

WILDLIFE

Destruction, Conservation and Biodiversity

John D. Harris
Paul L. Brown
Editors



Wildlife Protection, Destruction and Extinction Series

NOVA

WILDLIFE PROTECTION, DESTRUCTION AND EXTINCTION SERIES

WILDLIFE: DESTRUCTION, CONSERVATION AND BIODIVERSITY

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WILDLIFE: DESTRUCTION, CONSERVATION AND BIODIVERSITY

**JOHN D. HARRIS
AND
PAUL L. BROWN
EDITORS**

Nova Science Publishers, Inc.
New York

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LIBRARY OF CONGRESS CATALOGING-IN-PUBLICATION DATA

Wildlife : destruction, conservation, and biodiversity / [editors] ,John D. Harris and Paul L. Brown.

p. cm.

Includes index.

ISBN 978-1-61728-599-8 (E-Book)

1. Endangered species. 2. Nature conservation. 3. Nature--Effect of human beings on. I. Harris, John D., 1960- II. Brown, Paul L., 1958-

QH75.W528 2009

591.72'7--dc22

2009000171

Published by Nova Science Publishers, Inc. ✦ New York

CONTENTS

Preface	vii
RESEARCH AND REVIEW STUDIES	1
Chapter 1 Forest Ecosystems and Zoonoses <i>Nenad Turk, Josip Margaletic and Alemka Markotić</i>	3
Chapter 2 Contraction and Status of Maasai Lands as Wildlife Dispersal Areas and Implications for Wildlife Conservation in Amboseli Ecosystem, Kenya <i>Moses Makonjio Okello and Katie Grasty</i>	49
Chapter 3 Conservation During Conflict: Strategic Planning to Deal with War in Sub-Saharan Africa <i>Stephanie Prevost and Andrew T. Smith</i>	97
Chapter 4 Ecology of Soil Seed Bank in Conservation and Restoration of Endangered Plants <i>Yukio Honda</i>	111
Chapter 5 Mathematical Models of Diseases Spreading in Symbiotic Communities <i>Mainul Haque and Ezio Venturino</i>	135
Chapter 6 Effects of Chemical Contaminants on Wildlife: Identification of Biomarkers in a Sentinel Species <i>G.L. Poletta, A. Larriera, P. Siroski, M.D. Mudry and E. Kleinsorge</i>	181
Chapter 7 Evidence of Antimicrobial Resistance in Eurasian Otter (<i>Lutra</i> <i>Lutra</i> Linnaeus, 1758) Fecal Bacteria In Portugal <i>M. Oliveira, N. Pedroso, T. Sales-Luís, M. Santos-Reis, L. Tavares and C.L. Vilela</i>	201

Chapter 8	Behavior of Wild Animals Against Humans in Reservations, Sanctuaries, and Hunted Areas – Review and Theoretical Approach <i>Klaus M. Scheibe</i>	223
Chapter 9	Climate Change Effects on Wildlife Populations <i>Joerg Tews, Peter L.F. Fast and Marie Fast</i>	239
Chapter 10	A Sri Lankan Elephant Orphanage: Does It Increase Willingness to Conserve Elephants? How do Visitors React to it? <i>Clem Tisdell and Ranjith Bandara</i>	253
Chapter 11	Wildlife Conservation and the Value of New Zealand's Otago Peninsula: Economic Impacts and Other Considerations <i>Clem Tisdell</i>	277
SHORT COMMUNICATIONS		291
	Biological Monitoring Using a New Technique <i>Mariko Mochizuki, Makoto Mori, Ryo Hondo and Fukiko Ueda</i>	293
	GIS-Based Habitat Model of Javan Hawk-Eagle (<i>Spizaetus Bartelsi</i>) Using Inductive Approach in Java Island, Indonesia <i>Syartinilia, Satoshi Tsuyuki and Jung soo Lee</i>	301
	Conflicts with Humans and Conservation of Large Cats in Brazilian Ranches <i>Francesca Belem Lopes Palmeira</i>	313
	From Acceptance to Support: When Damage Compensation Turns into Performance Payments <i>Kathleen Schwerdtner Máñez</i>	325
	The Significance of Anthropogenic Impact on Forage Plant Species Richness in Structure of Ruminant Guilds: Food Benefits of Pastures with Two Forest Types <i>Ilya S. Sheremet'ev, Elena A. Pimenova, Irina N. Sheremet'eva and Valentina P. Verkholat</i>	333
Index		345

PREFACE

Wildlife includes all non-domesticated plants, animals, and other organisms. Domesticating wild plant and animal species for human benefit has occurred many times all over the planet, and has a major impact on the environment, both positive and negative. Wildlife can be found in all ecosystems, Deserts, rain forests, plains, and other areas—including the most developed urban sites—all have distinct forms of wildlife. While the term in popular culture usually refers to animals that are untouched by human factors, most scientists agree that wildlife around the world is impacted by human activities. This new book examines the destruction, conservation and biodiversity of wildlife.

As explained in Chapter 1, the turn of the century is characterized by occurring of many emerging and re-emerging zoonoses. Various factors that have contributed to the re-emergence of this infection include disturbances in natural ecosystems, increase in international transport of animals and humans and an improvement in diagnostic facilities resulting in better detection of these infections. Forests are complex natural ecosystems and home to a wealth of different organisms. They are among the greatest natural treasures from the perspective of its overall function that impacts the natural environment and the living conditions within. Mouse-like rodents that are known natural reservoir for numerous zoonoses (leptospirosis, tick-borne meningoencephalitis, lyme borreliosis, haemorrhagic fever with renal syndrome, etc.) form an important part of forest faunal community. The widespread geographic distributions of rodents harboring pathogens indicate considerable disease-causing potential essentially worldwide. The following species of mouse-like rodents are most common in the continental European forests: striped field mouse (*Apodemus agrarius* Pall.), yellow-necked mouse (*A. flavicollis* Melch.), wood mouse (*A. sylvaticus* L.), bank vole (*Clethrionomys glareolus* Schreib.), common vole (*Microtus arvalis* Pall.), field vole (*M. agrestis* L.), water vole (*Arvicola terrestris* L.) and the European pine vole (*M. subterraneus* de Sel.). The spread of certain zoonoses is dependent on the abundance of rodent populations, their distribution, mobility, feeding intensity, habitat conditions and reproduction potential, as well as the abundance and distribution of wild and domesticated animals susceptible to infectious disease. A large number of factors influence the population sizes of mouse-like rodents, and these can be classified into four basic groups: abundance and physiological state of the population, meteorological conditions, habitat and food sources, and natural enemies and diseases. The population abundance of each species changes in the course of a year or several years. Years with mild winters, dry springs and summers are favorable for increases in abundance of these species, which in turn can contribute to the

spread of individual zoonoses in forests. The objectives of interdisciplinary studies currently ongoing in Croatia are to define the distribution and genetic diversity of individual causative agents of certain zoonoses such as leptospirosis, lyme borreliosis and hemorrhagic fever with renal syndrome. In the same time, the level of infection among mouse-like rodents as the main reservoirs of these zoonoses in forest ecosystems is investigating on molecular level. Establishing the natural fruit-bearing cycle for woody plants is successfully used in assessing the possible growth in population numbers. Regular controls of rodent populations and their infectiousness is significant in planning epidemiological and sanitary measures in preventing outbreaks of epidemics and individual cases of illness among animal and human populations (forest workers, excursionists, mountaineers, soldiers, tourists, etc.).

Maasai group ranches are critical wildlife dispersal areas between Amboseli and Tsavo parks in Kenya. However, human activities are decreasing the quality and quantity of these dispersal lands. This study sought to establish the area and spatial location of all human activities by mapping and spatial analysis in relation to wildlife distribution in group ranches. In Kimana Group Ranch, the actual area covered by human activities was 57.83 km² (23%), but increased 55.74% with wildlife displacement. In Kuku Group Ranch, there were eleven clusters of human activities covering 24.4% of the ranch. The actual area was 38.31 km² (4%) but increased to 23.3% with wildlife displacement. In Mbirikani, human activities occupied an actual area of 16.85 km² (1.37%), which increased to 22.97% with wildlife displacement. In all group ranches, Maasai homesteads displaced more wildlife, followed by roads, and electric fences. The threat in Kimana was high proportion of areas taken by human activities both in the area taken as well as the spatial orientation that often blocked of wildlife movements. For Kuku and Mbirikani, the main threat was spatial arrangement of human activity clusters that threatened to block wildlife migration, even though more land was still available for wildlife and pastoralism. Chapter 2 shows the challenges of changing land uses and consequences for wildlife conservation in Amboseli Ecosystem. Wildlife dispersal area is increasingly shrinking due to human activities and changing land uses, making the future of conservation in the area challenging due to diminishing wildlife dispersal area.

Africa contains some of the most distinctive and valuable biological resources on Earth, yet the future for biodiversity in parts of sub-Saharan Africa is being compromised by the prevalence of wars and armed conflicts in this region. War yields a vast number of negative impacts on social, economic, and political conditions. Some of the negative impacts of war include the direct effect of war tactics, the appropriation of financial resources to support war rather than to benefit civil society, the displacement of people and the subsequent impact on resources by refugees, the deterioration of governments, and, perhaps most critical, the overexploitation of wildlife. These impacts cumulatively facilitate a downward spiral in biodiversity when appropriate conservation interventions cannot be accomplished. Much of sub-Saharan Africa has been ripped by wars, and for conservation measures to gain the upper hand will ultimately require the establishment of novel plans and strategies specifically designed to preserve biodiversity under these conditions. In Chapter 3, the urgent need for new and renewed efforts in regions torn apart by war is reviewed, along with the lessons that conservation organizations have learned using adaptive management in these circumstances. These lessons include advocating nature valuation, providing increased support for local stakeholders engaged in conservation work, integrating conservation approaches with the work of humanitarian organizations, and managing the plight of refugees.

Chapter 4 discusses soil seed banks, which have specific roles in conservation and restoration of plants. Material from a seed bank is less influential on the genotypes of local populations, since it pools the local endemic genotypes. In addition, a seed bank is expected to increase the genetic diversity of subdivided populations of endangered plants. In populations which have already disappeared due to habitat loss, the seed bank is the only hope to restore the populations. Hence, sound information on soil seed banks is essential to enhance the success of conservation and restoration in plant species. Recently, the author showed that seed dormancy, which has been considered the mechanism of a seed bank formation, is not essential for the persistence of the seed bank for at least 5 years (criterion of long-term persistence).

Many plants avoid germination under dense vegetation or in too deep soil because of the lowest competitive ability of seedlings in their whole life cycle and the limitation of nutrient reserves in seeds. Temperature fluctuations and/or light quality and quantity work as reliable gap-surface signals for many plants. Using such signals, many plants actually germinate at gap-surface with dexterity. Reversibility in the state of phytochrome (P_r and P_{fr}) must ensure the dexterous gap-surface detection in germination. Although some types of dormancy such as physical dormancy contribute to the persistence of a seed bank, dormancy mainly operates the temporal timing in germination. Thus, seeds avoid germination and form a seed bank under spatially and temporally unfavorable conditions where it can not expect reproductive success.

Since seeds of many plants can perceive the favorability in surrounding environments, the seed bank of a target species in the restoration may be accumulated in an unfavorable environment where reproductive success is not expected. For example, seeds of hygrophilous plants were actually sampled from dry soils of past wetlands. This trend holds true not only to target species in the restoration but also invasive plants. Surface soil may be polluted by invasive species seeds compared with deep soil. Restoration using a seed bank at surface soil actually raised an invader species rather than endangered plants in some cases. Samplings of a seed bank for restoration have been collected randomly in the local habitat. However, sampling design of a seed bank considering the unfavorability for both growth of the target species and invasive species will increase the success of the restoration using a seed bank. Several old fruits of lotus *Nelumbo nucifera* were recovered from a peat deposit at Kemigawa (Chiba Prefecture) in Japan. This lotus is currently called 'Ohga lotus' (Picture 1). Unfortunately, because all of the fruits were germinated, none was left for radiocarbon dating. However, wood from an old boat found at the same level in the peat deposit was dated roughly 3000 years old. Although this was not necessarily the age of the fruits, the recovery of the Ohga lotus is a symbolic occurrence indicating that a soil seed bank has the potential to restore past plant species that have disappeared from standing vegetation.

Symbiotic communities are relevant from the biologists' viewpoint. Diseases affecting interacting populations have earlier been considered in ecoepidemic models with interactions of competitive or predational type but also for mutualistic associations. In Chapter 5, the analysis is extended to populations experiencing mutualism, in the more realistic case in which the benefits of the symbiosis cannot exhibit unlimited growth as function of the ecosystem populations. The investigation of some such situations is not only biologically relevant, but it becomes important even from an economic point of view, like for instance the case of chestnut trees affected by chestnut cancer and several mushrooms. We model a symbiotic ecoepidemic system via a dynamical system, assuming that the return coming from

positive species interactions has an upper bound. We mathematically analyze its long-term behavior and identify conditions leading to disease eradication. Some new features characteristic of these models with respect to earlier ecoepidemic models with different underlying demographics are highlighted.

As presented in Chapter 6, current agriculture activities worldwide imply extended use of chemical complex mixtures. Roughly 85–90% of pesticides applied in agriculture never reaches target organisms, but disperse through the air, soil and water. Therefore, wildlife living in habitats adjoining heavily treated croplands is likely to be exposed to complex pesticide mixtures over extended periods.

One of the main challenges of the Environmental Toxicology is to relate the presence of a chemical in the environment with a valid prediction of the resultant hazards for those organisms potentially receptors. Alterations or malfunction of organism normal vital functions can be identified using *Biomarkers*, considered as measurable biochemical, histological, physiological, and morphological changes in response to xenobiotic undesirable action.

Environmental pollution may interfere with growth and development of organisms, but the induction of genetic damage due to long-term, low level chronic exposure to chemicals is perhaps the most relevant biological effect. It can cause a decrease in wildlife populations fitness by the effects of somatic and heritable mutations, that is, an increase in genomic instability. Therefore, the evaluation of the potential genotoxicity of a chemical product is essential for environmental hazard assessment and biodiversity conservation. Genotoxic biomarkers, specially non-destructive short term tests, provide a particularly promising alternative of increasing interest and relevance for measuring the potential effects in vertebrate species in both, laboratory and field studies. Moreover, if this assessment is done in species of particular ecological value, the information can be used to assess the impact of xenobiotics on both the species and the ecosystem. The identification of sentinel species as well as sensitive biomarkers of chronic genotoxicity represents an early warning system to detect adverse effects in natural environments.

Crocodylians are integral components of wetlands all around the world. Taking into account the agricultural frontiers expansion during the last years, many crocodylian populations live nowadays in habitats under a high contaminant pressure. Due to their biological characteristics they can be exposed to contaminants in all life stages. As a consequence, crocodylians world-wide appear as excellent model species of environmental pesticide contamination.

As explained in Chapter 7, bacterial antimicrobial resistance is a well recognized problem for human and animal health. Evaluation of antimicrobial resistance in enteric microbiota is a powerful tool to monitor selective pressure from drugs used for treating animal and human infectious diseases, or from compounds used in farming practices for prophylaxis. Screening antibiotic susceptibility patterns of wildlife animal isolates provides useful information on environmental contamination by resistant strains, deriving from contaminated effluents or from free-ranging animals that are potential vectors of resistance determinants.

Recently, we examined the antimicrobial resistance of *Escherichia coli* (n=7) and *Enterococcus* spp. (n=26) isolates obtained from 35 fecal samples from Eurasian otter (*Lutra lutra* Linnaeus, 1758) free-living in Pego do Altar and Monte Novo reservoirs and associated river stretches in Alentejo region, South Portugal. The 12 antimicrobials, tested as recommended in the Clinical and Laboratory Standards Institute guidelines, belonged to

different antimicrobial drug classes, acting through inhibition of transduction (n=6), cell wall synthesis (n=4), DNA gyrase (n=1) and folate synthesis (n=1).

Levels of resistance were different for the two bacterial genera considered. All *E. coli* isolates were susceptible to 5 of the antimicrobials tested, while none of *Enterococcus* spp. isolates was susceptible to all compounds. All enterococci were resistant to cephalixin, cephalexin, enrofloxacin and streptomycin. With exception of one *E. coli* isolate, all bacteria presented a multiresistant profile, being resistant to more than one antimicrobial drug class.

The animals sampled were not likely to have been subject to antibiotherapy. Therefore, low resistance levels were expected, since antimicrobial treatment exposure is still considered the major reason for emergence, selection, and dissemination of resistant bacteria. The multiresistant profile found in most isolates supports the hypothesis that environmental exposure of intestinal microbiota to antimicrobial agents may select for resistant bacterial strains, but the occurrence of point mutations or acquisition of transmissible mobile DNA elements responsible for antimicrobial resistance must also be taken into consideration.

The antimicrobial resistance profile of *E. coli* and *Enterococcus* spp. isolates from otters' fecal samples may provide useful information to assess the potential of antimicrobial resistance transmission from the environment contaminated by humans and domestic and wild animals, being particularly relevant in dams and rivers where human activities, such as farming or outdoor recreational activities, occur near or in the water. Resistance profiles should be taken upon consideration in future plans regarding management and conservation of otters, particularly in environments where cattle density near aquatic systems is high.

In nearly all hunted areas, game animals fly from humans, avoid being seen by seeking shelter during the day, and have a preference for nocturnal activity. This behavior has widely been assumed to be normal and shyness of all wild animals against humans has been accepted as natural behavior of these species, especially between hunters. On the other hand, in all non-hunted reserves wild animals display a behavior against humans very different from animals under human hunting pressure. This has been described as "national park effect". It consists of astonishing tolerance of potential prey animals towards humans, substantially reduced or even completely lacking flight behavior, and distinct daylight activity on open terrains. In Chapter 8, a general explanation of these effects is given based on the emotions of animals as well as on their learning behavior.

The response of inexperienced animals towards humans is based on general anxiety for unpredictable and possibly dangerous events. The emotion of general anxiety has to be distinguished from specific fear. Both processes can be modified by learning from experiences with humans. As hunting is the main cause for mortality in many game populations, hunting strategies will be the key factor to understand the learned behavior of deer towards hunters and tourists in a certain area. Theoretical learning curves are developed for different conditions. They support the importance of game sanctuaries and the development of drawback-free strategies for population regulation.

Additionally, the behavior of large predators towards humans can be interpreted based on general anxiety, specific fear, and learning. Recommendations are developed under these aspects for convenient strategies towards these species and to avoid conflicts.

To better understand human-wildlife conflicts, more experimental investigations on the learning behavior of the different species are required. Such investigations will open new ways to solve human – wildlife conflicts regarding ethical aspects.

It is now widely accepted that many wildlife species are under imminent threat as a result of climate change. As presented in Chapter 9, climate change effects on the demography of populations (i.e., changes in fecundity or survival rates) can be direct (i.e., abiotic through factors such as rainfall or temperature) or indirect through species interactions (i.e., through consumers, resources or competitors). Over time these processes and dynamics can result in positive, negative or neutral net effects with increasing, declining or stable population trends. For certain species groups it has been argued that shorter-lived species with higher fecundity might have a life span too short to develop behavioral adaptation to directional changes in their environment and are thus more sensitive to global change ('behavioral adaptation hypothesis'). In contrast, it has been postulated that short-lived and small-bodied species have a higher adaptation potential because (in the long term) shorter generation times allow higher rates of evolutionary adaptation ('structural adaptation hypothesis'). To evaluate these two hypotheses and to assess if and under which conditions net effects of climate change on species' demography are primarily positive or negative, we analyzed a selection of 47 peer-reviewed, empirical wildlife studies for the time period 1990-2007. Among all studies analyzed 73% reported negative climate change effects of which 60% were caused by biotic effects, i.e., indirect effects. There was an increased likelihood of positive effects amongst animals with shorter longevity (mean longevity = 13.3 and 5.7 years for negative and positive population effects, respectively). This suggests there may be an advantage to being shorter lived during periods of climatic change, and provides some support for the structural adaptation hypothesis. Mean number of generations studied was 4.1 ($n=34$, $SD=8.2$) and 9.3 ($n=12$, $SD=10.1$) among studies that reported negative and positive population effects, respectively. To our knowledge the results from this meta-analysis represent the first general assessment of climate change-induced demographic effects on wildlife populations.

Pinnawala Elephant Orphanage (PEO) was established in Sri Lanka in 1975 to provide a refuge for elephants that were injured, orphaned, abandoned or separated from their families/herds in the wild. The orphanage cares for such animals and it was hoped that after their rehabilitation, some would be successfully returned to the wild. It is mainly used as a facility for viewing elephants and providing visitors with elephant-based recreation. It attracts over 35,000 visitors (both local and foreign) per month on average. However, little or no attempt has been made to examine the reaction of visitors to its activities and its impact on their willingness to support the conservation of elephants. Chapter 10, after providing background on the PEO, reports findings from two visitor surveys (one of local visitors and one of foreign visitors) conducted at the PEO. It provides information on the characteristics of visitors, the satisfaction they gained from the visit, their attitudes towards the conservation of the elephant and the impact of their visit to the PEO on this, their reactions to the current facilities available at the orphanage, and their maximum willingness to pay (WTP) to enter the PEO. Some differences are evident between these two samples in relation to satisfaction received, responses to the WTP elicitation, and attitudes towards the information and interpretive facilities. For example, a higher percentage of Sri Lankan respondents compared to foreign correspondents said that their experience at the PEO had increased their support for the conservation of the Asian elephants, and while nearly all respondents thought that more should be done to conserve the Asian elephant, a larger percentage of Sri Lankans compared to foreigners thought that high income countries should help to pay for this. Nevertheless, the majority of the respondents (in both samples) indicated that their support for the conservation of the Asian elephant had increased with their visit to the Orphanage. This indicates that a

considerable unrecorded and as yet unutilized amount of support could be generated both financially and otherwise to conserve endangered species through wildlife-based refuges (combined with recreational facilities) such as those at the PEO in Sri Lanka. A particular feature of this article is its discussion of the role which wildlife refuges play in practice compared to the role they could play in the conservation of endangered species.

Valuing objects is a distinctive human trait. It is necessary for rational behaviour. Factors that are likely to influence valuations, the difficulties of getting agreements about valuations and the limited perspective of economics as a basis for valuation are discussed generally in this article. Attributes of Otago Peninsula that seem to be valuable and worth conserving are listed and discussed, taking into account possible conflicts in getting maximum value from these attributes. In Chapter 11, particular attention is given to the economic value of conserving wildlife species on the Otago Peninsula. As a result of the presence of these species and their use for tourism, expenditure of over \$100 million NZ is generated annually in the Dunedin regional economy (directly or indirectly) and 800-1000 full-time equivalent jobs are created. The economic opportunity cost of this wildlife conservation on the Peninsula is low and the economic benefits from this conservation are well in excess of the costs involved. When non-use economic values and the social values associated with Otago Peninsula are taken into account, this further adds to the value of conserving this wildlife. While there has been remarkable expansion in wildlife tourism on the Otago Peninsula and its economic impact in the Dunedin region in the last two decades, (especially in the viewing of Yellow-eyed Penguins), difficulties and constraints are emerging that are likely to hamper its future expansion. However, wildlife tourism on the Otago Peninsula will still have a huge economic impact on Dunedin's regional economy in the future. Consequently, even if assessed solely in terms of their economic value, the wildlife attractions of the Otago Peninsula are well worth conserving. Furthermore, the value of conserving biodiversity on the Peninsula exceeds its touristic and its economic value. Some conservation organizations (such as the Yellow-eyed Penguin Trust), even though not directly involved in tourism, add to its economic value as well as to its social value and promote the highly desired goal of conserving biodiversity.

Carnivores are frequently used for studies involving wildlife because they are positioned at the top of the food chain. The greater scaup (*Aythya marila*) is generally classified as a carnivorous bird that eats animals such as shellfish. However, it is known that this bird also uses feed of vegetable origin, depending on the environments in which it rests during migration. The often narrow classification of feeding habits is a daunting problem for studies of wildlife. To obtain a detailed understanding of the actual migratory flight path and the degree of contamination of the environment inhabited by migratory species is even more difficult. Thus, the data obtained from wildlife are usually distributed over a wide range, and outliers are often obtained. In the first Short Communication we investigated these problems using the data obtained in our studies of wildlife, and suggest the possibility of a new index for biological monitoring.

As explained in the second Short Communication, the Javan Hawk-Eagle (JHE) is categorized in the IUCN Red List of Threatened Species (CITES Appendix 2) as one of the world's rarest and most endangered raptors in the remaining original natural forests of Java, Indonesia. Since it is not feasible to conduct complete field surveys for a landscape-scale, this paper proposes a GIS-based extrapolation model based on local-scale model in order to generate a map of potential and present habitat suitability for JHE in the entire landscape.

Using autologistic regression, we developed a GIS-based habitat model for JHE in Java Island and subsequently estimated the population number of JHE. The obtained model will be the most useful for the wildlife management conservation planning process in order to help identify “hot spots” that are most likely to harbor JHE. Most of the predicted suitable habitats in Java Island are distributed in the mountainous area. The area with the largest proportion of suitable habitat for JHE is located in East Java, and then followed by West Java and the last in Central Java. Totally, about 41 locations (85%) of 48 historical localities recorded were recognized as suitable habitat. The estimated number of JHE pairs based on model extrapolation would place the population size about 108-542 (median = 325) pairs. Although this estimated population is higher compared to other studies, JHE had always been described as either rare or very rare. The apparent discrepancy between this estimated population and others, which might not suggest an increase in present JHE, may be explained by several reasons such as increased accessibility to formerly unexplored habitat and more recent satellite imageries and GIS techniques application used in estimation of suitable habitat of JHE and finally will allow a better population estimate.

Cattle depredations by large cats were recorded by ranch-hands for six years (1998 – 2003) in the *Ouro Branco* ranch, central-western Brazil. The mean annual depredation by these large cats represented about 18.9% of the cattle mortality and 0.4% of the cattle stock. Depredation was not occurred at random and was mainly associated with cattle’s age class, calving seasons, and spatial location. Some of the large cats depredation (22.3%; $n = 69$) were checked in the field and distinguished between puma (*Puma concolor*) and jaguar (*Panthera onca*) kills, from October 2002 to May 2003. Most of the depredation was caused by pumas (92.75%; $n = 64$) and few ones were caused by jaguars (7.25%; $n = 5$). In contrast, jaguars were the main victims of persecution by local poachers. In six years (1998 – 2003), three pumas and five jaguars were killed in the ranch and in three neighboring ranches. In addition, ranchers have offered three cows (USD\$ 365) as a reward for each large cat killed by local poachers. As explained in the third Short Communication, this control has become the main reason for the extermination of these large cats, particularly in areas not legally protected. Based on these results, non-lethal techniques should be encouraged to avoid depredations and, calves should be kept as far as possible from forest fragments. Also, it is necessary to have a scientific approach that comprises bio-ecological, socio-economic and cultural aspects to reduce the human-wildlife conflicts caused by depredation. Due to the great complexity of these interactions, a great effort must be made to guarantee large cats’ conservation in Brazilian ranches.

Damage compensation schemes are widely used as tools for the reconciliation of human-wildlife-conflicts. Two forms of compensation schemes exist: *ex ante* and *ex post*. While the latter is commonly used to compensate wildlife damages in many parts of the world, it is also often criticized for several reasons. Arguments against its use include the associated high transaction costs and the lack of those schemes to provide positive incentives for wildlife conservation. The importance of integrating positive incentives into conservation activities is not only highlighted by many economists, but also mentioned in the CBD. As a result, increasing attention has to be paid to the second form of compensation: *ex ante* compensation schemes. Changing compensation from one scheme to the other provides a high potential to increase public support for wildlife conservation. Instead of only distributing the damage costs more fair in the society as under *ex post* schemes, payments under *ex ante* compensation are directly linked to the number of animals including offspring. The aim of both instruments

is therefore fundamentally different: Whereas the first scheme seeks only to gain acceptance for damage-causing species, strives the latter for an active support. In that respect, *ex ante* compensations are payments for environmental services (PES). PES imply the need to address complex trade-offs between the “provider” and the “consumer” of an environmental good through compensations. Many scholars have assessed the advantages of PES over indirect approaches, but its application still remains “under-construction”.

A large amount of literature deals with the relevance of such payments for conservation activities, but the relation between *ex ante* compensation and payments for environmental services has not yet been mentioned in the literature. The fifth Short Communication aims to fill this gap by systematically looking at damage compensation schemes and payments for environmental services, arguing that an increased use of the latter will support wildlife conservation by shifting the focus from acceptance to support.

The last Short Communication deals with the relationship between species diversity of forage plants and structure of ruminant guilds at different stages of the disturbed communities. A general approach based on comparison of two systems of ruminant ranking, by their forage species richness and by abundance of ruminant species in a community. The number of plant species was considered as several variables regarding to forage value in diet of ruminants. It was found that species structure of the vegetation is at least a one of the conditions which determines the structure of the ruminant guilds. Population density of ruminants whose forage plant sets are more diverse is larger. The total number of forage plant species has a decisive significance, but not number of the most significant species. Anthropogenic disturbance of vegetation and change of plant species richness support change in structure of ruminant guilds.

RESEARCH AND REVIEW STUDIES

Chapter 1

FOREST ECOSYSTEMS AND ZOOZOSES

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Abstract

The turn of the century is characterized by occurring of many emerging and re-emerging zoonoses. Various factors that have contributed to the re-emergence of this infection include disturbances in natural ecosystems, increase in international transport of animals and humans and an improvement in diagnostic facilities resulting in better detection of these infections. Forests are complex natural ecosystems and home to a wealth of different organisms. They are among the greatest natural treasures from the perspective of its overall function that impacts the natural environment and the living conditions within. Mouse-like rodents that are known natural reservoir for numerous zoonoses (leptospirosis, tick-borne meningoencephalitis, Lyme borreliosis, haemorrhagic fever with renal syndrome, etc.) form an important part of forest faunal community. The widespread geographic distributions of rodents harboring pathogens indicate considerable disease-causing potential essentially worldwide. The following species of mouse-like rodents are most common in the continental European forests: striped field mouse (*Apodemus agrarius* Pall.), yellow-necked mouse (*A. flavicollis* Melch.), wood mouse (*A. sylvaticus* L.), bank vole (*Clethrionomys glareolus* Schreib.), common vole (*Microtus arvalis* Pall.), field vole (*M. agrestis* L.), water vole (*Arvicola terrestris* L.) and the European pine vole (*M. subterraneus* de Sel.). The spread of certain zoonoses is dependent on the abundance of rodent populations, their distribution, mobility, feeding intensity, habitat conditions and reproduction potential, as well as the abundance and distribution of wild and domesticated animals susceptible to infectious disease. A large number of factors influence the population sizes of mouse-like rodents, and these can be classified into four basic groups: abundance and physiological state of the population, meteorological conditions, habitat and food sources, and natural enemies and diseases. The population abundance of each species changes in the course of a year or several years. Years with mild winters, dry springs and summers are favorable for increases in abundance of these species, which in turn can contribute to the spread of individual zoonoses in forests. The objectives of interdisciplinary

studies currently ongoing in Croatia are to define the distribution and genetic diversity of individual causative agents of certain zoonoses such as leptospirosis, lyme borreliosis and hemorrhagic fever with renal syndrome. In the same time, the level of infection among mouse-like rodents as the main reservoirs of these zoonoses in forest ecosystems is investigating on molecular level. Establishing the natural fruit-bearing cycle for woody plants is successfully used in assessing the possible growth in population numbers. Regular controls of rodent populations and their infectiousness is significant in planning epidemiological and sanitary measures in preventing outbreaks of epidemics and individual cases of illness among animal and human populations (forest workers, excursionists, mountaineers, soldiers, tourists, etc.).

Key words: forest ecosystems, mouse-like rodents, zoonoses, population dynamics and abundance

Introduction

The turn of the century is characterized by occurring of many emerging and re-emerging zoonoses. Various factors that have contributed to the re-emergence of this infection include disturbances in natural ecosystems, increase in international transport of animals and humans and an improvement in diagnostic facilities resulting in better detection of these infections. It was recently reported that between 1940 and 2004, a total of 335 infectious diseases emerged in the global human population. The majority (60.3%) of emerging infectious diseases (EID) were caused by wildlife zoonotic diseases, while vector-borne diseases were responsible for up to 22.8% of these events.

Forests are complex natural ecosystems and home to a wealth of different organisms. They are among the greatest natural treasures from the perspective of its overall function that impacts the natural environment and the living conditions within.

With regard to biotic factors, the small rodents of the Muridae family (mice), subfamily Murinae (true mice) and Arvicolinae (voles) stand out as causes of damage to seeds, seedlings and young trees [Jensen 1983; Hansson 1985, 1992, 1994]. Mice and vole damage have been observed in forests in the form of bites of varying intensity on forest seeds, roots and lower stem of young plants (*Fraxinus angustifolia* Vahl., *Q. robur*, *Salix* sp., *Populus* sp., etc.) [Myllymäki, 1967]. Such damage has been particularly noticeable in years when the rodent populations were at their maximum [Krebs & Myres, 1974]. Furthermore, small rodents are also carriers of a range of infectious diseases that threaten the health of humans and of domestic and wild animals [Childs et al., 1985; Gratz, 1988]. They are known natural reservoir for numerous zoonoses (leptospirosis, tick-borne meningoencephalitis, lyme borreliosis, haemorrhagic fever with renal syndrome, etc.) form an important part of forest faunal community. The widespread geographic distributions of rodents harboring pathogens indicate considerable disease-causing potential essentially worldwide. The spread of certain zoonoses is dependent on the abundance of rodent populations, their distribution, mobility, feeding intensity, habitat conditions and reproduction potential, as well as the abundance and distribution of wild and domesticated animals susceptible to infectious disease.



Figure 1. Common oak forest (Photo by: Josip Margaletić).

Forest Ecosystems

Management and conservation of the optimal conditions for survival of forest stands are important tasks for the forestry profession. The success of natural reforestation is based on a regular, high-quality and rich seed harvest [Belletti & Lanteri, 1996]. All timber stand improvements taking place in forests have to be aimed at the production of the proper conditions for a good seed harvest. Reforestation has proven to be most successful when trees generate seeds and the soil is capable of seed germination and survival of seedlings. The periodicity of a partial seed harvest of the main forest species (*Quercus robur* L., *Fagus sylvatica* L., *Picea abies* (L.) H. Karst., *Abies alba* Mill, etc.) every two to five years and an abundant harvest every five to eight years is well documented [Elsner, 1993; Ducousso et al., 1993; Merzeau et. al., 1994; Nilson & Hjältén, 2003]. Many abiotic and biotic factors affect forest ecosystems [Torelli, 1994; Wühlisch et al., 1995; Kindvall et al. 2000; Kierdorf et al., 2004; Pernar et al., 2006; Idžojtić et al., 2008; Pernek et al., 2008]. Primarily, these are hydraulic land reclamation interventions, water, soil and air pollution, insects, fungal diseases, game, small rodents and the like [Berndt & Oberwinkler, 1992; Evans et al., 1992b; Diminić & Jurc, 1999; Chang, 2000; Chang & Matzner, 2000; Grubešić et al., 2004; Pernek et al., 2008].

Rodents are mammals with characteristic front, sharp incisors, a pair on the upper jaw and a pair on the lower one, that are used for gnawing [Delany, 1974] (Fig. 2). Rodents do not have eyeteeth, so there is an space without teeth between the incisors and molars.



Figure 2. Rodent jaw (*A. flavicollis*) with prominent front incisors (Photo by: Werner Heitland and Walter Bäumler, Munich/Freising, CD Biologie 99)

According to Wilson and Reeder [1992], the class of Mammalia is divided into 26 orders, including the order Rodentia (rodents) which is the largest in terms of the number of families and species. Of the approximately 5000 mammal species known today on Earth, about 2000 species belong to the order of rodents [Wilson & Reeder, 1992]. The phylogenetic relationship between 18 species of the European mice and voles is classified into three subfamilies using sequences of the mitochondrial cytochrome “b” gene, as researched by Martin et al. [2000]. Similar studies were described by Matson & Baker [2001] and Michaux et al. [2003, 2004]. Mice (Murinae subfamily) and voles (Arvicolinae subfamily) belong to the order Rodentia, suborder Sciurognathi and family Muridae [Wilson & Reeder, 1992]. There is great variation in the terminology of this family, with many known synonyms: Alticoli, Bramini, Clethrionomyini, Dicrostonychinae, Ellobiini, Fibrini, Lagurini, Lemminae, Microtinae, MicrotoscOPTINI, Myodini, Neofibrini, Ondatni, Phenacomyini, Pitymyini, Pliomyini, Pliophenacomyini, Prometheomyinae, Synaptomyini. The same authors divided the Muridae family into 17 subfamilies, 281 genera and 1326 species. The subfamily Arvicolinae (Gr.) (voles) covers 26 genera and 143 species.

The forest ecosystems of Europe are habitat for numerous species of voles, with just a few pointed out below.

1. Genus *Arvicola* [Lacepede 1799]
Synonyms: *Alviceola*, *Hemiotomys*, *Ochetomys*, *Paludicola*, *Praticola*
Species: *Arvicola terrestris* [Linnaeus, 1761]
2. Genus *Clethrionomys* [Tilesius, 1850]
Synonyms: *Craseomys*, *Glareomys*, *Eotomys*, *Eutomys*, *Evotomys*, *Neoaschizomys*
Species: *Clethrionomys glareolus* [Schreber, 1780] (Fig. 4)
3. Genus *Microtus* [Schränk 1798]
Synonyms: *Agricola*, *Ammomys*, *Arvalomys*, *Aulacomys*, *Campicola*, *Chilotus*, *Euarvicola*, *Herpetomys*, *Micrurus*, *Mynomys*, *Neodon*, *Pinomys*, *Scylvicola*, *Terricola*, *Tetramerodon*

Species: *Microtus agrestis* [Linnaeus, 1761]

Microtus arvalis [Pallas, 1778]

Microtus subterraneus [de Selys – Lang. champs, 1836]

Subfamily Murinae (III) (mice) covers 122 genera and 529 species. The synonyms are: Anisomyini, Conilurinae, Hydromyina, Phloeomyinae, Pseudomyinae, Rhynchomyinae.

Three species belonging to the genus *Apodemus* [Kaup, 1829] stand out and they are most frequently found in the forests of Europe:

1. *Apodemus agrarius* [Pallas, 1771] (Fig. 5)
2. *Apodemus flavicollis* [Melchior, 1834]
3. *Apodemus sylvaticus* [Linnaeus, 1758]

The synonyms of the genus *Apodemus* are as follows: *Alsomys*, *Carstomys*, *Nemomys*, *Petromys* and *Sylvaemus*. All author quotations of the genera and species of small rodents were adopted from Wilson & Reeder [1992]. Researching the evolution and genetic differences between the species *A. flavicollis*, *A. sylvaticus* and *A. microps* in the British Isles, Csaikl et al. [1980] stated that *A. sylvaticus* and *A. flavicollis* separated genetically 423,000 years ago.

Mice are characterized by long ears [longer than the hair on the head], long tail [longer than half the body], large eyes, slim body, acuminate snout and longer back legs. Voles are distinguished by short ears; majorities of the species have a short tail (shorter than half the body), small eyes, stout body, rounded snout and short back legs. Mice and voles are agile animals, distrustful and cautious [Bostrom & Hansson, 1981]. Digging abilities are well developed within many species. Their reproduction potential is very high [Kowalski, 1976]. In determining the species, familiarity with the habitat and morphology are particularly helpful [Niethamer & Krapp, 1979, 1982]. In terms of diet, most small rodents are polyphagous [Blaschke & Bäumlér, 1989; Heroldova, 1994]. Rodents live all over the world. They can be found in all types of forests, agricultural areas, pasture grounds, marsh lands and towns [Heitland & Bäumlér, 1999]. Mice and voles belong to a group of small mammals (Micromammalia) i.e. to the small rodents referring to all species of the class Mammalia (mammals), i.e. Rodentia order (rodents), whose adult individual mass is larger than two and smaller than 120 grams [Delany, 1974].

A. agrarius (striped field mouse) is characterized by an almost black, 3 mm wide central straight line along the entire body length, from the space between the ears to the tail. The fur is less smooth compared to *A. flavicollis* and *A. sylvaticus* [Gliwicz, 1980]. The tail length amounts to approximately two thirds of the total head and body length. The tail consists of 120 to 140 vertebrae. The back legs are more developed than the front ones and are used for jumping movements. The total head and body length ranges from 97 to 125 mm, the tail length from 60 to 90 mm and the body mass from 16 to 25 g [Niethamer & Krapp, 1978, 1982]. This species is widely distributed throughout Europe, from Finland in the north to Bulgaria in the south, inhabiting forest edges, glades, meadows, weed covered fields, parks, planting stocks, etc. In the lowlands in the large European rivers valleys, *A. agrarius* migrates in autumn from the meadows and fields into the forests and in reverse order in spring [Andrzejewski & Wroclawek, 1961]. Breeding takes place three to four times a year, with up

to six young per litter. Sexual maturity occurs at the age of eight weeks. Breeding starts in April and lasts till the first half of October. The seasonal changes in length and mass of the digestive system with a special reference to the surface area of the small intestine of adult animals have been studied by Borowska [1995]. She concluded that the reduction of intestinal parameters could have been caused by reduced metabolic needs and the termination of breeding in late autumn. The striped field mouse can live to an age of 18 months, while under optimal laboratory conditions the maximum age is extended to 4.5 years. The diet is largely comprised of food of animal origin (larvae and insect imago, mollusks, worms, etc.). Plant food consists mostly of seeds and fruit, while the share of green plant parts is substantially lower. During years of mass occurrence, considerable damage has been observed in nursery gardens and in forest, by gnawing the bark of poplar and other species.

A. flavicollis (yellow-necked field mouse) is distinguished by its intensive white belly and brown fur on the back, with a clearly marked border line along the flanks. On the lower part of the neck, there is a clearly marked transverse yellowish stripe or a round yellow spot. Unlike the wood voles (*A. sylvaticus*), this species is distinguished by a more intensive coloration on the belly and markedly brown fur on the back with a clearly marked border along the flanks [Niethamer & Krapp, 1978, 1982]. It is larger than *A. sylvaticus* and *A. agrarius*. The total head and body length range from 88 to 135 mm, tail length between 92 and 134 mm, and body mass of adults between 22 and 44 g [Bračiová & Macholán, 2006]. The species primarily inhabits older oak and beech forest stands with poorly developed undergrowth. The yellow-necked wood mouse is distributed in Europe from Sweden to Finland in the north to the Pyrenees in the south and the Balkan Peninsula in the east. Phylogeographic studies of the species were described by Michaux et al. [2003, 2004]. It feeds on tree seeds and only occasionally on herbaceous plants. Typically, an abundant oak and beech acorn harvest results in an increase in the number of this species [Ericsson, 1983]. Although it can also live in trees, the most frequent shelters with food storages are built in the ground up to 1.5 m in depth, depending on underground waters. The yellow-necked mouse is a twilight and nocturnal animal. It drops two or very rarely, three litters a year. The gravidity of females lasts from 2 to 25 days. In natural conditions, the lifespan is about two years. Breeding terminates during the winter season and continues again in mid to late February. Breeding is also possible during mild winters. The population in a given habitat varies throughout the year, with particular deviations over a number of years when cycles of over breeding appear on an average of every three years.

A. sylvaticus (wood mouse) often does not have a clearly marked yellow spot on the lower side of the neck and, if visible, it is usually elongated. It is distinguished by light grey fur on the back, with vaguely marked line towards the lighter to completely white belly. The variation in color on the sides is less pronounced compared to the yellow-necked wood mouse. The total head and body length ranges from 70 to 115 mm, tail length from 69 to 114 mm, and body mass of adults from 14 to 28 g. This species can be found almost everywhere on the European continent. It lives mostly in open and warm habitats at the forest edges, in parks, bushes and hedges [Hoffmeyer, 1973]. It is often found in agricultural areas, gardens and nursery gardens. It stores the food it gathers in underground corridors for use during the winter months and early spring [Wolton & Andrews, 1981]. This species has a relatively high breeding potential. Breeding begins in February and lasts till September and is interrupted during the winter, particularly if climatic conditions are unfavorable and if there is

insufficient food. It feeds on various trees seeds [Rogers & Gorman, 1995, Corp et al., 1997]. In years of over breeding, when the complete seed crop is destroyed, it can jeopardize the natural regeneration of the deciduous forests [Jensen, 1985]. This rodent causes damages to nursery gardens and forests by gnawing on the bark, root and buds of young woody plants, particularly the field ash. Population dynamic studies of the above species in Sitka spruce stands (*Picea sitchensis*) in northeastern England established that *A. sylvaticus* was dominant in clear cut areas [Fernandez et al., 1994].

