like that of all mammals, is made of keratin. Keratins are a broad class of fibrous proteins which exist in two major types, alpha-keratins and beta-keratins. An intrinsic difference in vertebrate keratins is that mammals (including giraffes) produce only alpha-keratins, while reptiles and birds produce both alpha-keratins and beta-keratins (Alibardi 2003; Fraser & Parry 1996; Marshall *et al.* 1991). Espinoza *et al.* (2008) have developed techniques for differentiating the hair keratin of elephants from those of giraffes using horizontal-attenuated total-reflection Fourier transform infrared (HATR FTIR) spectroscopy, followed by discriminant analysis. This was because both elephant and giraffe hair is extensively used to make indigenous artefacts (e.g. bracelets, earrings, finger rings, etc.) in the wildlife trade. Sadly, the implication is that elephants need protection, because they are on

Appendix I or II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), while giraffes do not! Yates *et al.* (2010) have extended this work by using cross-section analysis and light microscopy to analyse the tail hair morphology of 18 individual African elephants, 18 Asian elephants and 40 giraffes. Buys and Keogh (1984) note that giraffe hairs show a pigment-orientated feature in that in some of the lighter hairs, the pigment is seen on one side of the hair only.

The giraffe emits a scent that can be detected by humans over considerable distances. Dichloromethane extracts of hair samples from adult male and female reticulated giraffes were analysed by gas chromatography–mass spectrometry. Two highly odoriferous compounds, indole and 3-methylindole, identified in these extracts appear to be primarily responsible for the giraffe's strong scent. Other major compounds identified were octane, benzaldehyde, heptanal, octanal, nonanal, *p*-cresol, tetradecanoic acid, hexadecanoic acid and 3,5-androstadien-17-one; the last compound has not previously been identified from a natural source. These compounds may deter micro-organisms or ectoparasitic arthropods. Most of these compounds are known to possess bacteriostatic or fungistatic properties against mammalian skin pathogens or other micro-organisms. The levels of *p*-cresol in giraffe hair are sufficient to repel some ticks (Wood & Weldon 2002).

The skeleton

The first published description of the skeleton of giraffes was by Vosmaer (1787), followed by contributions from Pander and D'Alton (1823), Owen (1841), Mitchell (2009) and Damian *et al.* (2012). In many ways, the giraffe skeleton is quite typical of that of a herbivorous mammal. For example, like an average cow, it has 50 vertebrae: seven neck (cervical) (C1–C7), 14 thoracic (T1–T14), five lumbar (L1–L5), four sacral (fused into a single bone) and 20 tail or

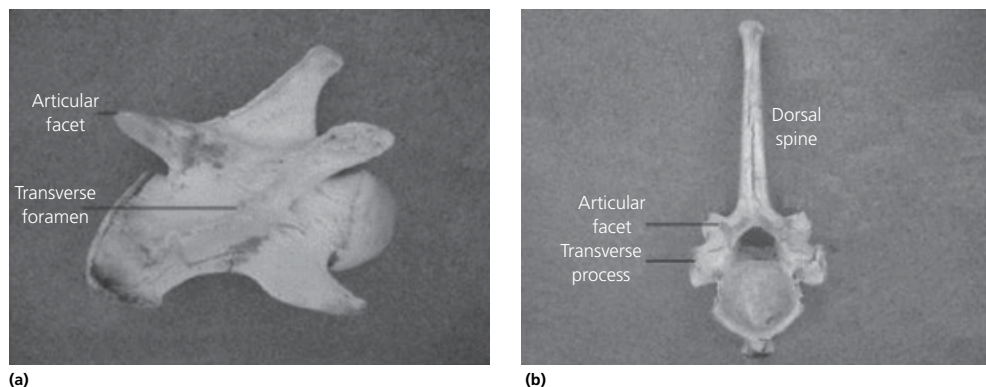


Fig. 4.2 Giraffe vertebrae C7 and T1. (a) Cervical vertebra 7 (lateral view). (b) Thoracic vertebra 1 (caudal view). 'Articular facet' is the articular facet on the caudal articular process. Source: adapted from van Sittert *et al.* (2010). Reproduced with permission of John Wiley & Sons.

caudal vertebrae. In comparison, a cow appears to have 7C, 13T, 6L, 5S and 18–21 caudal vertebrae.

There has been some debate over the classification of T1 (Fig. 4.2). Based upon the length, position and shape of the spinous and transverse processes, and on the position and orientation of the articular facets on the articular processes (e.g. Solounias 1999), T1 was proposed as a cervical vertebra (therefore making eight, an uncharacteristic mammalian number). However, using the defining characteristic of an attached rib that fuses with the sternum (Badlangana *et al.* 2009; Flower 1885; Mitchell & Skinner 2003; van Sittert *et al.* 2010), vertebra T1 is clearly thoracic, not cervical. Of course, the seven neck vertebrae are very long compared to most other mammals, and have only shallow dorsal spines, since the length of each vertebra is sufficient for the attachment of muscles. They also have a unique ball and socket joint (as does the camel) which allows the observed flexibility of the neck (Spinage 1968a). There is a significant increase in the elongation rate of vertebrae C2 to T1 after birth (van Sittert *et al.* 2010), resulting in the cervical vertebrae being 129% longer than the thoracic and lumbar vertebrae in adult giraffes (Slijper 1946). This postnatal elongation rate may be linked to the mechanics of normal birth. In normal giraffe birth (similar

to other ungulates), the extended forelegs appear first, followed by the head of the calf resting beside or between them (Dagg 2014; Dagg & Foster 1976). If the unborn giraffe had a neck length to foreleg length ratio of that of the adult animal (which is ca. 1.09 compared with ca. 0.72 in the foetus) (Mitchell *et al.* 2009), the neck and head would extend beyond the forelegs during birth, which could produce an increased risk of 'elbow flexion' and consequently a slow and difficult birth, perhaps resulting in death. The thoracic vertebrae have long dorsal spines (see Fig. 4.2b) to which are attached the muscles and ligaments of the neck. As noted, each of these thoracic vertebrae has an attached rib, seven of which are fused with the sternum and six to a cartilaginous support. The 14th rib is floating.

The bones of the leg are long and show some unique features. The humerus (the upper forelimb bone) articulates with a shoulder blade or scapula that is of the same length, making the front limb appear longer than the hindlimb. In fact, the front leg itself is only about 10% longer, but the long scapula acts as a kind of extension. The scapula of the giraffe is the longest and narrowest of all mammals and provides a large attachment area for muscles (Spinage 1968a). The radius (the ulna is present but not well developed) is actually longer than the humerus,

and articulates with the carpal or wrist bones. Two of the metacarpals (our hand bones) are nearly as long as the radius and are fused to form the 'cannon' bone. There is a corresponding lengthening of the hindlimb, with its three major bones: the femur, tibia and tarsus. The femur is noteworthy for its unusual large distal end, which articulates with the pelvic girdle. The hindleg also contains a metatarsal 'cannon' bone. It is usually thought that there is complete absence of metacarpals and metatarsals 1, 2 and 5, and therefore no 'false hoof'. However, metatarsal 2 often persists as a small sliver of bone. Digits 3 and 4 end in a horny cloven hoof. The foot of the giraffe reaches a diameter of 30 cm (12 in), and the hoof is 15 cm (5.9 in) high in males and 10 cm (3.9 in) in females. The rear of each hoof is low, and the fetlock (the hinged joint between the cannon bone and the pastern bone, or proximal phalanx) is close to the ground (Dagg & Foster 1976).

In addition to these large bones, the giraffe, like most mammals, has several loose, sesamoid bones. These are small 'bits' of bone that are generally located in a tendon or near a joint (such as the fetlock). Their function is not fully understood but it is thought they may play a role in changing the direction of muscle forces in a limb, or in protecting the tendons.

Bone structure

All animals must be built strongly enough to stand, and move, under their own weight (McMahon 1973). For a given mass of an animal (with increased length of leg bones and a consequent increase in loading forces), strength is usually provided by an increase in cross-sectional area of the bone (Cloudsley-Thompson 1976). So, the bones of small animals are generally relatively more slender than those of large animals (McMahon 1973). In giraffes, however, this does not seem to be the case. McMahon (1975), Hamilton (1978) and Geraads (1986) have all shown that giraffe metapodial bones

have a smaller diameter, and are therefore more slender, than predicted.

An alternative to increased diameter of limb bones for providing strength would be an increase in density, and Mitchell and Skinner (2003) suggest this might be the case for giraffe limb bones. In addition, they predict that giraffe neck vertebrae density should be relatively lower than that of short-necked animals, in order to reduce the weight of the head and long neck. Unfortunately, two further factors complicate this density prediction. First, the skeleton of the giraffe elongates during maturation, more rapidly than that of other mammals (Dagg 2014; Dagg & Foster 1976; Hall-Martin 1975). Second, giraffe diet has an average calcium to phosphate ratio (Ca:P) of 7.7:1 (Bredin *et al.* 2008; Mitchell & Skinner 2003; Pellew 1984c). At this level of phosphate, many herbivores will chew bones (osteophagia), a form of pica (eating substances that are largely non-nutritive, such as soil) (McDowell 1992; Underwood & Suttle 1999). Interestingly, osteophagia is a well-documented phenomenon in giraffes (Hall-Martin 1975; Langman 1978; Nesbit-Evans 1970; Western 1971; Wyatt 1971), which suggests that dietary deficiencies could occur in giraffe. If such dietary deficiencies are compounded by high growth rate, then bone formation (and hence density) may be compromised. Furthermore, the giraffe skeleton constitutes a greater proportion of its body mass than it does, for example, in cattle. Skeletal mass of cattle is about 15–20% of carcass mass (Muldowney *et al.* 2001), whereas in a mature male giraffe it is about 24% (Hall-Martin *et al.* 1977). This suggests that the absolute amount of calcium and phosphate required for bone production in giraffe might be proportionately higher.

To examine these issues, van Schalkwyk *et al.* (2004) collected the bones of seven giraffes and nine buffaloes from carcasses in Kruger National Park, South Africa. What they found was, firstly, that except for a small difference in lumbar vertebrae density, there were no differences between giraffe and buffalo bone densities,

suggesting no effect of anatomy or diet. In addition, the absence of any differences in density between individuals of different ages suggested that the high growth rate of giraffes does not affect their bone density, at least once they have reached maturity. There was also no difference in cross-sectional area of the limb bones. Thus, the authors conclude that the density of giraffe bones is not unique, that they are similar to those of another large herbivore of similar mass, and are not affected by factors that intuitively suggest that they should be unique.

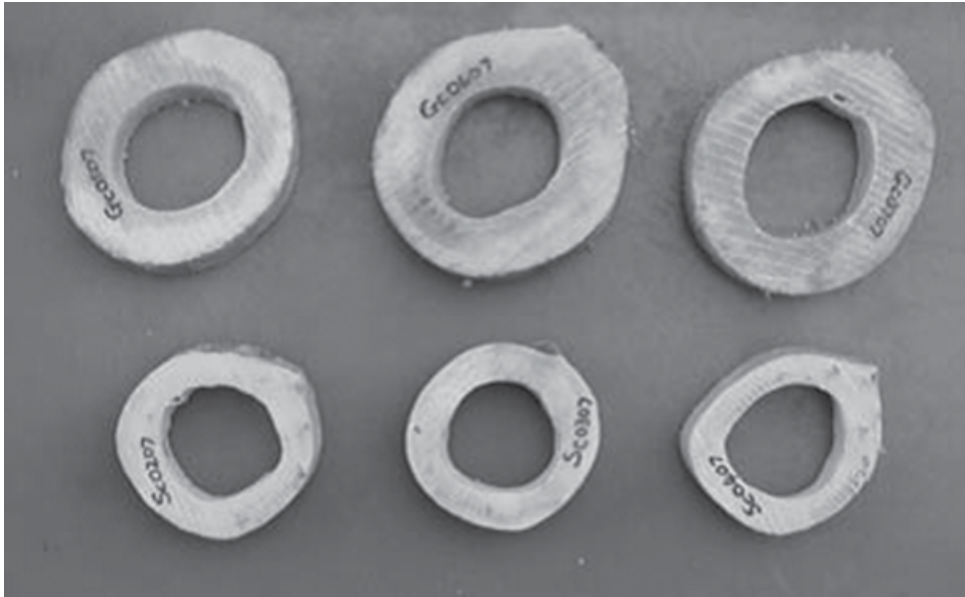
If not density, how is giraffe limb bone strength achieved? Van Schalkwyk *et al.* (2004) suggest a number of mechanisms. One might be that the limb bones are much straighter than they are in other artiodactyls and are therefore subjected to lower loading forces. Biewener (1983) measured curvatures (the distance that the mid-shaft deviates from a line joining the centre of the two articulating surfaces) for 11 artiodactyls ranging from hippopotamus (*Hippopotamus amphibius*) to dik-dik (*Madoqua kirkii*). He found that the giraffe femur mid-shaft deviated by 1.49 mm compared to an average of 7.3 ± 4.2 mm for the 10 other species. The curvature of the giraffe radius was 5.44 mm compared to 9.5 ± 2.7 mm for the other species. Additionally, both the femur and metacarpus in giraffes have diameters that are greater than equivalent bones in buffaloes (6.6 vs 4.9 cm for femurs, and 6.1 vs 3.9 cm for metacarpals). However, longer bones are expected to have a greater diameter (Alexander 1977; Alexander *et al.* 1979; Biewener 1983). So, for a bone that is 2–3 times longer in giraffes than in buffaloes, the diameter should be 2–3 times greater. It is not. Giraffe bone diameters are only about 1–2 cm greater than those of buffalo, giving the impression that giraffe bones are ‘slender’. On the other hand, the wall thickness of giraffe bones is significantly greater than it is in buffaloes (Fig. 4.3). Thus, the necessary strength for giraffe limb bones seems to come not from density but from a small increase in diameter, almost all of which is bone, rather than marrow.

In summary, these results of van Schalkwyk *et al.* (2004) indicate that, despite the unique anatomy of the giraffe, its high vertical growth rate, the high proportion of its body mass that is skeleton, and exposure to an adverse dietary Ca/P ratio, its skeleton is not unique with respect to bone density. Its bones have the same density as those of buffaloes, which have a very different anatomy, source of nutrients and a slower vertical growth rate. On the other hand, giraffe limb bones seem to have significantly thicker walls and are straighter than they are in other artiodactyls. These characteristics may be unique and may provide an explanation for how they support an elongated neck and how their long slender limbs support a large mass.

The skull

Skulls are important in mammal taxonomy, and that of the giraffe is no exception. Many anatomical observations have been made on the skull and its associated horn and teeth (Cobbold 1854; Granvik 1925; Kollmann 1920; Lankester 1907; Lönnberg 1912; Munoz 1949; Ridewood 1901; Roberts 1951; Roosevelt & Heller 1914; Rothschild & Neuville 1911; Shortridge 1934; Spinage 1968a; Thomas 1898, 1901; Willemse 1950). The most recent and detailed morphometric analysis is that of Seymour (2001), while Badlangana *et al.* (2011) used computed tomography (CT) scanning to examine the large frontal sinus. Appendix C in the updated edition of Dagg and Foster (1982) gives a detailed account of the skull and its associated structures.

The skull is large, but light for its size. Spinage (1968a) gives the weight for 16 males (average = 7.5 kg) and 10 females (average = 2.5 kg), with maxima of 11.3 kg and 4.0 kg respectively, but these are probably minus the lower jaw. Dagg (1965) gives an average of 9.9 kg for three male skulls with mandibles, and an average of 3.5 kg for seven female skulls with mandibles. The skull reaches a mean length of 63 cm in the adult female and 66.5 cm in the male, with



(a)



(b)

Fig. 4.3 Cross-sectional samples showing the difference in bone thickness between giraffe (*top row*) and buffalo (*bottom row*). (a) Femurs, (b) metacarpals. Source: van Schalkwyk *et al.* (2004). Reproduced with permission of John Wiley & Sons.

maxima of 71 and 74 cm respectively (Spinage 1968a). Seymour's (2001) examination of 142 adult skulls, using discriminant analysis, found

that of the 49 variables measured (cranial, mandibular and postcranial), only six showed a significant difference between males and females.

Five of these were associated with feeding and might be expected not to vary between the sexes. The sixth referred to the divergence of the parietal horn tips (see later). The occipitoparietal crest at the back of the skull is well developed and below it is a deep furrow where the strong neck muscles are attached (Rothschild & Neuville 1911). The occipital condyles (the bones which articulate with the neck) are extended and extremely rounded, enabling the giraffe to raise its head vertically, in line with its neck, when feeding on high trees (Spinage 1968). However, perhaps the most unique feature of giraffe skulls is the several air sinuses, particularly the relatively large 'frontal sinus'.

Both Colbert (1938) and Churcher (1978) noted that the giraffe had an extremely large sinus above the brain, extending into the occiput (the posterior portion of the skull). However, no detailed anatomical description was attempted until Badlangana *et al.* (2011) (Fig. 4.4). They examined the skulls of 14 individuals, from nine artiodactyl species using CT scans and three-dimensional image reconstruction programs (3D Slicer 3.5) (Fig. 4.5). In the giraffe, the frontal sinus starts in the frontal bone, extends backwards into the parietal and

interparietal bones and sideways into the temporal bones (Constantinescu & Constantinescu 2004). Within the parietal bones, the cranial vault (the space in the skull occupied by the brain) expands dorsally, resulting in a dome-shaped region at the bases of the ossicones (see later). The frontal sinus extends into that dome but, as shown in the CT reconstruction (Fig. 4.5), does not extend into the ossicones. However, the frontal sinus extends over the brain case and into the occipital bone. The sinus contains numerous plate-like trabeculae (see Fig. 4.4), and has a bony septum extending from the nasal bones to the occiput that completely divides the sinus into left and right halves. It is important to note that this frontal sinus is not unique to the giraffe. However, it is quite unique in terms of its absolute size and eventual position in the adult animal (Fig. 4.5). For example, using the cranial mass (g) divided by the frontal sinus volume (cm^3) (data from Badlangana *et al.* 2011, their table 1), we can obtain a number that indicates the size of this sinus relative to the skull. It ranges from a small number (large relative sinus size) to a larger number (small relative sinus size). In decreasing order of relative size, we get the following comparisons: an older giraffe (5.5+ years)

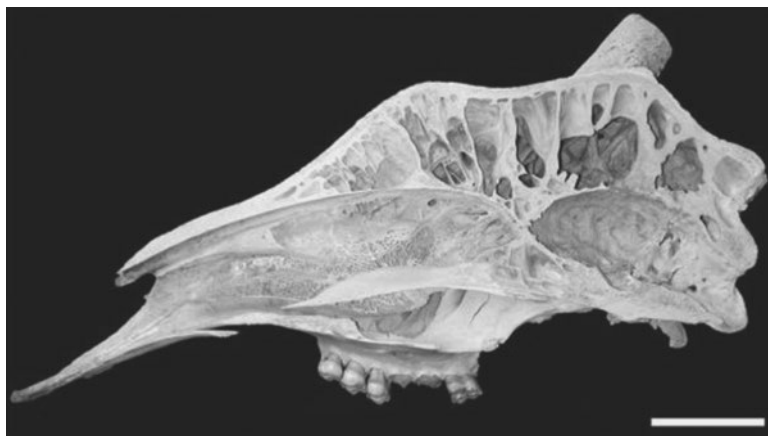


Fig. 4.4 Photograph of a mid-sagittal section of the right side of an adult giraffe skull showing the extent of the frontal sinus, extending over the brain case and into the occipital bone. A bony septum (not shown) divides the right and left halves of the frontal sinus. Trabeculae can be seen through the sinus. Scale bar = 10 cm.

Source: adapted from Badlangana *et al.* (2011). Reproduced with permission of John Wiley & Sons.

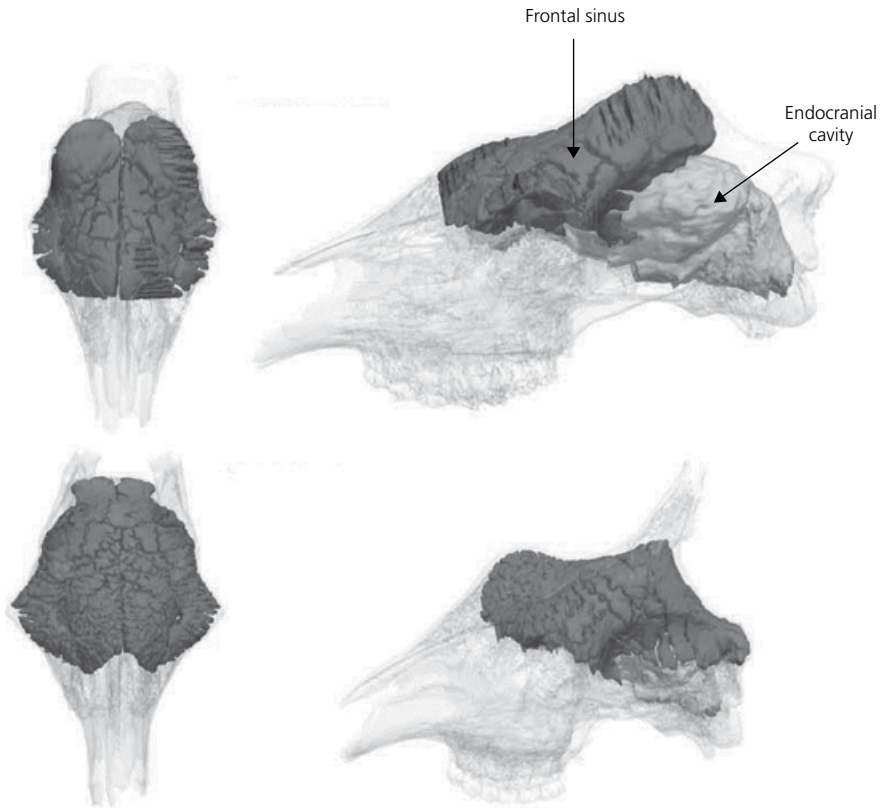


Fig. 4.5 Three-dimensional reconstructions of a neonate (0.5–1 year) (*top*) and an adult giraffe (>5.5 years) (*bottom*) skull showing the extent of the frontal sinus (in dark grey). Image views are left: dorsal, and right: lateral. The endocranial cavity is shown in light grey. Source: adapted from Badlangana *et al.* (2011). Reproduced with permission of John Wiley & Sons.

2780/4407.04 = **0.63**, a young giraffe (0.5–1 year) 460/117.74 = **3.91**, a warthog (*Phacochoerus aethiopicus*) 1260/274.8 = **4.5**, an okapi (*Okapia johnstoni*) 2500/417.06 = **5.99**, a wildebeest (*Connochaetes taurinus*) 1960/258.1 = **7.59** and a domesticated camel (*Camelus dromedarius*) 2800/165.89 = **16.88**. Clearly, in the adult giraffe the frontal sinus is both absolutely and relatively large in comparison to a sample of the other artiodactyls that Badlangana *et al.* (2011) studied, including the closely related okapi.

Why does the giraffe have this large space at the top of its skull? Several explanations have been suggested. These are all examined in some detail by Badlangana *et al.* (2011).

- Ganey *et al.* (1990) and Mitchell and Skinner (2003) suggest that it may assist in thermoregulation of the brain, in a head that is constantly under solar exposure.
- Mitchell and Skinner (2003) suggest that it effectively reduces the mass of the cranium while maintaining an overall 'large head volume' necessary for the support of the jaw muscles.
- Von Muggenthaler *et al.* (1999) believe that giraffes produce infrasonic vocalisations, and suggest that the frontal sinus may act as a resonance chamber for the production of such low-frequency sounds.
- The size and shape of the frontal sinus in the giraffe may represent an adaptation for

increasing the effective surface area for cranial contact during aggressive behaviours without increasing cranial mass. These behaviours include neck-sparring, clubbing and other dominance contests used in competition for mates and the establishment of hierarchies among individuals in bachelor herds (Kingdon 1979; Simmons & Scheepers 1996).

Unfortunately there is no firm evidence for any of these explanations.

The teeth

As already mentioned in Chapter 2, the generalised placental mammal has four types of teeth. The position and number of these teeth can be represented by a dental formula, which in humans is $\frac{2.1.2.3}{2.1.2.3}$. The upper numbers represent the teeth on one side of the upper jaw, and the lower numbers the teeth on one side of the lower jaw. The four successive numbers indicate the number of incisors, canines, premolars and molars. Typical formulae for a ruminant would be $\frac{0.0.2.3}{3.1.2.3} = 28$ (e.g. springbok) or $\frac{0.0.3.3}{3.1.3.3} = 32$ (e.g. giraffe). Therefore in the giraffe, the upper incisors and canines have been lost (being replaced by a hard palate) and the lower canines look like incisors, forming a row of eight chisel-shaped teeth. Also the lower canines are characteristically two or three lobed, effectively increasing the 'incisor row'. This row of eight teeth is arranged in an open half circle (Boué 1970), the teeth pointing forward, with the broad ends of the teeth adapted for stripping off leaves and smaller shoots during browsing, rather than cutting. The molar teeth are nearly square in section and both these and the premolars are adapted for grinding vegetable matter, their grinding surface having complex folds and sharp ridges, described in some detail by Singer and Boné (1960). There is typically a gap, called the diastema, between the incisors/canines and the grinding cheek teeth. Willemse (1950) noted that this diastema becomes longer in older giraffe.

Giraffes, like many browsers, have low-crowned (brachydont) teeth because their natural forage contains little or no abrasive components. On the other hand, grazers consistently have high-crowned (hypsodont) teeth, which protects against the abrasive silica contained in grasses. Clauss *et al.* (2007) have noted that this difference between 'attrition' for browsers and 'abrasion' for grazers frequently results in excessive tooth wear in captive giraffes, who are often fed a diet of alfalfa hay and food pellets (high in silica), rather than a browsing diet. The deciduous, or milk, teeth are the same as in the adult giraffe but with only 12 cheek teeth, the deciduous molars, giving a total complement of 20 teeth. These deciduous molars are finally replaced by the adult premolars.

Both deciduous and adult teeth appear over a sequence of time and can be used to age individuals (Hall-Martin 1975, 1976; Seymour 2001; Singer & Boné 1960), although there is undoubtedly considerable individual variation (Singer & Boné 1960, Figure 3). For both deciduous and adult teeth, the upper teeth tend to erupt before the lower. At approximately 4 weeks, the deciduous canines appear and all the milk teeth are present. At approximately 5.5 years all the adult teeth, apart from the canines, are present. These adult canines are present and fully functioning by about a year later. The height of the tooth, a combination of eruption and wear, can also be used to age individuals (Hall-Martin 1976), although individual diet clearly affects this (Clauss *et al.* 2007).

The horns or ossicones

The horn of the giraffe is different from the horn of bovids because it does not have a sheath made of keratin (the classic horn) and, unlike the antler of cervids (apart from the reindeer or caribou, *Rangifer tarandus*), it is permanent and does not show sexual dimorphism. To make this distinction, Lankester (1902) called it a 'vellericorn',

but in modern literature the term 'ossicone' is frequently used. However, Ganey *et al.* (1990) note that based on development, 'the giraffe horn is an unusual cranial exostosis that lacks clear delineation and categorisation as either horn or antler'. I will simply call them horns.

Five types of horns (parietals, median, occipitals, orbital and azygous) (four of which are paired) were identified by Lydekker (1904) and discussed by Spinage (1968), Dagg and Foster (1982), Ganey *et al.* (1990) and Dagg (2014). However, it should be noted that of the horns examined by Lydekker (1904), only the two parietals and the single median horn were consistent elements of all skulls that he examined. Some of these 'horns' may in fact be simply knobs of new bone growing on the surface of the skull (exostoses), that are a natural part of the giraffe ageing process, particularly that of male giraffes (see later). Ganey and colleagues (1990) looked at eight fresh specimens from the Busch Gardens Zoological Park, Florida, all of which had died recently in captivity. Spinage (1968b) examined the skulls of 52 giraffe in the British Museum and two in the National Museum in Nairobi. He also dissected the heads of three giraffes that had died in zoos: a week-old female, a 22-month-old female and a 23.5-year-old giraffe called 'Maud'.

The giraffe is unique among mammals in that the horns are present in the foetus. At what age they appear is unclear, but they were present in a 10-month-old foetus examined by Lankester (1907) and a 13-month-male foetus examined by Ganey *et al.* (1990). These are the so-called **parietal horns** (the pair clearly visible in both young and adult giraffe), which point backwards rather than standing upright. They are often asymmetrical in any one individual, leaning at different angles and differing in length by up to 35% (Rothschild & Neuville 1911).

There appears to be some disagreement over the presence of cartilage in the horn. A pad of cartilage was reported by Blumenbach (1805), and later by Murie (1872), at the junction of the horn with the skull, but Lankester (1907), looking at a new horn, says that 'it was composed

of a tough fibrocellular material with abundant, interspersed cellular elements.' Spinage (1968), examining a preossified horn (he shows a parasagittal section in his Figure 4), describes the substance of the horn as cartilage. However, Ganey *et al.* (1990) note that although radiographs of the skulls they examined indicated a radiolucency between the skull and the horn that could be consistent with cartilage, their histological studies demonstrate a tissue composed of dense connective material throughout foetal, neonatal and juvenile stages. They also state:

While sparse pockets of cartilage were found within the developing horn of the neonate that we examined, no cartilage was found in either of our juvenile specimens. Ossification is seemingly initiated from a fibrocellular component of the connective tissue, and only during the most accelerated rates of growth does a transition through fibrocartilage seem to occur.

Ossification of this cartilage/connective tissue commences after birth, and the bone of the horn usually fuses with the skull at about 4–4.5 years in the male and 7 or more in the female. However, Owen (1841) recorded a female of over 11 years in which the horns had not yet fused. Once fusion with the skull has taken place, growth in length and thickness still proceeds in the male and sometimes in the female, but much more slowly in the latter. This is by the deposition of bone over the whole surface of the horn, some 2 cm being added throughout life. This makes the male horns quite massive structures reaching a circumference of 22 cm and a length of between 10 and 25 cm (Dagg 2014). They are typically round in cross-section and terminally knobbed. Internally, the bone has an ivory-like compactness and hardness. Female horns rarely show the secondary bone deposition of the males and are slender, tapering structures, oval in cross-section. An exception was provided by 'Maud' in Spinage's skulls (1968). Her horns had formed terminal caps of extra ossification some 3–5 mm thick and of irregular appearance. The horn is usually capped with skin throughout life. The nature of the skin cap was partly described by

Nitsche (1898) and is said to be convoluted and corneous, comprising projecting epidermal papillae. However, the more recent study by Ganey *et al.* (1990) stresses that the horn is an extremely vascular tissue, supplied by the terminal branch of the external carotid artery, which is referred to as the cornual artery, and that a large vascular supply is provided to the skin. There are a few scattered bristly hairs. Neither the hair nor the skin is worn off in life, except at the tip. There is reduction in hair, probably resulting from changes which take place in the epidermis (Ganey *et al.* 1990) or in males during fighting (Dagg 2014).

All the above description is for the large parietal horns that are visible in all giraffes, both sexes and all subspecies. But how real are the other four horns?

The **median horn** originates in the same manner as do the parietals. A boss is formed in the frontal and nasal bones and is accompanied by dermal ossification which in the male eventually fuses with the boss. The fusion occurs later than it does in the parietals. In the adult, the horn bears a cap of horny skin. Almost all female skulls which Spinage (1968) examined were without a median horn. The exceptions were one or two specimens with a fused horn which appeared to be females, two specimens with a small, unfused cone of bone, and 'Maud'. The latter had a pronounced horn, 3.5 cm high. The occurrence of a median horn was used as a diagnostic character between northern and southern forms by Lydekker (1904) and de Winston (1897), and Spinage (1968) also says that the median horn shows least development in '*G. c. capensis*' (*G. c. giraffa*) and is greatest in *G. c. reticulata*. However, Dagg and Foster (1982) considered this character too labile to be diagnostic. Seymour (2001) confirms the first three observations using canonical analysis. He shows that giraffes with a greater median horn height (compared to the distance across the orbital ridges) originate from the north and those with a greater width than height come from the south. However, it is a ratio of dimensions, not an absolute height which is the perception an

observer would have. The posterodorsal region of the orbital rim is very pronounced, becoming more so with increasing age. Its rugose nature in adult males suggests that ossification is taking place over the apex and this may form a distinct knob called by some the **occipital horns** or **mizzen horns** (Dagg 2014). An orbital prominence may similarly develop into what some have called the **orbital horn** and could be seen as a protection for the eye when the giraffe makes sideways sweeps with its head.

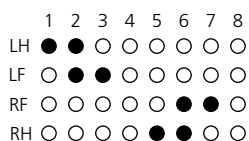
The so-called **azygous horn** lies just posterodorsal to the orbital boss, although it seems likely that Lydekker (1904) used this name in reference to the orbital, for the horn described by him could be an orbital horn. Unfortunately, it is now missing from the original skull. 'Azygous' is actually a misnomer for the horn, since the exostosis can be present on both sides of the head. It differs from other horns in that there is no boss. An azygous horn was present on one of the British Museum specimens and on both sides of the Kenyan Museum specimen examined by Spinage (1968). Singer and Boné (1960) observed it in three skulls.

These azygous horns would not appear to have any function other than that which the 'other exostoses' have. These other exostoses, or protuberances, can be extensive. In the male, and to a much less extent in the female, after the parietal and median horns have fused with the skull, a process of dermal bone deposition commences around them, gradually extending over the whole of the nasal, frontal, lachrymal, parietal and supraoccipital bones. The ossification is usually rough and flake-like, often projected into small pimples. The value of this bony covering of the arteries and veins of the upper part of the skull is self-evident when the giraffe's style of fighting is seen, a conclusion first reached by Urbain *et al.* (1944). This secondary ossification acts as a reinforcement of the skull, increasing with age as the frequency of fighting increases. The skull becomes stronger and heavier, thereby forming a more efficient weapon. A male wielding a skull of 11 kg of bone will have a considerable advantage over one armed

with only 7kg. Although some of these minor irregular protuberances could be traumatic, many cannot be of traumatic origin since they are present in old females that do not, as a rule, fight.

Movement

One of the most striking things about the giraffe is the 'effortless' way in which it appears to move. An adult giraffe can weigh up to 1950 kg (male) or 1200 kg (female), yet its movement appears almost weightless. Unlike a mammal such as a horse, the giraffe has only two different gaits: an ambling walk and a gallop. There is no intermediate trot. In addition, in marked contrast to most ungulates it does not employ the characteristic 'diagonal walk' in which right-front+left-rear are off the ground and moving forward, followed by left-front+right-rear moving forward, which is well described by Dagg and Foster (1976). The giraffe walks by swinging both legs on one side of the body forward at nearly the same time, and then both legs on the opposite side. In fact, the hindlegs leave the ground slightly ahead of the front legs. This type of gait is called a pacing gait and, it should be stressed, is not unique to the giraffe, being found in the okapi (*Okapia johnstoni*), camel (*Camelus dromedarius*), llama (*Lama glama*), topi (*Damaliscus lunatus jimela*), kongoni (*Alcephalus buselaphus*), wildebeest (*Connochaetes taurinus*), hyaena (*Crocuta crocuta*) and some canids, all with sloping backs. Below is a generalised diagram for the pacing gait. These diagrams were first devised by Muybridge in 1887, although this one is from Kar *et al.* (2003). Black circles indicate that the relevant foot is in its support phase (on the ground).



Of course, the giraffe doesn't fall over when only the legs on one side are on the ground, in

just the same way that in bipedal walking we don't fall over when we have only one leg on the ground. As noted above, the giraffe's two legs, on one side of the body, are not always off the ground together. In fact, the giraffe has all four legs on the ground for about 15% of the time (Dagg & de Vos 1968). The legs are not really flexed during each stride, producing a stiff-legged gait. When galloping, the hindlegs swing forward, around the front legs, before the latter move forward. During walking or galloping the giraffe's centre of gravity is partly controlled by the forward and backward movements of the head and neck (Dagg 1962). It is always said, and I have repeated this above, that giraffes walk or gallop but do not trot. In fact, this may not be totally correct. Let's look at these three types of gait. When most mammals walk, they move their feet in turn, always in the same order, at more or less equal intervals of time.

Walking giraffes move their feet with the forelegs moving slightly after the hindlegs of the same side. In trotting, a foreleg swings back while the hindleg on the same side swings forward, so there is a danger of the feet colliding, if the legs are long. In a pacing walk, the legs on one side of the body both swing forward, then both swing back, so the fore and hindfeet are kept well out of each other's way. The fact that some long-legged breeds of dog, as well as the okapi, wildebeest and camelids, also pace instead of trotting supports this explanation of the long-legged giraffe's pacing walk (Kingdon 1979). However, it may also have something to do with the long thoracic spines and sloping back since, as already noted, wildebeest, topi, kongoni and hyaena, all with sloping backs, do not trot either. With an increase in velocity, these species all change directly from a walk to a canter (slow gallop). This may explain the giraffe's unusual gait which in many ways looks more like a slow trot. However, Pennycuik (1975) considers pacing to be mechanically equivalent to a trot, so that giraffes may be said to pace or canter, with the pace gait replacing both the 'straight-backed' walk and trot.

Alexander (1989, 1992, 1996) has attempted to understand the dynamics of animal movement (from man to dinosaurs) by employing simple mathematical models and constructs. Do giraffes move according to the same biomechanical rules as other mammals, or is their movement unique? Dynamic similarity is a concept that applies to all moving systems. Two systems are dynamically similar if one could be made identical to the other by multiplying all lengths by one factor, all times by another factor and all forces by a third factor. For example, two pendulums of different lengths, swinging through the same angle, have dynamically similar motion. Alexander asks the question 'In what circumstances could different-sized animals move in dynamically similar ways?' Their bodies must be geometrically similar, and they must move at appropriate speeds. As animals walk or run, they rise and fall in each stride, gaining and losing potential energy. They also speed up and slow down in each stride, gaining and losing kinetic energy. If an animal of mass m is supported on legs of length L it has potential energy mgL , where g is gravitational acceleration. If it is travelling at speed v , its kinetic energy is $\frac{1}{2}mv^2$. Kinetic energy divided by potential energy = $(\frac{1}{2}mv^2)/(mgL) = \frac{1}{2}v^2/gL$. Dynamic similarity, and therefore generalisations between mammals, are possible for animals of different sizes if their speeds are such as to give them equal values of (v^2/gL) . This dimensionless quantity, v^2/gL , is called a *Froude* number after the Victorian engineer who used similar numbers to analyse wave resistance to the motion of ships. The advantage of the Froude number is that it is not tied to a particular model of walking. It simply suggests that similar-shaped animals, of different sizes, will tend to move in dynamically similar ways whenever possible – that is, when their Froude numbers are equal. They will make corresponding gait changes (from walk to trot, or from trot to gallop) at speeds which make their Froude numbers equal. In general, mammals ranging from small rodents to giraffes change from

walking to trotting at a Froude number of about 0.5, and from trotting to galloping at a Froude number of about 2.5.

However, dynamically similar movement implies more than just changing gaits at equal Froude numbers. It implies, for example, taking strides in proportion to leg length: when dogs and horses travel with equal Froude numbers we can expect the horses' strides to be four times as long as the dogs'. More generally, we can expect graphs of (stride length/leg length) against Froude number to be the same for different-sized animals. This is true for animals ranging from dogs to elephants, and including two-legged as well as four-legged species. The giraffe was not included in Alexander's Figure 2 (1996) but I have obtained the appropriate data from the literature. Christian *et al.* (1999) looked at 'limb swinging' in elephants and giraffe; they measured two giraffes from Allwetterzoo, Münster, Germany. The animals walked along a straight wall in their spacious enclosure without being influenced by any human. The walking speed of the two individuals was 1.1 m/s and 1.3 m/s, with little variation. Stride length divided by leg length was 1.27 ± 0.10 and 1.34 ± 0.17 . The Froude number was 0.08, which fits perfectly with Alexander's data showing that giraffes conform to this generalised model of mammalian biomechanics.

In addition to the anatomy and mechanics of movement, the speed of an animal is an important influence on its evolutionary fitness, mostly by affecting its ability to evade predators and find resources (Alexander 2006). However, while the biomechanics of locomotion are well studied (Alexander 2006; Biewener 2003), the evolutionary pressures influencing interspecific variation in speed have received far less analytical attention (Garland *et al.* 1998; Scales *et al.* 2009). As a consequence, although predator-prey arms races are often used to explain the speed of terrestrial mammals (Dawkins & Krebs 1979; Simpson 1944; Vermeij 1987), there has been no empirical testing of the suggestion. In

fact, three ideas have been put forward to explain herbivore speed.

- 1 The classic idea of strong evolutionary coupling between particular species, with the most vulnerable prey species (i.e. those most preyed upon) expected to be the fastest (the *specific coevolution hypothesis*; Ehrlich & Raven 1964).
- 2 If coevolutionary processes involve the wider community, with predators switching to slower, more catchable species in response to antipredator adaptations in their preferred prey, then the opposite pattern to (1) would be predicted. This scenario would promote diffuse coevolution where, ultimately, the most vulnerable species within the prey community are expected to be those with the strongest constraints on speed evolution (the *diffuse coevolution hypothesis*; Janzen 1980).
- 3 If the need to acquire resources has the potential to cause selection on animal locomotion (Gleiss *et al.* 2011; Pontzer 2012), we might expect that ungulates initially evolved adaptations for running to increase foraging efficiency where food sources are scarce, rather than to escape predators (the *foraging efficiency hypothesis*) (Janis & Wilhelm 1993). Support for this comes from palaeontological evidence which suggests that North American ungulates evolved long limbs before their predators (Janis & Wilhelm 1993).

In an attempt to throw light on this, Bro-Jørgensen (2013) examined the ecological links between sprint speed, predation risk and diet within the herbivore guild of the African savannah. This species-rich community, of which the giraffe is a part, is often seen as a classic example of predator-prey coevolution, and offers an opportunity to investigate the coevolutionary dynamics impacting on speed by using the method of Harvey and Pagel (1991), a comparative method with phylogenetic control (this takes into account, for example, that sable and roan antelope are similar in many ways simply because they're closely related, and is frequently

overlooked in simplistic comparative studies). The five main predators in the system are the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*) and wild dog (*Lycaeon pictus*) (Owen-Smith and Mills 2008; Sinclair *et al.* 2003). Of these, the first two are ambush predators relying primarily on surprise to overcome their prey (Bertram 1976; Hopcraft *et al.* 2005). The last three are pursuit predators, usually chasing their prey for more than 300m (Ewer 1973): the spotted hyaena and the wild dog are long distance runners relying on endurance, whereas both the stalk and chase are important components of the cheetah's hunting strategy (Hilborn *et al.* 2012; Kruuk 1972; van Larwick & van Larwick-Goodall 1970). Bro-Jørgensen's predictions were, first, that with the *specific coevolution hypothesis*, speed will be positively associated with high vulnerability to particular predator species, which are themselves expected to be relatively fast. Second, with the *diffuse coevolution hypothesis*, speed will be negatively associated with vulnerability to predators, as predators in this scenario prey preferentially on the slowest among their potential prey species. Third, with the *foraging efficiency hypothesis*, speed will increase with the dietary proportion of browse and fruit, as these food sources are less abundant than the other major vegetative component, grasses and sedges (Brashares *et al.* 2000; Shorrocks 2007).

Vulnerability of each herbivore species to each of the predators was compiled from Hayward and Kerley (2005), Hayward (2006) and Hayward *et al.* (2006a,b,c). Vulnerability was quantified by using the average Jacobs' index $D = (r - p) / (r + p - 2rp)$, where r is the proportion of the total kills at a site made up by a species, and p is the proportion availability of that prey species at the same site (Jacobs 1974). Data on maximum running speed were obtained from Christiansen (2002) for the mammalian herbivores and from Scott (1997) for the ostrich (*Struthio camelus*). The comparative method with phylogenetic control was used to

identify predictors of herbivore running speed (vulnerability to predators (Jacobs' index), the percentage of monocotyledons in the diet and body mass (logged)). The model with the lowest AIC (Akaike Information Criterion; Pagel 1999) score was selected as the final model. The model that best explained variation in herbivore sprint speed incorporated vulnerability to all five predators but neither diet, nor body mass were significant (Fig. 4.6). However, not all predators had the same effect on herbivore speed. An increased risk of predation by wild dogs, hyaenas or cheetahs was correlated with increased sprint speed but greater risk of predation by lions or leopards was correlated with reduced speed. This is consistent with the idea that running fast may not be a very helpful defence against a predator that attacks from ambush. Figure 4.6 shows that giraffes lie close to the isometric line, suggesting that they have evolved a running speed tuned to their predators and not as a by-product of their phylogeny.

Muscles

A giraffe's muscular system provides the pulling power to enable the above locomotion to take place. In fact, the muscular system consists of three types of muscle: skeletal, cardiac and smooth. I will discuss the cardiovascular system in the next chapter, and the muscular tongue when I look at the digestive system.

The muscles of the giraffe were initially described by several anatomists in the 19th and early 20th centuries (Joly & Lavocat 1845; Murie 1872; Owen 1841; Rothschild & Neuville 1911). The latter examined the omotrachelian muscle which extends from the scapula to the sixth and seventh cervical vertebrae. In mammals with shorter necks, it merely extends to the first cervical vertebra. Zuckerman and Kiss (1932), Willense (1958) and Angermeyer (1966) later described the neck and shoulder muscles, along with their innervation. Giraffes, like other ruminants, have no clavicle bracing the shoulder

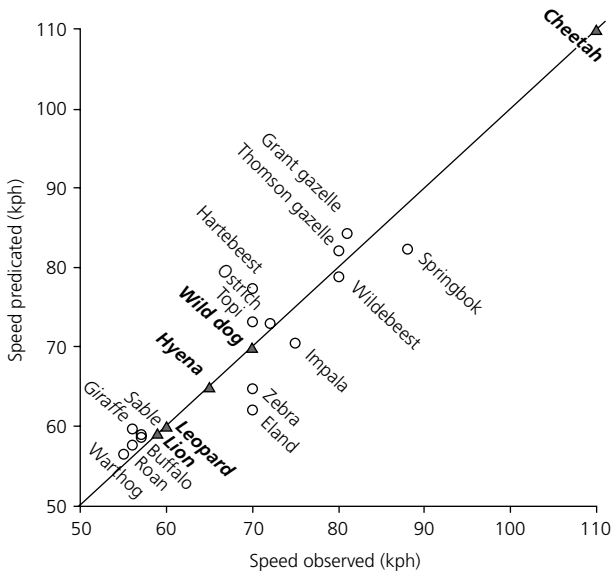


Fig. 4.6 Maximum running speed of African herbivores and their predators. For the herbivores (O), actual sprint speed is shown in relation to the speed predicted from the model based on vulnerability to the five main predators in the system. For reference, the speed of the predators (▲) is shown on the isometric line. Source: Bro-Jørgensen (2013). Reproduced with permission of John Wiley & Sons.

blade. Instead, the shoulder blades are embedded in thick muscle. They have no need of a brace since the legs move in one plane only.

Several large muscles (cephalohumerals, deltoids, triceps and latissimus dorsi) support the front end of the giraffe. The muscles of the legs, along with their innervation and blood supply, have been examined by Bego (1960) and Heinze (1964, 1965). Since the legs are long and stilt-like, the leg muscles are concentrated in the upper part of the leg and the hooves are controlled by long tendons. When the giraffe moves forward, it doesn't need to move the weight of the muscle, but simply swings the legs forward rather stiffly, rather like a pendulum (see above comments on the gait). Long tendons are also found in the neck. In fact, the remarkably long tendons are a feature of the giraffe's muscular system. Endo *et al.* (1997) looked at the muscles of the neck (longissimus, thoracic and cervical, spinalis and semispinalis, cranial muscles, caudal oblique of the head and the multifidus) and the nuchal ligament, and found that the muscles and their associated tendons had all been elongated during the course of evolution. The modified spinous processes provided the large attachment surface for the strong nuchal ligament and for the muscles of the second and other cervical vertebrae, while the muscle tendons had their origin in the ventrocaudally enlarged transverse process. They concluded that the modified muscles with their expanded belly and tendon have the functions of occupying the interspaces among the giraffe's long vertebrae, and also of supporting the head and

neck by means of their wide attachment to the altered vertebral processes.

Perhaps the most bizarre expanded tendon/muscle combination is that attached to the hyoid bone at the base of the tongue. In most mammals this is a short muscle that goes from the hyoid bone to the breastbone. Clearly, in giraffes this would pose a problem because of the long neck. Since a muscle can contract to a third of its length, this could result in the giraffe's larynx being pulled two-thirds of the way down its neck! So in the giraffe, this muscle starts at the breastbone as a fleshy muscle, then becomes a long tendon, then muscle, then tendon again, and finally muscle making attachment to the hyoid bone (Spinage 1968a). Although anatomical research is no longer very popular, two more recent papers have looked at the giraffe's muscles of mastication. Sasaki *et al.* (2001) looked at the largest of these 'eating' muscles, the masseter, and Furuuchi *et al.* (2013) examined the physiological cross-sectional area (PCSA) of four masticatory muscles. PCSA is critical for estimation of bite forces. Three adult giraffe were examined (two males and one female). They also measured muscle mass and fascicle (muscle fibre) length. Compared with the only other data available, the PCSA of giraffe medial pterygoid muscle was far higher than that of several other mammals (except pig). Since the medial pterygoid muscle plays an important role in the lateral movement of the jaw, this might suggest that lateral movement is a dominant component of jaw movement in giraffes.

CHAPTER 5

Physiology

Following on from the last chapter, this chapter will look at the sensory apparatus, internal organ systems and physiology of the giraffe

The sensory organs and nerves

The sympathetic innervation of the giraffe cardiovascular system was described by Nilsson *et al.* (1988). More recently, several people have looked at details of the central nervous system of the giraffe, including nuclear organisation, and found it to be basically similar to that of other ungulates (Badlangana *et al.* 2007a,b; Bux *et al.* 2010).

The mammalian corticospinal tract is known to contain axons that travel from the cerebral cortex to various levels of the spinal cord, and its main function is thought to be the mediation of voluntary movement. Badlangana *et al.* (2007a) describe the neuroanatomy of the corticospinal tract of the giraffe, which may present challenges because of the metabolism required for correct functioning and maintenance of very long axons. The spinal cord of the giraffe can be up to 2.6 m long. However, their study concluded that the spinal cord of the giraffe exhibited no unique anatomical features related to its length, and resembled that of a typical ungulate. Moving from anatomy to physiology, More *et al.* (2013) looked at sensorimotor control in the giraffe by analysing electrophysiology data, and sciatic nerve samples, from the

hindlegs of eight male giraffes. Sensorimotor control comprises both the time required to respond to a stimulus and the precision of stimulus detection. Both giraffes and other large animals must contend with greater sensorimotor delays and lower innervation density in comparison to smaller animals. This is true despite the fact that More *et al.* (2013) found the measured nerve conduction velocity of a giraffe ($50.4 \pm 20.0 \text{ ms}^{-1}$) was similar to that of other mammals with a similar mass ($83 \pm 13 \text{ ms}^{-1}$) (More *et al.* 2010). They point out that the giraffe's conduction velocity, like that of other large animals, is still not sufficiently high to maintain a nerve conduction delay relative to smaller animals. For example, in order to have the same absolute delays as a rat, which has an average nerve conduction velocity of 59.4 ms^{-1} (More *et al.* 2010), the giraffe would require a nerve conduction velocity of 650 ms^{-1} and therefore fibre diameters that were almost eight times the largest they measured.

While there are certainly advantages to being tall, there appear to be challenges as well and More *et al.* (2013) suggest that giraffes are less able to precisely and accurately sense and respond to stimuli using feedback alone, particularly when moving quickly. Larger animals are burdened with relatively long physiological delays, with implications for their behaviour, ecology and evolution, including constraining agility and requiring prediction to help control movements.

Perhaps one of the more interesting features of the nervous system is the extreme detour of the recurrent laryngeal nerve, about 4.6 m (15 ft) in the case of giraffes. Dawkins (2009) makes a convincing case that this detour is yet another piece of evidence for evolution. The nerve's route would have been direct in the fish-like ancestors of modern tetrapods, travelling from the brain, past the heart, to the gills (as it does in modern fish). Over the course of evolution, the neck extended, gills became part of the mammalian larynx (as well as the thyroid and parathyroid) and the heart moved lower in the body. The laryngeal nerve was caught on the wrong side of the heart and natural selection gradually lengthened the nerve by tiny increments to accommodate this, resulting in the circuitous route now observed. Not the work of an 'intelligent designer'!

It is generally stated that giraffes have excellent vision (Innis 1958), and certainly their visual excellence was legendary amongst game wardens (Bryden 1899). Giraffes are thought to detect movement at a distance of at least 2 km (Dagg & Foster 1976) and distinguish colours (Backhaus 1959). Partly this is due to characteristics of the giraffe's retina (Schiviz *et al.* 2008). Like all artiodactyls (in fact, most placental mammals), the retina of giraffes contains only two types of cone which provide the capacity for dichromatic colour vision.¹ It also has a

highly developed 'visual streak', which is an area of high acuity in the retina of many species. Unlike humans, the area of greatest acuity in their retina is not a single point, but rather an elongated 'streak' running across the retina. This allows for better detection of movement in the periphery. It typically lies horizontally at the level of the optic disc and has a high concentration of ganglion cells. In giraffes the streak extends dorsally which appears to be an adaptation to height. This means that when a giraffe looks down, images reaching the eye at a steep angle project onto areas of high cone density.

Although the anatomy of the giraffe eye has been examined by Johnson (1901), Ritland (1982) and Howland *et al.* (2004), the most extensive study has been carried out by Mitchell *et al.* (2013). They measured eye size, orbit orientation and retina surface area in 27 giraffes, of both sexes, ranging in age from neonates to mature adults, and compared their findings with data for other large mammals to assess whether the eye anatomy of the giraffe is unique, how it changes with growth and whether it explains their excellent vision. They found that giraffe eye volume increases from 33 mL at birth to approximately 65 mL in adults. The focal (axial) length increases from ca. 40 mm to 48 mm in adults, and retina surface area from ca. 3000 mm² at birth to 4320 mm² in adults. The orbital axis angle at birth is ca. 73° and the horizontal visual field is mainly monocular and panoramic. With age, the axis angle becomes more acute, to ca. 50° in adults, and the visual field more binocular. These results show that the giraffe eye and retinal surface area are larger than in other ungulates, and their visual fields more binocular, attributes which may explain their visual acuity.

Adult giraffes do not often make a noise audible to human ears, though they certainly have the vocal cords to do so. The myth that adult giraffes are silent, however, is false. They have been recorded making various noises, such as snorts, grunts, moans, bleats and coughs (Dagg 2014; Dagg & Foster 1982) and even a humming

¹While their Triassic ancestors were probably trichromatic, placental mammals are as a rule dichromatic. The ability to see long wavelengths (and thus separate green and red) was lost in the ancestor of placental mammals, though it is believed to have been retained in marsupials, where trichromatic vision is widespread. Dichromatic vision may improve an animal's ability to distinguish colours in dim light. Animals with dichromatic vision have two receptor types (light-sensitive cells in the retina of the eye) used in colour vision. This gives them limited colour vision, with the ability to see only one or two colours (such as blue and yellow). However, they can be better at differentiating between different degrees of luminance (how light or dark an object is), and at detecting hidden objects.

sound (Baotic *et al.* 2015). These last authors collected over 947 hours of audio material in three European zoos and quantified the spectral and temporal components of acoustic signals to obtain an accurate set of acoustic parameters. Besides the known, snorts and grunts, they detected harmonic, sustained and frequency-modulated ‘humming’ vocalisations during night recordings. However, the main vocal communication may involve infrasound (von Muggenthaler *et al.* 1999), too low for human ears to detect. This should not be surprising since other species, including elephants (Payne *et al.* 1986), rhinoceros (von Muggenthaler *et al.* 1992a) and okapi (Lindsey *et al.* 1999; von Muggenthaler 1992), are all known to use infrasound to communicate over distances.

Recordings were made of 16 reticulated giraffe, at two zoological parks in Carolina (von Muggenthaler *et al.* 1999). Audible signals contained frequencies from 11 Hz (75 dB±3) to 10,500 Hz (80 dB±3) (Hz=hertz, a unit of frequency, and dB=decibels, a logarithmic unit of intensity) with dominant frequencies between 150 and 200 Hz. Inaudible vocalisations measured from 14 Hz (60 dB±3) to 250–275 Hz (30 dB±3) with dominant frequencies between 20 and 40 Hz. A behaviour known as a neck throw appeared to be correlated with the signals, leading the researchers to theorise that Helmholtz resonance, $(V=c^2S)/(4p^2Lf^2)$ was responsible for the production of the vocalisations. Additionally, the decibel levels of the inaudible signals decreased rapidly over 40 Hz, which suggests that the vocalisation may be designed to be a covert form of communication. No signals occurred without the ‘neck stretch’ or ‘head throw’ behaviour. Both these behaviours involve the sudden raising of the neck or head, and are also seen in the okapi. Vocalisations occurred more frequently in adult males and young females when giraffes were separated.

How the infrasound is produced is not known. One possibility is that since giraffe vocalisations were only seen during the head throw behaviour, infrasound and other components of

giraffe communication might result from large volumes of air being forced up the neck, and/or possibly channelled through the posterior sinus (see Chapter 4). During the above study, von Muggenthaler *et al.* (1999) noticed a ‘shiver’ or vibration extending from the chest up the entire length of the trachea that occurred during some neck stretches that accompanied vocalisations. It is possible that this ‘shiver’ is air movement, and could be responsible for the infrasound.

The anatomy of the giraffe larynx has been described by Harrison (1980, 1981), Cano and Pérez (2009) and Erdoğan and Pérez (2013). The latter conclude that the anatomy of the larynx and its components in the giraffe, and horse, showed few differences and overall their laryngeal morphological features were similar.

What of the remaining senses – touch, taste and smell? Clearly, giraffe have a sense of touch because they rub their bodies against bushes, perhaps to relieve an itch (Dagg 2014). However, this could also be to remove parasites which are causing them more than just irritation. It would seem likely that both taste and smell are used to choose between plants, but clear tests have not been done. Pereira (2013) carried out some rather artificial experiments on a 3-year-old captive giraffe. She used a ‘discrimination task’ based on the protocols used to train dogs (i.e. search and rescue) to perform olfactory discrimination with multiple stimuli. Birch oil-scented cotton swabs were placed inside the target object which was presented to the subject with other visually identical, unscented objects made from PVC pipe. The results of this study show that a captive giraffe can choose a birch-scented object from an array of unscented objects more often than would be predicted by chance.