C. glareolus (bank vole) is distinguished by varying shades of dark brown fur on its back, with gray fur on the sides and white or yellowish fur on the belly (Fig. 3). The eyes and ears are larger compared to common voles and the European pine vole. The total head and body length ranges from 80 to 123 mm, tail length from 36 to 72 mm and body mass from 14 to 36 g. This species inhabits the forested zone of Europe [Chętnicki & Mazurkiewicz, 1994; Mazurkiewicz, 1994; Andrzejewski et al., 2000]. The distribution of the species was described using phylogeographic analysis by Karlsson [1987], Deffontaine et al. [2005], Kotlik et al. [2006] and others. The wood vole can be found in the lush undergrowth of deciduous and coniferous forests, at the forest edges, marshes, felling areas, bushes, parks, and the edges of plowfields [Mazurkiewicz, 1994; Chętnicki & Mazurkiewicz, 1994]. Breeding lasts from the second half of March to September, with three to four breeding events per year [Henttonen, 2000]. Its territorial behavior and the reproductive fitness of females has been studied and described by Koskela et al. [1997] and Rajska-Jurgiel [2000]. Studies on the relationship between the sexes of wood vole populations and its seasonal variations have been described by Kapusta et al. [1996], Kruczek & Pochron [1997], Kapusta et al. [1998], Yoccoz et al. [2000], Rajska-Jurgiel [2000], Marchlewska-Koj et al. [2003], Marchlewska-Koj et al. and others. From October to April, the vole feeds on tree bark, and can partially or completely debark young branches [Hansson & Zejda, 1977; Hansson, 1992]. The influence of feeding on the body mass and the energetic potential of the above species were investigated by Peacock & Speakman [2001]. In the laboratory and in field tests in Sweden, the damage caused by *C. glareolus* and *M. agrestis* on the native Scandinavian tree species (*Betula pendula*, *Sorbus aucuparia* and *Populus tremula*) were investigated from various regions and various phenological studies. The differences in preferences for shoots from different geographical regions was attributed to the chemical composition of the bark at the end of the growth period and during the freezing process in autumn [Hansson, 1994]. This species causes damage to field ash, willows, black poplar and other species [Obtel, 1973]. In northern Finland, a study on the susceptibility of common pine damage caused by mammals was conducted [Rousi, 1983]. A sample of 800 young plants showed that up to 15% were damaged by *C. glareolus*. In periods of high abundances of this species in the territory, some were even seen by day, unlike mice which are predominantly active by night [Wiger, 1979].

M. arvalis (common vole) is distinguished by yellow-grayish to grey-brown fur color on its back, depending on the geographical area, while its belly is grayish-white. This rodent has six warts on its hind foot, unlike the European pine vole which has five warts [Niethamer & Krapp, 1982]. It is very quick and an excellent climber. The head and body length ranges from 90 to 130 mm, tail length from 30 to 49 mm and body mass is between 14 and 50 g. The common vole is widely distributed through Europe, from the Baltic Sea to the Mediterranean. It predominantly inhabits higher ground, open areas, meadows, fields, forest edges, orchards, vineyards and nursery gardens. It inhabits soil that is rich in dry humus and avoids solid clay

soils, as it is unable to dig its underground corridors in these soils. It prefers habitats with short grass, arable land and roadsides. The common vole population is characterized by large deviations in number. The biological potential of the species is very high. Over breeding usually takes place every 3 to 4 years, with a mass occurrence interval usually occurring every 10 to 11 years. Mild winters in succession with low precipitation and wet summers are favorable for an increasing population. The lifetime of the vole is typically one year, with a maximum age of up to three years. The common vole, like almost all other voles, is a typical herbivore [Niethammer & Krapp, 1982]. It eats the green and succulent parts of various plant species, seed sprouts, roots, and bark of different woody species. During winter months with a high snowfall, when it is unable to find seeds, it gnaws young tree bark at the snow cover level. Young field ash plants are commonly damaged, as are many other tree species. Common voles gnaw the bark of young trees and attack the roots below ground level. Intense attacks will result into complete ringing or stem separation [Moraal, 1993]. In autumn, it migrates in great numbers to forested areas, nursery gardens and forest plantations, particularly inhabiting weed covered and untended habitats. The damage caused by voles is visible when the ground vegetation withers after the early frosts. The population number is not particularly influenced by dry or wet years. In general, the rapid population growth of small rodents is linked with their high reproduction ability and low mortality rate.



Figure 3. Forest (reddish) vole (*C. glareolus*) in nature (photo: W. Bäumler).

Microtus agrestis (field vole) is closely related to the common vole. It inhabits wet grassy areas of mixed forests, weed covered felling areas, open stands and the like [Niethammer & Krapp, 1982]. In Croatia, it inhabits the southern parts of the country [Kryštufek et al., 1989]. It is slightly larger than the common vole, with a body length ranging from 10 to 12 cm. Every 3 to 4 years, this species appears in larger numbers. Borowski [2003] studied the habitat elements of this species and its activity area in Slowinski National Park (Poland), and observed that this species primarily feeds on herbaceous plants, and the buds and bark of field ash, alder, willow, poplar and pine [Myllymäki, 1977; Hansson, 1986, 1991; Wheeler, 2005]. Hansson and Gref [1987] examined the bark of the species *Pinus contorta* and *P. sylvestris* for nutrients, certain mineral elements and resin acids. The samples used for the analyses came from three different provinces of *P. contorta* growing in Sweden, which attracted voles with varying intensity [particularly *Microtus agrestis*], and one province of *P. sylvestris* which the voles refused. The authors concluded that voles preferred *P. contorta* bark due to the lower fiber content. Young trees were gnawed at a height of 10 to 20 cm from the root or

were ringed [Bäumler, 1983; Bäumler et al., 1988]. This vole is primarily found in forest stands rich in ground vegetation. The optimal biotopes are moist habitats rich in food with dense grass vegetation. In such places, the population can grow to 100 and even 300 voles per hectare [Hansson, 1970]. In order to implement timely protection measures, it is necessary to be able to assess where a high population density of field voles can be expected [Bäumler et al., 1989]. Vegetation cover on newly afforested areas on rich soil is an ideal habitat for this. In such circumstances, the field vole population can obtain high numbers, until the vegetation cover is reduced after several years of trees growth. As winter progresses, food sources becomes less and less available and the hungry voles begin to feed on tree bark. This is a lower quality food, resulting in the death of a large number of voles. Mortality reaches its peak in February and March. If substantial damage is found in late winter or early spring, only a few voles can be caught in traps as this is the time when population of this species drops. Various studies on the population dynamics of *M. agrestis* often refer to the “summer crisis” [Myllymäki, 1997]. The phase of the increased breeding and rapid growth over the spring months, was followed by a crisis period. This recession phase, particularly with older animals having survived the winter, has been characterized by weight loss, reduced fertility and an increased disappearance of animals. In young animals, growth and the onset of sexual maturity was slowed. Meanwhile, changes in organs were in particular noticeable in the vole, such as enlargement of the spleen. Possible factors causing such changes could include poor nourishment quality, increased parasite load, more intensive competition for the growing population density in summer, hormonal growth changes and breeding power.

Arvicola terrestris (water vole) is a relatively large animal compared to other species of small rodents. The total head and body length of this rodent can be up to 20 cm. Its back is covered in brown fur. The weight of adult individuals ranges from 80 to 180 g. This species is distributed over a larger part of Europe, from Great Britain and Scandinavia in the north to the Mediterranean Sea coast. It lives in moist habitats, in smaller rivers and streams valleys, ponds shores, meadows, etc. Breeding occurs from the end of March to the end of September, 2 to 4 times per year. The species usually lives about two years. Severe damage caused by gnawing of young deciduous trees roots, especially oak, in forest stands and plantations are commonly attributed to *A. terrestris*. However, studies in Germany revealed that *Clethrionomys glareolus* and *Microtus agrestis* can cause similar damages where roots are easily accessible [Bäumler, 1989].

Microtus subterraneus (European pine vole) is distinguished by dark-grey fur on its back and lighter colored fur on the belly. It is characterized by very small eyes, smooth and thick fur, short tail and very short ears. The total head and body length ranges from 75 to 110 mm, tail length between 25 and 39 mm, and body mass from 12 to 24 g. It is distributed throughout most of the European continent and lives primarily in moist habitats such as river valleys, ponds and lakes shores, and wet meadows. Over breeding of the above species is very rare. The breeding takes place year round, up to 5 to 6 times in total.

Mycromys minutus (harvest mouse) is characterized by light brown fur on its back and yellowish-brown fur on its belly. The body length ranges from 5.8 to 7.6 cm. The tail is 7.2 cm long and is almost bare. It is distributed almost throughout Europe and it is active by day, and very good at climbing. It feeds on insects, seeds, buds and the like. Breeding takes place from March to August, 2 to 3 times per year. The lifetime of the mouse is from two to four years.

The population size of each species is directly influenced by abiotic and biotic factors, and varies throughout the seasons [Margaletić et al., 2005]. It is supposed that the numbers of these mammals will considerably increase in years where the influence of ecological factors was favorable; thereby increasing the threat of their harmful effects [Margaletić et al., 2002]. In order to maintain the natural balance in the forest ecosystem, it is important to permanently monitor the population dynamics of the small rodents and their infection by microorganisms and parasites. As small rodents have an extremely high biological potential in years when favorable conditions prevail, the population increases as does the damage. Some species can survive with less oxygen and stand lower or higher temperatures than any other mammal species, suggesting that they possess a very broad ecological valence.

The majority of small rodent species are polyphagous. Although they are typically herbivores, they also eat food of animal origin [Cook et al., 1995, Muzika et al., 2004]. Food eaten by humans used as bait in luring the animals into traps (live or dead animal traps of different types) is not necessarily attractive to mice and voles. Due to their large population numbers and significant ecological valence, small rodents are an important part of almost every forest ecosystem. They represent a significant group of animals connecting primary producers with higher trophic levels. They feed on green and succulent plant parts, seeds, roots and bark of ligneous species, young buds, insects and the like [Hamilton, 1941]. A study was conducted of the predation of small rodents on the sawfly population (*Cephalcia lariciphila*) during a sawfly invasion from July 1976 to January 1977 in areas covered with Japanese larch (*Larix kaempferi*). The rodents captured were the wood vole (*Apodemus sylvaticus*), bank vole (*Clethrionomys glareolus*) and common shrew (*Sorex araneus*). Intestinal analysis of the rodents showed that the sawflies comprised 70-90% of the diet of *A. sylvaticus*. The conclusion was that *A. sylvaticus* had a powerful potential in the biological control program for this insect [Don, 1979].

During years of over breeding, damage to forest stands, seeds, seedlings and young plants can be considerable [Niemeyer, 1993]. In the 1950s, intensive biological studies began on certain small rodent species to determine their distribution and the damages incurred to the economy, and various prevention methods were sought.

The ecology and biology of the small rodents in forest ecosystems was studied by Turček [1956]. He separated their influence on the forest ecosystem into the following groups: impact on the microclimate of sawflies and the upper soil layers, influence on airing and humidification of the soil, influence on the flow of inorganic and organic matter, influence on the abundance of harmful insects, influence on the maintenance of populations of various forest predators for which small rodents comprise the backbone of their diet, influence on succession in felling areas and influence on plants spread by seed circulation. Predation of small rodents on the pupae of the European pine sawfly *Neodiprion sertifer* was studied by Hanski & Parviainen [1985]. In the field, the authors set up individual cocoons (50 per habitat), in groups of 10 (20 such groups per habitat) and in groups of 50 (10 such groups per habitat) in 21 forested areas in Finland. The experiment proved that within a month, small rodents had destroyed 70% of all cocoons. The largest predators were *Sorex araneus* and *Clethrionomys glareolus*. The cocoons placed individually were most frequently destroyed by *S. araneus* while *C. glareolus* fed on the cocoons placed in groups.

The population density expressed as individual number or biomass per surface area or volume within a determined period of time has been the subject of numerous studies, particularly for species important from the perspective of health or the economy. Population

density refers to the number or mass (biomass) of individuals of certain species per surface area or unit volume. The population number of each species varies throughout the year. A year with favorable ecological factors contributes to an increased number of these mammals, thus also increasing the threat of damage they can cause.

Small rodent populations are influenced by many factors that can be classified into four basic groups:

1. Physiological Population Conditions

A possible increase of the number depends on the behavior and physiology, on the relationship between the sexes within the population, social relations, intraspecies competition, genetic predisposition and mortality rate [Kruczek & Golas, 2003].

2. Meteorological Conditions

The meteorological conditions that can influence an increase in rodent numbers include a dry and warm autumn, mild and dry winter or snowy climate without sudden temperature changes, free of ice cover, and high humidity, with gradual snow melt in spring, warm spring months (April, May) and a warm summer with a moderate quantity of precipitation required for successful vegetation growth [Hansen et al. 1999]. Furthermore, such conditions are favorable for the seed yields of woody plants that considerably influence the increased number of these mammals.

In Bialowieza National Park (eastern Poland), a study on the population dynamics of the species *Clethrionomys glareolus* (Schr.) and *Apodemus flavicollis* (Melch.) was carried out during the period from 1959 to 1991 [Pucek et al., 1993]. The study was conducted in a virgin-forest with common oak and hornbeam. During the 33 year period, with particularly detailed data from 1971 to 1991, a correlation in the population numbers of the above rodents was established with meteorological conditions, and the population size also correlated with the hornbeam, oak and maple acorn yield. The described results on the population dynamics of forest rodents are considered as typical for the lowland oak deciduous forests of Central Europe.

3. Habitat and Food Sources

Lush ground cover, particularly in untended and weed covered habitats, represents an important food source for small rodents [Capizzi & Luiselli, 1996]. The presence of herbaceous plants and cereal food sources, particularly during years of an abundant seed yield of woody plants species (oak, beech, etc.) is imperative for the feeding of overbred populations [Vander Wall, 1993, 1995, 1998]. Vincent [1977] found a positive correlation between rodent populations (*A. sylvaticus* and *C. glareolus*) and forest seed yield. An abundant seed yield stimulates reproduction and extends the reproductive period, thereby resulting in better survival rates for the young [Pucek et al., 1993; Löfgren et al., 1996; Ostfeld et al., 1997; Bergeron et al., 1998; Hulme & Hunt, 1999].

The impacts of habitat change on the structure and spread of single small rodent populations in the Czech Republic caused by forest cutting was investigated by Bryja et al. [2002].

4. Natural Enemies and Diseases

Natural enemies are, first and foremost, predatory animals such as mammals (fox, marten, polecat, weasel, badger, wild boar) and birds (buzzard, windhover, owls, crows) [Jedrzejewski et al., 1995; Korpimäki & Krebs, 1996]. Predators do not hunt individual rodents randomly. Originally, it was believed before that they primarily hunted diseased animals. However, this has proven not to be the case. Predators are not the “disease police”, as diseased mice are usually inactive and hide in their shelters. Most often they are trapped there by weasels. The majority of predatory species hunt moving individuals and the strong and dominant males that are particularly active on the ground surface. They jealously protect their territory, do not tolerate competitors in their area and remain in open areas much longer than females. The radius of their movement is much larger compared to that of the females. The catch of dominant males affects the social structure of the small rodent population, and the course of their breeding.

The number of rodents in forests in Europe and the USA have been investigated by many authors: Pelikan [1966a, 1971], Wiener & Smith [1972], Lidicker [1973], Gliwicz [1975], Tapper [1979], Chudoba & Huminski [1980], Bujalska [1981], Verme & Ozoga [1981], Jensen [1982], Hestbeck [1982], Gurnell [1985], Clarke [1985], Flowerdew [1985], King [1985], Kirkland et al. [1990], Zukal & Gaisler [1992], Zukal [1993], Haim & Izhaki [1994], Kirkland & Sheppard [1994], Krüger [1996], Hansen et al. [1999], Henttonen [2000], Rajska-Jurgiel & Mazurkiewicz [2000], Fasola & Canova [2000], Moses & Boutin [2001], Blundell et al. [2001], Miklos & Ziak [2002], Suzuki & Hayes [2003] and others. A four-year observation (1974–1978) of the population dynamics of the species *A. sylvaticus*, *C. glareolus* and *M. agrestis* in two-year old plantations covering 137 hectares of wet and lowland habitat of the Duisburg state forest (Germany) proved that the populations of the said species varied considerably from year to year. However, this oscillation was not of a cyclical nature [Pietsch, 1978].

Factors governing changes in number of small rodents include the type of vegetation and vegetation density, distance from agricultural crops, agricultural crop species and precipitation (rather than temperature) [Semizorova, 1971; Capizzi & Luiselli, 1996]. A massive food supply is a precondition for winter breeding, which also depends on another unidentified factor that could be a characteristic of the population itself [Smyth, 1966].

Several methods are used to observe the population dynamics of small rodents for the purpose of determining absolute and relative numbers. The absolute number is defined by the number of individuals of a certain species per surface area. The minimum squares method is used to establish the absolute values of the small rodent population. The method was suggested by Grodzinski et al. [1966] and modified by Zejda & Holišova [1971], Pelikan [1971] and Poole [1974].

The “Y” method is the most recent method of establishing the absolute number of small rodent. It was first applied by Kirkland and Sheppard [1994] when they were investigating the population dynamics in North America. The method offered good results in years of large

animal populations [Zukal & Gaisler, 1992]. The absolute number of small rodents can also be established using the method of “catch-recatch” [Bäumler, 1983; Gurnell & Flowerdew, 1994]. Relative number can be established in several ways, however the most commonly used is that of determining the percentage of individuals captured in traps in a transect with regard to the total number of prepared traps in that transect. The advantage of the linear transect method is that it is possible to establish the number of rodents in a larger area within a short period of time, as in this method, animals are only captured during a single night.

Stanko et al. [1999] conducted a comparison of the efficiency of sampling small rodents using two methods [bait traps and drop-in traps] in the flooded forests of eastern Slovakia. The authors proved that drop-in traps were more efficient in sampling shrews (*Sorex araneus*, *S. minutus*) and the common vole (*Microtus arvalis*), while *Apodemus flavicollis*, *A. microps* and *Clethrionomys glareolus* were found more frequently in bait traps.

In addition to direct methods, there are also other indirect methods that can be used to establish small rodent numbers. One such method is the method of counting holes per surface area, and another is the estimation of damage intensity on forest seeds and young plants. Other methods applied include following animal tracks and feces. These indirect methods, as described above, allows for the determination of population number without capturing individual animals.

Mathematical modeling of the population distribution of small rodents has been analyzed by the following authors: Brinbaum & Hall [1960], Chewing [1975], Stenseth et al. [1977], Conley & Nichols [1978], Southern [1979], Anderson [1982], Gustafsson [1983, 1985], Blundell et al. [2001], and others. Certain small rodent species breed mostly during the warm summer months, others in early spring and autumn, while there are yet other species for which air temperature has no significant impact on reproduction [Bronson, 1979].

The population density of some small rodent species varies during one or more years [Gliwicz, 1980; Henttonen, 2000]. Over multi-year periods, periodical population calamities can occur within these species. During these periods, they can cause damage to forest plants which can assume the characteristics of real disasters [Gliwicz, 1980; Lund, 1988]. The authors concluded that forest seeds were primarily damaged by mice, while roots and young plant bark were mostly damaged by voles [Moraal, 1993]. Most of this damage takes place in the late autumn and winter when there are large numbers of small rodents and food sources are limited. According to Myllymäkia [1977], the field vole (*Microtus agrestis*) is considered to be the main pest for forest plants. The southern border of its land area is in Croatia [Kryštufek et al. 1989]. Unlike the common vole (*Microtus arvalis*), the field vole is slightly larger and is not found on arable land. It is found in large numbers every 3 to 4 years. The influence of diet on the breeding of the species *Mus musculus* was studied by Olsen [1981], who concluded that the number of gravid females doubled when their food contained higher quantities of the plant hormone gibberelin. When this hormone was completely removed from the plants of their diet during the germination and intensive growth phases, female fertility was considerably reduced. The behavior among individuals of each sex and care in the upbringing of the young was investigated by Kowalski [1976], Meehan [1984], etc.

In order to successfully suppress the population, it is necessary to understand their senses (smell, touch, sight, hearing and taste) and reactions to certain stimuli. This was studied by Jensen [1975], Hoffmeyer & Sales [1977], Taylor & White [1978], Bronson [1979], Gipps [1981], Gyger & Schenk [1980, 1980, 1984], Wolton [1984], Zejda [2002], Gortat et al. [2004] and others.

In order to reduce the damage caused by small rodents, many scientists have investigated different methods to suppress their increasing numbers [Davis, 1956; Diehl, 1969; Greaves & Ayres, 1969, 1976; Greaves et al., 1977; Labov, 1981; Floody, 1981; Bäumler et al., 1983; Bäumler et al., 1989; Blaschke & Bäumler, 1989 and others]. Preventive methods used in forestry to fight small rodents, apart from forest cultivation techniques, include the use of repellents [Koehler & Johnson, 1983] and ultrasound and electromagnetic waves [Meehan, 1984]. In Poland, Borowski [1995] tested the effectiveness of the repellent Emol B to protect *Quercus robur* acorns from the damage caused by *C. glareolus* and *A. flavicollis* and the effect of the repellent on seed germination. It was established that the repellent provided no protection from the rodents.

Bäumler et al. [1990] conducted a laboratory and field study in which they treated the common oak acorn [*Q. robur*] with 18 plant extracts and chemical compounds used as repellents aimed at reducing losses caused by *Apodemus flavicollis* and *Clethrionomys glareolus*. The effect of the repellents on germination and growth was investigated. The results showed that treating the acorns with repellents was not advisable, as the protective effects of all the examined elements were of a limited duration and the risk of acorn damage caused by the repellents themselves was too great.

Other studies have revealed that electromagnetic waves negatively affect small rodent behavior. Animals exposed to waves run away from the electromagnetic field and become agitated to the extent that they stop taking food.

Biological rodent suppression includes using their predators, parasites or pathogenic microorganisms [Davis, 1956; Meehan, 1984]. The most frequent pathogenic microorganisms are certain bacterial species [Bykovsky & Kandybin, 1988]. The preparation of bacterial cultures intended for rodent suppression is very complex and requires a great deal of competence and caution on the part of the personnel in order to avoid the possibility of human or animal infection. The application of mechanical, genetic and chemical methods has been studied aimed at reducing the numbers of a single rodent species [Marsh, 1975, 1977]. The use of chemical means is, for the time being, the fastest means of suppressing over bred populations of these mammals. The activity of acute (instantaneous) rodenticides has been studied by Barnett et al. [1975] and others. These rodenticides cause a rapid toxic reaction soon after consumption. The first signs of poisoning and animal death are manifested within minutes or hours, depending on the substance. The disadvantage of today's rodenticides is that even very small quantities represent a significant threat to humans and to domestic and wild animals. Signs of poisoning in animals include strong convulsions, painful crying, creating agitation in other individuals and causing them to run away and avoid the offered toxic food. Over the past three decades, acute rodenticides have been used less frequently in deratization. The introduction of slow-acting rodenticides (anticoagulants) at the early 1950s marked substantial progress in suppressing small rodent populations. These agents prevent coagulation causing blood vessels to rupture in the poisoned animal. Death occurs due to bleeding, 4-12 days upon ingestion of the poisoned food. The toxic effects of first generation anticoagulants were studied by Hadler & Shadbolt [1975], Meehan [1984] and many others. The appearance of rodent resistance to anticoagulant rodenticides in the first generation significantly influenced the success of rodent suppression, as it was passed on to successive generations. Attempts were made to correct the failures to suppress resistant populations through the intensive application of fast-acting rodenticides; however, the expected results were not achieved. In the early 1970s, application of new chemical agents took place in

deratization, i.e. second generation anticoagulants. The results of these studies were published by the following authors: Hadler et al. [1975], Bull [1976], Grand [1976], Lund [1981a,b], Buckle et al. [1982], and others. In general, the suppression of warm-blooded animals is met with aversion, and this is particularly prominent today as the protection of the environment and biodiversity are considered to be the most important forest management objectives. Furthermore, some rodent species have a beneficial impact on forests, by feeding on harmful insect species or spreading spores and fungal mycelia, thereby creating fertile underground soil [Maser et al., 1976].

Only a relatively small number of chemical agents are used in deratization as fumigation rodenticides, as these have a very toxic effect on rodents. These agents are very effective as they penetrate into all crevices of varying materials, provided that the concentration level is adequate. They are particularly applicable in eliminating rodents in their underground corridors [Fluck, 1976; Greaves et al., 1977; Meehan, 1984 and others].

Over the past 30 years, most scientific papers have addressed the suppression of small rodents by means of temporarily or permanently regulating their breeding process. Reproductive obstruction can be achieved by the direct or indirect destruction of reproductive cells prior to fertilization [Marsh, 1973; Marsh & Howard, 1969]. Chemical agents can also be used to target the embryo in various stages of development. Irreversible sterility of animals can be achieved through steroid treatments immediately prior to or after the litter [Howard & Marsh, 1969, 1974]. The suppression of small rodents using chemical compounds that prevent the female from creating sexual pheromones would prevent the possibility of copulation [Whitten, 1956]. A comprehensive understanding of the biology of small rodents and regular observation of their population dynamics is necessary in order to effectively apply chemical sterilizing agents [Gwynn, 1972 a,b].

In order to improve the success rate of bait taken by small rodents, it is essential to have knowledge of their nutrition, how they approach food and their reaction to new food sources [Stefanova et al., 1995]. Water plays an important role in rodent nutrition [Knote, 1982]. The individuals of the genus *Apodemus* and *Pitymys* take relatively small quantities of water. Rodents often satisfy their need for water by drinking dew. If the food quantity is reduced for the species of the genus *Apodemus*, these rodents will soon afterwards proportionally reduce the quantity of water taken. Likewise, with increased quantities of food, the need for water is also increased.

The behavior of small rodents in their habitats is related to sex, sexual maturity, breeding conditions, season and genetics [Gipps, 1983; Mazurkiewicz, 1971, 1981; Rozenfeld & Rasmont, 1991; Kruczek, 1994, 1997; Horne & Ylönen, 1996]. Although the food that a certain rodent species eat in different areas of their distribution in different seasons is well known, how they choose their food is still poorly known. Experiments have shown that they prefer familiar food, and that they were able to determine which food was nutritious by its color and taste [Partridge & Maclean, 1981]. During their study of habitat selection for the species *Apodemus flavicollis* in acidophilic beech (*Fagus sylvatica*) forests in the western Pyrenees (Spain), Castien & Gosalbez [1994] established that during periods when beech seeds were easily available on the forest ground, the rodents preferred such habitats over others.

In order to survive, small rodents rely on their familiarity with their territory [Andrzejewski, 2002]. Apart from setting out to find food and water, they spend their time hiding from predators and many are not successful, thus contributing to the survival of their

various natural enemies [Southern & Lowe, 1982]. There are two essential moments in life of the small rodents; i.e. when they have to get up the courage to go out into an unknown area, as when the young go out exploring the area outside their shelter for the first time, and when [and if] they begin to go farther from the shelter. Studies have revealed after being removed from their habitat, rodents of the species *C. glareolus* were able to return even from a distance of 100 m [Saint-Girons & Durup, 1974]. They were able to orientate themselves according to the position of their habitat before and after being released. This orientation, however, is not the same with all individuals. In this respect, light conditions play a significant role [Karlsson, 1984]. The fact that small rodents avoid unknown objects can significantly thwart our understanding of their population biology. If individuals vary significantly with regard to their inclination to enter a trap, our estimates of their population density, breeding, survival, mobility and range from the habitat are then limited.

Experiments have revealed that hole-formed traps in which an animal drops in and is thus captured are suitable for young animals, but should not be used more frequently for catching the same animals [Beacham & Krebs, 1980]. Young voles can be trapped more easily, likely due to their lack of experience; however, once caught, individuals do not drop into the same trap twice. All studies carried out using live-traps allow the animals to “sample themselves”, and accordingly, our results depend greatly on changes in their behavior. For these reasons, multiple capturing methods should be used whenever possible and a comparison of the results obtained should be compiled in order to reach a conclusion on population changes.

In southern Europe, in normal conditions with respect to the duration of daylight, bank voles can be active both day and night, with a tendency of greatest activity at dawn and twilight [Greenwood, 1978]. During the summer months, they are more active by night. In order to conduct more detailed research into the activity rhythm of small rodents in natural conditions, researchers began to carry out radio monitoring, primarily of the species *A. sylvaticus* and *C. glareolus*. This proved to be much more difficult for the latter species, due to their substantially smaller size than *A. sylvaticus* [Wolton, 1983; Montgomery & Gurnell, 1985]. The results obtained suggested that greater activity of the wood vole by night makes the bank vole active more frequently at dusk. As for other species of small rodents, though not clearly proven for the bank vole, though there is indirect evidence supporting this, it was observed that the activity of a certain age or sex group could affect the activity of other individuals, i.e. a dominant male can limit the movement and activity of inferior individuals [Gipps, 1981].

Research to date has shown that males have a larger range from their shelters than females [Stoddart, 1977; Wolton & Flowerdew, 1985]. Studying the radius of movement of *A. agrarius* from their shelters, it has been proven that 60% of the sampled animals had an activity radius greater than 100 meters [Liro & Szacki, 1987]. The largest distance of movement exceeded 1000 meters. The manner of using and the level of marking territory also differed by sex.

Although females are capable of behaving much more aggressively under certain conditions and due to the influence of hormones, male bank voles and other mouse-like rodents are more inclined to injury than females, at least within higher density populations [De Jonge, 1980, 1983]. This could be due to a larger number of overlapping areas where they more frequently meet other unknown males they fight with, thus receiving serious injury, rather than more aggressive behavior than shown by females. On the other hand, females possessing a specific territory and will only meet female neighbors with which they are

already familiar in that territory and already have contact with them, rather than males that tend to spread out over a larger territory. It would appear that aggressive behavior among females is more linked to a specific territory than with males, they likely do not fight in boundary areas but their interaction seems to more a mutual avoidance connected with smell markings [Stoddart & Sales, 1985]. Aggression among male bank voles, and with other rodents, is likely dependent on the male sex hormone androgen [Gipps, 1983, 1984]. The sexual maturity of the bank voles, and with that the behavior caused by the sex hormones, is linked to the animal's chronological age and the season. Animals born early on in the breeding season usually drop their litter in the same year, while animals born later in the breeding season will only become sexually mature the following spring [Alibhai & Gipps, 1985].

Spatial behavior can directly affect the population ecology, e.g. the animals can mutually kill each other in a confrontation or one can expel another one from its habitat. This can also indirectly affect physiological processes such as social interactions, thus contributing to the prevention of reproduction.

There is no evidence that would suggest that bank voles in fact kill one another in confrontations or that an animal can physically expel another during such an interaction. What is well known is that in enclosed high density populations, the aggression of adult males affects directly impacts survival of the young [Gipps & Jewell, 1979].

The period of surface activity of *Apodemus* sp. has been studied using various methods, including capture in traps [Brown, 1969], radioactive marking [Kikkawa, 1959], observation via radio transmitters [Wolton, 1983, 1984], direct observation [Greenwood, 1978], and observation in the laboratory and enclosures [Miller, 1954, 1955; Ashby, 1969, 1972; Gurnell, 1975].

All the species of the genus *Apodemus* are primarily nocturnal animals. During the long winter nights, activity reaches its peak 2 to 4 hours after sunset and before dawn, while during the short summer nights, there is usually only one peak of activity in the middle of the night. It is believed that light is the main factor that controls the start of activity [Falls, 1968; Erkinaro, 1970]. Light intensity and the diurnal cycle determine when surface activity will begin, and therefore is closely linked to sunset. Though activity can be reduced during moonlit nights and under wet and cold conditions [temperatures below 3°C], the ecologically similar species of the genus *Peromyscus* showed increased activity during humid nights [Vickery & Bilder, 1981]. Food availability and avoidance of predators could be responsible for such behavior. Certain predators rely on sound in seeking out prey, and rain drops and moist rain litter can reduce the intensity of sound created by prey during its periods of activity, thus making it more difficult for the predator to find them. Smell traces can be also washed out, so that rainy periods are accompanied by an increase in activity [Smith 1979; Stoddart & Sales, 1985].

Studies to date have shown that when found on the surface, mice mainly explore the territory, searching for food or feeding [Watts, 1968; Zemanek, 1972]. In exploring its surroundings, the animal becomes familiar with the topography between the object and possible food and water sources, thus increasing its effectiveness in utilization of these sources, social interactions and interactions between the sexes, and the possibility of escape from possible predators [Barnett, 1958; Metzgar, 1967; Barnett et al., 1976].

When placed in new surroundings, the species of the genus *Apodemus*, like all small rodents, manifest a very high level of activity [Gurnell, 1972, 1975]. Many species of the

genus *Apodemus* are expert climbers [Montgomery, 1980a]. Studies indicate that the life of these animals in the trees is most probably not exclusively connected with seeking food and water, considering that they are often available on the ground [Montgomery, 1980b]. Their climbing could have another purpose. It has been proven that the yellow-necked mouse uses bird nests even at a height of 25 m, and often uses the lower branches so as to escape predators [Balat & Pelikan, 1959; Borowski, 1962].

Most species of the genus *Apodemus* are adapted to climbing on trees [Holišova, 1969]. Sampling of small rodents carried out in a Querceto-Carpinetum forest proved that the species *Clethrionomys glareolus* and *Apodemus flavicollis* were present in trees at a height of 3 meters from the ground as well as on the ground. Both sexes of various ages were found in the trees. Males prevailed in the sample of captured animals. Small rodents preferred oak to spruce trees. Animals were more frequently sampled on trees growing in groups rather than on isolated trees. *Apodemus flavicollis* can climb to a height of 25 m [Borowski, 1962] and there are cases when it was found in bird houses or nests [Balat & Pelikán, 1959]. It is believed that rodents use the bush and low vegetation when soundlessly moving over the territory, in order to remain unnoticeable to predators [King, 1975, 1985]. Life in the trees could be explained by the simple fact that mice explore them as much as they explore other parts within their habitat range. The branches that spread over the forest area could be privileged routes of passage as the animals can silently move over them, as opposed to bare ground surfaces where movements can cause noise and attract predator attention. This was proven for the yellow-necked mouse, which frequently uses the felled trees as its routes for movement [Olszewski, 1968; King, 1985]. The system of creating tunnels, apart from offering protection in severe weather conditions, represents a place for nesting and storing food, and a shelter to escape predators.

There are few studies of the number of animals residing in the tunnel systems. During the breeding season, research suggests that mice nest alone, although the females can be with the young [Walton & Flowerdew, 1985]. During winter, it would appear that mice can nest together (in groups of at least three animals), which is comprehensible due to the importance of conserving energy during the cold winters. It has been established that oxygen utilization per unit of body weight considerably decreases in groups of three, four or five individuals of yellow-necked mice [Fedyk, 1971]. This grouping is more pronounced at lower temperatures, although it is also evident at temperatures between 5–25°C. Saving energy is also seen through the use of deeper nests. Although the majority of tunnels are about 50 cm deep, some are placed even deeper with galleries and space for nests even up to 150 cm. At such depths, temperatures are relatively constant. The role of nests and burrows in the protection of habitat conditions, rather than their role as protection from predators, could be of special importance in the biology of *Apodemus* sp. and in the evolution of their underground shelters. In investigating the appearance and spread of young oak plants in Denmark, Jensen & Nielsen [1986] established that their appearance in groups were derived from the shelters of rodents feeding on acorns (*A. sylvaticus*, *A. flavicollis* and *C. glareolus*). Using radioactive acorn markers, during the following summer, the authors found them 37 meters from the tree. In studying the interaction between the seeds of common beech (*Fagus sylvatica* L.) and the forest rodents *C. glareolus* and *A. flavicollis* that feed on them, Jensen [1985] established that rodents were storing an average of five seeds in underground shelters at a distance from one to 13 meters from the place where the seed fell on the ground.

In studying the nocturnal movements of *A. sylvaticus*, the conclusion was that inferior males avoid contact with dominant males. This avoidance is probably the most frequent consequence of conflicts above ground [Brown, 1969, Brown & Pye, 1975]. The dominant/inferior relationship could be defined as a relationship between two animals where one subjugates the other in a fight; however, it has to be pointed out that this relationship can be predictably contrary in different areas and at different times [Kaufmann, 1983]. To be precise, these relations are interchangeable and are subject to environmental factors. There are examples that animals temporarily denied food became more subjugated in their behavior [Gurnell, 1972, 1977, 1978a, 1978b, 1981, 1985]. Biological processes, such as parasite infections, can also affect social relations. It has been shown that infections by nematodes reduce the likeliness of small mice to become dominant under laboratory conditions [Freeland, 1981; Rau, 1984]. It is important to stress that it is not clearly known whether dominant mice have an advantage in access to limited food supplies or whether they have greater opportunities for breeding, and if the vitality force of dominant mice is greater than that of inferior mice, simply because the inferior animals are limited in the use of their area and because they are forced to move around more frequently [Butler, 1980; Gaines & McClenaghan, 1980].

Animals living in a certain territory do not tolerate those that are only passing through and therefore these “transient individuals” are significant in the determination of their numbers during the annual population cycle. It has been shown that with an increase in population density, their spread increases proportionally and that reduced abundance in spring is proportional to the population density and only slightly higher in years when the density in early spring is greater [Trojan, 1965; Watts, 1969]. Studies on such changes in population density and social behavior of animals and a possible correlation with male aggression have given contradictory results. It would appear that the social structure changes in the late summer and autumn when their number starts to increase. The date this occurs is variable and depends in part on the population density; the higher the population density in early spring, the later this date [Flowerdew & Gardener, 1978; Flowerdew, 1985]. Seed collection is intensified during autumn and the quantity of seeds from trees directly affects the duration of mating in autumn [Gurnell, 1981]. Survival of the population, particularly of the young, is considerably improved at the beginning of this period, which could be explained by the disappearance of the founder of the spring population so that males become more tolerant to neighboring animals [Ylönen & Mappes, 1995]. However, the males continue to be sexually active, which is contradictory with the said connection between aggression and mating in males.

As for females, they do not spread out during spring and early summer. This could be explained by peaceful behavior of the males towards them so that they are not forced to spread out as the young and inferior males are. Individual female losses early in spring are likely due more to reproductive stress than to spreading out [Fairbairn, 1977]. Females independently choose other habitats if these are more suitable for improving their vitality. However, the evidence collected to date suggests that they tend to first choose reproduction over spreading out during first half of the breeding season, although higher densities can stop reproduction in females at that time [Watts, 1969; Horn & Rubenstein, 1984]. It has been proven that females show no changes in aggressive behavior with age [Gurnell, 1972; Ylönen et al., 1995].

Although the impacts of social behavior on population ecology can differ among closely related species, the way that wood voles change their population structure during the year is very similar to that of the species *Peromyscus maniculatus* in North America [Healey, 1967].

The population dynamics of the species *A. sylvaticus* and *A. flavicollis* differ in that the number of *A. flavicollis* increases early on with the arrival of the young, while during the early summer, the numbers of *A. sylvaticus* remains low during this time. Such differences in population dynamics between the species are characteristic of the differences in aggression levels and in the behavior of adult males towards the young [Hoffmeyer & Sales, 1977; Hoffmeyer, 1983].

Several species of small rodents co-inhabit most of the forest habitats throughout Europe. A discussion on their diets and the manner of food collection will mainly refer to the three species found in the forests of the majority of western, central and northern Europe: the wood vole, yellow-necked mouse and bank vole.

The species of the genus *Apodemus* are typical granivores, while the species of the genus *Clethrionomys* lie between granivores and herbivores [Madsen, 1995]. Pronounced changes in the diet by season are evident only for the food of animal origin in lime and hornbeam woods, with these studies primarily conducted in spring and autumn. With regard to seeds, its peak was reached in autumn during only one study, although in all oak and beech forests seeds were consumed to a larger extent in autumn and to a smaller extent during spring and summer [Holišova & Obrtel, 1979]. Morphological analysis of the intestines of two forest mice populations (*A. sylvaticus*) having different diets was conducted in the field by Corp et al. [1997]. One population inhabited sand dunes where food availability was scarce and as such the dominant food source was invertebrates. Another population inhabited a deciduous forest with greater food availability and the food source consisted mainly of seeds. The authors established that the population differences in the intestinal morphology that could be related to the different food source availability in the two habitats.

The tendency to take different food types, as revealed in a laboratory study, could be attributed to differences in nutritious content or the presence of repulsive substances among the types of food or the age of the food itself. In general, animals are more attracted to plant shoots rather than the older parts of aromatic plants. This currently suggests basic [Freeland, 1974] or stimulated chemical protection [Haukioja, 1980; Batzli, 1983]. However, testing of toxic substances could be in connection with the degree of inclination to specific plants, failed to reveal a mutual negative correlation for European small forest rodents. Thus, an item that attracts or rejects the rodent could be of a mechanical nature, i.e. bank voles avoid seeds with a hard shell but eat the fruit surrounding them [Miller, 1954; Watts, 1968; Zemanek, 1972].

Food selection is also linked to a limited quantity of certain food types. This is evident in the consumption of seeds in relation with sowing and also applies to the insects. As such, species of the genus *Apodemus*, in the majority of cases, focus their feeding area to the defoliators such as the larvae and pupae of the order Lepidoptera [Kulicke, 1963; Watts, 1968] and pupae of the wood wasps [Obrtel et al., 1978; Don, 1979].

The impact of food availability affects the competitiveness of related small rodent species. Bäumler and Brunner [1988] conducted a study in a forest stand in western Germany to establish whether damage in small forest planting stocks could be reduced through rivalry between various rodent species. A total of 125 kg of sunflower seeds were spread out on a one hectare plot over a six-week period while seeds were not added to a control plot. It was established that the population density of the species *Apodemus flavicollis* and *A. sylvaticus*

tripled on the experimental plot while the density of the harmful *Clethrionomys glareolus* was insignificantly reduced as compared to the control plot. A similar study was conducted in a common oak forest by Margaletić et al. [2002], with the addition of 130 kg of common oak acorns (*Quercus robur* L.) on a 1.44 hectare test plot surface. The results showed a statistically significant increase in the population of *Apodemus flavicollis*, *A. sylvaticus* and *A. agrarius*, while the population of *C. glareolus*, *Microtus agrestis* and *M. arvalis* were reduced.

Consumption of different foods in nature is influenced by external factors such as physical advantage, relative abundance and food distribution over space and time. It is important that the intake and consumption of energy and nutrients are balanced for different food species [Abt & Bock, 1998].

Taking into account the combined consumption of animal food, seeds and mushrooms and the inclination towards young plant shoots it would appear that the energy and nutritional content that are easily obtainable and of a high level are the essential factors by which forest rodents determine their food selection [Drozd, 1966, 1968, 1970; Holišova, 1971, 1972, 1975]. Only several food types are rejected as they contain toxic substances and it appears that the foods possessing the most balanced level of energy and nutrition are favored.

The range of food takes a central position in the relations among species in a biotic community. This can be also an important factor that influences population density and species dynamics [Smal & Fairley, 1980].

In Bavaria, a study on small rodent populations in mown and unmown areas was conducted on 52 test plots where the age of forest plants was between 2 and 12 years. Ruderal vegetation was eliminated in the course of July and August and rodents sampling was carried out in the period from September to November [Bäumler, 1992]. The study established that populations of *Clethrionomys glareolus* and *C. herborynus* were smaller in mown areas while *Apodemus flavicollis* was more abundant in mown areas. The effect of mowing was insufficient to create a long-term reduction in the vole population.

An analysis of the stomach contents of both species of the genus *Apodemus* showed fewer differences in types of food than in relation to the bank vole. Diet overlap between the yellow-necked mouse and bank vole is greater in the spring [Obrtel & Holišova, 1976, 1978, 1979, 1980, 1981]. It appears that the feeding circumstances are most favorable at that time, and become poorer in late summer. During that period and in autumn, the diets of these two species begin to vary; yellow-necked mice stick to foods of animal origin and seeds, while bank voles turn to green plant parts if the seed yield is insufficient. Within yellow-necked and wood mouse populations, there is significant diet overlap throughout the year [Berry & Tricker, 1969], which appears to increase from spring to autumn. However, the overall food spectrum of wood vole and bank vole is much broader compared to the yellow-necked mouse. These close food relations result in interspecies adaptation with regard to distribution and domination [Gurnell, 1985]. All three species of forest rodents require a certain quantity of concentrated food such as animal food, seeds and mushrooms. The species of the genus *Apodemus* are not able to survive only on plants, and it was revealed that bank voles die if their diet is confined to only plants for an extended period of time though they can survive without seeds [Holišova, 1971]. The acclimation period could be of considerable importance. Researchers also pointed out that bank vole increased their consumption of bait in traps when natural food conditions were poor [Obrtel & Holišova, 1974]. There is evidence that suggests that a lack of concentrated food sources affects the degree of growth and sexual maturity in

bank voles [Holišova, 1971]. Substantial seasonal and geographical differences in intestinal morphology and physiology suggest a temporary limitation, at least as far as food is concerned. Moreover, there is concrete evidence that a good yield of beech nuts positively impacts the growth and breeding of bank voles [Watts, 1969; Jensen, 1982, 1985], which is also true for wood mice [Gurnell, 1981]. Therefore, feeding experiments with seeds have revealed how diet can impact all forest rodents in terms of their growth, survival [Flowerdew et al., 1984], maturation, breeding [Jensen, 1982], migration and population density [Hansson, 1971b, 1979; Hansson & Zejda, 1977; Hansson & Larsson, 1978; Wolf, 1996].