The cardiovascular system

The 4–5 m elevation change that an adult giraffe experiences when obtaining a drink of water, or licking salt, is a serious problem. If not for a

series of one-way valves in the blood vessels of its neck (Mitchell *et al.* 2009), the extreme pressure would cause the blood vessels to break when the giraffe lowered its head, and conversely the giraffe would pass out from lack of blood when it lifted its head. In addition, giraffes can also adjust the capacity of the cardiovascular system, and are able to shrink and expand their blood vessels to change the volume of the cardiovascular system very efficiently. It has been estimated (van Citters *et al.* 1968) that distal parts of the arterial system can experience a variation of blood pressure of 400 mmHg and that arteries near the heart can be distended by pressures of over 300 mmHg.

Brøndum *et al.* (2007) measured blood pressure by the insertion of catheters into the central part of the carotid artery and jugular vein of five anaesthetised giraffes, suspended in an upright position. When the giraffe's head was lowered below heart level, the central arterial pressure decreased from 205 ± 14 mmHg to 139 ± 18 mmHg, and central venous pressure fell 2.9 ± 1.2 mmHg. Ultrasound images revealed a significant increase of the cross-section of the cranial part of the jugular veins from 0.12 ± 0.04 cm² to 3.16 ± 0.59 cm², leading to an estimated accumulation of 5 L of blood. This occurs in the network called the rete mirabilis. Just before reaching the brain, the external carotids divide into many small vessels that form this network. The elastic walls of this network expand when the head is lowered to hold more blood, so that the brain is not flooded by excess blood. In addition, when the head is raised, it retains blood so that the head is not depleted of blood while the system is readjusting to the pressure changes (Lawrence & Rewell 1948). The blood pressure in the brain of the giraffe is about 100 mmHg (similar to us, and most other mammals). This level is required to maintain an appropriate blood supply to all parts of the brain. The pulmonary blood pressure, produced by the right ventricle sending blood to the lungs, is approximately 38 mmHg, about double that of other ungulates.

To produce the necessary blood pressure to lift a column of blood to the brain, the giraffe's heart is a huge muscle, with some of its walls up to 8 cm thick and weighing 11 kg, and its resting heart rate is 65 beats per minute, enabling it to produce the 300/180 mmHg blood pressure needed for the blood to reach its head (twice that in humans). Additionally, the heart beats up to 170 times per minute, double that of humans. Perhaps as a consequence, giraffes have a relatively short lifespan of 20 years, and are prone to heart attacks.

It was previously thought that a giraffe had a really big heart, possibly 2.5% of the body mass (Goetz 1955; Goetz & Keen 1957), but recent research has shown this is not so. Instead, the giraffe has a relatively small heart and its power comes from a very strong beat as a result of the incredibly thick walls of the left ventricle. Mitchell and Skinner (2009) looked at the heart of 56 giraffes of all ages, including unborn individuals, culled in Zimbabwe. Heart mass increased almost linearly with body mass in both adults and foetuses, and the heaviest heart (7.8 kg) came from a 1441 kg adult male, which is only 0.54% of body weight. In fact, the relative heart mass (heart weight/body weight ratio) declined with growth and was on average $0.51 \pm 0.7\%$ which was not significantly different from that of mammals in general.

The right ventricle pumps the blood the short distance to the lungs and the muscle here is only about 1 cm thick. The left ventricle has to pump the blood all the way up to the head against the hydrostatic pressure of the blood already in the long vertical artery. A giraffe's left ventricle has therefore evolved to have thick muscle walls and a small radius, giving it great power to overcome this pressure (Fig. 5.1, top). The detailed anatomy has been described by Pérez *et al.* (2009). The thickness of the muscle wall is related almost directly to the length of the neck. For every 15 cm increase in the length of the neck, the left ventricle wall gets another 0.5 cm thicker. The calculations of Mitchell and Skinner (2009) gave a systemic

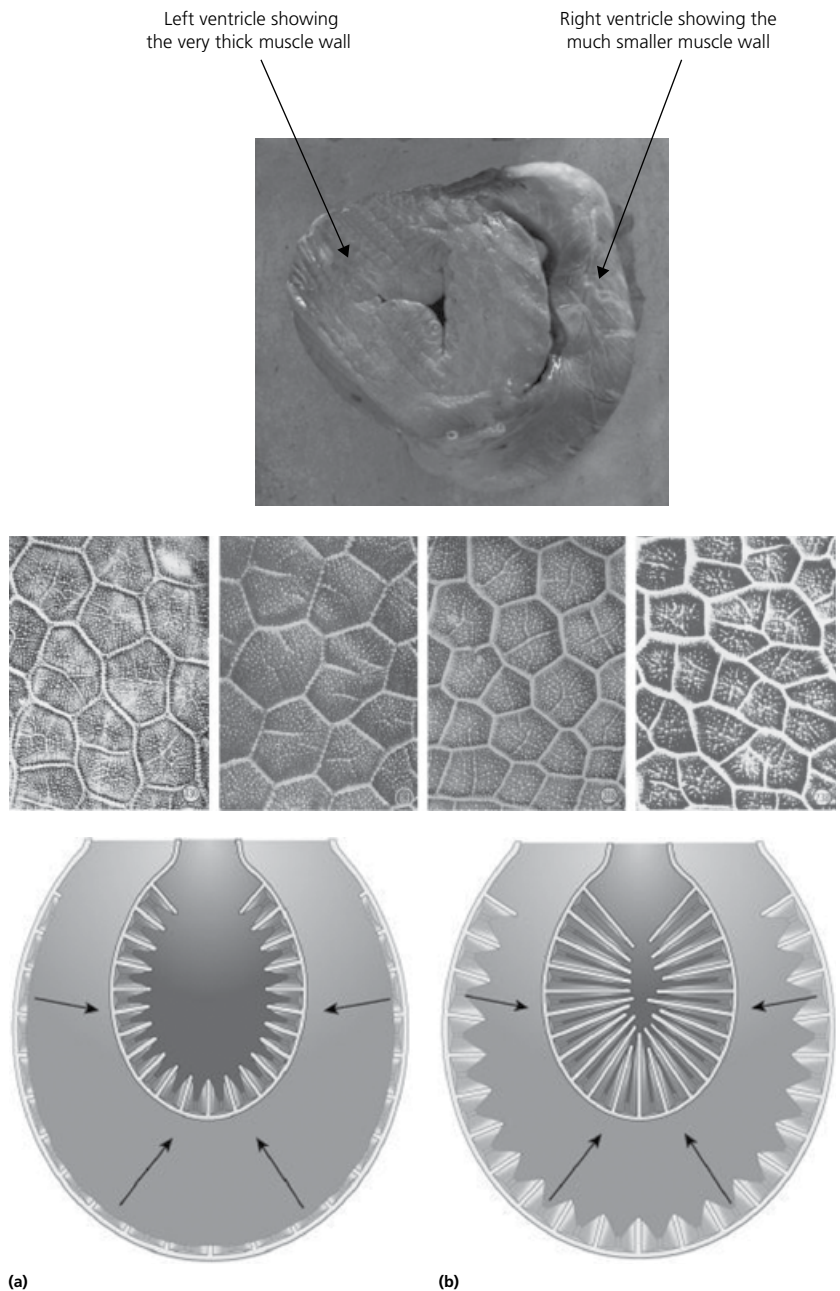


Fig. 5.1 (Top) Cross-section of the mid-point of the ventricles in a 1300 kg mature male giraffe (Mitchell & Skinner 2009). (Middle) Examples of differences in the height and prominence of the crests of the reticular mucosa of ruminants. Left to right: giraffe, suni (*Neotragus moschatus*), impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus*). (Bottom) Schematic representation of the reticulum in a relaxed and contracted state in (a) a typical 'browser' (with shallow reticular crests) and (b) a typical 'grazer' (with high reticular crests). Source: from Clauss *et al.* (2010) (drawings by Jeanne Peter).

blood pressure at the level of the heart, when the neck is at 55° to the vertical, of 208 mmHg in a giraffe of the average body weight in their study (775 kg). This pressure is almost twice the predicted value for other mammals of similar body mass. However, the authors point out that blood pressure in giraffes varies depending on the angle of the neck to the vertical (in addition to age and body weight). At an angle of 30°, it can be predicted to be 187 mmHg in a 775 kg giraffe, 216 mmHg at 60° and 247 mmHg at 90°.

Blood pressure also depends on neck length. Systemic blood pressure at birth in a giraffe (with a body mass of 100 kg; Skinner & Hall-Martin 1975) is the same as in other mammals but as giraffes grow and their necks elongate, it rises. These predicted blood pressures lie within the range of measured values. As Mitchell and Skinner (2009) point out, there are 29 measurements of giraffe systemic blood pressure reported in the literature and they were made in animals that had a similarly wide range of body masses, neck lengths and angles as their giraffes. These measurements give an average systemic blood pressure of 203 ± 41 mmHg (Goetz 1955; Goetz & Keen 1957; Goetz *et al.* 1960; Hargens *et al.* 1987; Linton *et al.* 1999; McCalden *et al.* 1977; Millard *et al.* 1986; Mitchell & Skinner 1993; Patterson *et al.* 1957, 1965; van Citters *et al.* 1966, 1968, 1969). The range in blood pressure values in the literature arises from the fact that individuals of different age and weight (the two are correlated, of course) were used, along with the animals having their necks at different angles. There is also the issue of the 'measurement situation' since blood pressure is very prone to effects of stress. Many of these blood pressure measurements were done under rather artificial 'captive' situations. One giraffe actually died during one of these measurements (Goetz *et al.* 1960). Probably some of the more reliable estimates are those of van Citters *et al.* (1966) and Warren (1974) since after

anaesthetisation and the stitching of a transducer into the right carotid artery, the animals were allowed to recover and walk about freely. As they walked about and browsed, their blood pressure ranged from 180/120 mmHg to 140/90 mmHg. The upper figure is the systolic figure and measures the pressure in the arteries when the heart muscle contracts. The bottom number, which is always the lower of the two numbers, measures the pressure in the arteries between heartbeats (when the heart muscle is resting between beats and refilling with blood). When one male galloped, its heart beat rate increased from below 60 to 170 beats per minute with a peak blood pressure of 230/125 mmHg.

The cardiovascular anatomy of the giraffe is essentially like that of other ungulates. Those vessels in the neck and legs are, of course, longer than many ungulates and they have an interesting structure. The carotid arteries have collagen fibres linked to the smooth muscle walls (Kimani 1981a), and microscopic examination shows that the tunica intima (the innermost layer of the carotid wall) contains a subendothelial elastic layer which changes in size along the length of the neck (Kimani 1983a). It gets progressively larger as you descend the neck towards the heart. The arteries below the level of the heart tend to have more muscular walls and smaller lumens than those above the heart (Maluf 2002). For example, while both the carotid artery (near the head) and the posterior tibial artery (in the leg) have identical total diameters of 3 mm, the leg vessel has a wall thickness seven times greater than the head vessel (Paton *et al.* 2009). Other work on the blood vessels of the giraffe are detailed in Kimani (1981b, 1983b), Kimani and Mungai (1983a) and Kimani and Opole (1991), on the carotid arteries. There is also work by Kimani (1987) on the vertebral artery, by Kimani *et al.* (1991) on the intercranial arteries and on the arterial system of the brain by Frackowiak and Jakubowski (2008).

The respiratory system

The elongated shape of the giraffe has produced relationships between structure and function that are different to those found in other mammals. This is true for the cardiovascular system (see earlier), the nervous system (Badlangana *et al.* 2007a), and skeleton (see Chapter 4). It is also true of the respiratory system. Clearly, a long neck will have a long trachea, and a long trachea suggests a large respiratory dead space (dead space is the volume of air which is inhaled, such as that in the mouth and trachea, that does not take part in gas exchange). In addition, the relatively small volume of the abdominal and thoracic cavities limits the space for lung expansion (Murie 1872). The former complication was noticed first by Vosmaer (1787) during his reconstruction of a giraffe skeleton. He found that the 'ribs formed a right angle with the spine and are rigid, incapable of being spread to facilitate respiration' (Vosmaer 1787).

Respiration, therefore, is achieved by the diaphragm. This conclusion was supported by the anatomical studies of Joly and Lavocat (1845) and Cobbold (1854). Cobbold later measured lung mass as an indicator of lung volume and in three animals found it to be 0.56%, 0.82% and 0.84% of body mass (Cobbold 1860) whereas allometric predictions suggest that its relative mass should be greater than 1% (Stahl 1967; Tenney & Remmers 1963). This small lung mass has been given as the reason for the supposed low exercise capacity of giraffes, most observations of which, however, are anecdotal and historical (e.g. Joly & Lavocat 1845; Lydekker 1901). In fact, the first formal analysis of giraffe respiratory anatomy was not made until Robin *et al.* (1960) found that dead space volume was nine times and total lung volume eight times that in humans. Also, the alveolar wall was thicker and the lung elastic fibres more numerous and coarser than they were in humans. Robin *et al.* (1960) concluded that to overcome the large

dead space, the lungs were disproportionately larger and the respiratory rate lower (8–10 bpm) than expected for similar-sized animals. Patterson *et al.* (1957, 1965) compared giraffe and cow respiratory characteristics and also found a large dead space volume in giraffes (2.6 mL/kg vs 1.0 mL/kg in cows), a lung mass of the expected 1% of body mass but a 'surprisingly small lung volume' and a higher respiratory rate. Inspiration time was prolonged compared to cows (ca. 2–3 s vs 0.9 s respectively), expiration time was similar (1.62 s vs 1.67 s) and the average ratio of inspiration time to expiration time was 1.2 in giraffes and 0.6 in cows (Patterson *et al.* 1965).

However, Hugh-Jones *et al.* (1978) came to different conclusions. They found that while the giraffe's dead space was ca. 3 mL kg⁻¹, it was 3.6 in deer (*Cervus elephas*), 3.1 in llama (*Lama glama*) and 1.8 in camels (*Camelus dromedarius*), and therefore not unusually large. They concluded that giraffes compensated for a long neck by having a trachea that was narrower than normal, resulting in greater resistance to airflow, which could explain the longer inspiratory time found by Patterson *et al.* (1965). Langman *et al.* (1982), who measured dead space volume, also concluded that it was not particularly large because the trachea, although long, was narrow and that resistance to airflow would be high. Therefore, increases in minute volume (the volume of gas inhaled or exhaled from the lungs per minute) would be brought about by increased respiratory rate, not tidal volume (the normal volume of air displaced between normal inhalation and exhalation when extra effort is not applied). However, it should be noted that these contrary conclusions were based on a total of nine giraffes, all young adults, of a body mass of 500–600 kg.

More recently, Mitchell and Skinner (2011) studied the respiratory anatomy of 46 giraffes. They quantified static lung volumes and dynamic lung volumes, and compared these to values that could be expected in similar-sized mammals, in order to establish whether the respiratory

system of giraffes is different to that of other animals. They measured lung mass and trachea dimensions, in both males and females, ranging in body mass from 147 kg to 1441 kg, and estimated static lung volumes (not affected by airflow) and dynamic lung volumes (affected by airflow), and developed allometric equations that related these to growth. These lung volumes were estimated because (1) the animals were dead and (2) giraffes cannot in any case be persuaded to breathe appropriately, on command. They found that relative lung mass was $0.6 \pm 0.2\%$ of body mass which was significantly less than in other mammals ($1.1 \pm 0.1\%$). Total lung volume was significantly smaller ($46.2 \pm 5.9 \text{ mL kg}^{-1}$) than in similar-sized mammals ($75.0 \pm 2.1 \text{ mL kg}^{-1}$). The lung volume/body mass ratio decreased with age, rather than increasing as it appears to do in other mammals. Tracheal diameter was significantly narrower than in similar-sized mammals but dead space volume ($2.9 \pm 0.5 \text{ mL kg}^{-1}$) was larger than in similar-sized mammals ($2.4 \pm 0.1 \text{ mL kg}^{-1}$). Their calculations suggest that tidal volume ($10.5 \pm 0.2 \text{ mL kg}^{-1}$) is increased compared to that in other mammals ($10.0 \pm 0.2 \text{ mL kg}^{-1}$) so that the dead space/tidal volume ratio is the same as in other mammals. Calculated functional residual capacity (the volume of air present in the lungs at the end of passive expiration) is smaller than predicted (53.4 ± 3.5 vs $33.7 \pm 0.6 \text{ mL kg}^{-1}$), as is expiratory reserve volume (the additional air that can be forcibly inhaled after the inspiration of a normal tidal volume) (47.4 ± 2.6 vs $27.2 \pm 1.0 \text{ mL kg}^{-1}$), but residual volume (the volume of air still remaining in the lungs after expiration) ($6.0 \pm 0.4 \text{ mL kg}^{-1}$) is the same as in other similar-sized mammals ($6.0 \pm 0.9 \text{ mL kg}^{-1}$). Their calculations suggest that inspiratory reserve volume (the additional air that can be inhaled after the inspiration of a normal tidal volume) is significantly reduced in size (11.6 ± 1.6 vs $3.8 \pm 2.4 \text{ mL kg}^{-1}$), and, if so, the capacity to increase tidal volume is limited. Calculated dynamic lung volumes were the same as in similar-sized mammals.

Overall, Mitchell and Skinner (2011) conclude that the static lung volumes of giraffes are smaller than expected for an animal of their body mass, probably because of the shape of their skeletons. Their dead space volume and tidal volume are much greater than expected because of their long necks, despite significant narrowing of their trachea which has the advantage of limiting increases in dead space volume. The main consequences of a small lung volume and a long trachea appear to be a reduced inspiratory reserve volume and high resistance to airflow. These limit the capacity to increase tidal volume, and prolong the time it takes to inhale and exhale a single breath. Nevertheless, the supply of oxygen to tissues is not compromised, although during exercise Mitchell and Skinner (2011) believe that lung anatomy may limit the aerobic capacity of giraffes. However, as Dagg (2014) has observed, a giraffe can outrun a horse and gallop at 60 km h^{-1} for at least 5 minutes (Langman *et al.* 1982).

The digestive system

In chapter 2 I mentioned briefly the two digestive systems of ruminants and non-ruminants. It is useful to elaborate on the ruminant system of ungulates before talking specifically about the giraffe.

Ruminants, apart from the four species of primitive ruminants called chevrotains, have a complex four-chambered stomach. Vegetation is swallowed and initially enters the first chamber or rumen. The coarsest plant particles (the cud) float to the top of the rumen, are regurgitated by its contractions and rechewed in the mouth (rumination). The rechewed food is then returned to the rhythmically contracting second stomach, or reticulum, for 'sorting'. Food particles are eventually pumped into the third stomach, or omasum (also known as the 'book organ' because of the leaf-like plates that line it), and filtered. The digestive process is completed in the fourth or 'true stomach'

(abomasum) and small intestine, and additional fermentation and absorption takes place in the caecum. In ruminants, therefore, cellulose digestion takes place, before normal digestion, in the rumen. Ruminants are therefore able to extract more nutrients from their plant food, but pass it through their digestive system very slowly, compared to hindgut fermenters. They require high-quality food. Ruminants can also recycle urea (normally a waste product excreted in the urine) and can therefore conserve water. In the ruminant stomach, the protein in the plant food is converted to ammonia and transported in the blood to the liver. Here it is converted to urea and transported back to the stomach where the micro-organisms use it as food. In addition to their role in cellulose fermentation, these micro-organisms excrete fatty acids which are used by their host. They also provide them with protein, as they pass down the ruminant's digestive system, mixed with the vegetable food (Demment & van Soest 1985).

However, although ruminants have a more efficient system for dealing with the cellulose component of plant food, and gain protein and fatty acids from the micro-organisms themselves, their one major disadvantage is that they cannot process food quickly. The more fibrous the food, the longer the process can take. When the protein content of plant food falls below about 6%, ruminants cannot process their food fast enough to maintain their weight and condition (McNaughton & Georgiadis 1986).

Another feeding distinction that has arisen in ungulates is that between grazers (roughage eaters), browsers (selective eaters) and mixed feeders (Estes 1991a; Hofmann 1968). Grazing ungulates feed on monocotyledonous plants (essentially grasses, but also reeds and rushes), while browsers, like the giraffe, feed on dicotyledonous plants (mainly tree foliage, but also fruits and herbs). Mixed feeders (e.g. elephant (*Loxodonta africana*) and impala (*Aepyceros melampus*)) are both grazers and browsers, often switching their foraging activity between the wet season (grass) and the dry season (foliage).

Some small browsers, such as klipspringer (*Oreotragus oreotragus*) and bushbuck (*Tragelaphus scriptus*), are extremely selective feeders, choosing food with the highest protein content. They tend to feed in short bouts and rarely fill the rumen more than half full before stopping to ruminate. Larger browsers such as giraffe, gerenuk (*Litocranius walleri*) and lesser kudu (*Tragelaphus imberbis*) need to take in more food and cannot afford to be as choosy. They often have larger and more subdivided stomachs designed to slow down the passage of food and allow more time for fermentation.

In contrast to these selective browsers, bulk grazers (Estes 1991a) such as waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer caffer*) tend to keep eating until the rumen is full, often regardless of grass quality. The different stomach chambers are more muscular and subdivided in order to churn, pump, sieve and filter the ingested food. The omasum, which in the selective browsers is simply a straining chamber, is highly developed. So-called roughage grazers (Estes 1991a), such as hartebeest (*Alcelaphus buselaphus*) and topi (*Damaliscus lunatus jimela*), are frequently more selective in the parts of the grass they eat and can consequently often survive on poorer grass swards. These dietary differences may aid the coexistence of herbivores (Shorrocks & Bates 2015).

Recently, Clauss *et al.* (2010) revisited these ruminant comparisons with particular reference to the second chamber, the reticulum. They examined differences in over 60 ruminant species of different body sizes and feeding types, including giraffes, but controlling for phylogeny in their comparisons. The reticulum has long been recognised in domestic ruminants as the site of particle sorting (Mathison *et al.* 1995; Okine *et al.* 1998; Reid 1985). In wild ruminants, empirical evidence also points towards the reticulum as the major site of particle sorting (Clauss *et al.* 2009a,b). In domestic ruminants, the two-phase contractions of the reticulum lead to an ejection of larger, floating

particles back into the rumen, while fluids and finer, denser particles pass into the omasum. In the second contraction phase, the reticulum contracts completely in cattle so that its lumen disappears, and the empty reticulum relaxes and refills with contents from the rumen.

How the anatomy of the reticulum, especially the unique shape of its lining mucosa, which is arranged in net-like ridges (hence the name 'reticulum') or 'honeycomb cells', accomplishes its function is unclear. However, the height of the reticular crests and the depth of the honeycomb structures vary considerably across species (Fig. 5.1, middle). Reticular crests are shallow in okapi (*Okapia johnstoni*), giraffe and deer, and higher in chamois (*Rupicapra rupicapra*), sheep and cattle (Burne 1917; Neuville & Derscheid 1929). Grazing ruminants tend to have higher reticular crests than browsers, and more pronounced crests (Hofmann 1969, 1973; Langer 1988). Hofmann (1973, 1989) suggested that, in general, browsing ruminants have a larger reticulum than grazers, something that Langer (1988) confirmed statistically using Hofmann's (1973) data. The suggested functional reason for this observation is that the entire reticulo-rumen might be involved in particle separation in grazers, in which rumen contents are prominently stratified, whereas in browsers the sorting mechanism might be spatially limited to the reticulum only, which might therefore need to be of a larger size (Clauss *et al.* 2009b,c; Hummel *et al.* 2009). Clauss *et al.* (2010) found that for a giraffe, rumen height was 75 cm, reticulum height was 32 cm, reticulum width was 18.8 cm and reticular crest height was 2 cm. Reticulum size was more or less constant in ruminants across both body size and feeding type (grazers or browsers). Linear dimensions generally scale allometrically, that is, to body mass^{0.33}, with or without controlling for phylogeny. Species that ingest a higher proportion of grass in their natural diet had both significantly larger (higher) rumens and higher reticular mucosa crests, but neither reticulum height nor reticulum width varied with feeding type. In browsing species with rumen contents

that may be less fluid and more viscous than those of the reticulum, incomplete closure of the lumen may allow the reticulum to retain the fluid necessary for particle separation. In grazing species, whose rumen contents are more stratified with a larger distinct fluid pool, a more complete closure of the reticular lumen due to higher crests may be beneficial as the reticulum can quickly refill with fluid rumen contents that contain presorted particles (Fig. 5.1, bottom).

The general anatomy of the giraffe's digestive system is much like that of any other ruminant. Tongue and mouth, oesophagus, four-chambered stomach, small and large intestine, caecum and colon. There are of course finer details, as in the reticulum's lining mucosa noted earlier, but the general anatomy is not much different to that of the well-studied cow. Such differences as do exist are mainly explained as the result of the giraffe's browsing diet, as opposed to a grazing diet, again as noted for the reticulum's lining mucosa earlier.

Some brief details now conclude this section. The giraffe's tongue is long (45–50 cm) and prehensile. From a distance, the tongue appears black but closer it is often described as bluish-black or even purple. The base is pink. It is frequently stated that the front part of the tongue has the dark pigmentation, under the epithelium, to protect it from the sun while eating. The tongue is covered by a mucous membrane, modified to form numerous thickened papillae which may, along with its thick saliva, protect it from sharp *Acacia* thorns. The tongue is extremely powerful (Sonntag 1922) with muscle fibres running both across and down the organ (Lahkar *et al.* 1992). The transverse muscles contract to extend the tongue, enabling it to grasp leaves, and the longitudinal muscles contract to bring the tongue, and its leaves, back into the elongated mouth.

The hard palette forming the roof of the mouth has 18 transverse folds with the free edges turned backwards (Pérez *et al.* 2012), which may help to direct food to the grinding cheek teeth. There are parotid, mandibular,

sublingual and buccal salivary glands (Kayanja 1973; Kayanja & Scholz 1974). There are small tonsils at the back of the throat (Hett 1928).

The four-chambered stomach is similar to most other ruminants and its general functioning has already been described, along with the more specific structure and function of the reticulum. In the first chamber, the rumen, fermentation begins and both Hall-Martin and Basson (1975) and van Hoven and Boomker (1985) describe in some detail the chemical contents. Kleynhans and van Hoven (1976) examined the rumen of eight adult female giraffe from the Transvaal and recorded 26 species of ciliates. The genus *Entodinium* with 11 species formed 41% of the total protozoa population. The holotrichs formed 19%, the genus *Enoploplastron* 16% and *Eodinium* 11% of the population.

The gross macroscopic anatomy of the intestine has been described by Pérez *et al.* (2009). When compared with the cow, the giraffe has a comparatively short small intestine and a comparatively long large intestine (25 m) which Pérez *et al.* (2009) suspected was associated with a browsing diet. The total length of small and large intestine and caecum is 76 m and Dagg and Foster (1982) give a detailed breakdown (Table B1, page 162) for 15 individuals. After the abomasum, or fourth stomach, digestion is completed in the small intestine and caecum, with only water absorption occurring in the large intestine.

The liver varies in shape, size and position and has been described by several anatomists (Cobbold 1854; Crisp 1864; Murie 1872; Schneider 1951; Stanley 1890; Wakuri & Hori 1970). The status of the gall bladder is equivocal. Cave (1950) dissected 19 giraffe and found only two with gall bladders, one of which was in a foetus. However, two more recent anatomists (Kobara & Kamiya 1965; Wakuri & Hori 1970) did find gall bladders in three adult individuals.

Like other ruminants, the giraffe has two kidneys which have been described in detail by Wroble (1965), Epelu-Opio (1975) and Maluf

(2002). A giraffe weighing about 1000 kg and eating 34 kg of *Acacia* leaves (containing 60% water) takes in 20.3 L of preformed water daily (C. R. Taylor, personal communication in Dagg & Foster 1976). Metabolic intake of water is estimated at 3.4 L/day. Thus, a fully grown giraffe would have at its disposal 23.7 L of water daily, or about 2.4 L/100 kg. By eating succulent leaves, a giraffe can therefore do without surface water. Maluf (2002) analysed the urine of 45 giraffes and found a blood urea nitrogen of 18 ± 8 mg/dL, a serum creatinine of 1.8 ± 0.4 mg/dL and a total plasma protein of 6.9 ± 1.1 g/dL (globulin 3.5 ± 0.9 g/dL and albumin 3.3 ± 0.5 g/dL).

The reproductive system

The reproductive system of the giraffe is essentially like that of other ungulates. In females there is a vagina, uterus and ovaries, and in males there is a penis, testes and associated glands (Harris 2010).

As with the other internal systems, early anatomists dissected a few giraffes and then examined, described and measured the organs. Murie (1872) measured the ovaries of one adult as $7 \times 2.5 \times 2.5$ cm. Lueders *et al.* (2009) give a value of 2.4×3.5 cm for the oval-shaped ovary. Hall-Martin and Skinner (1978) stated that embryos are free, unimplanted, in the uterus for 30 days. The implantation site was always found to be on the side of the corpus luteum. The giraffe has a typical ruminant macrocotyledonary placenta, which is implanted in both uterine horns, with the foetus located in the side of the corpus luteum (formed at the site of a follicle that has matured and released its egg. It secretes the hormone progesterone).

The number of cotyledons seems to vary considerably (cotyledons are 'villi' on the uterine surface of the placenta, surrounded by maternal blood, enabling the exchange of oxygen and nutrients with the foetal blood). Hall-Martin and Skinner (1978) counted the number of cotyledons as 149, 183 and 191 in

three pregnancies. Deka *et al.* (1980) found 178 cotyledons, but numbers recorded appear to range from 47 to 191. Ludwig (1962), who made the most detailed description of the giraffe placenta, did not enumerate the cotyledons of his two specimens. Hradecky *et al.* (1987), in comparing giraffe and okapi placentas, made the point that the number of cotyledons and structure of placental villi are sufficiently different to negate successful interspecific embryo transfer. The giraffe's placental villi are long, thin and sparsely branched, and the villi are of different lengths according to Ludwig (1962) who dissected individual villi. In contrast to other placentas from bovids, there are few trophoblastic binucleate cells, a finding also commented upon by Ludwig (1962). Glycogen was found in the amnion, but in no other regions (Ludwig 1962). Electron microscopic studies were reported by Reissig (1977). The placenta he studied had 167 cotyledons, which were of a brown colour on the maternal side. The umbilical cord inserts in the mid-portion of the two horns. Hradecky (1983) described the length of the cord as 140 cm in one specimen. Ludwig (1962) describes the vascular structure extensively.

Oestrous cycles occur every 14+ days, and last 24 hours (Hall-Martin & Skinner 1978). All types of giraffe examined have 30 chromosomes (2n); 28 are metacentric, the smallest pair are acrocentric (Hösli & Lang 1970; Huang *et al.* 2008; Koulisher *et al.* 1971; Taylor *et al.* 1967). Huang *et al.* (2008) suggest that translocations are mainly responsible for interspecific karyotype differences between giraffes and other pecorans, since they show a high degree of conservation in G-banding patterns, a technique used in cytogenetics to produce a visible karyotype by staining condensed chromosomes.

Before the paper of Hall-Martin *et al.* (1978), knowledge of reproduction in male giraffes was limited to some observations on the testicular artery and spermatozoa (Glover 1973), a description of the male genital tract and sperm (Velhanker *et al.* 1973), a note of

the reproductive status (Field & Blankenship 1973), and a discussion about reproduction in the giraffe in relation to environmental factors (Hall-Martin *et al.* 1975). The testes are descended at birth, contained in a pendulous scrotal sac and oval in shape. They measure 10/14 × 6/8 cm (excluding the epididymis). The epididymis (a narrow, tightly coiled tube connecting the rear of each testicle to its vas deferens) has no special giraffe features and consists of a well-demarcated head (caput), body (corpus) and tail (cauda), as in other mammals. Each vas deferens, which transports the sperm from the epididymis to the ejaculatory ducts) is about 60 cm long and leads to a prominent ampulla up to 10 cm in length. Conspicuous, paired, seminal vesicles, which secrete a significant proportion of the fluid that ultimately becomes semen, open into the urethra. The prostate gland, like that of other ruminants, consists of a glandular layer that surrounds the urethra (pars disseminata) and a main body. The bulbourethral glands (which contribute to the ejaculate) are oval and are situated in a fibrous capsule on the pelvic part of the urethra, covered by muscle. In mature males, the penis can measure up to 77 cm and has a marked downward, sigmoid flexure at the end. The penis retractor muscles are attached to the distal part of the flexure and are about 13 cm long (Hall-Martin *et al.* 1978). Giraffe sperm have an average head length of 5.77 µm and an average total length of 47.77 µm (Velhanker *et al.* 1973).

Growth

I have already touched on some aspects of giraffe growth in Chapter 4, for example the eruption of teeth. Here I briefly outline the growth statistics of giraffes, from birth to death, and detail some interesting aspects along the way.

The same variation, almost certainly for the same reasons, is seen for growth statistics as was noted at the beginning of Chapter 4 for adult

height and weight measurements. Behaviour associated with birth, such as birth site fidelity, will be examined later, although it is flagged up here. Giraffes normally give birth to one young. Occasionally twins have been recorded, but the norm is one calf. The average gestation period is approximately 15 months. Backhaus (1961) gives a range of 453–464 days, recorded from 35 captive females. A slightly different range (446–457 days) is given by del Castillo *et al.* (2005). Lueders *et al.* (2009) state that the gestation period for captive Rothschild's giraffes is about 470 days. Skinner and Hall-Martin (1975) say that for the southern giraffe, the 'gestation period is calculated as 457 days being the mean of 48 observations of other workers'. However, the earliest on record is 394 days (Lang 1955), a premature birth, and the longest 488 days (Robinson *et al.* 1965) for an old mother. Giraffe are iteroparous, characterised by multiple reproductive cycles over the course of their lifetime. The first birth occurs when a female is between 5 and 7 years of age, the interval between births is about 2 years, and female giraffe bear young throughout the year (Bercovitch & Berry 2010; Bercovitch *et al.* 2004; Dagg 2014), although conception peaks can coincide with increased rainfall (Hall-Martin *et al.* 1975).

The average height at birth, from records of seven captive giraffe, was found to be 1.67 m (Dagg & Foster 1976, Fig. 6.1). Newborn calves grow very quickly and these same seven giraffes had an average height of 3.06 m by 1 year (Dagg & Foster 1976, Fig. 6.1). From Dagg and Foster's table 10-3, the mean height (m) at birth for 30 captive giraffes is 1.68 ± 0.07 ($\pm 95\%$ confidence limits). From the same table, 21 'newborn' calves had an average weight (kg) of 57.48 ± 6.38 , therefore showing more variation. Skinner and Hall-Martin (1975) give a birth weight of 102 kg from measurements on wild southern giraffe. It should be noticed that this is almost twice as great as the Dagg and Foster (1976) figures for captive giraffe. But it should be noted that subspecies also differ in height and weight, as I indicated at the beginning of Chapter 4. However, it's a cautionary note

about using measurements, and observations, from captive giraffe.

Giraffes are often said to give birth in a 'calving ground' and that mothers will often return to where they were born to give birth to their own young (Estes 1991a; Kingdon 1997). However, the only serious test of this birthing site fidelity story (Bercovitch & Berry 2015a) did not confirm it. Giraffes appear to have no formal breeding season, although the published data is not 100% clear on this, as indicated by the contradictory statement that calving is often synchronised to provide safety in numbers against predators. This again may be a result of different subspecies, different geographical locations and different years when observations were made (see Chapter 6). Giraffes give birth standing up, so that the calf falls about 2 m to the ground. The newborn calf can stand and run within an hour of being born, at which point it will start to suckle its mother's milk. Calves remain reliant on their mother's milk for up to 9–12 months. Solid food (browse) can be eaten from about 4 months at which time calves begin to ruminate (Dagg 2014).

The colostrum² and milk of giraffe has been analysed by Stephan (1925), Aschaffenburg *et al.* (1962), Ben Shaul (1962), Glass *et al.* (1969), Hall-Martin *et al.* (1977a), Dagg and Foster (1982) and Petzinger *et al.* (2013). The colostrum has more fat, ash and protein content than the later milk, but less lactose. Aschaffenburg *et al.* (1962) note that the main characteristic of the milk was its high fat content, 12.5%. The contents of Ca pantothenate, riboflavin, thiamine and vitamin B₆ (pyridoxal) were similar to

²Colostrum is a form of milk produced by the mammary glands in late pregnancy. Most species will generate colostrum just prior to giving birth. Colostrum contains antibodies to protect the newborn against disease; it is lower in fat and higher in protein than ordinary milk. In humans, colostrum is known to contain immune cells (as lymphocytes) and many antibodies such as IgA, IgG and IgM (Ig=immunoglobulin). These are the major components of the adaptive immune system.

those in good-quality cow's milk. The contents of biotin and alpha-tocopherol were lower, and those of nicotinic acid, vitamin B₁₂ and vitamin A higher than in cow's milk. No carotenoids were present. Petzinger *et al.* (2013) found that reticulated giraffe milk was higher in dry matter during the first month of lactation (25.7% versus 17.9%), but had little change in sugar or crude protein. Fat was higher in the first month (11.0%), compared to the remainder of lactation (5.9%), and there was more fluctuation in the amount of fat than protein or sugar. The ash content of reticulated giraffe milk was fairly constant over lactation (0.98%), whereas the milk had higher calcium (1.48 kcal/g milk) during the first month, compared to later (1.00 kcal/g milk). The milk contained 36 mg protein/kcal during the first month and 47.3 mg protein/kcal for the remainder of lactation, possibly facilitating increase in growth rate for calves after the first month of life. Several growth curves have been published for life-time growth of giraffes and three published examples are summarised in Fig. 5.2.

Thermoregulation

Reference to the suggested role of the 'dark patches' on the skin with regard to thermoregulation has already been made in Chapter 4, as has the role of the frontal sinus. There is no experimental evidence for these two roles, although the 'dark skin patches' appear to contain more sweat glands (Mitchell & Skinner 2004) and infrared thermography shows that these dark areas radiate more heat (Hilsberg-Merz 2008; Kaspari 2008). Several other mechanisms of thermoregulation have been suggested, along with specific 'heat' problems that giraffes may have.

Giraffes are large mammals, living in hot, often dry places. Large animals have a smaller surface area to volume ratio, and therefore might lose less heat from their body surface than a smaller mammal (Dagg 2014). This was

one of the earliest explanations for Bergmann's rule, which is that larger animals have a lower surface area to volume ratio than smaller animals, so they radiate less body heat per unit of mass. Bergmann's rule states that within a broadly distributed taxonomic clade, populations and species of larger size are found in colder environments, and species of smaller size are found in warmer regions. Although originally formulated in terms of species within a genus, it has often been recast in terms of populations within a species. It is also often cast in terms of latitude. An often quoted example is that of Swedish moose (*Alces alces*) (Sand *et al.* 1995). However, Geist (1987) suggested that Bergmann's rule is false and that the correlation with temperature is spurious. Instead, Geist suggested that body size is proportional to the duration of the annual productivity pulse, or food availability per animal during the growing season.

More recently, in a dataset comprising 3561 mammal species, from 26 orders, Clauss *et al.* (2013) showed that while there is no significant correlation between latitude and body mass using conventional methods, this correlation is highly significant when the phylogenetic structure of the dataset is accounted for, therefore supporting Bergmann's original claim that the rule only applies to closely related species. Intriguingly for giraffes, Allen's rule may help them. This rule was proposed by Joel Asaph Allen (1877) and states that the body shapes and proportions of endotherms vary with climatic temperature by maximising exposed surface area to maximise heat loss in hot climates. The rule predicts that endotherms from hot climates usually have ears, tails, limbs, snouts, etc. that are long and thin while equivalent animals from cold climates usually have shorter and thicker versions of those body parts. This sounds like a giraffe. Of course, giraffes may also avoid overheating by seeking shade. However, several observations have failed to confirm this for giraffes in the wild (Innis 1958) or in captivity (Dagg 1970a).

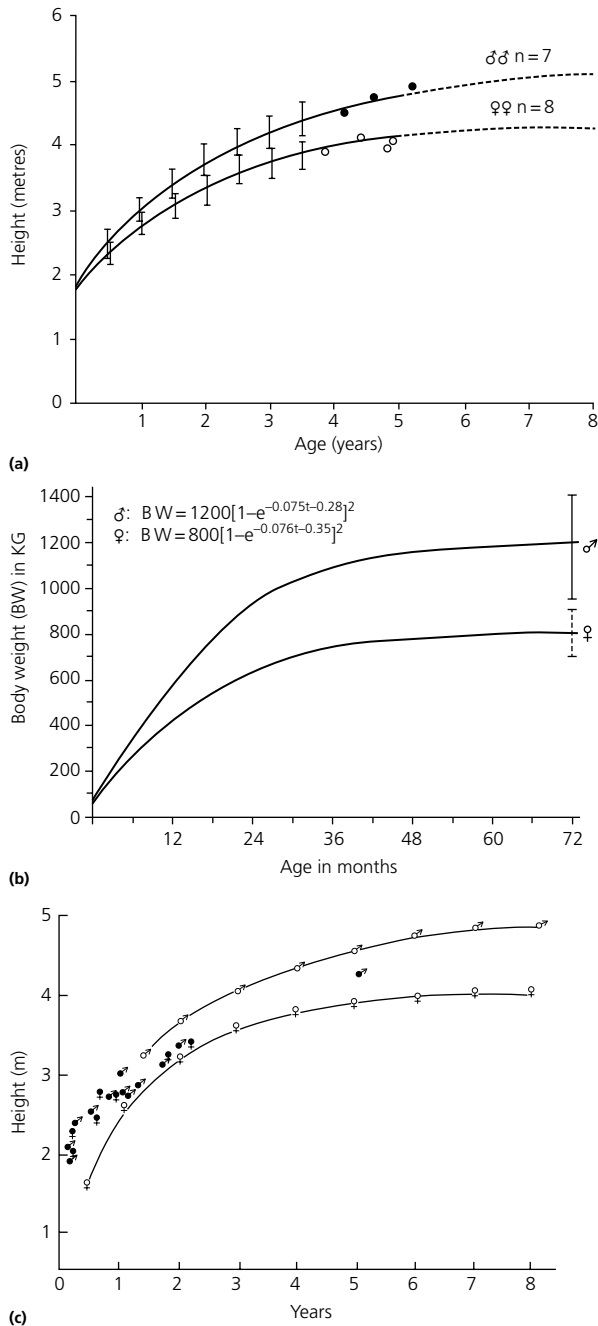


Fig. 5.2 Giraffe growth curves. (a) Average height versus age for 15 giraffes in the Serengeti (from Pellew 1983b; reproduced with permission of John Wiley & Sons). (b) Growth curves for male and female giraffe constructed from the von Bertalanffy growth equation (von Bertalanffy 1938). Range of measured weights indicated when available. Data from giraffe in Timbavati private reserve bordering the Kruger National Park (from Hirst 1975; reproduced with permission of John Wiley & Sons). (c) Growth curves of six wild and two captive giraffes. • Nairobi National Park data (Foster & Dagg 1972), ○ Backhaus (1961).

Another mechanism to combat rising temperature is to let it rise during the day and then reduce it at night. This is a trade-off between temperature rise, evaporative cooling and dangerous water loss. For example, the oryx (*Oryx gazella*) when deprived of drinking water employs various methods to minimise its water needs. These include allowing the body temperature to rise during the day (from a normal 35.7°C to 45°C) before beginning evaporative cooling, and concentrating the urine. Although the eland (*Taurotragus oryx*) is less desert adapted than the oryx, it can go indefinitely without drinking. It can allow its body temperature to rise as much as 7°C during the day and let the night temperature cool it down. This would be equivalent to using about 5 L of water per day in evaporative cooling (Shorrocks & Bates 2015). Giraffes may also do this. Langman *et al.* (1982) found that giraffe body temperatures ranged from 36.7°C on cool days to 39°C on hot days. They also found that giraffe body temperature rose during the day, to around

40°C, and fell at night to a lower 34°C (Langman 2012). Of course, as Langman *et al.* (1982) note, the above applies to large mammals, not small ones. But young giraffe are small. This may explain why calves spend much of their early life in hiding, in the shade (Dagg 2014). However, this may also be an antipredator behaviour. As is frequently the case, precise explanations, and disentangling correlating variables, are difficult without the required experimental and carefully taken observational data.

Giraffes do have sweat glands (Mitchell & Skinner 2004) but opinion is divided as to whether they function (Dagg 2014). Langman (2012) believes they are non-functional. There also appears to be nasal cooling (Langman *et al.* 1979). Giraffe nasal anatomy and respiratory system can combine to cause high respiratory evaporative heat loss and, theoretically, cooling of jugular venous blood (Mitchell & Skinner 2004), the large nasal cavity effectively acting as a small refrigerator (Dagg 2014).

CHAPTER 6

Individual behaviour

This chapter will look at mating, birth, infant care, fighting, feeding and daily patterns in individual behaviour. The first three of these form an examination of 'reproductive' behaviour. Sexual behaviour includes urine testing, the maintenance of a 'tending bond' by the male prior to mating, circling and foreleg lifting, and finally copulation and ejaculation. After birth the mother 'guards' the calf, which usually remains hidden. This 'birthing' strategy will be set in the context of other ungulates in Africa. Agonistic behaviour will include dominance and threat displays, submissive displays and fighting (often called necking).

Seeber *et al.* (2012) have recently produced a very nice inventory of giraffe behaviour. Such behavioural inventories are called ethograms. I will detail their inventory first, which probably includes all giraffe behaviours, including arguably less important ones. I will then examine in more detail those which I feel are most important in the wild, and for which there is abundant data, analysis and discussion. Behavioural studies on different animals, in different locations, by different people can only be legitimately compared if a standard set of categories (in other words, an agreed ethogram) is used. Unfortunately, many workers prefer to invent their own terms. The field observations of Seeber *et al.* (2012) were carried out in Hwange National Park, which covers an area of 14,650 km² in western Zimbabwe, estimated to contain a population of 2800 giraffe (HNP+adjacent areas). During 13

weeks (272 hours observation time), they made a total of 1264 sightings of giraffes. In addition, about 40 giraffes were observed in Entabeni Game Reserve, South Africa. They also examined 104 publications on giraffe behaviour, ecology and general biology for descriptions of behavioural patterns in the wild, previously noted by naturalists and field biologists. They classified natural giraffe behaviours (those observed in the wild) into 'activities' (involving only one giraffe) and 'interactions' (involving two giraffes).

Giraffe activities (one individual)

The single giraffe activities of Seeber *et al.* (2012) included *browsing*, *grazing*, *drinking*, *rumination*, *geophagy*, *osteophagy*, *scavenging* and *scanning* which will be examined in the next chapter when I discuss the giraffe's diet, in its broadest sense, and vigilance. They also list *walking* and *cantering* which I have described in Chapter 4. In addition, they list 11 further 'behaviours', which I briefly mention below, using bold to indicate the names they used.

Resting is when the body touches the ground and the legs are tucked underneath (Dagg 1970b; Innis 1958; Pratt & Anderson 1979). This is mostly seen in calves (Langman 1977), when the head tends to be erect. Resting is sometimes called 'recumbent sleep' (RS) (Tobler & Schwierin 1996). Adults do it for short periods,

often with the head curled and resting on the hip, and the eyes closed. This posture is sometimes called 'deep sleep' (DS) (Tobler & Schwierin 1996). They may well be **sleeping**, another of the individual behaviours listed by Seeber *et al.* (2012), although in the absence of electroencephalogram (EEG) recordings, this physiological state can only be assumed. Tobler and Schwierin (1996) made continuous video recordings of eight captive giraffe and concluded, from observing the animals' posture, that these giraffes 'slept' for 4.6 hours out of 24 hours, although DS was only 4.7% of this. These captive giraffes 'slept' mainly between 20.00 hours and 07.00 hours. Sicks (2012) also looked at 'deep sleep' in captive giraffes and found they averaged only 27 minutes at night in the DS position. Kristal and Noonan (1979), also watching captive giraffes, found that new-born calves spent 90% of their time in the DS position.

Related 'sleepy' behaviours are **drowse** and **yawn**. A yawn is when the animal opens its mouth, with the tongue sometimes protruded, the lower jaw sometimes moving sideways (Seeber *et al.* 2012). Drowse is when the animal stands with a rather relaxed neck and lowered head and seems not to *scan*. This is sometimes called 'standing up' (SS) (Tobler & Schwierin 1996). Rumination can occur while drowsing (Innis 1958). In wild giraffes, these resting phases appear to be rather short, sometimes following rumination, and are most apparent during the heat of the day. Usually the ears are relaxed (Dagg 1970b; Innis 1958).

The list of Seeber *et al.* (2012) is completed with nine other individual behaviours. A giraffe can **rub** its body/neck/head against an object, presumably to get rid of an itch (Dagg & Foster 1976). **Self-grooming** by biting its own body or legs is probably a similar reaction to an itch. They sometimes **lick** an object other than soil (*geophagy*, see later), perhaps to investigate it. Giraffes can stomp the ground with one foreleg, once or repeatedly. This **pawing** is rather rare and seems to be a displacement activity caused by an external threat (Innis 1958). Pawing is

sometimes followed, or preceded, by **snorting**, in which the giraffe blows air out through its nostrils. This also seems to be a reaction to a threat (Dagg 1971). More serious stomping in which the giraffe lifts both its front legs quickly, kicking or stomping them hard on the ground or eventually on a specific target (Dagg 1971; Dagg & Foster 1976; Putnam 1947; Roberts 1969), is a **predator defence**. Kicking is also done with the hindlegs (du Toit 2007) and giraffes have been observed to kill lions with these foreleg stomps (Campbell 1951; Dagg 1971; Dagg & Foster 1976; Puxley 1929). This is frequently seen in a female defending her calf and unfortunately, there are records of the young being accidentally killed (Percival 1924; Tjader 1910). A giraffe can sometimes **buck** (jump) while cantering or even while standing. It seems to be a defence reaction against birds such as oxpeckers (*Buphagus* spp.) and might, if the giraffe was standing, be followed by cantering for a short distance (Seeber *et al.* 2012). It is sometimes preceded by a shaking of the head and neck, in an attempt to get rid of the birds (Dagg 1971).

Oxpecker/ungulate associations are normally regarded as mutualistic because cleaners benefit from the consumption of ectoparasites (Attwell 1966) plus ear wax, blood and other edible material gathered from the host (Bezuidenhout & Stutterheim 1980), while hosts benefit because morbidity and mortality caused by ectoparasites are reduced (Lightfoot & Norval 1981; Norval *et al.* 1988), and oxpeckers' alarm calls warn of approaching predators (Attwell 1966). However, oxpeckers also open up old wounds, increasing the time taken for them to heal (Weeks 2000) and create fresh wounds (McElligot *et al.* 2004). This raises the possibility of parasitism, rather than mutualism, within the oxpecker–host relationship (Shorrocks & Bates 2015). This may explain why giraffes frequently show behaviours that appear to discourage these birds.

The giraffe can use its tail (**tail swishing**) to brush off flies from almost the whole of its trunk

(Dagg 2014). Tail swishing might also be a sign of irritation in alert situations. A young giraffe can sometimes be seen chewing, seen mainly in ruminating animals, but no bolus can be seen moving down the throat or returning between the chewing bouts. This is termed **idle rumination** by Seeber *et al.* (2012) and is usually observed in calves under the age of 6 months (Pratt & Anderson 1979).

Giraffe interactions (two individuals)

The behaviours that involve two individuals are divided into groups by Seeber *et al.* (2012): general interactions, bull/cow behaviours, cow/bull behaviours, bull/bull behaviour, interactions by calves and maternal behaviour. Once again, some of these will be dealt with in more detail later, the rest will be briefly listed next. The names used by Seeber *et al.* (2012) are again in bold type.

Their category of *general interactions* include 15 behaviours. These include several which could be seen as partitioning a continuous range of activities.¹ For example, **approach**, an animal moving towards a conspecific (but not threatening), and **nuzzling** (Bashaw *et al.* 2007; Pratt & Anderson 1979, 1985), in which an animal's muzzle touches a conspecific's nose or other area, other than flanks or anogenital area (which they term **investigate** (Bercovitch *et al.*

2006)), could be regarded as a continuous piece of behaviour. The same could be said of **yield** (Bashaw 2010) and **displace** (Bashaw 2010; Pratt & Anderson 1985) in which one animal avoids or is displaced by another. Also their behavioural category of **neck/rubbing** (Coe 1967; Bercovitch *et al.* 2006), as distinct from necking (see later), in which one giraffe rubs its head or neck against a conspecific's body, sometimes leading to an entwining of the necks, might be viewed as an extension of nuzzling.

Some behaviours in this category of general interactions are, I feel, more appropriate for other sexual categories and will be listed there. These include **sparring** (a less vigorous form of necking) (Coe 1967; Pratt & Anderson 1982), **flehmen** (urine testing) (Dagg & Taub 1970) and **investigate**. The remaining behavioural types in this category are **follow** (Pratt & Anderson 1985), in which one animal stays in proximity to another one and follows its movements in walk, **bump** (Bercovitch *et al.* 2006; Pratt & Anderson 1985) in which one giraffe pushes another one with its chest, **grooming** (Horwich *et al.* 1983) in which one animal grooms another's body or crest by licking or biting, and **mount** (Woods 1972) in which one animal stands right behind or on the side of another one, lifts its front legs on to the conspecific's body and attempts to mount it. This is distinct from the sexual mounting of a female by a male. Another 'out of context' behaviour is **nursing attempt** (Pratt & Anderson 1985), when a young giraffe attempts to suckle on the udder of a female that is not its mother. The last two categories are **vocalise** and **lick urine** (Dagg & Taub 1970) in which a giraffe licks another giraffe's urine from the ground. Licking urine from the ground is not to be confused with *urine testing*, which is performed by adult, and sometimes by subadult, bulls after stimulating a cow to urinate. Notice that several of these behaviours (e.g. nuzzling, bump and neck rubbing), involving bodily contact (Pratt & Anderson 1985), could be classified as *cow cow*, in the manner of the one below.

¹There are two types of measurement variables: continuous and discontinuous. Continuous variables, at least theoretically, can assume an infinite number of values between any two fixed points. Weight and height are examples. Discontinuous variables (meristic or discrete variables) have only certain fixed values with no intermediates. Number of teeth or offspring are examples. However, in behavioural studies, a continuum is frequently subdivided into classes, often for convenience. The problem then arises as to how finely this continuum is divided (Sokal & Rohlf 2012). This is not an error on the part of the behaviourist, but it certainly needs to be borne in mind, particularly with any statistical analysis.

The *bull cow* subcategory of Seeber *et al.* (2012) includes four types of male behaviour directed at females. These are usually sequential. Their *cow bull* subcategory simply includes four female reactions to these male advances and will be slotted in here. Starting with **mate guarding**, the male manoeuvres one female away from conspecifics and/or prohibits the approach of other males (Kingdon 1979; Pratt & Anderson 1982). The intensity of mate guarding, and how near the male remains to the guarded female, appears to be influenced by the proximity of other males, and also presumably by the female's oestrus state (Bercovitch *et al.* 2006). The female can **escape from the bull's** guarding attempt by cantering away, or she may **tolerate affiliation**. **Urine testing** is part of the male's investigation of the prospective mate, nuzzling a female's flanks to stimulate her to urinate (**stimulated urination** by the female) (Bercovitch *et al.* 2006). As she urinates, the male catches some urine in his mouth, usually leading to a **flehmen** response (Dagg & Taub 1970). Sometimes the male will taste urine from a female who is urinating anyway (Pratt & Anderson 1985). This is a behaviour whereby an animal curls back its upper lips, exposing its front teeth, inhales with the nostrils usually closed and then often holds this position for several seconds. It may be performed over a site or substance of particular interest to the animal. Flehmen (from the German verb *flehmen*, to bare the upper teeth) is performed by a wide range of mammals, including ungulates and felids. As with other mammals, the giraffe raises its head and curls up the upper lip, inhaling deeply, showing long saliva threads hanging from the mouth (Dagg & Taub 1970). By inhaling deeply, the giraffe presumably uses its vomeronasal organ (Jacobson's organ) to assess the female's oestrus state (Dagg & Foster 1976; Dagg & Taub 1970; Pratt & Anderson 1985).

As a preliminary to see if a female is ready to mate, the male may stand close behind, or follow, her, lifting one front leg repeatedly to touch the female's hindleg or flank. This behaviour is

termed **laufs Schlag** (foreleg lift), and Seeber *et al.* (2012) note that they only observed it when the male was mate guarding. The final category in this section is, of course, **mating**, assuming the female **tolerates the mating attempt**. In 17 years of research in Africa, I've only observed giraffes mating once. After several unsuccessful attempts (see also Kok 1982), the male mounted and, following intromission, the event was over within seconds.

Only four *bull bull* behaviours are listed by Seeber *et al.* (2012): **dominance gesture**, **submission**, **fight** and **play fight**. The first two are paired behaviours. One male shows a dominant posture while the subordinate male yields to avoid the dispute escalating. The dominance behaviour is often shown as an erect posture while standing still, with head high and neck vertical, or a tensed and arched neck when moving. Like many animals, there is a lateral presentation of the body to emphasise size (Estes 1991a, 1993). However, as Seeber *et al.* (2012) state, the visual signs of dominance can differ remarkably and can sometimes only be interpreted by the social context. The second two categories are both fighting (necking), with one judged to be 'not as powerful and as fast' as the real thing. Play fights, or practice fights, are frequently between adolescent males (Pratt & Anderson 1982). Serious fighting consists of two males raining blows on each other by swinging their head and neck against their opponent's neck, body and legs, using very powerful and fast blows (Innis 1958; Pratt & Anderson 1982). However, it should be noted that Pratt and Anderson (1982) only observed one 'violent' contest out of a total of 71 bouts observed. To increase their stability, the fighting individuals spread their front and hindlegs and lean against each other with their hindquarters touching (Innis 1958).

The last two categories of behaviour listed by Seeber *et al.* (2012) are *maternal behaviour* and *interactions by calves*. Since these are linked I treat them together here. **Neonate cleaning** (calves less than 1 month old) is when the mother licks

the new-born calf dry and eventually eats the foetal membrane (Knappe 1964; Loveridge *et al.* 2007). **Suckling initiation** (female approaches her calf and it suckles (Pratt & Anderson 1979, 1982)), **suckling prevention** (mother moves away or simply moves one of her hindlegs) (Pratt & Anderson 1979), **nurse** (mother lets the calf suckle while standing still), and **olfactory bonding** (Knappe 1964; Pratt & Anderson 1979) (mother licks and sniffs the calf) are all *mother calf* behaviours directed by the adult female. **Suckle** by the calf is the response to suckling initiation by the mother (Pratt & Anderson 1979, 1982). Mean duration of suckling has been recorded in the Serengeti National Park (Pratt & Anderson 1979) at 66 seconds and in Arusha National Park (Pratt & Anderson 1982) at 59 seconds, both for the Masai subspecies. In both studies, unsuccessful attempts by calves to suck outnumbered successful attempts. Suckling was initiated as frequently by the mother as by the calf, but the great majority of bouts were terminated by the mother, and a substantial number of suckling acts were prematurely terminated because other calves tried to join in the sucking. The oldest calf they saw being suckled in the Arusha National Park was 9 months, and in the Serengeti 22 months.

More 'playful' behaviours by the infant giraffe, noted by Seeber *et al.* (2012), are **tail chew** and **play**. The first involves chewing the tail of the mother or sometimes another juvenile (Horwich *et al.* 1983) and the second involves nosing, rubbing, sniffing, licking, kicking, gambolling and 'nasal-frontal greeting' (Pratt & Anderson 1979). Such 'frolicking' is a not uncommon behaviour among many young ungulates (Pratt & Anderson 1982), including domestic sheep and cows.

That completes the ethogram for giraffes, as listed by Seeber *et al.* (2012). In the next few sections I will add to this ethogram by examining in more detail the evidence for several debated behaviours. In the section on 'feeding', I discuss the single giraffe activities of *browsing, grazing, drinking, rumination,*

geophagy, osteophagy, scavenging and scanning postponed from the section above.

Fighting and the evolution of the giraffe's neck

Why does the giraffe have a long neck? The two main suggestions are that (1) long necks evolved because of competition with other browsers, allowing giraffes to feed above them ('competing browsers' hypothesis) (Darwin 1871), or that (2) the long neck evolved for direct use in intrasexual combat to gain access to oestrous females ('necks-for-sex' hypothesis) (Simmons & Scheepers 1996). Both are usually discussed as present-day explanations and not as phylogenetic ones, although the competition hypothesis could be stated in terms of 'past competition'. In fact, Mitchell and Skinner (2003), Simmons and Scheepers (1996) and Simmons and Altwegg (2009) all examined fossil evidence, but it must be borne in mind that the selective forces maintaining a morphological trait may not be the same as those giving rise to them in distant ancestors (Gould & Vrba 1982). Both suggestions could result in longer necks, and both are clearly advantageous to their bearers (Cameron & du Toit, 2007; Pratt & Anderson 1982, 1985) but see Chapter 7 about the flaws in competition evidence, and Shorrocks (2007) and Shorrocks and Bates (2015).

However, although both mechanisms can explain long necks in giraffes, until recently no tests have attempted to distinguish between them, in terms of both origin or maintenance of the long neck. And of course, the two hypotheses may not be mutually exclusive and both have their problems. The main challenge for the competing browser hypothesis is to explain why giraffes have remained about 2.5m taller than their tallest competitors for over 1My, when there are clearly costs in terms of predation rate, blood pressure and maintenance of skeletal lengthening (Mitchell *et al.* 2006; Warren 1974). Arguably, an animal half the size of the

present-day giraffe, in other words about 2.5 m high, would be sufficient to outcompete other browsers (but see Cameron & du Toit (2007) later when I look at the resource competition idea more fully). The main challenge for the sexual selection hypothesis is to explain why female giraffes also have long necks, even though their necks are shorter than those of males. Genetic correlations between the sexes is one explanation for male-like characters in females (Darwin 1871, Fisher 1930, Lande 1987, but see Stankowich & Caro 2009). Certainly artificial selection demonstrates close body size correlations between males and females, verified in field studies (see Andersson 1995). However, if there are costs to having a long neck and no benefits to females, one imagines that genetic correlations between female and male neck length should break down, resulting in a pronounced sexual dimorphism. Another possibility, although I suspect it would apply more to bovids than giraffes, is that the female's long neck is a male mimicry to protect her adolescent sons. Estes (1991b) details this hypothesis for bovids, where in wildebeest this even extends to a faux penile tuft in the female. Interestingly, young male giraffes do tend to leave the female group when they no longer 'look' like the females. Females having longer necks may prevent these younger males being subjected to aggressive *despotic competition* (Schein 1975).

Several lines of evidence support the sexual selection idea (I will defer the foraging competition evidence until later):

- 1 males with larger necks win most contests for access to oestrous females (Pratt & Anderson 1982, 1985)
- 2 oestrous females show preference for large-necked males, or darker, older males (Brand 2007; Pratt & Anderson 1985)
- 3 dominance contests involve prominent displays of the long neck by male giraffes during erect walking (Brand 2007; Dagg & Foster 1976; Estes 1991a)
- 4 sexually selected traits are condition dependent and costly (Andersson 1994; Darwin 1871;

Kodric-Brown & Brown 1984), for which there is some support from sex-biased mortality and physiological costs.

Numbers (1) and (2) are particularly important, and were partly examined by Pratt and Anderson (1982, 1985). They ranked males into three categories (*A* to *C*, with *A* the largest) based upon neck size and horn length. The larger giraffes had a stouter neck, massive horns and the addition of bone and knobs on the skull (see Chapter 4). *A* males were dominant over *B* and *C* males, and *B* males over *C* males, creating a dominance hierarchy. *A* bulls courted females more often than the other two ranks. Ranking was important in female choice since they allowed themselves to be urine tested more often by *A* bulls than *B* bulls, and they refused urine testing by *C* bulls 66% of the time. Of course, paternity tests are still required to confirm that these mating advantages lead to higher reproductive success.

Under sexual selection, males should have proportionally larger necks and heads than females, whereas the competing browsers idea predicts similar relationships for both sexes, assuming no intersexual competition for food. Sexually selected traits are more often positively allometric² than naturally selected ones among mammals (Kodric-Brown *et al.* 2006), but not universally so (Bonduriansky 2007; Cuervo & Moller 2009). Thus, positive allometry is more likely for male giraffes under sexual selection

²That is, larger giraffes will have relatively larger heads and/or necks. Not only are such positively allometric traits expected to provide the larger individual with greater competitive ability, but only larger animals can bear the 'costs' of having them. One interesting observation made by Simmons & Scheepers (1996) is that the ratio of an adult okapi's foreleg to neck is about 1:0.44 while for adult giraffes it is about 1:0.93. The neck of present-day giraffes is therefore about 2.1× longer than predicted by isometric increases. Interestingly, young giraffes (a few months old) have a ratio of 1:0.62, more similar to the okapi and possibly the giraffe's shorter-necked ancestors. The change from young to adult giraffes appears to be due to high neck growth, as indicated in Chapter 4.

than for females and this was investigated using 37 male and 45 female Namibian giraffes, culled from Etosha National Park (Simmons & Scheepers 1996). Heads were cut below the skull and weighed, and necks were cut from the shoulder to include all cervical vertebrae. However, only neck mass and not neck length was recorded. The authors assume that neck mass and neck length are correlated. They also note that older males have thicker necks, which may be important. Neck mass was plotted against body mass (minus the neck) to look for allometry and analysed using linear and reduced major axis regression (Sokal & Rohlf 2012). There was a clear trend for heavier males to have disproportionately heavier necks (slope $b=1.27$, $b_{\text{RMA}}=1.35$) and the slopes were significantly different from isometry ($t=4.33$, $P<0.005$). Females by contrast displayed isometry between neck mass and body mass ($b_{\text{RMA}}=0.986$, $R^2=82\%$, $N=43$). I'm unclear as to why an equivalent t value was not given.

Mitchell *et al.* (2009) also investigated the necks-for-sex hypothesis by examining 17 male and 21 female giraffes with body masses ranging from juvenile to mature animals from a culling operation in Zimbabwe in 2007–2008. They measured head mass, neck mass, neck length, leg length and the neck length to leg length ratio. All measurements were standardised by developing allometric (log-log) equations for each variable with respect to body mass. They report no significant differences in any of these dimensions between males and females of *the same mass*, although mature males, whose body mass is significantly (50%) greater than that of mature females, did have significantly heavier (but not longer) necks and heavier heads than mature females. They conclude that morphological differences between males and females are minimal, and that any differences that do exist can be accounted for by the larger final mass of males and that sexual selection is not the origin of a long neck in giraffes. Their conclusions therefore differed from the earlier study by Simmons and Scheepers (1996).

Simmons and Altwegg (2010) replied by publishing a new review of the issues involved in trying to distinguish between the necks-for-sex and foraging competition hypotheses. They revisited allometry, and they disagreed with the findings of Mitchell *et al.* (2009). An allometric relationship is represented by the equation:

$$T = aM^k$$

where T is the trait of interest (the neck mass or the head mass in this case), M is the body mass (excluding the neck and head mass to make T independent of M) and a is a constant. The exponent k determines whether the relationship between T and the body mass is isometric ($k \sim 1$), positively allometric ($k > 1$) or negatively allometric ($k < 1$). The Zimbabwean study (Mitchell *et al.* 2009) fitted linear regression models after taking the logarithm on both sides of this equation. Simmons and Altwegg (2010) reanalysed their earlier Namibian data using a non-linear least squares regression model (R Development Core Team 2009). In addition to whether k is significantly different from 1, there is also the question whether k differs between the sexes, and this approach allowed them to test this statistically. They modified the above equation to include sex (s : 0 = male, 1 = female):

$$T = (a + bs)M^{(k+cs)}$$

Parameters b and c estimate sex differences in the constant and in the exponent, respectively. They found that the results from the Namibia data were similar to those originally reported by Simmons and Scheepers (1996). Neck mass showed a positive allometric relationship to body mass in males with $k=1.34$ (95% confidence interval (CI) 1.16–1.51), and an isometric relationship in females with $k=0.90$ (95% CI 0.69–1.10) (Fig. 6.1a). This difference is significant (the confidence intervals do not overlap) and the values of k are similar to those obtained previously (Simmons & Scheepers 1996) using a different regression technique. Mitchell *et al.*

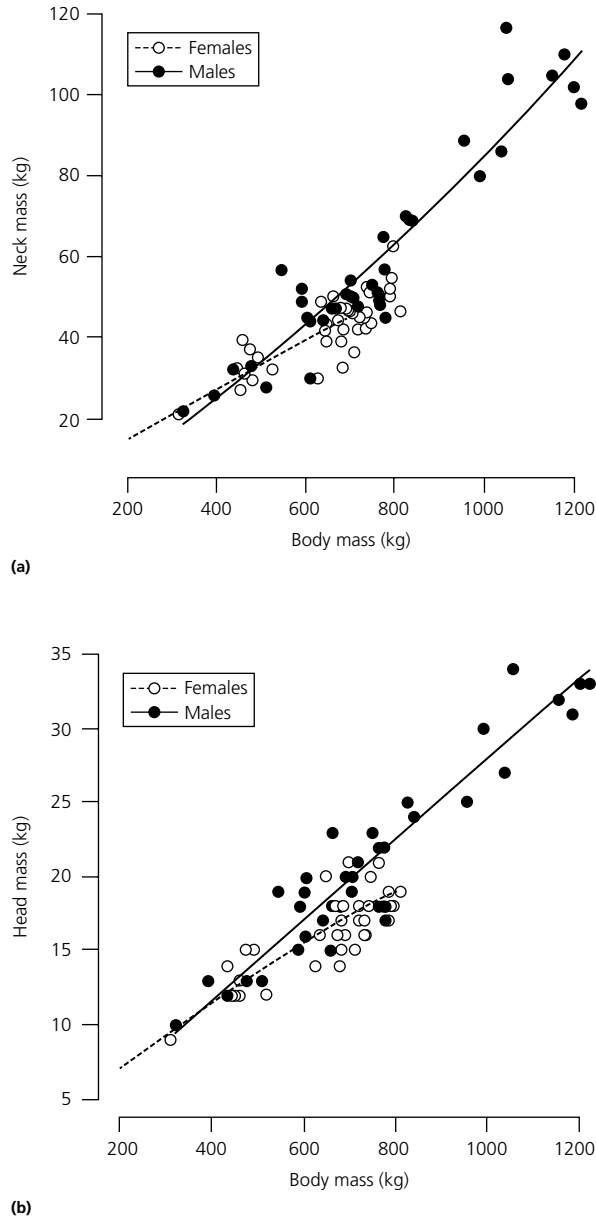


Fig. 6.1 Plots of body mass (kg) of 34 male and 43 female Numidian giraffes (a) with neck mass (kg) and (b) with head mass (kg). The fitted, and significant, non-linear regression lines are shown ($R^2 \sim 0.85$). Source: Simmons and Altwegg (2010). Reproduced with permission of John Wiley & Sons.

(2009) had reported $k=1.13$ for males and $k=1.06$ for females in their Zimbabwean giraffes. They interpreted this result as evidence for positive allometry in both sexes, although no

confidence intervals or significance levels for k , or differences between the sexes, are reported. In fact, the $k=1.06$ reported for Zimbabwean females (Mitchell *et al.* 2009) appears to reveal

isometry, not positive allometry, because it lies close to 1.00. Although these authors do not give confidence limits, this value is within the confidence limits for the Namibian sample. The data of Mitchell *et al.* (2009) therefore also appears to support the idea that female neck mass is directly related to body size ($k \sim 1$), while males show positive allometry ($k > 1$).

If sexual selection contributed to the evolution of the giraffes' large neck for clubbing opponents, we might also expect differences between the sexes in head mass. Simmons and Altwegg (2010) examined this possibility using their Namibian data (Simmons & Scheepers 1996) using the allometric methods described above. This indicated that males had significantly steeper allometric slopes than females (Fig. 6.1b) (males $k=0.96$ with 95% CI 0.83–1.09, females $k=0.73$ with 95% CI 0.56–0.90). The relationship was therefore isometric for males and negatively allometric for females, and the differences were significant ($P=0.049$). The Zimbabwean data showed similar trends with both estimates contained in the confidence intervals for the Namibian estimates (males $k=0.87$, females $k=0.80$) (Mitchell *et al.* 2009).

Notice, however, that neither the Namibian nor the Zimbabwean study allows us to refute one of the two major ideas for the giraffe's long neck. Perhaps predictably, Simmons and Altwegg (2010) conclude that both mechanisms may play a role in the origin and maintenance of this unique trait.

Dominance hierarchies

In their studies of giraffes in Arusha and Tarangire National Parks, Tanzania, Pratt and Anderson (1982, 1985) noticed that there was a clear dominance hierarchy among the males in each population, and this developed as they matured (Backhaus 1961; Coe 1967; Foster & Dagg 1972; Leuthold 1979; Moss 1975). Subjectively, they recognised three classes of bulls: *A*, *B* and *C*. As an individual matured from class *C* to class *B*, it increased in stature, the neck

became heavier and the horns longer and thicker. Bulls of class *A* also tended to be larger than class *B* bulls, but their main distinction was a stouter neck, massive horns and the addition of bone and knobs to the skull (see Chapter 4). The associations (solitary, bull groups, mixed groups) shown by these three categories of bulls also differed, and their data is shown in Table 6.1. Each bull was assigned to a class when seen for the first time, so that their rankings did not reflect the outcome of later contests observed. The interaction between these bulls, as they matured, established a dominance hierarchy, with the relative positions of individuals apparently established before they actually attained the *A* class. This 'previous' establishment of the hierarchy is demonstrated by the numbers that Pratt and Anderson (1985) observed sparring. Out of 298 observations they record, the males taking part were 254 *C* class bulls (38% of *C* class bulls seen), 44 *B* class bulls (12%) and no *A* class bulls. This suggests that by the time they reach the *A* category, bulls no longer need to actually fight. Social standing was manifested when a dominant individual obliged a subordinate male, by walking toward him or by merely staring at him, to move away from females. Table 6.2 shows the differing frequencies of 'wins' for each class of male giraffe.

Pratt and Anderson (1985) observed that sometimes when an *A* class bull joined a group of giraffes including cows and other bulls, he would single out the *B* bulls and send them off, while disregarding individuals of lower rank. This was almost always done when a female(s) was present. In 129 such displacements that they recorded, cows were present in all cases except one. The outcome of disputes tended to be settled in advance and potentially injurious conflicts were usually avoided, something that supports theory (Pusey & Packer 1997). Of course, television programmes might record the odd serious fight, but we should not be seriously influenced by what appears to be a rare occurrence.

Table 6.1 Associations shown by the three categories of giraffe bulls. Data from Pratt & Anderson (1982, 1985).

	C bulls		B bulls		A bulls	
	Observed	%	Observed	%	Observed	%
Solitary	76	6	194	19	95	25
All-bull groups	365	27	232	23	74	19
Mixed groups	889	67	590	58	212	56

Table 6.2 Frequency of 'wins' for the three classes of male giraffe. Data from Pratt & Anderson (1982, 1985).

		Winning bull		
		A	B	C
Losing bull	A	8	5	0
	B	28	28	1
	C	37	17	0

Theoretical predictions in pair-wise contests vary depending upon the situation. If opponents meet for only a single encounter, models based upon game theory predict that contestants will be more likely to escalate the fighting when the cost of injury is low relative to the value of the resource (Maynard Smith & Price 1973) (scenario I). When fighting has significant costs, disputes are more likely to be settled according to perceived asymmetries between the contestants (Maynard Smith & Parker 1976; Parker 1974) (scenario II), such as the differences noted above between A bulls and B and C bulls. In stable social groups where the same two individuals are likely to compete repeatedly and perceived differences are clearly detectable, the superior individual should consistently win each encounter and the inferior should defer to its opponent (scenario III). This would lead to a dominance relationship and it has even been suggested that this may even occur in the absence of the resource. In other words, individuals may compete for dominance *per se* and learn from the first few encounters with their opponents (Clutton-Brock & Parker 1995; Huntingford & Turner 1987). It would appear that giraffe males

fit scenario III, and that this outcome develops early in the life of the maturing bull. The only exception that occurs to me might be the giraffes of the desert region of north-west Namibia (Fennessy 2009; Fennessy *et al.* 2003). Here populations may be so widespread that social grouping and the availability of the resource are more restrictive, leading to scenario I.

Relevant to what has been said above about dominance hierarchies is the study of all-male herds of Thornicroft's giraffe, in Zambia (Bercovitch & Berry 2014). This study in Luangwa Valley, Zambia, is important for two reasons. First, it used an extensive 33 years of data on giraffes, in which each individual was identified by its pelage pattern. Very few long-term longitudinal studies of giraffes are available for analysis (or of many other ungulates) and this study will feature prominently in this book, along with the 6-year study of Kerry Carter and her colleagues in Etosha National Park (see Chapter 8). Secondly, the authors do not simply put forward one explanation for their observations, but rather several alternatives. In science (including African mammal ecology), this is always essential but frequently overlooked.

Adult male giraffes are most often observed as solitary individuals (Shorrocks & Croft 2009), but all-male herds of giraffes are reported throughout Africa (Bercovitch & Berry 2010b; Brand 2007; Dagg & Foster 1982; Estes 1991a; Leuthold 1979; Pratt & Anderson 1985). The main role of all-male giraffe herds has been presumed to be the establishment of dominance relationships, and to prepare males for possible future contests over access to sexually receptive

females (Coe 1967; Dagg & Foster 1982; Estes 1991a). This establishment of dominance hierarchies in preadult males is what appears to have taken place in the giraffes of Arusha and Tarangire National Parks detailed above (Pratt & Anderson 1982, 1985). However, extensive longitudinal data on individual giraffe has not been examined to test this inference.

Bercovitch and Berry (2014) examined this explanation but also posed five other alternative 'reasons' for these all-male herds. The six possibilities, along with what these authors think might be observed in each case, are:

- 1 *protection from predators*: all-male herd size should vary according to predator risk
- 2 *increased lifespan*: males residing in all-male herds should live longer than those that do not establish all-male herds
- 3 *improve competitive skills*: (a) male sparring (Coe 1967; Dagg & Foster 1982) should be common in all-male herds, and (b) all-male herds should be composed most often of males of similar age/size
- 4 *optimise foraging efficiency*: (a) all-male herds should prefer different habitats than solitary males or mixed-sex herds, and (b) all-male herds should consist of similar age/sized males foraging on foods that are most nutritious for their age/size class
- 5 *resource learning*: (a) all-male herds ought to contain a fully mature male, and (b) male-male associations should be weak to maximise the information obtained from multiple sources
- 6 *random formation*: the duration of time that male dyads were observed in the study area should correlate with their frequency of association in all-male herds.

In their study area,³ Bercovitch and Berry (2014) recorded all-male herds on 84 occasions,

³The study area (31°34'E to 32°05'E; 12°47'S to 13°25'S; approximately 750 km) incorporated the South Luangwa National Park and part of the adjacent eastern Game Management Area (Berry 1973, 1978). The study area has distinctive wet (November to April) and dry (May to October) seasons (Bercovitch & Berry 2010b).

which amounted to 33% of all observations of males (786) within a herd. Giraffes were recognised by their unique pelage patterns (see Chapter 8) that remain unchanged throughout life. The mean size ($\pm 95\%$ confidence limits) for mixed-sex herds (7.47 ± 0.87) was significantly larger than that of all-male herds (3.29 ± 0.37) (Mann-Whitney $U = 3148$, $P < 0.001$). Five males migrated into the area as mature adults, lived in the region for an average of 8.1 (± 2.6) years, were observed in mixed-sex herds, but were never recorded in all-male herds during the time frame. Of course, they may well have been in all-male herds prior to their arrival. A 'giraffe herd' consisted of all animals within sight of the observer that were, in general, engaged in the same activity such as foraging, drinking, moving and resting, and when travelling, they moved in a co-ordinated manner in the same direction (Bercovitch & Berry 2010b, 2013; Carter *et al.* 2013a,b; Dagg & Foster 1982; Leuthold 1979; Pratt & Anderson 1985). Association between pairs (dyads) of males was summarised using the formula $A + B_{(together)} / (A_{(without B)} + B_{(without A)} + (A + B)_{(together)})$.

Their conclusions on the six possible 'reasons' for all-male herds were as follows. I use the same numbers as above.

- 1 *Protection from predators*: habitat zone⁴ had no significant impact on whether a male giraffe joined an all-male herd or was a solitary individual ($X^2_{(3)} = 1.639$, $P = 0.651$) and habitat did not influence the size of all-male herds ($F_{(3,80)} = 1.546$, $P = 0.209$). All-male herds and mixed-sex herds were found in the same habitats in similar frequencies ($X^2_{(3)} = 1.934$, $P = 0.586$). Notice that actual predation was

⁴The habitat was subdivided into four major zones for analysis (Bercovitch & Berry 2010b; Berry 1973, 1978). (i) *Riverine*: the riparian forest region along the Luangwa River and its tributaries, (ii) *Woodland*: those areas dominated by mopane, munga and miombo (mostly *Brachystegia* and *Julbernardia*) vegetation. (iii) *Thicket*: those areas characterized by scrubland and dense thicket. (iv) *Open*: grassland areas with few or no trees, bushes or shrubs.

not analysed and this result relied upon the association between predator risk on ungulates and habitat type reported in the literature (buffalo (*Syncerus caffer*) (Prins 1996); puku (*Kobus vardonii*) and lechwe (*Kobus leche*) (Shorrocks & Bates 2015).

- 2 *Increased lifespan*: the five males who were never observed in all-male herds had a similar period of residency in the community as the males that formed all-male herds ($t_{32}=1.642$, $P=0.110$). However, the estimated age of death was not significantly different for males who did not join all-male herds, compared to those who did (Mann–Whitney $U=4.0$, $N_1=6$, $N_2=2$, $P=0.643$), but this may be entirely due to the low power of the test (Siegal & Castellan 1988; Sokal & Rohlf 2012) due to the small sample sizes.⁵
- 3 *Improve competitive skills*: Bercovitch and Berry (2014) established the age categories of all members of all-male herds in 65 cases (Table 6.3). Based upon birth records, size and appearance, males were classified as juvenile (birth to 2 years old), subadult (3–5 years old), young adult (6–9 years old) or mature adult/black bull (≥ 10 years of age). In this Zambian population, males had all black coat blotches at a mean of 9.4 years (Berry & Bercovitch 2012). The average age of death among male giraffes was about 16 years old. The maximum lifespan of male giraffes was about 22 years compared with a maximum lifespan of about 28 years for female giraffes. Over two-thirds (69%) of all-male herds were composed of males from different age categories. No sparring, or practice fighting, was observed in either the 17 all-male herds

Table 6.3 Composition of all-male herds in Thornicroft's giraffe (*Giraffa camelopardalis thornicrofti*), in South Luangwa National Park and the adjacent eastern Game Management Area, Zambia. Source: Bercovitch & Berry (2014).

Herd composition	Number of observations
All black bulls	3
Black bulls + young adult males	16
Black bulls + subadults	5
Black bulls + young adults + subadults	8
All young adult males	17
Young adult males + subadults	12
All subadults	3
All ages categories	1

with only young adults or the three all-male herds with only subadults. This result contrasts markedly with that of Pratt and Anderson (1982, 1985) described above. They observed 298 sparring events (129 contests or serious fights) over approximately a 3-year period of time in Arusha and Tarangire National Parks. I myself have seen sparring in Arusha National Park while on a brief visit, *en route* to Ngorongoro Crater and the Serengeti National Park.

- 4 *Optimise foraging efficiency*: only 23 all-male herds (see Table 6.3) contained males in the same age category. Neither habitat (see 3 above) or season ($\chi^2_{(1)}=0.394$, $P=0.530$) had a significant impact on whether a male would be sighted alone or in an all-male herd. All-male herds were not significantly more likely to be recorded during the dry, as opposed to the wet, season ($\chi^2_{(1)}=0.005$, $P=0.942$), and the size of all-male herds was independent of season ($\bar{x} \pm 95\%$ confidence limits) (wet: 2.79 ± 0.48 ; dry: 3.48 ± 0.29 ; $t=1.692$, $P=0.094$). Notice, however, that this last result is significant at the 10% level; that is, you would only expect this result 10% of the time by chance. There may be something worth investigating further here.

⁵This would be a type II statistical testing error, accepting the null hypothesis when it is in fact false. In other words, the two classes of giraffes may in fact have different survival rates but the test was unable to discover this. The 'power' of a test depends upon sample size and the type of test used. In general, parametric tests (e.g. ANOVA and t test) are more powerful than non-parametric ones (e.g. Mann–Whitney U), so long as the parametric assumptions are met.

- 5 *Resource learning*: slightly over half (50.7%) of the all-male herds contained a mature bull (see Table 6.3). Only 61/267 (22.8%) male dyads were observed together in all-male herds, and only 21 dyads were recorded in all-male herds on more than one occasion. In eight cases, males were observed in mixed-sex herds within 1 week of their sighting in an all-male herd and in 75% of cases, some or all of their male herd companions were observed with them in the mixed-sex herd. In six cases, the originating all-male herd contained a mature bull, but only one of the mixed-sex herds had a mature bull. Hence, all-male herds could function as a mechanism for younger males to follow older males to find females.
- 6 *Random formation*: among adult male subjects found together in all-male herds, the duration of coresidency in the population was not a factor influencing the strength of their Male/Male Association Index ($r_s = -0.275$, $P = 0.184$). The mean Male/Male Association Index was 0.006 (± 0.013 ; $N = 267$). Eliminating all dyads with zero association increased this to 0.030 (± 0.022 ; $N = 61$).

So what are the conclusions from this extensive data set and very detailed analysis? The first rather worrying conclusion is that even with 34 years data, the ability to distinguish between alternative hypotheses is not easy. On the face of it, there is little evidence for any of the six proposals put forward for the presence of male herds. One problem might be that although this giraffe population was observed for 34 years, the intensity of sampling may not have been large enough in each year. Another issue is that nearly half the all-male herds contained only two males, so that vigilance and predator protection would be minimal, although the authors say it would be significant. Without the predation data we just don't know. Another interesting difference with some previous studies is that all-male herds comprised only 11% of giraffe herds. This contrasts with other locations where all-male herds can be 20–25% of all herds

(Leuthold 1979; Pratt & Anderson 1985). The great value of this study is its longitudinal nature, providing accurate statistics for life history events. Although not significant at the 5% level, there is some suggestion that season might influence the group size of these all-male herds, with herds being larger in the dry season. Perhaps the most puzzling observation is the apparent lack of male–male contests, leading to the possibility that all-male herds provide a testing ground for the later dominance position of males. Either, for some reason, the Zambian sampling regime missed these events or these Zambian giraffes do not fight. Of course, given that male–male associations do not persist over time (Carter *et al.* 2013b), one can reasonably doubt that formation of all-male herds is an adaptive mechanism for establishing a rank order. Interestingly, Bercovitch and Berry (2014) conclude by saying 'Our data did not support the prediction that all-male herds form to enhance competitive skills, but we cannot dismiss the possibility that males gain fighting skills in all-male herds'.

Is birthing synchronised and is there birthing site fidelity?

In this section I look at two aspects of birthing that begin to move this chapter from individual behaviour to individual ecology. Population-level ecology and behaviour are examined in Chapters 6 and 7. The first behaviour is the distribution of giraffe births throughout the year. For example, is it seasonal, and if so why? Second, do females have preferred birthing sites, either because, for example, they have identified areas with excellent food resources or simply because some sites are familiar.

The phenology and synchrony of birth seasons in any tropical ungulate could be due to either of two major limiting factors: food supply and predation. However, phenology and synchrony address different questions. Phenology of births (time of year) is frequently stated to be

determined by food supply (Rutberg 1987), whereas birth synchrony (degree of co-ordination or spread) is an antipredator adaptation that could function in two different ways. High synchrony may occur through 'predator satiation' in species with precocious newborn (followers), whereas asynchrony may occur through 'predator avoidance' in species with non-precocious young (hiders). This division of ungulates into two categories was proposed by Jarman (1974). One group, the followers, comprise those species that are relatively large, eat abundant food such as grass, form large herds and have young that follow their mother from birth and are therefore very visible to predators. You would predict that predator satiation would be exploited by these ungulates, such as wildebeest (*Connochaetes taurinus*), topi (*Damaliscus korrigum*), buffalo (*Syncerus caffer*) and zebra (*Equus quagga*). The second of Jarman's two groups has a different suite of adaptive traits. These species are small to medium sized, territorial species that eat dispersed food, live at lower densities in small groups and hide their newborn young. These hiders include species such as impala (*Aepyceros melampus*), Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsoni*), waterbuck (*Kobus ellipsiprymnus*), oribi (*Ourebia ourebi*) and dikdik (*Madoqua kirki*). This group should not synchronise their births. They are not sufficiently abundant to satiate predators, and synchrony would result in greater rather than lesser predation (Ims 1990). Instead, this group should show the opposite trait of asynchronous births as a 'predator avoidance' behaviour. In other words, they should 'spread' their births throughout the year.

Giraffes, although large and visible, live at low density in relatively small groups (see Chapters 7 and 8). For the first week or more, mothers remain isolated with their calf, on guard against predators (Pratt & Anderson 1982), and the calf spends much of the day lying down and 'hiding' (camouflage has already been mentioned in Chapter 4). The mother often stays some distance away (100 m)

from the concealed calf and may leave it for up to 4.5 hours to find food and water (Pratt & Anderson 1982). Giraffes, therefore, do not fit easily into either of Jarman's categories, but are more similar to the latter group in their suite of adaptations (Sinclair *et al.* 2000).

In the Kruger National Park, peak births have been reported to occur in October to January (Stevenson-Hamilton 1947), February to April (Brynard & Pienaar 1960) and September to October (Pienaar 1963), perhaps suggesting no clear seasonal effect. Fairall (1968), also working in Kruger National Park, reported that two calving periods for the giraffe existed: February to March and August to October. Ansell (1960) found no evidence of a calving season for giraffes in Zambia. In Rhodesia (now Zimbabwe), Dasmann and Mossman (1962) reported that most births occurred in May during the dry season. In 1972, Foster and Dagg published the results of a 3-year (1965–1968) study of the biology of giraffes in Nairobi National Park. They found that calving was spread throughout the year (Fig. 6.2a), but again with possible peaks in the dry months, although no rainfall data is given. Interestingly, a chi-squared test for equality of births in all months (carried out by myself and summing sequential months in pairs to remove expected values less than 5) gives a value of $X^2_5 = 3.72$ ($P > 0.05$), which is therefore not significantly different from an even distribution across the months, although as mentioned earlier in this chapter, the small amount of data may not give the test sufficient power.

Leuthold and Leuthold (1975) examined the seasonal reproductive patterns of nine species of ungulates in Tsavo East National Park. Their graph for giraffes is shown in Fig. 6.2b. Not all births were observed directly and the authors had to estimate the month of birth from indicators such as the presence of the umbilical cord, which persisted for 6–8 weeks after birth. As a consequence, some of the births could not be certainly assigned to a specific month and therefore a ½ birth was assigned to the two adjoining months. This accounts for the ½ values in their

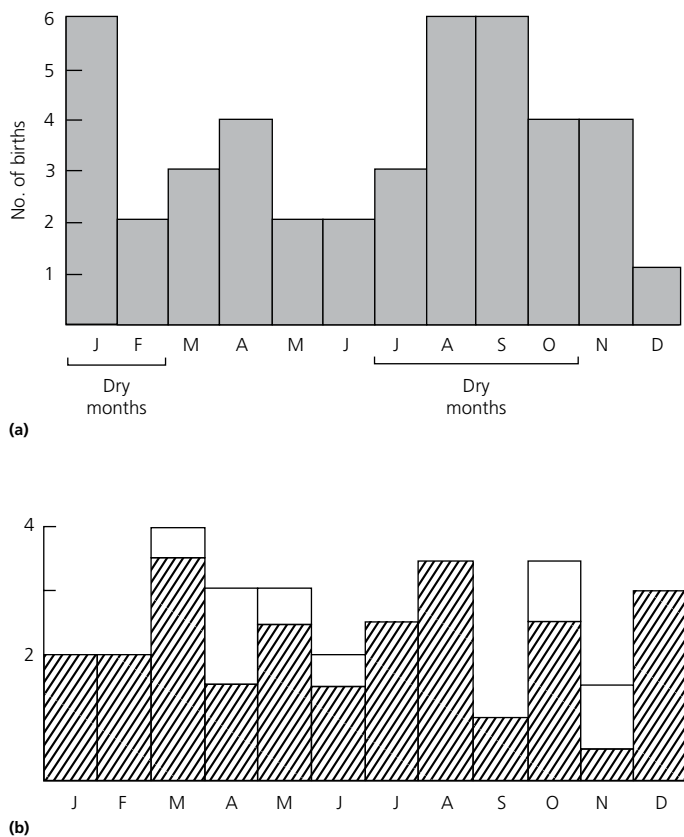


Fig. 6.2 Seasonal births in giraffes. (a) Nairobi National Park (Foster & Dagg 1972). (b) Tsavo East National Park (Leuthold & Leuthold 1975). Reproduced with permission of John Wiley & Sons.

graph. Although admitting the sample size is small (31), the authors conclude that the monthly distribution of births is regular and that 'The conclusion that reproduction in giraffe is non-seasonal seems warranted'. A chi-squared test (as above) gives a value of $X^2_5 = 1.21$, which certainly confirms their suspicion. In fact, this chi-squared value is rather low ($P > 0.90$), suggesting that the seasonal distribution might be more even than expected by chance. In Arusha National Park, Pratt and Anderson (1982) recorded the births of 22 calves during the year. They say 'In this small sample, there was no evidence of seasonality in calving'.

Sinclair *et al.* (2000) examined the factors determining the phenology and synchrony of

birth seasons of 13 species of ungulates in the Serengeti ecosystem, Tanzania. To examine the role of food supply, they measured green biomass of grass or tree shoots, and percentage crude protein. Births were determined from monthly sample counts covering the period 1967–1997. The seasonal distribution of births was compared to that predicted by the abundance of green biomass and percentage protein, and to an even (asynchronous) monthly distribution. Their results for giraffes are shown in Fig. 6.3. They conclude that giraffes, the only one of their species feeding on tree shoots, have their peak of births in the dry season although births occur frequently all through the year. Flowering, fruiting and new shoots of *Acacia*

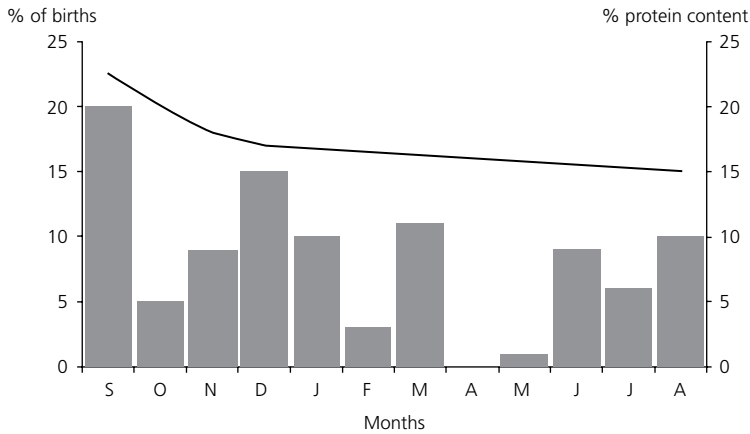


Fig. 6.3 Monthly distribution of giraffe births in the Serengeti 1967 to 1997. Histograms = months births. Line = % crude protein of food. Source: adapted from Sinclair *et al.* (2000). Reproduced with permission of John Wiley & Sons.

trees (a major food of giraffes) occur in mid dry season when crude protein levels reach $21.0 \pm 1.7\%$ of dry mass (mean ± 1 SE) compared to $15.3 \pm 0.9\%$ for older shoots later in the year (Pellew 1980). To detect the seasonality of births, Sinclair *et al.* (2000) used the non-parametric two sample Kolmogorov–Smirnov test. With this, they examined differences between observed birth distributions and (i) expected even distributions through the year ($K-S_{\text{even}}$) and (ii) expected distributions determined by biomass ($K-S_{\text{biomass}}$) and percentage protein ($K-S_{\text{protein}}$). For giraffes, these were $K-S_{\text{even}} = 0.19$ ($P = 0.016$), $K-S_{\text{biomass}} = 0.32$ ($P > 0.001$) and $K-S_{\text{protein}} = 0.15$ ($P = 0.108$). With an appropriate Bonferroni correction, distributions are significantly different ($P < 0.004$), suggesting that giraffe births, in the Serengeti, were not evenly spaced throughout the year, nor followed the biomass of their food. Giraffe births coincided with the flush of tree shoots and their high protein content, not with the amount of leaf biomass.

A similar seasonality in births was implied by the data of Hall-Martin *et al.* (1975) from Timbavati Private Reserve in the eastern Transvaal Lowveld of South Africa, May 1971 to July 1972. In fact, they analyse and display

(Fig. 6.4) the ‘conception date’ rather than the ‘birth date’ they observed, presumably obtained using their quoted value of 457 days for gestation (Skinner & Hall-Martin 1975). Giraffe calves (123) were judged to be newly born, or only a few days old, on the basis of size, coat texture and behaviour.⁶ These authors also estimated the ‘conception date’ for 12 foetal giraffes obtained from culling using the formula $W^{1/3} = a(t - t_0)$ of Huggett and Widdas (1951) where $W^{1/3}$ = cube root of foetal mass (measured from fresh specimens), a = the specific foetal growth velocity (calculated as 0.114 for giraffes; Skinner & Hall-Martin 1975), t = the age of the foetus in days, and $t_0 = 45.7$ (the gestation = 457 days; Skinner & Hall-Martin 1975).

In addition to this Timbavati Private Reserve data, these authors also present estimated, monthly, conception data for five other natural areas: (1) Langjan Nature Reserve in South Africa (15 observations), (2) Zululand in South Africa (16 observations), (3) Akira Ranch in Kenya (20 observations), (4) Nairobi National Park in Kenya (43 observations), the data of

⁶They note that the presence of an umbilical cord alone is not a reliable criterion of age in giraffes as it can be retained for up to 4 months.

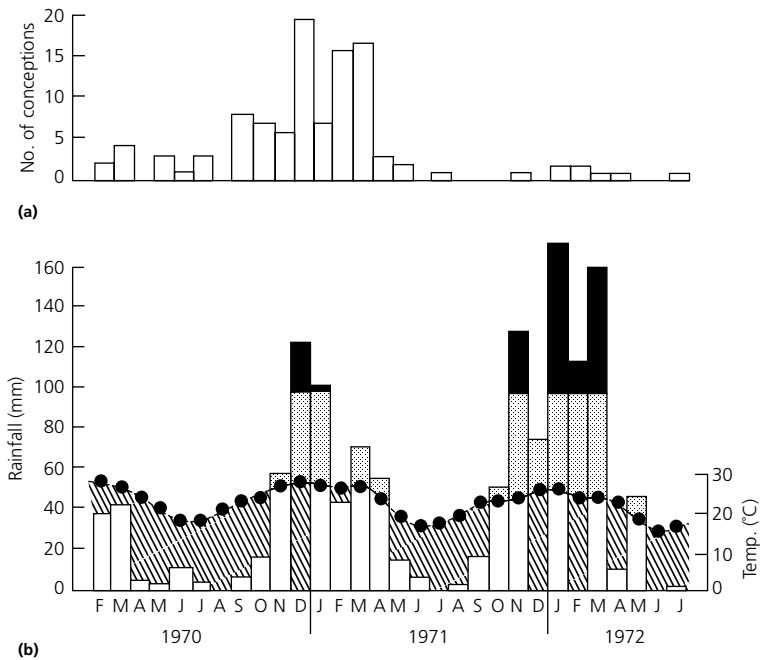


Fig. 6.4 (a) Histograms showing the number of conceptions per month in the Timbavati Private Nature Reserve (February 1970–July 1972). (b) Climatogram showing rainfall (histograms) and temperature (•) (with humid periods indicated by light stippling, per humid periods (>100 mm rainfall per month) shown in black and arid periods indicated by cross-hatching). Source: Hall-Martin *et al.* (1975). Reproduced with permission of John Wiley & Sons.

Foster and Dagg (1972) already examined above, and (5) Hans Merensky Nature Reserve, 70km northwest of Timbavati (143 observations). An examination of both sets of 'Timbavati' data clearly shows a seasonal aspect to this data. This appears to be correlated with both rainfall and temperature, although since these two aspects of climate are not independent, only one may be causal. Like Sinclair *et al.* (2000), they suggest new food. It is impossible to see what the data from Langjan, Zululand and Akira indicate since with such low numbers of observations, spread over 12 months, no statistical analysis can be performed. In fact, I randomly allocated 15 numbers (births) to 12 categories (months) and got very similar-looking graphs to those displayed by Hall-Martin *et al.* (1975) for these three sites. Random distributions are frequently thought to be meaningful because

people rather expect a random distribution to look more regular, which it is not, particularly when small numbers are involved.

The final set of data is taken from Bercovitch and Berry (2010a), using the large Zambian data set (33 years) already referred to above. Their data is shown in Fig. 6.5, and births ($n=35$) occurred in every month of the year. The modal birth month, May, was the first month following cessation of the rainy season, but females were as likely to bear offspring during the wet as during the dry season (binomial $P=0.311$). My chi-squared test (again as above) gives a value of $\chi^2_5 = 3.59$, confirming the non-seasonal nature of this data set. Because this giraffe data is so extensive, it is worth just summarising some other birth statistics that Bercovitch and Berry (2010a) give. Infant survivorship had no significant impact on interbirth

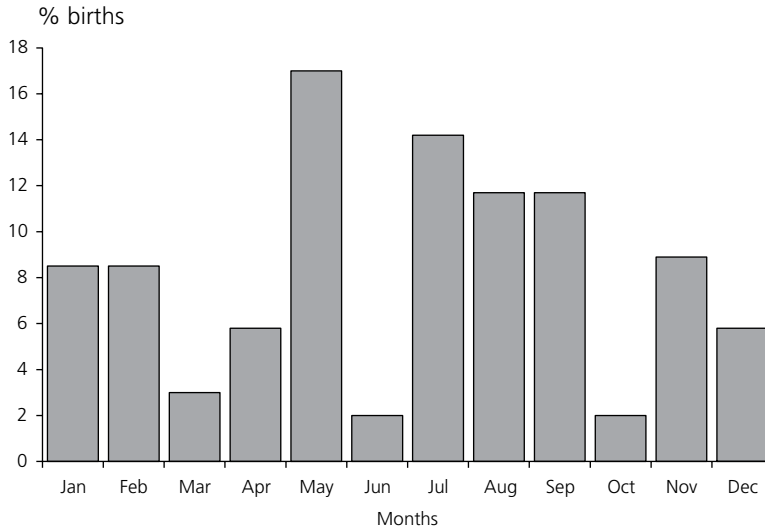


Fig. 6.5 Monthly distribution of giraffe births ($n=35$) in the Luangwa Valley, Zambia, 1970 to 2003. Source: redrawn using data from Bercovitch & Berry (2010a).

interval ($t=0.195$, $df=17$, $P=0.847$), so neonatal mortality was probably not a factor influencing reproductive rates. Across all births, the interbirth interval averaged 677.7 (± 182.4 ; $n=19$) days. Given the possibility that some exceptionally lengthy interbirth intervals (i.e. >1000 days) actually incorporate two births, they reanalysed a subset of the data by excluding these potential outliers. Within the more restricted sample, the average interbirth interval was 606.8 (± 76.5 ; $n=16$) days. Sex of calf had no significant impact on the length of the interbirth interval ($t=0.694$, $df=13$, $P>0.500$), and cows produced an unbiased sex ratio at birth (14:11; binomial $P=0.690$).

In conclusion, the question of whether giraffes are seasonal in their birthing pattern remains equivocal. Eight areas (seven in southern Africa) with adequate data say yes, six areas (three in East Africa and three in Zambia) with adequate data say no. At first glance, this could be seen as a southern Africa versus central/eastern African phenomenon. However, the Serengeti data of Sinclair *et al.* (2000) shows seasonality. Also Arusha, Tsavo and Nairobi are not exactly similar in their vegetation.

So is it subspecies, region, time period or observational bias? I have no idea.

The last birthing phenomenon that I will briefly examine is birthing site fidelity. Do giraffe females return to the same site to give birth? Although identifying factors that decrease offspring survival in the wild is difficult, one possible key component could be birth site location. This fidelity could be influenced by social factors, such as where other females within a group are also bearing offspring, and ecological factors, such as the extent of habitat cover and predator pressure (Bercovitch & Berry 2015). On the other hand, any lack of birth site fidelity could also be due to an adaptive mechanism, whereby females adjusted their parturition locations based upon yearly varying resource availability and/or predator pressure.

In the wild, calf delivery has been reported in female giraffes who isolate themselves from herd members (Dagg 2014; Langman 1977; Pratt & Anderson 1979), as well as those who bear progeny within a herd (Dagg 2014). Among those who bear offspring, about half remain alone with their calves up to 1 month after the birth (Pratt & Anderson 1979). Despite the lack of published

information based upon long-term studies, many African wildlife biologists have assumed that female giraffes return to 'traditional, highly localised, calving areas' (Kingdon 1997) and that they 'have preferred calving areas within their home range, to which each cow returns, alone, to drop successive calves' (Estes 1991a). The 33 years of Zambian data already referred to (Bercovitch & Berry 2015) examined this fidelity suggestion. In their study, these authors systematically recorded the location of the first sighting of all new calves, including the location of 50 calves born to individually recognised females. Calves were equally likely to be born during the wet and dry seasons (binomial $P=0.229$; $n=29$). Birth locations were distributed across the four ecozones⁷ in a pattern that was not significantly different from chance expectations (log-likelihood ratio $G=3.256$, $P=0.354$). They therefore found no evidence to support the suggestion that giraffe cows bear calves in specific birth locations, or that they return to preferred areas for bearing offspring. They did find that clustered conceptions could yield giraffe crèches within a single location, but found no evidence for temporal concentrations of births in a specific location. Although up to five calves could be born in a single locality, the distribution of birth sites was no different than expected based upon the distribution of ecozones in the study region. Intriguingly, while females did not seem to favour specific locations, individual females did have a tendency to avoid bearing consecutive calves at the same site when a previous calf did not survive the first year of life ($t=2.035$, $df. = 8$, $P=0.076$).

⁷The four ecological zones are based upon the predominant vegetation types present in each area (Bercovitch & Berry 2010b). They subdivided the habitat into four major ecozones for analysis. (i) *Riverine*: the riparian forest region along the Luangwa River and its tributaries, (ii) *Woodland*: those areas dominated by mopane, munga and miombo (mostly *Brachystegia* and *Julbernardia*) vegetation. (iii) *Thicket*: those areas characterized by scrubland and dense thicket. (iv) *Open*: grassland areas with few or no trees, bushes or shrubs.

Vigilance: an advantage of living in groups

Many savannah ungulates live in groups. There are benefits and costs to such behaviour (see Krause & Ruxton 2002 for a complete review), and before looking specifically at studies involving giraffes, I will briefly describe some of the stated antipredator benefits. These basically fall into three categories: increased vigilance (the 'many eyes' theory), predator confusion and dilution of risk.

Increased vigilance, with increased group size, is a consequence of more eyes looking for predators coupled with the transmission of information about detected predators throughout the group. As a result, an individual in a group does not need to detect a predator itself in order for it to be aware of the potential attack. The 'many eyes' idea suggests therefore that as group size increases, an individual's 'share' of the group vigilance can decline, leaving more time for other activities such as foraging. For example, Shorrocks and Cokayne (2005), looking at impala in Nairobi National Park, found that randomly selected females within breeding herds spent less time being vigilant in larger groups, and overall individuals spent more time foraging when they were less vigilant.

The second antipredator effect of living in groups, predator confusion, is thought to arise because of an inability of the predator to single out and attack individual prey within a group. They are distracted by too many targets. It is an appealing idea, but empirical support for the confusion effect is limited.

The 'dilution effect' basically suggests that there is safety in numbers. Included within this category of group benefits are two separate probabilities: a lower risk of detection and a lower risk of capture when detected (see Shorrocks & Bates 2015, Fig. 5.15, for a graphical illustration of this). The combination of the two probabilities will give the overall probability of being captured by a predator. However, for this to work, the predator must only take one

prey during an attack, and the probabilities must be 'appropriate'. For example, if the group is more easily seen from a distance, the overall group probability could rise and the 'safety in numbers' could disappear. In fact, the only data on this kind of risk assessment, in savannah ungulates, would suggest that the situation is even less straightforward. Creel and Creel (2002) calculated the 'risk of death' for an individual wildebeest, when the predator was the wild dog (*Lycaon pictus*), in the Selous Game Reserve, Tanzania. This measure of 'overall risk' took into account all the processes by which herd size might affect an individual's vulnerability to predation. These included 'risk of detection', the decision to hunt or not, the success of hunts, and the final 'risk of attack'. Their results suggest that the 'risk of death' does in fact change with group size. However, the lowest individual 'risk of death' was obtained when herd size is intermediate (around 40), not at the largest group size actually observed in the Selous Game Reserve. Larger groups of wildebeest are more easily detected than smaller groups and this cancelled out any benefit of reduced 'risk of attack'. This advantage, for individuals in groups of intermediate size, leads us to consider the distribution of group sizes naturally observed in savannah ungulates.

The distributions of group (herd) size have been recorded for several African ungulates (Creel & Creel 2002; Sinclair 1977; Wirtz & Lörcher 1982), including giraffes (Bercovitch & Berry 2009; Foster & Dagg 1972; Shorrocks & Croft 2009). They usually show a right-skewed frequency distribution (Fig. 6.6a). Small groups are very common, medium-sized and large groups less so. However, if we replot such distribution data, in terms of the group size experienced by each individual, we find that most individuals in fact choose to live in groups of intermediate size (Fig. 6.6b). For this giraffe example, the modal group is class 5. In other words, large giraffe groups are uncommon, small giraffe groups are common but comprise a relatively small number of individuals. Being in

a larger group might confer better antipredator advantages (higher vigilance, lower risk of attack), but being in too large a group has additional costs, such as increased competition for resources and, from the wildebeest example, higher risk of detection. There appears to be a medium group size that maximises the benefits and minimises the costs. Of course, these benefits and costs will vary from species to species, so we might expect group size to vary for savannah ungulates with different ecologies, and perhaps for giraffes in different habitats. However, the group size 'chosen' by most individuals always seems to be an intermediate one. Since details of 'predator confusion' and the 'dilution effect' have not been studied in giraffes (although they may be important), I will conclude this section by looking at vigilance, the presence of predators and conspecifics and how these interact with grouping behaviour.

In a 3-year study in the 350 km² Olkirimatian-Shompole Community Conservation Area in the South Rift Valley of Kenya, Creel *et al.* (2014) measured variation in antipredator responses (vigilance and group size), and the foraging costs of these responses, in five ungulates: zebra (*Equus quagga*), Grant's gazelle (*Nanger granti*), wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and giraffe. These ungulates made up more than 90% of the prey community available to the two locally dominant predators, lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*). This assessment of abundance was based on ground transects using distance sampling to account for variation in detectability (for the ungulates), and 396 days and nights of field observation and 43,318 photographs from motion-sensitive cameras deployed on a grid system for the carnivores. They recorded an animal as vigilant if 'it was stationary with its head held above shoulder height with the eyes and ears simultaneously focused, and not chewing or ruminating'. However, I believe this latter exclusion was mainly because they were also looking at the effect on foraging, in its wider sense, which

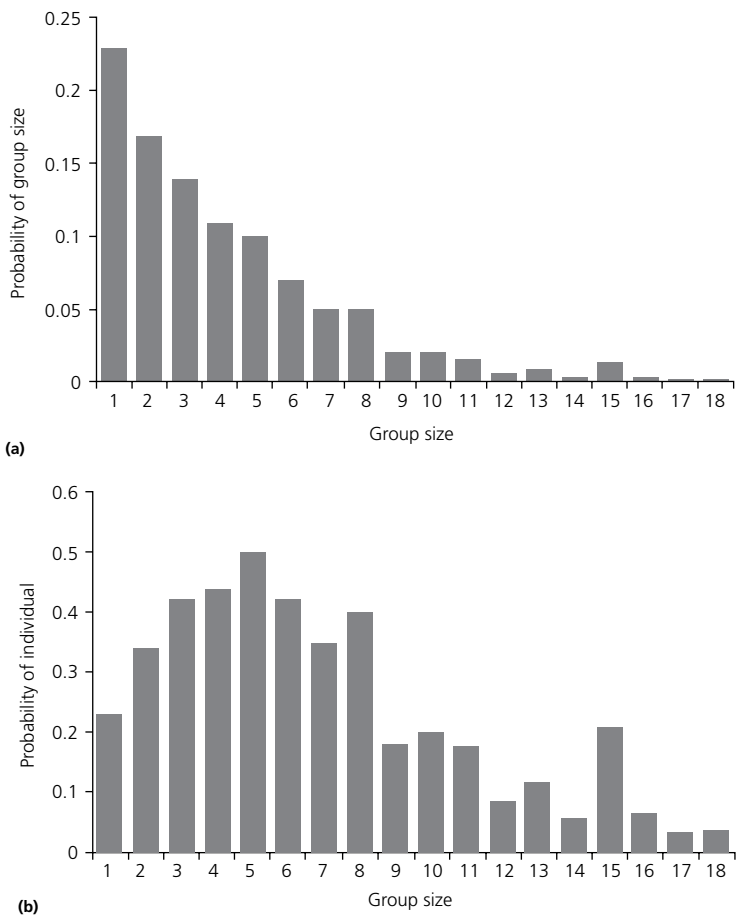


Fig. 6.6 Group (herd) size in giraffes. (a) Frequency of group size in giraffes, in Nairobi National Park. (b) Same data but showing the group size experienced by individuals. Data from Foster & Dagg (1972).

could include chewing and ruminating. If you are specifically testing the ‘many eyes’ idea then any vigilance should be recorded. Less restrictive definitions of vigilance allow the possibility that an animal can simultaneously be vigilant and ruminate. This is also an issue with the work of Cameron and du Toit (2005) below. However, the results of Creel *et al.* (2014) are very illuminating and the study is an excellent example of how wildlife research should be undertaken and analysed. Fig. 6.7a shows their results for the relationship between herd size and if predators were present or absent locally. Predators were classified as present at a distance

of 400 m or less. Zebras and impalas both aggregated into larger groups when predators were present, whereas wildebeests disaggregated into smaller groups, and Grant’s gazelles and giraffes showed weak responses. Fig. 6.7b shows their results for the ‘proportion of adults that were vigilant’ and the presence of predators. High levels of vigilance were seen in the species with the smallest groups, as revealed neatly by the mirror imagery of Figs 6.7a and 6.8b. Vigilance levels were lowest in obligate grazers that formed the largest herds (wildebeests and zebras), intermediate among mixed feeders with intermediate group sizes (impalas and

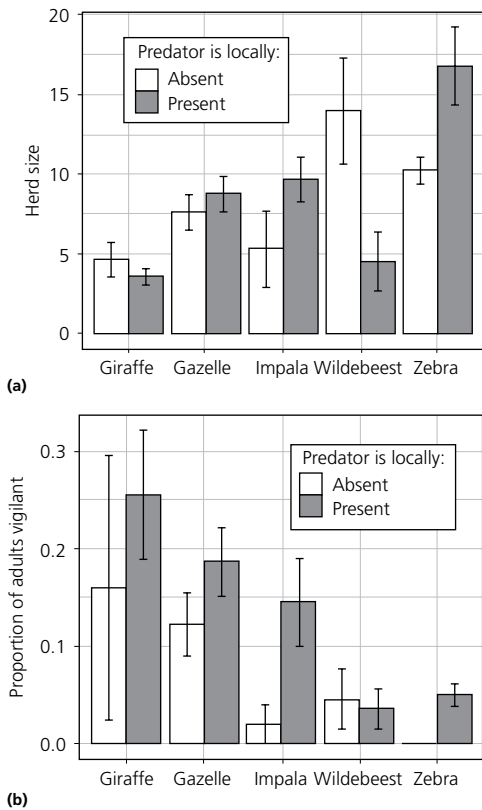


Fig. 6.7 (a) The relationship of herd size to the presence of predators for five ungulate species. The effects of variables other than predator presence were controlled in statistical analysis, but simple means and 95% confidence limits are shown here. (b) The relationship between the proportion of adults that were vigilant and the presence of predators. Predators were classified as present at a distance of 400 m or less for this figure, but similar patterns are seen if species-specific thresholds are used. The effects of group size and other variables on vigilance were controlled in statistical analysis, but simple means and 95% confidence limits are shown here. Source: Creel *et al.* (2014). Reproduced with permission of Oxford University Press.

Grant's gazelles), and highest for the obligatory browsing giraffes, which formed the smallest groups. Collectively, these results support the conclusion that grouping and vigilance are complementary responses to risk. This provides interspecific support for the 'many eyes' idea, but not intraspecific support.