Zoonoses

During evolution, a mutual adaptation of microorganisms and parasites to certain animal species and small rodents took place. Nowadays, small rodents represent an important source of infectious disease for numerous wild and domestic animal species and humans [Esch et al., 1975; Duszinski et al., 1978; Anderson & May, 1979; Boisseau-Lebreuil et al., 1980; Sebek et al., 1980; Sebek et al., 1980; Sterba et al., 1980; Twigg, 1980; Walter & Liebis, 1980; Healing, 1981; Langley & Fairley, 1982; Higgs & Nowell, 1983; Rau, 1983; Lee et al., 1990; Schmaljohn & Hjelle, 1997; Brummer-Korvenkontio et al., 1999; Fischer et al., 2000; Olsson et al., 2002]. This is in relation to the size of the rodent population, their distribution, mobility, feeding intensity, habitat conditions and breeding potential, and the number and spread of wild and domestic animals susceptible to the infectious diseases. Small rodents transmit infectious agents either actively (secretions or excretions) or passively (ectoparasites and endoparasites). A study conducted in the Ukraine (Kharkov district) from 1967 to 1981 proved that the bank vole (*C. glareolus*) was the main host for the tick (*Ixodes trianguliceps*) [Naglova & Naglov, 1983]. The spread of zoonoses transmitted by mice and voles can severely jeopardize the health and number of the susceptible wild animal species and can disturb the balance of the forest ecosystem or cause substantial damage in the organized breeding of wild game. Small rodents play an important role in the spread of infectious and parasitic diseases that are naturally transmitted to humans (trichinellosis, leptospirosis, tick encephalitis, lyme borreliosis, etc.).

Many factors influence the existence, spread and procedures of eradicating infectious diseases originating from small rodents. One such factor is the abundance and density of the rodent population, their spread and mobility, their way of life, feeding and breeding, and climatic and other features of the habitat, or the number, density and spread of wild and domestic animals and humans that are susceptible to a certain infectious or parasitic disease. As germ carriers, small rodents can temporarily or permanently release causative agents through secretions and excretions, thereby contaminating the environment they inhabit turning it into an intermediate and secondary source of infectious disease.

A reservoir of infectious disease is considered to be one or more animal or plant species in which the agent lives and multiplies and upon which their permanent continuation in nature depends. A source of infection is a place containing microorganisms prior to the appearance of the epizootiae/epidemiae with certain susceptible animal or human species and is of a more temporary character.

Epizootiology/epidemiology is an important branch of science concerning infectious diseases and dealing with the cause of origin, development and cessation of the

epizootiae/epidemiae and the methods of their suppression and prevention. Epizootia/epidemia is a common phenomenon of an infectious disease that tends to spread to one or more animal species or to humans in an area. The external factors influencing the micro- and macro-organisms are classified into five epizootiological/epidemiological groups, mutually connected in a closed epizootiological/epidemiological chain. These are virulence and infectious dose of microorganisms, sources of infection, manner of transmission of the infection, entrance of the infection into a host and host disposition. The lack of any group in the chain resulted in absence of the epizootia/epidemia itself. Rodents transmit infectious agents on their extremities via direct touch and by ectoparasites. The spread of a particular disease can oftentimes progress very rapidly due to the large number of rodents, their mobility and the fact that they easily come into contact with humans and domestic and wild animals. Gratz [1988] established that the main sources of leptospirosis are infected animals (primarily *Apodemus agrarius* and *Clethrionomys glareolus*) that release the infectious agents (bacteria of the genus *Leptospira*) through urination.

Leptospirosis is a zoonosis widespread throughout the world, caused by pathogenic members of the genus *Leptospira* with great impact on both human and veterinary public health. Leptospire are immunologically and genetically heterogeneous spiral-shaped microorganisms that comprise about 250 serovars organised into 24 serogroups and several species. Although leptospirosis was first described in Croatia in 1935 [Antunovic-Mikacic, 1935] our understanding of the circulating leptospiral serovars is still scarce. Various small rodents serve unambiguously as reservoir hosts for leptospire and they have potential to shed them in urine for extended periods. The urine of these rodents and domestic and wild animals contaminates grass, surface waters and marshy grounds where the leptospira survive successfully, so that such environments also represent sources of infection for animals and humans who can be infected by leptospira *per os* or through skin abrasions.

Leptospirosis is an endemic zoonosis in Croatia. Detailed analysis of *Leptospira* sp. strains among small rodents captured in 11 different regions of inland Croatia was recently done. Numerous *Leptospira* spp. strains were isolated from small rodents. Phylogenetic analysis revealed that the strains belonged to three different species: *L. borgpetersenii*, *L. kirschneri* and *L. interrogans*. *Mus musculus*, *A. sylvaticus*, *A. flavicollis* and *C. glareolus* showed the high infection level and confirmed their role as major reservoirs of the leptospire in the forest. Close interaction between humans, animals, soil and water in the regions defines a considerable hazard of leptospiral infection to the local population as well as for outdoor-reared domestic animals. For the first time the occurrence of serovars Tsaratsovo and Lora was reported in Croatia [Turk et al., 2003]. *Leptospira* infection was found also among the European brown bears (*Ursus arctos*) from three areas in Croatia. Based on the antibody titers, several serovars were implicated: Australis, Sejroe, Canicola and Icterohaemorrhagiae. There was a strong correlation between serovars in bears and serovars previously isolated from small mammals in Croatia [Modric & Huber, 1993]. A serology testing in patients showed 18 serological types of *Leptospira* detected, and serovars Sejroe, Pomona, Australis and Icterohaemorrhagiae prevailed [Peric et al., 2005].

Numerous small rodent species (*Apodemus sylvaticus*, *A. flavicollis*, *A. agrarius*, *Clethrionomys glareolus*, *Rattus rattus*, *R. norvegicus*, *Mus musculus* and others) are carriers of hemorrhagic fever with renal syndrome [Childs et al., 1985; Gratz, 1988; Childs et al., 1994; Schmaljohn & Hjelle, 1997; Kanerva et al., 1998; Golovljova et al., 2002; Heyman et al., 2002; Nemirov et al., 2002; Vapalathi et al., 2003; Bahr et al., 2004; Cvetko et al., 2005].

This disease represents a serious issue in human medicine due to the large number of disease and due to an insufficient degree of research of the disease infectious agent. The results on observing the populations of natural reservoirs of the hanta virus in the southwestern USA were described by Mills et al. [1999].

Hantaviruses are also endemic in Croatia [Markotić et al., 1996]. So far two viruses, Puumala and Dobrava have been identified as causative agents of hemorrhagic fever with renal syndrome in Croatia [Cvetko et al., 2005; Ledina et al., 2002; Markotić et al., 2002; Miletić-Medved et al., 2002]. Additionally, Tula virus, which is considered a non-pathogenic hantavirus was detected in small mammals. However, *Clethrionomys glareolus*, *Apodemus agrarius* and *Apodemus flavicollis* are the main reservoirs of hantaviruses in Croatia [Cvetko et al., 2005; Markotić et al., 2002; Miletić-Medved et al., 2002]. The incidence of HFRS varies in a cyclic fashion, with peaks occurring every couple of years, coinciding with peaks in rodent's population. Two large HFRS outbreaks were registered in Croatia in 1995 [Ledina et al., 2002; Markotić et al., 1996] and 2002 [Cvetko et al., 2005; Miletić-Medved et al., 2002] with more than 150 and 400 HFRS cases respectively. Dual infections with hantaviruses and leptospira were also detected in humans [Markotić et al., 2002] as well as in rodents [Cvetko et al., 2006].

In addition to leptospirosis and hemorrhagic fever, small rodents are also reservoirs for other zoonoses: lyme borreliosis, tularemia, plague, rabies, foot and mouth disease, etc.

Lyme borreliosis is a tick transmitted, multi-organ infection of humans and animals caused by spirochetes of the *Borrelia burgdorferi* sensu lato group [Hengge et al., 2003]. Lyme borreliosis is nowadays the most frequent human and animal disease transmitted by ticks in Europe and North America. In Euroasia, seven species of the *B. burgdorferi* sensu lato have been reported but at least five of these species are associated with Lyme borreliosis. Lyme borreliosis genospecies, *Borrelia burgdorferi* sensu stricto, *Borrelia afzelii*, *Borrelia garinii*, *Borrelia bissettii* and *Borrelia spielmanii*, were reported to cause human disease in Central Europe [Strle et al., 1997; Wang et al., 1999; Richter et al., 2004]. Lyme borreliosis spirochetes perpetuate in cycles involving rodent reservoir hosts, such as *Apodemus* spp. mice in Euroasia [Matuschka et al., 1992; Richter et al., 2004] or *Peromyscus leucopus* in North America [Anderson et al., 1986]. Such hosts readily become infectious to vector ticks and appear to remain so life-long. They serve as natural reservoirs of infection because numerous subadult vector ticks parasitize them. Fat dormouse (*Glis glis*) was reported to be similarly competent and locally important to these pathogens in central Europe [Matuschka et al., 1994]. The enzootic cycle of *B. burgdorferi* survives through the vector, the tick *Ixodes ricinus*, whose larvae parasitize small rodents. Humans and animals can be infected by the infected nymphs and adult tick stages as they feed on human blood. Humans most susceptible to lyme borreliosis are those who occasionally or regularly spend time outdoors, i.e. in geoeptizootiological areas suitable for the above disease [deciduous forests and the areas with characteristic vegetation, and with an average humidity over 80% that are suitable as habitats for reservoirs and vectors]. The risk of infection is higher during the warmer months of the year, as there is a seasonal connection of the incidence of the disease and the activity of reservoirs and vectors.

In Croatia, Lyme borreliosis is transmitted to humans and animals by *Ixodes ricinus* ticks, from which several strains of *Borrelia* have been evidenced [Rijpkema et al. 1996; Golubic et al. 1998]. There were also several reports about seroprevalence to *B. burgdorferi* sensu lato in humans and animals [Sepcic et al., 1994; Poljak et al. 2000; Turk et al. 2000; Mulic et al.

2006]. However, data on reservoir hosts for Lyme borreliosis pathogens in Croatia are still scarce [Golubic et al. 1998]. There is no data on *Borrelia* infection rates and the character of causative genospecies isolated or detected from fat dormouse in Croatia. To this date, there was only one seroepidemiological investigation showing no seropositivity to *Borrelia burgdorferi* sensu lato in 10 investigated dormice [Sepcic et al., 1994]. Recently, the role of fat dormouse (*Glis glis* L.) as reservoir host for spirochete *Borrelia burgdorferi* sensu lato in Croatia is proved [Turk et al., 2008].

There are some other zoonoses and vector-borne diseases with more or less documented evidence on epidemiological, clinical or etiological features. Croatia has a long tradition in research of zoonoses and vector-borne diseases with substantial collaboration among different professionals: epidemiologists, virologists, clinicians, veterinarians, zoologists, biologists, public health workers, basic scientists and others. With the new era of rising of emerging and re-emerging infectious diseases such ways of collaboration should be additionally supported and improved in the future.

References

- Abt, K. F. & Bock, W. F. 1998: Seasonal variations of diet composition in farmland field mice *Apodemus* spp. and bank voles *Clethrionomys glareolus*. *Acta Theriologica*, **43**[4]: 379–389.
- Alibhai, S. K. 1985: Effects of diet on reproductive performance of the bank vole [*Clethrionomys glareolus*]. *J. Zool.*, **197**: 300–303.
- Alibhai, S. K. & Gipps, J. H. W. 1985: The population dynamics of bank voles. *Symposia of the zoological Society of London*, **55**: 277–313.
- Anderson, J.F., Johnson, R.C., Magnarelli, L.A., Hyde, F.W. 1986: Culturing *Borrelia burgdorferi* from spleen and kidney tissues of wild-caught white-footed mice, *Peromyscus leucopus*. *Zentralbl Bakteriol Mikrobiol Hyg A*, **263**: 34–39.
- Anderson, R. M. & May, R. M. 1979: Population biology of infectious diseases: Part I. *Nature*, **280**: 361–367.
- Anderson, D. J. 1982: The home range: a new nonparametric estimation Technique. *Ecology*, **63**[1]: 103–112.
- Andersson, B. & Gustafsson, T. 1981: Relation between fertility and adrenal growth after mating in the bank vole, *Clethrionomys glareolus*. *Can. J. Zool.*, **59**: 329–331.
- Andersson, C. B. & Gustafsson, T. O. 1982: Effect of limited and complete mating on ovaries and adrenals in the bank vole, *Clethrionomys glareolus*. *J. Reprod. Fert.*, **64**: 431–435.
- Andrejwski, R., Babinska-Werka, J., Liro, A., Owadowska, E., Szacki, J. 2000: Homing and space activity in bank voles *Clethrionomys glareolus*. *Acta Theriologica*, **45**[2]:155-165.
- Andrzejewski, R. & Wroclawek, H. 1961: Mass occurrence of *Apodemus agrarius* [Pallas,1771] and variations in the number of associated Muridae. *Acta Theriologica*, **5** [13]: 173–184.
- Andrzejewski, R. 2002: The home range concept in rodents revised. *Acta Theriologica* **47**, Supplement [1]: 81-101.
- Ashby, K. R. 1967: Studies of the ecology of field mice and voles [*Apodemus sylvaticus*, *Clethrionomys glareolus*, *Microtus agrestis*] in Houghall Wood, *Duram. J. Zool.*, **152**: 389–513.

- Ashby, K. R. 1972: Patterns of daily activity in mammals. *Mammal Rev.*, **1**: 171–185.
- Bahr, U., Muranyi, W., Müller, S., Kehm, R., Handermann, M., Darai, G., Zeier, M. 2004: Bovine aortic endothelial cells are susceptible to Hantaan virus infection. *Virology*, **321**: 1–7.
- Balat, F. & Pelikán, J. 1959: On *Apodemus flavicollis* Melch. occupying nest boxes for birds. *Zool. Listy*, **3**: 257–287.
- Barčiova, L., Macholan, M. 2006: Morphometric study of two species of wood mice *Apodemus sylvaticus* and *A. flavicollis* [Rodentia, Muridae]: traditional and geometric morphometric approach. *Acta Theriologica*, **51** [1]: 15–27.
- Baril, C. & SaintGirons, I. 1990: Sizing of the *Leptospira* genome by pulsed-field agarose gel electrophoresis. *FEMS Mikrobiol. Lett.*, **71**: 95–100.
- Barnett, S. A. 1958: Exploratory behaviour. *J. Psychol.*, **49**: 289–310.
- Barnett, S. A. & Cowan, P. E. 1976: Activity, exploration, curiosity and fear: an ethological study. *Interdisciplinary Sci. Rev.*, **1**: 43–62.
- Barnett, S. A., Munroe, K. M., Smart, J. L. & Stoddart, R. C. 1975: House mice bred for many generations in two environments. *J. Zool. Lond.*, **177**: 153–159.
- Batzli, G. O. 1983: Responses of arctic rodent population to nutritional factors. *Oikos*, **40**: 396–406.
- Bäumler, W. & Brunner, M. 1988: Effect of food availability on competition between sympatric rodent species in forest plantation. *Anzeiger für Schädlingskde., Pflanzenschutz, Umweltschutz*, **61**[1]: 3–5.
- Bäumler, W. 1982: Ein Beitrag zur Prognose der Populationsentwicklung von Mäusen in Forstkulturen. *Anz. Schädlingskde., Pflanzenschutz, Umweltschutz*, **55**, 40–44.
- Bäumler, W. 1983: Integrated control of voles in forest plantations. *Anz. Schädlingskde., Pflanzenschutz-Umweltschutz*, **56**[5]: 94–98.
- Bäumler, W., Bachhuber, E. & Beck, C. 1989: The efficacy of various anticoagulants, against voles, pests in forestry. *Anz. Schädlingskde., Pflanzenschutz-Umweltschutz*, **62**[1]: 9–11.
- Bäumler, W., Fuhrmann, H., Lichtenwald, G., Morigl, R. & Wagner, A. 1983: Erfahrungen mit verschiedenen Ködermitteln und unterschiedlicher Ausbringungstechnik zur Bekämpfung forstschädlicher Wühlmäuse. *Anz. Schädlingskde., Pflanzenschutz, Umweltschutz*, **61**[3]: 3–5.
- Bäumler, W. 1989: Tree roots gnawed by voles. *Anz. Schädlingskde., Pflanzenschutz, Umweltschutz*, **62**[4]: 72–74.
- Bäumler, W., Mielke, H. & Zahner, V. 1990: Treatment of acorns with repellents against rodent damage. *Anz. Schädlingskde., Pflanzenschutz, Umweltschutz*, **63**[1]: 15–19.
- Bäumler, W. 1990: Development of woodland rodents in Bavaria. *Anzeiger für Schädlingskde., Pflanzenschutz, Umweltschutz*, **63**[2]: 96–99.
- Bäumler, W. 1992: Weed control and voles in forest plantations. *Anzeiger für Schädlingskde., Pflanzenschutz, Umweltschutz*, **65**[7]: 141–143.
- Bäumler, W. 1998: Predicting damages of voles in forest cultivations. *Anzeiger für Schädlingskde., Pflanzenschutz, Umweltschutz*, **71**: 117–120.
- Beacham, T. D. & Krebs, C. J. 1980: Pitfalls versus live-trap enumeration of fluctuating population of *Microtus townsendii*. *J. Mammal.*, **61**: 486–499.
- Belletti, P. & Lanteri, S. 1996: Allozyme variation among European beech [*Fagus sylvaticus* L.] stands in Piedmont, North Western Italy. *Silvae Getet.*, **45**[1]: 33–37.

- Berger, P. J. & Negus, N. C. 1982: Stud male maintenance of pregnancy in *Microtus montanus*. *J. Mammal.*, **63**: 148–151.
- Bergeron, J. M., Goulet, R. & Gozalezvoyer, A. 1998: The use of coniferous seedlings as alternative food to protect red oak [*Quercus rubra*] from vole girdling. *Scandinavian Journal of Forest Research*, **13**[1]: 50–53.
- Berndt, R. & Oberwinkler, F. 1992: Ultrastructure of septal pores of mycorrhiza-forming ascomycetes. *Mycologia*, **84**[3]: 360–366.
- Berry, R.J. & Rose, F.E.N. 1975: Islands and the evolution of *Microtus arvalis* [Microtinae]. *J. Zool.*, **177**: 395–407.
- Berry, R. J. & Tricker B. J. K. 1969: Competition and extinction: the mice of Foula, with notes of those of Fair Isle and St. Kilda. *J. Zool. Lond.*, **158**: 247–265.
- Birnbaum, Z. W. & Hall, R. A. 1960.: Small-sample distribution for multisample statistics of the Smirnov type. *Ann. Math. Statist.***31**: 710–720.
- Blaschke, J., & Bäumler, W. 1989: Micophagy and Spore Dispersal by Small Mammals in Bavarian Forests. *Forest Ecology and Management*, **26**: 237–245.
- Blundell, G. M., Maier, J. A. K., Debevec, E. M. 2001: Linear home ranges: effects of smoothing, sample size and autocorrelation on kernel estimates. *Ecological Monographs*, **71**[3]: 469–489.
- Boisseau-Lebreuil, M. T., Launay, H., Bailly-Choumara, H. & Beaucornu, J. C. 1980: Occurrence of adiaspores of *Emmonsia crescens* in the lungs of small mammals in northern Morocco. *Bulletien de la Societé and Ecology*, **8**: 61–66.
- Borkowska, A. 1995: Seasonal-changes in gut morphology of the striped field-mouse [*Apodemus agrarius*]. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **73**[6]: 1095–1099.
- Borowski, S. 1962: *Apodemus flavicollis* [Melchior, 1834] in the tops of tall trees. *Acta Theriol.*, **6**: 314.
- Borowski, Z. 1995: Testing of Emol B against damage caused to acorns by small mammals. *Sylwan.*, **139**[5]: 79–83.
- Borowski, Z. 2003: Habitat selection and home range size of field voles *Microtus agrestis* in Slowinski National Park, Poland. *Acta Theriologica*, **48** [3]: 325–333.
- Bostrom, U. & Hansson, L. 1981: Small rodent communities on mires: implications for population performance in other habitats. *Oikos*, **37**: 216–224.
- Bronson, F. H. 1979: The role of priming pheromones in mammalian reproductive strategies. In: Ritter, F.J. [ed.], *Chemical Ecology. Odour Communication in Animals*, 97–104.
- Brown, A. M. & Pye, J. D. 1975: Auditory sensitivity at high frequencies in mammals. *Adv. Comp. Physio. Biochem.*, **6**: 1–73.
- Brown, L. E. 1969: Field experiments on the movements of *Apodemus sylvaticus* L. using trapping and tracking techniques. *Oecologia*, **2**: 198–222.
- Brummer-Korvenkontio, M., Vapalahti, O., Henttonen, H., Koskela, P., Kuusisto, P., Vaheri, A. 1999: Epidemiological study of Nephropathia epidemica in Finland, 1989–96. *Scand. J. Infect. Dis.*, **31**: 427–435.
- Bryja, J., Heroldová, M., Zejda, J. 2002: Effects of deforestation on structure and diversity of small mammal communities in the Moravskoslezské Beskydy Mts [Czech Republic]. *Acta Theriologica*, **47**[3]: 295–306.

- Buckle, A. P., Rowe, F. P. & Husin, A. R. 1982: Laboratory evaluation of the anticoagulants coumatetralyl and brodifacoum against *Rattus argentiventer* in Peninsular Malaysia. *Trop. Pest Mgmt.*, **28**: 126–130.
- Bujalska, G. 1981: Formation of seks structure in populations of bank vole [*Clethrionomys glareolus* Schreber 1780]. *Wiad. Ekol.*, **27**: 37–48.
- Bull, J. O. 1976: Laboratory and field investigations with difenacoum, a promising new rodenticide. *Proc. 7th Vert. Pest Conf.*, 72–84.
- Butler, R. G. 1980: Population size, social behaviour and dispersal in house mice: a quantitative investigation. *Anim. Bihev.*, **28**: 78–85.
- Bykovski, B. A. & Kandybin, N. V. 1988: Biological principals, development and perspectives of the use of bacteria and viruses. In: Prakash, I. [ed.], *Rodent pest management*, CRC Press, 377 pp.
- Capizzi, D. & Luiselli, L. 1996: Ecological relationship between small mammals and age of coppice in an oak-mixed forest in central Italy. *Revue D'Ecologie-La Terre et la Vie*, **51**[3]: 277–291.
- Castien, E. & Gosalbez, J. 1994: Habitat selection of *Apodemus flavicollis* in a *Fagus sylvatica* forest in the Western Pyrenees. *Folia Zoologica*, **43**[3]: 219–224.
- Chang, S.-C. 2000: Soil nitrogen turnover in proximal and distal stem areas of European beech trees. *Plant and Soil*, **218**: 117–125.
- Chang, S.-C. & Matzner, E. 2000: The effect of beech stemflow on spatial patterns of soil solution chemistry and seepage fluxes in a mixed beech/oak stand. *Hydrological Processes*, **14**: 135–144.
- Chętnicki, W. & Mazurkiewicz, M. 1994: Dispersion of the bank vole in fine- and coarse-grained mosaics of deciduous and mixed coniferous forests. *Acta Theriologica*, **39**[2]: 127–142.
- Chewning, D. 1975: Migratory effect in predator-prey models. *Math. Biosciences*, **23**: 253–263.
- Childs, J. E., Korch, G. W. & Smith, G. A. 1985: Geographical distribution and age related prevalence of antibody to Hantaan-like virus in rat populations of Baltimore, Maryland, USA. *Amer. J. Trop. Med. Hyg.*, **34**: 385–402.
- Childs, J. E., Ksiazek, T. G., Spiropoulou, C. F., Krebs, J. W., Morzunov, S., Maupin, G. O. 2004: Serological and genetic identification of *Peromyscus maniculatus* as the primary rodent reservoir for a new hantavirus in the southwestern United States. *Journal of Infection Diseases*, **169**: 1271–1280.
- Chmiel, K. M. & Harrison, R. M. 1981: Lead content of small mammals at a roadside site in relation to the pathways of exposure. *Science of the Total Environment*, **17**: 145–154.
- Chudoba, S. & Huminski, S. 1980: Estimating numbers of rodents and edge effect using a modified version of the standard minimum method. *Acta theriologica*, **25**: 365–376.
- Clarke, J. R. & Egan, E. A. 1984: Wastage of ova: experimental studies in the field vole [*Microtus agrestis*], the bank vole [*Clethrionomys glareolus*] and wood mouse [*Apodemus sylvaticus*]. *Acta Zool. Fenn.*, **171**: 141–144.
- Clarke, J. R. & Hellwing, S. 1984: Fertility of the post-partum bank vole [*Clethrionomys glareolus*]. *J. Reprod. Fert.*, **68**: 241–246.
- Clarke, J. R. 1985: The reproductive biology of the bank vole [*Clethrionomys glareolus*] and wood mouse [*Apodemus sylvaticus*]. *Sym. Zool. Soc. Lond.*, **55**: 33–59.

- Conley, W. & Nichols, J. D. 1978: The use of models in small mammal population studies. *Spec. Publs Pymatuning Lab. Ecol.*, **5**: 14–37.
- Cook, S. P., Smith, H. R., Hain, F. P., Hastings, F. L. 1995: Predation of gypsy moth [Lepidoptera: Lymantriidae] pupae by invertebrates at low small mammal population densities. *Environ. Entomol.*, **24**: 1234–1238.
- Corp, N., Gorman, M. L., Speakman, J. R. 1997: Apparent absorption efficiency and gut morphometry of wood mice, *Apodemus sylvaticus*, from two distinct populations with different diets. *Physiological Zoology*, **70**[6]: 610–614.
- Csaikl, F., Engel, W. & Schmidtke, J. 1980: On the biochemical systematics of three *Apodemus* species. *Comparative Biochemistry and Physiology*, **65**: 411–414.
- Cvetko, L., Markotić, A., Plyusnina A., Margaletić, J., Miletić-Medved, M., Turk, N., Milas, Z., Avšič-Županc, T. & Plyusnin, A. 2005: Puumala virus in Croatia in the 2002 HFRS Outbreak. *Journal of Medical Virology*, **77**: 290–294.
- Cvetko L., Turk N., Markotić A., Milas Z., Margaletić J., Miletić-Medved M., Plyusnin A., Baranton G., Postic D. & Avšič-Županc T. 2006: Short report: dual infections with Puumala virus and *Leptospira interrogans* serovar Lora in a bank vole [*Clethrionomys glareolus*]. *Am J Trop Med Hyg*, **74**: 612–614.
- Davis, D. E. 1956: The frequency of reduction of rat populations by weather. *Ecology*, **37**: 385–387.
- Deffontaine, V., Libois, R., Kotlik, P., Sommer, R., Nieberding, C., Paradis, E., Searle, J. B., Michaux, J. R. 2005: Beyond the Mediterranean peninsulas: evidence of central European glacial refugia for a temperate forest mammal species, the bank voles [*Clethrionomys glareolus*]. *Molecular Ecology*, **41**: 1727–1739.
- De Jonge, G. 1980: Response to con- and heterospecific male odours by the voles *Microtus agrestis*, *M. arvalis* and *Clethrionomys glareolus* with respect to competition for space. *Behaviour*, **73**: 277–303.
- De Jonge, G. 1983: Aggression and group formation in the voles *Microtus agrestis* and *Clethrionomys glareolus* in the relation to intra- and interspecific competition. *Behaviour*, **4**: 1–73.
- Delany, M. J. 1974: The ecology of small mammals. Studies in biology, 51 Edward Arnold, London, 60 str.
- Diehl, F. P. 1969: Sound as a rodent-deterrend. *Pest Control* **37** [8]: 36–44.
- Diminic, D. & Jurc, M. 1999: Some aspects of *Sphaeropsis sapinea* presence on Austrian pine in Croatia and Slovenia. *Phyton: Annales Rei Botanicae*, **39**[3]: 231–234.
- Doby, J. M., Bigaignon, G. & Degeilh, B. 1992: Potential importance of the wood mouse [*Apodemus sylvaticus*] and bank vole [*Clethrionomys glareolus*] in the epidemiology of Lyme disease in the forest environment of western France, based on rodent-*Ixodes ricinus* relationships. *Bulletin de la Societe Francaise de Parasitologie*, **10**[2]: 271–293.
- Don, B. A. C. 1979: Gut analysis of small mammals during a sawfly [*Cephalcia lariciphila*] outbreak. *Journal of Zoology*, **188**[2]: 209–214.
- Drozd, A. 1966: Food habitats and food supply of rodents in the beech forests. *Acta Theriol.*, **11**: 363–384.
- Drozd, A. 1968: Digestibility and assimilation of natural foods in small rodents. *Acta Theriol.*, **13**: 367–389.

- Drozd, A. 1970: *Digestibility and utilization of natural foods in small rodents*. In: [Eds. Petruszewicz, K., Ryskowski, L.]: Energy flow through small mammal population. Polish Scientific Publishers, Warsaw, 127–129.
- Ducousso, A., Michand, H. & Lumaret, R. 1993: Reproduction and gene flow in the genus *Quercus* L. *Ann. Sci. For.*, **50**[1]: 91–106.
- Dunlap, J. M., Heilman, P. E. & Stettler, R. F. 1994: Genetic variation and productivity of *Populus trichocarpa* and its hybrids. VII. Two-year survival and growth of native black cottonwood clones from four river valleys in Washington. *Canadian Journal of Forest Research*, **24**[8]: 1539–1549.
- Duszynski, D. W., Ressel, D., Roy, S. A. & Castro, G. A. 1978: Suppressed rejection of *Trichinella spiralis* in immunised rats concurrently infected with *Eimeria nieschultzi*. *Journal of Parasitology*, **64**: 83–88.
- Elsner, G. 1993: Morphological variability of oak stands [*Quercus petraea* and *Quercus robur*] in northern Germany. *Ann. Sci. For.*, **50**[1]: 228–232.
- Eriksson, M. 1980: The adrenals of the wood mouse, *Apodemus sylvaticus* [Linné, 1758], at inhibition and regression. *Säugetierkundliche Mitteilungen*, **28**: 255–256.
- Eriksson, M. 1983: The follicle population in the ovaries of two wild mice, *Apodemus flavicollis* and *Apodemus sylvaticus*. *Canadian Journal of Zoology*, **61**: 195–201.
- Erkinaro, E. 1970: Effect on the length of the day and twilight on the phase relationship of the 24 hour periodicity of the field mouse *Apodemus flavicollis* Melch. in natural light. *Oikos*, **13**: 101–107.
- Esch, G. W., Gibbons, J. W. & Borque, J. E., 1975: An analysis of the relationship between stress and parasitism. *Am. Midl. Nat.*, **93**: 339–353.
- Evans, P. D., Michell, A. & Schmalzl, K. J. 1992b: Studies of the degradation and protection of wood surfaces. *Wood Sci. Technol.*, **26**: 151–163.
- Fairbairn, D. J. 1977: The spring decline in deermice: death or dispersal? *Can. J. Zool.*, **55**: 84–92.
- Falls, J. B. 1968: *Activity. Spec. Publ. Am. Soc. Mammal.*, **2**: 543–570.
- Fasola, M., Canova, L. 2000: Asymmetrical competition between the bank vole and the wood mouse, a removal experiment. *Acta Theriologica*, **45**[3]: 353–365.
- Fedyk, A. 1971: Social thermo-regulation in *Apodemus flavicollis* [Melchior, 1834]. *Acta Theriol.*, **16**: 22–29.
- Fernandez, F. A. S., Evans, P. R. & Dunstone, N. 1994: Local variation in rodent communities of Sitka spruce plantations: the interplay of successional stage and site-specific habitat parameters. *Ecography*, **17**[4]: 305–313.
- Fischer, O., Mátlova, L., Bartl, J., Dvorská, L., Melichárek, I., Pavlík, I. 2000: Findings of Mycobacteria in Insectivores and Small Rodents. *Folia Microbiol.*, **45**[2]: 147–152.
- Floody, O. R. 1981: The hormonal control of ultrasonic communication in rodents. *Am. Zool.*, **21**: 129–142.
- Flowerdew J. R., Gurnell J. & Gipps J. H. W., 1984: The Ecology of Woodland rodents Bank Voles and Wood mice. *Symp. zool. soc. Lon.*, 61–165.
- Flowerdew, J. R. 1985: The population dynamics of wood mice and yellow-necked mice. *Symposia of the zoological Society of London*, **55**: 315–338.
- Flowerdew, J. R. & Gardner, G. 1978: Small rodent populations and food supply in a Derbyshire ashwood. *J. Anima. Ecol.*, **47**: 725–40.
- Fluck, E. 1976: The odor threshold of phosphine. *J. Air Poll. Control Ass.*, **26**[8]: 795.

- Freeland, W. J. 1974: Vole cycle-another hypothesis. *Am. Nat.*, **108**: 238–245.
- Freeland, W. J. 1981: Parasitism and behavioural dominance among male mice. *Science*, **213**: 461–462.
- Greenwood, P. J. 1978: Timing of activity of the bank vole [*Clethrionomys glareolus*] and the wood mouse [*Apodemus sylvaticus*] in deciduous woodland. *Oikos*, **31**: 123–127.
- Gaines, M. S. & Mc Clenaghan, L. R. Jr. 1980: Dispersal in small mammals. *Rev. Ecol. Syst.*, **11**: 163–196.
- Gemmeke, H. 1981: Albumine differences of wood and yellow-necked mice [*Apodemus sylvaticus* and *A. flavicollis*, Mammalia, Rodentia] also electrophoretically demonstrable in dried muscles and skins. *Zeitschrift für Säugetierkunde*, **46**: 124–125.
- Gipps, J. H. W. 1983: Maturity, castration and behaviour of male bank voles, *Clethrionomys glareolus* [Mammalia]. *J. Zool.*, **200**: 197–203.
- Gipps, J. H. W. 1984: The behaviour of mature and immature male bank voles [*Clethrionomys glareolus*]. *Anim. Behav.*, **32**: 836–839.
- Gipps, J. H. W. & Jewell, P. A. 1979: Maintaining populations of bank voles, *Clethrionomys glareolus* in large outdoor enclosures, and measuring the response of population variables to the castration of males. *J. Anim. Ecol.*, **48**: 535–555.
- Gipps, J. H. W. 1981: Behavior of bank voles, *Clethrionomys glareolus*, in the field. *Journal of Mammalogy*, **62**: 382–384.
- Gliwicz, J., 1975: Age structure and dynamics of numbers in an island population of bank voles. *Acta theriologica*, **20**: 57–69.
- Gliwicz, J. 1980: Ecological aspect of synurbanization of the striped field mouse, *Apodemus agrarius*. *Wiadomosci Ekologiczne*, **26**: 117–124.
- Golovljova, I., Sjölander, B., Lindegren, G., Vene, S., Vasilenko, V., Plyusnin, A., Lundkvist, Å. 2002: Hantaviruses in Estonia. *J. Med. Virol.*, **68**: 589–598.
- Golubic, D., Rijpkema, S., Tkalec-Makovec, N., Ruzic, E. 1998: Epidemiologic, ecologic and clinical characteristics of Lyme borreliosis in northwest Croatia. *Acta Med Croatica*, **52**: 7–13.
- Gortat, T., Kozakiewicz, M., Barkowska, M., Chartytonik, U. 2004: The role of chemical information in shaping the spatial activity of bank voles in a free-living population. *Acta Theriologica*, **49** [4]: 465–477.
- Grand, M. 1976: Experimental results on a new anticoagulant rodenticide – bromadiolone. *Phytat.-Phytopharm.*, **25**[1]: 69–88.
- Gratz, N. G. 1988: Rodents and human disease: a global appreciation. In: Prakash, I. [ed.], *Rodent Pest Management*, 97–101.
- Greaves, J. H. & Ayres, P. 1969: Some rodenticidal properties coumatetralyl *J. Hyg., Camb.*, **67**: 311–315.
- Greaves, J. H. & Ayres, P. 1976: Inheritance of Scottish-type resistance to warfarin in the Norway rat. *Genet. Res.*, **28**: 231–239.
- Greaves, J. H., Choudry, M. A. & Khan, A. A. 1977: Pilot rodent control studies in rice fields in Sind, using five rodenticides. *Agro-Ecosystems*, **3**: 119–130.
- Greenwood, P. J. 1978: Timing of activity of a bank vole [*Clethrionomys glareolus*] and wood mice [*Apodemus sylvaticus*] in deciduous woodland. *Oikos*, **31**: 123–127.
- Grodzinski, W., Pucek, Z. & Ryszkowski, L. 1966: Estimation of rodent numbers by means of prebating and intensive removal. *Acta Theriol.*, **11**[10]: 297–314.

- Grubešić, M., Krapinec, K., Glavaš, M. & Margaletić, J. 2004: Body measurements and harvesting dynamics of the Fat Dormouse [*Glis glis* L.] in the mountainous part of Croatia. *Acta Zoologica Academiae Scientiarum Hungaricae*, **50**[4]: 271–282.
- Gurnell, J. & Flowerdew, J. R. 1994: Live trapping small mammals. Practical guide. *Occasional publication*, 1–36.
- Gurnell, J. 1972: Studies of the behaviour of wild wood mice *Apodemus sylvaticus* [L.]. Ph. D. thesis: University of Exeter.
- Gurnell, J. 1975: Notes on the activity of wild wood mice, *Apodemus sylvaticus*, in artificial enclosures. *J. Zool.*, **175**: 219–229.
- Gurnell, J. 1977: Neutral cage behavioural interaction in wild wood mice *Apodemus sylvaticus* [Linne, 1758]. *Saugetierk. Mitt.*, **25**: 57–66.
- Gurnell, J. 1978a: Observations on trap response in confined populations of wood mice, *Apodemus sylvaticus*. *J. Zool.*, **185**: 279–288.
- Gurnell, J. 1978b: Seasonal changes in numbers and male behavioural interaction in a population of wood mice, *Apodemus sylvaticus*. *J. Anim. Ecol.*, **47**: 741–755.
- Gurnell, J. 1981: Woodland rodents and tree seed supplies. In [Eds. Chapman, J. A. & Pursley, D.]: *The Worldwide Furbearer Conference Proceedings*, R. R. Donnelly and Sons Co., Falls Church, Virginia, U.S.A.: 1191–1214.
- Gurnell, J. 1985: Woodland rodent communities Symp. *Zool. Soc. Lond.*, **55**: 377–411.
- Gurnell, J. 1993: Tree seed production and food conditions for rodents in an oak wood in southern England. *Forestry*, **66**[3]: 291–315.
- Gustafsson, T. O. 1983: Reproduction and social regulation of sexual maturation in relation to population cyclicity in bank voles [*Clethrionomys glareolus*] Unpubl. Doctoral thesis: University of Lund.
- Gustafsson, T. O. 1985: Sexual maturation of *Clethrionomys glareolus*. *Annls. zool. fenn.*, **22**: 303–308.
- Gwynn, G. W. 1972a: Effects of a chemosterilant on fecundity of wild Norway rats. *Journal of Wildlife Management*, **36**[2]: 550–556.
- Gwynn, G. W. 1972b: Field trial of a chemosterilant on fecundity of wild Norway rats. *Journal of Wildlife Management*, **36**[3]: 823–828.
- Gyger, M. & Schenk, F. 1980: Effect of conspecific scent on ultrasound emission of the wood mouse [*Apodemus sylvaticus*]. *Behavioural Processes*, **5**: 311–322.
- Gyger, M. & Schenk, F. 1980: Semiotical approach to the ultrasonic vocalization in the woodmouse, *Apodemus sylvaticus*. *Behaviour*, **84**: 244–257.
- Gyger, M. & Schenk, F. 1984: Ultrasonic vocalization in the woodmouse. *Acta zool. fenn.*, **171**: 97–99.
- Haim, A. & Izhaki, I. 1994: Changes in rodent community during recovery from fire: relevance to conservation. *Biodiversity and Conservation*, **3**[7]: 573–585.
- Hamilton Jr., W. J. 1941: The food of small forest mammals in eastern United States. *J. Mammal.*, **22**: 250–263.
- Hansson, L. 1971b: Small rodent food, feeding and population dynamics: a comparison between granivorous and herbivorous species in Scandinavia. *Oikos*, **22**: 183–198.
- Hansson, L. & Zejda, G. 1977: Plant damage by bank voles [*Clethrionomys glareolus* [Schreber]] and related species in Europe. *EPPO Bull.*, **7**: 223–242.
- Hansson, L. & Zejda, J. 1977: Plant damage by bank voles [*Clethrionomys glareolus* Schreber] and related species in Europe. European and Mediterranean Plant protection

- Organization [EPPO]: Report of the joint FAO/WHO/EPPO conference on rodents of agricultural and public health concern. *Bulletin European and Mediterranean Plant Protection Organization*, **7**:223–242.
- Hansson, L. & Larsson, T. B. 1978: Vole diet in experimentally managed reforestation areas in northern Sweden. *Holarct. Ecol.*, **1**: 16–26.
- Hansson, L. 1979: Condition and diet in relation to habitat in bank voles *Clethrionomys glareolus*: population or community approach? *Oikos*, **35**: 55–63.
- Hansson, L. 1985: The food of bank voles, wood mice and yellow-necked mice. *Symp. Zool. Soc. Lond.*, **55**: 141–168.
- Hansson, L. 1986: Geographic, inherent variation in feeding behavior of a vole and its implications in pest control. *J. Mamm.*, **67**[3]: 587–589.
- Hansson, L. & Gref, R. 1987: Bark chemistry of *Pinus contorta* and *P. sylvestris* in relation to vole damage. *Scandinavian Journal of Forest Research*, **2**[3]: 359–363.
- Hansson, L. 1991: Bark consumption by voles in relation to mineral contents. *Journal of Chemical Ecology*, **17**[4]: 735–743.
- Hansson, L. 1992: Vole densities and consumption of bark in relation to soil type and bark mineral content. *Scandinavian Journal of Forest Research*, **7**[2]: 229–235.
- Hansson, L. 1994: Bark consumption by voles in relation to geographical origin of tree species. *Scandinavian Journal of Forest Research*, **9**[3]: 288–296.
- Haukioja, E. 1980: On the role of the plant defences in the fluctuation of herbivore populations. *Oikos*, **35**: 202–213.
- Heitland, W. & Bäumler, W. 1999: *CD Biologie 99*, München/Freising.
- Hadler, M. R. & Shadbolt, R. S. 1975: Novel 4-hydroxycoumarin anticoagulants active against resistant rats. *Nature*, **253**: 275–277.
- Hadler, M. R., Redfern, R. & Rowe, F. P. 1975: Laboratory evaluation of difenacoum as a rodenticide. *J. Hyg.*, **74**: 441–448.
- Hansen, T. F., Stenseth, N. C., Henttonen, H. 1999: Multiannual vole cycles and population regulation during long winter: an analysis of seasonal density dependence. *Am. Nat.*, **154**: 129–139.
- Hansson, L. 1970: Methods of morphological diet micro-analysis in rodents. *Oikos*, **21**: 255–66.
- Healing, T. D. 1981: Infections with blood parasites in the small British rodents *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*. *Parasitology*, **83**: 179–189.
- Healy, M. C. 1967: Aggression and self-regulation of population size in deer mice. *Ecology*, **48**: 377–392.
- Hengge, U.R., Tannapfel, A., Tying, S.K., Erbel, R., Arendt, G., Ruzicka, T. 2003: Lyme borreliosis. *Lancet Infect Dis* **3**: 489–500.
- Henttonen, H. 2000: Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjavi, Northern Finnish taiga. *Pol. J. Ecol.*, **48**: 87–96.
- Heroldova, M. 1994: Diet of 4 rodent species from *Robinia-pseudoacacia* stands in south Moravia. *Acta Theriologica*, **39**[3]: 333–337.
- Hestbeck, J. B. 1982: Population regulation of cyclic mammals: the social fence hypothesis. *Oikos*, **39**: 157–163.
- Heyman, P., Van Mele, R., De Jaegere, F., Klingström, J., Vandenvelde, C., Lundkvist, Å., Rozenfeld, F., Zizi, M. 2002: Distribution of hantavirus in Belgium. *Acta Tropica*, **84**: 183–188.