Another vigilance study, again on several species, was conducted by Périquet *et al.* (2010) who looked at vigilance while drinking. The study was conducted on giraffes, greater kudus (*Tragelaphus strepsiceros*), and plains zebras (*Equus quagga*), in Hwange National Park (HNP), Zimbabwe, between mid-September and mid-November 2008. The potential predator was the lion, which accounted for 10% (giraffe), 11–24% (kudu) and 5–7% (zebra) of lion kills in HNP. An animal was vigilant when 'it stood still on all four legs, with head raised above shoulder level and looked attentively at the surroundings, often with ears held forward'. They did not consider an animal was vigilant while moving. An animal's use of water was divided into three phases: approach, drinking and departure. Some results are shown in Fig. 6.8. Analyses revealed that the phase (approach, drinking or departure) influenced the proportion of time spent vigilant (giraffe: $F_{2,145} = 7.73$, $P = 0.001$; kudu: $F_{2,87} = 2.64$, $P = 0.077$; zebra: $F_{2,106} = 21.23$, $P < 0.0001$), with higher vigilance levels during the approach phase for all three species. Giraffes are particularly vulnerable to predators when drinking because of the splayed-legged posture they adopt. They generally spent the longest time drinking and showed the highest vigilance levels. In addition, the frequency of vigilance bouts was higher for giraffes, when lions were in the vicinity, during the drinking phase ($F_{1,58} = 5.05$, $P = 0.028$).

A third study that has looked at vigilance and group size in giraffes is that of Cameron and du Toit (2005). This study was conducted in Kruger National Park, South Africa. The woody vegetation in the area was dominated by *Acacia nigrescens* and *Sclerocarya birrea* trees, a typical giraffe habitat in this area. All the major predators of giraffes were present, with lions and spotted hyaenas comprising the largest threat to giraffes (Pellew 1984a). The study was conducted between July 2001 and July 2002. They 'located giraffes opportunistically while driving on predetermined routes through the study area during all daylight hours and recorded group composition as soon

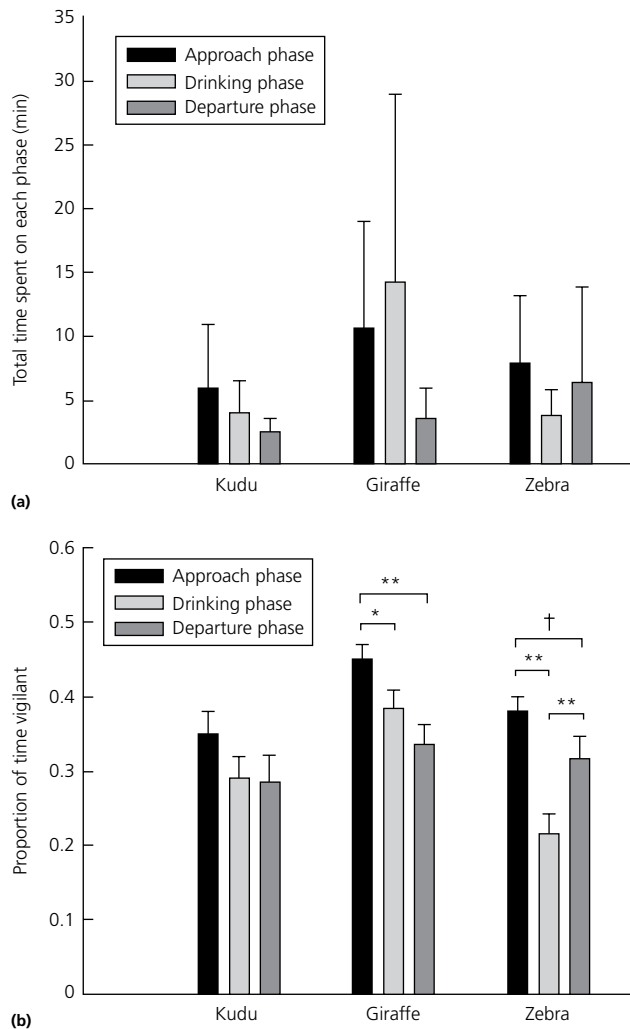


Fig. 6.8 (a) Average time + SD spent on each phase and (b) average vigilance levels + SE across the different phases (approach, drinking and departure) for the different study species. † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; t test with Bonferroni correction for multiple comparisons. Source: Périquet *et al.* (2010). Reproduced with permission of Elsevier.

as a group was encountered'. A group was defined as all giraffes within 100m of each other. This would allow the giraffes in a group to be quite widespread. Cameron and du Toit (2005) measured the neck angle, and the number of bites taken during a foraging episode (all continuous bites at one neck angle). Foraging episodes could therefore be terminated by a

change in the giraffe's neck angle or by a change from foraging to scanning, moving, interacting or grooming. Neck angles were divided into four categories based on the angle of the neck to the front leg: 45° (head low), 90°, 135°, 180° (head extended directly upwards) (du Toit 1990a).

Unfortunately, their definition of a 'scan' (what others have called vigilance) is different

from the two studies outlined above. They say '... those stands in which the giraffe had its head raised (135° or 180° neck angle), and which lasted at least 1 s without chewing, as a vigilance scan'.⁸ Shorter stands were considered part of foraging. One of their measures of vigilance was 'the proportion of foraging episodes that ended with a shift to scanning'. They also define a 'foraging bout', which was a combination of episodes and other behaviours at a single feeding station. Giraffes were considered to change feeding station when they took five consecutive steps without foraging. In practice, this meant changing trees, changing to the opposite side of a tree or moving away from the tree and then returning to the same tree.

They tested the relationship between group size and vigilance using ANOVA and only males showed a significant relationship with total group size ($F_{1,734}=4.41$, $P<0.05$), using the proportion of foraging episodes ending in a scan as the measure of vigilance. Proportion of time spent scanning during a foraging bout and frequency of scans per focal sample showed no significant relationship. However, their definition of scanning and vigilance is very different from

that of other researchers (Seeber *et al.* 2012) and it is difficult to know how to interpret their results with respect to total group size. However, females tended to end more foraging episodes with a scan when alone than when in a group (alone: 0.49 ± 0.03 , $N=90$; with bulls: 0.47 ± 0.06 , $N=33$; with other cows: 0.48 ± 0.01 , $N=562$; mixed: 0.44 ± 0.02 , $N=352$). However, the ANOVA is not significant: $F_{3,1033}=0.92$, $P=0.43$). In contrast, scanning behaviour by bulls was significantly influenced by group type. Bulls ended a foraging episode with scanning most frequently when they were in a group with other bulls and least frequently when they were alone (alone: 0.36 ± 0.04 , $N=190$; with other bulls: 0.52 ± 0.04 , $N=80$; with cows: 0.44 ± 0.03 , $N=200$; mixed: 0.41 ± 0.02 , $N=273$; ANOVA: $F_{3,739}=4.64$, $P<0.005$). In addition, when bulls were in a group with other bulls, their size influenced how often they scanned the environment. The largest bull ended a forage episode less often with a scan than did other bulls that were not the largest ($t_{359}=5.22$, $P<0.0001$). The frequency of scanning also differed significantly between the largest bull and the other bulls in a group ($t_{359}=2.53$, $P=0.01$). As a consequence of this, the total amount of time spent scanning during a foraging bout differed between the largest and smaller bulls ($t_{359}=3.01$, $P<0.005$).

The conclusion from these three studies of group size and 'vigilance' is that giraffes can respond to the presence of predators by changing group size, and change their degree of vigilance depending on perceived threats from both predators and conspecifics.

⁸At the start of this chapter, I described in some detail the giraffe ethogram outlined by Seeber *et al.* (2012). This is an important protocol for all comparative behaviour work, and vigilance is no exception. Their 'scanning' would be equivalent to what we have been calling vigilance. They define it as 'Vigilance is most obvious when the animal is standing still with an erect neck and appears to be actively watching, but scanning is apparently done synchronously with many other behaviours (e.g. while ruminating, walking, or between feeding bouts)'.

CHAPTER 7

Individual ecology

Following on from Chapter 6, this chapter will look at 'individual ecology'. The giraffe is a browser and this chapter will examine the species of tree used and evidence for selectivity. I will also look at the behaviour of browsing and the interaction between the individual giraffe and their 'thorn' tree food. How effective are the *Acacia* thorns, and in some areas the protective *Acacia* ants, in influencing the observed feeding patterns? The chapter will conclude by examining daily activity patterns, predators, competitors and mutualisms.

Of course, an individual's 'behaviour' and 'ecology' are intertwined, although traditionally the two aspects have frequently been studied by different people. Population behaviour and ecology are examined in Chapter 8. Although populations are made up of individuals, they have 'emergent' properties of their own. The types of questions we ask, and the techniques we employ, change as we move from studying individuals to studying populations. Asking how an individual giraffe is killed and by what predator (the interaction of two individuals) is different to asking the question 'are giraffe populations controlled or regulated by predators?'. Failure to realise this has frequently led field workers who see an individual 'predation event' to then assume that predators are important in regulating the population of which the individual is a part.

Daily activity in time and space

The daytime activity pattern of a giraffe varies throughout the 24 hours, as it does for other ungulates (Jarman & Jarman 1973; Leuthold 1977; Walther 1973). One of the earliest giraffe studies was that of Leuthold and Leuthold (1978b) in the southern part of Tsavo National Park, Kenya, near the Voi River. Observations were made from a vehicle, using 10 × 50 binoculars. During each period of observation, the authors concentrated on one individual giraffe and noted each change of activity to the nearest minute. They distinguished between four main categories of behaviour: (1) feeding, (2) ruminating, (3) standing/walking (including grooming and all social interactions), and (4) lying (with or without rumination). (2) and (4) clearly overlap and it is not clear in the subsequent analysis how this confluence was handled. The time that an individual spent in each activity was recorded as a percentage of each half hour, and also of the total observation time on any one day. The authors observed individuals at different times of year, and under different weather conditions, in order to assess both seasonal and day-to-day variations in behaviour patterns. Twelve individual giraffes (seven adult males, one subadult male and four adult females) were watched on 16 different days between 21 July 1971 and 6 July 1973 (a total of 230 hours).

It proved impossible to observe giraffes at night. The daily patterns of five individual giraffes are shown in Fig. 7.1. A feature of these activity patterns is their great variability. For example, the proportion of time spent feeding (the oblique cross hatching in Fig. 7.1) ranged from 15% to 49% in males and 25% to 70% in females. Since all these activities sum to 100%, this means that the other activities varied in a similar way. The temporal distribution of activities also differed considerably between different days.

What is surprising is that Walther (1973), with Thomson's gazelle, and Jarman and Jarman (1973), with impala, also found such wide variation, and yet concluded that there existed a basic activity pattern characteristic of the species, at a given time and place. Leuthold and Leuthold (1978) did note that relatively more giraffe were found 'lying' in larger, rather than in smaller, groups ($P < 0.001$) (no details of the statistical test are given). However, this observation fits well with the section in Chapter 6 on vigilance and 'many eyes'. In fact, Leuthold and Leuthold (1978) comment that 'Possibly, this reflects a greater "feeling of security" of individuals in larger groups'. In relation to 'weather' and the observed activity pattern, they did explore the 'heat load' idea put forward by Lewis (1975) to explain the activity pattern of African ungulates. In their giraffe data, Leuthold and Leuthold found that female giraffe fed less at high temperature (the dry bulb temperature at 1400 hours) ($r_s = -0.68$, $P < 0.05$), but not the males ($r = 0.19$, $P > 0.1$) (no degrees of freedom given). To examine their results for any general features in the activity patterns, and to investigate differences between the sexes, Leuthold and Leuthold accumulated all their records into half-hour intervals, for males and females separately. Males showed low levels of feeding throughout the morning and early afternoon, with a marked increase in late afternoon (ANOVA, $P < 0.01$). In females, the pattern was less pronounced (ANOVA, F not significant) and almost reversed, 'with relatively intensive

feeding in the early morning'. Leuthold and Leuthold comment on seasonal patterns but to be honest, they do not have the necessary data for an informed analysis. This is mainly because data is lacking for certain season/sex combinations and therefore comparisons are impossible. For example, they say '... the pattern of the male giraffe shown in Fig. 2a can be regarded as typical of the dry season in the area concerned, even though we do not have corresponding data for the green season'. However, if the corresponding data for the 'green season' is not available then you cannot say the 'dry season' data is typical of that season. The missing 'green season' behaviour pattern might in fact be the same as the 'dry season' one.

As a comparison to this early study of Leuthold and Leuthold (1978), I complete this brief examination of giraffe daily activity with a study by du Toit and Yetman (2005). This work compared the diurnal activity budgets of four species of African browsing ruminants that vary in body mass. These were steenbok (*Raphicerus campestris*), which is one of the smallest of all ruminants (11 kg), impala (*Aepyceros melampus*) (41 kg), greater kudu (*Tragelaphus strepsiceros*) (155 kg) and giraffe, which is the largest of all ruminants (828 kg).¹ Although this study looked at diurnal activity budgets, it had the overarching objective of investigating the effect of body size on behaviour. A fundamental idea about size in mammals is that if species in a herbivore assemblage all use the same quality food, and ingest it at roughly the same rate, then the total time spent on feeding (including walking to find food) should be positively related to body mass because of the increased metabolic requirements of larger animals (Peters 1983; Schmidt-Nielsen 1984). However, larger herbivores ingest food faster and have lower metabolic demands, frequently allowing them to use a

¹I quote the weights given by du Toit and Yetman (2005). Notice, however, that in Chapter 4 I concluded that an average weight for a male giraffe is about 1200 kg and for a female giraffe about 800 kg.

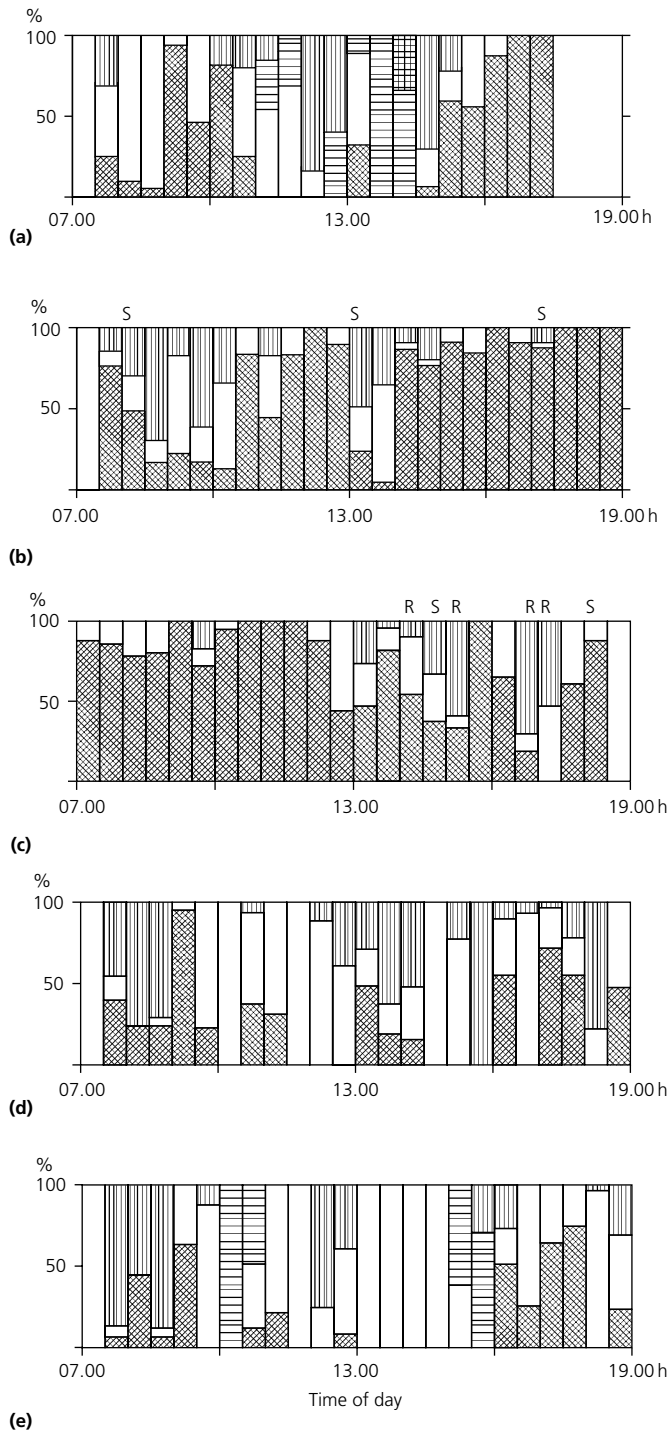


Fig. 7.1 Daily activity of five giraffe. (a) Subadult male, early dry season (July 1971). (b) Adult female, late green season (July 1972). (c) As (b) late green season (December 1971). (d) Adult female (in oestrus), hot season (March 1972). (e) Adult male accompanying (d) above (March 1972). Oblique cross-hatching = feeding, vertical hatching = ruminating (standing), horizontal hatching = lying (not ruminating), vertical/horizontal cross-hatching = ruminating (lying); grey = standing/walking and other activities; white = no data, R = rain, S = suckling. Source: Leuthold and Leuthold (1978). Reproduced with permission of John Wiley & Sons.

wider range of food than smaller herbivores (Bell 1971; Geist 1974; Jarman 1974). Essentially, this is because gut volume is a constant proportion of body weight, that is, it is essentially isometric ($\alpha \text{ mass}^{1.043}$) (Demment 1982; Parra 1978), while maintenance metabolism (a prime determinant of intake) is a fractional power of body weight, that is, it is allometric ($\alpha \text{ mass}^{0.75}$) (Kleiber 1975). As a consequence, larger herbivores may be able to reduce their foraging time, despite having greater absolute intake requirements, by increasing their intake rate and reducing their food quality, although they would prefer higher-quality food. The smaller ungulate species will feed more selectively on the highest quality plant parts available. This resource partitioning idea has become known as the Jarman–Bell principle, and I well remember its origins when Peter Jarman, Richard Bell and I were in the Zoology Department at the University of Manchester, England, studying for our respective PhD degrees.

In the study by du Toit and Yetman, focal animal observations (Altmann 1974) were performed on individuals within each species, from a 4×4 vehicle, using 7×50 binoculars. Only adult females were observed, and focal animals were either artificially marked with collars or individually identified from natural coat patterns or scars (see Chapter 8 for more on this type of identification). Observation periods were continuous and varied in duration, but were typically 3–5 hours long. Once a known individual had been recorded, it was not observed again until at least four observation sessions had been performed on other individuals of the same species. Therefore, any particular animal does not appear in their data set more than once per month, and observations were distributed over at least 20 individuals per study species. Observation sessions were preplanned, so that data collection for each species was spread across all hours between 0600 and 1800 hours, in every calendar month. A total of 1094 hours of observations was undertaken, during

which the following five classes of behaviour were noted: (1) *feeding*, (2) *moving* (walking, walking ruminating, running), (3) *standing* (ruminating, resting, alert, grooming, socialising), (4) *lying* (ruminating or resting), and (5) *obscured*. Some of their results are shown in Fig. 7.2. Using the four seasonal quarter years² as samples for each species, a Kruskal–Wallis test was used to see if the four species differed in their diurnal behaviours. Within this browsing guild of four species, increasing body size was associated with increasing time spent on feeding ($H = 12.11$, $P < 0.001$) (Fig. 7.2a) and moving ($H = 12.24$, $P < 0.001$) (Fig. 7.2b), but with decreasing time spent resting ($H = 12.73$, $P < 0.001$) (Fig. 7.2c). Giraffe was the only species to ruminate while walking (3.53% of total diurnal activity, and 26.9% of total ruminating time). There was also significant variation among the four species in the time spent running ($H = 9.02$, $P < 0.05$) and grooming ($H = 12.51$, $P < 0.001$), due to impala, which is a social and rather nervous or excitable species. The four species did not vary significantly in their time allocations to ruminating, being alert (vigilance) or non-grooming social interactions.

This study by du Toit and Yetman (2005) supports the idea that diurnal time spent feeding and moving, in a savannah ruminant, is positively associated with body mass (Owen-Smith 1988, 1992). This appears to be different from the pattern found in temperate ruminants (Belovsky & Slade 1986; Mysterud 1998; Pérez-Barbería & Gordon 1999). This suggests that similar ‘life styles’ (browsing and rumination) are over-ridden by environmental factors (temperate versus tropical) when determining how diurnal activity patterns are modified by body mass.

One suggestion (Mysterud 1998) is that in the tropics, the larger ruminants spend more time feeding during the day. Although in this present

²Quarter 1 = January–March, quarter 2 = April–June, quarter 3 = July–September and quarter 4 = October–December.

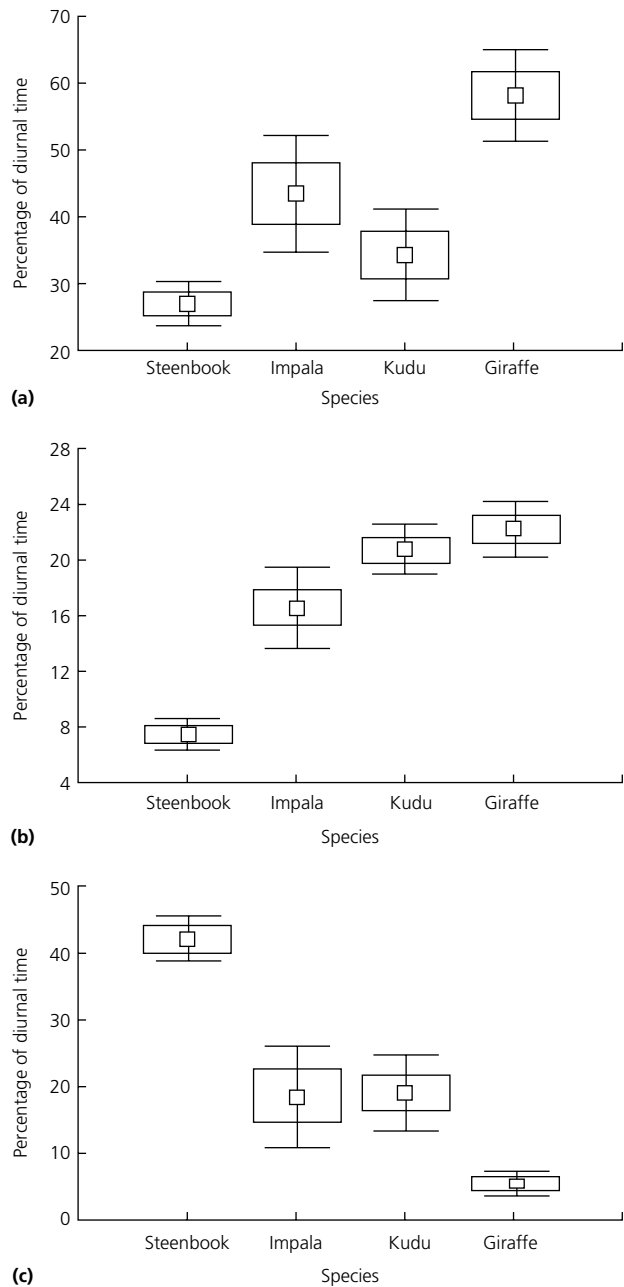


Fig. 7.2 Percentages of diurnal time spent (a) feeding, (b) moving and (c) resting by steenbok, impala, kudu and giraffe, plotted in order of increasing body size. Central square = mean, box = ± 1 standard error, bars = ± 1 standard deviation. Source: adapted from du Toit & Yetman (2005). Reproduced with permission of Springer Science and Business Media.

study du Toit and Yetman did not have suitable data to test this, they did have access to suitable data from previous work (du Toit 1993 and unpublished). They were able to quote that the ratio of diurnal: nocturnal activity (feeding and walking) was 0.579:1 for steenbok (11 kg) and 0.892:1 for kudu (155 kg), both in the dry season. This is consistent with Mysterud's idea. In fact, the temperate studies tend to be grazers or mixed feeders and this might also explain the differences between temperate and tropical above. For example, among African ruminants the larger browsers seem to spend more time foraging than similar-sized grazers (Owen-Smith 1992). A possible explanation for this is that the ratio of feeding to ruminating time differs between grazers (lower) and browsers (higher) because of differences in their fermentation rates (Owen-Smith 1982) of grass (slower) and browse (faster). Another reason, pointed out by du Toit and Yetman (2005), for the increased feeding time among larger browsers in African savannahs might be found in the physical properties of their browse. Large browsing ruminants in savannahs probably find it difficult to increase their food intake in proportion to their metabolic needs because they are constrained by the spines, thorns and branching architecture of their principal woody food plants (Cooper & Owen-Smith 1986; Leuthold & Leuthold 1978; Owen-Smith 1982; Pellew 1984b,c). This forces large ruminants like giraffe to increase feeding time to meet daily intake requirements. In fact, during the dry and early wet seasons giraffes, in the study by du Toit and Yetman, allocated disproportionately large amounts of diurnal time to feeding as compared with ruminating (58.3% to 13.1%). The authors believe this reflects the increased feeding time required by giraffes to meet their high intake requirements while cropping foliage from strongly spinescent and lignified twigs (see also Pellew 1984b,c). This is combined with the constraint that giraffes have in extending their rumination time. Giraffes differ from all other sympatric browsers, and

perhaps all other extant ruminants, in ruminating while walking. Giraffes are near the maximum size attainable by ruminants (Clauss *et al.* 2003) and therefore walking while ruminating (>25% of total rumination time in du Toit & Yetman 2005) might be an adaptation for alleviating this constraint.

In addition to temporal variations in foraging, there are also spatial differences. For example, I looked at foraging height in reticulated giraffe in Laikipia, Kenya (Shorrocks 2009). Continuous sampling was performed on 57 focal individuals. This involved observing individual giraffes for a continuous specified time of 10 minutes, and recording all instances of their behaviour in a number of categories. This was repeated, on different occasions, for the same focal individuals which could be recognised by their neck code (Shorrocks & Croft 2006, 2009). Habitats were classified as (1) open (open ground with a few sparsely distributed trees or shrubs), (2) semi-open (many trees and shrubs but with fairly large patches of open ground) or (3) dense (little open ground visible, with a dense covering of woody vegetation). From test observations to determine the range of behaviours performed by these giraffes, we had determined that the 'foraging' category could include the consumption of vegetation at five different height categories. These heights were measured relative to a giraffe in the field. They were: (1) above nose level (muzzle horizontal), (2) nose level, (3) from below the nose to half neck level, (4) half neck to shoulder level (neck more or less straight with back, and (5) below shoulder level (neck bent below line of back). The results are shown in Fig. 7.3. Giraffes spent a significantly greater proportion of their foraging time feeding at heights between shoulder and nose level than observed above nose level and below shoulder level ($P < 0.001$). Proportions of time allocated to feeding at different heights did not differ significantly between adults and juveniles ($P > 0.05$) (relative to their size), morning and afternoon ($P > 0.05$), or between different habitat types ($P > 0.05$).

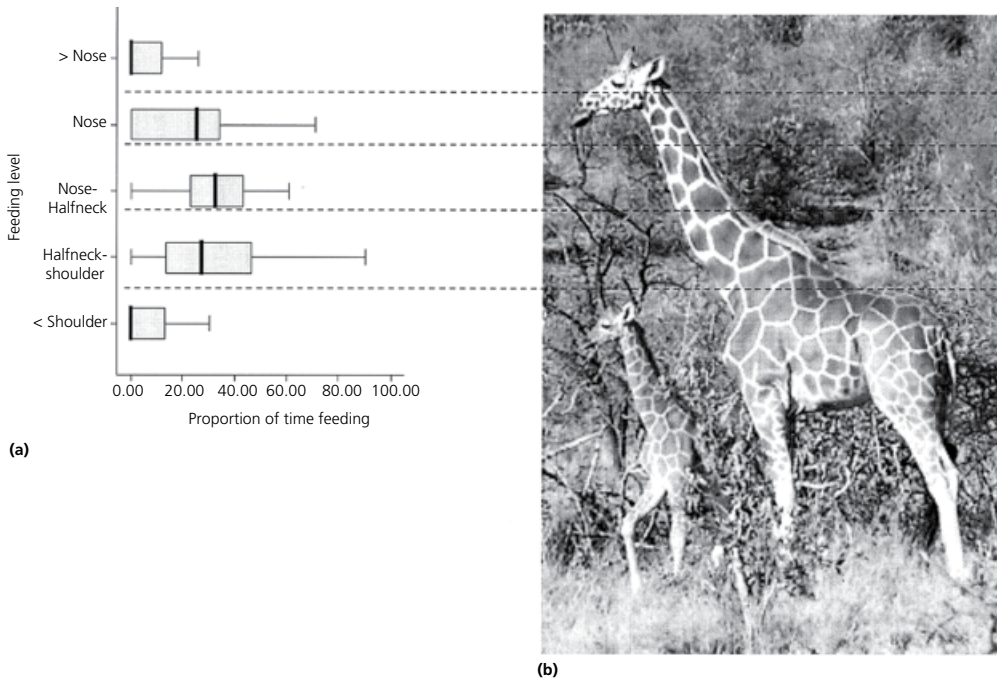


Fig. 7.3 Giraffe feeding heights. (a) Proportion of time spent at different levels. Box-whisker plots indicate median (black bar), quartile (boxes) and range (whiskers) of data for each feeding height category. (b) Location of feeding height categories superimposed on an adult reticulated giraffe.

Earlier, I asked the question: why does a giraffe have a long neck? Two main suggestions were put forward: (1) that long necks evolved because of competition with other browsers, allowing giraffes to feed above them ('competing browsers' hypothesis) (Darwin 1871) or that (2) the long neck evolved for direct use in intra-sexual combat to gain access to oestrous females ('necks for sex' hypothesis) (Simmons & Scheepers 1996). Suggestion (2) was discussed in Chapter 6. At this point, while looking at foraging height, it is appropriate to reconsider option (1). In fact, this first explanation has a long history and has become a key component of the explanation for coexistence among browsers. That is, because of body size and neck length, different species feed at different heights in the vegetation (Lamprey 1963; Leuthold 1978; McNaughton & Georgialis 1986). This 'niche' explanation has become accepted in

popular literature. In addition, it has also been suggested that competition between the sexes, in giraffes, is avoided because males can feed above the level of females (Pellow 1984a). However, despite its wide acceptance, the idea of feeding height separation among browsers had not been rigorously tested until the work of du Toit (1990a).

He observed the height at which four species of ungulate were browsing, in Kruger National Park (KNP), South Africa. These were giraffe, greater kudu, impala and steenbok, and the observation protocol was as described already for du Toit and Yetman (2005). Feeding height was divided into four classes for each species, using the angle (45°, 90°, 135° and 180°) made by the individual's neck, relative to its forelegs. Note therefore that the 'real height' categories are different for the four species. Each 'relative height' category (4) for each species (4) was given

a 'real height' value by physically measuring the height at which observed vegetation was foraged, for each species/'relative height' category (16 in all). Their results are shown in Fig. 7.4 (top). Giraffe allocated almost 90% of feeding time to feeding above the height ranges of kudu, impala and steenbok. Kudu allocated 33% of their feeding time to the height range 1.2–1.7 m, which was little used by giraffe and impala, and beyond the reach of steenbok. However, in this area of KNP, despite this clear stratification of feeding levels, there is still substantial overlap between kudu, impala and steenbok. What is

more, in areas of KNP where there is also nyala (*Tragelaphus angasi*), bushbuck (*T. scriptus*) and sunni (*Neotragus moschatus*), the overlap among the smaller browsers will be even more acute. In eastern Africa where there is also gerenuk (*Litocranius walleri*), another browser is added to this group. It would appear, therefore, that among the savannah browsers, only giraffe is separated by height of vegetation. However, it should be remembered that mature trees grow from seedlings and saplings. Excessive browsing by the smaller species on these young trees might have long-term consequences for the

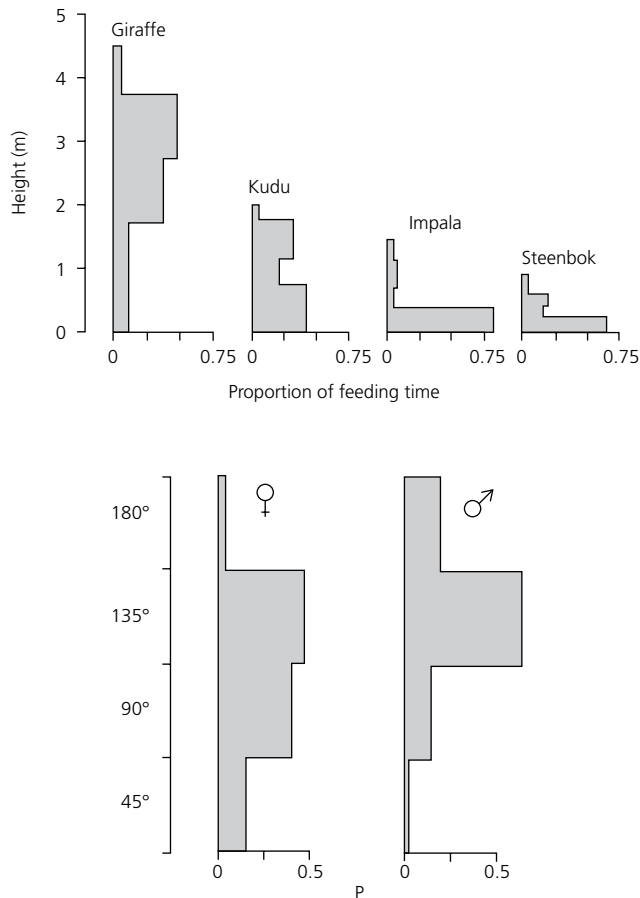


Fig. 7.4 (Top) Foraging height separation in South Africa (Kruger National Park) savannah browsers. (Bottom) Foraging height separation in male and female giraffe adults (South Africa, Kruger National Park). Source: du Toit (1990a). Reproduced with permission of John Wiley & Sons.

mature tree population. Browsing height stratification between giraffe and kudu + impala + steenbok does not exclude the possibility of resource competition, even between giraffes and the group of smaller browsers. Of course, there is also still the issue of why the giraffe neck needs to be so long. As discussed in Chapter 6, the 'competing browser hypothesis' needs to explain why giraffes have remained about 2.5 m taller than their tallest competitors for over 1 My, when there are clearly costs in terms of predation rate, blood pressure and maintenance of skeletal lengthening (Mitchell *et al.* 2006; Warren 1974). Arguably, an animal half the size of the present-day giraffe, in other words about 2.5 m high, would be sufficient to outcompete other browsers.

Du Toit (1990a) found that on average, giraffe bulls fed at a higher level in the vegetation than cows, spending 84% feeding above body height (neck angle $>90^\circ$), compared to 49% for females (Fig. 7.4 bottom). Bulls often had their head and neck extended vertically and may suffer an increased predation cost due to reduced vigilance when in this posture. Bulls may feed higher in the vegetation to gain access to more nutritious, protein-rich shoots in the upper canopy (Pellow 1984c). In fact, giraffes in general gain a nutritional advantage by foraging above the height of the other species, as they receive more biomass per bite higher in the canopy (Woolnough & du Toit 2001).

These ideas were further investigated by Cameron and du Toit in 2007. They wanted to know if the difference in leaf biomass available to giraffes at different heights in the canopy might be due to the foraging of smaller browsers, or the differential resource allocation within a tree. The Jarman–Bell principle mentioned earlier was of course developed for the African grazing guild. The larger species (buffalo *Syncerus caffer*, zebra *Equus quagga*, wildebeest *Connochaetes taurinus*) consume less leaf and more stem than the smaller-bodied species (Grant's and Thomson's gazelles, *Nanger granti* and *Eudorcas thomsonii*), which in the Serengeti

National Park results in a grazing succession (Bell 1970, 1971; Gwynne & Bell 1968; Shorrocks & Bates 2015). Originally it was thought that the larger species 'exposed' the high-quality forage for the smaller species (an instance of facilitation). But it appears that in fact, the smaller species, with narrower muzzles, deplete the highest quality parts of the forage, reducing the quality of the sward for the larger species. This would be competition, not facilitation. Is this what is happening with the vertical forage of the browsers? Are giraffes 'forced' to forage higher because of competition from the smaller species?

Cameron and du Toit (2007) erected 2.2 m high fences around individual *Acacia nigrescens*, 1 m from the outside canopy, that excluded smaller browsers. Only giraffes, that can forage above 2.2 m, were not excluded. Each fenced tree was paired with a nearby 'control' *A. nigrescens* tree, of a similar type (at least 4 m tall with branches at all foraging heights). These were maintained for a complete growing season (November 2001 to July 2003) at a savannah site in South Africa (Lion Sands Game Reserve in the Sabi Sand Wildtuin, part of the greater Kruger ecosystem) with an intact guild of indigenous browsing ungulates (giraffe, greater kudu, impala and steenbok).

Acacia nigrescens is a staple browse plant of giraffes in southern Africa (du Toit *et al.* 1990). Three levels of available browse were sampled: 1 m (available to steenbok, impala, kudu and giraffe), 2.5 m (available to kudu and giraffe) and 4 m (available only to giraffe). In order to provide a suitable index of browsing intensity (du Toit *et al.* 1990), the recent browsing of shoots, on a presence/absence basis, for 10 randomly selected shoots was recorded for each height level. To sample forage availability, they used the 'giraffe browse unit' (GBU). This is equivalent to the average twig pruned, or leaf stripped, by a giraffe in a single bite, which for *A. nigrescens* is 144 mm long (Woolnough & du Toit 2001). The GBU therefore includes the smaller bites of steenbok, impala and kudu.

It provides a measure of biomass return, to the browser, per bite and reflects both foliage depletion and foraging efficiency.

At each tree, five GBUs were clipped from around the canopy at each of the height levels (therefore 15 GBUs per tree). These GBU samples were then stripped of leaves, and the leaf and twig material air dried in the field and later oven dried at 60°C until mass was constant. Leaf dry mass, twig dry mass and twig proximal diameter were each recorded separately. Their results confirmed the findings of previous research, that there was a significant difference in forage availability at the different heights. There was less browse per GBU low in the tree and more at heights available only to giraffes (ANOVA, $F_{2,51} = 9.20$, $P < 0.0005$). There was no significant difference between control and treatment trees at any height before fencing. However, there was a significant difference from pre- to post-fencing between control and excluded trees at 1 m ($t = 2.62$, $P = 0.03$). At 2.5 m ($t = 1.30$, $P = 0.24$), and at 4 m ($t = 0.07$, $P = 0.95$) there was no significant difference. Forage availability was different at 1 m height between excluded and control trees ($t = 3.60$, $P = 0.005$) but not at 2.5 m ($t = 1.48$, $P = 0.16$) or 4 m ($t = 0.10$, $P = 0.92$). After fencing, there was still a significant difference in forage availability by height for the unfenced control trees, with less forage available at 1 and 2.5 m and significantly more at 4 m (ANOVA, $F_{2,22} = 5.54$, $P = 0.01$). In contrast, there was no difference in forage availability for the fenced trees (ANOVA, $F_{2,22} = 0.01$, $P = 0.98$). Notice that the fence had worked. No shoots were foraged on fenced trees at 1 m height. Because fences were 2.2 m high, they reduced but did not eliminate foraging at 2.5 m. Giraffes gain a foraging advantage by browsing above the reach of smaller browsers. Notice also that variation in leaf biomass per shoot, across browsing heights, diminishes significantly if the smaller browsers are experimentally excluded.

The conclusion can therefore be drawn that the observed variation in leaf biomass per GBU,

across the three feeding heights, must be due to depletion of leaf biomass by selective browsing at the lower levels. This supports the suggestion that giraffe feeding efficiency is reduced at low levels due to competition with the smaller browsers, who selectively reduced the overall forage quality. Competition may well drive the browsing height stratification in a similar way to that which we now believe drives the grazing succession of the grazers.

Another study of feeding height stratification is that of O'Connor *et al.* (2015). They examined possible competition between giraffes and camels at the Mpala Research Centre (MRC), Laikipia, Kenya, therefore a different subspecies to the studies of duToit and colleagues above. Spatially explicit 2-minute behavioural group scans were used to record frequency of feeding at different height categories, as well as the frequency of feeding on plant species. Only data from adult giraffe and adult female camels was recorded. Giraffes were observed between 6.30 am and 11.00 am and again from 3.00 pm to sunset, to avoid the midday period when animals are least active. The study area was divided into six sections that were visited in rotation to allow for even distribution of sampling effort across the MRC. Camel observations were made on the single accessible herd, over 5 days. The herd consisted almost exclusively of adult breeding females. The observer walked with the herders amidst the camels as they foraged across the landscape. Two-minute group scans were recorded on the first 15–20 adult female camels seen. Feeding heights for both species were determined using neck angles in the manner of du Toit and Yetman (2005), discussed above. Camels ($n = 340$, individual feed height mean = 1.36 m) fed significantly lower than male giraffes (Mann–Whitney U-test, $U = 34.5$, $P < 0.001$) and female giraffes ($U = 2504$, $P < 0.001$) (Fig. 7.5). Although camels are not a 'natural' component of this savannah system, they are increasingly important livestock in northern Kenya. This finding of forage separation helps to allay fears about forage

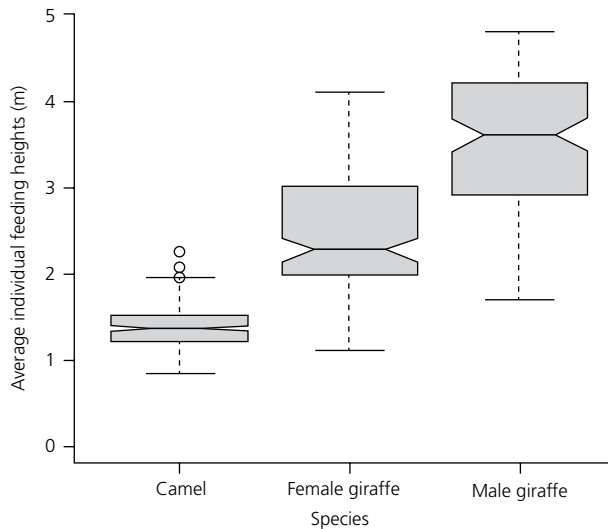


Fig. 7.5 Camel and giraffe feeding heights. Thick indented line represents median values, coloured areas show the range of the upper and lower quartiles. Range of the minimum and maximum values (excluding outliers) is shown by the dashed lines. Empty circles indicate the outliers. Source: O'Connor *et al.* (2015). Reproduced with permission of John Wiley & Sons.

competition among both ecologists (for giraffes) and pastoralists (for camels).

Sex ratios of giraffe groups are often different in dissimilar habitats, open vegetation tending to have groups with more females and dense vegetation areas more males. Young and Isbell (1991) looked at this on a ranch in south-central Kenya, and quantified the habitat differences of male and female groups. Intriguingly, they found that the preference for open habitats by female groups was in fact limited to groups with young. They therefore suggest that this difference is due to the avoidance of the predators of young giraffes. More relevant to this section, they also showed that the rate of giraffe feeding was highest at just above mid-body height (approximately 60% of adult giraffe height and similar to Fig. 7.3) (Shorrocks 2009). In dense habitats used by both male groups and female groups without young, both sexes fed mainly at heights where they could feed fastest (judged in terms of neck bending effort). In contrast, in open habitats used by female groups with young, females fed mainly at heights 'below

optimum' because these areas were dominated by short food plants. On the other hand, the dominant males accompanying these female groups fed at heights above optimum (they had to stretch) on rare tall trees, possibly to increase intrasexual vigilance. This study adds an extra dimension to the interspecific competition idea of Cameron and du Toit (2007), suggesting that both male and female giraffes sometimes forfeit feeding efficiency for reproductive gains.

Ginnett and Demment (1997) also examined the foraging behaviour of male and female Masai giraffes in Mikumi National Park, Tanzania. They explored the idea that sexual size dimorphism influences foraging behaviour, much as Cameron and du Toit (2007) had done for different species. This idea predicts that males will exhibit specific behaviours that increase their food intake rate above that of females. Foraging behaviour was examined 'within patches' (individual trees) and 'within habitats' (collections of trees). The prediction is that within patches, males should take larger bites, crop more quickly, chew less and chew

faster. Within habitats, males should increase the proportion of foraging time devoted to food ingestion as opposed to interpatch travel time and vigilance. In fact, what these authors found was that males spent less total time foraging than females but allocated a greater proportion of their foraging time to forage ingestion as opposed to travel between patches. There was no difference in rumination time between the sexes, but males spent more time in activities other than foraging and rumination, such as walking. Within patches, males took larger bites than females, but females cropped bites more quickly and chewed faster. Males had longer per-bite handling times than females but had shorter handling times per gram of intake and males also had longer residence times at trees. So, although not all the predictions were confirmed, overall the results agree qualitatively with the body size hypothesis.

Foraging and diet

In this section I'll look at what giraffes eat. Foraging has already been touched upon in the last section on the spatial use of a giraffe's environment. Here I look at a giraffe's diet (mainly browse from trees), but including grazing, geophagy, osteophagy and scavenging. I also examine some interactions with plant defences, including chemical defences, spines and ants. Detailing all the several hundred plant species that have been recorded as giraffe food would occupy a considerable amount of space and therefore I adopt the strategy employed by Anne Dagg (2014) in her giraffe book. I simply give a table of references (Table 7.1) and the number of plant species recorded as foraged. I will attempt to indicate the main species taken, when specified, and group the references according to their floral zone location. In practice, this also orders the table according to giraffe subspecies, although I suspect that the subspecies is unimportant in this context, since different races living in different areas appear to

take what is available in their location. In other words, the different subspecies of giraffe appear to have different diets simply because they live in different vegetation zones. In fact, as some of the studies show, evidence is equivocal that giraffes select species of tree (Pellew 1984b), although they do select within a tree, as shown in the last section. They also appear to select for leaf content (Caister *et al.* 2003).

There have been many attempts to classify the vegetation, or biotic, zones of Africa (Happold & Lock 2013). One of the most detailed was the UNESCO/AETFAT/UNSO Vegetation Map of Africa published in 1983 (White 1983) after more than 15 years of collaboration between UNESCO and AETFAT (Association pour l'Etude Taxonomique de la Flore de l'Afrique Tropicale). It was based on physiognomy and floristic composition, but not climate, and it included a total of 80 vegetation types and mosaics. Frank White (1983) recognised 17 major vegetation types, based on the cover and height of the vegetation, as well as the species involved. For example, forests were defined as all vegetation comprising a continuous stand of trees at least 10m tall with interlocking crowns. Woodland was defined as open stands of trees at least 8m tall, with a canopy cover of 40% or more, and with a ground layer usually dominated by grasses and other herbs.

This physiognomic approach to vegetation classification (looking at form or appearance) has largely been replaced by the phytosociological method which looks at species associations. However, in the context of Africa it is still frequently used because the 'physiognomy' of a plant is a useful, indirect, measure of the environment, particularly temperature, rainfall and soil. Although there have been several simplified versions of White's 1983 classification (Happold & Lock 2013; Shorrocks & Bates 2015), the MODIS IGBP Land Cover Classification (Hill *et al.* 2011) and Kingdon's (1989) map of African vegetation, I will place the 'diet' references for giraffe into one of White's original biotic zones (see Happold & Lock 2013, pages 64–65, for a coloured map and explanatory table).

Table 7.1 Major foraging studies carried out on giraffe.

Reference	Location	Giraffe race	Plant sp. eaten	Most eaten	Biotic zone	Vegetation
Caister <i>et al.</i> 2003	Dry season habitat, Niger	<i>peralta</i>	34	<i>Acacia nilotica</i> & <i>A. seyal</i>	Sahel savannah	Acacia wooded grassland
Caister <i>et al.</i> 2003	Koué-Harikanassou, Niger	<i>peralta</i>	34	<i>Combretum glutosum</i>	Sahel savannah	Acacia wooded grassland
Caister <i>et al.</i> 2003	Dollo Bosso, Niger	<i>peralta</i>	34	<i>Acacia senegal</i> & <i>A. siebriana</i>	Sahel savannah	Acacia wooded grassland
Ciofolo & Le Pendu 2002	Niger	<i>peralta</i>	45		Sahel savannah	Acacia wooded grassland
Ngog Nje 1984	Waza NP, Cameroon	<i>peralta</i>	22		Sudan savannah	Combretaceous shrub savannah
Lamprey 1963	Tarangire GR, Tanzania	<i>tippelskirchi</i>	40	<i>Acacia mellifera</i> & <i>A. drepanolobium</i>	Somalia-Masai bushland	Acacia-Commiphora
Hansen <i>et al.</i> 1985	Masai Mara NR, Kenya	<i>tippelskirchi</i>	8 genera	<i>Acacia, Olea</i> & <i>Grewia</i>	Somalia-Masai bushland	Acacia-Commiphora
Leuthold & Leuthold 1972	Tavo NP, Kenya	<i>tippelskirchi</i>	66	<i>Hymenodictyon parvifolium</i> & <i>Premna holstii</i>	Somalia-Masai bushland	Acacia-Commiphora
Foster 1966	Nairobi NP, Kenya	<i>tippelskirchi</i>	34	<i>Acacia drepanolobium</i>	Somalia-Masai bushland	Acacia-Commiphora
Pellew 1984c	Serengeti NP, Tanzania	<i>tippelskirchi</i>	45	<i>Acacia tortilis</i> & <i>Grewia bicolorifallax</i>	Somalia-Masai bushland	Acacia-Commiphora
Nesbit Evans 1970	Maralal, Kenya	<i>rothschildi</i>	42	<i>Acacia seyal</i> , <i>A. xanthophloea</i> , <i>A. gerrardii</i>	Somalia-Masai bushland	Acacia-Euclea bush
Chege 2015	Soysambu Conservancy, Kenya	<i>rothschildi</i>	22	<i>Acacia seyal</i> , <i>Maytenus heterophylla</i> , <i>A. tortilis</i>	Somalia-Masai bushland	Acacia-Commiphora
Nesbit Evans 1970	Soy, Kenya	<i>rothschildi</i>	21	<i>Acacia hockii</i> (pods)	Degraded – ranch	Grassland with <i>A. hockii</i> scrub
Pratt & Anderson 1982	Arusha NP, Tanzania	<i>tippelskirchi</i>	16+	<i>Croton macrostachyus</i>	Afro-montane forest and grassland	Albizia, <i>Calodendrum</i> , <i>Cassiporia</i> & <i>Croton</i>
Berry 1973	Luangwa Valley, Zambia	<i>thornicrofti</i>	19	<i>Securinea virosa</i> & <i>Kigalia pinnata</i>	Zambezian woodland	Mopane and munga woodland
Wilson 1969	Matopos NP, Zimbabwe	<i>giraffa</i>	20	<i>Acacia karroo</i> , <i>Albizia herveyi/versicolor</i> , mopane	Zambezian woodland	Miombo woodland
Makhabu 2005	Chobe NP, Zambia	<i>angolensis</i>	12+	<i>Capparis tomentosa</i> & <i>Combretum mossambicense</i>	Zambezian woodland	Acacia-Combretum
Sauer <i>et al.</i> 1977	Koos Meintjies NR, west Transvaal, SA	<i>giraffa</i>	29 incl. grass	<i>Acacia tortilis</i> & <i>Combretum hereroense</i>	Zambezian woodland	Acacia-Combretum

Oates 1972	North-eastern Transvaal, SA	<i>giraffa</i>	45	<i>Combretum apiculatum</i> & <i>Acacia nigrescens</i>	Zambezian woodland	Arid mopane woodland
Hall-Martin 1974	Timbavati NR, eastern Transvaal, SA	<i>giraffa</i>	44	<i>Combretum apiculatum</i> & <i>Acacia nigrescens</i>	Zambezian woodland	<i>Acacia-Combretum</i>
van der Schijff 1959	Kruger NP, SA	<i>giraffa</i>	43	No record	Zambezian woodland	Miombo woodland
Brynard & Pienaar 1960	Kruger NP, SA	<i>giraffa</i>	40	No record	Zambezian woodland	Miombo woodland
Fust & Loos 2015	Mogalakwena RC, SA	<i>giraffa</i>	25	<i>Acacia tortilis</i> , <i>Terminalia prunioides</i> & <i>A. nigrescens</i>	Zambezian woodland	<i>Acacia-Combretum</i>
Innis 1958	Eastern Transvaal, SA	<i>giraffa</i>	32		Zambezian woodland	miombo woodland
Kok & Opperman 1980	Willem Pretorius GR, SA	<i>giraffa</i>	25	<i>Acacia karroo</i> , <i>Asparagus laevis</i> , <i>Rhus undulata</i> & <i>Ziziphus mucronata</i>	Highveld	Highveld grassy shrubland with <i>A. karroo</i>
Marais <i>et al.</i> 2011; Cornelius <i>et al.</i> 2012	Nyaru Reserve, southern Cape, SA	<i>giraffa</i>	22	<i>Acacia karroo</i> & <i>A. cyclops</i> (<i>invasive sp.</i>)	South-west Cape	Mosaic thicket
Parker <i>et al.</i> 2003, 2005, 2006	Kariega GR eastern Cape, SA	<i>giraffa</i>	48	<i>Acacia karroo</i> , <i>Euclea undulata</i> & <i>Rhus longispina</i>	Coastal forest mosaic	Forest and thornveld

GR, Game Reserve; NP, National Park; RC, research centre; SA, South Africa.

Direct observation and faecal analysis are two commonly employed techniques for assessing the diet of wild herbivores (Field & Ross 1976; Landman & Kerley 2001; McInnes *et al.* 1983; Parker *et al.* 2003; van Aarde & Skinner 1975). However, both methods have their limitations in the way they quantify herbivore diets (Bookhout 1996; Dearden *et al.* 1975; McInnes *et al.* 1983; Norbury & Sanson 1992). For example, direct observation tends to be limited to daylight foraging and smaller species of browse might be overlooked. The observer also has to follow the focal animal and this may affect foraging patterns. Nevertheless, the diet of megaherbivores (herbivores >1000 kg) has traditionally been studied using direct observations, partly because megaherbivores are conspicuous and easy to observe. The approach is also simple, and relies on limited equipment. It has been extensively used for giraffes (e.g. Leuthold & Leuthold 1972; Parker *et al.* 2003; Pellew 1984b; van Aarde & Skinner 1975).

Giraffes are highly selective, compared to other megaherbivores, with regard to the precise part of a tree browsed. This is due to their unique foraging technique, whereby they strip the leaves off the terminal shoots of trees with their long tongue (Cooper & Owen-Smith 1986; Owen-Smith 1992). Typically, trees from the genus *Acacia* are the mainstay of giraffe diet (du Toit *et al.* 1990). However, most *Acacia* species are deciduous and lose their leaves during the dry or cold season (Parker *et al.* 2003). Consequently, giraffes include a greater proportion of evergreen or semi-deciduous vegetation in their diet during this period (Parker *et al.* 2003; Sauer 1983). For example, Parker and Bernard (2006) used direct observation to examine the diet of giraffes in the Eastern Cape Province, South Africa, between January 2002 and October 2003. *Acacia karroo* was the most important species in the diet. However, *A. karroo* is deciduous and members of the genus *Rhus* were more important in the winter months. In fact, these authors collected three foraging

statistics. First, by direct observation they recorded the frequency of plant species consumed, second, they collected fresh faecal samples (five groups of pellets) on a monthly basis, and third, they estimated the plant species in the areas used by giraffes, using the point centred-quarter method and 6–7 transects per site (Cottam & Curtis 1956; Parker *et al.* 2003). Relative dominance (= canopy cover of each species/total canopy cover × 100) was used to reflect the availability of each species (Parker *et al.* 2003). Finally they calculated the ‘strength of preference’ (SP = [% utilisation – % availability]/100) for each species (Caister *et al.* 2003). A value of zero would indicate that a species was eaten at the same frequency with which it occurred in the field. A positive value indicates a positive preference and a negative value an avoidance (Caister *et al.* 2003). Table 7.2 shows their results.

Direct observation clearly suggests that *Acacia karroo* and *Rhus longispina* were the two most important species, with the remaining species all below 6%. Giraffes only rarely consumed grass (but see Seeber *et al.* 2012). Faecal collections also showed *A. karroo* and *R. longispina* to be the most important species. Interestingly, grass appeared more important from the faecal samples, and a high proportion of epidermal fragments remained unidentified. However, the method of identifying browse did not have a significant effect on the results, except for the unidentified component. Both faecal analysis and direct observations detected similar seasonal changes in the frequency of occurrence of the five most important species (see Table 7.2). In total, these authors recorded 48 species (46 woody species, one shrub and one grass) of plant taken as food by giraffes (Parker & Bernard 2005). Parker and Bernard (2006) suggest that giraffes are selecting species of forage, because the value of their strength of preference (SP) statistic is greater than zero, for both the commonly used species. For *A. karroo*, SP > 0.19 for both their methods, and for *R. longispina*,

Table 7.2 Percentage occurrence of the five most important plant species in the diet of giraffe (across three sites and four seasons) in the Eastern Cape Province of South Africa. Results of direct observation, faecal analysis and the frequency (availability) of each plant species. Grass and unidentified components are included for comparative purposes.

Species	Observed	Faecal analysis	Availability
<i>Acacia karroo</i>	43.27	31.96	12.81
<i>Rhus longispina</i>	16.62	13.13	10.00
<i>Euclea undulata</i>	5.36	5.92	4.48
<i>Pappea capensis</i>	3.81	4.38	4.86
<i>Schotia afra</i>	3.20	3.21	1.95
Grass sp.	0.07	0.50	
Unidentified	0.36	14.21	

SP > 0.03 for both methods.³ However, since no statistical test is given, it is not clear if selection is really occurring.

Another example of seasonal change because a browse plant lost its leaves in the dry season is that of Sauer *et al.* (1977). In the arid bushland of the western Transvaal, they found that *Ziziphus mucronata* was consumed most in the wet season with a relative importance (RV)⁴ of 14.65%. However, it is a deciduous plant which sheds almost all its leaves at the end of April. From the beginning of May, the importance of *Z. mucronata* as a source of food declined and in the dry season it had a relative importance of only 0.65%. In the Serengeti National Park, Pellew (1984b) found that giraffes utilise the dominant species in approximate proportion to their availability, but show selection for shoots with very high protein content, and in the dry season a significant selection for phosphorus. Giraffes devoted more time to foraging as the biomass and quality of the food declined in the dry season.

Leuthold and Leuthold (1972) commented on the different percentages of *Acacia tortilis* browsed in two areas of Tsavo National Park,

Kenya. In their main study area, they recorded only 0.3% and 3.7% (green and dry season), while in 'other areas' they recorded 12% and 29%. They comment that 'These figures probably reflect real differences in availability and consumption, *A. tortilis* being relatively rare in the main study area, where a great variety of other species occur ...'. These authors also noted a seasonal shift in browse species taken, similar to that observed by Parker and Bernard (2006). They note that the species taken in the 'green season' are all deciduous, providing virtually no food once they have lost their leaves. The species dominant in the 'dry season' tended to show low percentages in the 'green season'. These 'dry season' species (*Boscia coriacea*, *Thylachium thomasii* and *Salvadora persica*) were evergreen, while *Euphorbia scheffleri* had succulent twigs and its fruits persisted long into the dry season. These selected 'dry season' species were all available to giraffes in the 'green season', but were rarely taken. Leuthold and Leuthold (1972) did in fact attempt to look at 'selectivity' on the part of feeding giraffes by assessing the vegetation available in a 1 km² area (using 50 90 × 5 m transects), during the dry season. However, they acknowledged the difficulty of assessing the vegetation available to the giraffes, stating that 'a representative sample was difficult to obtain in this case, as giraffe range over large areas in a short time, feeding

³Note, however, that no confidence limits or statistical tests are given. A Monte Carlo method (Manly 2006) could be used on such indices to provide confidence limits.