- Higgs, S. & Nowell, F. 1983: Infection patterns of *Eimeria hungaryensis* in the woodmouse *Apodemus sylvaticus*. *Parasitology* **87**: 217–222.
- Hoffmeyer, I. & Sales, G. D. 1977: Ultrasonic behaviour of *Apodemus sylvaticus* and *Apodemus flavicollis*. *Oikos*, **29**: 67–77.
- Hoffmeyer, I. 1973: Interaction in habitat selection in mice *Apodemus flavicollis* and *A. sylvaticus*. *Oikos*, **24**: 108–116.
- Hoffmeyer, I., Sales, G. D. 1977: Ultrasonic behaviour of *Apodemus sylvaticus* and *A. flavicollis*. *Oikos*, **29**: 67–77.
- Hoffmeyer, I. 1983: Interspecific behavioural niche separation in wood mice [*Apodemus flavicollis* and *A. sylvaticus*] and scent marking relative to social dominance in bank voles [*Clethrionomys glareolus*]. Ph. D. thesis: University of Lund.
- Holišova, V. 1969: Vertical movements of some small mammals in a forest. *Zool. Listy*, **18**: 121–141.
- Holišova, V. 1971: The food of *Clethrionomys glareolus* at different population densities. *Přírodov. Pr. Česk. Akad. Věd.*, **5**: 1–43.
- Holišova, V. 1972: The food of *Clethrionomys glareolus* in a reed swamp. *Zool. Listy*, **21**: 293–307.
- Holišova, V. 1975: The food eaten by rodents in reed seamps of Nesyt fishpond. *Zool. Listy*, **24**: 223–237.
- Holišova, V. & Obrtel, R. 1979: The food eaten by *Clethrionomys glareolus* in a spruce monoculture. *Folia zool.*, **28**: 219–230.
- Horn, H. S. & Rubenstein, D. I. 1984: Behavioural adaptations and life history. In: [Eds Krebs, J. R., Davies, N. B.], *Bihevioural ecology: an evolutionary approach* 2nd edn., Blackwell Scientific Publishers, London, 279–298.
- Horne, T. J. & Ylönen, H., 1996: Female bank vole [*Clethrionomys glareolus*] prefer dominant males: but what if there is no choice? *Behav. Ecol. Sociobiol.*, **38**: 401–405.
- Hulme, P. E. & Hunt, M. K. 1999: Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of pray. *Journal of Animal Ecology*, **68**[2]: 417–428.
- Idžojić, M., Pernar, R., Glavaš, M., Zebec, M. & Diminić, D. 2008: The incidence of mistletoe [*Viscum album* ssp. *abietis*] on silver fir [*Abies alba*] in Croatia. *Biologia*, **63**[1]: 81–85.
- Il'enko, A.I. & Krapivko, T.P. 1980: Variations in radiosensitivity of the common field mouse *Apodemus sylvaticus* related to dwelling conditions of the populations. *Radiobiologia*, **20**: 619–623.
- Jedrzejewski, W., Jedrzejewska, B. & Szymura, L. 1995: Weasel population response, home range and predation on rodents in a deciduous forest in Poland. *Ecology*, **76**[1]: 179–195.
- Jensen, T. S. 1985: Seed-seed predator interactions of European beech, *Fagus silvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos*, **44**: 149–156.
- Jensen, T. S. 1975: Trappability of various functional group of the forest rodents *Clethrionomys glareolus* and *Apodemus flavicollis*, and application in density estimation. *Oikos*, **26**: 196–204.
- Jensen, T. S. 1982: Seed production and out breaks of non-cyclic rodent populations in deciduous forests. *Oecologia*, **54**: 184–192.
- Jensen, T. S. 1983: Effect of small mammals on Danish forestry. *Dansk Skovforenings Tidsskrift*, **68**[4]: 332–348.

- Jensen, T. S. 1985: Seed-seed predator interactions of European beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos*, **44**: 149–156.
- Jüdes, U. 1979a: Ecological studies of the wood mouse [*Apodemus sylvaticus* Linné, 1758] and the yellow-necked mouse [*Apodemus flavicollis* Melchior, 1834] in the region of Kiel [Schleswig-Holstein]. I. Population density, weight changes, annual reproduction cycle, biological population parameters. *Zeitschrift für Säugetierkunde*, **44**: 81–95.
- Jüdes, U. 1979b: Ecological studies of the wood mouse [*Apodemus sylvaticus* Linné, 1758] and the yellow-necked mouse [*Apodemus flavicollis* Melchior, 1834] in the region of Kiel [Schleswig-Holstein]. II. Prenatal mortality. *Zeitschrift für Säugetierkunde*, **44**: 95–106.
- Kanerva, M., Mustonen, J., Vaheri, A. 1998: Pathogenesis of Puumala and other hantavirus infections. *Rev. Med. Virol.*, **8**: 67–86.
- Kapusta, J., Marchlewska-Koj, A., Olejniczak, P., Kruczek, M. 1996: Removal of the olfactory system modifies male bank vole behaviour in presence of females. *Behav. Process.*, **37**: 39–45.
- Kapusta, J., Marchlewska-Koj, A., 1998: Interfemale aggression in adult bank voles [*Clethrionomys glareolus*]. *Aggress. Behav.*, **24**: 53–61.
- Karlsson, A. F. 1984: Age-differential homing tendencies in displaced bank voles, *Clethrionomys glareolus*. *Anim. Behav.*, **32**: 515–519.
- Karlsson, A. F. 1984: Over-winter survival in a boreal population of the bank voles, *Clethrionomys glareolus*. *Canadian Journal of Zoology*, **66**: 1835–1840.
- Kaufmann, J. H. 1983: On the definitions and functions of dominance and territoriality. *Biol. Rev.*, **58**: 1–20.
- Kennedy, A. J., Penner, D. F. & Green, J. E. 1989: Small rodent populations and conifer seedling damage on reclaimed area in west central Alberta. *Cronicle*, **65**[4]: 271–275.
- Kierdorf, U., Konjević, D., Lazar, P., Šehić, M. & Grubešić, M. 2004: Malposition and loss of the left mandibular permanent canine in a male wild boar [*Sus scrofa* L.]. *European Journal of Wildlife Research*, **50**: 213–215.
- Kikkawa, J. 1959: Habitats of the field mouse on the Fair Isle in spring 1956. *Glasgow Nat.*, **18**: 65–77.
- Kindvall, O., Nordlander, G. & Nordenhem, H. 2000: Movement behaviour of the pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. *Entol. Exp. Appl.*, **95**: 53–61.
- King, C. M. 1975: The weasel *Mustela nivalis* and its prey in English woodland. *J. Anim. Ecol.*, **49**: 127–159.
- King, C. M. 1985: Interactions between woodland rodents and their predators. *Symp. Zool. Soc. Lond.*, **55**: 219–247.
- Kirkland, G. L. & Sheppard, P. K. 1994: Proposed standard protocol for sampling small mammal communities. In: Merritt, J.F., Kirkland, G.L. & Rose, R. K., [eds.], *Advances in the biology of shrews. Spec. Publ.* **18**: 277–283.
- Kirkland, G. L., Krim, P. M. & Klinedinst, Ch. A. 1990: Proposed standard protocol for sampling of small mammals. *Priv. Publ. Shippensburg*, 72–87.
- Knote, C. E. 1982: Liquid rodent baits. *Pest Control*, **50**[3]: 43–44.
- Koehler, C. E. & Johnson, R. J. 1983: Rodent repellents for conservation agricultural. *Proc. Nebr. Acad. Sci.*, Nebraska Wesleyan University, 101–124.
- Korpimäki, E., Krebs, C. J. 1996: Predation and population cycles of small mammals. *BioScience*, **46**: 754–764.

- Koskela, E., Mappes, T., Ylönen, H. 1997: Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. *J. Anim. Ecol.*, **66**: 341–347.
- Kotlik, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J. R., Searle, J. B. 2006: A northern glacial refugium for bank voles [*Clethrionomys glareolus*]. *PNAS*, **130**[40]: 14860–14864.
- Kowalski, K. 1976: *Mammals an Outline of Terriology PWN*, Polish scientific Publishers Warszawa, 408–419.
- Krebs, C. J. & Myres, J. H. 1974: Population cycles in small mammals. *Adv. Ecol. Res.*, **8**: 267–399.
- Krebs, C. J. 1978: A review of the Chitty hypothesis of population regulation. *Can. J. Zool.*, **56**: 2463–2480.
- Kruczek, M. 1994: Reaction of female bank vole *Clethrionomys glareolus* to male chemosignals. *Acta Theriol.*, **39**: 249–255.
- Kruczek, M. 1997: Male rank and female choice in the bank vole *Clethrionomys glareolus*. *Behavioural Processes*, **40**: 171–176.
- Kruczek, M., Pochron, E. 1997: Chemical signals from conspecifics modify the activity of female bank voles, *Clethrionomys glareolus*. *Acta Theriol.*, **42**: 71–78.
- Kruczek, M. & Golas, A. 2003: Behavioural development of conspecific odour preferences in bak voles, *Clethrionomys glareolus*. *Behavioural Processes*, **64**: 31–39.
- Krüger, F. 1996: Cuttings for the prognosis of abundances of, and damage to cause by epigaeically feeding voles [Microtinae], an alternative to trapping. *Anziger fur Schadlingskunde, Pflanzenschutz, Umweltschutz*, **69**: 1–6.
- Kryštufek, B., Tvrtković, N. & Mikuška, J. 1989: Distribution of the field vole [*Microtus agrestis*] in Yugoslavia. *Vestnik československé Společnosti zoologické*, **53**: 195–199.
- Kulicke, H. 1963: Kleinsäuger als Vertilger forstschädlicher Insecten. *Z. Säugetierk.*, **28**: 175–83.
- Kuthe, K. & Kramer, K. 1960: Damage by *C. glareolus* and *M. agrestis* in the forest. *Anz. Schadlingsk.*, **33**[6]: 92–93.
- Labov, J. B. 1981: Pregnancy blocking in rodents: adaptive advantages for females. *Am. Nat.*, **118**: 361–371.
- Langley, R. & Fairley, J. S. 1982: Seasonal variations in infestations of parasites in a woodmouse *Apodemus sylvaticus* population in the West of Ireland. *Journal of Zoolgy*, **198**: 249–261.
- Ledina D., Bradarić N., Borčić B., Turković B., Ivić I., Bakić J., Erceg M. & Tvrtković N. 2002: Dinara - new natural focus of hemorrhagic fever with renal syndrome in Croatia. *Croat Med J*, **43**: 576–580.
- Lee, H. W., Lee, P. W., Baek, L. J., Chu, Y. K. 1990: Geographical distribution of hemorrhagic fever with renal syndrome and hantaviruses. *Arch. Virol., Suppl.* **1**: 5–18.
- Lidicker, W. Z. 1973: Regulation of numbers in an island population of the California vole; a problem in community dynamics. *Ecol. Monogr.*, **43**: 271–302.
- Lögfren, O., Hörnfeldt, B., Eklund, U. 1996: Effect of supplemental food on a cyclic *Clethrionomys glareolus* population at peak density. *Acta Theriol.*, **4**: 383–394.
- Lund, M. 1981a: Hens, eggs and anticoagulants. *Int. Pest Control*, **23**[5]: 126–128.
- Lund, M. 1981b: Comparative effect of the three rodenticides warfarin, difenacoum and brodifacoum on eight rodent species in short feeding periods. *J. Hyg.*, **87**: 101–107.

- Lund, M. 1988: Rodent problems in Europe. In: Prakash, I. [ed.], *Rodent Pest Management*, CRC Press, Inc. Boca Raton, 29–38.
- Madsen, P. 1995: Effects of seedbed type on wintering of beech nuts [*Fagus sylvatica*] and deer impact on sprouting seedlings in natural regeneration. *Forest Ecology and Management*, **73**[1/3]: 37–43.
- Mappes, T., Ylönen, H. & Viitala, J. 1995: Higher reproductive success among kin groups of bank voles [*Clethrionomys glareolus*]. *Ecology*, **76**: 1276–1282.
- Marchlewska-Koj, A. 2000: Olfactory and ultrasonic communication in bank voles. *Pol. J. Ecol.*, **48**: 11–20.
- Marchlewska-Koj, A., Kruczek, M., Olejniczak, P. 2003: Mating behaviour of bank voles [*Clethrionomys glareolus*] modified by hormonal and social factors. *Mammalian Biology*, **68**: 144–152.
- Marchlewska-Koj, A., Kapusta, J., Kruczek, M. 2003: Prenatal stress modifies behavior in offspring of bank voles [*Clethrionomys glareolus*]. *Physiology & Behavior*, **79**: 671–678.
- Margaletić, J., Glavaš, M. & Bäumler, W. 2002: The development of mice and voles in an oak forest with surplus acorns. *Journal of Pest Science*, **75**[4]: 95–98.
- Margaletić, J., Božić, M., Grubešić, M., Glavaš, M. & Bäumler, W. 2005: Distribution and abundance of small rodents in Croatian forests. *Journal of Pest Science*, **78**[2]: 99–103.
- Markotić A., LeDuc J.W., Hlaca D., Rabatić S., Sarcević A., Dasić G., Gagro A., Kuzman I., Barac V., Avšić-Županc T., Beus I. & Dekaris D. 1996: Hantaviruses are likely threat to NATO forces in Bosnia and Herzegovina and Croatia. *Nat Med*, **2**: 269–270.
- Markotić, A., Nichol, S. T., Kuzman, I., Sanchez, A. J., Ksiazek, T. G., Gagro, A., Rabatić, S., Zgorelec, R., Avšuč-Županc, T., Beus, I., Dekaris, D. 2002: Characteristics of Puumala and Dobrava Infections in Croatia. *Journal of Medical Virology*, **66**: 542–551.
- Marsh, R. E. & Howard, W. E. 1969: Evaluation of mestranol as a reproductive inhibitor of Norway rats in garbage dumps. *Journal of Wildlife Management*, **33**: 133–138.
- Marsh, R. E. 1973: Potential chemosterilants for controlling rats. *Beihefte Z. Angew. Zool.*, **3**: 191–198.
- Marsh, R. E. 1975: Recent and future developments in rodenticides. *Bull. Soc. Vector Ecologists*, **2**: 1–56.
- Marsh, R. E. 1977: Bromadiolone – a new anticoagulant rodenticide. *EPPO Bull.* **7**: 495–502.
- Martin, Y., Gerlach, G., Schlötter, C., Meyer, A. 2000: Molecular phylogeny of European muroid rodents based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution*, **16**[1]: 37–47.
- Maser, C., Trappe, J. & Nussbaum, R. 1976: Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology*, **59**: 799–809.
- Matuschka, F.R., Fischer, P., Heiler, M., Richter, D., Spielman, A. 1992: Capacity of European animals as reservoir hosts for the Lyme disease spirochete. *J Infect Dis*, **165**: 479–483.
- Matuschka, F.R., Eiffert, H., Ohlenbusch, A., Spielman, A. 1994: Amplifying role of edible dormice in Lyme disease transmission in central Europe. *J Infect Dis*, **170**: 122–127.
- Mazurkiewicz, M. 1971: Shape, size and distribution of home ranges of *Clethrionomys glareolus*. *Acta Theriol.*, **16**: 23–60.
- Mazurkiewicz, M. 1981: Spatial organisation of a bank vole population in years of small and large numbers. *Acta Theriol.*, **26**: 31–45.

- Masurkiewicz, M. 1994: Factors influencing the distribution of the bank vole in forest habitats. *Acta Theriologica*, **39**[2]: 113–126.
- Meehan, A. P. 1984: *Rats and mice, their biology and control*. Research and Development Division, 383 pp.
- Merzeau, D., Comps, B., Thiébaud, B. & Letouzey, J. 1994: Estimation of *Fagus sylvatica* L. mating system parameters in natural populations. *Ann. Sci. Forestières*, **51**[2]: 163–173.
- Metzgar, L. H. 1967: An experimental comparison of screech owl predation on resident and transient white-footed mice [*Peromyscus leucopus*]. *J. Mammal.*, **48**: 387–391.
- Miklos, P. & Ziak, D. 2002: Microhabitat selection by three small mammal species in oak-elm forest. *Folia Zoologica*, **51**[4]: 275–288.
- Miletić-Medved M., Markotić A., Cebalo L., Turković B. & Avšič-Županc T. 2002: Haemorrhagic fever with renal syndrome in Croatia. *Lancet*, **360**: 415–416.
- Miller, R. S. 1954: Food habits of the wood mouse, *Apodemus sylvaticus* [Linné, 1758] and the bank vole, *Clethrionomys glareolus*, [Schreber, 1780] in Whytam Woods, Berkshire. *Säugetierk. Mitt.*, **2**: 109–114.
- Miller, R. S. 1955: Activity rhythms in the wood mice, *Apodemus sylvaticus*, and the bank vole, *Clethrionomys glareolus*. *Proc. Zool. Soc. Lond.*, **125**: 505–519.
- Mills, J. N., Ksiazek, T. G., Peters, C. J., Childs, J. E. 1999: Long-term studies of hantavirus reservoir populations in the southwestern United States: a synthesis. *Emerg. Infect. Dis.*, **5**: 135–142.
- Michaux, J. R., Magnanou, E., Paradis, E., Nieberding, C., Libois, R. 2003: Mitochondrial phylogeography history of the wood mouse [*Apodemus sylvaticus*] in the western Palearctic region. *Molecular Ecology*, **12**: 685–697.
- Michaux, J. R., Libois, R., Paradis, E., Filippucci, M. G., 2004: Phylogeographic history of the yellow-necked fieldmouse [*Apodemus flavicollis*] in Europe and in the Near and Middle East. *Molecular Phylogenetics and Evolution*, **32**: 788–798.
- Montgomery, W. I. & Gurnell, J. 1985: The behaviour of *Apodemus*. *Symp.zool.Soc. Lond.*, **55**: 89–115.
- Montgomery, W. I. 1980a: Spatial organization in sympatric populations of *Apodemus sylvaticus* and *A. flavicollis* [Rodentia, Muridae]. *Journal of Zoology*, **192**: 379–401.
- Montgomery, W. I. 1980b: The use of arboreal runways by the woodland rodents, *Apodemus sylvaticus* [L.], *A. flavicollis* [Melchior] and *Clethrionomys glareolus* [Schreber]. *Mammal Review*, **10**: 189–195.
- Montgomery, W. I. 1980c: Population structure and dynamics of sympatric *Apodemus* species [Rodentia, Muridae]. *Journal of Zoology*, **192**: 351–377.
- Moraal, L. G. 1993: Prevention of vole damage on trees. *Research Report*, **93**[7]: 1–15.
- Moses, R. A., Boutin, S. 2001: The influence of clear-cut logging and residual leave material on small mammal populations in aspen-dominated boreal mixedwoods. *Can. J. For. Res.*, **31**: 483–495.
- Muzika, R. M., Grushecky, S. T., Liebhold, A. M., Smith, R. L. 2004: Using thinning as a management tool for gypsy moth: the influence on small mammal abundance. *Forest Ecology and Management*, **192**: 349–359.
- Myllymäki, A. 1967: Damage caused by voles on garden plants, field crops and forest trees in Finland. *Maatalous Koetoim.*, **21**: 183–194.

- Myllymäki, A. 1974b: Experience from an unsuccessful removal of a semi-isolated population of *Arvicola terrestris*. *Proceedings of the International Symposium on Species and Zoogeography of European Mammals*, 376–387.
- Myllymäki, A. 1977: Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos*, **29**: 468–493.
- Myllymäki, A. 1977: Outbreaks and damage by the field vole *Microtus agrestis* [L], since World War II in Europe. European and Mediterranean Plant Protection Organization[EPPO], *Report of the joint FAO/WHO/EPPO conference on rodents of agricultural and public health concern*. EPPO Bulletin, 177–207.
- Mulic, R., Antonijevic, S., Klismanic, Z., Ropac, D., Lucev, O. 2006: Epidemiological characteristics and clinical manifestations of Lyme borreliosis in Croatia. *Mil Med*, **171**: 1105–1109
- Naglova, G. I. & Naglov, V. A. 1983: Data on the distribution and ecology of *Ixodes trianguliceps* [Ixodidae] in the Kharkov region. *Parazitologiya*, **17**[5]: 409–410.
- Nemirov, K., Andersen, H. K., Leirs, H., Henttonen, H., Vaheri, A., Lundkvist, Å, Plyusnin, A. 2004: Saarema hantavirus in Denmark. *Journal of Clinical Virology*, **30**: 254–257.
- Nemirov, K., Henttonen, H., Vaheri, A., Plyusnin, A. 2002: Phylogenetic evidence for host switching in the evolution of hantaviruses carried by *Apodemus* mice. *Virus Research*, **90**: 207–215.
- Niethamer, J. & Krapp, F. 1978: Handbuch der Säugetiere Europas: Nagetiere 1/1. *Akad. Verlag Wiesbaden*, **1**: 281–381.
- Niethamer, J. & Krapp, F. 1982: Handbuch der Säugetiere Europas: Nagetiere 2/1. *Akad. Verlag Wiesbaden*, **2**: 51–491.
- Niemeyer, H. 1993: New points on vole control in North Germany. *AFZ, Allgemeine Forst Zeitschrift*, **48**[5]: 228–229.
- Nilson M. E. & Hjältén, J. 2003: Covering pine-seeds immediately after seeding: effects on seedling emergence and on mortality through seed-predation. *Forest Ecology & Management*. **176**: 449–457.
- Nygren, J. 1980: Allozyme variation in natural populations of field vole [*Microtus agrestis* L.]. III Survey of a cyclically density-varying population. *Hereditas*, **93**: 125–136.
- Obrtel, R. 1973: Animal food of *Clethrionomys glareolus* in a lowland forest. *Zool. Listy*, **22**: 111–126.
- Obrtel, R. & Holišova, V. 1976: Trophic Diversity and dietary overlap of two sympatric rodents. *Zool. Listy*, **25**: 217–227.
- Obrtel, R. & Holišova, V. 1978: Variation in trophic niche of *Clethrionomys glareolus* in the two different habitats. *Folia zool.*, **21**: 193–202.
- Obrtel, R. & Holišova, V. 1979: The food eaten by *Apodemus sylvaticus* in a spruce monoculture. *Folia zool.*, **28**: 299–310.
- Obrtel, R. & Holišova, V. 1980: The food eaten by *Apodemus flavicollis* in a spruce monoculture. *Folia zool.*, **29**: 21–32.
- Obrtel, R. & Holišova, V. 1981: Mean individual dietary diversity and its variation in selected small rodents. *Folia zool.*, **30**: 11–22.
- Obrtel, R., Zejda, J. & Holišova, V. 1978: Impact of small rodent predation on an overcrowded population of *Diprion pini* during winter. *Folia zool.*, **27**: 97–110.
- Olsen, P. 1981: The stimulating effect of a phytohormone, gibberellic acid, on reproduction of *Mus musculus*. *Aust. Wildl. Res.*, **8**: 321–325.

- Olsson, G. E., White, N., Ahlm, C., Elgh, F., Verlemyr, A. C., Juto, P. & Ralo, R. T. 2002: Demographic Factors Associated with Hantavirus Infection in Bank Voles [*Clethrionomys glareolus*]. *Emerging Infectious Diseases*, **8**[9]: 924–929.
- Olshewski, J. 1968: Role of uprooted trees in the movements of rodents in the forests. *Oikos*, **19**: 99–104.
- Ostfeld, R. S., Manson, R. H. & Canham, C. D. 1997: Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology*, **78**[5]: 1531–1542.
- Partridge, L. & Maclean, R. 1981: Effects on nutrition and peripheral stimuli on preferences for familiar foods in the bank vole. *Anim. Behav.*, **29**: 217–220.
- Peacock, W. L., Speakman, J. R. 2001: Effect of high-fat diet on body mass and energy balance in the bank vole. *Physiology & Behavior*, **74**: 65–70.
- Pelikan, J. 1966: Analyse von drei populations dynamischen Faktoren bei *Apodemus flavicollis* [Melch.]. *Zeitschrift für Säugetierkunde*, **31**: 31–37.
- Pelikan, J. 1971: Calculated densities of small mammals in relation to quadrat size. *Anales zoologici Fennici* **8**: 3–6.
- Pelz, H. J. 1980a: Population ecology of the striped field mouse, *Apodemus agrarius* [Pallas, 1771], on the western border of its range in eastern Hesse. I. Demography and reproduction. *Zeitschrift für Angewandte Zoologie*, **67**: 179–209.
- Pelz, H. J. 1980b: Population ecology of the striped field mouse, *Apodemus agrarius* [Pallas, 1771], on the western border of its range in eastern Hesse. I. Choice of biotope and behaviour. *Zeitschrift für Angewandte Zoologie*, **67**: 209–223.
- Pernar, N., Bakšić, D., Antonić, O., Grubešić, M., Tikvić, I. & Trupčević, M. 2006: Oil residuals in lowland forest soil after pollution with crude oil. *Biomedical and Life Sciences and Earth and Environmental Science*, **177**[1-4]: 267–284.
- Pernek, M., Hrašovec, B., Matošević, D., Pilaš, I., Kirisits, T. & Moser, J. C. 2008: Phoretic mites of three bark beetles [*Pityokteines* spp.] on Silver fir. *Journal of Pest Science*, **81**[1]: 35–42.
- Pernek, M., Pilaš, I., Vrbek, B., Benko, M., Hrašovec, B. & Milković, J. 2008: Forecasting the impact of the Gypsy moth on low hardwood forests by analyzing the cyclical pattern of population and climate data series. *Forest Ecology & Management*, **255**[5]: 1740–1748.
- Petrusewicz, K., [ed.] 1983: Ecology of the bank vole. *Acta theriologica*, **28**[1]: 1–242.
- Petrusewicz, K., Gorecki, A., Grodzinski, W. & Kozłowski, J. 1983: The concept of productivity and energetics. In: Petrusewicz, K., [ed.], Ecology of the bank vole. *Acta theriologica*, **28**[1]: 128–133.
- Pietsch, M. 1978: Four-year studies on the population dynamics and home range the wood mouse [*Apodemus sylvaticus*], bank vole [*Clethrionomys glareolus*] and field vole [*Microtus agrestis*] in a young conifer plantation in the western Ruhr. *Zeitschrift für Angewandte Zoologie*, **65**[4]: 461–475.
- Poljak, I., Troselj-Vukic, B., Miletic, B., Morovic, M., Ruzic-Sabljić, E., Vucemilovic, A., Materljan, E. 2000: Low sero-prevalence of Lyme Borreliosis in the forested mountainous area of Gorski Kotar, Croatia. *Croat Med J*, **41**: 433–436.
- Poole, R. W. 1974: *An Introduction to Quantitative Ecology*. Mc Graw–Hill Kogakusha, Ltd., Tokio, str. 31–43.

- Pucek, Z., Jedrzejewski, W., Jedrzejewska, B. & Pucek, M. 1993: Rodent population dynamics in primeval deciduous forest [Bialowieza-National-Park] in relation to weather, seed crop, and predation. *Acta Theriologica*, **38**[2]: 199–232.
- Rajska-Jurgiel, E. 2000: Breeding dispersal in *Clethrionomys glareolus* females. *Acta Theriologica*, **45**[3]: 367–376.
- Rajska-Jurgiel, E., Mazurkiewicz, M. 2000: "Single-capture" rodents: vagrants or just newly weaned young? *Acta Theriologica*, **45** [4]: 485–490.
- Rau, M. E. 1983: Establishment and maintenance of behavioural dominance in male mice infected with *Trichinella spiralis*. *Parasitology*, **86**: 319–322.
- Rau, M. E. 1984: Loss of behavioural dominance in male mice infected with *Trichinella spiralis*. *Parasitology*, **88**: 371–373.
- Richter, D., Klug, B., Spielman, A., Matuschka, F.R. 2004: Adaptation of diverse Lyme Disease spirochetes in a natural rodent reservoir host. *Infect Immun*, **72**: 2442–2444.
- Rijpkema, S., Golubic, D., Molkenboer, M., Verbeek-De Kruif, N., Schellekens, J. 1996: Identification of four genomic groups of *Borrelia burgdorferi* sensu lato in *Ixodes ricinus* ticks collected in a Lyme borreliosis endemic region of northern Croatia. *Exp Appl Acarol*, **20**: 23–30.
- Rogers, L. M. & Gorman, M. L. 1995: The diet of the wood mouse *Apodemus sylvaticus* on set-aside land. *Journal of Zoology*, **235**: 77–83.
- Rozenfeld, F. M. & Rasmont, R. 1991: Odour cue recognition by dominant male bank voles *Clethrionomys glareolus*. *Anim. Behav.*, **41**: 839–850.
- Saint-Girons, M. C. & Durup, M. 1974: Homing in *Apodemus sylvaticus* and *Clethrionomys glareolus*: ecological factors, learning and memory. *Mammalia*, **38**: 389–404.
- Sebek, Z., Sixl, W., Stunzer, D., Troger, H. & Chambouris, R. 1980: Blood parasites and parasitic tissue protozoa of small wild mammals of Greece. *Folia Parasitologica*, **27**: 203–206.
- Sebek, Z., Sixl, W., Stunzer, D., Valova, M., Hubalek, Z. & Troger, H. 1980: Blood parasites of small wild mammals in Styria and Burgenland, Austria. *Folia Parasitologica*, **27**: 295–301.
- Semizorova, I. 1971: Changes in the numbers of Muridae on selected plots in 1967 and 1968 as a function of ecological factors. *Prace Vyzkumneho Ustavu Lesniho Hospodarstvi a Myslivosti*, **40**: 105–119.
- Sepcic, J., Morovic, M., Poljak, I., Ruzic-Sabljić, E., Matrljan, E., Sepic-Grahovac, D., Milohanic, S. 1994: Prevalence of *Borrelia burgdorferi* antibodies in a high risk zone for multiple sclerosis [Gorski Kotar, Croatia]. *Neurol Croat*, **43**: 241–246.
- Smal, C. M. & Fairley, J. S. 1980: Food of wood mice [*Apodemus sylvaticus*] and bank voles [*Clethrionomys glareolus*] in oak and yew woods at Killarney, Ireland. *J. Zool.*, **191**: 413–418.
- Smith, J. C. 1979: Factors affecting the transmission of rodent ultrasounds in natural environment. *Am. Zool.*, **19**: 432–442.
- Smyth, M. 1966: Winter breeding in woodland mice, *Apodemus sylvaticus*, and voles, *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford. *J. Anim. Ecol.*, **35**[3]: 471–485.
- Schmaljohn, C. S. & Hjelle, B. 1997: Hantaviruses: a global disease problem. *Emerg. Infect. Dis.*, **3**: 95–104.

- Schindler, U. 1954: Mäuseschäden und Mäusebekämpfung in Niedersachsen 1951-53. Forstwiss. *Centralbl.* **73**, 240–251.
- Schindler, U. 1963: *Clethrionomys glareolus* damage to Scots Pine buds. *Allg. Forstzeitschr.*, **18**[21]: 359–360.
- Southern, H. N. & Lowe, V. P. W. 1982: Predation by tawny owls [*Strix aluco*] on bank voles [*Clethrionomys glareolus*] and wood mice [*Apodemus sylvaticus*]. *J. Zool.*, **198**: 83–102.
- Southern, H. N. 1979: The stability and instability of small mammal populations. In: Stoddart, D. M., [ed.], *Ecology of small mammals*, 103–134.
- Stanko, M., Mosansky, L., Fricova, J. & Casanova, J. C. 1999: Comparison of two sampling methods of small mammals in the margin of a lowland forest. *Biologia*, **54**[5]: 595–597.
- Stefanova, Z., Neychev, H., Ivanovska, N. & Kostova, I. 1995: Effects of a total extract from *Fraxinus ornus* stem bark and esculin on zymosan and carrageenan induced paw oedema in mice. *Journal of Ethnopharmacology*, **46**[2]: 101–106.
- Stehn, R. A. & Jannett, F. J. 1981: Male induced abortion in various microtine rodents. *J. Mammal.*, **62**: 369–372.
- Stenseth, N. C., Hansson, L., Myllymäki, A., Anderson, M. & Katila, J. 1977: General models for the population dynamics of the field vole *Microtus agrestis* in Central Scandinavia. *Oikos*, **29**: 616–642.
- Sterba, J., Tomsikova, A., Prokopic, J. & Novackova, D. 1980: A serological proof of adiaspiro mycosis in wild rodents. *Folia Parasitologica*, **27**: 377–381.
- Stoddart, D. M. 1977: Two hypotheses supporting the social function of odorous secretion of some Old World rodents. In: [Eds. Mozell, M. M. & Muller-Schwarze, D.] *Chemical signals in vertebrates*. Plenum Publ. Corp., N.Y., 333–356.
- Stoddart, D. M. & Sales G. D. 1985: The olfactory and acoustic biology of wood mice, yellow-necked mice and bank voles. *Sym. Zool. Soc. Lond.*, **55**: 117–139.
- Strle, F., Picken, R.N., Cheng, Y., Cimperman, J., Maraspin, V., Lotric-Furlan, S., Ruzic-Sabljić, E., Picken, M.M. 1997: Clinical findings for patients with Lyme borreliosis caused by *Borrelia burgdorferi* sensu lato with genotypic and phenotypic similarities to strain 25015. *Clin Infec Dis*, **25**: 273–280.
- Suzuki, N., Hayes, J. P. 2003: Effects of thinning on small mammals in Oregon coastal forests. *J. Wildl. Manage.*, **67**[2]: 352–371.
- Tapper, S. C. 1979: The effect of fluctuating vole numbers [*Microtus agrestis*] on a population of weasels [*Mustela nivalis*] on farmland. *J. Anim. Ecol.*, **48**: 603–617.
- Tähkä, K. M., Teräväinen, T. & Wallgren, H. 1982: Effect of photoperiod on the testicular steroidogenesis of the bank vole [*Clethrionomys glareolus*]: an in vitro study. *Gen. Comp. Endocr.*, **47**: 377–384.
- Tähkä, K. M., Teräväinen, T. & Wallgren, H. 1983: Testicular steroid metabolism in juvenile bank voles [*Clethrionomys glareolus*]: an in vitro study. *Gen. Comp. Endocr.*, **51**: 394–400.
- Taylor, P. K. & White, P. M. 1978: Changes induced in rat trigeminal nuclei by whisker removal. *Proc. Univ. Otago Med. School.*, 28–56.
- Torelli, N. 1994: Relationship between tree growth characteristics, wood structure and utilization of beech [*Fagus sylvatica* L.]. *Holzforschung und Holzverwertung*, **45**[6]: 112–116.
- Trojan, P. 1965: Intrapopulation relations and regulation of numbers in small forest rodents. *Ekol. Pol.*, **13**: 143–168.

- Turk, N., Modric, Z., Marinculic, A. 2000: Serologic studies on canine Lyme borreliosis in the Zagreb area [Croatia]. *Vet arhiv*, **70**: 39-45.
- Turk, N., Milas, Z., Margaletić, J., Starešina, V., Slavica, A., Riquelme-Sertour, N., Bellenger, E., Baranton, G. & Postic, D. 2003: Molecular characterization of *Leptospira* spp. isolated from small rodents in Croatia. *Epidemiol. Infect.*, **130**[1]:159-166.
- Turk, N., Milas, Z., Margaletić, J., Turk, R., Barbić, Lj., Konjević, D., Perić, S., Štritof, Z., Starešina, V. 2008: The role of fat dormouse [*Glis glis* L.] as reservoir host for spirochete *Borrelia burgdorferi* sensu lato in the region of Gorski Kotar, Croatia. *Eur J Wildl Res*, **54**: 117-121.
- Turček, F. J. 1956: Quantitative experiments on the consumption of tree-seeds by mice of the species *Apodemus flavicollis*. *Suomal. Eläin-ja Kasvit. Seur. Van. Tiedon.*, **10**: 49-59.
- Twigg, G. I. 1980: A review of the occurrence in British mammals of the major organisms of zoonotic importance. *Mammal Review*, **10**: 139-149.
- Vander Wall, S. B. 1993: Seed water content and the vulnerability of buried seeds to foraging rodents. *Am. Midland Nat.*, **129**: 272-281.
- Vander Wall, S. B. 1995: Influence of substrate water on the ability of rodents to find buried seeds. *J. Mammal.*, **76**: 851-856.
- Vander Wall, S. B. 1998: Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology*, **79**: 233-241.
- Vapalahti, O., Mustonen, J., Lundkvist, Å., Henttonen, H., Plyusnin, A., Vaheri, A. 2003: Hantavirus infections in Europe. *The Lancet Infectious Diseases*, **3**: 653-661.
- Verme, L. J., Ozoga, J. J. 1981: Changes in small mammal populations following clear-cutting in upper Michigan conifer swamps. *Can. Field Nat.*, **95**: 253-256.
- Vickery, W. L. & Bilder, J. R. 1981: The influence of weather on rodent activity. *J. Mammal.*, **62**: 140-145.
- Viitala, J. & Hoffmeyer, I. 1985: Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus*: social odour, chemistry and biological effects. *Ann. Zool. Fennici*, **22**: 359-371.
- Walter, G. & Liebisch, A. 1980: The ecology of some blood protozoa of wild small mammals in North Germany. *Acta tropica*, **37**: 31-40.
- Walton, J. B. & Andrews, J. F. 1981: Torpor induced by food deprivation in the wood mouse *Apodemus sylvaticus*. *Journal of Zoology*, **194**: 260-263.
- Wang, G., van Dam, A.P., Dankert, J. 1999: Phenotypic and genetic characterization of a novel *Borrelia burgdorferi* sensu lato isolate from a patient with Lyme borreliosis. *J Clin Microbiol*, **37**: 3025-3028.
- Watts, C. H. S. 1968: The foods eaten by wood mouse [*Apodemus sylvaticus*] and bank voles [*Clethrionomys glareolus*] in Wytham Woods, Berkshire. *J. Anima. Ecol.*, **37**: 25-42.
- Watts, C. H. S. 1969: The regulation of wood mouse [*Apodemus sylvaticus*] numbers in Wytham Woods, Berkshire. *J. Anima. Ecol.*, **38**: 285-304.
- Wegge, P. 1967: Damage by small rodents in forestry [in Norway]. *Norsk Skogbr.*, **13**[5]: 155-156.
- Wendland, V. 1981: Cyclic population changes in three mouse species in the same woodland. *Oecologia*, **48**: 7-12.
- Westlin, L. M. 1982a: Sterile matings at the beginning of the breeding season in *Clethrionomys glareolus* and *Microtus agrestis*. *Can. J. Zool.*, **60**: 2568-2571.

- Westlin, L. M. 1982b: Increased fertility in young primiparous female bank voles, *Clethrionomys glareolus*, treated with prolactin or progesterone after mating. *J. Reprod. Fert.*, **66**: 113–115.
- Westlin, L. M. & Gustafsson, T. O. 1983: Influence of sexual experience and social environment on fertility and incidence of mating in young female bank voles [*Clethrionomys glareolus*]. *J. Reprod. Fert.*, **69**: 173–177.
- Westlin, L. M. & Gustafsson, T. O. 1984: Influence of age and artificial vaginal stimulation on fertility in female bank voles [*Clethrionomys glareolus*]. *J. Reprod. Fert.*, **71**: 103–106.
- Wheeler, P. 2005: The diet of field voles *Microtus agrestis* at low population density in upland Britain. *Acta Theriologica*, **50** [4]: 483–492.
- Whitten, W. K. 1956: Modifications of the oestrus cycle of the mouse by external stimuli associated with male. *J. Endocr.*, **13**: 399–404.
- Wiener, J. G. & Smith, M. H. 1972: Efficiency of four types of traps in sampling small mammals populations. *J. Mammals*, **53**: 868–873.
- Wiger, R. 1979: Demography of a cyclic population of the bank vole [*Clethrionomys glareolus*]. *Oikos*, **33**: 373–385.
- Wilson, D. E. & Reeder, D. M. 1992: *Mammal species of the world*. Smithsonian Institution Press, Washington and London, 501–753.
- Wolff, J. O., 1996: Population fluctuations of mast-eating rodents are correlated with production of acorns. *J. Mammal.*, **77**: 850–856.
- Wolton, J. B. & Andrews, J. F., 1981: Torpor induced by food deprivation in the wood mouse *Apodemus sylvaticus*. *J. Zool.*, **194**: 260–263.
- Wolton, R. J., 1983: The activity of free-ranging wood mice *Apodemus sylvaticus*. *J. Anima. Ecol.*, **52**: 781–794.
- Wolton, R. J., 1984: Individual recognition by olfaction in the wood mouse, *Apodemus sylvaticus*. *Behaviour*, **88**: 191–199.
- Wolton, R. & Flowerdew, J. R., 1985: Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. *Sym. Zool. Soc. Lond.*, **55**: 249–275.
- Wühlisch, G. von, Krusche, D. & Muhs, H.-J., 1995: Variation in temperature sum requirement for flushing of beech provenances. *Silvae Gen.*, **44**: 343–346.
- Ylönen, H. & Viitala, J., 1985: Social organization of an enclosed winter population of the bank vole *Clethrionomys glareolus*. *Ann. Zool. Fennici*, **22**: 353–358.
- Ylönen, H., Pusenius, J. & Viitala, J., 1985: Impact of kinship and familiarity on the annual social organization and population dynamics of *Clethrionomys* and *Microtus* voles. *Ann. Zool. Fennici*, **32**: 225–232.
- Ylönen, H., Mappes, T., 1995: Spacing behaviour and key resources: an experiment on seasonal preferences of male bank voles, *Clethrionomys glareolus*, for food and females. *Ann. Zool. Fennici*, **32**: 445–448.
- Yoccoz, N., Hansson, L., Ims, R. A., 2000: Geographical differences in size, reproduction and behaviour of bank voles in relation to density variations. *Pol. J. Ecol.*, **48**: 63–74.
- Zejda, J., & Holíšova, V., 1971: Quadrat size and the prebaiting effect in trapping small mammals. *Annales Zoologici Fennici*, **8**: 14–16.
- Zejda, J., 1961: Age-structure in populations of the bank vole, *Clethrionomys glareolus* Schreber 1780. *Zool. Listy*, **10**, 249–264.
- Zejda, J., 1962: Winter breeding in the bank vole, *Clethrionomys glareolus* Schreber 1780. *Zool. Listy*, **10**, 249–264.

- Zejda, J., 1966: Litter size in the bank vole, *Clethrionomys glareolus* Schreber 1780. *Zool. Listy*, **10**, 249–264.
- Zejda, J., 1967: Mortality of the population of *Clethrionomys glareolus* in the boottomland forest in 1964. *Zool. Listy*, **16**: 221–238.
- Zejda, J., 2002: Yellow necked mouse attaced a dead bank vole. *Acta Theriol.*, **47**[2]: 221–222.
- Zemanek, M., 1972: Food and feeding habits of rodents in decidous forest. *Acta Theriol.*, **17**: 315–325.
- Zukal, J. & Gaisler, J., 1992: Testing of a new method of sampling small mammal communities. *Folia Zoologica*, **41**[4]: 299–310.
- Zukal, J., 1993: Estimation of ecological parameters of small mammal communities by a new method of sampling. *Folia zoologica*, **42**[1]: 1–12.

Chapter 2

CONTRACTION AND STATUS OF MAASAI LANDS AS WILDLIFE DISPERSAL AREAS AND IMPLICATIONS FOR WILDLIFE CONSERVATION IN AMBOSELI ECOSYSTEM, KENYA

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Abstract

Maasai group ranches are critical wildlife dispersal areas between Amboseli and Tsavo parks in Kenya. However, human activities are decreasing the quality and quantity of these dispersal lands. This study sought to establish the area and spatial location of all human activities by mapping and spatial analysis in relation to wildlife distribution in group ranches. In Kimana Group Ranch, the actual area covered by human activities was 57.83 km² (23%), but increased 55.74% with wildlife displacement. In Kuku Group Ranch, there were eleven clusters of human activities covering 24.4% of the ranch. The actual area was 38.31 km² (4%) but increased to 23.3% with wildlife displacement. In Mbirikani, human activities occupied an actual area of 16.85 km² (1.37%), which increased to 22.97% with wildlife displacement. In all group ranches, Maasai homesteads displaced more wildlife, followed by roads, and electric fences. The threat in Kimana was high proportion of areas taken by human activities both in the area taken as well as the spatial orientation that often blocked of wildlife movements. For Kuku and Mbirikani, the main threat was spatial arrangement of human activity clusters that threatened to block wildlife migration, even though more land was still available for wildlife and pastoralism. This work shows the challenges of changing land uses and consequences for wildlife conservation in Amboseli Ecosystem. Wildlife dispersal area is increasingly shrinking due to human activities and changing land uses, making the future of conservation in the area challenging due to diminishing wildlife dispersal area.

Key words: Amboseli Ecosystem, contraction of corridors, Kenya, wildlife dispersal

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Introduction

The Maasai people have tolerated wildlife and practiced pastoralism alongside wildlife use of their range for many years without actively seeking benefits or significantly harming wildlife until very recently (Cheeseman 2001). The changing socio – economic realities and shrinking land involves real and opportunity costs as wildlife disperses and destroys property, competes for land and resources and endangers human life (Sindiga 1995). It is the socio – economic struggles of the impoverished and poor Maasai that is leading to alternative land uses that are neither ecologically compatible with range use or with wildlife conservation (Campbell *et al.* 2000, 2003). Wildlife has failed to contribute to the majority of the Maasai in terms of socio – economic livelihoods, and therefore is not regarded highly as an alternative land use option in the area (Okello^a 2005, Western 1982). It is therefore mostly displaced or regarded as a burden and vermin in sharing of their communal rangelands (Sibanga & Omwenga 1996, Sindiga 1995). In order to promote conservation in the wildlife dispersal area between Tsavo and Amboseli national parks in Kenya, it is important that local people who live side by side with wildlife and bear wildlife – related losses during dispersal benefit from wildlife (Okello *et al.* 2003, Newmark & Hough 2000, Beresford & Phillips 2000, McNeely 1993).