⁴Relative importance = (% observations + % time)/2 (van Aarde & Skinner 1975).

intermittently as they move'. Twenty plant species offering food during part or all of the dry season were chosen and their frequencies in the habitat compared with those in their food records (their Table 3, in which only 19 species are shown). Unfortunately, their chi-squared analysis on this data is incorrect since they use percentages, which is not allowed for this test. I have recalculated their Table 3 to obtain numbers rather than percentages (observed) and recalculated expected values by multiplying the number of browse records (1280) by the plant frequencies in the habitat. The results are now very significant, and slightly different to those indicated in the original paper. Within the 'ever-green' species, *Salvadora persica* and *Azima tetracantha* appear to be avoided, while *Thylachium thomasi*, *Boscia coriacea*, *Acacia tortilis/velutina* and *Cadaba farinosa* are taken in larger numbers than expected. Within the species only providing browse for part of the dry season, *Cordia ovalis* and *Calyptrotheca taitensis* are taken less than expected, while *Melia volkensii* and *Combretum ukambense* are taken more. However, the

authors are very cautious about interpreting these results because it is technically very difficult to assess the frequency of browse species availability. They quote the case of *S. persica* which appears to be avoided. This species grows in dense clumps and the plants in the centre of these clumps are unavailable to giraffes. Their availability from transect data may therefore be overestimated considerably, and the apparent avoidance might be an artefact.

Oates (1972) looked at the food of giraffes in dry mopane woodland in the north-eastern Transvaal, South Africa. Forty-five species were recorded as browsed and the author calculated a ratio of 'preference' = (% taken by giraffes)/(% in the field). Unfortunately, ratios are not ideal measurements (Sokal & Rohlf 2012) because the errors in each measurement are magnified in the ratio. As a simple visual method, I have instead plotted the results as a scatter graph, with a 45° line indicating equality (dashed line) (Fig. 7.6) and a solid line indicating the linear regression. This regression line is calculated without the outlying point given by *Colophospermum mopane*,

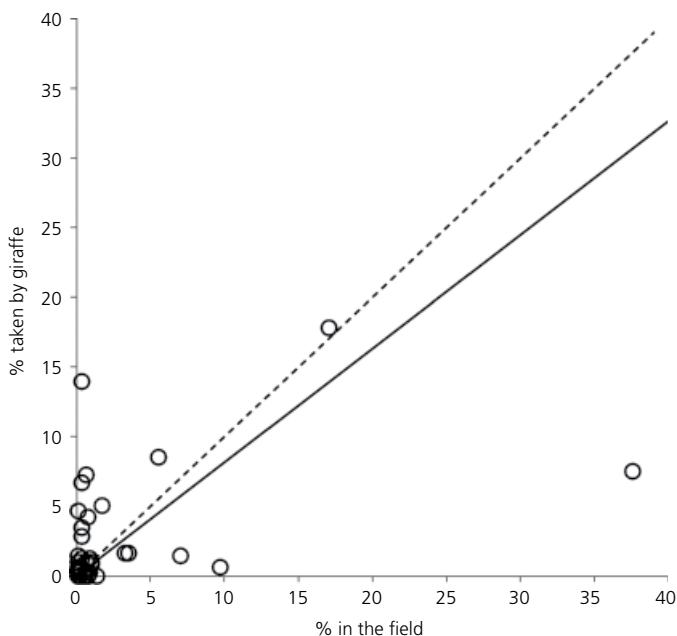


Fig. 7.6 Food 'preference' of giraffe in the north-western Transvaal of South Africa. Data from Oates (1972).

a tree seemingly avoided by giraffes. However, this data point is strange because although *C. mopane* is taken much less frequently than apparently available, it is still the third most browsed species among the 37 plants taken. This work was carried out in a mopane woodland and therefore this tree is the most common species. It seems likely that giraffes actually 'prefer' this species but that it cannot be consumed enough to equal the field percentages. Its leaves are certainly protein rich and they are consumed by many wildlife species and domestic animals. I leave the data point on the graph for readers to contemplate the difficulties of measuring, and equating, abundance in the field with percentages eaten by giraffes. Without this one data point, the slope of the fitted regression line is not significantly different from 1.00, which would indicate little choice of the 45 plant species available. However, without detailed statistical tests, that take account of natural variation, we can still probably say that the most browsed species (17.8%), *Combretum apiculatum*, is taken in the same proportion as in the field (17.04%), with just three species (*Acacia nigrescens* 13.96%, *Dichrostachys cinerea* 7.27% and *Ziziphus mucronata* 6.68%) appearing to be taken in greater frequency than in the field. Notice that *Z. mucronata* was also a 'preferred' species in Sauer *et al.* (1977), mentioned earlier.

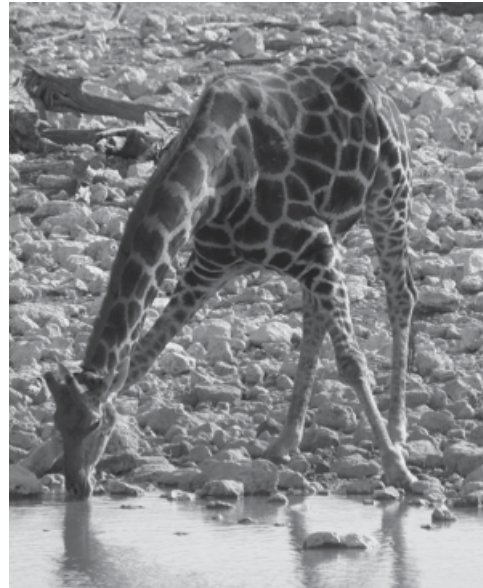
Caister *et al.* (2003), examining the foraging preferences of *Giraffa camelopardalis peralta* in Niger, found that nursing cows showed an avoidance of tannins. Bulls and non-nursing cows, however, preferred hi-protein and high-fat forage, while subadults showed a strong preference for high protein and carbohydrate content and moderate tannin levels. *Combretum glutinosum* was the 'preferred' species for adults of both sexes in one study area, while in two others it was *Acacia nilotica*, *A. seyal*, *A. senegal* and *A. siebriana*. Hall-Martin and Basson (1975) and Dougall *et al.* (1964) have analysed general stomach contents for protein and crude fibre, but no species are specifically identified. Working in the Jack Scott Nature Reserve

(JSNR), South Africa, Sauer *et al.* (1982) noted that the percentage utilisation of *A. caffra* by giraffes was significantly correlated with seasonal changes in protein content (Kendall Partial Rank Coefficient (τ) = 0.67) and with fat content (τ = 0.67). *Acacia caffra* is the most important and preferred food plant of giraffes in JSNR. On the other hand, percentage utilisation correlated negatively with crude fibre content (τ = -0.67). The protein content was highest in new growth sampled in JSNR during October 1975 (18.6%), gradually decreasing until September 1976. A similar picture emerged for another important food plant, *A. karroo*, with percentage utilisation significantly correlated with protein content (τ = 0.96) and negatively correlated with crude fibre (τ = -0.98). Similar findings were found in other species, for example, *A. senegal*, *Combretum apiculatum*, *C. hereroense*, *C. zeyheri*, *Colophospermum mopane* and *Dichrostachys cinerea*.

It would appear that giraffes do 'select for' certain properties of their browse (e.g. high protein and fat) and 'select against' certain properties (e.g. tannin and fibre). Clearly, giraffes browse some plant species more than their frequencies in the wild might suggest, if feeding were random. However, whether this is selection for certain species or simply selection of the best available at the time is difficult to know. Preference is a notoriously difficult thing to measure, since it not only depends on the item apparently selected but on what other items are available. Giraffes may not be selecting for species of browse *per se*. In fact, because giraffes switch their 'preferred' browse between seasons and sites, it would appear that they do not. It seems more likely that they simply take the forage most easily available or that provides the best nutrition at the time. They may prefer species A but when it drops its leaves or their tannin content gets too high, they may eat species B. If this second alternative is available for longer, the giraffes may be observed to take more of this species, even though it is not the most preferred.

Water is also an essential part of a giraffe's daily requirements (Fig. 7.7a). It comes in two forms: liquid form in rivers and pools and as 'metabolic' water in the browse. In fact, many savannah mammals get their water from their food. As with food intake, there is a diurnal pattern of behaviour. One study that examined this pattern is that of du Preez and Grobler (1977). During 19 censuses carried out in Etosha National Park, between August 1971 and February 1973, they observed 14 mammal species, including giraffes, and ostrich drinking water from waterholes. Most of the ungulates (e.g. wildebeest, springbok, gemsbok, hartebeest, kudu and eland) were daytime drinkers. Lions and hyaenas drank mainly at night. Giraffes were unusual in drinking all through the day, although there are 'peaks' around twilight. Weir and Davison (1965), working at Wankie (Hwange National Park, Zimbabwe), noted a similar peak in drinking between 1600 and 2000 hours.

One of the most thorough studies of water access in wild herbivores was carried out in Hwange National Park, Zimbabwe (Valeix *et al.* 2007). These authors studied 10 herbivore species, including three that browse (giraffe, impala and greater kudu), and monitored 12 waterholes in 2003 (19.44 hours of observation) and nine waterholes in 2004 (18.48 hours of observation). The study took place in the dry season (May/July to August/October). The two years had different rainfall levels (474mm in 2003 and 770mm in 2004). Each waterhole was visited twice a month, with a 24-h monitoring effort coinciding with the full moon and a 12-h monitoring effort when no moon was present. They considered the effect, on drinking, of *water abundance* (dependent on dry years or the dry season), *thermoregulation* (because waterholes are often surrounded by open areas that are overutilised and trampled, offering little shade), *perceived predator risk* (giraffes drinking are very vulnerable because they have to splay their legs; Fig. 7.7a) and *interference competition* from elephants who can be the major source of



(a)



(b)

Fig. 7.7 (a) Giraffe drinking in Etosha National Park, Namibia. Photograph by Bryan Shorrocks. (b) Reticulated giraffe in Laikipia, Kenya, eating soil (geophagy). Photograph by Bryan Shorrocks.

aggressive interactions. The waterhole area was defined as a circle of 100m radius, and observers recorded whether the herbivores drank or not. The time when a group entered the waterhole area minus the time when the first animal of the group drank was regarded as the 'access time', in other words, how long it took before an individual of the group actually drank. The probability of drinking once in a waterhole area differed between species, and ranged from 0.61 for giraffes to 0.91 for buffaloes. The value for giraffes is quite low, suggesting they were frequently 'discouraged' from drinking. For giraffes, the mean time to accessing water was 12 minutes, but with high variability. For many species, the probability of drinking was higher, and the time spent accessing water lower, in 2003 (lower rainfall) and higher towards the end of the dry season, but not for giraffes. However, giraffes were influenced by other factors. 'Access time' decreased significantly with higher temperatures and larger group size, and increased when the distance to vegetation cover increased, and the number of elephants increased. 'Probability of drinking' increased with larger herd size and decreased when the distance to vegetation cover and numbers of elephants increased. Thermoregulation seemed to play an important role in the time spent accessing water. During hotter periods, herbivores avoided staying in open areas where solar radiation was high. This was particularly the case for the largest herbivores (giraffe, buffalo and zebra), which is consistent with the idea that body size has a major effect on heat balance, with larger mammals heating and cooling less rapidly than small ones (Peters 1983).

The last nutritional topic that I will briefly outline includes the already listed behaviours of geophagy (e.g. eating soil and salt licking) (Fig. 7.7b), osteophagy (chewing bones) and scavenging (e.g. eating the afterbirth) (Seeber *et al.* 2012). Giraffes require an estimated 20g calcium (Ca) and 10g phosphorus (P) per day from birth to 5 years of age for the growth of their unique skeletons (Mitchell & Skinner

2003; Mitchell *et al.* 2005). After this age, daily requirements in both sexes are lower but rise in lactating females (Mitchell *et al.* 2005). Nesbit Evans (1970) observed a Rothschild's giraffe eating the stomach contents of an eland (*Taurotragus oryx*) carcass and Western (1971) recorded several Masai giraffes apparently 'chewing' the bones of a Grant's gazelle (*Nanger granti*). Wyatt (1971) and Leuthold and Leuthold (1972) also observed Masai giraffes 'chewing' bones.

Osteophagy is common in domestic stock suffering from phosphorus deficiency (Nesbit Evans 1979), but Western points out in his note that although it is difficult to assess if this osteophagia is a result of phosphorus deficiency, the soils in the area where he observed giraffes chewing are highly alkaline and saline, and chemical analysis of plants that giraffes eat suggest that it is unlikely that calcium, sodium, magnesium or potassium are in short supply. Western (1971) believed that osteophagia was unlikely to offset any mineral deficiency in giraffes as it appeared to be an uncommon occurrence. However, Langman (1978), working from 1972 to 1974 in Timbavati Reserve bordering Kruger NP in South Africa, observed 60 examples of osteophagy + geophagy. From his description, the giraffe involved seemed to actively search for both bones and soil. They adopted a searching posture which involved lowering the head and walking across an area looking down at the ground. When an area for geophagy or osteophagy was located, the giraffes assumed the drinking position. They then proceeded to pick up bones or soil, stand up and point the nose up and the head back. Langman states that 'The high frequency of pica (geophagy and osteophagy) in the southern giraffe indicated that the minerals obtained in this manner are an important dietary supplement'. However, I am not convinced that 60 observations, on an estimated 600 giraffes over 2 years, is in fact a high frequency.

However, because giraffes in the wild are, more or less, exclusive browsers, the changes in

pica that were observed could be related to the rise and fall of various minerals in leaves. The pica observations, in addition to being mostly in the dry season (90%), also had two distinct peaks, one in April and the other in October. The first peak in April coincides with the beginning of the dry season. The second peak in October corresponds with the onset of the rainy season. Langman believes that the mineral content of leaves changes dramatically at both these times, although no experimental data is supplied. However, as Bredin *et al.* (2008) have more recently pointed out, analyses of giraffe skeletal biology (Mitchell *et al.* 2005; van Schalkwyk *et al.* 2004) suggest that by selective browsing alone, giraffes are probably able to obtain sufficient Ca for skeletal growth. Sources of sufficient P are more obscure, although Pellew (1984c) showed significant selection by giraffe cows for P-rich browse in the wet season of East Africa, and by bulls throughout the year. One possibility is that they obtain P by eating bones. To explore this further, Bredin *et al.* (2008) immersed samples of cervical vertebrae and metacarpal shafts in the rumens of five fistulated Merino sheep, for a period of up to 30 days. The effect was compared to immersion in two other liquids, distilled water and artificial saliva, again for 30 days. Distilled water had no effect on the bones. Dense bones (metacarpal shaft) were softened by exposure to the saliva and rumen fluid, but did not lose either calcium or phosphorus. In saliva and rumen fluid, the cancellous bones (vertebrae) also softened, and their mass and volume decreased in the saliva, but in neither fluid did they lose significant amounts of calcium and phosphorus. However, there appears to be no evidence that giraffes select for cancellous bone, which is easier to crush. Bones selected by giraffes range from fresh to weathered, and from dense non-porous bones to bones that are porous and often brittle. Bredin *et al.* (2008) therefore conclude that although saliva and rumen fluid can soften ingested bones, there is an insignificant digestion of bones in the rumen to provide the giraffe

with any quantity of Ca or P. At least in the rumen of Merino sheep.

The role of plant defences

Herbivore-induced defences may be placed in several categories: (1) plant resistance traits that reduce herbivore performance or damage, such as thorns (Stapley 1998) or tannins (Caister *et al.* 2003), (2) tolerance traits, such as mass compensatory regrowth, that reduce negative effects when herbivore damage has already occurred, and (3) phenological 'escape' that reduces plant availability when herbivores are most active.⁵ Fornara and du Toit (2007) attempted to measure these 'browsing induced responses' on stands of *Acacia nigrescens* in Kruger National Park, South Africa. They wished to investigate the possibility of 'browsing lawns', as a counterpart to 'grazing lawns' (McNaughton 1984). During the 2-year field study (2003–2004), they measured plant tolerance, resistance and phenological traits, while comparing variation in leaf nitrogen and leaf area across stands of *A. nigrescens* that had experienced different intensities of browsing from herbivores, including giraffe, kudu, impala and steenbok.

Browsing studies had been conducted in this ecosystem since the 1970s (du Toit & Owen-Smith 1989; du Toit *et al.* 1990; Owen-Smith 1979, 1990), and it is thought that browsing ungulate density, and woody vegetation cover, have existed in an equilibrium for decades, possibly centuries, throughout the study area (du Toit 2003). What they found was that trees in heavily browsed stands developed (1) tolerance traits such as high regrowth abilities in shoots and leaves, high annual branch growth rates, extensive tree branching and evidence of internal

⁵One habitat-induced protection was uncovered by Bond & Loell (2001) who found that *Acacia davyi* had low browsing on steep slopes that were not favoured by giraffes.

nitrogen translocation, and (2) resistance traits such as close thorn spacing. However, phenological 'escape' responses were weak even in heavily browsed stands. Overall, browsing strongly affected plant morphofunctional traits and decreased both the number of trees carrying pods and the number of pods per tree in heavily browsed stands. They conclude that 'tolerance' and 'resistance' traits may occur simultaneously at heavily browsed sites, but that this was at the expense of reproductive success. It appears that heavy browsing can maintain *A. nigrescens* in a state that is analogous to a grazing lawn, because large herbivore browsing induces changes in resource allocation and plant architecture, which increases the regrowth of foliage. In fact, this is a 'pruning effect' familiar to all gardeners. Similar effects have been noted by Milewski and Madden (2006).

One of the interesting interactions that occurs with browsing ungulates is that between ants and the would-be browser. In about 10% of spiny *Acacia* species, the base of their spines becomes greatly expanded, forming a pseudogall. These are not true galls because they are not induced by the insect. The ants chew a hole in the new, soft, green pseudogall and hollow out the inside as a site for a mini-colony. As the gall grows older, it darkens and becomes harder and more protective. The colony of ants established on an *Acacia* tree aggressively removes any insect herbivore, frequently consuming them, and even attack mammalian herbivores, such as giraffe. A particularly detailed study of these ant-*Acacia* mutualistic systems has been carried out in the Laikipia District of central Kenya (Goheen & Palmer 2010; Palmer *et al.* 2013; Stanton *et al.* 2002; Young *et al.* 1997). In this semi-arid bush savannah, *Acacia drepanolobium*, the whistling thorn, often makes up 95% of the trees (about 2000 trees/ha). Since virtually all whistling thorns over 0.5 m tall are occupied by ants, it has been estimated that acacia ants may account for up to 25% of the animal biomass in this ecosystem. In most plants there is a pair of scale-like appendage at the base of

the leaf stalk, or petiole. In whistling thorn, these stipules are developed into a formidable pair of thorns, up to 7 cm long. Between 5% and 40% of these paired thorns share a hollow inflated base that is 1.5–3.5 cm in diameter. Ants produce winged, reproductive forms that disperse to found new colonies. These newly mated, winged females explore the exterior surfaces of whistling thorn looking for new, unoccupied galls. Having found a suitable swollen thorn, the female removes her wings, initiates a conversion of her flight muscles into food and chews an entry hole into the swollen thorn. She then plugs up the hole from the inside and remains sealed within the swollen thorn until her first workers are produced.

Acting together, ants and sharp thorns form a quite effective defence against browsing by small to medium-sized herbivores. Madden and Young (1992) reported a negative correlation between the number of swarming ants and the duration of feeding bouts for giraffe calves ($r = -0.91$, $P < 0.05$). Adult giraffes feeding seemed less sensitive, with a positive but non-significant correlation with ant swarming ($r = 0.41$, $P = 0.10$). A study by Martins (2010) also demonstrated protection for *Acacia drepanolobium* provided by ants. He examined browsing by two subspecies of giraffe, Masai and reticulated, in Kenya. Time spent approaching individual trees and then browsing, for both giraffes subspecies, is shown in Fig. 7.8. *Cremogaster mimosae* appears to be the most aggressive and effective deterrent to giraffe browsing, with *C. nigriceps* less so, and *Tetraponera penzigi* not at all.

Thorn removal experiments have been carried out with both a tethered goat and free-ranging giraffe by Milewski *et al.* (1991), on the Athi Plains, Kenya. *Acacia* branches were offered to the goat, which clearly preferred to feed on branches with the thorns experimentally removed. With the giraffe experiment, 50 *Acacia seyal* were chosen, in an area of approximately 1 hectare, and two matched branch pairs were selected on each tree. One branch was randomly selected and all its thorns removed (the experimental branch),

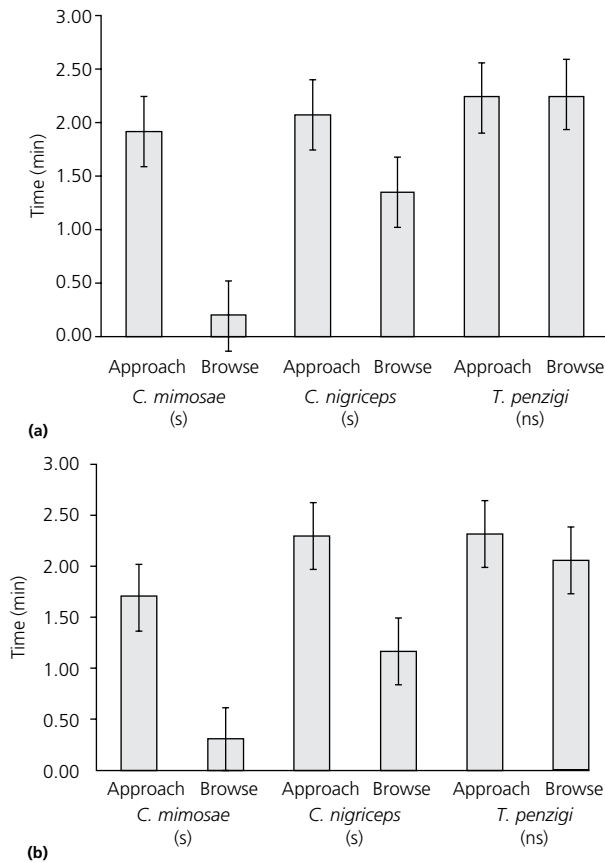


Fig. 7.8 Time spent browsing by (a) Maasai giraffe and (b) reticulated giraffe on *Acacia drepanolobium* inhibited by different ant species (mean $\pm$ SE). s = significant, ns = non-significant. Source: Martins (2010). Reproduced with permission of John Wiley & Sons.

while the other was left untouched (the control branch). Identification tags were placed at the base of both branches, in the same position. The trees were resurveyed at 3 weeks, 1 month, 2 months, 3 months, and 16 months. The results are striking. In the 3 weeks between clipping the thorns and the first resurvey of the trees, giraffes fed upon 26 of the experimental branches, but only four of the control branches. This difference continued through 3 months of surveys. Not only were giraffes more likely to feed on experimental branches, but these branches also suffered significantly greater branch tip loss and greater stripping damage than did control branches. In total, branches whose thorns had been removed lost an

average of 39% of their original length in the first 3 months after clipping, whereas control branches lost an average of only 5%. Even 16 months after the initial clipping, experimental branches were on average 12.9 cm shorter than at the beginning of the experiment, whereas control branches were on average 1.5 cm longer.

These authors also looked at thorn length in a 'natural experiment' (see Diamond 1986). This was provided by the reluctance of giraffes to feed in the vicinity of the 3-year-old research camp, located in *Acacia* woodland. Seven 200 m line transects were run from the middle of the camp, in all directions. One or two branches 1.7–2.0 m off the ground were

surveyed on each *Acacia* tree encountered within 5 m of each transect. Three representative thorns and three representative leaves were measured on each branch. In addition, giraffe dung was recorded for 1 m on either side of each transect. This provided an index of giraffe presence, calculated as the sum of the rankings of mean number of dung piles per 10 m section of the transect, and the percentage of sections with dung. Results for two *Acacia* species are shown in Fig. 7.9. With more giraffes (distance from camp), thorns get longer and leaves get shorter. So the giraffes affect the trees in two ways: they reduce the

foliage and they induce the tree to produce longer thorns for protection.

Interactions with other species

Interactions between species have been given many different, often confusing names. However, a simple and unambiguous method of classification is to use the 'effect' that individuals of one species have upon the population growth of another species and vice versa (Shorrocks & Bates 2015). We ask the question: in the presence of species A (+), does species B (1) increase its numbers (+), (2) not change its numbers (0), or (3) decrease its numbers (–) relative to when species A is absent (–)? The same question is asked of species A in the presence of species B. The answers can be conveniently summarised in a 3×3 table (Table 7.3). Because of the symmetry in the table, there are actually only six types of interaction. These are frequently called neutralism (00), commensalism (+0), predator/prey, parasite/host, herbivore/plant interactions (+–), amensalism (0–), competition (– –) and mutualism (+ +). Neutral interactions may well be very common in many ecosystems, but do not contribute to the dynamics of the system, and would be regarded by most ecologists as uninteresting. Commensalism could be regarded as an extreme example of mutualism in which the beneficial effect of one species on the other is rather weak and undetectable. Amensalism could also be regarded as an extreme example of competition, in which the adverse effect of

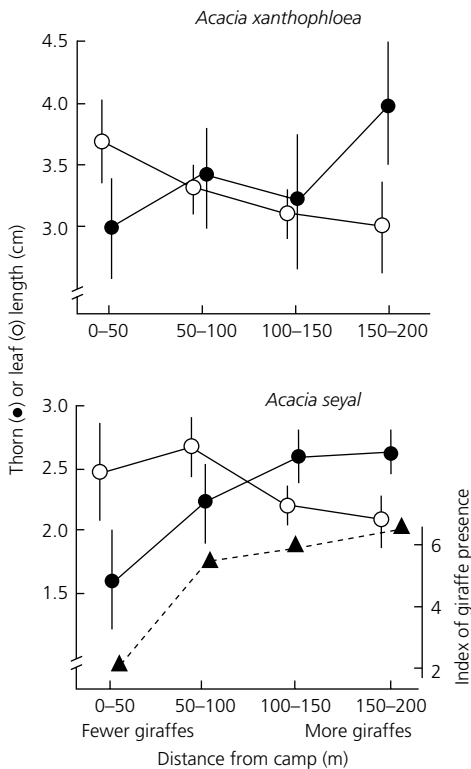


Fig. 7.9 Changes in thorn and leaf length in *Acacia xanthophloea* and *Acacia seyal* along a gradient away from the research camp (increasing giraffe density). Bars are one standard error. Closed circles = thorn length; open circles = leaf length; triangles = the index of giraffe dung presence. Source: adapted from Milewski *et al.* (1991). Reproduced with permission of Springer Science and Business Media.

Table 7.3 A simple classification of species interactions (from Shorrocks & Bates 2015).

		Effect of A on B		
		+	0	–
Effect of B on A	+	++	+0	+–
	0	0+	00	0–
	–	–+	–0	––

one species on the other is much greater than the reciprocal effect. This section of Chapter 7 will therefore briefly examine only three types of interaction between giraffe and other savannah species: 'predator/prey' (+ -), competition (- -) and mutualism (+ +). One example of mutualism given above, between ants and *Acacia drepanolobium*, is possibly to the detriment of giraffes. Below I briefly catalogue the species involved and outline some details of the interactions.

Predator prey type interactions (+ -)

This type of interaction actually encompasses three interactions that may appear rather different. They certainly tend to be studied by different ecologists. They all have in common the fact that one species (carnivore, parasite or herbivore) consumes the body, or part of the body, of another species (prey, host or plant). Giraffe feeding has already been discussed. Dynamic aspects are unclear. Pellow (1983, 1984b) suggests that in the Serengeti, at the time of his study, giraffes had a major impact on *Acacia* regeneration, removing up to 85% of the new shoot production. The retarding effect of giraffe browsing on the growth rates of the trees is considerable. Pellow points out that it takes an *A. tortilis* seedling some 36 years to exceed the maximum browse reach of an adult bull giraffe, approximately 2.8 times longer than when unbrowsed. The corresponding retarding factors for *A. hockii* and *A. xanthophloea* were 2.8 and 4.8 respectively. In this Serengeti study, the maximum impact of giraffe browsing occurred when the trees were between 2 and 3 m. At this height, the growth rate of *A. tortilis* averaged only 11 cm per year. Above this height, the rate accelerates, reaching 33 cm per year between a height of 5 and 6 m. In the Serengeti, these variations in height-specific growth rates reflected the feeding heights of the various age and sex categories in the local giraffe population. Browsing impact also varied throughout the year, being greatest in the dry season when tree production rates decline. However, these high

off-take rates are really caused by the double perturbations of elephant impact and the reduction of fire, and 'there is no short-term evidence that the giraffe impact is curtailing plant productivity' (Pellow 1984b). In this Serengeti study, the daily consumption rates by adult male and female giraffe were estimated to be 19.0 kg dry matter day⁻¹ and 16.6 kg day⁻¹ respectively, equivalent to 30.8 g min⁻¹ and 22.2 g min⁻¹ of actual feeding time.

Ruess and Halter (1990) similarly report giraffe damage to *Acacia* species in the Serengeti. They comment that the successful regeneration of trees and eventual recovery of the Seronera woodlands will be influenced by both burning and the browsing pressure of giraffe. These two agents of tree damage are inter-related. For example, heavy browsing prevents trees from maturing to larger size classes, rendering them vulnerable to fires. Also heavy browsing, without fire, results in dense regeneration thickets, essentially changing the structure of the habitat. Birkett (2002) and Birkett and Stevens-Wood (2005), working in Laikipia, Kenya, also noted that heavy browsing by giraffes reduced tree (*A. drepanolobium*) growth rates and increased their susceptibility to drought. The combination of low rainfall and heavy browsing by elephants, black rhinos and giraffes therefore led to rapid tree loss.

Dharani *et al.* (2008) found significant differences in growth of plant height, canopy cover and stem diameter of *Acacia xanthophloea* trees in fenced plots as compared with unfenced plots. This occurred in both the wet and dry seasons, when Rothschild's giraffes were excluded. Effects of giraffes on *Acacia* have also been documented in South Africa (Bond & Lofell 2001). Working in the Ithala Game Reserve in Kwa-Zulu Natal, these authors measured giraffe browsing damage on four species of *Acacia*: *caffra*, *davyi*, *karroo* and *nilotica*. In addition, *A. gerrardii* and *A. tortilis* were monitored for mortality. Twelve sites were monitored, six in high-density giraffe areas and six in low-density areas. Browse lines were significantly higher in

high (4.9 m) versus low (2.6 m) giraffe density areas ($t_{10} = 4.86$, $P < 0.001$). There were also significantly fewer pod-bearing trees below the browse line in high (21 out of 383 trees) versus low (154 out of 467 trees) giraffe density areas ($X^2 = 47.1$, $P < 0.001$). The frequency of browse-damaged branch tips was significantly higher for all four *Acacia* species examined, and mortality of trees was significantly higher for 4/6⁶ *Acacia* examined, for trees in high-density giraffe areas. Tree mortality was correlated with twig-tip estimates of browse damage by giraffe (Spearman's $r_{10} = 0.72$, $P < 0.05$). The authors conclude that 'Giraffe do not, as yet, appear to be negatively influencing *Acacia* recruitment'. And yet they also state that *A. davyi* has already disappeared from high-density giraffe areas, except on steep slopes not reached by giraffes. A similar fate is predicted for *A. caffra*. *Acacia karroo*, which showed high mortality in heavily browsed areas, continued to produce foliage, but the constant browsing pressure may weaken these trees. The concern is that the population would be seriously affected if additional pressures of drought or disease were imposed. Interestingly, *A. tortilis* showed no negative effects of giraffe presence, and this is a dominant savannah species (Pellew 1983). Could it be resistant to giraffe browsing?

Another report of giraffe being the 'predator' is that of Fleming *et al.* (2006). They examined the relationship between giraffes and *A. nigrescens*, in an *A. nigrescens* (marula, knobthorn) savannah ecotype of Kruger National Park, South Africa. The flowers of *A. nigrescens* are an important food source for giraffes in the late dry season when browse is extremely limited and of low quality (du Toit 1992). Therefore, even though *A. nigrescens* flowers contain almost

three times as much condensed tannin as leaves, giraffes in fact consume large quantities (~85% of flowers within reach), frequently resulting in a distinct browse line on the trees. No enclosure was used to exclude giraffes. In effect, the authors used a 'natural experiment' (see Diamond 1986) by examining flowers 'within reach' versus 'out of reach' of giraffe browsing. Exposure to giraffes was associated with a significant reduction in abundance of *A. nigrescens* flowers and pods, but not leaves. Trees had significantly fewer flowers ($t_{74} = 8.20$, $P < 0.001$) and fruit ($t_{85} = 3.63$, $P < 0.001$) for heights within giraffe browse range. This substantial consumption of flowers therefore had a negative effect on the fecundity of *A. nigrescens*, significantly reducing fruit set at heights on trees that were accessible to giraffes. Fruit set increased above the reach of giraffes, suggesting successful pollination by insects. These results indicate that giraffes are flower predators of this *Acacia* species, in South Africa. A similar study by du Toit (1990b) also showed giraffes to be a 'predator' of *Acacia* flowers. Miller (1994) also documents the fate of *Acacia* pods, from production on the tree to destruction on the ground. Giraffes were a major agent of browsing directly from the tree. They were never observed to take them from the ground.

When people think about 'predator/prey' (+ -) interactions and giraffes, they usually think of large carnivores, although disease organisms come into this category, and frequently have similar dynamics. The main large predator of giraffes is the lion (*Panthera leo*) (Berry 1973; Dagg & Foster 1982; Hall-Martin 1974). Mitchell *et al.* (1965) in Kafue Park (Zambia), Foster and Kearney (1967) in Nairobi Park (Kenya), Pienaar (1969), Owen-Smith and Mills (2008) in Kruger Park (South Africa), Loveridge *et al.* (2006) in Hwange National Park, Zimbabwe, Hirst (1969a) in Timbavati Private Reserve (South Africa), Kruuk and Turner (1967) in the Serengeti National Park (Tanzania) and Schaller (1972) in the Serengeti and Manyara Parks (Tanzania) all report lions killing giraffes.

⁶There was insufficient data for the other two species. Only three *Acacia gerardii* were monitored in the high-density giraffe area, and no *A. tortilis* were found in low-density giraffe areas. However, no dead *A. tortilis* out of 41 trees examined were seen in high-density giraffe areas.

However, Brenneman *et al.* (2009) report that in Murchinson Falls National Park (Uganda), a wildlife ranger with 13 years experience had never observed lion preying on giraffe. Even where lion predation is reported, numbers are small compared to other prey. For example, Schaller (1972) in Manyara notes that buffalo comprised 62.0% of kills, while giraffe were only 2.0%. In Kafue equivalent comparisons were buffalo (30.5%), giraffe (0%), in Nairobi NP wildebeest (48.3%) and giraffe (3.9%), and in Kruger NP wildebeest (23.6%) and giraffe (3.9%). Of course, one must remember that 2.0–3.9% of a giraffe population might well be more severe than 23.6–48.3% of a wildebeest population. Bothma and Walker (1999) say that lions sometimes kill giraffe ‘... with a specialised technique ...’, knocking the animal off its feet so that it cannot use the hooves of its powerful front feet to deliver accurate blows. However, no reference is given. Pienaar (1969) noted that in two separate studies, 1933–1946 and 1954–1966 in Kruger NP, out of 46,181 known wildlife kills, 675 were lion on giraffe. This is only 1.46% of wildlife kills. In two of these years, specifics were recorded for 108 giraffe killed by lion. Of those giraffe that could be reliably aged, 64 were adult, 18 were subadult and juvenile, and 12 were calves. Of course, calves will be under-represented in data of this type because the carcasses will rapidly be consumed and not recorded.

One nice study of lion predation is that of Hayward and Kerley (2005) in which data from 23 studies, over 48 different spatial locations or temporal periods throughout the lions’ distribution, was examined. Lions preferred prey in the weight range 190–550 kg, and gemsbok (*Oryx gazella gazella*), buffalo (*Syncerus caffer caffer*), wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*) and giraffe are all significantly preferred. That is, they are taken in greater frequency than they occur locally. Giraffe were recorded as prey in 24 out of the 48 different locations and while giraffe made up only 3.71% of the available prey, they represented 6.32% of actual kills.

Of course, direct observations of lion attacks are rare and are usually anecdotal, or inferred from carcass records.

A novel approach to lion predation is that of Strauss and Packer (2013). They recorded predation marks on live giraffe in Serengeti National Park, Tanzania, in three different regions of the Park, between 2008 and 2010. Only some lion attacks are fatal (Schaller 1972), and surviving prey often show bite wounds or claw marks. Strauss and Packer (2013) state that lion claw marks are distinctive and can be differentiated from marks inflicted by other predators (of course, since lions are the only serious predator of giraffes, almost all marks will be caused by lions). However, interpretation of claw marks requires caution. For example, an absence of claw marks in an age–sex class is likely to indicate that all attacked individuals die, rather than no individuals are attacked. In this study, giraffes were photographed and identified using the pelage pattern unique to each animal. In total, 702 giraffe photographs (132 calves, 187 subadults and 383 adults) were examined for predation marks, almost all of which were on the flank, rump or hindlegs. Giraffes were placed into three age categories: calf (0–1 year), subadult (1–5 years) or adult (>5 years). An estimated 10.6% of giraffes (13.1% of giraffes >1 year old) showed evidence of surviving at least one lion attack and the estimated prevalence of claw marks was significantly higher among adults (17.6%) than subadults (3.7%) ($\chi^2_1 = 21.34$, $P < 0.0001$). There were two very interesting non-significant effects on frequency of claw marks. In the one area they tested (Seronera), they found no difference in mean herd size between individuals with claw marks ($n = 57$) and those with no marks ($n = 292$) ($t_{10} = 0.97$, $P = 0.33$) and there was no difference in the height of adult giraffes with claw marks versus those with no marks ($z_{20,28} = -1.06$, $P = 0.29$, two-sided Mann–Whitney U-test), suggesting that both herd size and size of the individual were unimportant in influencing lion attacks. This is surprising,

since both have been suggested as deterrents to predation. For the two areas where most data was collected, Seronera and Kirawira, there are suggested indications of sex differences, age differences and location differences for claw mark prevalence (Fig. 7.10).

Although lions are clearly the main predators of giraffes, there is certainly evidence that they are eaten by spotted hyaenas (*Crocuta crocuta*) (Bearder 1977). Working in the Lowveld of South Africa, Bearder recorded one young giraffe killed by hyaenas. Furthermore, in 527 hyaena scats and 200 regurgitations, he found 304 and 43 identifiable giraffe remains, respectively. However, these remains may well come

from old lion kills. In fact, giraffe remains were most common during the dry winter months when they are most vulnerable to lion predation (Hirst 1969a). Hans Kruuk (1972), working in both the Serengeti Park and Ngorongoro Crater (Tanzania), recorded no spotted hyaena kills of giraffe, or even any hyaena scavenging a giraffe carcass. A leopard was once seen feeding on a young giraffe (Pienaar 1969) and Scheepers and Gilchrist (1991) have recorded leopards killing giraffe calves in Etosha National Park, after two carcasses were found in trees bearing claw marks.

We know from serological studies that many African mammals contract diseases of various

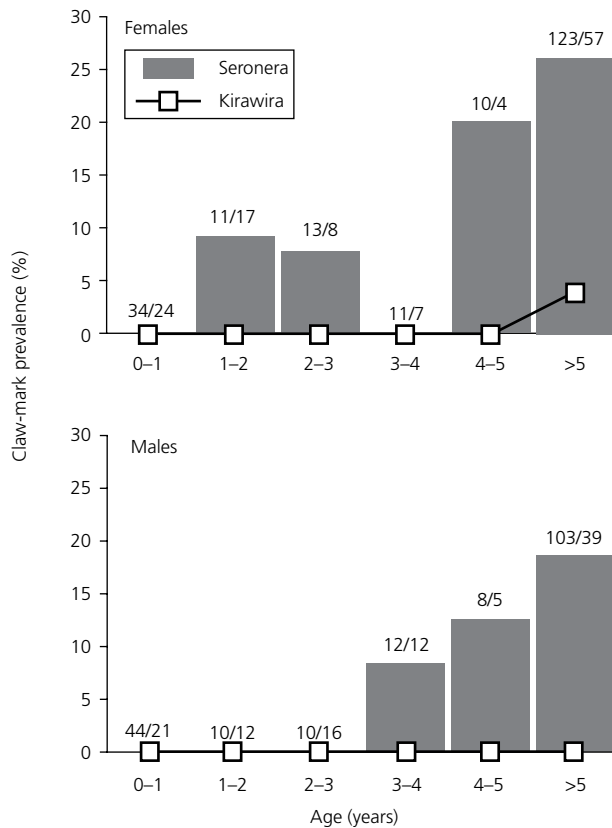


Fig. 7.10 Age and sex patterns in claw mark prevalence among giraffes in two areas of the Serengeti system (Seronera: grey histograms; Kirawira: squares). Sample size is shown above each data point for Seronera/Kirawira. The adult class (>5 years) includes all individuals between 5 and 25 years. Source: Strauss and Parker (2013). Reproduced with permission of John Wiley & Sons.

kinds. In other words, when tested, they are found to contain antibodies to various pathogens. For example, many giraffes carry antibodies to Crimean-Congo haemorrhagic fever⁷ (CCHF) (Sonenshine 1994). However, this type of serological data does not tell us how severe the effects of the pathogens might be. A high seroprevalence (many individuals having antibodies) may simply indicate that most animals become infected early in life, but that the resulting disease is mild and most animals recover and become immune. Alternatively, the same high seroprevalence might indicate that the population has recently been exposed to a highly virulent disease, and that only those individuals that survived (and are therefore sero+) are now present. However, although we do not know how severely these pathogens affect most savannah animals, we do know that some pathogens cause high mortality in some species. The most dramatic African wildlife epidemic was the rinderpest epidemic that spread throughout sub-Saharan Africa, from about 1890. Rinderpest is a highly contagious viral disease of cattle, domestic buffalo and some species of wildlife, including giraffe. The name is German, meaning cattle plague. It is characterised by fever and high mortality. Rinderpest virus is a single-stranded RNA virus in the family Paramyxoviridae, genus *Morbillivirus*. It is immunologically related to canine distemper virus, human measles virus, peste des petits ruminants virus and marine mammal morbilliviruses. The pandemic that occurred at the end of the 19th century was initiated by the accidental introduction of a few infected cattle into the Horn of Africa in 1890. This caused a major pandemic which spread mainly via the movement of cattle along trade routes. It moved

westward and southward and reached southern Africa in 1896. Unfortunately, wild ungulates are infected by contact with cattle drinking at the same water, etc., and we know that giraffe were certainly part of this epidemic in 1913–1921, 1931, 1937–1941 and 1960 (Simon 1962). More recently, another rinderpest outbreak that raged across much of Africa in 1982–1984 is estimated to have cost at least US\$500 million in domestic livestock losses.

Another disease that has had severe effects on wildlife populations is anthrax (*Bacillus anthracis*). After a susceptible host ingests spores, the bacilli enter the bloodstream, replicate exponentially, and produce fatal septicaemia. In the Kruger ecosystem in southern Africa, epidemics occur in episodes of 6–20 years. These episodes tend to occur during dry periods, and in seasons when overabundant populations of herbivores are congregating around stagnant surface water. Most mammal species in Kruger are susceptible to anthrax. There have been recorded outbreaks in Etosha National Park, Namibia, the Luangwa Valley (1987) and Queen Elizabeth National Park, Uganda (1959, 1962, 1991 and 2004–2005) (Shorrocks & Bates 2015). Ebedes (1976) records five cases of anthrax in giraffe in Etosha National Park between July 1967 and June 1974. Kaitho *et al.* (2013) recorded 11 carcasses of reticulated giraffe in the Mwea NR, in Kenya. Anthrax was rapidly confirmed using bacteriological methods.

Parasites comprise both ectoparasites (ticks, lice, fleas and hippoboscids) and internal parasites such as nematodes, flatworms and bacteria. Sachs and Debbie (1969) record parasitic infections of ‘game animals’, and although mainly detailing antelopes and wildebeest, they also briefly mention those found on/in giraffe. Giraffe are noted to be ‘more or less heavily infested (with ticks) depending on the season’ and that *Monodontella giraffae*, a nematode, is found in their liver. *Anaplasma* spp. have been identified in the blood of giraffes (Augustyn & Bigalke 1974) and seroprevalence of antibodies to *Anaplasma* spp. has been found in Kenyan

⁷CCHF is a widespread tick-borne viral disease that is endemic in Africa, the Balkans, the Middle East and Asia. While clinical disease is rare in infected animals, it is severe in infected humans, with a mortality rate of 10–40%. *Hyalomma* species are considered the primary vectors.

giraffe (Ngeranwa *et al.* 2008). Walker (1974) and Theiler (1962) recorded several species of ticks on giraffe, particularly *Amblyomma* species, *Hyalomma* species and *Rhipicephalus* species, and Alasaad *et al.* (2012) recorded the mite *Sarcoptes scabiei*. At least seven species of parasitic worm are known from giraffe (mainly southern subspecies) along with several viruses and other pathogens. Anne Dagg (2014) gives a three-page list of parasites and pathogens recorded for giraffe.

Perhaps surprisingly, the giraffe attracts a large variety of tick species, 'surprisingly' because the tick must climb up the giraffe's extremely long, short-haired legs. At least 28 species have been associated with giraffes: 17 from Kenya, 19 from Ethiopia, nine from Tanzania, six from Sudan and two from the Transvaal. Of course, this distribution may reflect the distribution of zoologists studying ticks! One widely spread species is *Amblyomma hebraeum* (Fig. 7.11), the bont tick, found in South Africa, Swaziland, Botswana, Zimbabwe and southern Mozambique, which transmits *Ehrlichia ruminantium* and *Theileria mutans*. The transmission of disease is a common feature of tick biology. *A. hebraeum* adults feed on cattle, sheep, goats and large wild ruminants, particularly giraffes, African buffalo (*Syncerus caffer*) and eland (*Taurotragus oryx*), and also on warthogs (*Phacochoerus africanus*) and black

(*Diceros bicornis*) and white rhinoceroses (*Ceratotherium simum*). Immatures infest the same hosts as the adults but also small antelopes, helmeted guineafowls (*Numida meleagris*), scrub hares (*Lepus saxatilis*) and leopard tortoises (*Geochelone pardalis*). A tick found in areas inhabited by giraffes, *Rhipicephalus appendiculatus*, is repelled by p-cresol, one of the giraffe skin compounds (Wood *et al.* 1975).

Competition (– –)

The essence of interspecific competition is that individuals of one species suffer a reduction in fecundity, survival or growth as a result of resource exploitation (resource competition), or interference (interference competition), by individuals of another species. It is frequently highly asymmetric, that is, the consequences are often much greater for one of the species involved. In discussions of interspecific competition, one frequently encounters the term *ecological niche*. This term was first used by Joseph Grinnell in 1917 to mean simply the range of physical conditions under which a species could survive and reproduce. It thus had only physical dimensions. Now, however, ecologists include resource dimensions, such as tree species, leaves or fruit, foraging height, and so on. Only part of each niche dimension is visualised as being used, often described as a 'utilisation function', and represented in models as a normal curve. For example, a seed-eating bird might take all seeds between small and large, but prefer (and therefore use more) seeds of intermediate size. Figs 7.3, 7.4 and 7.5 are examples with giraffe.

Although many field biologists may not be aware of it, the Lotka–Volterra model of two-species competition (Lotka 1932; Volterra 1926) has had an important influence on how field biologists think about competition. From this theoretical model, and early laboratory studies, arose the widely held view that interspecific competition led either to competitive exclusion of one species or coexistence. The Lotka–Volterra model predicts that coexistence will only occur if intraspecific competition is greater



Fig. 7.11 Postage stamp showing giraffe and an associated tick.

than interspecific competition, for both species. This condition is achieved if the two species occupy different niches. Then, individuals of each species will meet individuals of their own species more frequently than they meet individuals of the other species. One of the weaknesses of this 'solution' to the coexistence problem is that the Lotka–Volterra model does not predict how dissimilar the two niches have to be. Later models, exemplified by MacArthur and Levins (1967) and May (1973), attempted to rectify this and define the limits to similarity that would allow coexistence. These models, using normally distributed resource utilisation curves and competition between three species along one niche dimension, suggested the simple solution that $d/w > 1$ would lead to stable coexistence (where d = the distance between adjacent resource utilisation curve peaks and w = the standard deviation of these curves). However, Abrams (1983) found that alternative resource utilisation curves and competition in several dimensions would often lead to lower values of d/w being compatible with coexistence. There may be no general, precise solution to this problem, and savannah ecologists may have to measure specific resource utilisation curves and dimensions, as indicated for foraging height previously. In theory, interspecific competition is obviously important.

But how important are these theoretical effects in the real world? There is no doubt that competition *sometimes* affects populations. Equally, no one now believes that it is always of over-riding importance in each and every case. If other agents (e.g. lions, rinderpest and lack of rain) keep numbers low, so that competition is negligible, then competition cannot be a potent force in controlling populations. If several browsing species coexist, and use the habitat in slightly different ways (have slightly different niches), is this evidence of competition? Many ecologists think it is, and believe these patterns are the result of past competitive interactions (the 'ghost of competition past'; Connell 1980). However, as Begon *et al.* (1996) say, 'The trouble

is ... there is no proof'. The danger with using pattern to infer process (and this includes the statistical techniques of correlation and regression) is that usually an identical pattern can be caused by more than one causative agent. A 'competition pattern' could be present as a result of non-competitive influences. Giraffe and kudu may well forage at different heights (see Fig. 7.4), as a result of past competition. They may also do this simply because they are different sizes, a result of past phylogenetic pathways that have nothing to do with competition. We have to distinguish between species traits being the specific result of competition (and therefore indicating past competition) and being simply adaptations to a general mode of life. Resource partitioning and niche studies provide a start to examining interspecific competition, but savannah ecologists need to collect additional data to strengthen any competitive interpretation. This could include, for example, evidence of present resource limitation, observed niche shifts when one species is absent (a natural experiment), and looking for alternative explanations.

It is against this general competition background that I now detail some giraffe examples, remembering that the foraging height studies, mentioned previously, are a good example of resource partitioning studies. Two early examples of this type of niche study are those of Lamprey (1963) in Tarangire National Park, Tanzania, and Leuthold (1978) in Tsavo East National Park, Kenya. Lamprey examined ecological separation by habitat and food. There are clearly some separations between the species. For example, Grant's gazelle favoured 'grassland', while giraffe favoured 'open woodland' and lesser kudu favoured 'dense woodland'. It was noted that giraffe preferred zones containing *Acacia mellifera* and *A. drepanolobium*. Of course, it must be remembered that 'habitat' and 'forage' are not independent 'niche dimensions'. In fact, they may only represent one dimension. Giraffe may prefer the 'open woodland' habitat because of its structure, enabling better visibility for group communication or

predator warnings, and simply forage the trees found here. Or they may prefer these two *Acacia* species and therefore are found in 'open woodland' where these trees grow.

Leuthold looked specifically at browsers and again their habitat use and diet. Also included was 'season', but this is not a niche dimension. It simply makes the niche different between seasons – browsers cannot use only one season. With browse, giraffe had some percentage overlap with renekus (0.2–13.8%) and kudu (0.1–10.9%), depending on the species of browse examined, but what this implies for competition, or lack of it, is not known since we do not know if resources are limiting. Combined 'niche overlaps' are calculated, which implicitly assumes they are independent, by multiplying food × habitat overlap. Clearly, they are not independent.

Another 'resource partitioning' study is that of Dekker *et al.* (1996) which looked at habitat partitioning on a game ranch by the Limpopo River, South Africa. They measured a total of 13 'environmental' variables, in eight plant communities, and analysed their results using correspondence analysis, a multivariate statistical technique conceptually similar to principal component analysis, but applied to categorical rather than continuous data. They predict where you might find a number of ungulate species, including giraffe. Their correspondence analysis showed that giraffe were found mainly in *Colospermum mopane* woodland, with 0–750 shrubs ha⁻¹, >6 m from shade and 1000–1500 m from water. The highest degree of spatial separation of the ungulates in the study area occurred in the warm, dry season (August–November). This apparently coincides with the period at which resources are most limited in the area, presumably implying that competition is a factor. In fact, however, simply ignoring their 13 variables and the correspondence analysis, the three browsers – giraffe, kudu and impala – appear 'separated' simply by type of woodland, rather than any of the other variables (their Figure 2) (foraging height was not measured explicitly).

A more recent example of a 'niche' study is that of Makhabu (2005), working in the northern part of Chobe National Park, Botswana. Four species that browse (elephant, giraffe, kudu and impala) and three 'niche dimensions' (woody plants browsed, plant parts taken and browsing height used) were examined. Plant parts taken were placed into four broad categories: leafless shoots, shoot with leaves, leaves only and bark. Using a road transect, animals were initially observed from a vehicle, with binoculars. After taking observations, the tree species was confirmed, and because of the 'fresh, wet, bites', the plant parts taken and height browsed could be checked. Overlap in resource use was assessed using Schoener's index (Schoener 1970). This equals:

$$O_{jk} = 1 - \frac{1}{2} \sum_{i=1}^n (P_{ij} - P_{ik})$$

where O_{jk} is the overlap between browsing species j and k . P_{ij} is the proportion of all browsing events on resource category i by the herbivore species j , and P_{ik} is the same for browsing species k , and n is the number of resource categories. The index O_{jk} can be calculated separately for the three resource categories and take the range 0 (no overlap in resources) to 1 (complete overlap in resources). Overlap is frequently considered significant if equal to or greater than 0.6, but I suspect that Monte Carlo analysis is required to compute the distribution of O_{jk} and determine the true 5% and 1% values. With this reservation in mind, giraffe had, for plant species, $O_{jk} < 0.6$ with elephant, but > 0.6 for kudu and impala. There was no overlap in plant parts browsed between elephant and the other species. Impala and giraffe overlapped during the dry season while impala and kudu overlapped in the wet season. Overlap between giraffe and impala was lower during the wet season than during the dry season. There was no difference between the dry- and wet-season overlaps in plant parts browsed by other species. Browsing heights are shown in Fig. 7.12 and resemble those of du Toit and O'Connor *et al.* mentioned earlier in this

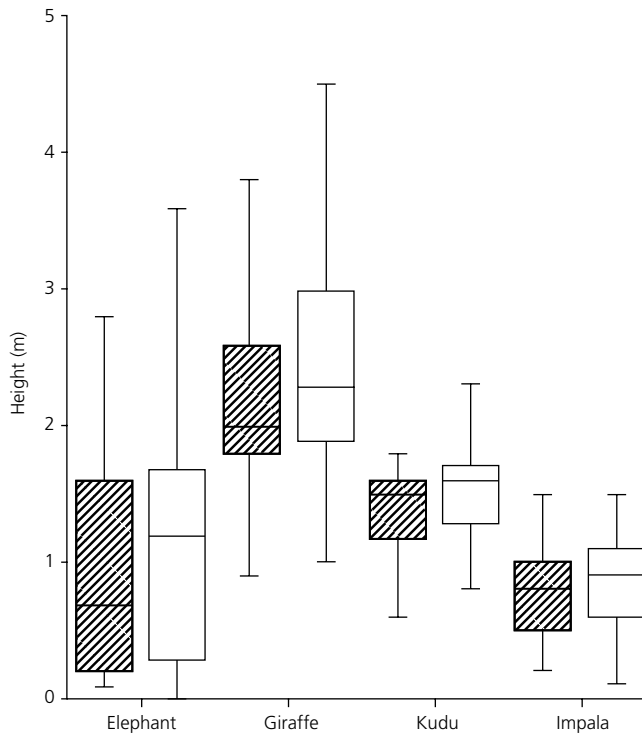


Fig. 7.12 Box plots (25th to 75th quartiles) showing location and variation in heights browsed by four species during the wet (hatched) and dry (open) seasons. The line in the box is the median, and the lines outside the box show the minimum and maximum values within the next 25th quartile from the box. The $\circ$ symbols beyond the lines are outlying observations. Source: adapted from Makhabu (2005). Reproduced with permission of Cambridge University Press.

chapter. Combining all three resource dimensions suggests that giraffe only overlaps to any extent with kudu. For wet and dry season, the value of O_{jk} for giraffe with elephant was 0.01 and 0.01, for kudu 0.10 and 0.12 and for impala 0.03 and 0.02. Of course, if species of tree, height of browsing and plant part taken are not independent resources, then these overlaps are far too small. This would happen, for example, if browse height and tree species were closely correlated.

Of course, even if these niche studies tell us nothing about competition and how it structures these browsing communities, they may provide useful information for giraffe conservationists. If giraffe prefer, for example, open woodlands of *Acacia mellifera* and *A. drepanolobium*, it might be important to have such zones in areas where giraffe are introduced (see Chapter 9).

Mutualism (+ +)

In addition to being a herbivore (a predator of plants), giraffe can also be beneficial to plants. For example, Miller (1996) investigated the role that giraffe have in the seed dispersal of thorn trees. *Acacia* can be either indehiscent or dehiscent. The pods of the former remain on the tree until eaten or knocked off by browsers or other physical agents such as wind. Dehiscent pods open on the tree, exposing seeds to physical forces such as wind or gravity which disperse the seeds from their open pod. Miller (1996) carried out the research in the Nylsvley Nature Reserve, Northern Transvaal, South Africa, in a 2 hectare patch of *Acacia* savannah. Three species were studied: two indehiscent species (the umbrella thorn, *A. tortilis*, and the Egyptian thorn, *A. nilotica*) and one dehiscent species (the sweet thorn,

A. karroo). All three species were abundant in the study area. Seed dispersal was assessed by collecting dung and calculating the number of *Acacia* seeds deposited by each herbivore species (five mammals and one bird), per hectare. The results for the giraffe (mean $\pm$ SE) were *A. tortilis* 2952 ± 644 , *A. nilotica* 1060 ± 308 and *A. karroo* 452 ± 132 . These seed densities are for four 0.25 hectare areas, collected every 2 weeks between May and August 1992. Clearly giraffe mainly browse the dehiscent pods and since they also deposited more dung outside the ground shaded by the trees (>3 m), are effectively dispersing seeds away from the parent tree. This is particularly important because in an enclosed area, free from browsers, pod fall declined significantly with distance from the tree base (*A. tortilis*, $F_{1,4} = 107.5$, $P < 0.0001$; *A. nilotica*, $F_{1,4} = 44.8$, $P < 0.05$).