Agriculture is now being viewed as a positive source of income and food despite its consequences and unsustainability. Also the growing population has encouraged subdivision, which is also supported by the government in an effort to encourage individual land ownership and increase quality of local land stewardship (Galaty 1992). The older generations want to secure their right to the land before their children come of age and increase the number of people that the land must be shared. Current communally owned group ranches are now being subdivided privately – owned individual parcels (Galaty 1992, Pickard 1998, Seno & Shaw 2001, Okello 2005). Many Maasai have taken to renting out their land to members of other tribes as a way to make more money. This has caused a large influx of these non-Maasai peoples and an increase in cultivation. These changes in land use and land tenure have resulted in the encroachment on wildlife dispersal areas (Newmark 1993). Agriculture also decreases the water available to wildlife and cattle. Agriculture consumes 400% more water than humans and animals combined (Barrow *et al.* 1993). This can be a significant problem in semi-arid areas where water is a limiting resource.

Pastoralists incur losses through transmission of diseases from wildlife carriers to livestock. An example of such a disease is Malignant Catarrhal Fever which can be transferred from wildebeest (*Connochaetes taurinus*) to cattle (Ottichilo 1999). Agriculturists also struggle as they are faced with the threat of aggressive crop raiding animals such as the African elephant (*Loxodonta africana*). Elephants also kill livestock, destroy water supplies, demolish grain stores and houses, injure and even kill people. These problems tend to be the worst during the wet season (Western 1975, Newmark 1994). These are the times of the most intense conflicts because agriculture is at its peak and the species disperse from the protected areas because food is abundant outside in the dispersal areas (Western 1975). However, intense conflicts also occur in dry area wildlife concentration areas where people, livestock and wildlife compete for resources (Okello 2005). These human-wildlife conflicts create frustration and animosity towards the wildlife and may result in retaliation killings (Okello 2005, Sindiga 1995, Mwale 2000).

Changing land uses in Amboseli area are also driven by socio –economic and political forces operating locally and nationally in Kenya (Campbell *et al.* 2003). Land use policy over the years that have taken Maasai range and confined them to group ranches has been counter productive to their communal ownership of resources as practiced in pastoralist regimes. Lack of education and political empowerment of the Maasai have also contributed to their poverty levels as economic investment in this rangelands has been neglected by Kenyan political class for many years, sidelining them from equitable sharing and access to national resources. Pastoralism has been constrained by shrinking land resources, poor beef markets, scarcity and high costs of veterinary services, and historical injustices and prejudices against the Maasai (Campbell *et al.* 2003). In recent years, with increasing population in the less than a third arable land in Kenya, immigration into Maasai land to cultivate “idle land” has increased stress to land and few water resources (used for irrigation cultivation). With increasing Maasai population of over 4% (Ntiati 2002, Campbell *et al.* 2000), resource and land competition has increased, leading to degradation of rangelands and increasing poverty among the Maasai. The increasing poverty and human population is leading to socio – economic changes that involve incompatible land use practices (such as cultivation) and resource use competition and conflicts.

Wildlife has begun to contribute tangible benefits to the Maasai as they seek alternative sources of income to the declining pastoralism. But the benefits are now taking a new dimension different from the passive tokens (such as sharing tourism revenue, building schools and clinics for the local people or education bursaries) that have been attempted for over the past 20 years (Western 1982, Campbell *et al.* 2000, Campbell *et al.* 2003). As the Maasai struggle to make a living, they are turning to wildlife resources and especially the associated tourism activities as an alternative source of livelihood. The desire is for more tangible and direct benefits (Okello^a 2005) different from previous strategies of tokens. This would not only offset the costs they incur as a result of wildlife dispersal from Amboseli and Tsavo West / Chyulu National Parks, but also rightly benefit from these resources which have benefited the government and tourism investors at their expense (Honey 1999, Ceballos-Lascurain 1996). This is important to avoid the possibility of wildlife being completely displaced from Maasai communal rangelands where they disperse as a result of embracing alternative land uses and hostility to wildlife conservation (Western 1982, Western 1994, Okello^a 2005). Until recently, except a few cases of conservation areas being leased by tourism investors in group ranches directly benefiting local communities, there has been no sustainable and consistent flow of benefits to local communities derived from wildlife presence on their land (Sindiga 1995, Cheeseman 2001).

There are two possible ways in which local communities can directly benefit from wildlife resources: consumptive and non-consumptive utilization. Consumptive utilization has specific requirements (Du Toit 2001), especially through game ranching and cropping. It has been attempted in Kenya, but remains controversial (Hackel 1999, McNab 1991) due implementation difficulties as well as the potential to encourage illegal wildlife killing through commercial poaching and bushmeat trade (Barnett 2000, Okello & Kiringe 2004). Some of the problems with game cropping include a multitude of genetic and population dynamics problems, as well as increased difficulty in instilling hunting ethics in rural poor societies whose impoverishment will create a dependence on such resources, leading to potential over - exploitation (Macnab 1991). However, no successful conservation is possible in most third world countries where local communities livelihoods are mostly resource –

dependent, and especially where they incur costs and are benefiting (Alpert 1996, Adams & Hulme 2001, Beresford & Phillips 2000, Hackel 1999, Newmark & Hough 2000). Literature is endowed with many suggestions and strategies that have been proposed to share benefits with local communities or involve them in resource conservation process (Western 1982, Newmark & Hough 2000, Western 1994) or addressing their socio – economic development and needs (Norton – Griffiths & Southey 1995, Emerton 2000, Ferraro & Kiss 2000, McNeely 1993, Okello *et al.* 2003).

Non-consumptive utilization such as ecotourism appears to have fewer impacts on wildlife species and potentially more profitable option where the tourism potential exists (Honey 1999, Okello *et al.* 2005) such as Amboseli ecosystem where tourism is well developed (Okello^c 2005). In view of lack of official government compensation for most damages from wildlife or significant direct benefits from wildlife to most Maasai (Sindiga 1995), there is now promotion of ecotourism ventures that will allow Maasai benefit directly from wildlife – based ecotourism ventures as both a livelihood and direct contribution to wildlife conservation (Sindiga 1995). There is now a strong movement of establishment of community and landowners private wildlife sanctuaries that will be owned and managed (for some cases in partnership with tourism investors) in Amboseli and other pastoral areas in Kenya (Western personal communication). The evolution of community owned wildlife sanctuaries in the Amboseli area is a new movement that seeks not only to expand range for dispersing wildlife but establish conservation as a competitive land use option in the rapidly changing socio – economic fabric of the area and changes in land tenure regime.

Kimana Community Wildlife Sanctuary (now leased by African Safari Club) pioneered this in 1996 (Lichtenfeld 1998), but now each of the six group ranches in Tsavo – Amboseli Ecosystem are making their own initiatives (Okello *et al.* 2003). David Western (personal communication) notes that private sanctuaries in Kenya now support over 75% of the wildlife biodiversity in Kenya. But challenges against this still remains. After much land loss historically (Cheeseman 2001), most Maasai hesitate to set aside more of their land for use for conservation as they fear that it easy for them to loose the land. Exploitation by local elites, professional management and lack of equitable sharing of benefits from such investments remains a hindrance to these initiatives (Lichtenfeld 1998), unless the wildlife sanctuaries are owned by individual land owners. Further, it seems that land is still needed for more direct economically rewarding land uses such as pastoralism and agriculture (Okello in press).

Since 1960's, the Maasai have lived in group ranches, which are expansive communal lands with legally known and registered ownership and membership. The aim of creating the Maasai into group ranches was to increase livestock production from pastoralism and prevent further loss of their land to government or other ethnic communities (Frakin 1994). The management of group ranches has been taken over by elites who continually exploit resources and associated benefits without sharing it equitably and widely with other communal land owners, or managing the communal land for greater public good. This, among other reasons (Ntiati 2002) has led to disillusionment with group ranch communal ownership, and failure in maintaining environmental integrity or inspiring greater socio – economic growth from pastoralism (Cheeseman 2001, Galaty 1992). Issues of land are emotive and where it's a primary source of livelihood, its ownership, uses and stewardship becomes of great political, social and economic interest (Kituyi 1990, Juma & Ojwang 1996, Galaty 1992, Ogolla & Mugabe 1996, Seno & Shaw 2002). It is for this reason that land use changes must be

understood and discussed in the context of socio – economic livelihoods and political dispensation (Campbell *et al.* 2003).

Many Maasai believe that if they owned their own land, they would secure it better, be better stewards of it, secure development loans through offering land as collateral, use it in a way that best meets their interests, and have their children become land owners of group ranches and preventing further loss of Maasai land to government or other ethnic communities in Kenya (Ntiati 2002, Campbell *et al.* 2000, Fratkin 1994). Land use changes such as agriculture expansion is also contributing to the shift in land ownership as many Maasai are turning into agropastoralism from purely pastoralism (Okello *et al.* 2003, Campbell *et al.* 2003). This shift in land use is potentially harmful to both pastoralism as a socio – economic and cultural practice as well as wildlife, which shares the range with Maasai livestock (Bourn & Blench 1999). Now group ranches in Amboseli area are at various stages of subdivision, with some like Kimana Group Ranch having been fully sub – divided while others like Mbirikani and Eselenkei making progress towards sub - division (Ntiati 2002).

Group ranch subdivision and incompatible land uses to conservation could lead to people fencing off land and excluding the wildlife (Ntiati 2002, Mwale 2000). The community group ranches in Amboseli area are key wildlife dispersal and migration corridor for wildlife wet season dispersal from parks (Amboseli, Tsavo West, Chyulu and Kimana Community Wildlife Sanctuary). Dispersal is important for wildlife well being, as well as for genetic and population viability. For example, in the wet season when forage and water is widely available, over 80% of wildlife disperses from dry season concentration area (such as Amboseli) into the entire ecosystem (Western 1982). Island biogeography theory (Young and McClanahan 1996) predicts that insularized protected area (such as through incompatible land uses and encroachment of human structures and activities) will have increased incidences of species extinction and reduced population genetic diversity (Fahrig 1997, Meffe & Carroll 1997). This is already believed to be happening in protected areas of East Africa (Soule' *et al.* 1979, Western & Ssemakula 1981, Newmark 1996, Burkey 1994, Okello & Kiringe 2004). Insularization not only affects wildlife populations directly, but fans unending human - wildlife conflicts that lead to wildlife persecution and retaliatory killings (Kenya Wildlife Service 1994, Okello^a 2005, Sindiga 1995, Campbell *et al.* 2000, Mwale 2000, Hoare & Du Toit 1999, Harris & Shaw 1997, Siex & Struhsaker 1999, Thouless & Sakwa 1995), and prevents harmonious sharing of land between people, wildlife and livelihood practices (Makombe 1993, Mwalyosi 1992)

Loss of dispersal areas and migration routes is becoming a big threat to protected areas and their diversity (Okello & Kiringe 2004). This process of insularization is caused by urbanization, fragmentation of habitats, inadequate dispersal area access, the displacement of wildlife through incompatible land uses, and illegal wildlife poaching for trophies or bush meat (Harris & Shaw 1997, Newmark 1996). Wildlife habitats, which once formed continuous large blocks of land, are being broken into several isolated pockets that are no longer available to wildlife during its ranging (Newmark 1996, Meffe & Carroll 1997). The establishment of wildlife corridors linking parks could help to reduce the potential loss of species and ease the threats to biodiversity in protected areas (Newmark 1993, Meffe and Carroll 1997). Dispersal areas also help stabilize the diversity of species of an ecosystem by increasing the rate of immigration and emigration. Insularization effects on a wildlife population can be seen when a small number of individuals of a certain species undergoes a catastrophic decline because of environmental changes, genetic problems, or other random

events due to their isolation in a limited geographic range (Cunningham & Saigo 1999, Young & McClanahan 1996).

The postulates of the island biogeography theory have been shown to apply to parks within East Africa (Western & Ssemakula 1981, Newmark 1993, 1996; Burkey 1995). The threat of biodiversity loss is an eminent one for East African protected areas as they become increasingly insularized by the growing human population in surrounding areas outside protected areas, human activities such as settlement, agricultural cultivation, and active elimination of wildlife on land adjacent to parks (Newmark 1996, Okello & Kiringe 2004). In Amboseli area, attributes associated with rapid population growth and land use changes threaten to completely isolate protected areas from each other (Okello 2005). There is a likelihood that protected areas will lose a significant proportion of their large mammal fauna if they became completely insularized (Burkey 1995).

Several researchers have worked on the issue related to land use changes and implications for wildlife conservation in the Amboseli region (Western 1982, Campbell *et al.* 2003, Worden *et al.* 2003, Noe 2003). However, their work sampled along a catena transects and was assessed land use changes at a landscape level. The method was also mostly aerial based (using light aircraft and satellite images). Their work has provided useful insights on root causes and nature of land use changes. However, a land – based assessment that comprehensively maps and provides information on total coverage and spatial location of all human land uses would be critical for both monitoring purposes, as well as clearly indicating how much land and where it is for wildlife dispersal and pastoralism. This paper sought to provide this ground - based complete assessment of size and location of all human structures / activities that lead to wildlife dispersal area contraction, and relationship of these structures and activities on wildlife presence. The specific objectives were to:

- i. Determine the total coverage of different land uses practices in three critical group ranches (Kuku, Kimana and Mbirikani) between Amboseli and Tsavo national parks, and what proportion of land still remains for wildlife ranging and where within the group ranch.
- ii. Determine spatial location of these human activities and consequences for wildlife dispersal
- iii. Establish the average minimum distance wildlife keep away from each of the various human structures and activities.
- iv. Establish habitat associations of large wild mammals in the dispersal area
- v. Discuss the implications of these findings for the status of Kuku Group Ranch as a wildlife resident and dispersal area for neighboring protected areas.

Study Site

Tsavo - Amboseli area is a major block for wildlife conservation and covers a large area where large mammal species move freely in area communally owned by the Maasai (Wishitemi & Okello 2003). This ecosystem is also home to renowned protected areas such as Tsavo East and West, Chyulu and Amboseli National Park. It comprises an important area for ecotourism that brings Kenya lots of foreign revenue through the tourism industry (Okello *et al.* 2005).

This work was done on a landscape level in three group ranches: Kuku, Kimana and Mbirikani over a period of four years for three weeks in wet season when wildlife disperses in April and November between 2003 and 2007 beginning in Kuku Group Ranch (April 2003, November 2003 and April 2004), Kimana Group Ranch (November 2004, April 2005, November 2005 and April 2006) and Mbirikani Group Ranch (November 2006, April 2007 and November 2007).

The group ranches are located in southern Kenya bordering Tanzania, in the new Oloitokitok District. Kuku Group Ranch covers an area of 960 km², Kimana Group Ranch an area of 251 km² while Mbirikani Group Ranch area is 1,229 km². Most of the area in Oloitokitok District is semi-arid and arid rangeland with a bimodal rainfall pattern (Waters & Odero 1986). This is caused by Kenya's location in the Inter-Tropical Convergence Zone. This is where the northeast and southeast trade wind air masses meet and are forced upwards, expanding, cooling and producing rain (Waters & Odero 1986). The amount of rainfall received in KGR is also influenced by its proximity to Mt. Kilimanjaro. Mt. Kilimanjaro casts a rain shadow affect over the region where moisture in the clouds is lost as air masses move up the south side of the mountain and arrive on the north side of the mountain dry (Katampoi *et al.* 1990).

The area gets long rains occur from March to early June and the short rains occur in October and November. The average annual rainfall received in KGR is 210 mm with 30% being received during the short rains and 45% received during the long rains (Irigia 1995). The vegetation of KGR is mainly composed of woody or bushy grassland and open grasslands. Dominant tree geneses consist of *Acacia*, *Balanitis* and *Commiphora* species (Livestock Production Department 1989; Ngethe *et al.* 1990). For rainfall, KGR experiences a bimodal rainfall pattern, receiving a yearly average between 400 and 500 mm. The long-rain season occurs between March and May and the short-rains from October to December (Livestock Production Department 1989). The majority of KGR is a semi-arid rangeland mostly unsuitable for agricultural practices (Ngethe *et al.* 1990).

The rangelands in the area have a variety of habitats including dense and open shrubland, bushland, and woodland. The dominant vegetation in the riverine habitat is *Acacia xanthophloea* and the drier regions are dominated by *Acacia tortillis* and *Acacia mellifera* (Irigia 1995). Soils in this region are classified as volcanic soils which are generally highly saline and alkaline. In addition, the soils in the KGR area are shallow due to the recent volcanic activity of the region. This volcanic soil is generally unproductive, but near water sources can be extremely fertile (Katampoi *et al.* 1990). Areas further away from water sources are suitable only for pastoralism and wildlife grazing.

The group ranches are part of the Tsavo-Amboseli ecosystem and are situated between Amboseli National Park, Tsavo East and West National Parks, and the Chyulu Hills (figure 1). Together, these group ranches create wildlife corridors and dispersal areas that connect the park islands, allowing the parks to support large populations of seasonally migratory mammals (Western 1975). The group ranches also support large populations of wildlife on their own. In support of this wildlife, Kimana Community Wildlife Sanctuary was established in 1996 (Lichtenfeld 1998). It provides a concentration area in the group ranch for resident and migrating species between protected areas in the ecosystem.

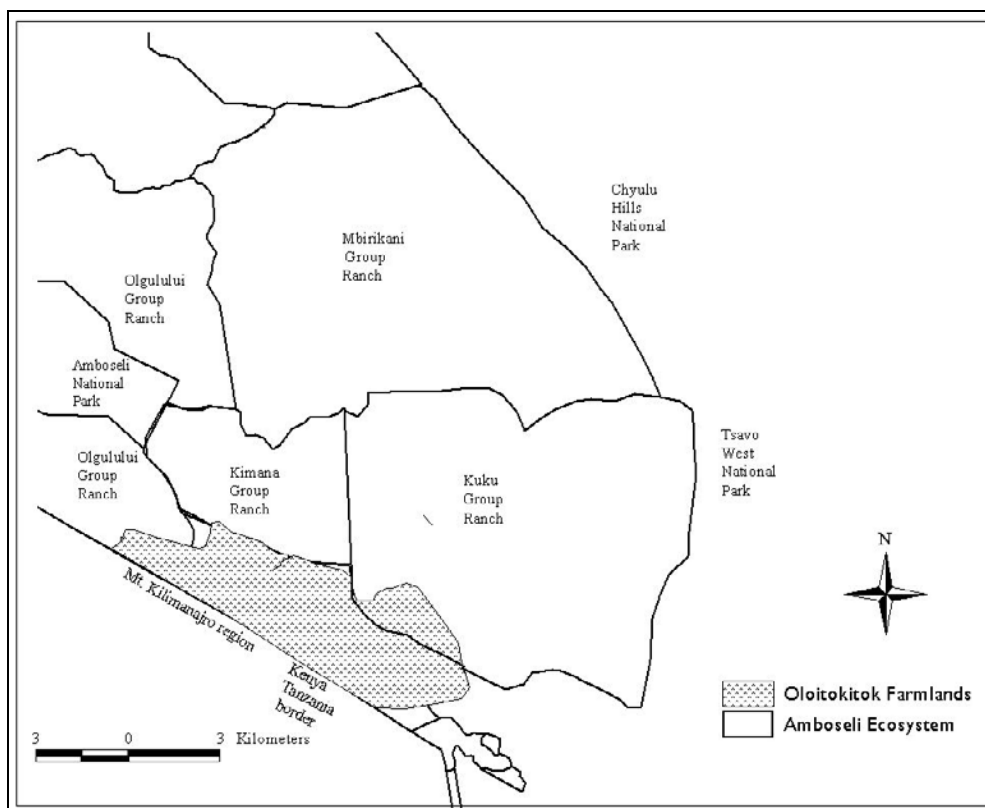


Figure 1. The three critical dispersal areas of Kuku, Kimana and Mbirikani Maasai group ranches between Amboseli National Park on the west and Tsavo West / Chyulu Hills national parks on the east.

In the past, the pastoralist Maasai practices were compatible with wildlife due to the fact that there was a larger space and range similarity in feeding strategies between livestock and most wild large herbivores. Originally, the group ranch was set up to protect the Maasai from losing more land than it had already lost to the colonizing British and other Kenyan ethnic tribes (Campbell *et al.* 2000). KGR had a population of 12,988 people in 1999 (Republic of Kenya 2001) and is now growing. The last census estimated the group ranch to have a density of 36 people per km² (Republic of Kenya 2001), with the Oloitokitok District having an estimated population growth rate of 5.6% compared to the national average of about 3.6% (Government of Kenya 1999). This increasing population size has put pressure on dispersal area resources, such as land and water (Newmark 1993). At the same time, there is a shift in the definition of wealth by the Maasai; originally the Maasai defined their wealth by the number of children and livestock but this is changing to cash and private land (Campbell *et al.* 2000).

This socio – economic changes are increasing demand for group ranch subdivision so that people individually feel secure in land ownership. Newer government policies aim to provide a framework for dismantling communal ownership of land and nomadic pastoralism into individual ownership in support for group ranch subdivision (Graham 1989; Galaty 1992). Kimana is now fully subdivided, and all Maasai group ranches have already begun the process. As subdivision occurs, the Maasai will no longer be able to support their large herds of

livestock without depletion of land resources. In response, many Maasai are becoming agro-pastoralists (Okello 2005) despite the old belief that to till the land is a curse (Seno & Shaw).

Also land tenure policy promoting subdivision and private ownership has increased the opportunity for migrant farmers to lease subdivided land, hence accelerating agriculture expansion in the area (Okello 2005). This switch to agriculture causing serious problems since cultivation is considered one of the most serious threats to wildlife conservation in this region (Okello & Kiringe 2004, Pickard 1998). Almost all agriculture that takes place in these group ranches requires the use of irrigation except in the areas near Kilimanjaro where rain fed agriculture is possible. The use of irrigation reduces water quantity available to other land uses such as pastoralism and wildlife (Campbell *et al.* 2000).

Methods and Materials

This work was done in the wet season when rain had caused growth of forage in all areas of the ecosystem, and when the limiting presence of water has been removed (Western 1975) due to rain water gathering in many places other than dry season concentration areas that have permanent water sources (such as Amboseli, Kimana Swamp and Osoit Pus Swamp). During this season, wildlife ranges widely, and its use of land and resources is largely constrained by human interactions rather than ecological constraints. The primary purpose of wildlife sighting was to establish the closest distance they maintain to human structures and activities (in the wet season when ecological constraints are relaxed) as an index of displacement, rather than on wildlife distribution and density which can be best done by over flight procedure (Worden *et al.* 2003)

Spatial location, area and wildlife displacement effects was assessed for Maasai homesteads (*bomas*), roads, markets, electric fences, learning and social institutions, and agriculture. Wildlife sightings and ranging in relation to these structures in terms of distance away was also evaluated. Groups of researchers traveled throughout the group ranches collecting data in two research sessions in November 2004 and April 2005

Bomas

A boma, a Maasai homestead, consisted of a group of housing units arranged in a circle around a central livestock area and surrounded by a fence, usually of Acacia branches. All bomas in the Kimana group ranch outside of the electric fences (Namelok and Kimana) were mapped using Global Positioning Systems (GPS) (Version III Plus, Germin Corporation 1999). The general location as well as the coordinates of each boma was recorded. Multiple GPS coordinates along the perimeter of the bomas were taken in order to obtain the diameter and area of the entire compound. The number of housing units (Enkaji) within each boma, and the permanence of housing units (based on the dominant materials from which the roof and walls were constructed) and whether the housing units were occupied or abandoned were noted to get information on vital boma statistics as well as permanency of settlements based on materials used to construct housing units within homesteads. The average area covered and diameter (determined using a rangefinder: Bushnell® Laser Rangefinder, Yardage Pro™ 400,

Bushnell Corporation, USA) of the bomas, as well as the average number of housing units, and number of families were calculated.

Roads

In order to map, establish location and area of roads, GPS points were taken at every one kilometer on road segments of main roads, and every half kilometer on straight segments of minor or feeder roads. If the road curved, a GPS point was taken at each curve. All roads in Kimana Group Ranch were mapped. The length of each road segment was recorded from a vehicle odometer, while road segment of widths were determined using a rangefinder (Bushnell® Laser Rangefinder, Yardage Pro™ 400, Bushnell Corporation, USA). An average of several width lengths of roads taken at every GPS together with road length gave both road network mileage as well as area covered. The entire road reserve was included in width determination.

Markets

In order to estimate the area of each market, the market center was identified and a GPS reading taken. The market radius was then determined by walking from the center point in eight straight transect lines to the end of the market in the four primary (N, S, E, W) and in the four secondary (NW, NE, SE and SW) compass directions. In each direction, a GPS point was taken on the far side of the last. Further, the total number and type of structures at each market (stone, tin/timber and mud) were recorded as an indicator of the economic status and permanency of the market center. For analysis, stone structures were considered as permanent, tin/timber as semi-permanent and mud as temporary structures. All structures and activities (shops, social areas, and residential areas) associated with market activities and functions were deemed to be enclosed within the market. The area of each market was determined from the average of radius obtained using a rangefinder (Bushnell® Laser Rangefinder, Yardage Pro™ 400, Bushnell Corporation, USA) in the eight compass directions using the formula of the circle (πr^2). The spatial location of the map was taken by taking points around the periphery of each market, and this was also used to calculate the area from GIS for comparison purposes.

Electric Fences

The spatial locations of electric fences (Kimana and Namelok), their circumferences and area were determined from spatial GIS maps generated after driving or walking around the entire fence and taking GPS points. At all fence corners, GPS points were taken; as well as at all openings, gates, and curved segments. The perimeter of the power house structure was also determined by taking GPS points at the midpoint as well as the four corners in order to determine its total area. Notes on fence conditions, damages and power supply were also taken.

Kimana Community Wildlife Sanctuary (KCWS) and Other Institutions

All public and government institutions (churches, schools, government offices, health facilities, social halls etc.) within Kimana Group Ranch, including KCWS, were mapped with GPS. First, GPS readings were taken at the center of each institution. If the area of the institution was small enough for its boundaries to be within viewing distance, GPS points were taken at the four corners of the institution's perimeter. For such institutions, an estimation of the area was determined from units of length and width obtained using a rangefinder (Bushnell® Laser Rangefinder, Yardage Pro™ 400, Bushnell Corporation, USA). Institution's land and other structures such as gardens and playgrounds were included as part of the area of that institution. For each institution, the number of structures was counted and each was classified according to its building material as stone (a permanent structure), wood/tin (semi-permanent), or mud (temporary). If the property was very large, such as KCWS, it was mapped by walking or driving around its perimeter and taking multiple GPS points at many points, particularly where curving in the perimeter occurred. The area of big institutions was obtained from spatial analysis after GPS points had been plotted on a GIS program.

Agriculture Outside Kimana Electric Fences

All agricultural areas outside the electric fences agricultural clusters were identified and mapped using the GPS equipment. GPS readings were taken at every corner of the entire cultivated area and any point where the perimeter of cultivated areas. The location of agriculture (rainfed and or irrigation - dependent) was mapped and the area outside the fences determined from GIS spatial analysis.

Livestock

When livestock was seen in proximity to wildlife, its identity (cattle, sheep / goats and donkeys) and the number of each livestock type were established and the nearest distance of each kind to a given species of wild large mammal was established. This was done every time wildlife and livestock were in close proximity.

Wildlife Ranging Outside Electric Fences

All large mammalian wildlife in the Kimana Group Ranch outside of fenced areas as well as inside electric fences was mapped whenever they were sighted. The animals consisted of all primates and any mammals larger than a Kirk's Dik-dik (*Madoqua kirkii*). Once wildlife was sighted, GPS coordinates were recorded at those points by driving or walking to that location. The wildlife species name and the number of individuals in each group were recorded. The general habitat type (Open grassland, Open woodland / shrubland, dense woodland / shrubland, and riverine), distance to any livestock type, human structure and

activity within view (by eye or binoculars) were noted. Wildlife displacement distances by these human structures and activities were obtained from average distances between wildlife and these structures and activities.

Further Data Analysis

All data of human structures and activities as well as wildlife and livestock distribution were compiled into Excel[®] 2002 for Windows (Microsoft Corporation, Troy, New York) for processing so as it can be subjected to statistical as well as spatial analysis. All Global Positioning System (GPS) coordinates were entered into a Geographical Information System (GIS) using ARCVIEW[®] software Version 3.3 (Environmental Systems Research Institute, Inc., 2000). Maps were generated showing spatial distribution and area covered by these structures and activities. Spatial analysis showed the relationship of human structures and activities in relationships to each other and wildlife distribution in the group ranch. Other parameters of the structures and activities (such as area and perimeter) were either obtained from actual field dimensions determined (radius, lengths and widths) or GIS maps for larger ones (such as KCWS and electric fences) where that was only possible after spatial analysis. From these determinations, the total area taken up by human structures and activities individually and collectively was calculated.

An average minimum distance for each wildlife species and overall for all wildlife species was calculated to show effect of displacement by human structures and activities, and livestock. Further, from these average distances, the actual area of each structure and activity was adjusted to include wildlife displacement. This total area of wildlife displacement was determined by adding to each structure / activity the average displacement distances to shape dimensions (radius, length or width) of human structures and activities taken and new area determined. The new area was determined for discrete units (such as a single *boma*, a road segment, cultivated plot, one fence etc) and then for entire human structures and activities (such as total for all one hundred *bomas*, all roads, all fences etc).

In order to understand habitat associations with wildlife and livestock, the mean group size of each species of wildlife and livestock types were determined for each habitat type. Chi Square Cross – tabulations (Zar 1999) was used to establish whether livestock or wildlife was dependent or independent of habitat type in terms of its distribution of habitat use (using number of sightings and total number of individuals seen in each habitat).

Results

A) Kuku Group Ranch

The actual area taken by human structures and activities in Kuku Group Ranch was 38.31 km², which was about 4% of the group ranch (table 1). However, factoring in the minimum average distance wildlife kept away from human structures and activities (figure 2), land taken away from wildlife use by human structures and activities increased to 223.70 km², about 23.3% of the group ranch, leaving about 76.7% of Kuku open for pastoralism and wildlife ranging.

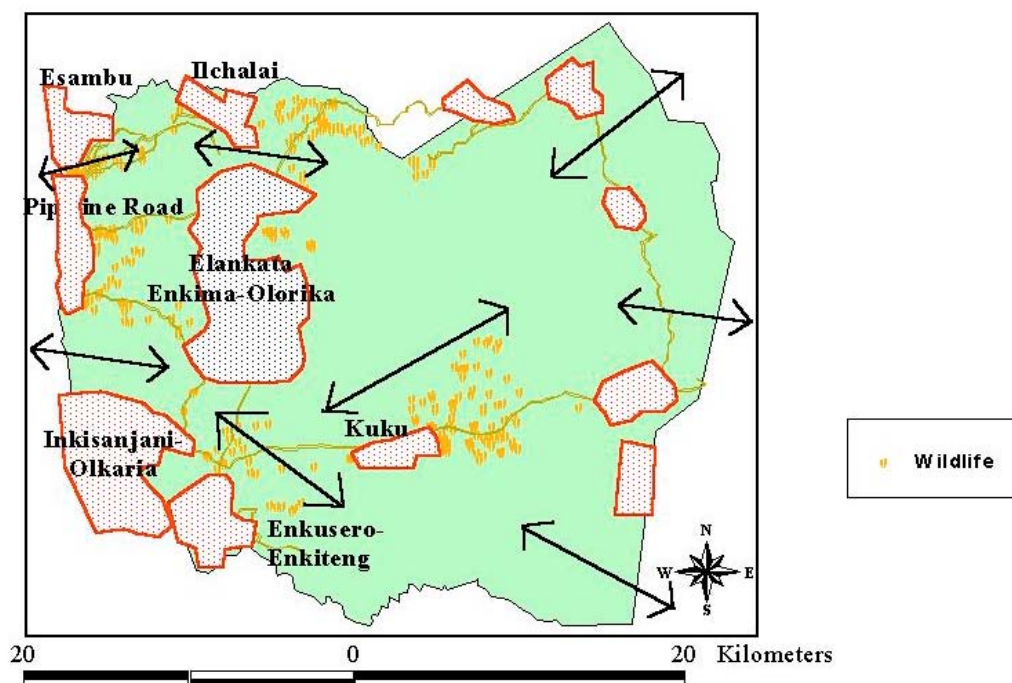


Figure 2. Wildlife distributions and cluster areas of human activity and structure concentration in Kuku Group Ranch. The arrows shows current available migration routes that wildlife can follow between Tsavo West / Chyulu National Park on one side, and Kimana Community Wildlife Sanctuary on another.

Table 1. Area occupied by various human structures and activities, inclusive of wildlife displacement space in Kuku Group Ranch

Variable	Maasai settlements (Bomas)	Roads		Agriculture			Other structures
				Total	Rainfed	Irrigated	
Average distance to closest wildlife (km)	0.43 ± 0.07^1	0.13 ± 0.01		0.57 ± 0.22	0.02 ± 0.01	0.64 ± 0.24	-
Average radius/width (km)	0.02 ± 0.005	0.003 ± 0.13		-	-	-	-
Average radius/width inclusive of distance wildlife keeps off (km)	0.45	0.13		-	-	-	-
Total area actually taken by human structure / activity (km ²)	0.34	Total area: 1.12 km ²	Total length: 222.36 km	30.25	16.19	14.06	6.60
Total area inclusive of distance wildlife keeps off structures / activities (km ²)	151.88	29.35		42.47	16.40	23.78	-
Proportion (%) of actual areas structure/activity covers in KGR	0.04	0.12		3.15	1.67	1.46	0.69

Table 1. Continued

Variable	Maasai settlements (Bomas)	Roads	Agriculture			Other structures
			Total	Rainfed	Irrigated	
Proportion (%) of structure/activity inclusive of space wildlife keeps off the human structure / activity in KGR	15.80	3.10	4.42	1.71	2.48	-
Magnitude of increase (times) from actual to that inclusive of wildlife displacement	442.78	26.21	1.40	1.01	1.69	-

Average estimates of distance and area are all in kilometers (mean $\pm$ SE)

However, spatial examination showed that human structures and activities were concentrated in several clusters of multiple – use areas where several structures and human activities occurred together (figure 2). The five clusters of multiple human structures and activities taking up the greatest area of Kuku were Elankata Enkima-Olorika (76.36 km²), followed by Inkisanjani-Olkaria (50.55 km²), Engusero Enkuteng (19.52 km²), Pipeline road (13.8 km²) and the Iltilal Market (13.04 km²). There were about twelve such clusters of human activities and structures, which together occupied a total of 234.2 km² (about 24.4%) of the group ranch land (table 2). This left an about 75.6% of land outside such clusters available for pastoralism and wildlife ranging.

Of human activities and structures, agriculture occupied the largest actual area of 30.25 km² (3.15%) of Kuku, followed by institutional structures (6.60 km²; 0.69% of Kuku), then roads (1.12 km²; 0.12% of KGR) and lastly by Maasai settlements (*bomas*) (0.34 km²; 0.04%).

Table 2. Areas pf clusters of human structures and activities in Kuku Group Ranch. These clusters run north - south direction in the western part of Kuku Group Ranch hence creating a spatial barrier to dispersing wildlife from Kimana Wildlife Sanctuary to Chyulu Hills / Tsavo West National Parks through Kuku Group Ranch

Name of human structures / activity clusters	Perimeter (km)	Area (km ²)
Elankata Enkima - Olorika	46.69	76.36
Ilchalai	17.34	11.01
Elonkati	11.06	6.51
Oltiasika	12.22	8.43
Luca Ecotourism Camp	8.52	5.06
Iltilal Market	14.14	13.04
Olpusare	13.36	9.59
Kuku	13.36	8.57
Engusero - Enkuteni	19.33	19.52
Inkisanjani - Olkaria	33.05	50.55
Pipeline Road	20.74	13.8
Esambu	16.94	11.76
Total perimeter and area	226.75	234.2
Proportion of area in group ranch		24.40%

The average minimum distance of each *boma* from wildlife (0.43 ± 0.07 km) was smaller than the average distance of agricultural from wildlife (0.57 ± 0.22 km). Maasai *bomas* had the largest total area (151.88 km^2 ; 15.80%) inclusive of the area of wildlife displacement, despite having the smallest actual area in the group ranch (table 1). The total area inclusive of wildlife displacement for agriculture ranked second (42.47 km^2 ; 4.42%) to settlements, followed by roads (29.35 km^2 ; 3.10%).

Table 3. Numbers and sightings of most frequently seen large wild mammals in various habitats across of Kuku Group Ranch. Human activities have precluded use of certain habitats such as the riverine habitats where agricultural activities are concentrated

Some common species	Dense Woodland / Shrubland	Grassland	Open Woodland / Shrubland	Riverine
Kirk's Dik Dik (<i>Madoqua kirkii</i>)	23 (13 ¹)	0 (0)	37 (19)	0 (0)
Grant's Gazelle (<i>Gazella granti</i>)	4 (1)	131 (12)	282 (38)	0 (0)
Impala (<i>Aepyceros melampus</i>)	62 (10)	1 (1)	225 (24)	0 (0)
Thomson's Gazelle (<i>Gazella thomsonii</i>)	1 (1)	91 (12)	146 (19)	0 (0)
Common Wildebeest (<i>Connochaetes taurinus</i>)	0 (11)	168 (11)	429 (28)	0 (0)
Common Zebra (<i>Equus burchelli</i>)	32 (5)	186 (13)	1245 (75)	2 (1)
Total number of wild large mammals seen ²	193	735	2816	123
Total number of sightings of wild large mammals	48	56	262	19
Percentage (%) of number in each habitat	4.99%	19.01%	72.82%	3.18%
Percentage (%) of sightings in each habitat	12.47%	14.45%	68.05%	4.94%

¹ Values in parentheses for some of the common large mammal species seen represents the total number of sightings (times) that species was seen over the study period of 10 days of each study session.

²This includes the 22 large mammal species observed in Kuku Group Ranch. Some were very rare such as vervet monkeys, sykes (blue) monkey.

Among agriculture activities, Irrigated agriculture (that uses water from key rivers) took up less actual area in Kuku Group ranch (14.06 km^2 ; 1.46%) compared to rain fed agriculture (16.19 km^2 ; 1.67%), which uses rain water especially in areas close to Mt. Kilimanjaro that receives relatively more rainfall than the lower rangelands. However, irrigated agriculture displaced more wildlife (0.64 ± 0.24 km) than rain fed agriculture (0.02 ± 0.01 km),. Therefore the total area inclusive of wildlife displacement of irrigated agriculture was also

higher (23.78 km²; 2.48%) for irrigated agriculture compared to rain fed agriculture (16.40 km²; 1.71%).

The magnitude of increase in area from actual area occupied by a human structure / activity to area inclusive of wildlife displacement was dependent on the frequency (number of times) and coverage the specific structure / activity occurred in the group ranch. The highest magnitude was for *bomas* with the magnitude of wildlife displacement area of wildlife to actual area being 442 times followed by roads (26.21 times). Agriculture, because of its low frequency and confinement close to water sources and close to Kilimanjaro, had a comparatively low magnitude of 1.40 times inclusive of wildlife displacement compared to its actual area (table 1).

Wildlife seemed to avoid areas with clusters of concentrated human activities / structures (figure 2). The land between the two biggest clusters: Elankata Enkima-Olorika cluster and Inkisanjani-Olkaria was about only 10 km apart and potentially one of the main migration routes wildlife uses to Kimana Group Ranch and eventually into and from Amboseli National Park. The other land open for wildlife movement was between Ilchalai cluster and Elankata Enkima-Olorika cluster, which was relatively more smaller (less than 4 km apart), but critical for wildlife dispersing directly into Kimana Community Wildlife Sanctuary to and from the group ranch. Use of such spaces could also be affected by snares recovered close to some of these clusters, especially near agriculture areas in riverine habitats.

Open woodland / open shrubland habitats had many wild mammals (72.82%) seen, as well as frequency of sightings (68.05%) in the group ranch (table 3). Fewer numbers and sightings of large wild mammals occurred in riverine habitats where most irrigated cultivation is located. The total number of wildlife species sighted was dependent (Chi-square cross tabulations; $\chi^2 = 687.15$; $df = 15$; $p < 0.001$) on the habitat type, as was the frequency of wildlife large mammal sighted ($\chi^2 = 75.85$; $df = 15$; $p < 0.001$).

Minimum distance different livestock types kept from wildlife was significantly different from each other ($F = 7.96$; $df = 2, 84$; $p < 0.001$). The shoats (goats and sheep together) significantly displaced wildlife than both cattle and donkeys. However, the displacement distance of wildlife between cattle and donkeys was similar.

No significant correlations were found between livestock group size and the distance wildlife kept away from livestock. A positive but insignificant relationship (Pearson's correlation; $r = 0.119$; $p = 0.4$) was found between livestock group size and the minimum distance wildlife kept away. Further, positive but insignificant correlation ($r = 0.159$; $p = 0.37$) was also found between shoats (sheep and goats together) group size and the distance wildlife kept away from them.

B) Kimana Group Ranch

All human structures and activities displaced wildlife (inclusive of wildlife displacement) from a total area of 140.01 km² (55.74% of KGR), leaving only about 44% of KGR available for both wildlife and pastoralism (table 5). However, only 57.83 km² (about 23% of Kimana) was actually taken by all human structures and activities in the group ranch. Institutions occupied only a small actual area of Kimana, but displaced wildlife from a total area of about 5.2 km² (2.07%) with a 0.18 ± 0.06 km of wildlife displacement distance (table 5). *Bomas*, also took a small total actual area of about 0.24 km² (1.09%), but the area increased to the

second highest wildlife displacement, of 28.11 km² (11.19%), with a wildlife displacement distance of 0.23 ± 0.04 km.

Kimana Community Wildlife Sanctuary covered the largest area (24.04 km², 9.57%) among the community / public institutions within the group ranch (table 5). Besides KCWS, a further potential 67.43% of the land (without correcting for wildlife displacements) was available for wildlife, but this shrank to only 34.89% of land available to wildlife in the rest of the group ranch (besides KCWS) when wildlife displacement effects from human activities and structures were considered.

There were a total of 100 *bomas* outside of the electric fences in Kimana Group Ranch occupying only about 0.24 km² (1.09%) of Kimana actual area (table 5). The average number of housing units per *boma* was 6.21 ± 0.21 . Of the total number of housing units, 56% were thatched, 18% tin, 13% dung, 10% plastic, 0.2% concrete, and 0.5% unfinished. Permanent house units made of concrete *bomas* were rare (only 1 during entire study).

All the roads covered a network of 219 kilometers and covered an actual area of only 1.69 km² (0.47%) of Kimana. But this area increased to the highest wildlife displacement area (38.22 km², about 13.79%) of all structures / activities (table 6a). These roads had an average wildlife displacement distance of 0.18 ± 0.02 .

Table 4. Average group sizes of some common large wild animals and livestock within and across habitats in Kuku Group Ranch

Species	Across Habitats	Dense Woodland/ Shrubland	Grassland	Open Woodland/ Shrubland	Riverine
Impala (<i>Aepyceros melampus</i>)	8.2 ± 1.5^1	5.9 ± 2.1	-	9.4 ± 1.9	-
Vervet Monkey (<i>Cercopithecus aethiops</i>)	4.8 ± 1.7	-	-	-	5.3 ± 2.2
Sykes Monkey (<i>Cercopithecus mitis</i>)	6.5 ± 1.0	-	-	-	6.5 ± 1.0
Common Wildebeest (<i>Connochaetes taurinus</i>)	15.3 ± 4.2	-	15.3 ± 5.3	15.3 ± 5.6	-
Common Zebra (<i>Equus burchelli</i>)	15.6 ± 1.7	6.4 ± 1.7	14.3 ± 2.8	16.6 ± 2.1	-
Grant's Gazelle (<i>Gazella granti</i>)	8.2 ± 1.1	-	10.9 ± 2.8	7.4 ± 1.1	-
Thomson's Gazelle (<i>Gazella thomsonii</i>)	7.4 ± 1.2	-	7.6 ± 1.8	7.4 ± 1.7	-
Maasai Giraffe (<i>Giraffa camelopardalis tippelskirchi</i>)	6.2 ± 1.4	7.8 ± 3.2	-	6.2 ± 1.7	-
Kirk's Dik-dik (<i>Madoqua kirkii</i>)	1.9 ± 0.1	1.8 ± 0.2	-	1.9 ± 0.1	-
Savannah Baboon (<i>Papio cynocephalus</i>)	16.3 ± 5.4	7.0 ± 5.0	-	21.3 ± 8.5	10.5 ± 4.5
Cape Buffalo (<i>Syncerus caffer</i>)	15.4 ± 7.0	-	-	14.3 ± 9.0	-
Lesser Kudu (<i>Tragelaphus imberbis</i>)	2.3 ± 0.5	1.3 ± 0.3	-	3.3 ± 0.3	-
Common Eland (<i>Taurotragus oryx</i>)	13.5 ± 5.5	4.0 ± 2.0	27.4 ± 20.3	9.3 ± 2.5	-

Table 4. Continued

Species	Across Habitats	Dense Woodland/ Shrubland	Grassland	Open Woodland/ Shrubland	Riverine
Wildlife ²	10.5 ± 0.8	4.3 ± 0.7	13.1 ± 2.3	11.2 ± 1.0	6.5 ± 0.9
Cattle	34.2 ± 3.9	30.7 ± 8.7	52.2 ± 24.5	32.8 ± 4.6	53.8 ± 16.1
Donkeys	7.8 ± 2.9	3.3 ± 1.9	-	8.9 ± 3.6	-
Goats and Sheep	57.6 ± 6.0	75.6 ± 16.8	45.0 ± 25.0	54.5 ± 6.6	25.0 ± 5.0
Livestock	42.5 ± 3.4	50.7 ± 9.7	45.1 ± 17.2	40.7 ± 3.8	41.7 ± 12.3

²Some species were sighted only once in some habitat and so they are not listed here

Table 5. Actual area occupied by human structures as well as associated wildlife displacement area in Kimana Group Ranch.