Acacia pods are consumed by many large herbivores, particularly during the dry season when other food sources are scarce (Coe & Coe 1987; McNaughton & Georgiadis 1986; Miller 1995a,b; Pellew 1984b,c). Seeds from indehiscent *Acacia* pods are adapted to dispersal by herbivores owing to their high nutrient content, rounded form, strong scent and hard seed coat which resists fracturing during mastication (Coe 1985; Gwynne 1969; Lamprey 1967; Miller & Coe 1993). In fact, Miller (1996) only observed seeds to germinate from dung and never from undigested pods. Miller (1995) had previously examined the fate of *Acacia* seeds by feeding them to captive large herbivores,⁸ including giraffe. In one experiment, carried out in 1991, between 95.6% (*A. tortilis*) and 99.1% (*A. nilotica*) of seeds consumed were never voided. A year later, a similar experiment yielded figures of 90.0% (*A. tortilis*), 91.2% (*A. nilotica*), 77.9% (*A. karroo*),

90.7% (*A. hebeclada*) and 95.9% (*A. robusta*). However, despite the high percentage mortality, many seeds survive, are dispersed and have higher germination rates. For 1000 *A. tortilis* seeds within pods on the tree, 77.8% are eaten, of which 10% survive gut passage, of which 32.3% germinate. Therefore 7 out of 1000 *A. tortilis* seeds eaten survive the passage through a giraffe's digestive system. Or and Ward (2003) have documented an interesting three-way interaction between *Acacia*, large mammalian herbivores (including giraffe) and bruchid beetles.

Two species of oxpeckers, the yellow-billed (*Buphagus erythrorhynchus*) and the red-billed (*B. e. africanus*) are aberrant starlings endemic to Africa. They spend most of the day actively clambering about on ungulates, and the association is usually described as an example of an interspecific cleaning relationship, and therefore mutualistic (Dickman 1992). Cleaners benefit from the consumption of ectoparasites (Attwell 1966) plus ear wax, blood and other edible material gathered from the host (Bezuidenhout & Stutterheim 1980). Hosts benefit from the attentions of oxpeckers in several ways. For example, morbidity and mortality caused by ectoparasites are reduced (Lightfoot & Norval 1981; Norval *et al.* 1988), oxpeckers' alarm calls warn of approaching predators (Attwell 1966) and hosts spend less time self-grooming (Mooring & Mundy 1996). Also, in a mutualistic association, hosts might be expected to solicit the attentions of oxpeckers as is actually observed in impala (*Aepyceros melampus*) (Mooring & Mundy 1996), zebra (*Equus quagga burchelli*) and desert warthog (*Phacochoerus aethiopicus*) (Breitwisch 1992). Grobler and Charsley (1978), in Rhodes Matopos National Park, Zimbabwe, recorded nine sightings of *B. africanus* on giraffe. In fact, giraffe appear to be the fifth most preferred host after buffalo, white rhinoceros, zebra and eland. Hustler (1987), also working in Zimbabwe, recorded 36 sightings of *B. africanus* and 64 sightings of *B. erythrorhynchus* on giraffe. Red-billed oxpeckers used giraffe significantly more than yellow-billed oxpeckers did ($\chi^2 = 7.84$, $P < 0.01$).

⁸Note that there are problems in studying animals in captivity. First, provision of food *en masse* may cause ingested food to be insufficiently utilised. Second, there may be water imbalance problems due to more water being provided than in the wild. Third, the digestive morphology of captive ungulates differs substantially from that of wild conspecifics (Hofmann 1989). Fourth, captive mammals are often fed a very acid, fruit-rich diet dissimilar to their natural one.

CHAPTER 8

Social networks, movement and population regulation

In the last two chapters I looked at the individual behaviour and ecology of the giraffe. In this chapter I examine how these actions and interactions, affecting one or two individuals, translate into population-level processes. Of course, individuals make up populations, but at the population level we tend to ask different types of question. For example, in Chapter 7 I listed the parasites and predators that are recorded as infesting or killing giraffe. In this chapter we ask 'do these deaths and infestations affect population numbers?'. The answer is certainly not simple. Just because giraffe are dying from lion predation does not mean that lions are in any way affecting populations. They are certainly affecting the individual giraffe concerned, but whether this 'individual effect' translates into a 'population effect' requires further investigation. For example, diseases and predators may simply be taking old or undernourished individuals that are already 'lost' to the reproductive population.

I will examine two main topics. First, I will look at the complex social networks that exist in giraffe populations. We believe that giraffes live in 'fission-fusion' societies, in which animals frequently leave or join groups. This type of social network requires very careful and detailed data collection, and subsequent analysis. This was attempted, many years ago, by Dagg and Foster (and detailed in their 1976 book), in Nairobi National Park (NP), but new computer techniques and ideas on social network analysis

have enabled this to be examined in far more detail. This is one of the giraffe projects I started in 2001, in Laikipia (Kenya), on reticulated giraffe, and continued with Kerry and John Carter in Etosha NP (Namibia) on the Angolan giraffe.

In order to understand the giraffe social network data that has been published, I will briefly examine some network ideas and statistics. Values of 'home range' will be conveniently detailed in this section since 'fission-fusion' societies involve movement of giraffes. Ingress and egress will lead naturally into the second section of this chapter since rates of movement influence population numbers locally. However, both movement and population size are influenced by environmental conditions. The 'desert giraffe' of Namibia have a different population structure than do the giraffe of the southern or eastern savannahs, or of the miombo woodlands. These varying structures will be described where possible, with examples of population sizes and movement. Local population size is influenced by net movement, birth and death, and the environmental agents that act on these events. Animals starve, are preyed, parasitised or fall victim to disease. These agents will be rediscussed for populations of giraffe in widely separated regions of Africa, leading on to the final short chapter on conservation strategies.

Of course, if you are looking at a specific animal population in order to try and understand its social network or its numerical changes, you

need to know many details. Social network analysis requires repeated recognition of individual giraffes. Estimation of population size, perhaps over several consecutive years, requires methods or techniques that give accurate and unbiased numbers. And if you wish to predict future population events, you need details of birth rates and death rates, and how they change over time. You need to know what agents are responsible for these rate changes, such as food shortage, disease and predation. The final description may involve a detailed mathematical model or computer simulation of the population. In practice, only a few single-species populations of savannah animals have received this amount of detailed attention, and to my knowledge no giraffe populations to date. Probably the closest was the viability analysis of the West African giraffe by Desbiez and Leus (2009) (see Chapter 9), using a Vortex (v9.92) simulation model of the giraffe population.

Recognising individuals

In most cases the population sizes, or densities, obtained for giraffe are estimates. It is very rare that all animals or plants can be counted. Of course, if individuals can be recognised repeatedly when observed on subsequent occasions, then very good population data can be obtained. With static organisms, like trees for example, this usually involves simply tagging the individual tree with a marker and recording its position with a global positioning system (GPS). Birkett (2002) carried out this type of census on individual whistling thorn (*Acacia drepanolobium*) trees in Sweetwater Game Reserve, in the Laikipia area of Kenya. With animals, that are mobile, identifying individuals can be more difficult, although not impossible. Schaller (1972), in his study of Serengeti lions, found that he could recognise about 60 lions by their individual natural markings such as a missing ear, tail or other deformity. However, many more lions were marked by placing coloured metal tags in their ears. Caro (1994)

(cheetahs) and Maputla *et al.* (2013) (leopards) both used the pattern of spots to identify individuals. In Mole National Park, in northern Ghana, bushbuck were uniquely identified using a combination of their spot and line body markings (Dankwa-Wiredu & Euler 2002).

The earliest attempt to undertake this type of individual recognition with giraffe was that of Foster (1966) in Nairobi National Park. A photograph of each giraffe was glued to a 4' × 6' data card and taken into the field. Cards were divided by sex, pattern (regular or irregular) and age (adults and immature) to make visual scanning of the cards easier. He was able to individually recognise 65 adult males, 72 adult females and 30 immature giraffe, a total of 167 individuals. Rachel Brand (2007) and Kerryn Carter (2013) compiled similar photographic records for giraffe in Etosha National Park, Namibia. Suraud (2009) and Suraud and Dovi (2006, 2007) have compiled photographic records of 164 Niger giraffe (*G. c. peralta*), and, using pelage pattern to identify individuals, estimated the size of this important population. A photographic database was also made by Stutzman and Flesch (2010) to help identify individuals of Thornicroft's giraffe in Zambia's Luangwa Valley. A standardised area of the shoulder was used for individual identification. Lee and Bond (2011) compiled a photographic record of Masai giraffe in the Tarangire-Manyara Ecosystem, Tanzania, as did Dautrey (2013) for Rothschild's giraffe in the Soyambu Conservancy, Kenya. One of the most recent accounts of using a photographic database is that of Brown (2015). He is collecting photographs of Rothschild's giraffe in Murchison Falls National Park, Uganda, using standardised survey routes (road transects) through the Park (see later). To date, his team have identified 650 unique giraffe individuals.

Some animals, such as zebra, have the equivalent of barcodes on their body and these have been used to identify individuals (Briand Peterson 1972). I developed a similar coded system for identifying reticulated giraffe in Laikipia, Kenya (Shorrocks & Croft 2006, 2009) (Fig. 8.1).

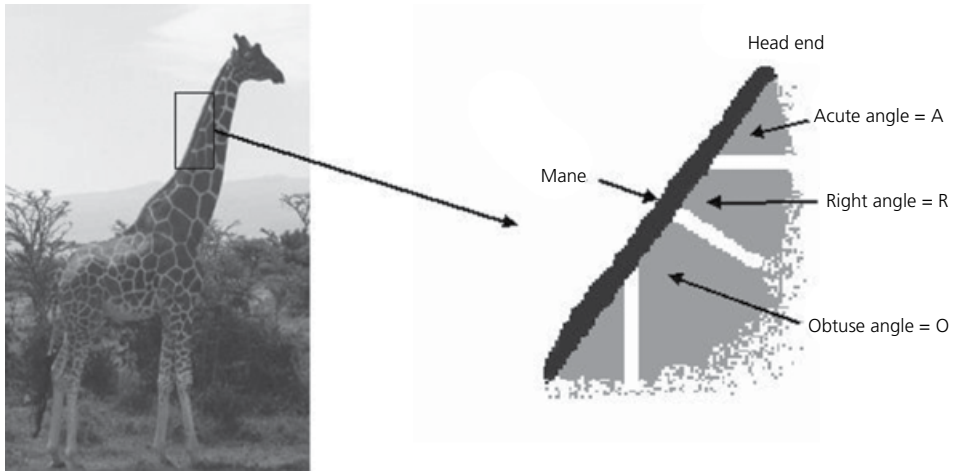


Fig. 8.1 Reticulated giraffe and diagram explaining the ‘neck code’ used by Shorrocks and Croft (2009) to identify individual giraffe. Reproduced with permission of John Wiley & Sons.

The ‘neck pattern’ is converted to a ‘neck code’, written for each individual. The neck pattern that is coded is the section that runs along the back of the neck, adjacent to the mane. The yellow lines of the giraffe’s pattern that reach the mane are coded according to the angle they make with the mane, starting at the head end. Three types of line are recognised: right-angled lines (R), acute-angled lines (A) and obtuse-angled lines (O). Obviously, each giraffe has two codes, one for the right-hand side of the neck, the other for the left. The right-hand code for the giraffe in Fig. 8.1 is ROAARAAROO. With three types of line (R, A and O) and 10 positions on the neck, there are 3^{10} (=59,049) permutations. If both sides of the neck are observed there would be 3^{20} or 3,486,784,401 permutations. The advantage of this type of linear code is that it can be stored in a simple computer database, and new sightings checked against the stored codes each day. This computerised searching is far more efficient than looking through photographs and allows hundreds of individuals to be recognised. Photo-identification software, such as Wild-ID (www.dartmouth.edu/~envs/faculty/bolger.html) can also be used to facilitate individual identifications.

However, although being increasingly used for giraffe studies, there are problems with misidentification with such software (Morrison *et al.* 2011). Halloran *et al.* (2014) have examined the use of computer-aided photo-identification in Thornicroft’s giraffe. They used Wild-ID (version 1.0; Hanover, NH, USA) (Bolger *et al.* 2011, 2012). Bolger *et al.* (2012) had in fact tested the accuracy of Wild-ID on a set of Masai giraffe photographs with some success. However, the accuracy of the software had only been evaluated with photographs standardised by angle (between photographer and subject) and by portion of the animal photographed. Of course, collecting such standardised photographs minimises identification error, perhaps suggesting that the software can be used more widely. In practice, long-term photographic data sets cannot always be controlled for fine-scale factors like angle and portion of the body because of challenging field conditions, or rarity and elusiveness of the target species. Consequently, testing the applicability of Wild-ID with a large non-uniform data set is important for any future, widespread adoption of computer-aided photo-identification.

Halloran *et al.* (2014) attempted to do just that. They analysed 817 Thornicroft’s giraffe

photographs taken from March to October 2009. The study area was approximately 2800 km² in the southern portion of South Luangwa National Park and the Lupande Game Management Area, Zambia (Becker *et al.* 2013). Photographs were not taken at standardised angles, or of particular portions of the animal, as in Bolger *et al.* (2012). Photographs were therefore 'pre-treated' to help the computer-aided identification (Fig. 8.2). They also classified each image according to the quality of the photograph (image blur, background complexity, presence of sky, presence of other giraffe patterns that pretreatment failed to remove) in order to assess the effect on the computer software. Wild-ID processes the images by comparing the geometric arrangement of image features in possible pairs of images and generating a 'goodness-of-fit' score (from 0 to 1) for each pair (Bolger *et al.* 2011). Once all the pairs have been scored, the program ranks the top 20 best matches for each image. The software user can then confirm or reject any potential matches. If all potential matches are rejected, then the image is considered to have 'no match'. To assess the performance of Wild-ID, they compared its match with matches identified using a traditional visual analysis, carried out by personnel trained in giraffe identification. Any discrepancies between computer-generated matches and those generated by visual inspection were considered errors by the computer software. Notice, however, that error is of two types: false acceptance error (FA) and false rejection (FR) error. FA error occurs when an image is wrongly matched with an image of another individual. FR error occurs when an image is labelled as having 'no match' when a match actually exists.

Of the final 552 images analysed, visual analysis revealed that 323 of the 552 photographs had a match (58.5%). The Wild-ID program identified a match for 166 of the photographs (30.1%). All of the 166 matches the program identified were correct, thus no images were mismatched and the FA error was 0%.

However, using the whole giraffe, Wild-ID failed to identify 157 of the possible 323 matches due to FR error. Thus, 157 of the 552 images were incorrectly identified, resulting in an identification error of 28.4%. This suggests that using Wild-ID on non-uniform photographs is much less effective at correctly matching photographs than reported for uniform photographs (Bolger *et al.* 2012). The error was reduced by masking the background (down to 13.4%), using only the neck and flank of the focal giraffe (17.2%) or using only the flank (13.8%). Similar levels of error have been reported for other photo-identification software (Kehtarnavaz *et al.* 2003; Kelly 2001; Speed *et al.* 2007; van Tienhoven *et al.* 2007). Confusingly, Lee *et al.* (2013), in a short report with no data, suggest that Wild-ID has '...the lowest pattern identification error rate (less than or equal to 0.007) of any photo-identification system currently available'. It may be that programs like Wild-ID can help sort photographic databases so that a smaller number require confirmation by eye, rather like my neck codes for reticulated giraffe. But I believe it is essential that additional visual inspection should still be carried out.

When natural markings are not available, individuals can be artificially marked. Traditionally, radio transmitters were attached to collars which fitted around the animal's neck. Although older radio collars were quite big, and only used on large mammals, modern radio collars can be quite small. For example, in Comoé National Park, Ivory Coast, kob antelopes (*Kobus kob*) were fitted with nylon radio collars (total weight about 200 g) and located twice a day by triangulation (Fischer & Linsenmair 2001). Tiny radio ear-tags have been used successfully on bushbuck (Dankwa-Wiredu & Euler 2002). The most hi-tech development is the attachment of satellite transmitters to radio collars. In north-western Namibia, Lindeque and Lindeque (1991) attached 12 kg collars, containing both traditional VHF transmitters and UHF satellite transmitters, to seven elephants. A single individual within a family unit was collared, so that in effect

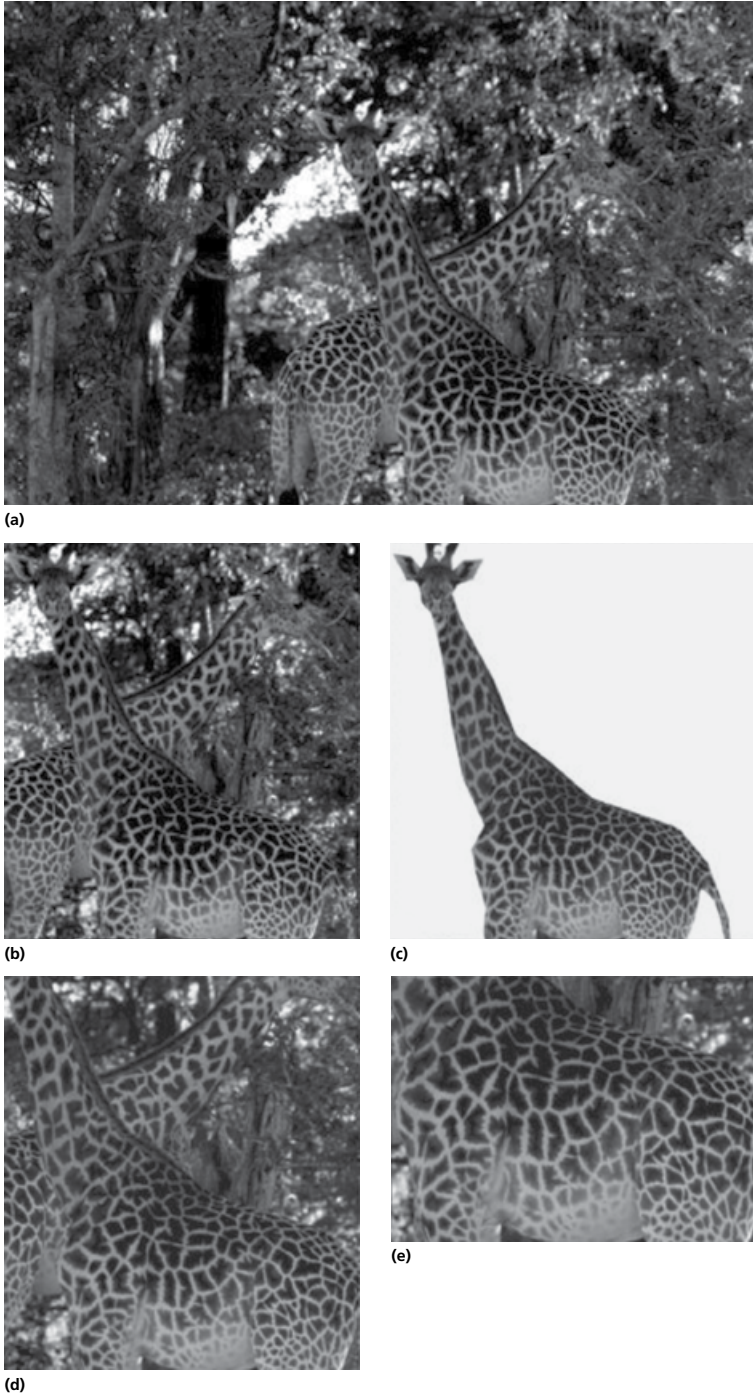


Fig. 8.2 Photographs in various stages of pretreatment. (a) Original, untreated photograph. (b) Photograph after cropping to the body of the focal giraffe. (c) Photograph after background has been masked. (d) Photograph after neck and flank crop. (e) Photograph after flank crop. Source: Halloran *et al.* (2014). Reproduced with permission of John Wiley & Sons.

seven groups of elephants were tracked. Hensman *et al.* (2014a,b) fitted collars to sable antelope (*Hippotragus niger*) in the Okavango Delta, Namibia. These collars had a GPS unit, UHF and VHF transmitters, and batteries designed to last a year. A single female in each of three sable herds was collared. Data stored in the collars was downloaded periodically, using a UHF modem with VHF R-1000 telemetry receiver that was used to get within 500 m of the herd.

These developments in tagging African mammals are mirrored in the use of 'collars' on giraffe. Early collars were often made by the researcher themselves, and were radio transmitters with no GPS ability (Langman 1973). In this study, the completed collar weighed 3.5 kg. Seven giraffe were collared in the Hans Merensky Nature Reserve, South Africa, and individuals were located by radio triangulation. Moving to more recent times, du Toit (1990c) fitted radio collars to three giraffe, four kudu, two impala and two steenbok in Kruger National Park, South Africa, in order to investigate the relationship between range size and body mass. Fennessy (2009) fitted GPS collars on three male and one female giraffe, in the northern area of the arid Namib Desert, to investigate range size. In an arid area such as this, in which mammal ranges can be very large, the GPS collar is an important research item. Suraud (2011) equipped eight *peralta* giraffe with satellite collars in order to study seasonal movements. Mónico and Ortega (2012) fitted GPS collars to five giraffe in Garamba National Park, Democratic Republic of Congo, and Deacon (2012) fitted eight giraffe with GPS collars in Kgalagadi Transfrontier Park, South Africa. No details of the collars are given in any of the last three reports. Deacon gives more details in a later report (Deacon & Smit 2013), saying that the GPS unit was attached using a novel head harness, rather than a collar around the neck. The head harness had been developed, and refined, by fitting it on 48 different giraffe skulls and live specimens. After 18 months there were no problems, injuries or mortalities.

Of course, one of the problems with fitting collars (as opposed to taking photographs) is that the giraffe has to be anaesthetised by darting. The process is not without its dangers and fatalities. GPS collars are important for establishing giraffe ranges and the movement of individuals. But for social network analysis and most population studies, the photographic database, with or without programs such as Wild-ID, are the better, and safer, option. We must always remember that population ecology is the appliance of science and not the science of appliances.

Estimating population size

Moving on from marking individuals for range estimation or social network analysis, I now look briefly at population estimation techniques, with some giraffe examples.

When animals are marked, released and recaptured (or otherwise re-examined) at a later date, an estimation of their population size/density can be made. If (1) marked and unmarked animals behave in the same way (marks do not affect capture, which is true of natural marks like body patterns in giraffe) and (2), the population is closed (no input or loss), then the ratio of marked individuals to the total population size is equal to the ratio of marked recaptures to the total size of a second sample. If we denote the unknown population size as P , the size of sample 1 as n_1 , the size of sample 2 as n_2 , and the number marked in sample 2 as m , then the equality stated above can be written:

$$\frac{P}{n_1} = \frac{n_2}{m}$$

This is known as the Lincoln–Peterson estimate (Seber 1982). The main problem of this method of population estimation involves the second condition above: that the population remains closed between the two sampling events. This closure includes not only migration of individuals, but also birth and death. One

solution to this would be to take the second sample immediately after release of the first, marked sample. However, this would inevitably mean that condition (1) was violated, because the marked individuals would be more likely to be recaptured. Because of this, the two sampling events (marking and recapturing) (or photographing and rephotographing) are usually at least two consecutive days apart. To overcome the problem of input and output, you have to estimate the rate of gain or rate of loss. If either of these can be done, then a suitable adjustment can be made to provide a correct estimate of population size. To do this, at least one more sampling of the population must be done, and individuals caught on different days must be marked in a distinctive way (or a daily photographic record kept). However, this is only a 'day' mark and individuals need not be identifiable. Details of these multiple mark/release/recapture methods will not be given here but they can be found in Seber (1982).

Intriguingly, one of the first people to use these multiple recapture methods was Jackson (1933) who employed it for estimating populations of tsetse flies in East Africa.

Most uses of this technique in savannah systems have employed the simple Lincoln–Peterson estimate, and the results must therefore be viewed with some caution. For example, Kruuk (1972) marked 51 spotted hyaenas (*Crocuta crocuta*) in the relatively small Ngorongoro Crater, northern Tanzania. By subsequently resighting these marked individuals (recaptures), he estimated that there were about 385 adult hyaena in the Crater. Maputla *et al.* (2013) estimated that a leopard population, in Kruger NP, comprised 19 individuals based on 'mark-recapture' photographic data from motion-sensitive camera traps. All the 'photographic' studies of giraffe could use the Lincoln–Peterson estimate for calculating population sizes (although the removal method discussed later is probably more appropriate). With enough 'resightings' in the database, it might even be possible to use more sophisticated

multiple recapture methods. Stutzman and Flesch (2010) (Thornicroft's giraffe) and Lee and Bond (2011) (Masai giraffe) both mention that they intend to use 'mark recapture' in their research reports, but do not actually present population estimates. Brown (2015), for a population of Rothschild's giraffe in Murchison Falls NP, provides numbers that can be used to give a Lincoln–Peterson estimate of $n = (356/118) \times 294 = 887$. This 2007 figure is reasonably close to that of 757 from an aerial survey in about 2012.

Another method of estimating population size that uses marked, or naturally identifiable, animals is the 'removal' method. Animals are not, in practice, removed (because they would be replaced by new animals moving into the area), but simply identified. On each successive sampling occasion, the number of 'new' unmarked (unknown) animals will decrease until all the animals have been marked (identified). An early use of this method was by Pratt and Anderson (1982) on Masai giraffe in Arusha NP, Tanzania. They say that '... at the end of the study the number of known individuals was 462 and still increasing slowly'. They tallied the cumulative first sightings of giraffe and fitted a generalised logistic model to the data. The estimate of total population size obtained was 471. Figure 8.3 shows separate cumulative numbers for male and female giraffe in the relatively small (c. 100 km² of land) Manyara National Park, Tanzania (van der Jeugd & Prins 2000). Lines are fitted second order polynomials. Predictably, the male and female lines look quite different. Males roam extensively, while females are frequently more sedentary. The local female population appears to be heading for an asymptote of around 40, perhaps a little higher. The male line shows no sign of an asymptote, probably because a much larger and wide-ranging population is being measured. Although Surau and Dovi (2006, 2007) and Surau (2008) do not show a cumulative graph of numbers in their Niger giraffe census, they do effectively employ this method, since they state

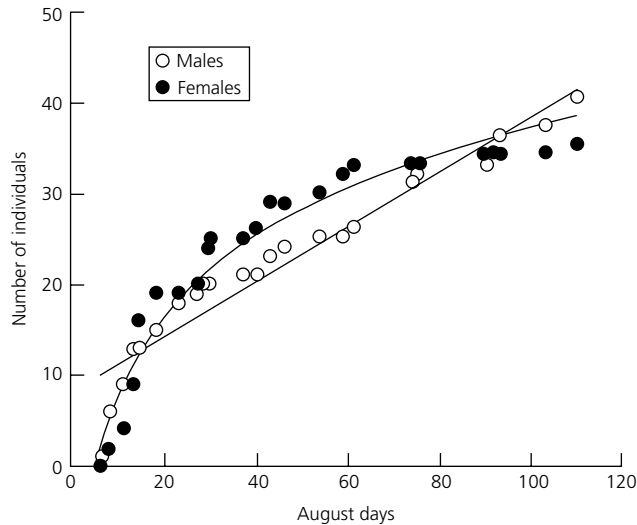


Fig. 8.3 Cumulative graphs of newly recognised giraffes in Manyara National Park, Tanzania, showing separate lines for males and females. Source: van der Jeugd & Prins (2000). Reproduced with permission of John Wiley & Sons.

that one of the objectives of the study is to 'count every individual' and that they continued their transects '... until no new giraffes were discovered'. Of course, once again, this method only works if the population is confined to the area in question. Otherwise you are estimating the population of an unknown area. Additionally, it is not usually necessary to continue observing the population until every animal has been recorded. Since the number of 'new' animals drops progressively, it is usually possible to extrapolate to 'no new' animals, using some form of regression technique.

Most population surveys in savannah habitats involve some type of transect. A line is travelled at a constant pace, by the observer, and all animals seen are counted. Sometimes a straight line transect is walked on foot, but more frequently a road transect is driven in a vehicle. This is often more convenient, and safer. The fact that the road transect is not a straight line does not really matter. The transect method is the same. In effect, a strip either side of the road is sampled. If the sample strip is a random sample of the study area, and if all animals within the strip are seen, then the estimation of den-

sity, or numbers, is relatively easy. For example, imagine that observers in a game reserve drive along its network of roads (20 km) observing all giraffe within 100 m either side of the road. They see 32 giraffe. The density (D) of the population would be $D = n / (2aL)$ where n = the number of animals (32), a is half the strip width (0.1 km), and L is the length of the transect (20 km). This would equal $D = 32 / (0.2 \times 20) = 8.0$ giraffe per km². In practice, it is never so simple. The width of the strip will rarely be constant. For example, if the transect runs through dense vegetation the observed strip will be narrower. If the transect runs through open grass savannah, the observed strip might be wider. One answer to this problem is to record the sighting distance to each animal, and use this to estimate an average value for a . Population density is then estimated by:

$$D = \frac{n}{2L} \left(\frac{1}{n} \sum \frac{1}{r_i} \right)$$

where n and L are as before, and r_i is the observed distance to each sighted animal i . For example, Table 8.1 shows data from a road transect of reticulated giraffe in Laikipia, Kenya.

Table 8.1 Sighting distances for reticulated giraffe in Laikipia, Kenya. Note that this transect, with nine giraffe sightings, was chosen to illustrate the technique. On some drives you may see only one or two, or even no giraffes. Source: unpublished data from Shorrocks.

Animal number	1	2	3	4	5	6	7	8	9
Sighting distance r_i	150	140	140	150	110	100	120	120	125

The transect length was 24 km. The estimated density is therefore:

$$D = \frac{9}{2(24)} \left(\frac{1}{9} \left[\frac{1}{0.15} + \frac{1}{0.14} + \frac{1}{0.14} + \dots + \frac{1}{0.125} \right] \right)$$

= 1.96 giraffe per km². But note that this example uses only one morning road transect (for ease of calculation and illustration), in which nine giraffe were seen, and should not be taken as a ‘good’ estimate of giraffe density for the Laikipia region. For example, in the afternoon transect we saw no giraffe, making the day’s estimate 0.98 giraffe per km², a more representative value for Laikipia.

Although this estimate is one way to allow for variable strip width, it still assumes that all animals within the strip are seen. It assumes what is called a rectangular detection function (Fig. 8.4, line a). In practice, the probability of detection falls off the further an animal is from the line transect baseline, even for a tall animal like giraffe. Line b in Fig. 8.4 is the simplest such relationship. With this detection function, only half the animals within your transect strip would be seen, and in effect a is half the value you think it is. The constant a is therefore more than just the strip width. It estimates how wide the strip would be if every organism was seen and none were missed, and there are numerous ways of estimating it (Buckland *et al.* 2001, 2004). The shaded area in Fig. 8.4 encloses the general zone for detection functions for wildlife populations. Eltringham *et al.* (1998) used a road transect (393 km) to estimate numbers of large mammals in the Mkomazi Game Reserve (2850 km²), northern Tanzania. Four surveys, each lasting 3–4 days, were undertaken during the 1996 dry season when the animals were

more easily seen because of the sparse vegetation. In 477 sightings of giraffe, they saw 2761 individuals, and estimated the 1996 dry season population to be 979 with a standard error of 84. The authors can therefore be 95% certain that the actual giraffe population lies between 811 and 1147. Shorrocks *et al.* (2008) used distance sampling to estimate densities of zebra, impala and dikdik, in Laikipia, Kenya. Dunham and du Toit (2013) sampled 36 transects totaling 94.15 km, four times over 2 days. Using the distance analysis (Buckland *et al.* 2001, 2004), they were able to estimate detection functions for nine species and therefore their densities, but not unfortunately for giraffe. Simple road transects were used by Caro (1999) to estimate the abundance of mammals (including giraffe) in Katavi National Park, Tanzania. To overcome potential variable strip width, Caro’s team did two things. First they divided the park into seven areas and drove a transect (at <10 km h⁻¹), once a month along minor tracks in each area. Second, they made continuous estimates of sighting (strip) width during the transects. Giraffe had a mean density of 2.21 per km². Waltert *et al.* (2009) working in the Katavi–Rukwa NP/GR system in western Tanzania, using walked transects and the software DISTANCE 4.1, estimated giraffe densities of 0.98 per km² (Katavi National Park) and 0.44 per km² (Rukwa Game Reserve). This difference in numbers between national parks and games reserves is not uncommon.

The type of transect most associated with savannah is probably the aerial survey (Norton-Griffiths 1978). Rather than walking or driving the sampled strip, it is flown over, in a light aircraft, and the animals counted from the air. Sometimes, particularly if the animals are in

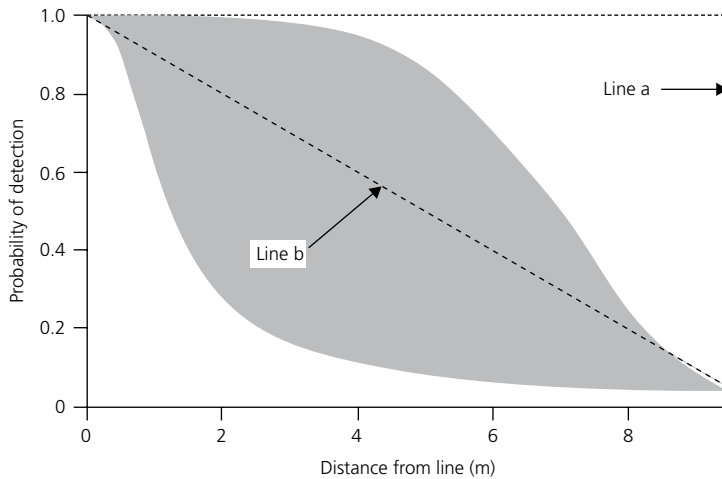


Fig. 8.4 Detection functions of a line transect survey. Source: Shorrocks and Bates (2015).

groups, they are photographed and counted later. The technique was pioneered by Bernhard and Michael Grzimek (1960a,b), who used it in the Serengeti ecosystem in the late 1950s. The flying method remains essentially unchanged today (Foguekem *et al.* 2010), although the statistical analysis surrounding it has become something of an industry. Only aircraft with high wings give an unobstructed downwards view. An observer sits in the back of the aircraft and, using markers placed on the window and wing struts, 'views' a transect strip on the ground, and counts the animals visible. These markers are positioned while the aircraft is on the ground. If W is the required strip width during the survey and H is the flying height chosen, then w (the strip width on the ground) is obtained from $w = W \times h/H$. This width, w , can then be marked on the hangar floor and the position of the markers on the window and the wing strut can be adjusted until they are in line with the margins of this width in the hangar. The pilot simply has to fly at height H for the observer to 'see' a transect of the required width on the ground below.

In East Africa such aerial surveys normally travel at 160 km h^{-1} , at a height of 100 m, giving a transect width of 150 m. In open terrain and/

or with conspicuous animals, the height can be greater and in more wooded terrain and/or with less visible animals, the height can be lower. Two observers can be employed, one on each side of the aircraft. Cameras can also be fitted to the underside of the aircraft and photographs taken of a transect strip directly below, rather than to each side.

Of course, not all the savannah area being studied is usually flown over. This would require many hours of expensive flying time. The study area is sampled and the total population, or density, is estimated (Parker *et al.* 2011). Aerial surveys usually underestimate the populations on the ground (Caughley 1974; Craig 2004). Giraffe are particularly cryptic from the air, notably in the late morning when they move to the shade of large trees. The proportion seen declines with flight speed and observer inexperience.

A classic example of this type of aerial survey, that counted giraffe, is that of Watson *et al.* (1969a). They surveyed nine large mammals in the Mkomazi region of northern Tanzania and southern Kenya. They used a system of stratified random samples (random samples in specific areas) and flew strips of 440 m width, from an aircraft travelling 100 m above the ground at

130 km h⁻¹. One area was totally counted to check the transect sample method and gave very similar results to the sample. Estimates and standard errors were computed using the methods of Jolly (1968). Estimated giraffe numbers were 225 ± 114 , so the standard error was computed to be quite large. The published paper provides a very nice summary of the problems involved with aerial sampling and the difficulties of maintaining the aircraft at the correct height. A similar classic aerial survey is that of Watson *et al.* (1969b), in the Loliondo Controlled Area of northern Tanzania. Once again, they did a total count in one area (155 km²) to compare with the sample count (10 samples covering 16.8 km²) in the same area. The results for giraffe were: number counted 281, estimate from sampling 295 with 95% confidence limit (CL) of 164–426. Other examples of aerial surveys that have included giraffe are Sommerlatte and Williamson (1995) (Murchison Falls NP, Uganda), Lamprey (2000) (Queen Elizabeth NP and Murchison Falls NP, Uganda), Omondi *et al.* (2007) (Waza NP, Cameroon), Potgieter *et al.* (2009) (Zakouma NP, Chad), Chase (2011) (northern Botswana) and Rwetsiba *et al.* (2012) (Murchison Falls NP, Uganda).

Declining numbers and distributions of many wildlife populations, particularly giraffes, call for data at ever increasing levels of spatial resolution, prompting questions about the precision of sample survey estimates. While sample surveys are less costly, total surveys are thought to be more reliable. Georgialis *et al.* (2011) made a direct comparison between these two methods for wildlife in the Laikipia District, Kenya, discussing their strengths and weaknesses. They found that neither total nor sample surveys yield accurate population estimates. Both methods in fact tend to underestimate numbers, with the bias varying among species, observers and habitats (see also Caughley 1974; East 1999; Redfern *et al.* 2002). Undercounting appeared to be slightly greater in the total count than the sample survey, but on average, differences were not large. However, comparison factors, such as

cost and the scope of information provided, revealed huge differences in favour of sample surveys.

Although aerial surveys with light aircraft remain the most commonly used technique for counting large mammals in African savannahs, there are drawbacks. These include safety issues (Watts *et al.* 2010) and logistical issues, namely the lack of airfields or even appropriate aircraft in some areas of Africa (Vermeulen *et al.* 2013). Moreover, these operations are quite expensive for most African wildlife managers, and it is therefore difficult to plan long-term and regular surveys. As a result, in many African protected areas, the interval between two successive surveys can often be as great as 10–25 years (Dunham 2012). This makes it difficult to quantify accurately any short-term change in wildlife populations (Ferreira & Aarde 2009). As a result, some populations may collapse between two surveys because no appropriate action had been taken (Bouché *et al.* 2011, 2012). Unmanned aerial systems (UAS), using small drones, may be more cost-effective, safer and capable of reaching more remote areas (Lisein *et al.* 2013). These authors tested the accuracy of drone counts in Nazinga Game Ranch (940 km²) in Burkina Faso, using a fixed wing, small UAS, equipped with an autopilot and digital camera, and a ground control station comprising a tablet computer. Transect surface area estimation was found to be good, although no actual animals were counted in this trial. However, the use of small UASs in big mammal surveys opens up interesting prospects for the future.

Another hi-tech development in ‘counting’ mammals (also used in behavioural studies) is the camera trap (Abu Baker & Brown 2014; O’Connell *et al.* 2011; Swann *et al.* 2010). These are placed in fixed transects or grids and are remotely activated by a motion sensor, an infrared sensor or a light beam. They are usually baited to attract the mammal in question. For example, in the duiker example (Abu Baker & Brown 2014), the bait was alfalfa-based pellets, and camera photos were each given an ID, date,

time, species, number of individuals, sex, posture and specific individual whenever possible (marks such as chipped horns). Camera traps are being used in the Serengeti NP, Mara GR, Samburu NR and Laikipia (Mpala Research Centre) to watch and monitor wildlife, including giraffe. In Etosha NP, Dean (2012) reports on camera traps that have taken over 7000 pictures of giraffe since they were set up in 2010 by Dr Wendy Turner, of the University of California, Berkeley (Krishnappa & Turner 2014). Their original use was to study anthrax transmission at carcass sites.

So far, the methods of estimating animal populations that I have outlined have involved counting animals directly. However, ecologists frequently count the signs left by animals rather than the animals themselves, such as footprints, feeding signs and dung. So far as I'm aware, these methods have not been applied to giraffes but with elephants, counting dung is a frequently employed method of population estimation and could be used for giraffes. An excellent elephant example is the survey of Jachmann (1991) carried out in the Nazinga Game Ranch, Burkina Faso, in western Africa. The vegetation is a tall grass, tree and shrub savannah with *Vitellaria paradoxa*, *Terminalia* spp., *Combretum* spp., *Acacia* spp. and *Detarium microcarpum* as the dominant trees. Jachmann estimated the elephant population by four methods, unfortunately not all in the same year: aerial counts of elephants (both total and sample), line transect foot surveys of elephants, vehicle road surveys of elephants and a dung count using quadrats. The 'dung' quadrats were positioned along the line transect used for the foot survey. Of course, simply counting the number of dung piles is not enough to estimate the elephants producing them. Jachmann had to estimate two other things: the rate of dung production and the rate of dung decay. Defaecation rate was estimated by following elephants on foot for several hours. Dry season defaecation rate was estimated at 14.1 droppings/elephant/day, while the wet-season rate

was estimated at 27.2 droppings/elephant/day. By watching 31 droppings, over several weeks, the decomposition rate was estimated to be 0.59%/day.

Table 8.2 shows the estimates of population size obtained by the various methods. Using the total aerial survey as the best estimate, we might believe that the dung count gives a very good estimate of the elephant population at Nazinga. A study by Olivier *et al.* (2009) used dung surveys to estimate population size, and extracted an age structure from boli diameters for the elephants living in the Maputo Elephant Reserve, Mozambique. Their estimates were based on published defaecation rates, dung decay rates, distance sampling techniques and 1672 dung piles encountered on 204 line transects. Comparison with a 1995 dung survey (de Boer *et al.* 2001) suggested that the elephant population was stable.

In the end, which method is best for estimating giraffe population size will depend on the size of the area, the suspected size of the population, the person-power available and money. With small restricted areas, with a small population, the total count using a database of photographs will be best. In larger areas, with more widespread populations, this could still be used but the 'removal' method with extrapolation might be best. With huge areas like many of the larger national parks, road and flight surveys are probably the only way, although with road

Table 8.2 Elephant population estimates in the Nazinga Game Ranch, Burkina Faso (from Jachmann 1991).

Survey method	Year	Population estimate
Aerial (100% coverage)	1989	366
Aerial (6.1% coverage)	1988	610
Foot transect	1987	487
Foot transect	1988	306
Vehicle road transect	1988	293
Dung count	1987	353–396*

* Two different assumptions about dung dynamics.

surveys there is no reason not to use a digital camera at the same time.

To end this section on population techniques, I will pause to consider why we need accurate data on numbers of African mammals, including giraffes. I believe there are two main uses. First, these numbers inform population models which attempt to describe, and understand, the ecological processes that determine population numbers. Without the estimated numbers of real populations, we would have nothing to compare our predictions to. Secondly, they alert managers, ecologists and conservationists to changes in populations (trends) that we should know about. I therefore end this first section by describing a nice study that looked for such population trends in savannah mammals.

The Masai Mara ecosystem comprises the Masai Mara National Reserve and the adjoining group ranches. The National Reserve is a formal conservation area owned by the government of Kenya, while the group ranches are privately owned. The main land uses are pastoralism, tourism and agriculture. Since 1977 the Department of Resource Surveys and Remote Sensing has carried out systematic survey flights to estimate the wildlife populations. Ottichilo *et al.* (2000) used census data spanning the years 1977 to 1997 to look for population trends in several species. The giraffe data is shown in Fig. 8.5. Many species showed a significant trend ($P < 0.05$), all of them downwards. Declines for individual species were warthog 88%, buffalo 82%, giraffe 79%, eland 76%, waterbuck 76%, topi 73%, Coke's hartebeest 66%, Thomson's gazelle 62% and Grant's gazelle 52%. There were no significant downward trends in elephant, impala and ostrich. Livestock populations (cattle, sheep, goats and donkeys), which were also examined, did not show any significant downward trend. This decline of most wildlife in the Masai Mara ecosystem could be due to a number of factors, acting individually or in combination. These include counting errors and biases, climatic effects, habitat changes, competition for forage,

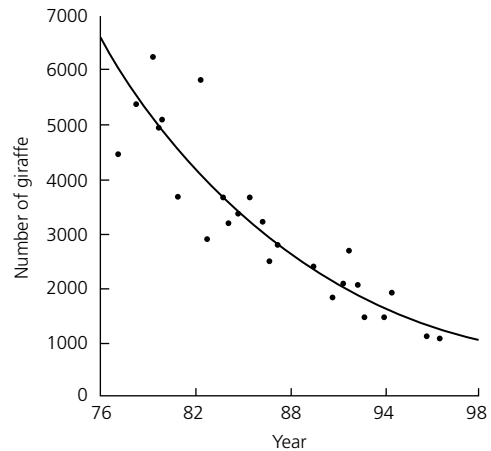


Fig. 8.5 Population trends for giraffe in the Masai Mara ecosystem between 1977 and 1997. Source: modified from Ottichilo *et al.* (2000). Reproduced with permission of John Wiley & Sons.

and poaching. Although difficult to assess, the authors conclude that counting errors and climate can be discounted. Counting errors tend to increase the variation around the population estimate rather than introduce a systematic effect, such as that observed here. Also the method of data collection did not change over the 20 years. There were severe droughts in this part of Africa during 1984, 1986 and 1993 which would have affected vegetation growth and potentially herbivore numbers, but any effect could not be detected in the data. A combination of the last three factors, which are known to be present, could be responsible. Sadly, Ogutu *et al.* (2011) report that the Mara situation has not improved. Losses are estimated at 95% for giraffes, 80% for warthogs, 76% for hartebeest and 67% for impala.

Dispersal and home ranges

Home range is the area in which an animal lives and travels. The concept can be traced back to a publication in 1943 by W. H. Burt, who constructed maps delineating the spatial extent, or outside boundary, of an animal's movement

during the course of its everyday activities. Associated with the concept of a home range is the concept of a utilisation distribution, which takes the form of a two-dimensional probability density function that represents the chance of finding an animal in a defined area within its home range. In other words, if you take a cross-section through an animal's home range, its abundance does not follow a rectangular distribution but is more like a normal curve. This is also true of continental distributions (Shorrocks & Bates 2015). The home range is typically constructed from a set of location points that have been collected over a period of time identifying the position in space, and time, of an individual. Such data can be collected by observation of individually recognised animals (e.g. using a photographic database) and in the past this was the only way. Now this data can be collected automatically using collars placed on individuals that transmit through satellites and GPS technology, at regular intervals (see earlier section).

The oldest and simplest method of calculating home range is to find the minimum convex polygon (MCP). The MCP completely encloses all data points by connecting all the outer locations. However, using this method has several drawbacks. These include the fact that it is a non-parametric technique and therefore not informative about areas of high utilisation. It is also sensitive to sample size; the more observations, the larger the MCP tends to be. Therefore it is difficult to compare two sets of range sizes if based on different sample sizes. It is also sensitive to data points that are outliers, and it could therefore include areas never used by the animal and give a false impression of range size and extent. There are some methods derived from the MCP that try to account for outliers, excluding some points. These include the arithmetic mean peeled polygon, the harmonic peeled polygon and the recalculated arithmetic mean peeled polygon (Kenward 1987). All of these have the same problem, which is that locations are considered singly. This means that not all

points in a cluster, far from the centre, are removed in a x^{th} percentile 'peeled' polygon. This is clearly an issue with giraffe that tend to occur in groups. Alternative approaches might do better by considering the percentage to be removed as a group and calculating areas based on sets of points removed rather than removing them singly.

The best known methods for constructing utilisation distributions are the so-called bivariate Gaussian or normal distribution kernel density methods (Seaman & Powell 1996; Silverman 1986; Worton 1989). This group of methods is part of a more general group of parametric kernel methods that employ distributions other than the normal distribution as the kernel elements associated with each point in the set of location data. Rather than just seeing a polygon with an empty interior, you see an enclosed space with interior isoclines representing frequency of occurrence within the range outline.

Non-parametric method extensions to the kernel approach are Burgman and Fox's alpha-hull method (Burgman & Fox 2003) and Getz and Wilmer's local convex hull (LoCoH) method (Getz & Wilmer 2004; Getz *et al.* 2007). Although currently, more software is available to implement parametric than non-parametric methods, there is some suggestion (Getz *et al.* 2004, 2007) that LoCoH methods generally provide more accurate estimates of home range sizes and have better convergence properties as sample size increases than parametric kernel methods. Several computer programs are available to carry out these analyses. For example, ARCVIEW (now known as ArcGIS for Desktop) can be downloaded at www.esri.com/software/arcgis/arcgis-for-desktop.

Over the years there have been several measurements of giraffe movement and home range using both photo-recognition and tracking devices. Foster and Dagg (1972) reported home ranges for giraffe in Nairobi National Park as 62 km² for adult males and 85 km² for adult females. However, males in particular are thought to move out of the Park. The radio

collar work of Langman (1973) is another early example already mentioned. The ranges reported were MPCs, although not named as such.¹ The mean home range was 22.8 km² for adult males, 24.6 km² for adult females and 12.8 km² for juveniles. The home ranges reported had at least one permanent watering point and three seasonal watering points, and the observed home ranges overlapped to a large extent. Daily movements depended on the age and sex of the giraffe as well as weather conditions. The mean daily distance travelled was 5.9 km for adult males, 2.9 km for adult females and 3.3 km for juveniles. Other examples of home range estimates are as follows.

- Berry (1978) in Luangwa Valley, Zambia, in which the average range for males (n=14) was 82 km² and for females (n=6) was 68 km².
- Leuthold and Leuthold (1978a) in Tsavo NP, Kenya, in which average home range was 160 km², the largest male range being 650 km² and for a female 480 km².
- Van der Jeugd and Prins (2000) in Lake Manyara NP, Tanzania, in which the average home range was 8.6 km², but with large variation among individuals.
- Fennessy (2007), reporting work by Jean-Patrick Suraud using a photographic database, gives home range areas for giraffe in arid areas of Niger as 842 km² for males and 367 km² for females.
- Fennessy (2009) in the arid northern Namib Desert. Estimates of home range size were calculated using data from individually identified giraffe and the GPS satellite collars fitted to four giraffes. For males the average home range was 513.9 km², with a range of 26.7–1950 km². For females the average was 199.5 km², with a range of 12.9–1098 km².

- Gieling (2011) in Entabeni Game Reserve, South Africa, recorded very small ranges of about 25 km², which was the size of the reserve, and this may have artificially limited the movements of giraffe.

All these studies suggest that measured giraffe home ranges can vary from about 13 km² to about 1950 km², although the average is usually between about 68 km² and 514 km². There is a suggestion that males have larger home ranges than females, and that arid environments promote larger home ranges. Certainly those measured by Fennessy in the arid Namib Desert, and the ones estimated by Suraud in an arid area of Niger, are the largest on record. Unfortunately, as Fennessy (2009) says, none of the studies of range size have collected enough sightings for the estimated MPC to approach convergence. Because of this (the issue of sample size already mentioned), making comparisons between areas and sexes is quite difficult. However, I'm sure that the larger home ranges estimated in arid environments are relatively real, given that arid environments will probably mean that giraffe populations are lower and that fewer sightings are therefore taken. These reduced sightings would have the opposite effect to that observed, and imply that home ranges in arid environments may be even larger than the large ranges actually estimated.

As a final comment on home ranges, the work of du Toit (1990c) is worth noting. He looked at home range data for four browsing ungulates in Kruger National Park (KNP), South Africa, and how this related to their body mass. The four species of browser were giraffe, greater kudu, impala and steenbok. In general, home range area has been found to scale with body mass with an exponent greater than 0.75, suggesting that larger animals appear to forage over a proportionally greater area than predicted from metabolic requirements alone (which would be $M^{0.75}$). Du Toit used the same technique (two to four radio collars on each species) in the same area (KNP) to allow comparison. The mean home range for giraffe was 282 km².

¹'Home ranges were measured from plotted locational data. Boundaries for purposes of discussion were determined by connecting the outermost sightings.'

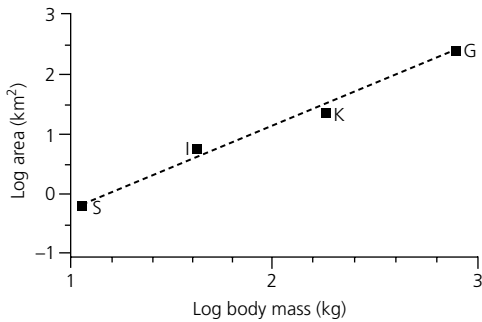


Fig. 8.6 Double-log plot of the relationship between home range area (km²) and body mass (kg). Points (■) are mean values for steenbok (S), impala (I), kudu (K) and giraffe (G). The regression line (dotted) is $\log(\text{area}) = 1.38(\log \text{body mass}) - 1.62$, $r^2 = 0.99$, $P < 0.01$. Source: du Toit (1990c). Reproduced with permission of John Wiley & Sons.

For this savannah area, home range area (A_{hr}) scaled on body mass (M) as $A_{\text{hr}} = 0.024M^{1.38}$ ($r^2 = 0.99$) (Fig. 8.6). One suggestion for why the exponent 1.38 is greater than 0.75, put forward by du Toit, is that 0.75 sets a minimum metabolic limit but that animals will forage outside this core area for feeding sites of high quality.

Herd size

Before moving on to look at giraffe social networks, let me say a few words about giraffe herd size. The perceived advantages of living in groups have already been discussed in Chapter 6. Here I simply report observed distributions of herd size. Figure 8.7 shows a selection of measured examples. Distributions are usually similar although some workers have recorded longer tails to the distributions, for example, Leuthold (1979) and Shorrocks and Croft (2009) (Fig. 8.7 middle). Interestingly, in regard to this longer tail, seen in some distributions, Shorrocks and Croft (2009) estimated individual giraffe separation distances (Fig. 8.8) and found that (1) most giraffes in a group were quite close together and (2) this distance did not change with group size, suggesting perhaps that the larger groups, some-

times seen, are real and not two or more groups passing through each other.

Several people have reported that group size can change with season or habitat. For example, Leuthold (1979), working with Masai giraffe, in Tsavo East NP, Kenya, noted that most groups had between one and 10 individuals, rather like those in Fig. 8.7, with a maximum of 35 and a mean of 3.8. However, in the western part of the Voi River area the average group size was 4.6, while in the eastern part of the Voi River area the average was significantly lower at 3.3. Le Pendu *et al.* (2000), working in Niger with *peralta*, found that group sizes were significantly smaller during the dry season than during the rainy season (one-tailed Mann-Whitney $U = 4131$, $P < 0.01$). In the rainy season, with 99 groups the mean group size was 9.4, while in the dry season, with 111 groups the mean group size was six. Brand (2007) recorded the size of giraffe groups in Etosha NP (Fig. 8.9) and again noted that group sizes were larger in the rainy season. In Manyara NP, van der Jeugd and Prins (2000) noted a significant effect of month on group size ($F_{6,472} = 2.60$, $P < 0.05$), but no two months differed significantly from each other (Scheffé multiple comparisons). In fact, in this case the differences between months were not clearly a seasonal trend.

Finally, Bercovitch and Berry (2009), working with the already mentioned long-term data of Thornicroft's giraffe, in South Luangwa Valley NP, Zambia, also noted that herd sizes were larger in the rainy season. Average herd size was significantly larger (5.6 ± 4.0), and more variable (coefficient of variation (CV) = 71%), during the wet than during the dry season (5.0 ± 3.3 ; CV = 66%; $t = 2.190$, $df = 979$, $P = 0.029$). In fact, giraffe herd size altered as a function of month (ANOVA: $F_{11,969} = 2.185$, $P = 0.013$), but Tukey's *post hoc* multiple comparisons tests of pair-wise differences between individual months were not significant, rather like the Manyara data. Herds of size 1 and herds of size >1 were found in similar frequencies during both wet and dry seasons

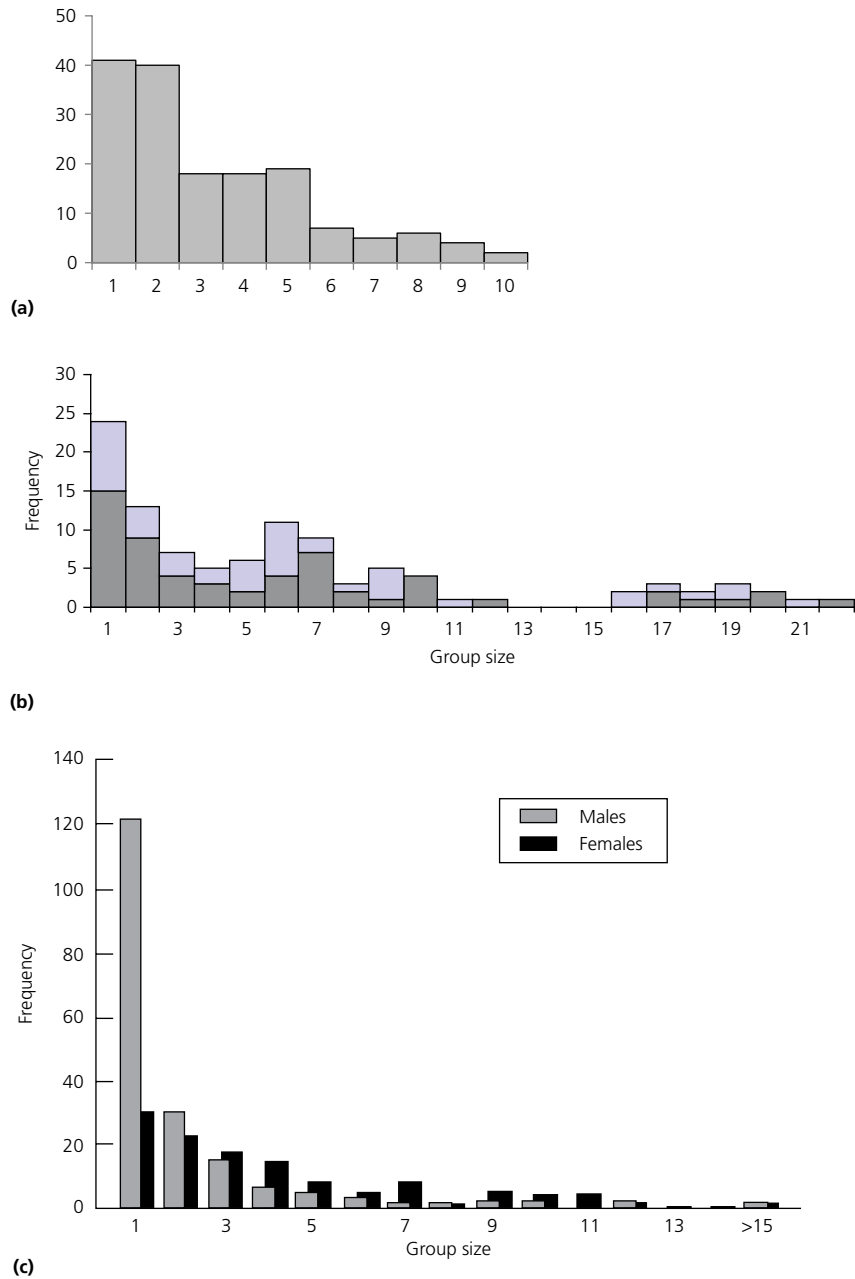


Fig. 8.7 Distributions of giraffe group size. From top to bottom, (a) Masai giraffe in Nairobi NP, Kenya (Foster 1966). (b) Reticulated giraffe in Laikipia, Kenya, 2005 (light grey) and 2006 (dark grey) (Shorrocks & Croft 2009). (c) Masai giraffe in Manyara NP, Tanzania (van der Jeugd & Prins 2000). Reproduced with permission of John Wiley & Sons.