Human structures and activities in Kimana Group Ranch	Perimeter (km)	Area of KGR actually taken (km ²)	Proportion (%) of total KGR area	Area of KGR actually taken inclusive of wildlife displacement (km ²)	Proportion (%) of total KGR inclusive of wildlife displacement
Amboseli Sopa Lodge	3.02	0.11	0.04	5.2 (all institutions together)	2.07 (All institutions together)
SFS Center for Wildlife Management Studies	1.52	0.14	0.06		
Kimana Secondary school	1.67	0.14	0.06		
Commercial Cultural <i>Manyattas</i> (three at Amboseli, Sopa Lodge and KCWS)	0.5	0.03	0.01		
Churches	6.21	0.19	0.08		
Schools	4.28	0.28	0.11		
Government offices	2.08	0.12	0.05	28.11	11.19
<i>Bomas</i>	-	0.24	1.09		
Agriculture	-	0.69	0.27		
Other Institutions	0.37	0.002	0.0006	-	-
Electric Fences	-	52.98	21.10	69.29	27.61
TOTAL of all human structures and activities	-	57.83¹	23.02	140.01	55.74
Kimana Community Wildlife Sanctuary (KCWS)	21.85	24.04	9.57	-	-

¹Adjustment to areas was done to eliminate double counting for structures and activities within electric fences. No wildlife was therefore seen in human activities enclosed within electric fences (markets, institutions). No wildlife was also seen close to agriculture found outside electric fences

Table 6a. Area of roads including wildlife displacement effect in Kimana Group Ranch

Type of road (all were marrum roads)	Total length (km)	Average width (km)	Total area (km ²)	Percentage (%) of group ranch	Road area and displacement (km ²)	Percentage (%) of group ranch with displacement
Isinet - Kimana main road	16.28	0.019	0.30	0.12	3.06	1.22
Amboseli road (off main Kimana – Oloitoktok road)	21.60	0.008	0.18	0.07	3.84	1.53
Other major roads	113.58	0.008	0.94	0.37	20.20	8.04
Other minor roads	67.74	0.004	0.27	0.10	11.11	3.00
Total	219.20	0.010	1.69	0.47	38.22	13.79

Table 6b. Perimeters and areas of the two electric fences within Kimana Group Ranch

The electric fence location	Perimeter (km)	Area (km ²)	Percentage (%) of KGR	Displacement area (km ²)	Displacement Percentage (%) of KGR
Kimana	34.51	42.39	16.88	53.07	21.12
Namelok	16.35*	10.59*	4.22	16.22	6.46
Total	50.86	52.98	21.10	69.29	27.61

*Area and perimeter within Kimana Group Ranch. Total Namelok Fence was 18.11 km² and total perimeter was 21.15 km as covers part of Mbirikani and Olororashi group ranch

Table 6c. Perimeters and areas of markets within Kimana Group Ranch

Market name	Perimeter (km)	Area (km ²)	Percent (%) of KGR
Kimana	3.50	0.48	0.19
Namelok	1.05	0.06	0.02
Mbironi	0.72	0.01	0.00
Other small markets	1.74	0.04	0.01
Total	7.01	0.58	0.23

Table 6d. Wildlife displacement by livestock within Kimana Group Ranch

Livestock Type	Mean distance to a wildlife (km)
Sheep / Goat (<i>Ovis aries</i> / <i>Capra hircus</i>)	0.17 ± 0.03 ¹ 0.24 ± 0.04 ² 0.20 ± 0.03³
Cattle (<i>Bos Taurus</i>)	0.15 ± 0.00 ¹ 0.23 ± 0.04 ² 0.18 ± 0.03³
Donkey (<i>Equus arsinus</i>)	0.05 ± 0.03¹
Livestock	0.21 ± 0.02

¹ November 2004 ² April 2005, ³ Average (in bold), respectively

The largest actual space in the group ranch was taken by electric fences, both covering an area of 52.98 km² (21.09%) of Kimana Group Ranch (table 6b), but this area increased to 69.29 km² (27.58%) of wildlife displacement (table 5), with wildlife keeping a distance of 0.07 ± 0.04 km, the smallest of all average distances to wildlife. Kimana fence covered an area about four times larger (42.39 km², 16.88%) than Namelok fence (10.59 km², 4.22%) and was approximately 2.2 times longer (table 6b). With wildlife displacement, Kimana fence took up still a larger area (53.07 km², 21.12%) more than Namelok fence (16.22 km², 6.46%).

Out of all the human structures and activities, markets took up the smallest proportion of the group ranch, (0.58 km², 0.23%) (table 6c). The two largest markets were Kimana (0.48 km², 0.19% of KGR) and Namelok (0.06 km², 0.02% of KGR). The majority of all the institutions and markets were inside Kimana and Namelok electric fences. No wildlife was sighted in close proximity to markets and institutions because almost all of them were enclosed in the electric fences. Agriculture was mainly located inside the electric fences, and what was outside was very small, covering an actual area of 0.89 km² (0.27% of KGR). However, no wildlife was sighted in close proximity to these agricultural areas, so it was not possible to get minimum distance to wildlife, but was definitely more than viewing distance, even for primates that raid crops.

The displacement of wildlife by livestock was 0.21 ± 0.02 km (table 6d). Shoats (sheep and goats together) displaced wildlife the most in Kimana (0.20 ± 0.03 km). Cattle displaced wildlife by 0.18 ± 0.03 km, while donkeys displaced wildlife the least (0.05 ± 0.03 km) (table 6d).

The average group size of wild large mammals was 7.32 ± 0.41 individuals (table 7). The riverine habitat supported the largest group size of 10.50 ± 1.19 individuals per group; however these were only primate species (table 5). Dense woodland/shrubland habitat had an average of 7.55 ± 1.26 individuals per group, open woodland/shrubland had 7.28 ± 0.47 while grassland had 6.71 ± 1.00 individuals per group (table 7).

The abundance of wildlife (in terms of numbers) was different among habitat types ($\chi^2 = 3942.80$, $df = 3$, $p < 0.001$), neither was the frequency of sightings of wildlife species similar ($\chi^2 = 547.89$, $df = 3$, $p < 0.001$). Wildlife use of habitats (in terms of numbers) was dependent on habitat types ($\chi^2 = 62.97$, $df = 6$, $p < 0.001$). Similarly, wildlife frequency of sightings was also dependent on habitat type ($\chi^2 = 7.46$, $df = 6$, $p < 0.001$).

Elephants had an average group size of 3.08 ± 0.69 individuals (table 7) in the group ranch and were found in all habitats except the riverine habitats. Elephants were displaced the most by electric fences (0.40 ± 0.06 km), followed by livestock, roads, *bomas* and least by institutions.

Human structures and activities concentrated mostly inside and immediately around electric fences, along roads, along major rivers and market centers (figure 3). The *bomas* tended to clump along the electric fences, along the road and around major agricultural areas. However, wildlife was distributed all across the group ranch, but were in higher densities near Amboseli National Park and in areas with less human activities and structures (figure 3), and close to water source. Livestock sightings were common around the *bomas* and also throughout the group ranch where pasture was found. Elephant signs primarily were found all around KGR except near electric fences and *bomas* (figure 3).

The concentration of *bomas* and agriculture were cutting the south western entry of wildlife into KCWS from the rest of the group ranch and Amboseli National Park. The potential migratory routes without the electric fences would be much more direct (figure 3) than the current potential ones. Hence, the remaining corridor between the Namelok and Kimana fence to KCWS was only 1.82 km between Namelok fence and *boma* clusters, and even small gap of 111.75 meters between these *boma* clusters and Kimana fence (figure 3).

The location of the fences was such that the area they occupied inhibited wildlife access to Kimana Sanctuary (figure 3). The southern boundary of the sanctuary was blocked almost completely by Kimana fence, and about half of the western boundary was blocked by Namelok fence. Only about five kilometers remained potentially open between the two fences for wildlife to use to enter the sanctuary (figure 3).

Table 7. Average group sizes of wildlife within and across habitats in Kimana Group Ranch

Species	Dense woodland/ shrubland	Grassland	Open woodland/ shrubland	Riverine	Average in Kimana Group Ranch
African Elephant (<i>Loxodonta africana</i>)	1.00* ¹ 4.50±2.50 ² 3.33 ± 1.92³	6.00*	4.25 ± 1.38 2.86±0.74 2.63 ± 0.68	-	4.00 ± 1.09 3.22±0.74 3.08 ± 0.69
Black-backed Jackal (<i>Canis mesomelas</i>)	-	-	3.00* 2.00* 2.50 ± 0.50	-	3.00* 2.00* 2.50 ± 0.50
Common Eland (<i>Tragelaphus oryx</i>)	-	-	1.00 ± 0.00 1.00±0.00 1.00 ± 0.00	-	1.00± 0.00 1.00±0.00 1.00 ± 0.00
Grant's Gazelle (<i>Gazella granti</i>)	5.50 ± 1.50 2.67 ± 0.67 4.00 ± 2.05	3.00 ± 1.00 12.5±1.70 3.00 ± 3.00	5.27 ± 1.00 8.15±1.66 7.35 ± 1.10	-	5.95 ± 0.87 8.48±1.68 7.42 ± 1.06
Impala (<i>Aepyceros melampus</i>)	10.53 ± 3.88 9.67±2.96 9.78 ± 2.84	-	4.63 ± 0.79 9.70±1.21 8.64 ± 1.12	-	6.32 ± 1.23 9.69±1.13 8.82 ± 1.05
Kirk's Dik-dik (<i>Madoqua kirkii</i>)	1.40 ± 0.25 2.50±1.50 1.80 ± 0.80	-	1.69 ± 0.17 1.50±0.34 7.35 ± 1.10	-	1.61 ± 0.14 1.75±0.41 1.86 ± 0.22
Lesser Kudu (<i>Tragelaphus imberbis</i>)	1.00 ± 0.00 1.00* 1.00 ± 0.00	-	1.00± 0.00	-	1.00 ± 0.00 1.00* 1.00 ± 0.00
Maasai Giraffe (<i>Giraffa camelopardalis</i>)	2.50 ± 0.00	4.00*	4.68 ± 0.64 6.47±2.38 6.42 ± 1.67	-	4.21 ± 0.54 6.33±2.25 6.07 ± 1.47
Plains Zebra (<i>Equus burchelli</i>)	8.25 ± 1.90 9.20±2.06 9.50 ± 2.67	12.00* 9.17±1.00 9.57 ± 1.03	6.27 ± 0.59 9.21±1.03 8.88 ± 0.82	-	6.79 ± 0.60 9.21±0.85 8.99 ± 0.71
Sykes Monkey (<i>Cercopithecus mitis</i>)	3.00*	-	-	9.00*	9.00* 3.00* 6.00 ± 3.00
Savanna Baboon (<i>Papio cynocephalus</i>)	12.67 ± 5.92	-	15.00 ± 2.64 16.50±5.50 17.33 ± 3.28	17.00* 14.00* 15.50 ± 1.50	14.29 ± 2.53 15.67±3.29 15.00 ± 3.20
Thomson's Gazelle (<i>Gazella thomsonii</i>)	2.00*	3.00* 6.00±2.92 6.00 ± 2.92	2.31 ± 0.37 13.63±6.24 6.48 ± 2.68	-	2.32 ± 0.35 11.08±4.49 6.40 ± 2.27

Table 7. Continued

Species	Dense woodland/shrubland	Grassland	Open woodland/shrubland	Riverine	Average in Kimana Group Ranch
Vervet Monkey (<i>Cercopithecus aethiops</i>)	7.33 ± 2.73 15.50±14.50 11.00 ± 6.72	-	7.13 ± 1.53 4.33±1.35 6.70 ± 1.17	10.00* 1.50±0.50 9.50 ± 0.50	7.68 ± 1.26 5.38±1.99 7.39 ± 1.23
Average wildlife group size in the group ranch	5.90 ± 0.96 7.75±1.96 7.55 ± 1.26	5.40 ± 1.78 9.33±2.30 6.71 ± 1.00	4.87 ± 0.32 8.02±0.64 7.28 ± 0.47	12.00 ± 2.52 5.57±4.18 10.50 ± 1.19	5.15 ± 0.31 8.02±0.58 7.32 ± 0.41

*Species was only seen once in this habitat. ¹ November 2004. ² April 2005. ³ Average (in bold), respectively.

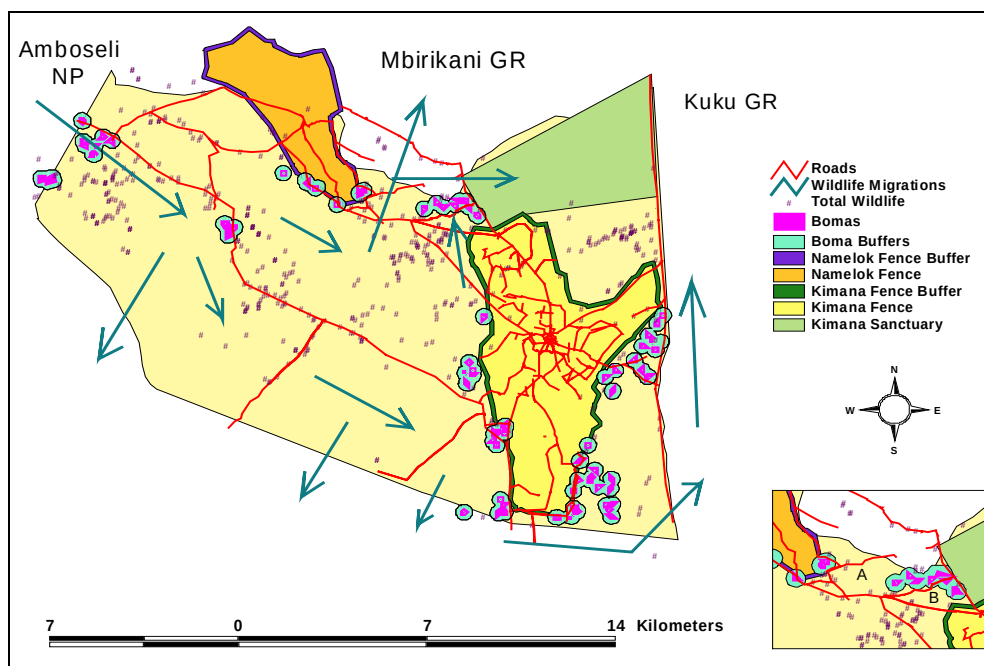


Figure 3. Present potential migration routes of wildlife from Amboseli to KCWS. Inset: Remaining corridor for wildlife migration into KCWS (A=1,820.17m, B=111.75m).

C) Mbirikani Group Ranch

Human structures occurred across the entire group ranch (figure 5), taking up an actual area of 16.85 km² (1.61%) of Mbirikani (table 8). However, when wildlife displacement was taken into account, the area covered by human structures increased by 16.75 times to 282.27 km² (23.33%) of the group ranch. Agricultural areas took up 12.76 km² (1.28%) of the actual area in the group ranch, followed by *bomas* (0.14%), roads (0.12%), airstrips (0.03%), water pipeline points (0.03%), and institutions (0.01%). However, when wildlife displacement was factored in, the road network covered the largest portion of the group ranch (10.43%), followed by *bomas* (10.33%), agricultural areas (1.70%), institutions (0.68%), water pipeline

Table 8. Area occupied by human structures in Mbirikani Group Ranch

Variable	Overall	Maasai Bomas			Roads*				Agriculture	Institutions	Airstrip	Water pipeline points and tanks	Total
		Occupied	Abandoned	New	Overall	Minor	Major	Main					
Average distance from wildlife to nearest structure (m)	237.39 ± 21.92	-	-	-	180.54 ± 10.65	-	-	-	89.50 ± 82.15	333.33 ± 22.10	35.82 ± 7.35	108.00 ± 53.70	-
Average radius/width (m)	23.24 ± 0.84	23.90 ± 0.99	19.63 ± 1.03	21.73 ± 2.25	2.34 ± 0.06 ^b	8.95 ± 0.52 ^b	2.91 ± 0.04 ^b	2.08 ± 0.03 ^b	Length: 126.5 ± 28.5 Width: 126.0 ± 46.0	Radius: 16.63 ± 2.84 Length: 82.61 ± 28.51 Width: 48.89 ± 12.44	-	Radius: 5.77 ± 1.48 Length: 10.63 ± 3.08 Width: 5.63 ± 3.47	-
Total area of MGR actually taken by human structures (km ²)	1.78	1.64	0.13	0.02	1.48**	0.55	0.51	0.41	12.76	0.13	0.39	0.31	16.85
Area of MGR occupied by actual structure areas (%)***	0.14	0.13	0.01	0.002	0.12	0.04	0.04	0.03	1.28	0.01	0.03	0.03	1.61
Total area of MGR taken inclusive of wildlife displacement (km ²)	126.90	106.71	17.87	2.32	128.13	44.32	49.03	34.79	16.93	8.30	0.57	1.44	282.27
Area of MGR occupied inclusive of wildlife displacement (%)	10.33	8.68	1.45	0.19	10.43	3.61	3.99	2.83	1.70	0.68	0.05	0.14	23.33
Magnitude of increase (times) from actual area to that inclusive of wildlife	71.29	-	-	-	86.57	-	-	-	4.65	63.85	1.46	4.65	16.75

points (0.14%) and airstrips (0.05%). Roads also had the largest magnitude of increase in terms of wildlife displacement (86.57 times the actual area), and airstrips (1.46 times) had the least (table 8).

Areas with high concentrations of *bomas*, roads and other human activities were located in eight clusters of human settlements in Mbirikani group ranch (figure 4). The clusters covered 239.13 km² (20.38%) of the dispersal space in the ranch (table 9). The largest cluster occurred along the Pipeline-Main Road (128.07 km², 11.34%). This large cluster bisects the group ranch, leaving only 2.35 km of the main pipeline road open for wildlife dispersal. The Oldonyo-Wuas Ecotourism Area (43.30 km², 3.52%) was the second largest cluster, followed by the Kimana Swamp-Esambu cluster (42.14 km², 3.43%), the Ilchalai Swamp cluster (13.62 km², 1.11%), the Namelock cluster (7.72 km², 0.63%), the Olubili cluster (3.12 km², 0.52%), and the Eleenkati cluster (0.97 km², 0.08%). The smallest group of settlements occurred in the southeast section of the group ranch (figure 4) at the Lemasusu cluster (0.19 km², 0.02%). These clusters left 70.62% (989.80 km²) of the space (table 9), and nine potential routes for wildlife dispersal left open in Mbirikani group ranch (figure 5).

Table 9. Clusters and areas of human settlements and activities in Mbirikani Group Ranch

Name of human structures / activity clusters	Perimeter(km)	Area(km ²)	Area (%) in Mbirikani Group Ranch
Namelok Cluster (A)	15.26	7.72	0.63
Kimana Swamp- Esambu Cluster (B)	49.39	42.14	3.43
Ilchalai Swamp Cluster(C)	21.47	13.62	1.11
Pipeline- Main Road Cluster (D)	76.43	128.07	11.34
Oldonyo-Wuas Ecotourism Area (E)	34.93	43.30	3.52
Olubili Cluster(F)	7.82	3.12	0.25
Elenkati Cluster (G)	6.58	0.97	0.08
Lemasusu Cluster (H)	2.67	0.19	0.02
Total	214.55	239.13	20.38

The majority of *bomas* identified were occupied *bomas* (73%), with 14% abandoned, 131% unclassified, and 2% new (table 10). Occupied *bomas* covered the largest amount of space (23.90 ± 0.99 m). The majority of the structures within the *bomas* were temporary (70%), followed by semi-permanent structures (20%), incomplete structures (7%) and permanent structures (3%).

Wildlife utilized all of Mbirikani group ranch but was displaced by structures, especially within clusters (figure 4). The average minimum distance of all wildlife to all human structures in Mbirikani was 190.29 ± 9.28 m. Large mammal species kept the farthest from institutions (326.73 ± 35.28 m), followed by *bomas* (234.84 ± 20.96 m), water resources (194.33 ± 75.77) roads (182.17 ± 10.74), agricultural activities (89.50 ± 82.15), and airstrips (35.82 ± 7.35). These distances varied among structures (F = 3.849, df = 4, p = 0.004). The mean minimum distance between wildlife and airstrips was significantly less than between wildlife and *bomas* (p = 0.037), and the mean minimum distance between wildlife and

airstrips was less than between wildlife and institutions ($p = 0.015$). However, all other differences were not significant.

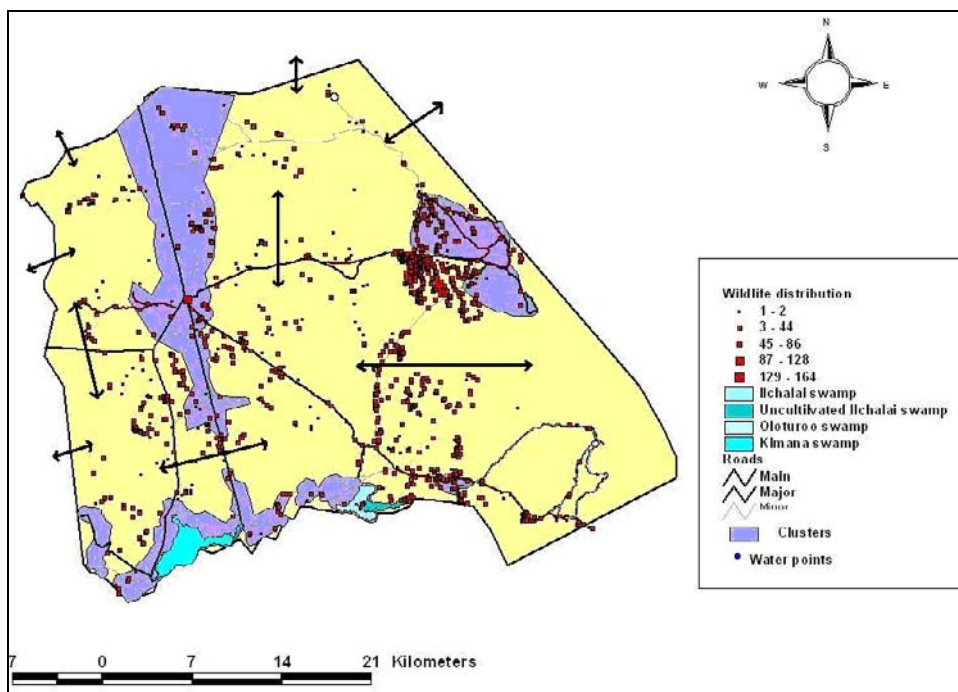


Figure 4. Clusters of multiple human activities and structures in relation to wildlife.

Table 10. Parameters associated with Maasai settlements (*bomas*)

<i>Boma</i> type	Mean radius $\pm$ SE (m)
Occupied	23.90 $\pm$ 0.99
Abandoned	19.63 $\pm$ 1.03
New	21.73 $\pm$ 2.25
Overall average	23.24 $\pm$ 0.84
Structure type	Number (%)
Temporary	1900 (70%)
Semi-Permanent	543 (20%)
Incomplete	191 (7%)
Permanent	77 (3%)
Total number of structures within <i>bomas</i>	2711
<i>Boma</i> type	Number (%)
Occupied	548 (73%)
Unclassified	87 (11%)
Abandoned	106 (14%)
New*	12 (2%)
Total number of <i>bomas</i>	754

*New *bomas* was a category only included in the most recent data collection, therefore it is an under estimate.

Table 11. Average group size of common large mammal species among habitats in Mbirikani Group Ranch

Wildlife Species	Across Habitats	Dense Bushland	Dense Shrubland	Open Bushland	Open Shrubland	Grassland	Riverine / Swamp
Coke's hartebeest	2.85 ± 0.63	8.00	–	–	2.60 ± 1.17	2.57 ± 0.72	–
Common eland	5.56 ± 1.24	8.00 ± 0.00	4.92 ± 1.35	3.00	2.83 ± 0.79	7.80 ± 3.51	–
Common warthog	2.60 ± 0.52	–	1.50 ± 0.22	–	2.80 ± 0.97	3.00 ± 0.58	–
Common wildebeest	15.21 ± 1.12	28.00 ± 22.00	19.88 ± 8.66	5.00	10.14 ± 1.77	16.23 ± 1.33	7.50 ± 3.50
Common zebra	11.86 ± 0.77	3.40 ± 0.81	11.29 ± 2.92	7.25 ± 1.31	9.70 ± 0.86	13.47 ± 1.19	8.63 ± 1.59
Fringe-eared oryx	6.04 ± 1.89	1.67 ± 0.33	10.00 ± 0.00	–	8.56 ± 5.27	3.92 ± 1.86	–
Gerenuk	3.27 ± 0.29	–	3.54 ± 0.96	3.33 ± 0.80	3.24 ± 0.36	3.08 ± 0.67	–
Grant's gazelle	7.34 ± 0.50	5.50 ± 2.50	2.50 ± 0.50	4.71 ± 1.23	7.16 ± 0.66	8.06 ± 0.81	–
Impala	6.87 ± 0.98	22.5 ± 2.75	5.23 ± 1.01	4.00 ± 1.00	5.94 ± 1.21	5.00 ± 3.51	–
Kirk's dik dik	1.57 ± 0.15	2.00 ± 1.00	1.67 ± 0.19	1.00	1.33 ± 0.21	–	–
Lesser kudu	1.25 ± 0.25	–	1.50 ± 0.50	–	1.00	1.00	–
Maasai giraffe	6.22 ± 0.62	6.33 ± 1.86	6.25 ± 0.66	13.00 ± 10.07	5.72 ± 0.75	6.43 ± 2.27	–
Thomson's gazelle	5.65 ± 0.66	1.22	2.00	1.50 ± 0.50	7.59 ± 2.35	5.49 ± 0.68	3.00
Yellow baboon	10.40 ± 2.96	1.00	–	17.00	12.40 ± 5.21	11.50 ± 1.50	1.00
All wildlife	9.52 ± 0.26	9.12 ± 1.82	6.17 ± 0.55	5.48 ± 1.02	7.36 ± 0.35	11.60 ± 0.43	7.40 ± 1.91
Cattle	88.48 ± 4.80	–	24.57 ± 4.15	29.00 ± 6.00	60.92 ± 8.58	111.31 ± 5.91	24.55 ± 0.55
Shoats	84.06 ± 6.95	–	–	–	66.05 ± 8.79	102.53 ± 10.10	–
Donkeys	4.21 ± 0.79	–	2.00	–	3.75 ± 0.95	4.67 ± 1.14	–
All livestock	89.66 ± 4.81	–	24.86 ± 3.99	29.00 ± 12.97	62.71 ± 5.59	114.25 ± 5.42	24.55 ± 7.40

*Single value was due to the species being sighted only once

Note: African civet, African elephant, African wild dog, black-backed jackal, common waterbuck, golden jackal, oribi, spotted hyena, swamp cat, and topi were all observed four times or less and were therefore not included as a commonly sighted animal

Livestock displaced wildlife at an average minimum distance of 329.62 ± 10.89 m in Mbirikani group ranch. Cattle displaced wildlife the most (357.63 ± 14.84 m) and donkeys displaced wildlife the least (161.87 ± 23.43 m), while shoats displaced wildlife at an average distance of 247.17 ± 18.36 m. There was also a significant and positive correlation between the number of cattle in a herd and the mean minimum distance maintained by wildlife ($r = 0.131$, $p = 0.030$, $n = 277$). Therefore, as cattle group size increases, the mean minimum distances maintained by wildlife increase. There was no significant correlation between the shoats group size and the mean minimum distance kept by wildlife to the herd ($r = -0.167$, $p = 0.136$, $n = 81$), or the donkey group size and the mean minimum distance of wildlife from that herd ($r = 0.435$, $p = 0.120$, $n = 14$).

Table 12. Total numbers (and frequencies of sightings) of common large mammal wildlife species seen* in different habitats in Mbirikani Group Ranch

Wildlife Species	Grassland	Open Bushland	Dense Bushland	Open Shrubland	Dense Shrubland	Open Woodland	Wetland	Abundance across habitats (%): presence across habitats (%)
Coke's hartebeest	36 (14)	0 (0)	8 (1)	13 (5)	0 (0)	0 (0)	0 (0)	57 (0.4); 20 (1.5)
Common eland	78 (10)	3 (1)	16 (2)	17 (6)	64 (13)	0 (0)	0 (0)	178 (1.4); 32 (2.4)
Common warthog	10 (3)	0 (0)	0 (0)	14 (4)	3 (2)	0 (0)	0 (0)	27 (0.2); 9 (.7)
Common wildebeest	4,025 (248)	5 (1)	56 (2)	578 (57)	159 (8)	0 (0)	2 (3)	4825 (36.8); 319 (23.5)
Common zebra	2,747 (204)	29 (4)	17 (0)	1,048 (108)	158 (14)	0 (0)	69 (8)	4068 (30.5); 338 (24.9)
Fringe-eared oryx	47 (12)	0 (0)	5 (3)	77 (9)	40 (4)	0 (0)	0 (0)	169 (1.3); 28 (2.1)
Gerenuk	40 (13)	20 (6)	0 (0)	136 (42)	46 (13)	0 (0)	0 (0)	242 (1.8); 74 (5.5)
Grant's gazelle	1,032 (528)	33 (7)	11 (2)	838 (117)	25 (10)	0 (0)	0 (0)	1939 (14.8); 264 (19.4)
Impala	15 (3)	8 (2)	90 (4)	95 (16)	115 (22)	0 (0)	0 (0)	323 (2.5); 47 (3.5)
Kirk's dik dik	0 (0)	1 (1)	4 (2)	8 (6)	20 (12)	0 (0)	0 (0)	33 (0.3); 21 (1.5)
Maasai giraffe	45 (7)	39 (3)	19 (3)	263 (46)	125 (20)	15 (1)	0 (0)	50(3.9); 80 (5.9)
Thomson's gazelle	511(94)	3 (2)	2 (1)	129 (17)	2 (1)	0 (0)	3 (1)	650 (5.0); 116 (8.5)
Yellow baboon	23 (2)	17 (1)	0 (0)	62 (5)	1(1)	0 (0)	1 (1)	104 (0.8); 10 (0.7)
Total number (and frequency) of large mammals	8, 609 (738)	158 (28)	228 (20)	3,278 (438)	758 (120)	15 (1)	75 (13)	13,121 (1,358)
Total number (frequency) of large mammals (%) in each habitat	65.6 (54.3)	1.2 (2.1)	1.7 (1.5)	25.0 (32.3)	5.8 (8.8)	0.1 (0.1)	0.6 (1.0)	-----

The average minimum distance of large mammals to humans in Mbirikani was 299.02 ± 11.30 m. The mean minimum distances wildlife kept from structures, livestock and humans differed ($F = 39.734$, $df = 2$, $p < 0.001$). The overall mean minimum distances of wildlife to structures in Mbirikani was less than those from wildlife to livestock ($p < 0.001$) and wildlife and humans ($p < 0.001$).

Grassland habitats had the highest wildlife average group size (11.60 ± 0.43 m), followed by dense bushland habitats (9.12 ± 1.82 m), riverine or swamp habitats (7.40 ± 0.35 m), dense shrubland habitats (6.17 ± 0.55 m), and open bushland habitats (5.48 ± 1.02). Across all habitat types, the average group size of all livestock was 89.66 ± 4.81 , compared to an average wildlife group size of 9.52 ± 0.26 m (table 11). The average group size of livestock was the highest in grassland habitats (114.25 ± 5.42), followed by open shrubland habitats (62.71 ± 5.59), open bushland habitats (29.00 ± 12.97), and, lastly, dense shrubland habitats (24.86 ± 3.99).

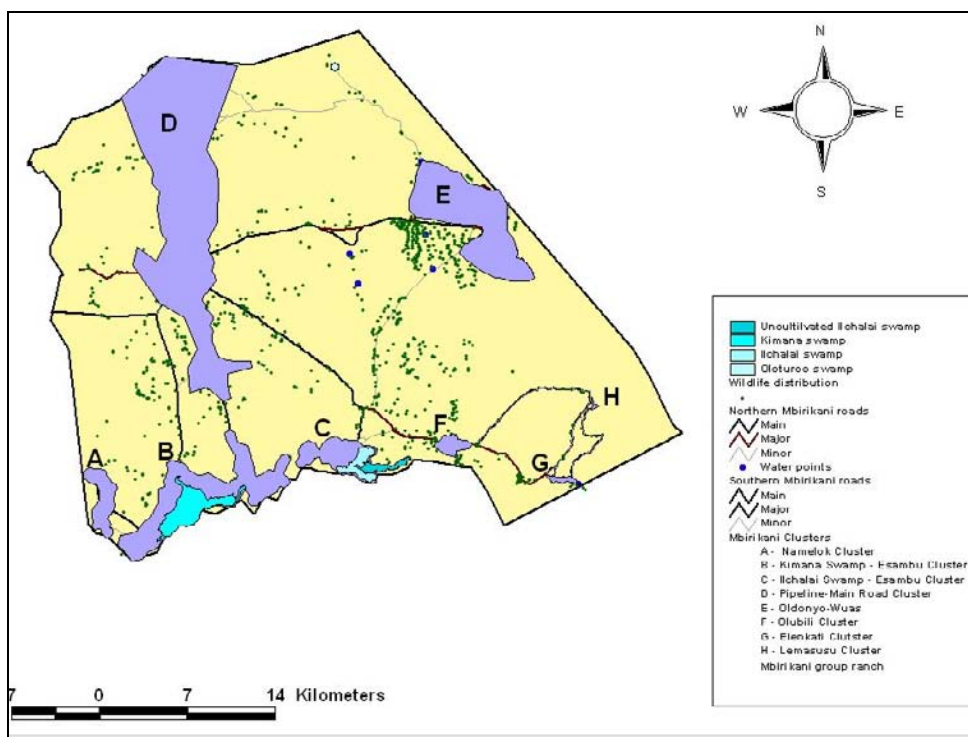


Figure 5. Wildlife distribution and abundance in relation to clusters of human structures/activities and potential wildlife movement routes.

Grassland habitats had the highest number of wildlife sightings (53.7%), followed by open shrubland (33.0%), dense shrubland (8.7%), open bushland (2.1%), dense bushland (1.4%), and wetland habitat (1.0%). The sightings (table 12) of wildlife species seen was dependent on habitat type ($\chi^2 = 381.519$, $df = 24$, $p < 0.001$). Grassland habitats supported the greatest number (table 12) of common wildlife mammals (65.6%), followed by open shrubland habitats (25.0%), dense shrubland habitats (5.8%), dense bushland habitats (1.7%), open bushland habitats (1.2%), wetland habitats (0.6%), and open woodland habitats (0.1%).

The abundance (in numbers) of the wildlife species seen was also dependent on habitat type ($\chi^2 = 4748.348$, $df = 24$, $p < 0.001$).

Discussions

Protected areas for wildlife conservation without their dispersal areas are becoming ecologically unsustainable islands surrounded by incompatible land uses (Morell 1996, Western 1997, Okello & Kiringe 2004). But it is the local people that live on the land that will decide the fate of wildlife conservation (Western 1982). In order to make a living, the local people in most third world countries, often poor and impoverished, will do what it takes to survive. Therefore, local communities in Amboseli area are increasingly replacing wildlife with livestock and agriculture which have a direct economic value to them (Berger 1993, Norton - Griffiths). Money that accrue from wildlife – based tourism benefits mostly the government exchequer, the elitist tourism investors, stakeholders and investors, but significantly less to the local people (Gakahu & Goode 1992).

Wildlife cannot be utilized the same way as livestock, as wildlife hunting was banned in Kenya in 1977 (Sindiga 1995). If wildlife could be economically useful to local communities, it would gain value and be legitimate for local people to be expected to protect them. Since the government owns wildlife in Kenya, people do not mostly view it as their resource, but as a government property. They view wildlife as enemies from whom they should be protected from. As long as people see wildlife as a competitor for the increasingly limited land and its resources without marching significant benefits, conservation cannot prevail (Sibanda 1996, Nicholson 2001, Ogolla & Mugabe 1996). This partly explains agriculture's rapid expansion and popularity in the Amboseli area (Okello 2005). The desire for the Maasai to diversify income from the increasingly expensive, uneconomical and unpredictable pastoralism is another strong reason for agriculture expansion.

Many Maasai in Amboseli area now believe that agriculture is more productive than pastoralism or wildlife conservation as a land use, however unprofitable or unsustainable it may be. It is for this reason that the majority of people in Amboseli Ecosystem have switched from traditional pastoralists to mixed agro-pastoralism (Pickard 1998, Campbell *et al.* 2000, Okello 2005). Even though the Maasai in this area believe that agricultural expansion is taking away livestock and pastoral lands in the group ranch, but they do not necessarily see it as a problem (Okello 2005). This is because agriculture reduces their dependence on pastoralism as a source of food, and is mostly confined within the electric fences, along the fertile riverine habitats where wildlife – related damages are minimized, and they use rivers to irrigate their crops throughout the year.

But agriculture is mostly incompatible land uses to the ecology of the Amboseli Area. It heavily relies on irrigation from the few rivers available, thereby affecting water flow and volume in rivers. Agriculture is also leading to rapid conversion of critical wetlands (such as Kimana and Ilchalalai swamps) used by both livestock and wildlife foraging especially in the dry season (and drought) when pasture is limited. This is destroying these rare and critical habitats in the ecosystem and also affecting human use of critical resources (plants, ethno - botanical resources, drinking and domestic water use, and water for livestock) found in these habitats.

There is also likely to be farmer – herder, farmer – wildlife, herder – wildlife and human – human conflicts (as noted by Campbell *et al.* 2000) as resources in these critical habitats diminish and competition for access intensifies. These conflicts eventually affect wildlife more (Sindiga 1995, Okello^a 2005), and inevitably leads to wildlife displacement from use of such habitats. About sixteen years ago in 1990, it was estimated that the Nolturesh river in Kuku Group Ranch alone was irrigating 80% of the farms in Olorika and Kisanjani areas while only about one percent of the land in Kuku was being cultivated for agriculture (Ngethe *et al.* 1990). This work showed an increase of agricultural cultivation in Kuku Group Ranch to over three percent. It is this steady increase in irrigated agriculture in the entire ecosystem (also reported by Campbell *et al.* 2003) that is of concern to wildlife conservationists, even though the proportion of total agriculture (irrigated agriculture in particular) still covers a small portion of the ranch.

Irrigated agriculture poses many direct (habitat loss, pollution from fertilizers and pesticides) and indirect threats (competition for water, human – human conflicts, human – wildlife conflicts) to wildlife conservation in the area. In Kuku Group Ranch, most rivers are now dry downstream, with diversion of main rivers occurring within a quarter of their causeway from the river sources. This diversion of sometimes entire rivers upstream is not only illegal (but is never enforced by ministry of water resources or National Environmental Management Authority, NEMA) but also denies the majority of people, livestock and wildlife users downstream. This water shortage downstream affects the use of the group ranch, concentrating human activities along river causeways and encouraging degradation water sources (such as swamps, riverine habitats and springs).

Even though most riverine habitats are still available, especially in Kuku and Mbirikani Group Ranch (with only 16% converted into agriculture in Kuku Group Ranch), most rivers in Kimana have been diverted into irrigation to the extent that most have only dry riverbeds downstream making most riverine habitats less useful to dependent wild animals such as bushbuck, reedbuck, sykes and vervet monkeys and riverine habitats dominated by *ficus* and *acacia* spp to die out. All riverine woodlands are also under siege from charcoal makers, hence putting more pressure on this habitat. Irrigated agriculture uses heavy pesticides and herbicides in production of onions, tomatoes, maize and beans. Most of these chemicals percolate into the few existing river systems and are already causing further harm to water users and polluting the environment (Githaiga 2003).

Most farming areas are also illegal bushmeat hotspots where wildlife is snared and killed for by casual cultivators who stay up late in nights guarding their crops from wildlife raiding. Active illegal killing is also an attempt to reduce the density of wildlife around farms as a way of controlling crop raiding. So even though irrigated agriculture takes a smaller portion of the group ranch, its direct and indirect effects on conservation are many. Therefore, this is possibly why wild mammals kept a longer distance from irrigated agriculture because of harassment, destruction of riverine habitats, snaring and actual harm cultivators subject them to. This has been the reason many wildlife species has been exterminated in former wildlife ranges where agriculture has been established in Kenya (Milton 2000, Mwale 2000), and is gradually taking root in Tsavo – Amboseli Ecosystem.

The fact that the majority of land in Kuku and Mbirikani group ranches is not converted into human structures and activities means that critical areas of migration, dispersal and habitat types are still potentially available in the group ranch. This result is partly because the land is not suitable for agriculture due to ecological constraints (lack of sufficient rainfall and

poor shallow soils), thus discouraging the relatively lucrative and economically attractive agriculture activities in the rangelands, except along rivers, swamps and areas of more reliable rainfall. Another reason why much land remains is the relatively wildlife -tolerant Maasai culture and pastoralism lifestyle that shares range with wildlife (Wishitemi & Okello 2003) without unnecessarily harming it. With the right economic incentives and direct benefits suggested by Norton -Griffiths & Southey (1995, Ferraro & Kiss (2000), and restructuring of pastoralism and communal ownership of resources (Kituyi 1990, Galaty 1992, Mwalyosi 1992, Ntati 2000), wildlife dispersal can be allowed alongside traditional pastoralism. The Maasai should be encouraged to embrace economic activities associated with wildlife (such as ecotourism and merchandizing tourist souvenirs). With now beef markets being reconstructed in the country and political willingness to invest in semi arid and arid lands (ASAL), these rangelands can be maintained for both pastoralism and wildlife use to the benefit of the local community (Makombe 1993, Lichtenfeld 1998, Noe 2003, Wishitemi & Okello 2003).

The Maasai homesteads (*bomas*) occupied the smallest amount of area in all group ranches, but the total displacement effects and displacement distance were relatively high. Maasai *bomas* support several families and livestock. They tend to have high concentration of humans and associated activities such as noise that greatly displace most wildlife. Further, the plant resources in wildlife habitats surrounding *bomas* are heavily used for charcoal production, wood fuel, medicinal purposes and construction materials (Kiringe & Okello 2005, Sindiga 1995; Okello & Kiringe 2004). The land surrounding *bomas* are also over-utilized by livestock. Mwalyosi (1992) found that livestock grazing affected plant species composition and contributed to severe soil erosion. Livestock in high density severely trample and deplete the vegetation cover, as well as in the areas surrounding *bomas*. *Bomas* are also spreading throughout group ranches as human population increases, thereby increasing land degradation and hence displacement of wildlife. As more adults leave to establish new *bomas* to make room for new families, the number of *bomas* in the group ranch will inevitably increase, further displacing wildlife. The overall effect of *bomas* is magnified dramatically due to the high number of *bomas* with associated human presence and activities. Maasai *bomas* are a hub of activities in the rangeland and the demands for individual household further fragments the rangeland and make it inaccessible to most dispersing wildlife.

Unlike in the years past, markets and most *bomas* are becoming permanent at their sites mostly because of the ongoing group ranch subdivision into individual land ownership, the expansion of agriculture and the protection afforded by the electric fences. As the *bomas* become permanent they also displace wildlife permanently in areas wildlife once roamed freely across the group ranch dispersal areas and block migration corridors between protected areas. For example, the very small gap leading to Kimana Community Wildlife Sanctuary (KCWS) will be blocked by a cluster of human settlement and agriculture within few years. This increasingly makes Kimana no longer available as a wildlife dispersal area because only less than half of Kimana group ranch land is still available for wildlife use, even with a designated but small and increasingly insularized KCWS.