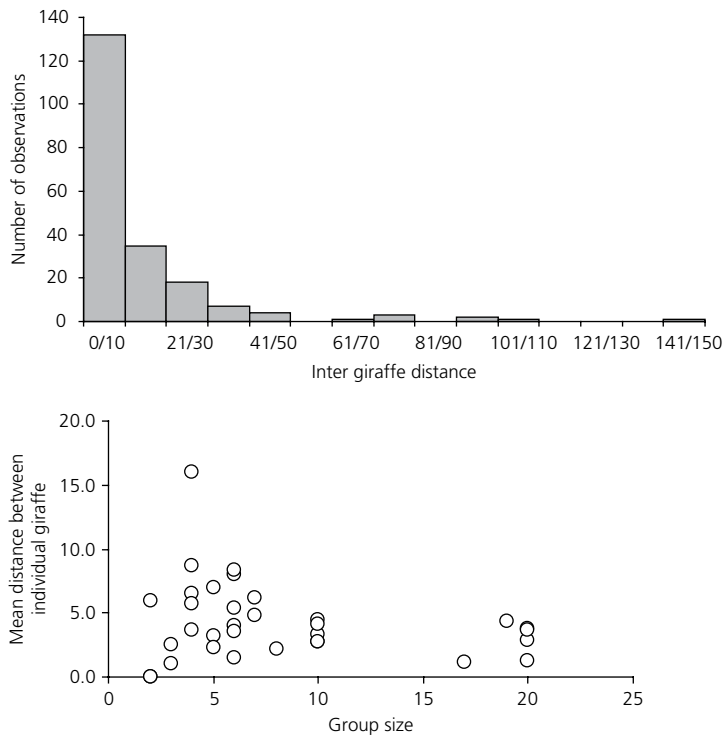


Fig. 8.8 (Top) Frequency of giraffe separation distances. Distance = one giraffe length = 1.75 m. (Bottom) Mean distance between individuals in a group and the size of the group. Both graphs are for the 2006 data of Shorrock & Croft (2009).

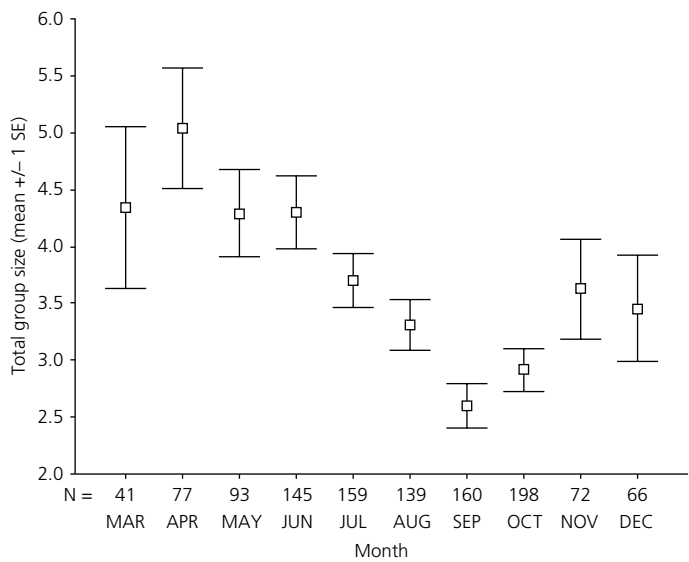


Fig. 8.9 Variation across the months in mean total group size of giraffe in Etosha National Park, Namibia. Bars are one standard error. Source: Brand (2007). Reproduced with permission.

($X^2=0.525$, $df=1$, $P=0.469$). Bercovitch and Berry (2009) also noted a habitat difference. Solitary animals were more likely to be seen in riverine and thicket habitats, whereas herds of several individuals were more likely to be found in open and woodland habitats ($X^2=24.58$, $df=3$, $P<0.001$). Among non-solitary animals, herd size was significantly different across habitat type ($F_{3,977}=3.024$, $P=0.029$). A Tukey's *post hoc* multiple comparisons test revealed that the result was a consequence of the largest herds (5.7 ± 3.7) occupying open areas, whereas the smallest herds (4.1 ± 2.5) were noted in thicket areas.

Social networks

Early work on giraffe social structure and giraffe groups tended to concentrate on group composition (all male, mixed, etc.) and the types of interactions between individuals of the same, or different sexes (Foster 1966; Leuthold 1979; Pratt & Anderson 1982, 1985), and this is still usefully being recorded nowadays (e.g. Bercovitch & Berry 2013; van der Jeugd & Prins 2000). Some of this work has already been discussed in Chapter 6. Working in Manyara NP, Tanzania, van der Jeugd and Prins (2000) looked at the associations between giraffe individuals, and their estimation of numbers and group sizes have already been mentioned in this chapter (Figs 8.3 and 8.7). Although not employing social network techniques, as outlined below, they clearly make social network-like comments. They note that females did not associate randomly, but were found more commonly in small groups. In contrast, males associated randomly, and were mostly observed in groups of one. Only one 'fairly stable group' of giraffes was noted in Manyara, judged on their higher association levels compared to other individuals. Necking contests with newly arrived males were common in this group.

Social network analysis has been widely used in the social sciences for many years but has only been used by researchers of animal behaviour over the past decade (reviewed by Croft *et al.* 2008; Krause *et al.* 2007; Wey *et al.* 2008). However, such analysis has now allowed the detection of subtle interactions in the social organisation of many animal species that had not previously been described, and the range of network measures now available makes it a very powerful analytical tool. In savannah species there has been revealing work on Grevy's zebra (*Equus grevyi*; Sundaresan *et al.* 2007), reticulated giraffe (Shorrocks & Croft 2009), the Angolan giraffe (Carter *et al.* 2013a,b), Thornicroft's giraffe (Bercovitch & Berry 2013), and the savannah elephant (*Loxodonta africana*; de Silva & Wittemyer 2012). An excellent introduction to the subject can be found in Croft *et al.* (2008), with important comments on hypothesis testing in networks in Croft *et al.* (2011). Before looking at the giraffe examples in more detail, I will briefly examine elements of network terminology and methods.

The essential elements of a network are nodes and edges. In biology, the nodes are individual animals and the edges are observed interactions between two individuals (called a dyad). Although it would be possible to observe actual interactions in giraffe (see Chapter 6), in practice the 'interaction' is usually inferred, rather than observed. Data on group composition is frequently available because individual giraffe can be identified either by 'coding the neck pattern' or by compiling a photo-database for the area of study (see earlier). If two individuals are seen in the same group, then they are presumed to interact.

As an illustration, Fig. 8.10 shows the social network for 80 giraffes sampled in Kenya in 2006. Each dot (node) represents one individual giraffe (identified by a number) and the lines indicate that two individuals were seen in the same group at least once, and therefore presumed to interact. The network was produced using the computer program NETDRAW (using the

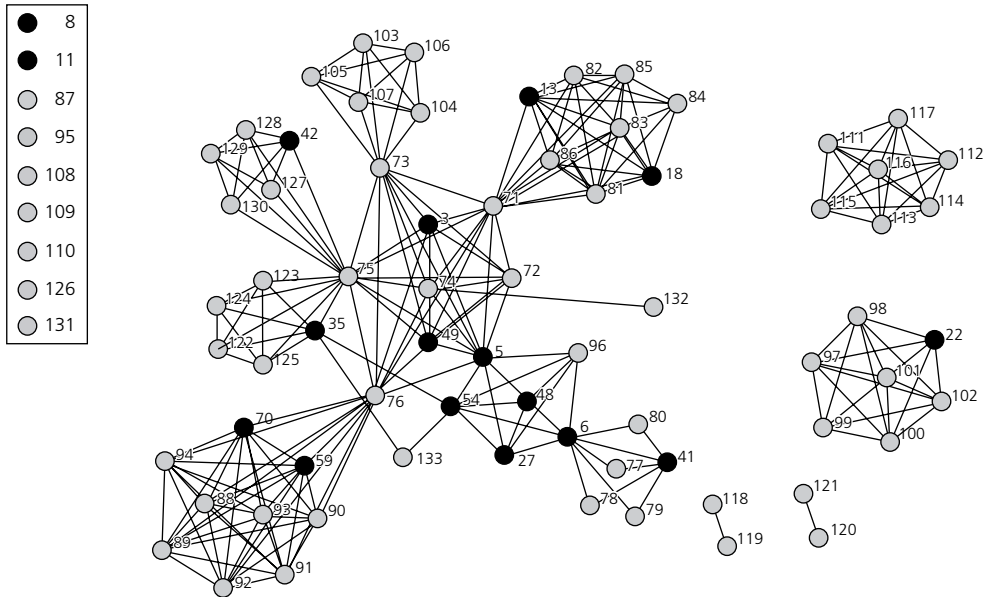


Fig. 8.10 The social network for 80 giraffes sampled in 2006, in Laikipia, Kenya. Each dot represents one individual giraffe (identified by a number) and the lines represent the fact that two individuals have been seen in the same group at least once. The network is determined by these links between individuals. The position of groups or individuals in the diagram is for visual clarity only. Black dots are individuals first seen in 2005 and grey dots are individuals first seen in 2006. Source: Shorrocks and Croft (2009). Reproduced with permission of John Wiley & Sons.

spring-embedding function), and is determined by the links between individuals. When some interactions (edges) are stronger (= more observations), the network can be adjusted accordingly. In the figure, black dots are individuals first seen in 2005, and grey dots are individuals first seen in 2006. Quantitative analysis is carried out not on these graphical representations of networks, but on a matrix of values that conveys the same information. Many of these matrices only contain simple binary data. For example, in the giraffe matrix for the network in Fig. 8.10, all the individuals were listed along both top and side, and in each cell (apart from the diagonal) of the matrix a value was written. If two individual giraffe were never seen together this was a 0, and if two giraffe were seen in the same group it was a 1. The 1s translate into the edges in the network graph. If sufficient data is available, the 1 can be replaced by

a larger number, indicating the frequency of that edge. These are edge weights and, if available, should always be used. If there is not enough data to use the edge weights then probably there is not enough data to allow a meaningful analysis of the social network. Alternatively, a measure of association can be used as the edge value. For example, Carter *et al.* (2013a,b) used the half-weight index (HWI), which is the most appropriate association index when both members of the pair are located infrequently in each sampling period (sighting) (Cairns & Schwager 1987). The index is defined as:

$$\text{HWI} = y_{ab} (y_{ab} + y_a + 0.5y_a + y_b)$$

where y_{ab} is the number of times both giraffe a and giraffe b are sighted in the same group; y_a is the number of times giraffe a is observed but

not giraffe b ; y_b is the number of times giraffe b is observed but not giraffe a ; and y_0 is the number of times giraffe a and giraffe b are not seen in a group. The HWI produces a value between 0 (a pair of animals are never seen together) and 1 (a pair of animals are always seen associating in the same group).

Analysis of the network matrix can be carried out using UCINET (Borgatti *et al.* 2002). This is a comprehensive computer package for the analysis of social networks and can deal with very large data sets. The current version is 6.587 (6 September 2015). Integrated with UCINET is NETDRAW, written by Steve Borgatti. Another useful tool is SOCPROG (Whitehead 2009). This is a series of MATLAB programs for analysing data on social structure, population structure and movements of identified individuals. For those not running MATLAB on their computer, there is a compiled version that will run without MATLAB.

Using the above software, analysis of networks can be extensive. However, simply stated, detailed examination tends to focus on two things: (1) who are the important individuals in the network? and (2) what is its structure? Question (2) can partly be answered by looking at the network graph, but more sophisticated tools are available that search for components and sub-structures. One parameter is the average *clustering coefficient* (C), which is a measure of the local ‘cliquishness’ of the network and is calculated as the mean fraction of all possible connections that occur in a local neighbourhood (Newman 2003). C lies in the range 0–1. It measures the probability that two of one’s network neighbours are themselves neighbours. For the network in Fig. 8.10, the mean C is 0.89. Knowledge of C may contribute to our understanding of a population’s susceptibility to epidemics. For example, high levels of clustering may decrease the spread of a disease in a population, because the infection will be contained among a few individuals that are highly interconnected.

Question (1) focuses on individuals and their connection to other individuals. For example, the *degree* of an individual is the number of

other individuals joined to it. The mean degree (k) of the network in Fig. 8.10 is 5.47. The *mean path length* (L) is calculated as the mean number of connections in the shortest path between two individuals in the network. This is calculated among ‘reachable’ pairs of nodes or, in other words, pairs of nodes in the same component. The observed mean path length for the giraffe population was 3.06.

The mean degree of the networks suggests that on average, a given giraffe is connected to approximately five or six others. Knowledge of the degree of an individual could be important in predicting the probability that a disease will spread through a population. If the infected individual is highly connected, then the probability that the infection will spread in the network will be greater than if the individual has a low degree. The mean path length of reachable pairs in the network suggests that any two giraffes can be connected on average via 1–3 others. L is a global network measure and can be used to predict how quickly information and disease will spread through populations, with information and disease spreading more quickly between any two individuals with smaller values of L .

Finally, a network approach may allow us to identify the role of individuals in maintaining social structure. In the Laikipia study, certain individuals may provide important links in the social network. For example in Fig. 8.10, individuals 71 (an adult female), 73 (an adult female), 75 (a juvenile) and 76 (a young male) were important in joining smaller groups into one central social network.

Temporal dynamics are also becoming a key issue for many ecological and evolutionary questions. These dynamics include both changes in network topology and the ‘information’ flow through the network. Network analyses that ignore or do not adequately account for these temporal dynamics can result in inappropriate inferences (Blonder *et al.* 2012). This paper presents an overview of time-ordered networks, and reviews available methods and software.

Giraffe social networks

So far there have only been a handful of social network studies on giraffes. The earliest work of Shorrocks and Croft (2009) has already been mentioned in the previous section and illustrated in Fig. 8.10. This preliminary study was carried out in Laikipia, Kenya, on reticulated giraffe in 2006 and 2007. The study then moved to Namibia using a population of Angolan giraffe (Carter *et al.* 2013a,b) and, in addition, was able to use records from the prior giraffe work of Brand (2007), also carried out in Namibia. The two PhD programmes (Rachel Brand and Kerry Carter) formed a unique and valuable database and allowed subsequent analysis of giraffe social networks. The study was conducted in the Okaukuejo area of Etosha National Park, Namibia (19°10'S, 15°54'E). Data on group compositions was recorded for a total of 1531 giraffe groups during the two study periods: period 1 (P1) between May 2004 and January 2006 and period 2 (P2) between May 2009 and April 2010. Only giraffe groups for which at least 80% of group members were identified were included in the analyses (601 in P1 and 501 in P2). These groups included 301 individually identified females and 324 males, of all ages.

The approximately 1000 km² study area was divided into four 65 km road transects, which included tourist roads plus a number of staff-only access roads. This set of four transects was searched for giraffes once or twice per week on average. All observations were recorded from a vehicle and all driving was confined to roads, owing to Etosha National Park requirements. During transects, the identity, sex and age class of all individuals encountered were recorded. Age classes were categorised as juvenile (<18 months), subadult (18 months to <4 years) or adult (4+ years) (Le Pendu & Ciofolo 1999). These were adapted from the size criteria used in previous studies of giraffe (Dagg & Foster 1982; van der Jeugd & Prins 2000). A group was defined as one or more giraffes that were foraging or moving

together, but were not moving past each other in opposite directions. In fact, giraffe groups were usually self-defining as the distances between individuals were much less within a group compared to between groups. All individuals in a group were deemed to be associating and solitary giraffes were recorded as groups of one. Many female giraffes in the study area appeared to be sedentary and consistent in their spatial use among seasons (Carter & Brand, unpublished data), enabling data to be collected from these individuals throughout the year. Individual giraffes were identified using the unique coat patterns on both sides of their entire body and all giraffes sighted were entered into a database and given an identification number.

All identifications were carried out by matching photographs of individuals with those in the database by eye. During P2, the photographic identification software Wild-ID (Bolger *et al.* 2012) was used, with all matches done by Wild-ID also confirmed by eye. If Wild-ID did not match an individual with any giraffes in the database, the matching process with the entire catalogue of photos of individual giraffes was repeated by eye. The strength of association between pairs of giraffes was calculated using the half-weight index (HWI) already mentioned. In order to avoid 'autocorrelation', a common problem with spatial or temporal data (Lennon 2000), the period between sampling was set at 1 day as giraffes' group compositions have been reported to change almost daily (Moss 1976). Le Pendu *et al.* (2000) reported that giraffes seen on consecutive days had an approximately 50% chance of still being with a particular companion from the first day, on the second day. Therefore giraffes were expected to have adequate opportunity to change associates between days.

Comparison of the social structure of the Etosha population of giraffes between 2004–2005 and 2009–2010 showed that pairwise associations (HWIs) and various network structures were similar between the two study periods. The networks suggested a highly

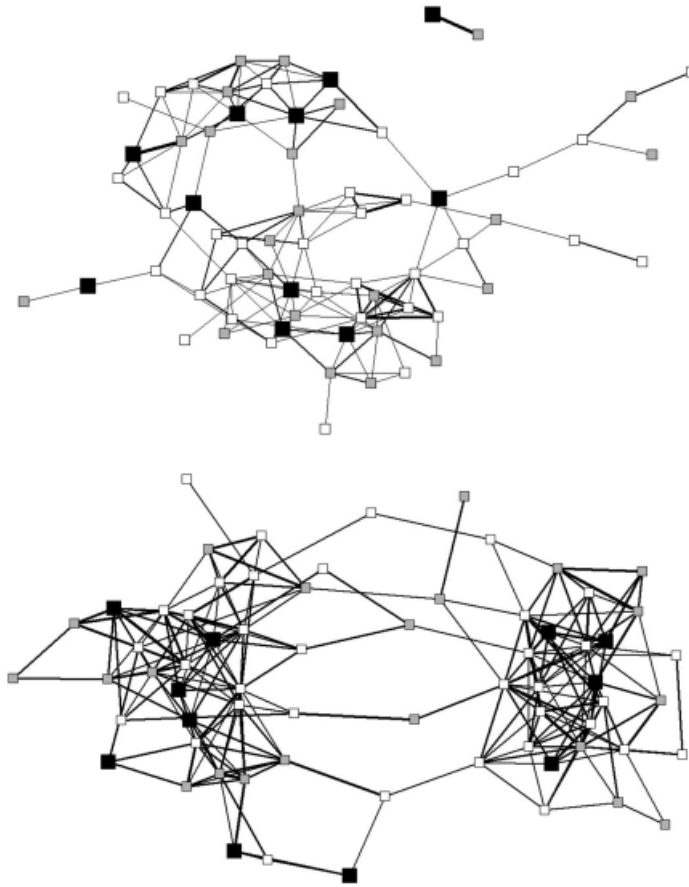


Fig. 8.11 Social networks of female giraffes sighted at least eight times in Etosha National Park during (*top*) period 1 (2004–2005, $n = 73$) and (*bottom*) period 2 (2009–2010, $n = 70$). Each square represents an individual giraffe included in the analysis. The thicknesses of the lines (ties) represent the strengths of association (HWI) between pairs. Black squares represent 11 younger females and grey squares represent 24 older females sighted at least eight times in both study periods. White squares represent females sighted at least eight times in a particular study period, but not both study periods. Only individuals and ties with HWIs ≥ 0.20 are shown. Source: Carter *et al.* (2013b). Reproduced with permission of Elsevier.

interconnected population with short path measures, that did not appear to differ between males and females (Fig. 8.11). Two adult age cohorts were used to investigate whether a female's age influenced her sociability. Analysis found that as younger females reached adulthood, they associated with greater numbers of females, whereas older adult females did not change their numbers of associates over time. In both study periods, all giraffes were con-

nected into one large network component, so that all individuals seen at least six times in the study population were highly interconnected, either directly or indirectly. The mean densities² of the networks were similar in both study periods (P1: 0.033; P2: 0.046). The network

²The density of a weighted network is calculated by dividing the sum of all HWIs by the total number of possible ties (Borgatti *et al.* 2002).

diameter³ indicated that no giraffe was more than four steps away from any other giraffe in the network, in either study period. The mean geodesic distances (path lengths) among giraffe pairs were small in both study periods (P1: 1.806; P2: 1.746), suggesting a cohesive network in which information or disease would quickly reach all giraffes. From the matrices of association, it was found that the giraffe network connections were sparse in the sense that in P1, only 24% and in P2, only 31% of possible pair-wise associations were observed.

Despite the Etosha giraffes exhibiting high levels of variability in grouping patterns, a property of higher fission-fusion species (Aureli *et al.* 2008; Carter *et al.* 2013a,b), the population's social network and pair-wise relationships were generally stable over time, except for male–male relationships. This temporal stability suggests that no major stochastic processes occurred in the study population between the two periods, enabling a somewhat stable population of interacting animals to coexist. The mosaic of tree and shrub communities in the area, with different flowering and fruiting phenologies, provides these giraffes with flushes of leaves, fruit and flowers to eat throughout the year (Brand 2007). It is therefore likely that such perennial food resources, coupled with permanent water resources, provide a sufficient level of environmental predictability throughout the year so that social relationships are not disrupted by seasonal movements out of the National Park. Female giraffes formed long-term associations with other females (over at least 6 years) whereas male–male giraffe associations in P1 did not appear to continue through to P2, even though 58 males were sighted in the

area during both study periods and some males exhibited weak, but long-term, relationships with females. This sex difference may be the result of the more sedentary nature of female giraffes, which form a stable population within an area (Berry 1978; Moss 1976; Pratt & Anderson 1982; van der Jeugd & Prins 2000), enabling repeated associations with the same individuals over time. Female giraffes of all age cohorts may benefit from associating with each other by obtaining knowledge about food availability, and adult females may obtain reproductive benefits from forming long-term preferred associations with other females. In contrast, male giraffes might incur reproductive costs if they associated with males of the same age cohort, which would be in direct reproductive competition. In addition, as male giraffes mature, their lifestyle changes considerably as they become increasingly solitary and adopt a roaming strategy to search for females (Bercovitch *et al.* 2006; Clutton-Brock 1989; Dagg & Foster 1982; Pratt & Anderson 1982, 1985). Therefore, the ranging patterns and reproductive strategies of males may vary with age (Brand 2007), thereby reducing the incentive for males of different age cohorts to associate for more than brief periods.

Despite these differences in sociability between giraffe sexes, the social network analysis did not find significant sex differences in any network metrics, suggesting that both males and females contributed equally to the network structure. However, there were fewer males than females in the final analyses, and no network metrics of male giraffes were significantly different from those calculated using randomly generated networks, suggesting either that all males were moving and associating randomly or that the male data did not have sufficient statistical power to distinguish the patterns in the data from random expectations.

Older females showed stability across both study periods in their mean HWIs and in their network strengths and numbers of associates,

³The diameter of a network is the largest geodesic distance (path length) between pairs in the network and provides a measure of the number of social connections between pairs that have the greatest separation (the size of the network) (Hanneman & Riddle 2005).

suggesting stability of relationships. The numbers of associates of the younger and older females did not differ between cohorts in P1 when the younger females were subadults. However, when the younger females matured to adults in P2 (4–8 years old), they had significantly more associates than the older females (>8 years old). The younger females also increased their network measure of strength in P2 yet the mean HWI of the younger females was similar in both study periods (P1: 0.048; P2: 0.065), suggesting that the increase in strength was due not to their stronger bonds with associates, but rather their associations with a greater number of females.

As immature females matured to young adults, it seems they became more gregarious and less selective in their choices of associates. This behaviour is perhaps akin to the dispersal phase of female horses, *Equus caballus*, that leave their natal group during their first oestrus and interact with various social groups and potential mates for a few years, before eventually choosing a group to which they become loyal (Linklater & Cameron 2009). Little is known about the dispersal of immature giraffes (but see Bercovitch & Berry 2010a). However, based on the variation in spatial overlap of relatives in the Etosha population, Carter *et al.* (2013a,b) suggest that female giraffes may show dispersal patterns similar to those of young females of many mammal species, with some females dispersing and others remaining philopatric within the same population (reviewed by Clutton-Brock & Lukas 2012). Despite the increase in the numbers of apparently weak relationships of maturing young females, both the younger and older females formed long-term associations with each other over a 6-year period. Younger or naive individuals may choose to associate with others that have a greater level of experience or knowledge, and noticeably, giraffe herds are often led by middle-aged or old females (Pratt & Anderson 1985).

In Carter *et al.* (2013a,b), 47 skin-biopsied females⁴ that were each seen at least 10 times during the Etosha study were used for closer investigation of the influences of genetic relatedness and spatial overlap on female–female relationships. The study population exhibited very low levels of genetic variation (35 alleles over 12 microsatellites), confirming previous genetic analysis of the same population using dung samples (Brand 2007). The mean $\pm$ SE number of alleles per locus was 2.92 ± 0.26 and the average observed heterozygosity $\pm$ SE was 0.459 ± 0.058 . The matrices of relatedness and percentages of spatial overlap between female pairs showed weak but significant positive correlations,⁵ suggesting that pairs inhabiting similar areas were often not closely related (Hemelrijk Rr tests ($\times 1000$): 95% kernel $r = 0.13$, $N = 47$, $P < 0.001$; 50% kernel $r = 0.16$, $N = 47$, $P < 0.001$). However, some pairs with high relatedness values showed a large proportion of spatial overlap, suggesting that at least some females showed natal site fidelity or that related females sometimes travelled together. There was a weak but significant positive correlation between relatedness and the proportion of time (HWI) that female pairs spent together (Hemelrijk Rr tests ($\times 1000$): $r = 0.14$, $N = 47$, $P < 0.001$), which was not greatly influenced by the amount of spatial overlap between pairs (partial Hemelrijk Rr tests ($\times 1000$) controlling for the percentage of spatial overlap between

⁴Skin biopsies were collected under the supervision of the Etosha National Park veterinarian using a remote biopsy dart delivery system (DanInject CO₂ powered).

⁵To investigate the relationships between the matrices of pair-wise association (HWI), genetic relatedness and spatial overlap of 47 female giraffes, full and partial Mantel tests were performed in SOCPROG 2.4 (Whitehead 2009) with 1000 permutations, using the Hemelrijk Rr test (Hemelrijk 1990) as in Bashaw *et al.* (2007) and Gero *et al.* (2008). The Hemelrijk Rr test ranks values in each row of the matrix and therefore controls for individual differences in sociability (Gero *et al.* 2008; Hemelrijk 1990).

pairs: 95% kernel $r = 0.09$, $N = 47$, $P = 0.014$; 50% kernel $r = 0.07$, $N = 47$, $P = 0.036$). This suggests that the amount of time related females spent together was not strongly affected by how much they overlapped spatially.

Giraffes demonstrate structured social patterns even though they do not exhibit complex co-operative behaviours. Therefore, giraffes may fit into route B (Aureli *et al.* 2008) which proposes the evolution of higher fission-fusion dynamics, in which fission-fusion groups develop from solitary rather than group-living animals. Fission-fusion species on this evolutionary path could shift towards more cohesive groups with greater social complexity and communication abilities if ecological conditions allowed (Aureli *et al.* 2008). Such transitions from solitary animals through to fluid group structures, and finally to stable groups, have also been suggested for models of primate social evolution (Shultz *et al.* 2011).

Examining the long-term data for Thornicroft's giraffe in South Luangwa, Zambia, Bercovitch and Berry (2012) found that giraffe herd composition was based upon long-term social associations that often reflected kinship, with close relatives significantly more likely than non-relatives to establish herds. Mother/offspring dyads had the strongest associations, which persisted for years. Within the study population, giraffe herds were composed of subsets of specific individuals. Considering all possible dyads of co-resident giraffe⁶ revealed an average dyadic association index of 0.097 (± 0.120 ; median = 0.055; range = 0.000–1.000). Both the

sex of a giraffe and kinship⁷ influenced the probability of herd formation and the strength of social associations. Only 11% of female–female dyads did not form a herd with each other, while 30% of male–male dyads were never observed together in a herd. Female–female dyads were significantly more likely to associate in a herd than were other sex combinations (Kruskal–Wallis test $\chi^2 = 57.25$, $n_1 = 189$ (male/male), $n_2 = 57$ (female/female), $n_3 = 244$ (male/female), $P < 0.001$), a finding that remained consistent when analysis was restricted to adult giraffe (Kruskal–Wallis test $\chi^2 = 53.14$, $P < 0.001$). *Post hoc* pair-wise comparisons showed significant differences between all possible pairings by sex (male/male versus female/female, Mann–Whitney $U = 83.0$, $P < 0.001$; female/female versus male/female, $U = 268.5$, $P < 0.001$; male/male versus male/female, $U = 3196.5$, $P = 0.032$). Kinship influenced the magnitude of the dyadic association index. While 57% (20/35) of kin dyads established strong social associations, that is, those >1 SD above the mean, only 7% of non-kin (33/455) had strong social associations ($\chi^2 = 83.86$, $df = 1$, $P < 0.001$). Although the number of years of overlap between pairs of giraffe did not significantly differ between kin and non-kin (7.47 ± 5.02 versus 7.59 ± 3.89 ; $U = 7552.5$, $P = 0.61$), the association index of kin was significantly greater than that of non-kin (0.327 ± 0.218 versus 0.105 ± 0.096 ; $U = 2325$, $P < 0.001$).

Giraffe therefore live in a complex society characterised by marked flexibility in herd size, with a large proportion of the variance in herd composition being due to kinship and sex. Both the Etosha giraffe study and the Luangwa giraffe study highlight the importance of long-term studies of wild giraffe populations, with known or genetically determined pedigrees.

⁶Because of the length of the data set (34 years), these authors could not subject the whole data to traditional social network analysis, because giraffes at year 1 were unable to associate with giraffes at year 34, not because of choice but because of death. Association was therefore only calculated for dyads around during the same time interval (called co-resident giraffes in their paper).

⁷Because individuals could be recognised by their pelage patterns, and these patterns do not change with age, mother–calf relationships could be followed over time.

Population regulation and size

What changes numbers? The simple answer to this question is, of course, birth, death, immigration and emigration. However, in their book *The Biology of African Savannas*, Shorrocks and Bates (2015) suggest that savannah ungulates are regulated through their food supply (what ecologists call 'bottom-up regulation'), determined ultimately by rainfall, rather than 'top-down regulation' via parasites and predators. Unfortunately, as they also point out, the only detailed, long-term population studies that suggest this directly are for wildebeest (Mduma *et al.* 1998, 1999), buffalo (Sinclair 1974, 1977) and zebra (Georgialis *et al.* 2003, 2011) in East Africa, although much of the excellent long-term work in Kruger NP, South Africa, suggests a similar conclusion. However, there is very suggestive evidence that this bottom-up regulation regulates other savannah ungulates, including giraffe. Therefore, below I will examine the evidence for the population regulation of savannah herbivores, by examining the few surveys that include several species, of which one is frequently the giraffe. In a book specifically on giraffes, the aim is to show that (1) these 'patterns' appear to be widespread among African savannah herbivores, including browsers, (2) where possible giraffe populations fit these patterns, and therefore (3) the problems of giraffe population regulation may not be unique to giraffes. Until we have long-term detailed studies of at least one giraffe population, like those of the Serengeti wildebeest and buffalo, this is all we have to inform our thoughts on population regulation. Intriguingly, the superb Luangwa NP data set, already mentioned many times, collected by Phil Berry and analysed so expertly by Fred Bercovitch, might just be sufficient for the task.

One of the important pieces of evidence for the role of food in regulating African savannah ungulate populations is the presence of a correlation between rainfall and ungulate biomass. What is more, this type of association usually

involves data points from many different savannah areas, suggesting that the relationship is not restricted to one particular African region. Coe *et al.* (1976) first showed that the total biomass of large savannah herbivores was positively correlated to mean annual rainfall. They used data from 20 wildlife areas of southern and eastern Africa, in which rainfall varied from less than 200 to more than 1100 mm per year. Since primary production is also positively related to mean annual rainfall in African savannah systems, Coe *et al.* (1976) considered that the herbivore biomass/rainfall relationship reflected the effects of water availability on the herbivores' food supply. This is the mechanism implicated in the wildebeest, buffalo and zebra case studies mentioned above.

However, the analysis reported by Coe *et al.* (1976) referred to large herbivore communities as a whole rather than to particular species. What is more, it was confined to what are sometimes called arid/eutrophic savannas (Huntley 1982), characterised by high soil nutrients, relatively low rainfall and a low biomass of high-quality vegetation supporting a high total biomass of large herbivores. Bell (1982) suggested that the herbivore biomass/rainfall relationship could be modified by soil nutrient status and that the positive correlation observed by Coe *et al.* (1976) only applied to savannas with high soil nutrient status (e.g. soils of volcanic origin). Bell (1982) suggested that for savannas with low nutrient soils, the relationship might even 'reverse' at high rainfall. Such savannas would include the miombo woodlands of south-central Africa whose pre-Cambrian rocks frequently weather into highly leached soils with low supplies of nutrients.

The biomass/rainfall relationship was therefore re-examined by East (1984) for individual species, with soil nutrient status being taken into consideration. These relationships are shown in Fig. 8.12. Three classes of soil nutrient status were distinguished following the broad classification used by Bell (1982): high (volcanics), medium (rift valley sediments) and

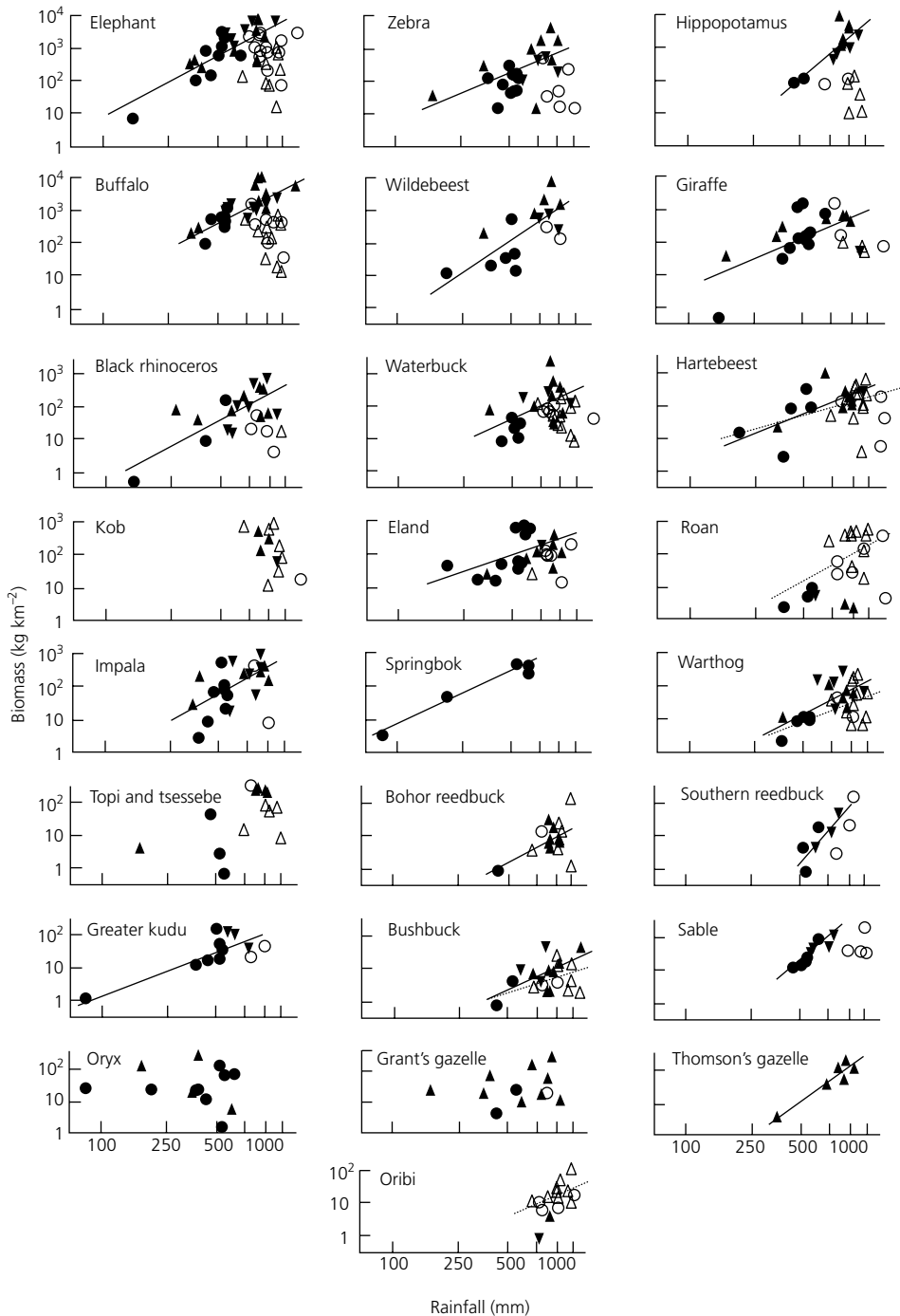


Fig. 8.12 Biomass/rainfall relationships for 25 herbivores species. Symbols indicate different nutrient status: high (▲), medium (▼), low with annual rainfall ≤ 700 mm (●), and low with annual rainfall > 700 mm in southern and eastern Africa (○) and West Africa (△). Closed symbols are arid/eutrophic savannahs and open circles are moist/dystrophic savannahs. Statistically significant regressions ($P < 0.05$) are indicated for arid/eutrophic savannahs as solid lines and for all savannahs in areas of low nutrient status as dotted lines. Source: East (1984). Reproduced with permission of John Wiley & Sons.

low (basement and basin sediments, granitic shields and Kalahari sands). Areas of low soil nutrient status were further subdivided into those with mean annual rainfalls of less than or equal to 700 mm and those greater than 700 mm. Least squares regression analysis, of log-transformed data, revealed significant relationships ($P \leq 0.05$) in arid/eutrophic savannahs for 19 out of 23 species for which sufficient data was available. Of the four remaining species, roan antelope had few data, topi/tsessebe had $P = 0.075$ and oryx and Grant's gazelle showed little association with rainfall. Notice that on soils of low nutrient status, some species (elephant, zebra, buffalo, giraffe, black rhinoceros and eland) do show a decline in biomass at rainfall greater than about 700 mm (open symbols in Fig. 8.12), although the regression for arid/eutrophic savannahs is still significant (solid line in Fig. 8.12). Significant relationships between biomass and rainfall are also seen in several species on poor nutrient soils (hartebeest, roan, warthog, bushbuck and oribi) (Fig. 8.12 dotted lines).

Although this survey of East (1984) is not a detailed examination of population processes, as were the studies on wildebeest, buffalo and zebra, nonetheless the evidence for a bottom-up regulation of savannah herbivores seems quite clear. What is more, there are other field studies, not as detailed as those of wildebeest and buffalo in the Serengeti, that enforce this view obtained from the relationships in Fig. 8.12. Macandza *et al.* (2014) conclude that although faecal nutrient levels for sable antelope appeared only marginally limiting under the conditions that prevailed during the study, malnutrition could have contributed to the population decline by sable during a persistently low-rainfall period. Studies on greater kudu populations in Kruger NP, over the period 1974–1984 (Owen-Smith 1990), also reveal the controlling influence of annual rainfall on population dynamics, mainly through calf survival, but also through yearling and adult survival. This is particularly interesting because the greater kudu is predominantly a browser, like

the giraffe, rather than a grazer like wildebeest and buffalo.

Mills *et al.* (1995) confirmed the strong positive influence of annual rainfall on changes in the abundance of kudu, as well as buffalo and waterbuck, in the central region of Kruger. Rainfall appears to determine primary production and this, in turn, regulates population size. This is a useful, general statement about the population regulation of savannah herbivores. It appears to apply to many African species, in many African savannahs. Of course, there will be interesting and instructive exceptions. In the Serengeti ecosystem, for example, populations of wildebeest and buffalo before 1960 were undoubtedly affected by rinderpest, an exotic disease. In many other parts of Africa, the interaction between the rinderpest virus and wild and domestic populations of ruminants was the principal factor that kept these populations at reduced levels for many years (Sinclair 1979). However, we should note that rinderpest may be exceptional as a disease, since it was exotic, not endemic, and may have had more devastating results as a consequence.

Many disease outbreaks seem to occur at the end of the dry season. This has been noted for rinderpest in the Serengeti (Sinclair 1979), rinderpest in Manyara (Prins 1996) and anthrax in Kruger NP (Pienaar 1961, 1967). This may imply that disease is often removing individuals that are already dying through starvation.

In Lake Manyara NP, both buffalo numbers and lion numbers are exceptionally high. Lion predation on buffalo is also quite significant, amounting to some 89% (Prins 1996). Many other authors have reported high predation rates in savannah ungulates, but it is difficult to know how to interpret these. This data often comes from carcasses that are found and identified as 'predator kills'. Predator kills are identified by seeing predators at a kill, seeing claw marks on kills without predators and even by hearing 'killing' noises the previous night. However, we know that even lions can obtain up to 15% of their diet by scavenging (Schaller 1972)

so that many of these 'predator kills' might be deaths from other causes. Predators pick out individuals in poor condition and this implies that predators are often removing individuals that are already dying through starvation and/or disease. In fact, many authors have questioned the role of predators in regulating savannah herbivores (Eloff 1984; Hirst 1969a; Mills 1984; Pienar 1969; Schaller 1972). Equivocal support for this view is provided by a removal exercise carried out in Kruger NP. In the late 1970s it was speculated that lion and spotted hyaena were responsible for the local decline of wildebeest and zebra populations (Smuts 1978). As a result, the largest systematic culling operation in Kruger's history took place. Over a 5-year period, 445 lions and 375 spotted hyaena were killed, but the reduction had no detectable influence on the population trends of the wildebeest and zebra (Whyte 1985). Unfortunately, the cull had no detectable influence on the lion and hyaena population either so the proposed regulatory effect of these two predators was still unclear.

Mills and Shenk (1992) present some evidence for the 'impact' of lion predation on wildebeest and zebra populations in the south east of Kruger NP. Using intensive observations, over a 4-year period, they estimated wildebeest, zebra and lion population size. They also estimated the number of 'killing' lions (females) and their individual annual kill rate (seven wildebeest and eight zebra). They used these two parameters to estimate the death rate of both prey species and, coupled with an estimate of prey fecundity, used these parameters in a simulation model. The model was then used to predict the predator numbers necessary to 'stabilise' the population, such that it showed little change over a 4-year period (like the wild prey populations). Unfortunately, there is no regulation in this model (no density dependence) and the delicate balance observed relies on the model makers. If fecundity, or kill rate, rose by as little as 10%, the population of prey simply went into exponential increase (or into exponential decline if they fell by 10%). The model demon-

strates that predation, if very high, can have an impact on prey, but not a regulating effect. There is an important difference between predation being an 'important source of mortality' and 'predation regulating populations' of savannah herbivores.

Quite recently, two excellent analyses of long-term population counts for savannah ungulates have claimed to show that predators influence population numbers. One of these was in the Kruger ecosystem of South Africa (Owen-Smith & Mason 2005; Owen-Smith *et al.* 2005) and the other was in the Serengeti-Mara ecosystem of East Africa (Sinclair *et al.* 2003). In both cases there is certainly something very interesting happening demographically, but whether this is caused by predation is debatable. In the Serengeti-Mara, Sinclair *et al.* suggest that a 'natural experiment' (Diamond 1986) has taken place. They suggest that in an area of the northern Serengeti, poaching and indiscriminate poisoning removed the majority of carnivores (lion, spotted hyaena and jackals) for an 8-year period (1980–1987), citing Sinclair (1995). However, there are no predator population numbers to confirm this, and what the Sinclair (1995) paper actually says is 'there is some circumstantial evidence that lions, which are the main predators in the area, disappeared: roar counts were considerably lower in the study area in 1990 compared to other parts of the Serengeti (Packer 1990)'. Notice that only lions are mentioned and the comparison is with 'other parts' at this time, not the northern area prior to this date.

In the contiguous Masai Mara Reserve predator populations are thought to have remained intact (Brotten & Said 1995). During the period of 'predator removal', five smaller-bodied species (<150 kg) – oribi (*Ourebia ourebia*), Thomson's gazelle (*Gazella thomsonii*), warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*) and topi (*Damaliscus lunatus jumela*) – increased markedly in density in the northern Serengeti (no predators) relative to their population in the Mara (predators present). These northern Serengeti populations declined once predators returned to the area, after 1987. In contrast, the abundance

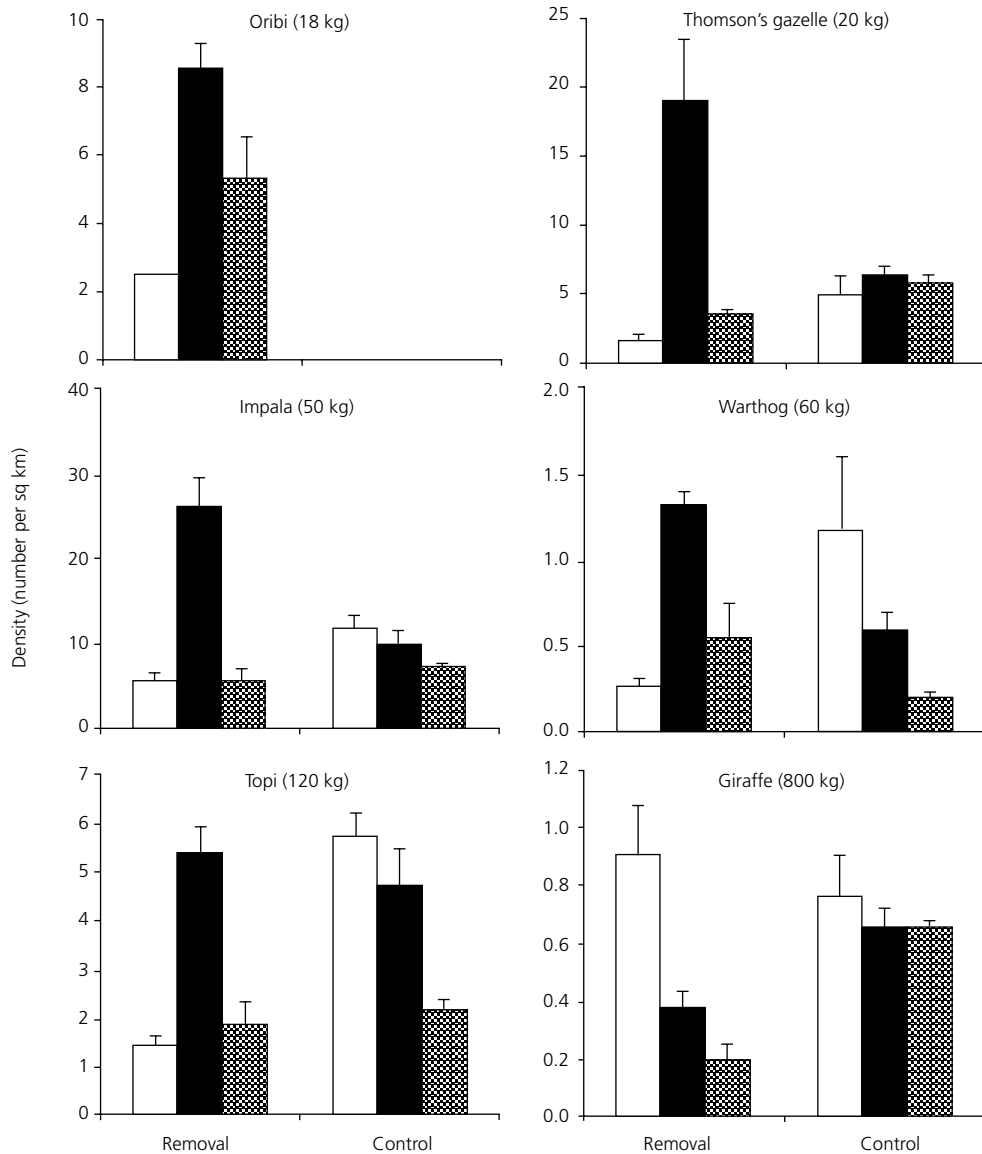


Fig. 8.13 Densities of six ungulates in a 'predator removal' area in northern Serengeti compared with an adjacent 'control' in the Mara Reserve. The period before predator removal (open bar) is for 1967–1980, the period of low predator numbers due to poaching (solid bar) is for 1981–1987, and the period after predators returned (shaded bar) included years from 1989 onwards. There is no control for oribi because they do not occur in the Mara. Error bars are one standard error. Source: Sinclair *et al.* (2003). Reproduced with permission of Nature Publishing Group.

of a large ungulate, the giraffe, did not increase during the predator removal period (Fig. 8.13). In fact, the density of giraffe declined over this period in the northern Serengeti, although not in

the Mara. Clearly, there is reason to think that something happened in the northern Serengeti during the period 1981–1987 that did not happen in the Mara. Was this due to a relaxation of

predation? I think the evidence is equivocal. The evidence for reduced predators (perhaps only lions) is circumstantial. However, we do know that buffalo numbers in this northern area of the Serengeti were seriously reduced due to poaching about this time. Sometime between 1976 and 1982, approximately 85% of buffalo (about 9000 animals) in northern Serengeti were removed by poachers (Dublin *et al.* 1990; Sinclair 1977). This did not happen in the Mara Reserve. So would this have affected all the small-bodied animals, except giraffe, through competition for grazing rather than size? We probably don't know but it's a possible scenario. Of course, prey size affects predation (Sinclair *et al.* 2003). For example, adult predation by lions accounts for virtually 100% of adult deaths for oribi (*Ourebia ourebia*), impala (*Aepyceros melampus*) and topi (*Damaliscus*

lunatus jumela) in the Serengeti ecosystem, while for giraffe it is about 5%, and for black rhinoceros (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibius*) and elephant (*Loxodonta africana*), it is virtually zero. Small prey have more predator species (Sinclair *et al.* 2003). Of course, large herbivores start their life smaller and therefore being a large adult might not protect the species from serious predation.

In conclusion, I feel the balance of evidence is for bottom-up regulation of African savannah herbivores, both grazers and browsers. The giraffe seems to fit this picture, with rainfall being an important influence on population numbers. Giraffe biomass in arid areas is always going to be lower.

We now move on to the final chapter on conservation.

CHAPTER 9

Conservation status and wildlife reserves

This chapter will look at the main dangers to giraffe survival as a species, in the wild. Giraffe tails are highly prized by many African cultures. The desire for good luck bracelets, fly whisks and thread for sewing or stringing beads has led people to kill the giraffe for its tail alone. Giraffes are easily killed and poaching, now more often for meat and hide, continues today. But is hunting and poaching the main reason for any decline in giraffe numbers? In order to make reasoned judgements on this topic, we require reliable estimates of giraffe numbers, not just 'perceived wisdom'. Are giraffes really decreasing? Is this a long-term event or is it a short-term result of climatic fluctuations? Of course, even 50 years ago Africa was a very different place when people like Foster and Kearney (1967) and Watson *et al.* (1969a) estimated giraffe numbers in East Africa. Less of the natural habitat had been removed and there were fewer people wanting land for agriculture. I won't go all the way back to those times in order to access changes, because although numbers of almost all African mammals have changed since then, there is no going back to those times. I will therefore use, as my baseline, the work by Rod East finally published in 1999.

Reasons for giraffe decline: what factors might be involved?

There are numerous reasons for the monitored wildlife decline in Africa, and I briefly outline these now. Population changes in wildlife, including giraffe, could be caused by:

- 1 predation by humans. This might include trophy hunting for skins and tails, hunting for meat or removing perceived 'pests'
- 2 predation by other predators, for example lions
- 3 disease, such as rinderpest or anthrax
- 4 competition with other browsers, for example kudu (resource competition for browse) or elephants (interference competition at waterholes or tree damage).
- 5 food shortage, via rainfall and other climatic changes
- 6 habitat loss, due to both agriculture and urbanisation
- 7 an environmental change affecting birth rate
- 8 a systematic error in undercounting of modern estimates of giraffe numbers.

Explanations (2), (3), (4) and (5) have already been examined in Chapter 7. Before looking at further evidence on this matter (beyond that already stated in Chapter 7), I would have probably predicted that (7) is possible but unlikely,

(2), (3) and (4) were not the reason, that (5) might be, that (1) and (6) are the traditional reasons given by conservationists, and that (8) needs checking by looking at census data rather than just perceptions. Of course, the reason for any decline does not have to be the same in all areas of Africa where giraffes are found. Giraffes could be seriously hunted in one area and have their habitat seriously reduced in another. A third area might have suffered severe drought, since desertification is a continuing problem in Africa, as elsewhere. Lastly, of course, numbers might well be rising in some areas and declining in others. So before we look at these possibilities further, what do the conservationists say about giraffe populations?

Numbers and population trends in 1998

The *Antelope Database 1998*, published by the IUCN, was the culmination of more than 15 years of painstaking efforts by Rod East. Between 1988 and 1990, he completed a country-by-country survey of sub-Saharan Africa which the IUCN published as Parts 1, 2 and 3 of *Antelopes: Global Survey and Regional Action Plans*. Five years later, East produced a series of Antelope Survey Updates, seven of which were published by the IUCN between August 1995 and January 1998. The whole series of reports and updates was finally capped by the production of the *Antelope Database 1998*, which was published a year later. Giraffes were included in this 'antelope' database and I use East's 1998 conclusions and predictions as the starting point for my examination of giraffe numbers.

These estimates of giraffe numbers (and the other larger herbivores mentioned in East's database) were obtained largely from aerial surveys (see Chapter 8), which underestimate numbers. East suggests, from published survey work at the time, that the correction factor for this undercounting will be $\times 1.1$ to $\times 2.5$ for the

larger species such as giraffe. In fact, in his table of estimates for giraffe populations in various African countries, he uses a correction factor of $\times 1.3$ to allow for this undercounting. Below I summarise his country-by-country¹ assessment of the status of the giraffe 18 years ago. I have précised the text and changed the tense to suit a summary of a past report. Otherwise the content is the same as in the original. I have added East's estimated numbers, in bold, at the end of each country section. In some cases this is simply shown as 'extinct' or 'vagrant'. I use East's nomenclature in my summary. That is, (1) western giraffe (*G. c. peralta*, *antiquorum*, *congoensis*), (2) Nubian/Rothschild's giraffe (*G. c. camelopardalis*, *rothschildi*), (3) reticulated giraffe (*G. c. reticulata*), (4) Masai giraffe (*G. c. tippelskirchi*), (5) Thornicroft's giraffe (*G. c. thornicrofti*), (6) southern giraffe (*G. c. giraffa*, *angolensis*, *infumata*, *capensis*, *wardi*). It is important to remember that what is said refers to 1998 and not the present day.

Mauritania

The western giraffe was originally found in south-eastern Mauritania, but was now extinct.

Population extinct.

Mali

The western giraffe originally occurred widely in central Mali, in the Sahel zone and northern savannah woodlands. However, by the time of East's report it had been exterminated over almost all of its former range by uncontrolled hunting for meat and hides. By the late 1980s, it had disappeared completely from Boucle du Baoule, Bafing and other areas in the west. In 1996, the country's last surviving giraffe population (<10 individuals) was found in the Ansongo-Menaka Partial Faunal Reserve on

¹East uses countries to summarise his conservation data because he argues that it is countries that will have, or not have, conservation policies. Present-day conservation bodies, such as the IUCN, tend to focus their estimates, or guesstimates, on subspecies.

the Niger border in the east. Rod East notes, however, that this reserve had been severely affected by incursions of livestock and the encroachment of human settlements. He also comments that although the Malian authorities took active steps in the early 1990s to protect the reserve's giraffe population, habitat degradation was likely to continue. **Population <10, declining.**

Niger

The western giraffe formerly occurred on the northern bank of the Niger River from the Mali border to south of Niamey, and in west-central Niger from Agadez southwards to the Zinder area near the Nigeria border. Uncontrolled hunting and the expansion of agriculture, along with the inevitable land clearance and desertification of the Sahel, had caused a major contraction in its range. By 1988 the country's estimated total giraffe population had decreased to <100, with the largest numbers in the Boboye region to the south of Niamey. East believed it was now extinct in west-central Niger. In July 1998, a population of 68 giraffes survived in the Koure area, 50–70 km east of Niamey. In addition, a few individuals from Mali occasionally wandered into Niger (Ayorou area), and a few individuals (possibly wanderers from Koure) were seen occasionally in the Gaya area near the Benin border. The Koure population increased with the birth of 16 young in 1998.² **Population 70, increasing.**

Senegal

Giraffes were originally found in the savannah woodlands and Sahel zone of central and eastern Senegal. However, they suffered severely from uncontrolled hunting, and by the late 1950s only a few survivors persisted in the east. By the time of East's report, they were extinct. Attempts to reintroduce the species to

Niokolo-Koba National Park from Cameroon in the early 1970s were unsuccessful. **Population extinct.**

Guinea

Formerly occurred in the savannahs of northern Guinea, but now extinct. **Population extinct.**

Burkina Faso

The Niger River had generally been regarded as an effective barrier to the extension of the giraffe's geographical range southwards into the apparently suitable savannah woodland habitat of Burkina Faso and adjoining countries such as Ivory Coast and Ghana, which lie to the south of the Niger. At the time of East's report, giraffe were known to occur as rare vagrants in Burkina Faso; for example, in the early 1980s a pair of giraffes wandered from the Mali–Niger border area south-westwards across the country and ended up near Nazinga Game Ranch in the south. **Population vagrant, declining.**

Nigeria

The western giraffe had been recorded in the past from scattered localities, mainly to the north of the Niger and Benue Rivers. In 1998 it was thought to be extinct except for occasional vagrants which wander into north-eastern Nigeria from Waza National Park in Cameroon. **Population extinct.**

Chad

Giraffes formerly occurred widely in central and southern Chad. However, they were eliminated from substantial parts of their former range by uncontrolled hunting and the effects of drought, but in 1998 survived quite widely in the south. The largest surviving population was in Zakouma National Park, where numbers had increased substantially with the rehabilitation of this park during the 1990s. At this time, they were also reappearing in Siniaka Minia Faunal Reserve to the west of Zakouma. Elsewhere populations were generally low and decreasing. **Population >830, increasing.**

²See later in this chapter for more details of this population which has already been mentioned in Chapter 7.

Cameroon

The western giraffe formerly occurred widely in the northern savannah woodlands and Sahel zone, but in 1998 was largely restricted to protected areas, i.e. national parks and hunting zones. Waza National Park protected an important population, with estimated numbers between 1000 and 2000 individuals over the period 1962–1994, although a 2-day census of wildlife around all of Waza's waterholes in May 1994 produced a lower population estimate of 340. The results of a 1995–1996 survey of Waza's wildlife populations was not yet available. Giraffes still occurred widely at lower densities in Bouba Ndjida, Benoue and Faro National Parks and the adjoining hunting zones of North Province, which is the species' natural southern limit in Cameroon. **Population 1360, stable.**

Central African Republic

The western giraffe originally occurred widely in its northern savannah woodlands, but it had been reduced to very low densities, or even eliminated, by poaching over a large part of its former range. The main surviving population, in Manovo-Gounda-St Floris National Park, numbered in the thousands until recently but by 1998 had been reduced to a few hundred. **Population >550, declining.**

Congo-Kinshasa

In 1998, giraffes were confined to the Garamba National Park area in the north east. East notes that although formerly widespread in the southern part of the park, giraffes now tended to use the peripheries of the park and the adjacent reserves, where woodland density had increased. This change was thought to be due to an increase in the elephant population reducing the woodland in the central area. While the Garamba giraffe population was not greatly poached, it was nevertheless more vulnerable at the edges of, and outside, the park. **Population 280, stable.**

Sudan

Giraffes formerly occurred widely in southern, central and north-eastern Sudan, with the Kordofan race (*antiquorum*) said to occur to the west of the Nile and Nubian/Rothschild's giraffe (*camelopardalis/rothschildi*) to the east. By 1998 they had been hunted to extinction over most/all of their former range in central and north-eastern regions. For example, the last herd in Dinder National Park was destroyed by poachers in 1985 and it no longer survived in Radom National Park. During the early to mid 1980s, Nubian/Rothschild's giraffes occurred in large numbers in parts of the south east. For example, there were estimated populations of 8770 in the 22,800sq km Boma National Park and 4530 in the 68,000sq km Jonglei Canal survey area. They still survived in significant numbers in the south east. For example, herds of up to 28 had been observed recently by UN pilots in eastern equatorial region. To the west of the Nile, the western (Kordofan) giraffe was reported to be scarce in the 1970s. By 1998 there was no recent information on this subspecies' status or continued occurrence in Sudan. **Population unknown, declining.**

Eritrea

The Nubian giraffe had formerly occurred in the south-western savannahs but was now extinct. **Population extinct.**

Ethiopia

Giraffes formerly occurred widely in the western and southern lowlands, with the Nubian giraffe (*camelopardalis*) in the west and south west and the reticulated giraffe (*reticulata*) in the south. A marked decrease in Ethiopia's giraffe population as a result of overhunting was evident by the early 1970s. By 1998 total numbers were thought to be no more than a few hundred and were probably continuing to decrease. By 1998 the Nubian giraffe survived in small, but declining numbers in Omo National Park-Tama Wildlife Reserve and perhaps elsewhere in the west and south west, for example, Gambella

National Park and the western lowlands. Much of this subspecies' former range had either been heavily encroached by settlement and cultivation (e.g. Gambella) or affected by military activity and insecurity. The species had disappeared from Mago National Park during the 1990s. The reticulated giraffe survived in small numbers in Borana and was reported by local people to occur in south-western Ogaden. **Population Nubian >160, declining; reticulated >140, stable/declining.**

Somalia

The reticulated giraffe had formerly occurred in the south, between the Juba River and the Kenya border. In the early 1980s, it survived locally within its former range but its numbers had been greatly reduced by poaching. By 1998 it survived in only a few areas, for example Bush Bush National Park, probably in declining numbers. **Population unknown, declining.**

Uganda

Most of Uganda's surviving population of Nubian/Rothschild's giraffe occurred in Murchison Falls National Park, where numbers were gradually increasing. Kidepo Valley National Park formerly supported the country's largest protected giraffe population, but this had decreased to a mere five animals by 1995. Three giraffe (one male, two females) were successfully translocated to Kidepo Valley from Lake Nakuru National Park in Kenya in 1997, in an attempt to promote the recovery of the Kidepo population. The only other giraffe population known to survive in Uganda comprised a very small number in Pian-Upe Game Reserve in the Karamoja region. **Population 145, stable/increasing.**

Kenya

In 1998, the reticulated giraffe still occurred widely within its historical range in northern Kenya, north of the Tana River and east of the Rift Valley. The bulk of the subspecies' population occurred on unprotected rangeland, particularly

in Wajir, Garissa and Marsabit districts. Relatively small numbers occurred in protected areas such as Marsabit and Meru National Parks and the privately owned Lewa Downs Wildlife Conservancy. East comments that while Kenya's population of reticulated giraffe appeared to be in reasonably good shape, large parts of its range in the north of the country were virtually unadministered and poaching was prevalent. Giraffe meat, hides and tail hair were valued commodities, and little could be done to protect giraffes outside parks and reserves if poaching pressures increased to high levels across northern Kenya. The Masai giraffe occurred widely in protected areas and unprotected rangeland in southern and eastern Kenya. The largest population occurred in Kajiado district, with major populations in other areas such as the Mara ranches, Tsavo National Park and surrounds, Laikipia³ and Tana River districts. The Tsavo population had decreased substantially in recent years. The Nubian/Rothschild's giraffe occurs in western Kenya, where naturally occurring giraffes are now rare. It has been introduced successfully to Lake Nakuru and Ruma National Parks. **Population Rothschild's >140, stable/increasing; reticulated >27,680, stable/declining; Masai 17,330, declining.**

Tanzania

The Masai giraffe remained widespread and common over substantial parts of its historical range, which included most of the country north of the Rufiji River, although it had disappeared from extensive areas of central and coastal Tanzania. Large populations survived in the Serengeti, Tarangire and Ruaha ecosystems, Moyowosi-Kigosi, Katavi-Rukwa and the northern sector of Selous Game Reserve. Most of these populations were thought to be stable but the Serengeti population, formerly the largest protected giraffe population in Africa, decreased from an estimated 8830 in

³In 16 years of working in Laikipia I have never seen Masai giraffe, only reticulated giraffe.

1989–1991 to 6170 in 1996, possibly because of poaching and/or disease. **Population 28,860, stable/declining.**

Rwanda

By 1998, the Masai giraffe did not occur naturally in Rwanda, but in 1986 six Masai giraffe from Kenya were introduced into the southern part of Akagera National Park. This population had increased to about 20 by 1994. East thought that it had probably been unaffected by recent invasions of cattle into the northern part of the park. **Population 20, stable/declining.**

Angola

Giraffe had formerly occurred in the mopane/acacia savannahs of southern Angola. In the late 1960s a few hundred were reported to survive in the Mupa National Park-Cafima area in the south west and the Mucosso area in the south east but by the early 1980s, they had largely disappeared from these areas. East believed it was almost certainly extinct in 1998. **Population extinct?**

Zambia

In 1998, Thornicroft's giraffe, which is endemic to the Luangwa Valley, was more numerous than at any time in the last 50 years. For example, the total population of this subspecies was estimated to be about 250 in the 1950s and 450 in the early 1980s. The bulk of the population occurred in Lupande Game Management Area and South Luangwa National Park. It appeared to be expanding its range northwards towards North Luangwa National Park. The giraffe was not subjected to illegal hunting in the Luangwa Valley and its numbers were thought to be regulated by environmental factors such as elephant density and the availability of browse. The southern giraffe survived in small numbers in Sioma Ngwezi National Park within its former range in the south west. This park had been severely affected by poaching for more than 20 years. **Population Thornicroft's 1160, stable; southern giraffe rare.**

Mozambique

Giraffe formerly occurred in southern Mozambique, mainly to the south of the Save River. By the early 1970s it had been eliminated from most of its former range, and the few surviving animals were restricted to the area between the Limpopo River and Kruger National Park on the South African border. East thought that by 1998 it may be extinct, but that it should return to Mozambique with the current rehabilitation of the wildlife areas of Gaza Province. **Population extinct?**

Namibia

Giraffe formerly occurred in the northern savannahs, extending into the semi-desert Kaokoland in the north west. In 1998 it still occupied a large part of its former range, mainly in protected areas (especially Etosha National Park) and on private farmland. The largest population on communal land was the unique desert giraffe population of Kaokoland. Its numbers and distribution are continuing to expand on private land in the northern farming districts. **Population 6690, increasing.**

Botswana

Giraffe formerly occurred widely in the savannahs of northern and central Botswana. In 1998 it still occupied a substantial part of its former range, with the largest numbers in the northern region. It was common in Chobe and Makgadikgadi-Nxai Pan National Parks and Moremi Game Reserve. It was widespread and locally common throughout the rest of the northern region, especially in and around the Okavango Delta. There was also a substantial population in Central Kgalagadi Game Reserve. **Population 11,700, stable/increasing.**

Zimbabwe

Giraffe formerly occurred widely in western and southern Zimbabwe, but was naturally absent from the Zambezi Valley and other areas in the east and north. It still occurred widely in wildlife areas within its former range, with the

major populations in Hwange National Park and adjoining areas of north-western Matabeleland, and on private conservancies and game ranches in the south-eastern Lowveld. **Population 5430, stable/increasing.**

South Africa

Giraffe was originally found mainly in the northern Lowveld and Bushveld. It had been eliminated from large parts of its former range by overhunting and the expansion of agriculture, but survived in Kruger National Park which in 1998 supported a major population. The giraffe had been reintroduced widely to protected areas and private land within its former range. It had also been introduced to extralimital areas, such as Hluhluwe-Umfolozi and other protected areas in KwaZulu-Natal and Double Drift Reserve in the Eastern Cape. **Population 7880, stable/increasing.**

Swaziland

East thought that the giraffe may have occurred formerly in northern Swaziland, to the north of the Nkomati River, but that any indigenous populations that might have existed were now extinct. Six animals from Namibia were introduced to Hlane Game Reserve in the 1970s but had never been bred up. A small population from the Kruger National Park area of South Africa had been bred from a mother-son union in Mlilwane Wildlife Sanctuary, and giraffe from South Africa had also been introduced to the privately owned Mkhaya, Mhlosinga and Mbuluzi Nature Reserves. **Population unknown.**

In conclusion, East suggests that total numbers of each 'subspecies' are of the following order:

- western giraffe: 3500 (decreasing)
- Nubian/Rothschild's giraffe: 500 in Uganda, Kenya and Ethiopia, plus unknown but probably larger numbers in Sudan (stable/increasing in Uganda and Kenya, decreasing elsewhere)
- reticulated giraffe: 36,000 (stable/decreasing)
- Masai giraffe: 60,000 (stable/decreasing)

- Thornicroft's giraffe: 1200 (stable)
- southern giraffe: 40,000 (increasing).

East estimated that the total population of the species in 1998 was approximately 141,000 (excluding the Sudanese population), including >50,000 in and around protected areas and >8000 on private land. East predicted that in the future the species' Red List status was unlikely to change as long as good populations continue to be effectively protected in a substantial number of parks and reserves and on private land. However, he also predicted that if present trends continued, the western and Nubian/Rothschild's giraffes and possibly also the reticulated subspecies would eventually be reduced to a few, small protected populations while the abundance of the southern giraffe would continue to increase. How correct was he?

Numbers and population trends in 2015

The most recent IUCN assessment (Fennessy & Brown 2010) available when this book went to press says that the giraffe is listed as Least Concern⁴ because the species remains widespread, with a total population probably numbering more than 100,000 individuals. However, they point out that a recent preliminary population estimate suggests a decline in the total population has taken place. This is perhaps not surprising. When in early 2015 I revised my book on African savannahs (Shorrocks & Bates 2015), and redrew all the distribution maps for the mammals, I realised that in just 6 years

⁴'Least Concern' (LC) is defined by the IUCN as 'as evaluated but not qualified for any other category', which is rather nebulous. Previously, in 1996, the IUCN had categorised giraffe as Lower Risk/conservation dependent (LR/cd). LR/cd was a higher risk category than LC. LR/cd is part of the IUCN 1994 Categories & Criteria (version 2.3), which is no longer used in evaluation of taxa, but persists in the IUCN Red List for taxa evaluated prior to 2001, when version 3.1 was first used.

(from the first edition) almost all had reduced their distribution and that their populations had become more fragmented. Giraffes are simply following the unfortunate trend in African wildlife. Fennessy and Brown (2010) do say that 'Some populations remain stable, or are even increasing [see later] but others are in a more precarious position ...'. In West Africa, the only surviving giraffes are a small population in south-western Niger (Boulet *et al.* 2004). This appears to be the only surviving wild population of the West African giraffe (*G. c. peralta*), since a small population observed in the Ansongo-Menaka Partial Faunal Reserve in Mali, on the border of Niger, is thought to be extinct. Fennessy and Brown (2010) say that 'Giraffe are still present in northern Cameroon, southern Chad, Central African Republic and in Garamba National Park in north-eastern Democratic Republic of Congo', although the reference they give is that of East (1999). There is limited information on the status of giraffe in Sudan, west of the Nile, where, the IUCN report says '... they were not recorded at all during the course of recent surveys ...'. It is known they still occur in the south east (in Boma National Park) (estimated 404) (Fay *et al.* 2007). In East and north-east Africa, giraffes still occur in relatively large numbers in northern Kenya, mainly outside protected areas, in south-western and southern Ethiopia, Somalia, and in small numbers in a few protected areas in Uganda. They are now thought to be extinct in Eritrea. They remain relatively widely distributed through southern Kenya and Tanzania. Of some concern is the status of Rothschild's giraffe, for which the only remaining naturally occurring population is in Murchison Falls National Park, Uganda (see later section for Kenya). The latest figure for Rothschild's giraffe is <1200) (IUCN GOSG Specialist Group 2016 Red List assessment, personal communication).

The 2010 IUCN (Fennessy & Brown 2010) report acknowledges that there is an isolated population of Thornicroft's giraffe in the Luangwa Valley (Zambia), but provides no numbers. Ciofolo and Pendu (2015) say it is

present in large numbers. Berry and Bercovitch (2015) suggest an estimate of between 500 and 600 individuals, and that numbers have been fairly stable over the last 50 years.

In southern Africa, giraffes are common both inside and outside a number of protected areas in Namibia, Botswana, Zimbabwe and South Africa. In Angola, they are thought to be extinct (Crawford-Cabralo & Veríssimo 2005).⁵ A few animals are reported to still survive in Sioma Ngwezi National Park in south-western Zambia, while in Mozambique, a few individuals still occur in the area adjacent to Kruger National Park. Giraffes have been introduced to Swaziland (Ciofolo & Pendu 2015) with stock from South Africa and Namibia. They have also been introduced to a number of reserves in KwaZulu-Natal and the Eastern Cape (Ciofolo & Pendu 2015).

The IUCN 2010 report singles out two subspecies with a higher risk (Endangered): the West African giraffe (ssp. *peralta*), with a total population of <200, and Rothschild's giraffe (ssp. *rothschildi*) with a total population of 'well below 2,500 mature individuals'.

Dobson (2015) quotes the latest figures for the nine subspecies as Angolan giraffe <15,000, Kordofan giraffe <2000, Nubian giraffe <650, South Africa (Cape) giraffe <17,000, West Africa giraffe ~400, reticulated giraffe <4700, Rothschild's giraffe <1100, Thornicroft's giraffe <550 and Masai giraffe ~37,000.

Examples of population change

Before looking at some examples of population change, I will examine three relevant topics that involve the basic reproductive rate (R_0). R_0 is the

⁵However, the Giraffe Conservation Foundation (GCF) says on its website that South African giraffe were introduced into Kissama NP and had increased to 20 by 2013. Other than these introduced giraffes, it is uncertain if giraffes occur elsewhere in Angola. There is some evidence that giraffes move across the Namibian/Angola border.

average number of offspring produced by an individual.⁶ It is usually calculated from a life table of age-specific female survival (l_x) and age-specific births (m_x). The relevant topics are therefore length of life (maximum x), age-specific death (l_x) and age-specific birth (m_x).

How long can giraffes live in the wild, that is, what is a reasonable estimate for maximum x ? Berry and Bercovitch (2012) used their extensive data on Thornicroft's giraffe to try and estimate this. Using lifetime data on male deaths and disappearances, combined with cross-sectional records on coat colour transformation, they concluded that the average age of death for male giraffes was approximately 16 years. The maximum for males was approximately 22 years. Females were estimated to have a maximum lifespan of about 28 years. I will therefore take this value of 28 as the final value of x for female giraffes. We therefore require values of our life table data until l_{28} and m_{28} . In fact, this value of x is similar to maximum ages estimated by Bristol Foster for two female Masai giraffe, from old photographs, of 24+ (Dagg & Foster 1982).⁷ Female giraffe usually produce only one young, and Bercovitch and Berry have estimated the interbirth interval for Thornicroft's giraffe as 677.7 ± 182.4 days, which is approximately 23 months. Therefore with this information, and assuming a sex ratio, at birth, of 1:1, we could predict an estimated value⁸ of $m_x = 0.25$. Leuthold and Leuthold (1978) also estimate these quantities for Masai giraffe in Tsavo National Park. They estimated

an average of 22.6 months between parturitions, which is close to that estimated by Bercovitch and Berry on a different subspecies, in a very different geographical area. They also estimate $m_x = 0.31$. Since the two average times between births, noted above, are in fact slight less than a year, a value of m_x slightly higher than the estimate of $\frac{1}{4}$ is probably more correct, and therefore I will use this value of 0.31 in the life tables.

However, females do not reproduce when young. The average age of first birth was 6.4 ± 0.7 years in Thornicroft's giraffe (Bercovitch & Berry 2009) although they state that females come into oestrus for the first time at about 4 years (Berry & Bercovitch 2013). This value of 4 years is also quoted by Hall-Martin and Skinner (1978) and I therefore assign values of $m_x = 0$ for the first 4 years.

Survival estimates (l_x) are difficult to find for giraffe. Often field workers record 'disappearance' rather than actual death (e.g. Leuthold & Leuthold 1978). Their values, obtained from 'resighting' individuals in photographs, give rather severe yearly 'survival' rates of 'adult and subadult' = 0.91, second year = 0.80 and first year = 0.33. The life table resulting from these values of l_x and m_x is shown in Table 9.1. The calculated value for R_0 is 0.71, which clearly suggests a declining population. Leuthold and Leuthold (1978) do in fact say 'Giraffe density in our study area is low compared with most other areas for which data is available'. This was in Tsavo between 1969 and 1971. They point out that Tsavo East lies in an area of relatively low and irregular rainfall and that as a consequence, food resources for herbivores are rather low and unpredictable. To make matters worse, they note that 'large tracts of original woodlands, the main sources of food for giraffes, have been transformed into more open habitats offering less woody vegetation, in terms of both volume and variety'. These vegetation changes had possibly been compounded by interference competition by elephants. So $R_0 = 0.77$ may well be near the truth for this Tsavo population, at this time.

⁶Note that R_0 for animals with discrete generations is also the net rate of increase. For continuous breeding species with overlapping generations, R_0 only has the function stated. The instantaneous rate of increase would be λ , or r .

⁷In fact, the difference between 24 and 28 may not be important since the last few values of x make very little difference to R_0 . In Table 9.1, for example, the first 15 years of a surviving female's reproductive life contributes 90% to total R_0 , and the last 7 years only 10%.

⁸One young every 2 years, therefore one female every 4 years = m_x of $\frac{1}{4}$.

Table 9.1 Life table for giraffe using the survival values from Leuthold and Leuthold 1978 (1st column). See text for the m_x values. The average number of offspring produced by an individual is only 0.77.

	Years	l_x	m_x	$l_x \cdot m_x$
	1	1.00	0	0.00
0.33	2	0.33	0	0.00
0.80	3	0.30	0	0.00
0.91	4	0.27	0	0.00
0.91	5	0.25	0.31	0.08
0.91	6	0.23	0.31	0.07
0.91	7	0.21	0.31	0.06
0.91	8	0.19	0.31	0.06
0.91	9	0.17	0.31	0.05
0.91	10	0.16	0.31	0.05
0.91	11	0.14	0.31	0.04
0.91	12	0.13	0.31	0.04
0.91	13	0.12	0.31	0.04
0.91	14	0.11	0.31	0.03
0.91	15	0.10	0.31	0.03
0.91	16	0.09	0.31	0.03
0.91	17	0.08	0.31	0.02
0.91	18	0.07	0.31	0.02
0.91	19	0.07	0.31	0.02
0.91	20	0.06	0.31	0.02
0.91	21	0.05	0.31	0.02
0.91	22	0.05	0.31	0.02
0.91	23	0.05	0.31	0.01
0.91	24	0.04	0.31	0.01
0.91	25	0.04	0.31	0.01
0.91	26	0.03	0.31	0.01
0.91	27	0.03	0.31	0.01
0.91	28	0.03	0.31	0.01
			R =	0.77

Life table data is also available for the Masai giraffe in the Serengeti National Park. Pellew (1983a,b,c) made extensive studies of several populations and these have been re-examined by Strauss *et al.* (2015) who computed population growth rates (λ) for several populations, using a Leslie matrix methodology (Caswell 2001). These are shown in Table 9.2. These figures are almost as bad as for Tsavo East in 1969–75 (λ would have been 0.97 for the Tsavo data). From these two detailed examples, Tsavo and Serengeti, giraffe populations do not appear to be in great

shape. It is interesting to note that a value of $m_x = 0.31$, as in the Tsavo table, is probably quite natural for giraffe. One young about every 22 months seems a reasonably estimate and it is hard to see how this might change drastically even with moderate food shortages (as was the case in Tsavo). For example, in my Tsavo XL spreadsheet, to get a value of $R_0 = 1.02$ requires $m_x = 0.41$, which implies a birth every 15 months. However, changing l_x does have a marked effect. For example, in my Tsavo XL spreadsheet, changing first year survival from 0.33 to 0.43 (a 30% increase) produces a value of $R_0 = 1$. Changing adult survival from 0.91 to 0.94 (a 3% increase) produces a value of $R_0 = 1.10$. Increasing both by just 3% produces $R_0 = 1.13$. So I would tentatively predict that mortality of young and/or adults is the key, not low birth. But what long-term population numbers do we have for giraffe? Here are some examples.

In Chapter 8 (Fig. 8.5), I detailed the estimated Masai giraffe numbers for the Masai Mara ecosystem in East Africa (Ottichilo *et al.* 2000). Census data for the years 1977–1997 presented by Ottichilo *et al.* (2000) suggests a 79% decline in giraffe numbers. In 2011 they reported that the situation had not changed, with losses estimated at 95% for giraffe. This looks like an approximately 14–18% yearly decline over 30 years. This is a severe decline, but interestingly not as severe as would have been predicted using the Tsavo data. In the Laikipia District of Kenya, Muchoki (2000) used aerial surveys of the Ewaso Nyiro Basin to estimate numbers for reticulated giraffe (Table 9.3). This represents over a 50% decline in the 20-year period. What is more, these figures may be overestimates since the IUCN survey (East 1999) gives a figure of only 1510 individuals for Laikipia. Bouché *et al.* (2009) carried out an aerial sample count in the Northern Central African Republic at the end of the dry season in June 2005, covering an area of 85,000 km² of complex landscape, including national parks and hunting areas. Their results showed a dramatic drop in wildlife populations compared to a survey done in 1985.

Table 9.2 Values of female survival (l_x), female births (m_x) and λ for populations of Masai giraffe in the Serengeti National Park. Data from Pellew (1983) and Strauss *et al.* (2015).

	Pellew (1975–1977)	Strauss <i>et al.</i> (2008–2010)	
	Serengeti (Seronera)	Serengeti (Seronera)	Serengeti (Kirawira)
l_x calves	0.42	0.57	0.67
l_x subadults	0.92	0.79	0.85
l_x adults	0.95	0.84	0.89
m_x	0.32	0.26–0.32	0.26–0.32
λ	1.03	0.92–0.93	0.99–1.00

Table 9.3 Estimated numbers for reticulated giraffe in Ewaso Nyiro Basin on Laikipia. Data from Muchoki (2000).

Year	Numbers
1977	6398
1990	5419
1994	2118
1997	2903

In the 20-year period, wildlife populations declined, on average, by 65%. They highlight poaching as a possible cause. The giraffe population went from an estimated 1750 (coefficient of variation (CV)= 22%) in 1985 to 535 (CV=42%) in 2005, a decline of 69%.

Not all estimates of giraffe populations show decline, however. Stoner *et al.* (2006) collated aerial census data collected during the late 1980s to early 2000s for large herbivore populations in eight large census zones in Tanzania. Although most ungulates, such as Thomson’s gazelle, Grant’s gazelle, hartebeest and zebra, declined, giraffe only declined in one area (Katavi NP). In the remaining seven areas (Burigi-Biharamulo GR, Ruaha NP/Kisigo GR/ Rungwa GR, Tarangire NP, Moyowosi-Kigosi GR, Selous GR, Serengeti NP, Ugalla GR), Masai giraffe numbers were viewed as stable.⁹

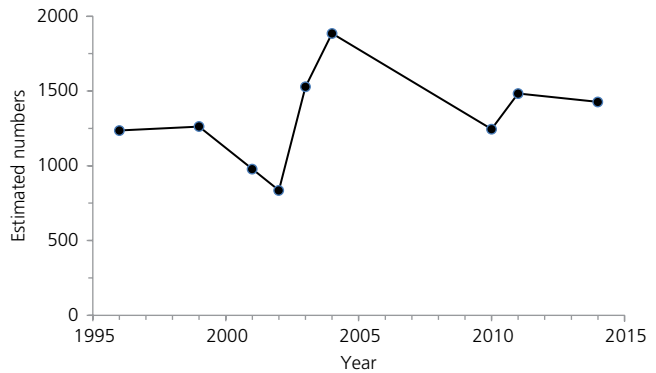
⁹Significant ($P < 0.05$) based on Mann–Whitney tests performed across grid cell densities at the start versus finish of 10 years.

Ogutu and Owen-Smith (2005), looking at data from Kruger NP in South Africa, record an increase in the giraffe population over the period 1965–1994. Although there are fluctuations, the population of giraffe increased from about 3000 to 5000 over this period. Chirima and Owen-Smith (2012), using the same aerial survey data, confirm this Kruger increase by noting that giraffe also expanded their range in the KNP. They occurred throughout the southern half of the KNP, and continued expanding their presence in the northern half of the KNP during the survey period¹⁰ (likelihood ratio statistic= 9.454, $df=3$, $P=0.024$), particularly in the far north ($z=6.907$, $P=0.001$). Chase (2013) and Chase *et al.* (2015) provide wildlife population estimates from aerial surveys of Chobe District and Chobe NP, Botswana (Fig. 9.1). Although the estimated numbers fluctuate and confidence intervals will be large, there is no evidence of decline in this period from 1996 to 2011.

One of the remarkable ‘rescues’ has been the increase in Niger’s population of West African giraffe from about 49 in 1996 to about 310 in 2011 (AWF 2013). This subspecies was once very widespread over northern Africa, including

¹⁰To establish whether the distribution of a species had changed significantly between the two periods, they dropped the three-way or two-way interaction terms from models incorporating region and period as factors, checking whether the omission brought about a significant reduction in model fit.

Fig. 9.1 Giraffe population estimates from eight dry season aerial surveys over Chobe District and Chobe NP, 1996–2011. Data by kind permission from Chase (2013) and Chase *et al.* (2015).



large parts of the Sahara Desert (Ciofolo 1995). Indeed, it is probably the giraffe carved into the stone surface shown in Fig. 1.2. At the end of the 19th century this subspecies was found in Gambia, Mauritania, Senegal, Mali, Nigeria and Niger, but now it is only found in Niger. Traditionally the cause is said to be hunting, increased agriculture with resultant deforestation and habitat loss and fragmentation (Ciofolo 1995; Suraud 2009). Interestingly, the rate of increase (λ or r) for this population between 1996 and 2009 appears to be extremely constant, resulting in exponential growth, since on a natural log plot the data fits a straight line (Fig. 9.2). Poaching largely stopped, there were development and education activities in the local communities, and there were no major droughts.

An assessment of the likely causes

In my list of possible causes at the beginning of this chapter, and in Chapter 7, I suggested that predators (2) and parasites (3) kill giraffe, but not in sufficient numbers to warrant us suspecting them as the reason for the decline in giraffe populations. In addition, we have to remember that both predators and parasites tend to kill individuals already weakened by other factors, such as starvation. In effect, they take individuals that are already dying. There is little evidence

for competition (4) as the downward driving force either, although elephants may sometimes exert exploitation competition at water-holes (see Chapter 7). There is some evidence that food shortage (5) might be important, via rainfall (see Chapter 7). There is no evidence for causes (7) and (8). However, poaching (1) is important. For example, in the Katavi-Rukwa ecosystem of western Tanzania, Martin and Caro (Caro 2008, 2010, 20011; Martin & Caro 2012), using 'snowballing techniques', interviewed known illegal hunters, which in turn led to further contacts. They estimated that the total number of illegal hunters operating out of an area adjacent to Katavi NP and Rukwa GR was 115 (mean = 10.5/village, SD = 3.8, range 2–16). These poachers enter the KNP and RGR frequently (mean = 4.6 (SD = 2.9) and 2.3 (SD = 2.1) trips/month in wet and dry seasons, respectively) for 1–7 days, sleep in the bush and hunt small game for the pot using muzzle loaders and sometimes dogs. The estimated number of giraffe killed per year was 98. Notice this is largely hunting for meat, although hides are also a marketable quantity. Strauss (2009) reports on the illegal hunting of giraffe in Tanzania. She noted that in 2007, 210 giraffes were slaughtered in a 10-month period in the West Kilimanjaro corridor in northern Tanzania. Hunters target giraffes for meat, hide and tail hair. A more recent motivation for hunting giraffes is the fallacy that consumption of giraffe bone marrow or brains can treat

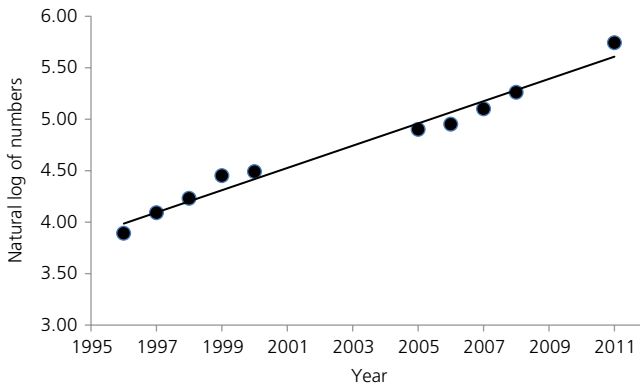


Fig. 9.2 Numbers of West African giraffe (logarithms to the base e) from 1995 to 2011. $R^2=0.97$, $F=3.11$, $P<0.0001$. Data from Surau (2009) and AWF (2013).

HIV/AIDS.¹¹ Giraffes are hunted with guns, dogs and snares and the choice of technique appears to vary by region.

In a more recent paper (Strauss *et al.* 2015), decline of giraffe in the Serengeti NP was examined using a 'decision table'. Three areas were examined: Seronera (central), Kirawira (west) and Bologonja (north). Densities of giraffe have declined in the Serengeti NP from about 1.5–2.5 individuals km^{-2} in the 1970s to around 0.3–0.4 giraffes km^{-2} in the 2000s. They looked at four possible causes of this decline: food supply, predation, parasites and poaching. Predation, by lions, was not large. The observed number of potential kills was only 0–6 per year, and there was no relationship between lion population size and giraffe kills. Low levels of parasite eggs were found in giraffe faeces. However, giraffe made up 45% of all snare reports. They suggest that lower recruitment (Table 9.2 m_x) may result from a reduction in diet quality, owing to the replacement of preferred trees with unpalatable species,¹² while decreased adult survival results from illegal harvesting. The latter appears to have had a greater impact on giraffe populations bordering the western and northern Serengeti. Bercovitch *et al.* (2014) reported that although

only a single confirmed case of direct illegal hunting of giraffe had been recorded in South Luangwa NP within the last few years, snaring of other animal species did kill giraffe. Recently, up to five giraffe snaring incidents per year have been reported. However, Bercovitch *et al.* (2014) conclude that although snaring and illegal hunting are potential threats to Thornicroft's giraffe, none of these human activities appears to be a major threat at present.

Habitat loss, and fragmentation, may be the most potent factor in the decline of giraffe, and most other African wildlife. Historically, habitat loss was the second most important reason for species decline, the first reason being species introduction. This is no longer the case. Globally in the 21st century, habitat loss is the primary cause of species extinction and decline. Riggio *et al.* (2013) note that in 1960, 11.9 million km^2 of savannah had fewer than 25 people per km^2 . The comparable area shrank to 9.7 million km^2 by 2000.

If 'bush meat' hunting and habitat degradation are the main causes of giraffe decline, what is the solution? Perhaps well-managed, conserved areas.

Protected areas as islands

Protected areas are an important tool for conservation. Ideally, they provide a refuge for wildlife. However, there are dangers and they

¹¹'Giraffe brains sold as HIV-AIDS cure hoax.' *Arusha Times*, 4–10 Sept 2004, 1.

¹²The unpalatable *Acacia robusta* and *Commiphora trochae* have replaced preferred species such as *Acacia senegal*.

must be managed, not simply left to manage themselves (Soulé *et al.* 1979). Protected areas are in fact 'islands' in a 'sea' of unfavourable habitat. This is the area of geographical ecology known as island biogeography. Larger islands contain more species. Although the specific relationship between number of species (S) and island area (A) can vary, it has traditionally been viewed as a power function:

$$S = cA^z$$

where c is a constant giving the number of species when A has a value of 1 (often specific to a taxon), and z encapsulates the relationship between species number and area. By taking logarithms of both sides of this 'species-area' equation, we get:

$$\log S = \log c + z \cdot \log A$$

That is, on a double-log plot ($\log S$ vs $\log A$), we see a straight line relationship between S and A , with z the slope of the line. The species–area relationship has been found to apply to a wide variety of taxonomic groups (e.g. plants, insects, fish, birds and mammals) and to a wide variety of types of island, including 'virtual' islands (e.g. lakes, mountain tops and protected areas). Sadly, intact African savannahs are increasingly only found in protected areas. Some of these protected areas are now under threat. Over 200 km² of Selous Game Reserve has been approved by the Tanzanian government for open pit uranium mining that will pollute the air, water and soil. Selous Game Reserve was designated a UNESCO World Heritage Site in 1982, but UNESCO permitted the Tanzanian government to redraw the park boundary so that the mine would not be within the park in order to quell international outrage. No doubt there will be more 'islands' threatened in the future.

As already stated, these national parks, game reserves and private reserves are increasingly 'islands' of relatively intact savannah fauna

and flora in a 'sea' of degraded habitat. What does island biogeography tell us about the numbers of species in these savannah islands? Before we consider African savannah islands specifically, it will be useful to examine briefly the reasons that have been put forward for the island species–area relationship. There have been two main themes, not necessarily unconnected. The original explanation, put forward by MacArthur and Wilson (1967), is known as the 'dynamic theory of island biogeography'. It proposed that species number (on an island) is a dynamic balance between two forces, immigration and extinction, and that these are in turn modified by island size and isolation. Figure 9.3 summarises the situation proposed by the dynamic theory. Two example immigration curves and two example extinction curves are shown. When an island is empty of species, any new arrival will contribute to the rate of immigration of new species. As species number on the island increases, the number of new species arriving will fall and in theory will reach zero when all the potential colonists have arrived. Islands that are near the source of the colonists (the mainland for real islands) and large islands (large targets) will have higher rates of immigration. Extinction rate will rise when there are more species on the island. This is thought to occur because with more species, competitive exclusion becomes more likely and the population sizes will, on average, be lower. This latter will make them more susceptible to chance extinction. A similar reasoning would suggest that smaller islands would have higher rates of extinction. For example, the rate of ungulate extinction in Tanzanian reserves correlates significantly with reserve area ($r = -0.93$, $P < 0.02$) (Newmark *et al.* 1994). Where the extinction curve and the immigration curve cross gives the dynamic equilibrium species number for a particular island. The theory therefore explains why smaller islands have fewer species and suggests that more isolated islands will also have fewer species.

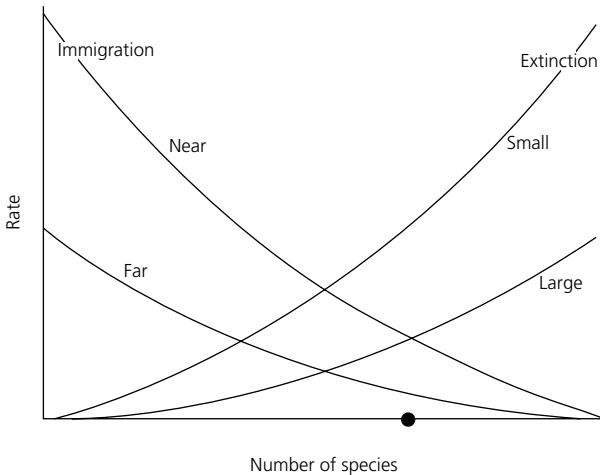


Fig. 9.3 MacArthur and Wilson's (1967) equilibrium theory of island biogeography showing the rate of immigration and extinction plotted against the number of resident species on the island. The predicted equilibrium between immigration and extinction, for a large island and a near source of colonists, is shown by the • symbol.

The second major theme put forward to explain the species–area relationship is that of habitat diversity (Lack 1969, 1976). Essentially, this states that larger islands will have more habitats and an area with more habitats will have more species. Of course, this explanation could be incorporated within the dynamic theory because habitat diversity, linked to island size, could be one of the reasons for the different extinction curves in Fig. 9.3.

One of the earliest attempts to apply island biogeography ideas to savannah reserves was that of Miller and Harris (1977). They examined 13 East African savannah parks and looked at the relationship between area and species number. Their results are shown in Fig. 9.4a. The fitted relationship is $S = 35A^{0.02}$. The regression is not significant ($F = 0.17$, $P = 0.69$). Soulé *et al.* (1979) published another set of data for 20 East African areas (Fig. 9.4b) in which the species–area relationship was $S = 18A^{0.13}$, and this time the regression was significant ($F = 24.67$, $P = 0.0001$). Soulé and colleagues make the point that without ‘active’ intervention, newly isolated communities such as national parks and other protected areas tend to show species loss. This is known as relaxation. In effect, the isolated area travels ‘down’ the species–area curve, from a higher point (larger area and more species) to a lower point (smaller area, fewer species).

As protected areas become smaller and more isolated, the rate of species loss increases because populations are smaller and therefore more prone to extinction and recolonisation is less likely because of intervening, unsuitable habitat. Of course, the traditional theory of island biogeography suggests that the species going extinct will be lost at random, whereas in reality certain species are more prone to extinction. These might include, for example, larger herbivores like giraffe with special habitat requirements. Smaller ‘islands’ will probably have fewer habitats and this will almost certainly be a major factor in the higher extinction rate found in smaller areas. Soulé and colleagues estimate that simply due to benign neglect, many of the smaller African savannah reserves would lose up to 10–20% of their large mammal species in 50 years following isolation. If this is true, it suggests that protected areas will either have to be enormous or that they will require active intervention to maintain an intact fauna.

In response to the Soulé predictions, Weston and Ssemakula (1981) published their own data set of the ungulate species in 19 eastern African parks and reserves (Fig. 9.4c). The species–area relationship was $S = 16A^{0.03}$ and the regression was not significant ($F = 0.93$, $P = 0.35$), suggesting that smaller parks do not have fewer species.

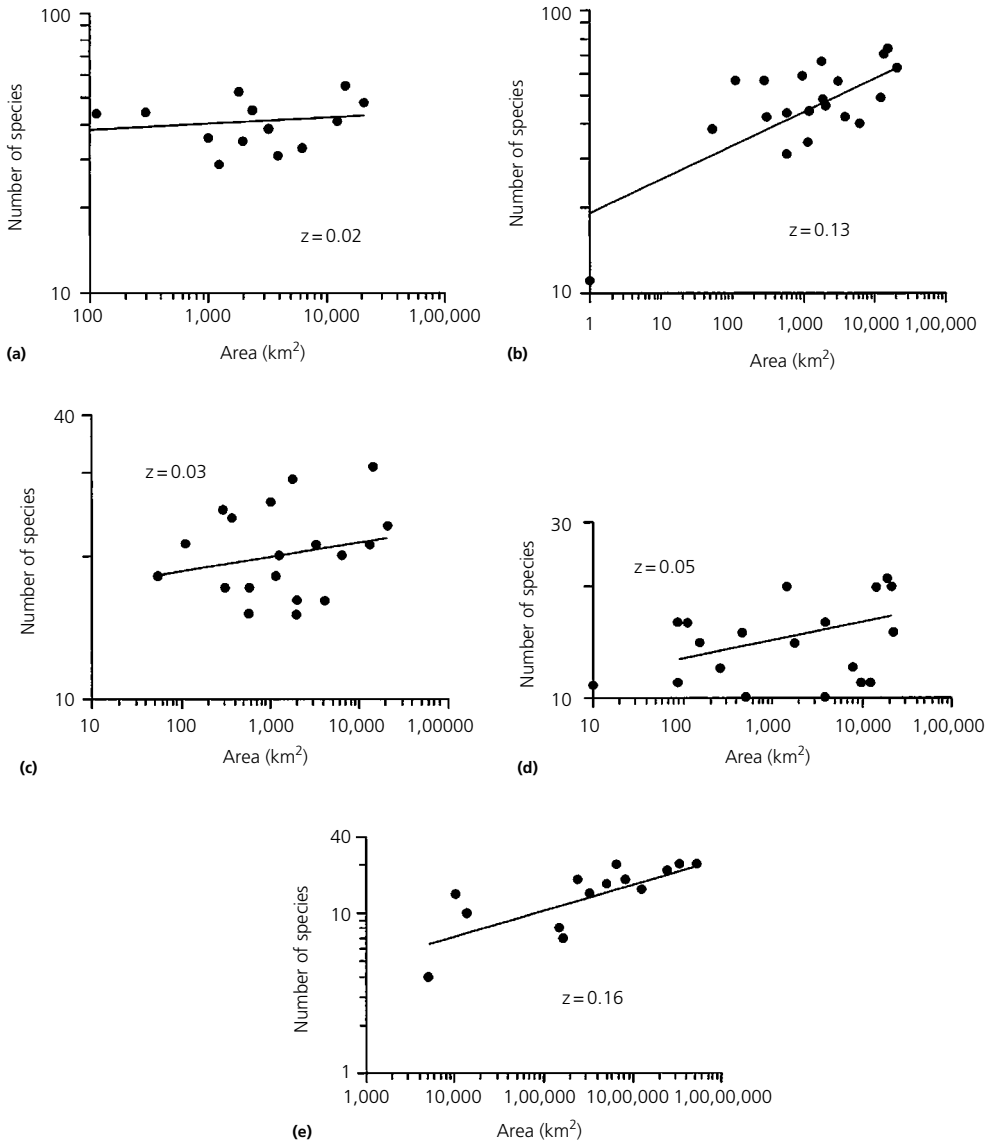


Fig. 9.4 Species–area graphs from five African savannah studies. Each graph shows the value of z for the data collected. (a) 'Large mammals' in 13 East African parks (Miller & Harris 1977). (b) 'Large mammals excluding insectivores, rodents, bats, and lagomorphs' in 20 East African areas (Soulé *et al.* 1979). (c) 'Ungulate species' in 19 East African parks and reserves (Western & Ssemakula 1981). (d) 'Large herbivores' in 20 African reserves (East 1983). (e) 'Bovids' in 14 Tanzanian ecological areas (Wragg 2002). The text in quote marks above indicates the species used, in the author's own words.

These authors are also more pessimistic about the survival of large mammal species in reserve islands. They believe that the extinction rates used by Soulé *et al.* were too high, having been

derived from studies on 'true' oceanic islands. Savannah reserves (at least in East Africa) continue to experience immigration because, Weston and Ssemakula claim, 'extensive livestock

ranching is not necessarily inimical to wildlife'. They conclude that the 'significance of island biogeography to the design of nature reserves is limited, at least in the savannahs'. Finally, a geographically more extensive data set was published by East (1983). He looked at 'large herbivores' (Fig. 9.4d). The species–area relationship was $S = 11A^{0.04}$ and the regression is not significant ($F = 1.81$, $P = 0.19$).

Of course, one of the problems here is that different studies seem to show both significant and non-significant species–area relationships. It's not easy to see why. There are differences in the data, even the sizes of the same protected areas are frequently different. In some cases the species chosen are difficult to discover because terms like 'large mammals' and 'large herbivores' are used. Back in 2002, Fiona Wragg and I collated a large data set from Tanzanian protected areas (Wragg 2002). This looked specifically at bovids because a specific species–area curve probably only exists for ecologically similar species. It also looked at 14 contiguous ecological areas, rather than the 24 gazetted parks for which we had data. So, for example, the 'Serengeti island' = Serengeti NP + Ngorongoro CA + Maswa GR + Masai Mara NR + Ikorongo-Grumeti GCA, and 'Selous island' = Selous GR + Mikumi NP. This is quite important since two adjacent reserves clearly constitute one 'island'. The data was compiled from a very extensive literature search (over 200 sources), and confirmed by using the IUCN African Antelope Database (East 1998). The species–area relationship is shown in Fig. 9.4e. The species–area relationship is $S = 2A^{0.16}$ and the regression is very significant ($F = 16.15$, $P = 0.002$). Although not shown, we also had data for the larger set of all ungulates. Here the species–area relationship is $S = 1.5A^{0.19}$ and the regression is again very significant ($F = 14.73$, $P = 0.002$). Both these results suggest that there is a species–area relationship for both bovids and all ungulates, at least in Tanzania, indicating that the kind of effect suggested by Soulé *et al.* (1979) might occur for these savannah

species. It should be noted that none of our protected areas had the full complement of Tanzanian bovid species (35). Extrapolating Fig. 9.4e until $S = 35$ suggests that an area of more than 200 million km² would be needed to preserve this number of species. In other words, an area larger than Tanzania. This suggests strongly that protected areas cannot be run on the principle of 'benign neglect'. That is, they cannot simply be established and left. Even in the largest protected areas such as the Serengeti complex and Selous complex in Tanzania, or the Kruger ecosystem in southern Africa, species will be absent or eventually lost naturally, even without the added burden of poaching. Intervention and management are required as illustrated below.

One of the main problems with these virtual islands we call national parks is the fragmentation that inevitably occurs (Galvin *et al.* 2007). As noted above, small islands 'relax' over time and lose species. In addition, the prevention of migration between these island reserves can be crucial. Many biologists believe that the re-establishment of ancient migration routes is the key to the survival of African wildlife. In 2006 an international agreement was signed that will create the Kavango Zambezi (KAZA) Transfrontier Conservation Area. KAZA will link together 36 national parks located in Angola, Botswana, Namibia, Zambia and Zimbabwe. This will be the largest wildlife island on the African continent composed of about 440,000 km². The first phase of the establishment of Greater Limpopo Transfrontier Park involved removal of a fence between the eastern side of Kruger National Park, South Africa, and Limpopo National Park located in Mozambique. Following the removal of the fence, animals from Kruger NP were able to migrate into Mozambique that was depleted of wildlife due to the past civil war. However, the negative trade-off of fence removal was the significant rise in poaching within Kruger NP that even the South African army and the use of a drone cannot seem to control. Money obtained from

poaching is helping to fund African terrorist groups, making this a global concern.

Protected areas for giraffe

Giraffe now largely inhabit protected areas, although large areas of 'semi-protected' ranch land like Laikipia, in Kenya, still host populations of giraffe.¹³ How does real-life island biogeography map onto the theory in the section above? I will look briefly at one or two examples.

When Lydekker (1904) first described Rothschild's giraffe, the subspecies inhabited the region from the Rift Valley of west-central Kenya, across Uganda to the River Nile and northward into southern Sudan. At the present time, habitat fragmentation is thought to have confined the subspecies to 12 'populations' in 12 conservation islands. The Kenyan populations appear to have been derived from a single, endemic population dispersed when the defunct Soi army base, located in far western Kenya, near Eldoret, was opened for resettlement in the late 1970s. According to the latest report by the Giraffe Research and Conservation Trust (2015),¹⁴ seven of these Kenyan islands contain a total of only 320 Rothschild's giraffe, established by direct counts. They were unable to verify the survival, or size, of the other five populations. The most recent estimate for these five was from 2010 and totalled fewer than 90 individuals. In fact, many of the so-called populations that were counted were very small and little more than 'groups' in zoological gardens (Ruko Conservancy 9; Giraffe Centre Nairobi 10). Ruma NP (68), Lake Nakuru NP (89), Soysambu Conservancy (78), Kiglio Conservancy (32) and Mwea NR (34) had the largest populations.

Brenneman *et al.* (2009) looked at the population in Lake Nakuru NP where, they report, there had been a rapid decline in numbers from 153 individuals (1995) to 62 individuals (2002).¹⁵ In 2002 there were three main concerns. The first was a possible food shortage created by the observed decline in preferred browse, *Acacia xanthophloea*. The second was lions preferentially preying on juvenile giraffe, and the third was a possible genetic effect from inbreeding depression. Brenneman *et al.* (2009) carried out molecular analysis on the Lake Nakuru population and found little evidence for inbreeding depression. The inbreeding estimator (F_{is})¹⁶ of 0.044 indicates only a 3% chance that two alleles in an individual were transmitted from a common ancestor (Kuehn *et al.* 2003), diffusing the argument for inbreeding depression. Brenneman *et al.* (2009) suggest that the 1994 El Niño-induced drought (rainfall in the Rift Valley lake systems fell by roughly half per year) (Ngaira 2006) reduced the regrowth ability of acacia, and may have contributed to the giraffe decline. They point out that under free-ranging conditions, giraffe would have had the opportunity to migrate into other areas of the Rift Valley. This is clearly one of the problems of a conservation island and the variable carrying capacity of small reserves must be appreciated by managers. Unfortunately, fragmentation is a problem for many giraffe populations in Africa and a clear danger. Without natural migration between patches, regional conservationists should practise unnatural movement, by translocation.

Moving individual giraffe

There are two reasons for re-introductions: (1) reintroduction of extinct populations to an area, and (2) introduction to new areas, usually

¹³www.laikipia.org/

¹⁴The Trust was founded by Zoe Muller to help in the conservation of the Rothschild's giraffe. See <http://ptes.org/wp-content/uploads/2015/09/Kenya-giraffes-project-update.pdf> for the report and <http://giraffetrust.org/> for the Trust.

¹⁵Clearly there has been an increase in the last 13 years.

¹⁶Introduced by S. Wright in 1931.

for commercial operations and private game reserves. Of course, (2) is important not only for giraffes and other wildlife but for Africans. The desire of overseas tourists to experience African wildlife, in its natural habitat, has resulted in Africa having one of the strongest tourist growth markets, with most destinations showing consistently above average increases in arrivals and receipts. Between 2000 and 2005, international tourist arrivals to Africa increased from 28 million to nearly 40 million, an average growth of 5.6% a year, compared to a worldwide 3.1% a year. In the same period, Africa's international tourism receipts doubled from US\$10.5 billion to US\$21.3 billion. Total travel and tourist revenues for the whole of Africa were expected to generate \$73.6 billion of GDP in 2005, equivalent to 8.8% of the regional economy. The tourist sector also provided 3,877,200 jobs directly and a total of 10,647,000 jobs indirectly in 2005, or 6.8% of all employment in sub-Saharan Africa. According to UNWTO figures for 2005, the number of visitors to sub-Saharan Africa from outside the region increased 13%, to 23.1 million. The most rapid growth was recorded in Kenya, where the number of visitors increased 26% on 2004, and Mozambique, where the number of visitors increased a massive 37%. Many of the African countries that support large areas of savannah habitat are high on the tourist list.

Most of this tourism is due to wildlife, and interest in African wildlife centres on savannah ecosystems with their charismatic large herbivores, including giraffe, and carnivores. In Botswana it is estimated that wildlife viewing accounted for about half of the total overseas' tourist expenditure and generated up to \$3 million income for the government in 1990. About half of this was from entry fees and about a fifth from tax revenues (Modise 1990). In Kenya, in 1995, about 70% of the tourist income (\$500 million) could be attributed to wildlife tourism, and government revenues from this were in excess of \$20 million (Republic of Kenya 1996). Key wildlife species are especially highly valued.

For example, in Kenya the net global returns to the 1.5 million wildebeest of the Masai Mara National Reserve have been estimated at between \$125 and \$150 per animal per year (Norton-Griffiths 1995). In Amboseli National Park the viewing value of a lion has been estimated to be in excess of \$0.5 million (Thresher 1981) and the flamingos of Lake Nakuru National Park had an annual tourist value of between \$3 million and \$5 million (Earnshaw & Emerton 2000).

If wildlife is worth so much, via tourism, isn't this a way to ensure that wildlife is protected? Isn't it an investment worth protecting for its financial return, in addition to its aesthetic and scientific value? The answer is yes. But the financial returns must filter down to the local farmers, ranchers, hunters and poachers who would otherwise see a better profit in the demise of wildlife.

However, it has long been recognised that there are factors to consider when moving giraffe (or any mammal) to a new area (Hall-Martin & Graff 1978). These are (1) were giraffe present in the area in recent memory, (2) is there appropriate browse and water, (3) where will the animals come from, i.e. what subspecies will be used, and (4) are there remains of a different subspecies still living there or near? A population viability analysis (PVA) is essential for determining (2). This is a species-specific method of risk assessment frequently used in conservation biology. It brings together species characteristics and environmental variability to forecast population health and extinction risk, thus ensuring that the population of a species is self-sustaining over the long term. Such an analysis has been carried out for the West African giraffe (Desbiez & Leus 2009). A Vortex (v9.92) simulation model of the giraffe population, using Monte Carlo simulations, was used to predict likely outcomes under different scenarios. Because of stochastic events incorporated into the model (such as environmental variability), each model run gives slightly different predictions. Each scenario was therefore iterated 500 times.

The authors of this PVA report for the West African giraffe suggest the following: (1) monitor the environment closely to detect catastrophes early, so they can be mitigated, (2) maintain a core population at all cost, (3) enable giraffe to disperse, (4) establish additional populations, and (5) monitor the rate of habitat loss. Clearly (2), (3) and (4) are closely linked and habitat loss is again prominent.

Conclusions

Numbers as such are not a worry, apart from very small populations susceptible to stochastic perturbations. Trend is more important. Small populations are always vulnerable, so the Niger giraffes are not secure. Thornicroft's is not so small as to be influenced by stochastic events and appears to be stable. Other subspecies (with modest populations) are declining and therefore there is a worry, because continued decline will bring them into the small population zone of eventual extinction (Gilpin & Soulé 1986).

Small populations have a number of problems. First there are demographic effects, where the effect of random variation in reproduction and mortality rates is much higher for small populations than large ones. Random variation in demographic rates will cause a small population to fluctuate randomly in size and the smaller the population, the greater the probability that fluctuations will lead to extinction. For example, the probability that all offspring in a generation will be of the same sex (assuming an equal sex ratio) is $1/2^{n-1}$. With a 'population' of three individuals, the probability of them all being the same sex is 0.25. For 20 individuals, this becomes 0.000000048.¹⁷ Annual variation in environmental factors such as rainfall and temperature can produce 'good' and 'bad' years when birth rates and death rates are 'good' or

'bad'. These demographic fluctuations will again be more severe for small populations.

A third problem for small populations is genetic consequences. Conservationists are frequently concerned about a loss of genetic variation in small populations. There are two issues. Reduction of fitness caused by the unmasking of recessive deleterious alleles (Lande 1994; Lynch *et al.* 1995), through increased homozygosity and/or reduced allozyme variability (Brock & White 1992; Pray *et al.* 1994; Vrijenhoek 1994), that is, the number of different alleles at the same genetic locus. There are two mechanisms operating in small populations that influence these two types of genetic variation: 'genetic drift' and 'inbreeding' (non-random mating). Drift is when, by chance, deleterious alleles become more frequent and are 'fixed' in a population. Any allele, deleterious, beneficial or neutral, is more likely to be lost from a small population's gene pool than a large one. Basically, the problem with either inbreeding or drift is that recessive deleterious alleles become homozygous and 'visible', and/or a population loses genetic variation and the ability to adapt/evolve to changing conditions.

A related topic is that of the effective population size (Wright 1931). This is almost always lower than the actual arithmetic mean population size. It is affected by variance in reproductive success, non-equal sex ratios and variation in population size. For example, if a population of giraffes, say 30, has only 10 females, and only half of these females reproduce, then the effective population size is much lower than the observed population of 30. If this population of 30 had estimated numbers of 30, 28, 28, 30, 32, 32 over a series of 6 years then the arithmetic mean of 30 is a realistic estimate of that population. However, if the past years' numbers had been 30, 10, 10, 15, 20, 30 then it is the harmonic mean that better represents this population (16) and its predicted genetic make-up. This is less than the arithmetic mean (19) of the population size. The harmonic mean tends to be dominated by the smallest bottleneck that the population goes through.

¹⁷Although a biased sex ratio is more likely and will have an effect on the 'effective population size'.

Examples of genetic consequences that have happened in two inbred populations that have gone through bottlenecks are cheetahs, who suffer with low infant survivability and a decrease in birth rates, and northern elephant seals, who have had cranial bone structure changes to the lower mandibular tooth row. The wolves on Isle Royale, a population restricted to the island in Lake Superior, have bone malformations in the vertebral column in the lumbosacral region. These wolves also have syndactyly, which is the fusion of soft tissue between the toes of the front feet. I'm not aware of any published reports of similar consequences for small giraffe populations, but people may not have looked.

I will conclude this chapter, and this book, by using a paragraph from East's 1998 summary of the state of antelope species, replacing the word 'antelope' that he used by the word 'giraffe' and adding 'sub' to species. It's perhaps salutary that 18 years later the same words are still relevant.

Africa's wildlife faces an uncertain future. Rapid growth of human populations and expansion of human activities is accelerating the destruction of wildlife populations and their habitats. In this situation, the goal for international giraffe conservation policy is to ensure the long-term survival of all giraffe subspecies by maintaining as many viable populations as possible of each subspecies in as wide a range of its habitats as are practical. Key words in this goal are 'possible' and 'practical'. To succeed, giraffe conservation must not be an end in itself, but part of an overall environmental and biodiversity conservation strategy which takes full account of, and is integrated with, human development needs.

Conservation of giraffe therefore requires preservation of as many areas as possible of suitable habitat sufficiently large to support healthy populations, and restriction of offtake levels as necessary within these areas to enable viable populations to persist. This can include a range of land-use options, from strictly protected national parks and reserves where consumptive use of wildlife is not permitted, to areas of natural habitat which are managed for sustainable utilisation, e.g. through trophy and/or meat hunting, as part of multiple resource use systems.

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