Most permanent *bomas* were concentrated around roads and water resources, where distribution of critical resources and services influence people's settlement patterns. Permanent *bomas* and created barriers to wildlife that lead to a lasting loss of wildlife dispersal space. Temporary *bomas* are constructed out of leaves, grass, trees, mud and cow dung, and are traditionally used by the nomadic pastoralists during grazing in unsettled open

rangelands. When traditional pastoralists traverse the entire group ranches, their livestock goes with them, spreading the impact of both humans and livestock in the ranch, but such effects of temporary *bomas* help diversify and fertilize the range. Therefore the impacts of temporary *bomas* are less severe and are easily reversed than permanent *bomas*, thereby displacing wildlife less. Nevertheless, this does not eliminate resource competition between livestock and wildlife especially when they occur in preferred habitats that have abundant forage, water and less inhabited by people. Most, *bomas* are also constructed in areas with good soil and drainage conditions (Lamprey & Reid, 2004), and will be abandoned if natural resources in the area declines. Therefore, temporary *bomas* may actually consume more space in the group ranch than the clustered permanent *bomas*, by moving from place to place and consuming resources for their construction more frequently.

Every wildlife species have tolerance levels of human and livestock presence (Bourn & Blench 1999). Most zebra, wildebeest and gazelles seem to tolerate livestock and will sometimes be seen to graze side by side. However, where competition for forage occurs (like wild browsers and goats) or where livestock is accompanied by much noise and human presence (such as noisy bells hung on goats to establish the location of dispersing ones) displaces wildlife more. Sheep and goats were the cause of the most displacement of wildlife. This may due to their large group size and feeding strategy; they compete with both wild grazers and browsers. They were also most common in dense bush/shrubland, where wildlife occurs in the largest groups outside of riverine habitats.

Cattle are bulk feeders (Bergstrom & Skarpe 1999) and often grazed in open woodland or shrubland habitats. In some cases, large herds of cattle displaced wildlife more than shoats and donkeys due to their large size and numbers. The noise and presence of herders may also displace wildlife more than the actual forage competition between livestock and wildlife. It was very common to see wildebeest and zebra grazing in close proximity to cattle in the group ranch, especially in cases where herders are absent. Donkeys displaced wildlife the least. They are also bulky but nonselective feeders (Bergstrom & Skarpe 1999), hence competing less for forage with wildlife. They also grazed in relatively smaller groups and without a Maasai herder. The seasonal migration patterns and foraging strategies of wildlife and livestock are similar that their competition for pasture and water is occurring throughout the year (Berger 1993). This suggests that there is direct competition for resources between wildlife and livestock, often leading to displacement, especially of wildlife in the dry season when forage and water are scarce (Western 1975, Okello 2005).

Our general observation was that most group ranches were generally overgrazed, with some areas severely degraded and eroded to be suitable wildlife range. Overgrazing, especially during the dry season, prevents the ecosystem from its normal cycle and leads to the loss of many plant species. Some areas have plant composition that is mostly temporary annual plant species or invader species indicative of a degraded range (Bolen & Robinson 1999, Heady & Heady 1982). The Maasai group ranch owners must be encouraged to monitor livestock stocking rates as well as ecological integrity of the group ranch if it is going to support both livestock and wildlife use of range. There is however strong need to help the Maasai get inclined to fewer but healthier herds of livestock that can survive prolonged droughts and diminishing range. Breeding of better variety of livestock with local Maasai ones will improve the quality of livestock (for beef or milk) and help reduce excessive herds that cause degradation on the range and reduce its value to both livestock and wildlife.

Since people's presence also cause wildlife displacement of their own, the number of herders accompanying livestock could also increase the distance wildlife was displaced from livestock. In addition to competition for space and resources, the presence of livestock may be enough to displace wildlife because of their associated noises (bells and bleating) and scent (Bergstrom & Skarpe 1999). The Maasai utilized open wooded or scrubland habitats to graze their livestock and collect plant resources (Kiringe & Okello 2005). Since wildlife also preferred open wooded or scrubland habitats, competition for resources ensues. In this regard, wildlife is competing with an additional human presence in the habitat they depend on for their survival needs (Kiringe & Okello 2005, Western 1982).

Since the Maasai range has diminished throughout history, they have become more sedentary as they have also now been confined into group ranches which are also undergoing sub – division into individual land ownership. This increases their dependence of smaller parcels of land, and with increasing droughts, livestock gets compressed in small unproductive areas and hence increases overgrazing and degradation (Morell 1996, Western 1977, Lado 1992). This overgrazing becomes more pronounced in long dry seasons when they also more intensely compete with wildlife for forage and pasture. This situation creates more conflicts between the Maasai and wildlife leading often to persecution of wildlife (spearing, snaring and actively displacing) to minimize competition for space and other land resources and conflicts with wildlife (Western 1982).

Another fragmenting land use also associated with much noise and both human and motor traffic is the roads. Roads can restrict animal movements since noise and traffic can be extremely alarming to animals and add to the edge effect caused by roads. The restricted movement of animals caused by unplanned network of roads can interfere with wildlife activities such as searching for prey, mates and seeking cover thereby confining them only to ranges where they feel free and safe. In extreme cases, such fragmentation can cause local extinctions (Fahrig 1997). The continuous soil compaction, caused mainly by vehicle weight, reduces the ability of the soil to recover because of the lack of roots anchorage (Ceballos-Lascurain 1996). This in-turn creates an increase in surface run-off, which causes erosion and further degradation to the vegetation of the area. Herders of livestock tend to stick close to the roads of the area, which also leads to more wildlife displacement. Vehicles also displace wildlife because of potential harm in accidental deaths from vehicle traffic. The number of road kills may be less in group ranches, but may be significant on main roads that link major towns in the area and elsewhere in Kenya. Further, roads have great fragmentation effect because of their relatively huge network that keeps changing because of poor conditions. This degrades and destroys wildlife habitats and fragments the dispersal areas which may not be useful, even if available.

In Mbirikani Group Ranch, the roads only took up a small actual area of the group ranch, but displaced wildlife the most out of any human infrastructure due to the noise, danger and much traffic. The construction of the road network in Mbirikani effectively split the group ranch into six fragmented sections. As the population grows in the group ranches, it is likely that the traffic and noise produced by the roads will also increase further displacing wildlife. If this occurs, the wildlife populations in the group ranch will not be able disperse across Mbirikani, but will return to protected areas of origin, effectively blocking movements between the protected areas. It is important that no more roads are constructed in such a way as to prevent any further truncation of the ecosystem.

Wildlife requires quality habitat and space in order to thrive (Bolen & Robinson 1999). Range requirements by wildlife include food, proper cover or room to flee and opportunities for reproduction and nurturing of young (Heady and Heady 1982). Habitats that are heterogeneous and offer many of these will be used more by wildlife. In this work, riverine habitats had few animals because they were also areas of high agriculture and human concentration. Some primates (such as sykes and baboons) prefer this area as natural habitats, but can also be drawn to them for crop raiding or gathering what agriculture produce is left behind after harvesting crops. This intensifies human – wildlife conflicts and can lead to intense persecution and even permanent displacement of wildlife (Siex & Struhsaker 1999, Hoare & Du Toit 1999). Open woodland / shrubland offer heterogeneity in terms of browse, grass and cover (thermal, escape and nesting) and hence supported higher diversity of animals. Grasslands, however, may support large group sizes due to large herd grouping patterns of most plain grazers such as zebra, wildebeests and gazelles (Estes 1997).

The abundance and frequency of sightings of wildlife were all dependent on habitat type. This could be either because of habitat visibility differences, sampling bias (not sampling all habitats equally, although an effort was made to minimize this error), or simply because certain species prefer certain habitats. For example, animals such as the arboreal sykes monkey (*Cercopithecus mitis*) can only be found in riverine habitats (Estes 1997) where they feed on fruits and leaves (Estes 1997). This means that the integrity of certain habitats (especially open wooded or open shrublands, and riverine habitats) is very critical for wildlife viability in dispersal areas. The dispersal areas should offer quality diverse habitats with sufficient supply of shelter, cover, forage and water to remain useful to dispersing wildlife. Otherwise even if the dispersal space is available but the quality of the dispersal areas or migration corridors is low (due to livestock overgrazing, depletion of plant cover by humans or fragmentation by roads and settlements) or unsafe for wildlife, they will not be used (Fahriq 1997), and the effect will be the same as if the dispersal area and migration corridors had been blocked or converted to alternative uses (Newmark 1996).

Land use changes in the group ranches are a key reason for contraction of wildlife dispersal space in the Amboseli Ecosystem. Currently, most group ranches in Amboseli Area have resolved to sub – divide group ranches into individually owned parcels of land. Agriculture expansion is the most dominant driving force for sub – division, together with poor stewardship of group ranch resources by elected group ranch officials and land ownership demands by the new Maasai generation (Campbell *et al.* 2003, Ntiati 2002, Okello^a 2005). Further, members desire economic diversification and empowerment through access to credit facilities, which require land as collateral. Recent droughts and sedenterization of the Maasai into group ranches have increased competition for land, water and pasture required by livestock among communities in Kajiodo district (Campbell *et al.* 2003).

Group ranch subdivision will affect wildlife just as it will affect pasotalism. Small pieces of land will make pastoralism expensive practice, reducing Maasai herd sizes and causing abandonment of pastoralism as a livelihood or practicing it in combination with other livelihood options. Pastoralism is declining mainly because of reduced government free veterinary services and lack of structured market for beef products from livestock, and reduced land that encompasses dry and wet season grazing areas for the Maasai. However, people with large livestock numbers are opposed to group ranch sub-division, as it will greatly reduce access to abundant communally owned pasture and water, threatening any

remaining form of pastoralism and irreversibly altering the Maasai lifestyle and culture (Okello *et al.* 2003).

Negative implications for wildlife resulting from subdivision and group ranch fragmentation will be immense from immediate conversion, selling and cutting off migration and dispersal areas in initial excitement of private ownership as people claim and fence off their individual parcels of land (Ntiati 2002). This will encourage expansion of incompatible land use practices, human structures and activities that will diminish further wildlife (and pastoralism) range. This will increase competition for land and other critical resources leading to more social conflicts. Wildlife populations dependent on migrations may collapse (Burkey 1994, Newmark 1996), especially on short term. For example, in Okavango Delta in Botswana over 50,000 wildebeests were found dead in 1983 along a new fence which prevented them from reaching water (Conniff 1999). This is what is widely predicted (Ntiati 2002), but this view is also ignorant of what has also happened elsewhere (Maasai Mara and Kaputei areas) in the long run, when individual land owners pulled down fences and jointly owned critical resources (pasture, water, range) with individual shares equivalent to legal land owned in the pooled land.

There is indeed a possibility that individual landowners may merge their land into large blocks of land for access to sufficient pasture and water especially in dry season and prolonged droughts. These actions may potentially restore the back to dispersing wildlife. Land owners in known critical wildlife migration routes can be encouraged to begin ecotourism ventures to benefit from wildlife on their land, or they negotiate with conservation NGO's and government agencies to maintain landscapes for pastoralism and wildlife conservation at a concession fee or economic easement programs (Ferraro & Kiss 2000). This might be easier because negotiations will be with known legal land owners who can easily enter into contracts and reach agreements unlike the current complex management regime where sometimes consensus is difficult to reach and benefits are not distributed equitably among group ranch members (Lichtenfeld 1998). Therefore group ranch sub – division poses both challenges as well as opportunities for maintaining dispersal areas and migration routes for wildlife.

In Kuku Group Ranch, a more clear threat to wildlife dispersal space is the growing spatial proximity in a north – south direction of major human cluster of activities along pipeline road and western part of KGR. The two biggest clusters of human activities in Kuku are Kisanjani and Elankata Engima-Ilchalai. Both of these multiple use clusters have gotten larger over the years due to agriculture expansion that also attracts concentration of settlements and markets centers. The area between these two clusters was commonly been used by elephants, wildebeest, Zebra and eland migration between Kimana Community Wildlife Sanctuary to the chyulu Hills and Tsavo West National Parks. It is still one of the visibly active migratory routes for wildlife in the ecosystem, but the gap between these clusters is rapidly continuing to close due to growing number of cultivators in these clusters. This would confine the wildlife to only using the narrow space between the Elankata Engima-Olorika and Inkisanjani clusters, which is already unsuitable due to known frequent bush meat illegal killings around Inkisanjani cluster and towards Rombo group ranch for the wildlife meat market in Tanzania. These three clusters growth is fragmenting Kuku Group Ranch and likely to truncate Kuku dispersal area by blocking complete migration of wildlife between the Amboseli / Mt. Kilimanjaro and Tsavo/Chyulu systems. Therefore spatial growth and arrangement of clusters can be a significant threat to the wildlife dispersal area, even if

the actual area taken up by human activities and structures in the group ranch is small, or there is still vast unconverted land available for dispersal. Contraction of corridors due to spatial location and growth is becoming a more frequent direct threat to wildlife dispersal in the ecosystem (Noe 2003).

On a landscape level, there is still sufficient undeveloped wildlife dispersal area (shared with livestock) in Kuku Group Ranch. However, this does not mean that the remaining space is in good ecological state as suitable wildlife range. There may be dispersal land available, but if its overgrazed, degraded and depleted of vegetation cover, or is a hot spot for wildlife snaring and illegal killing, such area will not be used by wildlife for dispersal or as migration corridors. A good example is the avoidance of agricultural areas near Inkisanjani and along the pipeline road as these areas are hotspots for wildlife snaring (KWS Problem Animal Control Records, Oloitoktok).

There are places of abundant wildlife away from human clusters at the center of Kuku Group Ranch that were having no settlement or human activities. With vast areas of the group ranch still intact, focus need to be placed on opening up the migration gap (Lindenmayer & Nix 1993) between Ilchalai and Elankata Enkima-Olorika clusters as well as between Inkisanjani – Okaria and Elenkata Enkima – Olorika clusters for wildlife migration between Tsavo West / Chyulu and Kimana Kimana Wildlife Sanctuary / Amboseli National Park system to be complete. Recent studies (Okello^b 2005, Okello^c 2005) have investigated the possibility of establishing *Olosoito – Motukanju Wildlife Conservancy* which is already underway from December 2005. This wildlife sanctuary is expected to replace the Ilchalai – Esambu clusters and open a direct dispersal route of wildlife from Kimana Community Wildlife Sanctuary to Chyulu Hills / Tsavo West National Park. The wildlife conservancy is expected to be modeled on a multiple use resource area principles, and not the national park model (Beresford & Phillips 2000). Tourism revenue from tourism would go directly to the community and access to pasture and water by the community allowed on a controlled manner during droughts or prolonged dry seasons (Okello *et al.* 2003) so that the conservancy retains relevancy to the community even during decline in tourism revenue.

The importance of a new wildlife sanctuary in Kuku Group Ranch would be legitimizing wildlife conservation as land use option that brings revenue directly to the community or land owners, thereby also securing more range for wildlife. This would directly benefit long ranging species like elephants, which are also ecologically important and tourism flagship species (Waithaka 1996, Western 1989). It would help reduce the negative attitudes towards elephants as destructive and number one problem animal in the area (Thouless & Sakwa 1995, Hoare & Du Toit 1982, Nyeki 1992, Okello^a 2005). Partnership with tour companies and investors would boost the economic potential of the area (Ceballos-Lascurrain 1996), while management would benefit from funds and expertise of the tour investor while community involvement would legitimize it a community enterprise (Okello^c 2005, Ogolla & Mugabe 1996). Many group ranch members want the conservation area established before sub – division and jointly owned by the community (Okello in review, Newmark 1996; Meffe and Carroll 1997).

In Kimana Group Ranch, the threat to wildlife dispersal areas and corridor is both spatial and size. A big space has been taken over by human structures, and wildlife greatly displaced by especially *bomas*, roads and electric fences and agriculture. The fact that we could not see any wildlife close to agriculture area is evidence for agriculture's high wildlife displacement potential (Mwale 2000). People think by persecuting wildlife, they will push them far away

from farms and therefore reduce crop raiding. Further, the people who farm spend lots of energy guarding their crops day and night using noise, fire and other crude weapons which further scare, intimidate and displace wildlife. Many farm attendants are hired laborers and do not have enough money to live on. Most engage in snaring gazelles, giraffes and zebra for easy bush meat. Another threat is spatial arrangement of human structures and activities. For example, the electric fences sealed in most rivers and watering points, and were constructed directly in the migration paths leading to the critical Kimana Swamp located in KCWS, hence cutting off critical dry season wildlife grazing area and access to water. These dual aspects have greatly compromised KGR as a viable dispersal area, and more able to negatively affect economical and ecological viability of KCWS.

In Kimana, confining *bomas* to market areas or inside the electric fences may be a useful strategy to confine human settlements to one location where wildlife has already been displaced anyway. The problem with this is that it is not consistent with the Maasai's pastoral lifestyle, and the land inside the fence can not sustain many people in these relatively small areas that have already been subdivided into privately owned parcels of land. Already markets are dense populated and are competing for scarce amenities such as clean water and firewood to supply energy needs. The heavy traffic and density of people inside these market settlement clusters inside fences would create even larger wildlife displacement. The land that remains outside electric fences can have clearly defined uses in a comprehensive land use plan (Sibanda 1996), while maximizing suitable uses for land in areas in which it dominates. The disadvantage with this is that it will need legal instruments and institutions for enforcement, and the Kenyan government has little capacity and proven success in enforcement of its policies especially in regards to environmental management.

The electric fences in Kimana Group Ranch have not only displaced wildlife, especially elephants by taking dispersal area, but due to their spatial location, have also deflected human - wildlife conflicts to other areas such as agricultural areas on the slopes of Mount Kilimanjaro. They have shifted the problem rather than solving it. Although it has succeeded in excluding most wildlife, it is simply a matter of time before it is destroyed due to neglect. It is surprising that most causes to its damage are human – caused and not elephants. Further, these electric fences were put up without carrying out environmental impact assessments on effects to wildlife dispersal and encouragement of agriculture it would create. They have completely cut off the majority of east-west corridors, and reduced wildlife access to water, since almost all water sources were enclosed within the fence. Further, there has been no local ownership of the fence and they (especially Kimana) are falling in disrepair (with wires cut and solar panels missing). Once the elephants discover the fence is faulty, it will be destroyed immediately and difficult to repair or reinstate because of associated expenses (Thouless & Sakwa 1995). Funds for maintenance and running costs were not factored in the fence plan, hence its deplorable state and lack of ownership.

Though the establishment of Kimana Community Wildlife Sanctuary was a good economic and conservation initiative, it will not remain viable partly because it adopted a park model and not other suitable alternatives (Beresford & Phillips 2000, Wishitemi & Okello 2003). It needs the surrounding dispersal areas that are quickly disappearing as well as corridors to the other protected areas. If the wildlife sanctuary is not ecologically viable, it will not attract tourists or tourism investors to lease it or run it jointly with the community and remain economically profitable (Gowdy 1997). Without profits, there will be no benefits from KCWS directly and significantly coming to the community anymore. KCWS brings in excess

of Ksh 8 Million to the group ranch yearly. But disagreements between the investor and local Maasai about access to KCWS resources (forage and water especially during dry seasons and droughts) are slowing down local appreciation for wildlife in the group ranch. Future proposed community wildlife sanctuaries can avoid these pitfalls (Okello *et al.* 2003). The local community needs to take action to avoid insularizing KCWS and to allow wildlife migrations between it, Amboseli and Tsavo West/ Chyulu Hills Parks to make this pioneer community conservation initiative succeed and remain viable.

In Mbirikani Group Ranch, even though most of the group ranch is still available for wildlife, the spatial placement of the eight clusters in the group ranch has greatly affected the dispersal corridors, and the movement of wildlife. Human settlements tend to concentrate around water resources, which are a scarce resource in the dryland ecosystem (Githaiga *et al.*, 2003). Settlements are also found along the main road from Loitokitok to Emali, and along the pipeline road between Inkisajani and Mbirikani markets that follows the water pipeline to Nairobi (Campbell^a *et al.*, 2003). Only nine potential routes were still open for wildlife dispersal. However, these dispersal routes have not been assessed ecologically, for adequate water and forage resources. If the ecological conditions in these areas are poor, the potential routes could be detrimental rather than beneficial to wildlife populations in the area. As immigration and population continue to grow (Thompson & Homewood, 2002), development in the group ranch will expand, further reducing the space available to wildlife. The migration gap left open along the main pipeline road may eventually close and seal off the east-west migration routes that link the Chyulu Hills to Amboseli National Park, thus effectively ending migration between the two parks. As Amboseli is too small to support the wildlife populations on its own, species will suffer and possibly go extinct.

The ecological integrity of Mbirikani Group Ranch is critical for the success of wildlife in the region, as the group ranch provides the most direct route for wildlife from Amboseli National Park to Tsavo National Park. But the amount of development in the group ranch has cut off wildlife from critical resources. The Namelok, Kimana Swamp-Esambu, and Ilchalai Swamp-Esambu clusters on the southeast end of Mbirikani effectively sealed off the swamps from wildlife, depriving the migrating animals a source of water. These clusters both cut off the swamps and the migration route to the Kimana Community Wildlife Sanctuary, an important dry season grazing and resident area for wildlife. Since water is the limiting factor on the amount of wildlife and livestock that Mbirikani group ranch can support, the loss of swampland habitats will eventually be highly detrimental to the success of many species in the group ranch. The presence of water-independent species such as the eland (*Taurotragus oryx*), fringe-eared oryx (*Oryx beisa callotis*), and gerenuk (*Litocranius walleri*) demonstrate that there were wildlife in the region that are adapted to low water availability (Reid, 2007), but most species still need access to water resource in order to survive.

Way Forward

The Tsavo - Amboseli landscape needs a well-defined land use plan that will guide establishment of new agriculture areas, areas of new settlement, markets centers and cluster growth and use of water resources. Collaborative initiatives and consensus building is needed to achieve this. New human activities should be confined within existing clusters, while trying to control expansion into existing wildlife migration routes and key dispersal areas.

The spread of agriculture, especially irrigated, needs to be strictly monitored because of the drastic effects it has on the environment. The riverine habitats are essential to the wildlife (also man and livestock) that is dependent on its water resources. The amount of water that farmers can extract from a river should be limited for the protection of wildlife habitats as well as access to water downstream by wildlife, humans and livestock.

Fire can help stimulate forage productivity and control pathogens and parasites for both wildlife and livestock, and together with grazing of herbivores in appropriate stocking densities help maintain a diversity of natural habitats in the ranch, as noted by Makombe (1993). A mosaic of habitats would encourage high biodiversity and density of wildlife. Various scenarios for wildlife conservation, corridors and migration routes need to be explored and discussed as group ranch dissolution progresses and individual ownership replaces the communal ownership practiced by the Maasai for many years. With the human population in Maasailand increasing at a rate of about four percent per year, further efforts towards preserving the dispersal areas and corridors on a landscape level is essential to safeguard wildlife and pastoral resources (Wishitemi & Okello 2003). Implications for wildlife and pastoralism should be anticipated and interventions established to preserve the landscape. As it stands now, the rangeland in Kuku Group Ranch is still available for wildlife and livestock despite expanding clusters and threat of agriculture expansion and associated consequences. This study provides good ground – based baseline information on current land uses and potential remaining areas for wildlife and pastoralism in Kuku Group Ranch, even for monitoring purposes. It is the ecological integrity of the available area that should be investigated further to ascertain its status as a suitable wildlife range.

More work is needed to establish the exact displacement effects of human structures and activities to wildlife. While this work considers the average distance as an index of such displacement, such distance may be affected by other factors such as habitat quality, animal density and distribution and season of the work. It may be important to evaluate such distances in relation to habitat and distribution variations so as to establish the actual additional displacement of human structures and activities. Further, use of the land may differ between day and night. It is likely that wildlife is less affected at night by human activities and therefore uses a much wider area than that deemed to be displaced. Nevertheless, it's an important first step to addressing wildlife displacement apart from actual area taken away from wildlife as dispersal area.

The community and other stakeholders need to be aware of the threats of human structures and expansion, together with group ranch subdivision poses to wildlife and pastoralism way of life. As a way forward, it is important to use this information to establish a comprehensive and binding land use plan for the ecosystem, maintaining uses where they are suitably established, but outlawing uses where they are socio – economically and ecologically unviable. Further, critical dispersal areas and migration areas between protected areas, as shown in this study, need to be established and recognized. The landowners or group ranch members in such areas should be compensated to allow the area to be leased at market prices as a wildlife dispersal or migration areas, or if owners are individuals, be encouraged to form linked private wildlife sanctuaries. These sanctuaries would benefit from the lucrative tourism industry in the area and generate direct and significant revenue to its owners, as well as expand range through expanded wildlife dispersal and migration space outside protected areas.

Another conservation option is to have the identified viable and critical corridors recognized and established (figure 6). This would involve negotiations with blocks of land owners (where subdivision has already taken place) or group ranch leadership (where land is still under communal ownership) through a lease or compensation program (Ferraro & Kiss 2000) from a conservation fund established by stakeholders. Such land would be available for wildlife as priority, but may be used for pastoralism during droughts or long dry season. The other option is to encourage landowners to pool together land (as seems to be now happening) and form privately owned wildlife sanctuaries to tap into the lucrative tourism industry in the area. This would also bring direct benefits from conservation (through establishment of campsites or leasing to ecotourism investors, and money going to known landowners). Such land would also be used sustainably for pastoralism with owners' deliberately reducing livestock stocking density, and ensuring habitat quality and diversity for wildlife. Such private conservation areas would expand range and dispersal area for wildlife from the nearby protected areas as well as economic benefits (Ferraro & Kiss 2000), but will have to still be linked to each other by viable corridors and migration routes.

As of right now, wildlife still utilizes the most group ranches, but with the increasing development, it is not certain that wildlife will still be able to survive in the areas it does now. Several steps must be taken in order to prevent development from becoming more detrimental to the wildlife corridors and populations. Improving the status of local communities, though managing population increase, improved livelihoods, and poverty reduction can help reduce the impacts of humans around protected areas. Creating programs for sustainable natural resource use, such as harvesting of medicinal plants, and the creation of rural based education is important for conservation objectives to be met. Most importantly, the communities must benefit from the wildlife they support for conservation to succeed (Okello & Kiringe, 2003). Additionally, the local communities receive no compensation for wildlife-induced losses such as crop trampling or predation of livestock. This imbalance must change in order for human-wildlife conflict to be mitigated (Okello & Kiringe, 2003).

Protected areas are highly important to species conservation. Since it is neither practical nor ethical to expect a community to support wildlife without any benefits (Okello & Kiringe, 2003), a community owned and operated protected areas can provide both a stop-over area for wildlife in route from the Chyulu Hills to Amboseli National Park, and a source of money for the community. However, as the population in the group ranch has grown, the protected area may become unviable without adequate dispersal spaces and links to other protected areas.

A land-use policy would also help to regulate the types of land use in the rangelands that are incompatible with conservation and protection of wildlife. Additionally, a protected landscape model could potentially provide a way to prevent further degradation of the corridors in Mbirikani Group Ranch. A protected landscape model (IUCN Category V) encourages a working environment of high natural or cultural value so that safeguarding the integrity of the area is vital to the protection, maintenance and evolution of such areas, and provides a way for local communities to be involved in conservation objectives (Okello and Wishitemi, 2003). Also, the application of the protected landscape model would protect wildlife, without displacing the people in the group ranch, as a national park or community sanctuary would. In Kenya, where land is a highly valued resource, this model would help to balance the local people and wildlife's needs.

It is clear that it is not only the area human structures and activities take away from wildlife in key critical dispersal areas, but its spatial arrangement and orientation of these

structures and activities. Kuku and Mbirikani Group ranch may have most of the wildlife dispersal area still available, but its spatial proximity and orientation clearly block direct wildlife movements and dispersal between the protected areas. For Kimana Group Ranch, the electric fences and human settlement not only take most of the area away, but the orientation and proximity to each other is blocking wildlife dispersal into the Kimana Community Wildlife Sanctuary and to other protected areas. The threat is therefore both in proximity of clustered settlements, the area taken away and orientation of these clusters (figure 6).

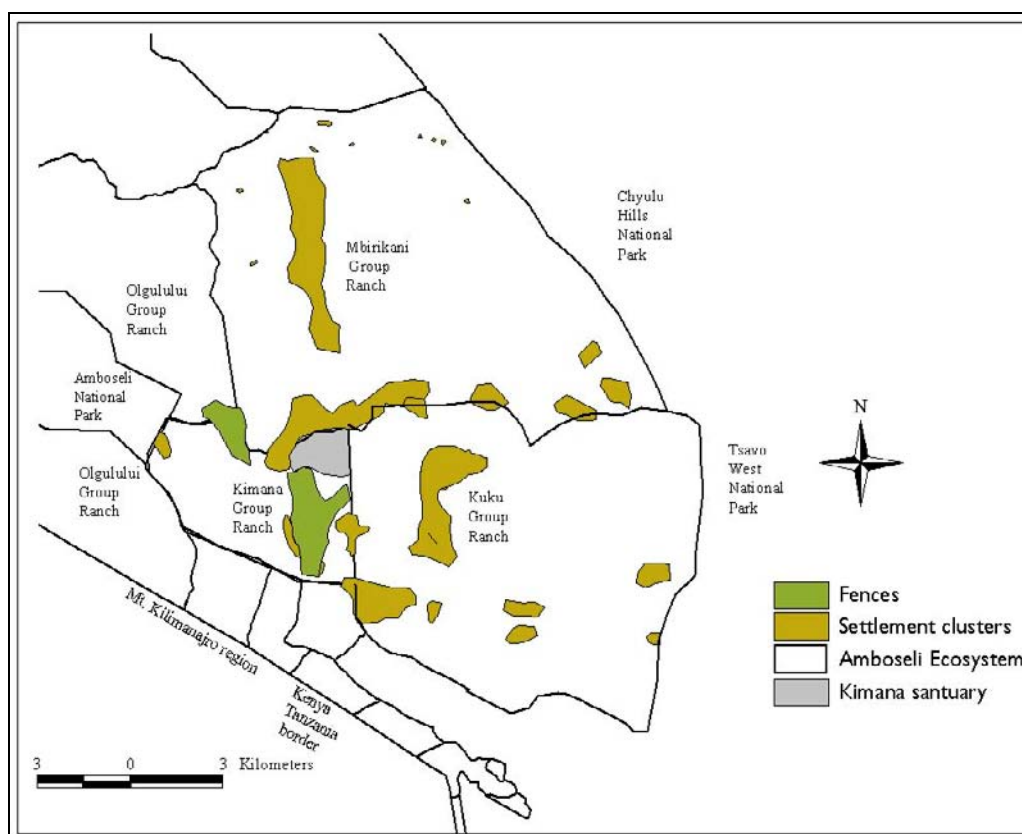


Figure 6. Clusters of human settlement and activities in three group ranches (Kuku, Kimana and Mbirikani) and how they spatially block direct wildlife movements and dispersal between Amboseli National Park on the west and Tsavo / Chyulu national parks on the west.

So the area taken away, additional wildlife displacement due to the activities and human traffic, and spatial orientation (figure 6) emerges as the three critical issues central to the contraction of wildlife dispersal space in group ranches in the Amboseli Ecosystem. The other emerging reality is that due to increasing land use changes as well as human population (natural increase and immigration will continue to displace wildlife and/or take away critical wildlife areas and insularize protected areas, thereby affecting their future viability as conservation enclaves. It is important to institute a land use plan so that all the land uses will be optimized and located in suitable areas without negatively affecting other land uses. It is also important to ensure that the land uses will be compatible with the ecology and culture of the area. Resource use (such as water and land) between different land uses must be done in

such a way that does not negatively impact the other. Land use policy and effective government institutions of regulating and managing such use is needed and critical to the survival of Amboseli Ecosystem.

Acknowledgements

We would like to thank The School for Field Studies and its Center for Wildlife Management Studies in Kenya for all logistical and financial support for this research. We thank research assistants who participated in the work: Paul Haverkamp, Salaash Olekoisseba, Paul Marias, Paul Sipaya, John Mpaa, John Karine, Wilson Musikeri, Simon Fayioki, David Kirembu, Abdi Kumbi, Moses Waema and Sarah Yerian. We thank John Kioko, Dan Manina and Amanda Huelat for helping with GIS spatial analysis. We also thank the officials and group ranch members in Kuku, Kimana and Mbirikani group ranches for allowing us to do this work on their ranches. We also thank the Kenya Wildlife Service Rangers for providing security from wildlife. We are also grateful to research teams in April 2003, November 2003 and April 2004: Stefanie Berg, Adrienne Metz, Julia Dreher, Lindsay Wieland, Marc Chipault, Nicole Seveageau, Jenny Glazier, Rachel Nichols, Bronwyn Llewellyn, Angela Schacht, Corrina Beale, Erika Pickett, Julie Widholm, Megan Morse, Michelle Gooch, Patrick Ayscue, Sean Tuley, Bradley Haley, Meghan Dinneen, Heidi Esh, Breeane Geery, Vanessa Knowles, Stephanie Martin and Regina Webb. Our local Maasai guides Isaiah and John Mpaa while John and Tim were our Kenya Wildlife Service guards. We also thank research teams of November 2004 and April 2005: Jackie, Amis, Daniel Mannina, Meghan Massaua, Tessa Dawson, Bryce Bunker, Amanda Huelat, Kaira Wagoner, Siv Tang, Jeff Cherian, and Therese Tepe, Leann Wilkins, Robyn Carver, Lacey Doucet, Hance Ellington, Justine Ma, Megan McNaught, Miguel Ordenana, Margrett Reinert, and Benjamin Still. We thank the November 2006, April 2007 and November 2007 research teams: Harper Addison, Sarah Coven, Karen Klinger, Amanda LaVoie, Julius Pasay, Skylar Stalians, Annie Putnam, and Summer Chrisman, Ian Haskins, Tracie Hiatt, Kelly Hillbun, Sarah Martin, Jessy Mortimer, Alida Ovrutsky, Angela Reid, Jake Rudolph, Amy Seaman, Shelby Schwartz and Megan Sweetwood, Aimee Weiss, Melissa Anderson, Quintana Baker, Jennifer Cotey, William Farmer, Rebecca Fuda, Alexandra Kamins, Ryan Lisson, Alexis Mincer, Corey Vane, and Kayla Yurco. Lastly, I thank anonymous reviewers for comments on earlier manuscripts.

References

- Adams, W. M. & Hulme, D. 2001. If community conservation is the answer in Africa, what is the question? *Oryx* 35(3): 193 – 200
- Alpert, P. 1996. Integrated conservation and development projects. examples from Africa. *Bioscience* 46(11): 845 - 855
- Barrow, E. Lembuya, P., Ntiati, P. & Sumba D. 1993. Knowledge, attitudes and practices concerning community conservation in Kuku and Rombo Group Ranches around Tsavo West National Park. *Community Conservation Discussion Paper No. 12, African Wildlife Foundation Discussion Papers Series*. 65 pp.

- Bergstrom, R. & C. Skarpe. 1999. The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *African Journal of Ecology* **37**: 12-26.
- Barnett, R. 2000. Food for thought: the utilization of wild meat in Eastern and Southern Africa. TRAFFIC East / Southern Africa. Nairobi, Kenya.
- Beresford, M. & Phillips, A. 2000. Protected landscapes: a conservation model for the 21st Century. *The George Wright Forum* **17**: 15 - 26
- Berger, D.J. 1991. *Wildlife extension: participatory conservation by the Maasai Of Kenya*. African Centre For Technology Studies, Nairobi.
- Bolen, E.G. & Robinson, W.L. 1999. *Wildlife Ecology and Management*. Fourth edition. Prentice-Hall, Inc. New Jersey.
- Bourn, D.& Blench, R.. 1999. *Can Wildlife Livestock Co-exist: An Interdisciplinary Approach*. Overseas Development Institute Research Study. UK
- Bonkounougou, E.G. (Year Unknown). Biodiversity in drylands: challenges and opportunities for conservation and sustainable use. The World Conservation Union.
- Burkey, T. 1994. Faunal Collapse in East African Game Reserves Revisited. *Biological Conservation* **7**(1): 107-110
- Campbell, K and Hofer. M. 1995. *People and wildlife: spatial dynamics and zones of interactions*. Pg 534-570 in A. R. E. Serengeti II: dynamics, management, and conservation of an ecosystem. The University of Chicago Press, Chicago.
- Campbell, D.J., Gichohi, H., Mwangi, A., & Chege, L. 2000. Land Use Conflict in Kajiado District, Kenya. *Land Use Policy* **17**: 337 – 348
- Campbell, D.J., Gichohi, H., Reid, R., Mwangi, A., Chege, L., & Sawin, T. 2003. Interactions between people and wildlife in Southeast Kajiado District, Kenya. The Land Use Change, Impacts and Dynamics (LUCID) Project. *Working Paper Series Number 18*. International Livestock Research Institute (ILRI), Nairobi, Kenya. Website: [http:// www.lucideastafrica.org](http://www.lucideastafrica.org)
- Campbell^b, D.J., Lusch, D.P., Smucker, T., & Wangui, E.E. 2003. Root Causes of Land Use Change in the Loitokitok Area, Kajiado District, Kenya. The Land Use Change, Impacts and Dynamics (LUCID) Project. *Working Paper Series Number 19*. International Livestock Research Institute (ILRI), Nairobi, Kenya. 32 pp.
- Campbell^a, D.J., Gichohi, H., Mwangi, A., & Smucker, T. 2003. Globalization and Local Heterogeneity: An overview of diversity in land use and development issues in Loitokitok Division, Kajiado District, Kenya. The Land Use Change, Impacts and Dynamics (LUCID) Project. *Working Paper Series Number: 21*. International Livestock Research Institute (ILRI), Nairobi, Kenya. 36 pp.
- Cheeseman, T. 2001. *Conservation and the Maasai in Kenya: Tradeoff or Mutualism?* On “Policy Failure in Kenyan Conservation and Maasailands. Cheesemans’ Ecology Safaris. Web document
- Ceballos-Lascurain, H. 1996. *Tourism, ecotourism and protected areas: the state of nature based tourism around the world and guidelines for its development*. IUCN, Gland, Switzerland and Cambridge UK.
- Cunningham, W.P. & Saigo, W.B. 1999. *Environmental Science*. Fifth ed. The McGraw Hill Companies, Inc. USA.
- Du Toit, J. T. 2002. Wildlife harvesting guidelines for community – based wildlife management: a southern African perspective. *Biodiversity and Conservation* **11**: 1403 – 1416

- Estes, R.D. 1997. *The Behavior Guide to African Mammals*. Russel Friedman Books. South Africa
- Emerton, L. 2000. Economic incentives for biodiversity: How Eastern African countries are making biodiversity attractive. *Innovation: Biodiversity for Secure Livelihoods in Africa* 7(1): 17 - 20.
- Environmental Protection Authority. 2004. Environmental protection and ecological sustainability of the rangelands in Western Australia. *Position Statement* No. 5 Perth, Western Australia 33 pp.
- Fahrig, L. 1997. Relative Effects of Habitat Loss and Fragmentation on the Population Extinction. *Journals of Wildlife Management* 61(3): 603-607.
- Ferraro P. J. & Kiss, A. 2000. Direct payments to Conserve Biodiversity. *Science* 298: 1718 - 1719
- Fratkin, E. 1994. Pastoral Land Tenure In Kenya: Maasai, Samburu, Boran, And Rendille Experiences 1950 - 1990. *Nomadic Peoples* 34: 55 – 68.
- Fratkin, E., 1997. Pastoralism: Governance and Development Issues. *Annu. Rev. Anthropol* 26:235-61
- Gakahu G.C. & Goode B.E. (1992). *Ecotourism and Sustainable Development in Kenya*. Wildlife Conservation International, Nairobi, Kenya. 321 pp.
- Graham, O. 1989. A land divided: The impact of ranching on a pastoral society. *Ecologist* 19(5): 184-185.
- Galaty, I. 1992. The land is ours: social and economic factors in the privatization, sub – division and sale of Maasai ranches. *Nomadic peoples* 30: 26 - 40
- Githaiga, J. M., Red, R., Muchiru, A. N., & van Dijk, S. 2003. Survey of Water quality changes with land use type in the Loitokitok Area, Kajiado District, Kenya. The Land Use Change, Impacts and Dynamics (LUCID) Project. *Working Paper Series* 35. International Livestock Research Institute (ILRI), Nairobi Kenya. 28 pp.
- Groom, R. 2005. Ecological Changes due to Land Subdivision in Maasai Pastoral Communities. University of Bristol and African Conservation Centre. 34 pp.
- Gowdy, M. J. 1997. The value of biodiversity: markets, society, and ecosystems. *Land Economics* 73(1): 25-41.
- Government of Kenya, 2001. Kajiado district development plan 1997-2001. *Office of the Vice- President and Ministry of Planning and National Development*. Government Printers, Nairobi, Kenya
- Hackel, J. 1999. Community conservation and the future of Africa's wildlife. *Conservation Biology* 13(4): 726-734pp.
- Harris, L. K. & Shaw, W.W. 1997. Urban Neighbors' wildlife-related attitudes and behaviors near federally protected areas in Tucson, Arizona, USA. *Natural Areas Journal* 17(2): 144-148.
- Heady, H.F. & Heady, E.B. 1982. *Range and Wildlife Management in the Tropics*. Longman Inc., New York.
- Hoare, R. E., & Du Toit, J.T. 1999. Coexistence between people and elephants in African savannas. *Conservation Biology* 13: 633-639.
- Honey, M. 1999. *Ecotourism And Sustainable Development: Who Owns Paradise?* Wasland Press, Washington D.C. Juma, C. & J.B. Ojwang. 1996. In *Land We Trust: Environment, Private Property and Constitutional Change*. Initiatives Publishers. Nairobi, Kenya

- Irigia, B. K. 1995. Kenya Wildlife Service environmental impact assessment of the proposed Kimana Wildlife Sanctuary. *Community Wildlife Service*, KWS, Nairobi. 29 pp.
- Katampoi, K., Genga, G., Mwangi, M., Kipkan, J., Seitah, J., Van Klinken, M., & Mwangi, S.M. 1990. Kajiado District Atlas. ASAL Programme Kajiado, Kajiado, Kenya.
- Kenya Wildlife Service. 1994. *Human wildlife conflicts in Kenya*. A five persons report. Kenya Wildlife Service, Nairobi, Kenya. 18pp.
- Kiringe, J. W. & Okello, M. M. 2005. Use and availability of Tree and Shrub resources on Maasai Communal Rangelands near Amboseli, Kenya. *African Journal of Range and Forage Science* **22**(1): 37 - 46
- Kituyi, M. 1990. *Becoming Kenyans: Socio – Economic Transformation of the Patorial Maasai*. Acts Press. Nairobi, Kenya.
- Lado, C. 1992. Problems of Wildlife Management and land use in Kenya. *Land Use Policy* **24**: 169-184.
- Lamphry, R.H., Reid, R.S. 2004. Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife?. *Journal of Biogeography* **31**: 997-1032.
- Lichtenfeld, L. 1998. Local Participation and Conservation in Kenya: A case study of the Kimana Community Wildlife Sanctuary. *Paper prepared for the 12th Annual Meeting of the Society for Conservation Biology*, July 13th-16th, 1998.
- Lindenmayer, D. A. & H. A. Nix. 1993. Ecological Principles for the Design of Wildlife Corridors. *Conservation Biology* **7**(3): 627-630.
- Livestock Production Department Range Planning Unit. 1989. Development Plan for Kuku Group Ranch. Government of Kenya, Nairobi, Kenya.
- Lusigi, W. 1981. New approaches to wildlife conservation in Kenya. *Ambio* **10** (2&3): 1943 - 1967
- MacKinnon, J., Child, K. & Thorsell, J. (eds.). 1986. *Managing Protected Areas in the Tropics*. IUCN. Gland, Switzerland. 295pp.
- Macnab, J. 1991. Does Game Cropping Serve Conservation? A Reexamination Of The African Data. *Canadian Journal of Zoology* **69**: 2283-2290.
- Makombe, K. 1993. Sharing the Land: Wildlife, People, and Development in Africa. IUCN/Rosa *Environmental Issues Series No.1*. IUCN/Rosa, Harare, Zimbabwe.
- McNeely, J. 1993. Economic Incentives for Conserving Biodiversity: Lessons for Africa. *Ambio* **22**(2): 144-150
- Mech, S.G. & Hallett, J.G. 2001. Evaluating the effectiveness of corridors: a genetic Approach. *Conservation Biology* **15** (2): 467 – 474.
- Meffe, G.K. & C.R. Carroll. 1997. *Principles of Conservation Biology*. Second edition Sinauer Associates, Inc. Sunderland, Massachusetts.
- Milton, S.J. 2000. *Biodiversity and Conservation in the Real World*. Inaugural Address. June 2000. University of Stellenbosch. South Africa.
- Morell, V. 1996. Surrounded! Civilization is encroaching on Nairobi National Park (Nairobi wild side). *International Wildlife* **27**(4): 38-44.
- Mwale, S. 2000. Changing Relationships: The history and future of wildlife conservation in Kenya. *Swara* **22**(4): 11-17.
- Mwalyosi, R. 1992. Influence of livestock grazing on range condition in south-west Maasailand, Northern Tanzania. *Journal of Applied Ecology* **29**, 581-588.

- Ngethe, S.J., Wafula, H.O. & Munyugi, J. 1994. *Contribution to a conservation based management plan for Kuku and Rombo Group Ranches*. Unpublished report. Kenya Wildlife Service. Nairobi, Kenya.
- Nicholson, C. F. 2001. Environmental Impacts of Livestock in the Developing World. *Environment*. Web document: findarticles.com
- Noe, C. 2003. The Dynamics of land use changes and their impacts on the wildlife corridor between Mt. Kilimanjaro and Amboseli National Park, Tanzania. The Land Use Change, Impacts and Dynamics (LUCID) Project. *Working Paper Series* Number 31. International Livestock Research Institute (ILRI), Nairobi, Kenya. Website: [http:// www.lucideastafrica.org](http://www.lucideastafrica.org)
- Norton-Griffiths, M. & Southey, C. 1995. The opportunity costs of biodiversity conservation in Kenya. *Ecological Economics* 12: 125-139.
- Norton-Griffiths, M. 1996. Why Kenyan Conservation is Failing. *Swara* (Special 40th anniversary edition): 6-8. O'Connell-Rodwell, C.E., T. Rodwell, M. Rice and L.A. Hart.
2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biological Conservation* 93: 381-391.
- Ntiati, P. 2002. Group Ranches Subdivision Study in Loitokitok Division of Kajiado District, Kenya. The Land Use Change, Impacts and Dynamics (LUCID) Project. *Working Paper Series* Number 7. International Livestock Research Institute (ILRI), Nairobi, Kenya. Website: [http:// www.lucideastafrica.org](http://www.lucideastafrica.org)
- Newmark, W.D. 1993. The Role and Design of Wildlife Corridors with Examples from Tanzania. *Ambio* 22: 500-504.
- Newmark, W.D. 1994. The conflicts between wildlife and local people living adjacent to protected areas in Tanzania: human density as a predictor. *Conservation Biology* 8(1): 249-255.
- Newmark, W.D. 1996. Insularization of Tanzanian Parks and the Local Extinction of Large Mammals. *Conservation Biology* 10(6), 1549-1556.
- Newmark, W. D., & Hough, J. L. 2000. Conserving wildlife in Africa: Integrated conservation and development projects and beyond. *Bioscience* 50(7): 585 – 592.
- Nyeki, D.M. 1992. *Wildlife Conservation and Tourism in Kenya*. Jacaranda Designs, Ltd, Nairobi. .
- Ogolla, B. D. & Mugabe, J. 1996. Land tenure systems and natural resource management. In: Juma, C. and Ojwang, J. B. (eds.), *In land we trust: environment, private property and constitutional change*. ACTS Environmental Policy Series No. 7. Initiative Publishers. Nairobi.
- Okello^a, M. M. 2005. Land Use Changes and Human - Wildlife Conflicts in the Amboseli Area, Kenya. *Human Dimensions of Wildlife* 10(1): 19 – 28
- Okello^b, M. M. 2005. An assessment of the large mammal component of the proposed wildlife sanctuary site in Maasai Kuku Group Ranch near Amboseli, Kenya. *South African Journal of Wildlife Research* 35 (1): 63 - 76
- Okello^c, M. M. 2005. A Survey of Tourist Expectations and Economic Potential for a Proposed Wildlife Sanctuary in a Maasai Group Ranch near Amboseli, Kenya. *Journal of Sustainable Tourism* 13 (6): 566 - 589

- Okello, M.M. In review. Maasai Landowners' Opinions And Support For The Establishment Of A Wildlife Conservancy In Kuku Ranch Near Amboseli, Kenya. *Journal of East African Natural Resource Management*
- Okello, M. M., Wishitemi, B.E.L & Lagat, B. 2005. Tourism Potential and achievement of Protected Areas in Kenya: Criteria and Prioritization. *Tourism Analysis* **10** (2): 151 – 164
- Okello, M.M. & Kiringe, J. W. 2004. Threats to biodiversity and their implications in protected and adjacent dispersal areas of Kenya. *Journal of Sustainable Tourism* **12**(1), 55-69.
- Okello, M.M., Seno, S.K., & Wishitemi, B. L. 2003. Maasai community wildlife sanctuaries in Tsavo – Amboseli Ecosystem, Kenya: management partnerships and their conditions for success. *Parks* **13**(1) 7 - 15.
- Okello, M.M., S.G. Manka & D.E. D'Amour. 2008. The Relative Importance of Large Mammal Species for Tourism in Amboseli National Park, Kenya. Accepted in *Tourism Management* **29** (4):751 - 760.
- Ottichilo, W.K., J. de Leeuw, & Prins, H. H. T. 1999. Population trends of resident wildebeest [*Connochaetes taurinus* (Neumann)] and factors influencing them in the Maasai Mara ecosystem, Kenya. *Biological Conservation* **97**:271-282.
- Pickard, J. 1998. Recent trends and implications of group ranch sub-division and fragmentation in Kajiado District, Kenya. *The Geographical Journal* **164**(2): 202.
- Republic of Kenya, 2001. 1999 *Population and Housing Census*: Population Distribution by Administrative Areas and Urban Centers. Volume 1. Government Printer, Nairobi, Kenya. 158pp.
- Reid, A. *Impacts of Human Development on Wildlife Dispersal Areas in Mbirikani Group Ranch near Amboseli*, Kenya: A spatial analysis of human structures, agriculture, livestock, and wildlife 2007. Unpublished report. SFS Center for Wildlife Studies, Nairobi, Kenya. 34 pp.
- Seno, S.K. & Shaw, W. W.. 2002. Land Tenure Policies, Maasai Traditions, and wildlife conservation in Kenya. *Society and Natural Resources* **15**: 79-88.
- Sibanda, B. M. C,& Omwega, A.K. 1996. Some reflections on conservation, sustainable development and equitable sharing of benefits from wildlife in Africa: the case of Kenya and Zimbabwe. *South African Journal of Wildlife Research* **26**(4): 175 –181.9
- Sindiga, I. 1995. Wildlife-Based Tourism In Kenya: Land Use Conflicts And Government Compensation Policies Over Protected Areas. *The Journal of Tourism Studies* **6**(2): 45 – 55.
- Siex, K. S., & Struhsaker, T. T. (1999). Colobus monkeys and coconuts: A Study of perceived human – wildlife conflicts. *Journal of Applied Ecology* **36**: 1009-1020.
- Sitati, N.W., Walpole, M.J., Leader-Williams, N. 2005. Factors affecting susceptibility of farms to crop raiding by African elephants: using a predictive model to mitigate conflict. *Journal of Applied Ecology* **42**: 1175-1182.
- Soule, M.E., Wilcox, B.A., & Holtby, C. 1979. Benign neglect: a model of faunal collapse in game reserves of East Africa. *Biological Conservation* **15**: 259-272.
- Thouless, C.R. & Sakwa, J. 1995. Shocking elephants: Fences and crop raiders in Laikipia District, Kenya. *Biological Conservation* **72**: 99-107.
- Thompson, M. & Homewood, K. 2002. Entrepreneurs, elites and exclusion in Maasailand: trends in wildlife conservation and pastoralist development. *Human Ecology* **30**(1): 107-138

- Waithaka, J. M. 1996. *Elephants: A keystone species*. pp. 284-285 In: McClanahan, T.R. and T.P. Young (eds.), *The East-African Ecosystems and their Conservation*. Oxford University Press (OUP), New York.
- Waters, G. & Odero, J. 1990. *Geography of Kenya and the East African region*. MacMillan Education Ltd, London. 287pp.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal* **13**: 265-286.
- Western, D. 1982a Amboseli National Park: Enlisting landowners to conserve migratory wildlife. *Ambio* **11**(5): 302 – 308
- Western, D. 1982b. The environment and ecology of pastoralists in arid savannas. *Development and Change* **13**: 183-211.
- Western, D. 1989. The ecological role of elephants in Africa. *Pachyderm* **12**: 42-45.
- Western, D. 1994. *Ecosystem conservation and rural development: the case of Amboseli*. In: Western, D., Pearl, M.C. (eds.). *Conservation for the twenty - first century*. Pages 15 - 52. Oxford University Press, New York
- Western, D. 1997. Nairobi National Park is slowly being strangled by development. *Swara* **19**(6) and 20(1): 19-20.
- Western, D. & Ssemakula, J. 1981. The future of Savannah ecosystems: ecological islands or faunal enclaves? *African Journal of Ecology* **19**: 7-19.
- Wishitemi, B.E.L. & Okello, M. M. 2003. Application of the Protected Landscape Model in Southern Kenya. *Parks* **13**(2), 12 - 21
- Worden, J., Reid, R. & Gichohi, H. 2003. *Land use impacts on large wildlife and livestock in the swamps of the Greater Amboseli Ecosystem*, Kajiado District, Kenya. The Land Use Change, Impacts and Dynamics (LUCID) Project. Working Paper Series Number 27. International Livestock Research Institute (ILRI), Nairobi, Kenya. Website: [http:// www.lucideastafrica.org](http://www.lucideastafrica.org)
- Young, T.P., & McClanahan, T.R. 1996. *Island Biogeography and Species Extinction*. In *East African Ecosystems and Their Conservation*. T. R. McClanahan & T. R. Young (Eds.). Pages 292 – 293. Oxford University Press, New York. 452 Pp.
- Zar, J.H. 1999. *Biostatistical Analysis*. Fourth ed. Prentice Hall, Inc. Upper Saddle River, New Jersey. 663 pp.

Chapter 3

CONSERVATION DURING CONFLICT: STRATEGIC PLANNING TO DEAL WITH WAR IN SUB-SAHARAN AFRICA

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Abstract

Africa contains some of the most distinctive and valuable biological resources on Earth, yet the future for biodiversity in parts of sub-Saharan Africa is being compromised by the prevalence of wars and armed conflicts in this region. War yields a vast number of negative impacts on social, economic, and political conditions. Some of the negative impacts of war include the direct effect of war tactics, the appropriation of financial resources to support war rather than to benefit civil society, the displacement of people and the subsequent impact on resources by refugees, the deterioration of governments, and, perhaps most critical, the overexploitation of wildlife. These impacts cumulatively facilitate a downward spiral in biodiversity when appropriate conservation interventions cannot be accomplished. Much of sub-Saharan Africa has been ripped by wars, and for conservation measures to gain the upper hand will ultimately require the establishment of novel plans and strategies specifically designed to preserve biodiversity under these conditions. The urgent need for new and renewed efforts in regions torn apart by war is reviewed, along with the lessons that conservation organizations have learned using adaptive management in these circumstances. These lessons include advocating nature valuation, providing increased support for local stakeholders engaged in conservation work, integrating conservation approaches with the work of humanitarian organizations, and managing the plight of refugees.

Introduction

War negatively affects biodiversity on all levels, from genetic biodiversity to ecosystem biodiversity (McNeely 2003a). Yet biodiversity conservation during times of war and armed

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conflict is very controversial because many view it as choosing nature over the welfare of humans (Douma 2000). However, in consideration of the bigger picture, the drastic impacts that such conflicts can have on the environment are all the more reason to focus and intensify conservation efforts in militant regions.

It is widely known that Africa's environmental health, biodiversity, and ability to sustain residents has been degraded and continues in that direction throughout most of the continent. All agree that the environmental degradation in Africa is caused by a number of interconnected factors including, but not limited to, rapid population growth, poverty, deforestation, development, and political corruption. But one factor that has often been left out in much of scientific literature and analyses (until recently) is the impact of war and armed conflict on environmental degradation. This exclusion is probably due to a lack of concrete data on the environmental impacts caused by armed conflict. The main reason why so little data have been collected regarding this issue is that most conservation efforts are usually terminated in regions where armed conflicts arise. The purpose of this paper is to show the urgent need for conservation efforts in the violent and war-torn regions of sub-Saharan Africa and to direct the implementation of conservation efforts to manage, heal, and prevent the impacts of social conflicts on humans and the environment.

Africa's Importance in Biodiversity Conservation

Africa is a unique continent composed of 119 ecoregions (WWF 2004), some of which are the world's most diverse, species-rich areas. WWF (2004) performed a biological value assessment based on biological distinctiveness, which can be described as the combined aspects of species values (richness and endemism) and non-species values (unusual evolutionary and ecological phenomena, rare habitat types, large intact ecosystems, higher taxonomic uniqueness, and the overlap of these factors). The conclusions made about the overall biological distinctiveness of Africa, ranked on the above criteria, are that 55 of Africa's ecoregions are globally outstanding, 17 are regionally outstanding, 23 are bioregionally outstanding, and 24 are locally important. And the most biologically distinct biome in Africa, tropical and subtropical moist broadleaf forest, has 62% of its total area (2,171,610 km²) affected by armed conflicts, which is the highest percentage compared to the continent's other biomes (Shambaugh et al. 2004).

Positive Aspects of War

Wit (2000) observed some war-related benefits to biodiversity and the environment in African countries. Areas that had been isolated due to danger and insecurity have done quite well or even flourished in biodiversity. Isolated areas along Mauritania's coast during the Polisario war provided optimum habitat for the rare Monk seal (*Monachus monachus*) and, further inland, the Adrar Mountain habitat for the vulnerable Barbary sheep (*Ammotragus lervia*) was also isolated. Landmines protected both of these habitats. Also, during the 1970s, every Nigerian military governor wanted to defend his own protected area (Wit 2000).

Although there are these positive benefits to the environment from armed conflicts in Africa, no researcher could effectively argue that they outweigh the negative consequences of

war. For example, war in Africa has been directly responsible for local extinctions such as that of the Western Black Rhino (*Diceros bicornis*) in the Chad Basin and the Northern White Rhino (*Ceratotherium simum*) in the Democratic Republic of Congo (Wit 2000). Often times, the benefits caused by war are also counteracted by consequences. The civil war in the Democratic Republic of Congo (DRC) caused a collapse in the timber industry, but it also increased the number of people that depend on firewood for fuel (Draulans & Van Krunkelsven 2002). Benefits, as outlined here, are unfortunately short-term and often only endure for the duration of the war (Blom 2000). It also has been argued that wartime benefits no longer apply to conflicts in the 21st century (Dudley et al. 2002).

Negative Impacts of War

The negative impacts of warfare on biodiversity can be categorized on multiple levels. Armed conflicts impact nature both directly, through local extinctions and overexploitation, and indirectly by obstructing good governance, an essential requirement for long-term conservation. War, directly and indirectly, induces a shift toward instability in social, economic, and political conditions, resulting in the potential for extensive damage to environmental ecosystems and decreases in biodiversity (Shambaugh et al. 2004).

Bruch (2000) describes four ways in which war negatively impacts the environment. First, war tactics can target the environment, whether they are intentional or unintentional. Second, war impacts the environment because of the rising need for funds to cover military expenses, which leads to excessive extraction of natural resources from the local area. A third major impact caused by war is the overexploitation of vital resources to meet the needs of displaced persons and refugees. Finally, the deteriorating impacts that war has on government and law enforcement open up the way for increases in the amount of illegal and armed activities.

War Tactics

Violent conflicts have had catastrophic impacts on Africa's environment since the 19th century colonial period. Whether the impacts were intentional or unintentional, the results have been devastating. The European colonial government in South Africa resorted to warfare tactics that intentionally damaged the environment at the expense of the enemy, a practice that has been termed 'ecocide.' South Africa targeted the natural resources vital to Black African armies instead of the armies themselves (Levine 2004). The environmental impacts of such tactics, unsurprisingly, have increased exponentially over the centuries in response to the growth of technology (Levine 2004). South African soldiers also targeted the locals' crops and other food sources. They flattened fields repeatedly with motorbikes and trucks and nearly wiped out a crucial food source for indigenous natives during times of drought, the fruit of the native *oshipeke* bush (Kreike 2004).

During the 20th century Apartheid Wars, the South African Defense Force implemented the use of 'killing zones' as a warfare tactic against the South West African People's Organization. To enforce restrictive boundaries, South Africa stationed soldiers to shoot any person or cow that crossed the border and bulldozed all of the vegetation along a strip at the

border so patrols could identify trespasser tracks on the bare soil (Kreike 2004). The effects of killing zones and the terror they caused still impacts local productivity, income, and the environment today (Kreike 2004).

The establishment of the border also forcibly removed Black Africans from their settled homes and farmland onto less suitable land, requiring them to clear natural bush habitat to rebuild farm infrastructure, which significantly reduced food production and availability (Kreike 2004). Millions of blacks were forced into the most resource-poor and ecologically vulnerable lands in South Africa (Homer-Dixon 1993). By 1980, the rural density of the Ciskei homeland was 82 people/km², whereas the surrounding Cape Province had a rural density of 2 people/ km². The 1980 report also determined that 50 percent of the land suffers moderate to severe erosion and 40 percent of pasture was overgrazed (Homer-Dixon 1993). With high birth rates, resource depletion, lack of employment, and social damage from Apartheid, Homer-Dixon (1993) termed conditions in Ciskei homelands as a “subsistence crisis.”

An example of an unintentional direct impact of war on the environment and wildlife is explosives. In the 1994 war in Rwanda, bombs certainly killed all life, not only humans, and the water quality in the Nile basin became poor primarily due to corpses in the rivers, which decreased the entire basin’s health and biodiversity (Kanyamibwa 1998).

Military Finance

During times of conflict, war economics always takes precedence over the good of long-term, formal economics. Militias in Africa have intensified the effects of over-harvesting large mammals and poaching endangered species, such as the African Elephant (*Loxodonta africana*) and the extremely rare mountain gorilla (*Gorilla beringei*), because of their need for meat and other animal products to sustain themselves and to fund their war efforts (Plumptre 1997; Dudley et al. 2002). The warlord, Charles Taylor, supported his militant activities in the Liberian civil war by selling timber, gold, and diamonds (Douma 2000). Angola was plundered for its resources in teak, ivory, diamonds, and petroleum to cover war expenses (Bruch 2000).

Displaced People and Refugees

Tours of refugee camps in Liberia, Sierra Leone, and Guinea by the Environmental Foundation for Africa between 1999 and 2000 showed the devastating impacts of forced migration on the environment such as trampled lands, the absence of trees, and extensive ecosystem degradation from having to support 5-20 times more people than normal (Garnett 2000).

Hundreds of thousands of Rwandan refugees were forced into northwestern Tanzania in the 1990s, where Tanzania, a signatory to the Geneva Convention of 1951 and the Organization for African Unity (1969), was quite hospitable to them until the land and the government became so overburdened by the repercussions of the Rwandan refugee presence (Smith 2001). Smith (2001) describes the negative consequences of the refugees in regards to environmental damage, destruction of infrastructure, social problems, and security problems.

A number of experts, including the Ngara Development Trust Fund, quantified a few of the environmental impacts caused by the massive number of refugees in Tanzania, estimating that the refugees in the Kagera region consumed one million liters of water per day and used up 3,500 hectares of forest for firewood within six months, causing massive depletions of Tanzania's water and forest resources (Smith 2001). An equally large number of Rwandan refugees also crossed the border into what was Zaire at the time as a result of the same 1990s civil war propagating another civil war in the Democratic Republic of Congo as they struggled to find the resources they needed to survive (McNeely 2003b).

Government Deterioration

The breakdown of effective government and law enforcement after the onset of war causes major increases in the amount of illegal activities, such as poaching. The poaching of gorillas and elephants thrived during Congo's war (Bruch 2000). The lack of control over poaching facilitates the ability of militias to fund their war efforts (Plumptre 1997; Dudley et al. 2002), and can even urge poachers and others engaged in the illegal exploitation of resources, who derive benefits from the collapse of law enforcement, to support the continuation of the conflict (Blom 2000; Wit 2000). Because social institutions control the illegal bushmeat trade, increases in poaching rates within national parks and other protected areas cannot even be counteracted by four-fold increases in protected area patrol efforts (de Merode et al. 2007).

Overexploitation: The Most Critical Factor

The scarcity of natural renewable resources from overexploitation plays an enormous role before, during, and after conflicts. Homer-Dixon et al. (1993) attribute overexploitation and natural resource scarcity, prior to the onset of conflict, to three factors: (1) the overconsumption of resource capital; (2) the increase in human population; and (3) the disparity of resource access between the rich and the poor. The deficiency in critical resources caused by these three factors and the resulting ecosystem vulnerability then worsens the area's social, economic, and political conditions. The deterioration of these conditions creates self-reinforcing, positive feedback loops that facilitate further environmental damage and overexploitation of resources. A lack of resources in combination with the above conditions is believed to contribute to the onset of armed conflict and war. The conflict then adds yet another element to the system of feedback loops, amplifying the effects that the deteriorating conditions have on each other and the environment (Homer-Dixon et al. 1993; Dudley et al. 2002).

The Democratic Republic of Congo and Rwanda are two examples that were studied before, during, and after armed conflicts. Glew and Hudson (2007) found that, in both countries, illegal resource exploitation prior to conflicts was simply intensified when conflicts arose and tended to fuel the hostilities. Their study also recorded that overexploitation increased between 1999 and 2000 in DRC, after peace negotiations occurred, and between 1995 and 1996 in Rwanda after its conflicts ceased. Recent reports from DRC indicate that poaching of elephants in Africa's oldest national park, which intensified during the brutal

1998-2003 war, continues today; it is estimated that 20 percent of the elephant population has been killed in 2008 alone (Bavier 2008). Rwanda also reported impacts of wartime resource exploitation long after its peak in 1996 (Glew & Hudson 2007). McNeely (2003b) agrees that, as bad as war can be for biodiversity, peace can certainly be worse.

The increase in overexploitation of natural resources during war can be attributed to four factors: (1) the decreased capacity of the state to enforce law and control illegal activities; (2) the increased dependency on natural resources for subsistence due to a collapse in the economy and sometimes restricted access to other resources; (3) the changes in supply and demand for natural resources such as timber, ivory, and diamonds to provide general income and finance the war; and (4) the shift of mindset among residents regarding ownership of natural resources from belonging to individuals or entities to belonging to no one or everyone (Candotti 2000). Findings from a study on the environmental impacts of conflict in ten sub-Saharan countries support the above factors as the sources of the majority of environmental damage from war (Glew & Hudson 2007). Data from this study show that only 4.6 and 8.4 percent of the environmental impacts of warfare between 1990 and 2005 can be attributed to direct and indirect effects of military activities, respectively, whereas 87 percent of reported impacts within the 15-year period could be attributed to changes in socioeconomic conditions caused by the war.

Impacts of War on Conservation

Kanyamibwa & Chanterreau (2000) classify the impacts of war on conservation into eight categories based on the effects of conflicts across Africa's Albertine Rift. The most common (and the most significant) impact that war in Africa has on conservation is the interruption or termination of conservation efforts. The remaining seven categories of impacts are reduction or end of monetary support from donors, institutional capacity loss due to conservation staff mortality, changes in the mentality and priorities of staff as they struggle for survival, changes in rural mentality leading to an increase in illegal use of resources and poaching, refugee presence, environmental degradation and biodiversity loss, and the indirect and long-term consequences including erosion, pollution and improper waste disposal. Most, if not all, of the above impacts occur across Africa as a result of armed conflicts.

Considerations for Conservation during Conflict

Some conservation strategies prefer to separate humans from conservation entirely. While this strategy has its debated costs and benefits for conservation, it is impossible to implement when social conflicts arise in the area. Conservation during wars and armed conflicts necessitates a combined conservation and human-based approach. Stemming from the inseparability of humans and environmental conservation, armed conflicts pose logistical problems for conservation because of the danger in residing within an area of violent conflict and thus, the conservation organization's potential capacity loss from war-related deaths of staff members (Blom 2000; Kanyamibwa & Chanterreau 2000).

Analyses have shown that war cannot be predicted in Africa based on the existence of particular factors or conditions. Shambaugh et al. (2004) looked for correlations between the

onset of African armed conflicts and human population density, cultural diversity, biological value, habitat degradation, and indices of poverty including gross domestic product and other socioeconomic attributes. They found that ecological degradation is not consistently a cause or consequence of conflict across the entire continent despite other support for this theory (Homer-Dixon et al. 1993; Dudley et al. 2002). Nor did they find correlations between most of the socioeconomic factors and conflict intensity levels (Shambaugh et al. 2004). The only significant correlation they found is that a lower per capita gross domestic product corresponds with higher conflict intensity levels.

The scientific literature has left out an important implication of war that conservation organizations must be prepared for in Africa. Although many conservation biologists acknowledge the role that social factors have on the environment and in conservation efforts, the extent of the impacts that war in Africa can have on the mental conditions of refugees and other war victims are not acknowledged in the literature. Refugees from Rwanda, for example, have suffered from posttraumatic stress syndrome after exposure to massacre, genocide, gang rape, HIV, and other traumas (Smith 2001). Not only is it an additional challenge for conservationists to communicate and work with these traumatized victims, but the refugees cause further problems for themselves that can easily impact conservation negotiations and strategies. In the overpopulated Rwandan refugee camps in Tanzania, the Rwandans fought with each other resulting in many brutal killings and even accidental killings of Tanzanians (Smith 2001). Between July 1994 and January 1995 (as tensions continued to rise between Rwandans themselves and between Rwandans and Tanzanians), Tanzanian authorities had to increase the number of Tanzanian police officers from 5 to 43 at the Benaco refugee camp, which still remained far too small a number (Smith 2001).

Conflicts can also vastly increase the number of stakeholders that conservation organizations and entities must consider. In addition to the general stakeholders involved in nearly every biodiversity conservation effort (e.g. local people, local industries, national governments, etc.), the presence of war can easily double or even triple the number of stakeholders. Some of the new stakeholders that need to be involved in the midst of armed conflicts are rebel groups and their allies, the national army, local NGOs, poachers, illegal loggers and crop growers (now unhindered by law), intervention forces that aim to stabilize the region, foreign armies of nearby countries, refugees from other countries/regions, foreign resource extraction companies, consumers of products from conflict areas, international conservation organizations, development organizations, and humanitarian organizations that provide aid during the conflict (Blom 2000). When planning protected area management, stakeholders have shown an eagerness to be more involved, but it could be critical to keep in mind that the development of a network of partnerships between parties requires flexibility, special consideration for each situation, and time for capacities and roles among stakeholders to work themselves out on their own (Rutagarama & Martin 2006).

Considering the above implications of warfare in Africa and the vast number of potential stakeholders, it is no wonder that so many conservation efforts have ceased when conflicts arose. However, research and adaptive management that has taken place during the wars in Africa can offer conservation biologists practical knowledge about planning and implementing conservation strategies under such conditions, even when success seems impossible.

Suggestions for the Future of Conservation during Conflict

Some of the actions that are generally necessities for successful biodiversity conservation in warring African countries are (1) controlling illegal extraction or use of natural resources to fund war efforts; (2) spreading awareness about the values of nature; (3) providing support for local stakeholders; (4) integrating environmental conservation with war-relief humanitarian organizations; and (5) managing the flow of refugees to avoid the irreversible environmental degradation caused by excessively high human densities in small areas (Wit 2000).

Controlling Resource Use

Bruch (2000) suggests that the establishment and enforcement of criminal liability by an international court can prevent militias from causing unnecessary “environmental atrocities” to fund war efforts during periods of armed conflicts. Another, similar strategy Bruch proposes is the creation of a system of civil liability for environmental damage where individuals or parties would not be criminally liable for their destruction, but would be monetarily responsible. The hope of these strategies is that the liability factor will deter individuals or groups from being careless about the effects of their warfare tactics and from using ecocide strategies against their enemies. While these prevention methods have potential benefits, they also have their flaws, and their effectiveness has not yet been tested in the African context.

A more promising suggestion is the use of international bans on imports and trade embargoes to restrict the ability of militias to finance their efforts by marketing exploited, natural resources (Bruch 2000; Wit 2000). This strategy can be particularly useful in places such as Angola and Sierra Leone, where militias extract and trade diamonds to obtain guns (Bruch 2000), or in Liberia where they harvest timber to finance violence (Garnett 2000).

Advocating Nature Valuation

The WWF was able to improve the setting for biodiversity conservation in Eastern Congo simply by educating military commanders of rebel groups about the natural values of the region (Wit 2000). However, if conditions among locals and the Tragedy of the Commons do not support nature valuation at the utilitarian level, like they did in Congo, the spiritual valuation of nature is supported by some of Africa’s indigenous cultures. Spiritual valuation based on indigenous cultural values has resulted in the indirect conservation of biodiversity through native protection of ‘sacred groves’ in Ghana, Tanzania, and Kenya (Barrow & Pathak 2005). The deterioration of indigenous culture over the years, however, has decreased the number of sacred groves (Barrow & Pathak 2005). Yet these declines can still be reversed if conservation organizations take initiative and make the appropriate efforts to promote nature valuation and cultural renewal.

Garnett (2000) emphasizes the need for education in developed countries about nature’s values and the poor condition of what is left of the natural resources in overexploited countries such as Liberia and Sierra Leone. People in developed nations have contributed to this overexploitation as consumers of products.

Providing Support

The WWF-East African Regional Programme has effectively shown that conservation organizations have the ability to conserve resources and maintain good local relations by supporting some of the local stakeholders (Wit 2000). By providing sufficient monetary compensation to staff working at the various world heritage sites in DRC, international assistance also provides for the 10-15 family members that each of the staff supports (Candotti 2000). Committed international support is especially vital when national governments break down in conflict-ridden countries (Hart 1997).

Implementation of the Nyungwe Forest Conservation Project in 1987 to assist the Rwandan government in conserving and managing the Nyungwe Forest Reserve has provided insights into what kind of protected area management can withstand a transition from peace to violent civil war and still maintain some control. Fimbel and Fimbel (1997) found that local participation in the project is what kept it running after the expatriate staff left the country after the outbreak of war in 1994. After the project's supervisors were evacuated and all other conservation efforts in the area ceased, only 40 local junior staff remained to protect the Nyungwe Forest Reserve. The newly reorganized team managed to perform daily patrols of the reserve throughout the 5-month war without salaries or communication with the previous senior staff. Upon remission of the war, the Wildlife Conservation Society continued to pay staff salaries, provide assistance, recruit more Rwandans to the project, and give moral support to the staff, all of which has helped the project to progress and reinstate the reserve's former tourism, research, and public awareness programs. The Nyungwe Forest Reserve was designated as a national park in 2002 (Rutagarama & Martin 2006). The significance of the trials and tribulations of the Nyungwe Forest Conservation Project is that committed project leaders and personnel from the local population, with some assistance from a non-governmental organization free of political ties, can be a key to conservation success, especially where political instability is a factor (Fimbel & Fimbel 1997).

Local village chiefs in the Democratic Republic of Congo have also shown a significant degree of control over the bushmeat trade in rural areas, which depended primarily of legal bushmeat and was consistent both in and out of wartime (De Merode & Cowlshaw 2006; De Merode et al. 2007). The chiefs accomplished this by recovering automatic weapons and discouraging the presence of military personnel and the illegal trade of protected species, both of which disrupted village trade. Thus, in these situations, supporting local village chiefs and their authority could definitely help conservation efforts. De Merode and Cowlshaw (2006) even suggest that management partnerships forged between village chiefs, or traditional authorities in general, could be influential in reestablishing political control over the military's illegal bushmeat trade in urban areas, where it is prevalent.

Integrating Approaches with Humanitarian Organizations

Teaming up and collaborating with local organizations, especially humanitarian organizations such as the Red Cross, can be especially important (Kanyamibwa & Chantereau 2000; Shambaugh et al. 2004). During times of conflict, conservation funding usually decreases and humanitarian funding increases (Garnett 2000) making collaboration with human relief organizations all the more beneficial. Educating humanitarian workers about the

importance of the environment to long-term human welfare can help integrate conservation efforts into relief work that would have otherwise disregarded environmental impacts completely in many cases (Garnett 2000).

One example of how both humanitarian and conservation efforts can work together but toward their respective goals is distributing food, especially protein sources in urban areas, which can help reduce poverty and damper the bushmeat trade. A study showed that urban bushmeat sales of protected species, which are generally larger and therefore more desirable, in DRC increased five-fold during wartime compared with times of peace (De Merode & Cowlishaw 2006). The study attributed the increase not only to the loss of control over poaching, but also to increased need in urban areas because their previous supply of bushmeat and domestic meat from other sources had been disrupted by the ensuing warfare.

Some would also argue that conservation initiatives could not be met without first taking care of humanitarian issues. Because so many conflicts are dealt with by wars and violence, Kanyamibwa (1998) asserts that to establish peace and a stable conservation program in Rwanda or nearby African countries, social and political problems need to take priority or efforts will be short-lived.

Managing Refugees

The worst environmental degradation caused by refugees occurs within and around the organized refugee camps, but if refugees settle in small camps near preexisting villages and are integrated into the regular population and economy, less environmental damage results (Ketel 2000; UNEP 2000). Ketel (2000) emphasizes the need for humanitarian and environmental agencies to further develop their policies and environmental guidelines for all operations, create field manuals, and train those already responsible for implementing projects.

A study on land use patterns in the Horn of Africa, where an excessively large number of African refugees reside, worked out a resettlement design that takes into account the pastoral land use of locals, agricultural land use by refugees, and severe droughts that are commonplace in the region. Unruh (1993) claims that encouraging exchange relationships between pastoralists and farmers could facilitate a sustainable multiple land use system based on grain crop forage values and vulnerabilities to drought. If pastoralists will consider trading for or purchasing crop residues as dry-season fodder for their livestock from refugee farmers, the carrying capacity for livestock can be maximized while still minimizing the amount of overall land use (Unruh 1993). This interaction between refugees and pastoralists not only helps refugees to become integrated into the preexisting economy, a known benefit that minimizes environmental impact (Ketel 2000; UNEP 2000), but also provides a source of income to rural refugees (Unruh 1993).

Further Insights

Candotti (2000) explains that the WWF also has determined five fundamental necessities for conservation planning and implementation during wars in Africa. The WWF's theories about what is required for conservation efforts in the midst of armed conflict is based on its

long history of conservation work in the Democratic Republic of Congo, beginning decades before, and continuing through, the political instability and warfare this country has been experiencing since 1991 (Candotti 2000). The WWF first stresses the importance of a long-term vision and the vital role it plays in driving the four remaining necessities. Next, the WWF emphasizes the importance of maintaining a strategic partnership with environmental authorities. The third necessity is organizational adaptive management, which enables conservation organizations to make quick, adaptive decisions in response to changing situations. Fourth, conservation efforts during conflicts have demonstrated that flexible and independent core minimum funding is needed to maintain operations when other funding falls through. Finally, effective, long-term conservation during times of war will not be able to succeed without forging links with local and international entities and strategically working together to integrate approaches.

Conclusion

Conditions in some of the most distinct and ecologically important regions in the world are deteriorating at a rapid rate because of war and political instability. No longer can conservation organizations cease or postpone their efforts when wars arise in Africa without risking very serious loss of biodiversity, environmental damage, natural resource depletion, and ecosystem failure in some of the most diverse and unique ecoregions on the planet. Although there remains a lack of research and conservation experience under war-related conditions, the knowledge that has been acquired provides us with practical and effective strategies to derive the maximum amount of benefit from conservation efforts during times of war in Africa. Among the most important of these suggestions are effective methods for controlling trade of overexploited resources, instilling a sense of value for nature among local stakeholders, providing support for as many locals as possible during the course of the conflict, collaborating and strategizing with humanitarian organizations to improve human and environmental conditions during and after the war, and organizing the migration of refugees to prevent overexploitation and depletion of resources within ecosystems.

References

- Barrow, E., and Pathak N. (2005). Conserving "unprotected" protected areas - communities can and do conserve landscapes of all sorts. In J. Brown, N. Mitchell, & M. Beresford (Eds.), *The protected landscape approach: linking nature, culture and community* (pp. 65-80). Cambridge, United Kingdom: The International Union for the Conservation of Nature.
- Bavier, J. Ivory Poachers Decimate Congo Elephant Population. (2008 August 25). Available from: *Planet Ark World Environmental News* <http://www.planetark.com/avantgo/dailynewsstory.cfm?newsid=49920>.
- Blom, E. (2000). Conclusions and recommendations. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 165-170). Leiden, The Netherlands: Commission for International Nature Protection.

- Bruch, C. E. (2000). An overview of legal mechanisms for conserving biodiversity during armed conflict. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 141-144). Leiden, The Netherlands: Commission for International Nature Protection.
- Candotti, S. (2000). The evolving role of an international conservation organisation in times of war: WWF in the Democratic Republic of Congo. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 21-38). Leiden, The Netherlands: Commission for International Nature Protection.
- De Merode, E., & Cowlshaw D. (2006). Species protection, the changing informal economy, and the politics of access to the bushmeat trade in the Democratic Republic of Congo. *Conservation Biology*, **20**, 1262-1271.
- De Merode, E., Smith, K. H., Homewood, K., Pettifor, R., Rowcliffe, M., & Cowlshaw, G. (2007). The impact of armed conflict on protected-area efficacy in central Africa. *Biology Letters*, **3**, 299-301.
- Douma, P. (2000). The destruction of nature as collateral damage: how wars can obfuscate the protection of nature. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 1 - 8). Leiden, The Netherlands: Commission for International Nature Protection.
- Draulans, D., & Van Krunkelsven, E. (2002). The impact of war on forest areas in the Democratic Republic of Congo. *Oryx*, **36**, 35-40.
- Dudley, J. P., Ginsberg, J. R., Plumptre, A. J., Hart, J. A., & Campos, L. C. (2002). Effects of war and civil strife on wildlife and wildlife habitats. *Conservation Biology*, **16**, 319-329.
- Fimbel, C., & Fimbel, R. (1997). Rwanda: the role of local participation. *Conservation Biology*, **11**, 309-310.
- Garnett, T. (2000). War and nature: the impact of conflict on the environment in the Upper Guinea Forest. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 59 - 80). Leiden, The Netherlands: Commission for International Nature Protection.
- Glew, L., & Hudson, M.D. (2007). Gorillas in the midst: the impact of armed conflict on the conservation of protected areas in sub-Saharan Africa. *Oryx*, **41**, 140-150.
- Hart, J. (1997). Conservation in crisis. UNESCO Sources, Retrieved 12 August 2008, from Academic Search Premier database.
- Homer-Dixon, T. F., Boutwell, J. H., & Rathjens, G. W. (1993). Environmental change and violent conflict: growing scarcities of renewable resources can contribute to social instability and civil strife. *Scientific American*, **268**, 38-45.
- Kanyamibwa, S. (1998). Impact of war on conservation: Rwandan environment and wildlife in agony. *Biodiversity and Conservation*, **7**, 1399-1406.
- Kanyamibwa, S., & Chanterreau, O. (2000). Building regional linkages and supporting stakeholders in areas affected by conflicts; experiences from the Albertine Rift region. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 45 - 58). Leiden, The Netherlands: Commission for International Nature Protection.
- Ketel, H. J. (2000). Environmental impact and mitigation of mass refugee and migrant situations. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit

- (Eds.), *Nature in war: biodiversity conservation during conflicts* (pp. 161 - 164). Leiden, The Netherlands: Commission for International Nature Protection.
- Kreike, E. (2004). War and the environmental effects of displacement in southern Africa (1970s-1990s). In W. G. Moseley, & B. I. Logan (Eds.), *African environment and development: rhetoric, programs, realities* (pp. 89 – 110). Aldershot, United Kingdom: Ashgate Publishing Limited.
- Levine, R. S. (2004). African warfare in all its ferocity: changing military landscapes and precolonial and colonial conflict in southern Africa. In R. P. Tucker, & E. Russell (Eds.), *Natural enemy, natural ally: toward an environmental history of warfare* (pp. 65 – 92). Corvallis, Oregon: Oregon State University Press.
- McNeely, J. A. (2003a). *War and tropical forests: conservation in areas of armed conflict*. New York: The Haworth Press.
- McNeely, J. A. (2003b). Conserving forest biodiversity in times of violent conflict. *Oryx*, **37**, 142-152.
- Plumptre, A. J., Bizumuremyi, J., Uwimana, F., & Ndaruhebeye, J. (1997). The effects of the Rwandan civil war on poaching of ungulates in the Parc National des Volcans. *Oryx*, **31**, 265-273.
- Rutagarama, E., & Martin, A. (2006). Partnerships for protected area conservation in Rwanda. *The Geographical Journal*, **172**, 291-305.
- Shambaugh, J., Jackson, N., Gylee, R., Oglethorpe, J., Kormos, R., Balmford, A., Hales, J. D., Kanyamibwa, S., Burgess, N., Garnett, T., & Morjan, M. D. (2004). Armed conflict and the African environment. In World Wildlife Fund (Ed.), *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment* (pp.125-128). Washington, DC: Island Press.
- Smith, C. D. (2001). *Ecology, civil society and the informal economy in northwest Tanzania*. Aldershot, United Kingdom: Ashgate Publishing Limited.
- UNEP (United Nations Environmental Programme). (2000). *Pre-assessment of the environmental impact of refugees in Guinea. 2000 report*. Nairobi, Kenya: UNEP.
- Unruh, J. D. (1993). Refugee resettlement on the Horn of Africa: the integration of host and refugee land use patterns. *Land Use Policy*, **10**, 49-66.
- Wit, P. (2000). The impacts of conflicts on nature and environment. In E. Blom, W. Bergmans, I. Dankelman, P. Verweij, M. Voeten, & P. Wit (Eds.), *Nature in war: biodiversity conservation during conflicts*. Leiden, The Netherlands: Netherlands Commission for International Nature Protection.
- WWF. (2004). *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment*. Washington, DC: Island Press.
- Reviewed by Professor Ben A. Minter, Human Dimensions Faculty, School of Life Sciences, Arizona State University (editor of: *Reconstructing Conservation: Finding Common Ground*. 2003. Island Press).

Chapter 4

ECOLOGY OF SOIL SEED BANK IN CONSERVATION AND RESTORATION OF ENDANGERED PLANTS

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Abstract

Soil seed banks have specific roles in conservation and restoration of plants. Material from a seed bank is less influential on the genotypes of local populations, since it pools the local endemic genotypes. In addition, a seed bank is expected to increase the genetic diversity of subdivided populations of endangered plants. In populations which have already disappeared due to habitat loss, the seed bank is the only hope to restore the populations. Hence, sound information on soil seed banks is essential to enhance the success of conservation and restoration in plant species. Recently, I showed that seed dormancy, which has been considered the mechanism of a seed bank formation, is not essential for the persistence of the seed bank for at least 5 years (criterion of long-term persistence).

Many plants avoid germination under dense vegetation or in too deep soil because of the lowest competitive ability of seedlings in their whole life cycle and the limitation of nutrient reserves in seeds. Temperature fluctuations and/or light quality and quantity work as reliable gap-surface signals for many plants. Using such signals, many plants actually germinate at gap-surface with dexterity. Reversibility in the state of phytochrome (P_r and P_{fr}) must ensure the dexterous gap-surface detection in germination. Although some types of dormancy such as physical dormancy contribute to the persistence of a seed bank, dormancy mainly operates the temporal timing in germination. Thus, seeds avoid germination and form a seed bank under spatially and temporally unfavorable conditions where it can not expect reproductive success.

Since seeds of many plants can perceive the favorability in surrounding environments, the seed bank of a target species in the restoration may be accumulated in an unfavorable environment where reproductive success is not expected. For example, seeds of hygrophilous plants were actually sampled from dry soils of past wetlands. This trend holds true not only to target species in the restoration but also invasive plants. Surface soil may be polluted by invasive species seeds compared with deep soil. Restoration using a seed bank at surface soil actually raised an invader species rather than endangered plants in some cases. Samplings of a seed bank for restoration have been collected randomly in the local habitat. However,

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sampling design of a seed bank considering the unfavorability for both growth of the target species and invasive species will increase the success of the restoration using a seed bank. Several old fruits of lotus *Nelumbo nucifera* were recovered from a peat deposit at Kemigawa (Chiba Prefecture) in Japan. This lotus is currently called ‘Ohga lotus’ (Picture 1). Unfortunately, because all of the fruits were germinated, none was left for radiocarbon dating. However, wood from an old boat found at the same level in the peat deposit was dated roughly 3000 years old. Although this was not necessarily the age of the fruits, the recovery of the Ohga lotus is a symbolic occurrence indicating that a soil seed bank has the potential to restore past plant species that have disappeared from standing vegetation.



Picture 1. Ancient lotus (*Nelumbo nucifera*) called ‘Ohga lotus’ that was recovered at Kemigawa in Japan. Ohga lotus grows at Experimental Station for Landscape Plants in Japan with maintenance of the same genotype as the individual recovered from the soil. *Nelumbo nucifera* seeds have physical dormancy, which contributes to long-term persistence in soil. Photo by Fumiko Ishizuna.

Introduction

Against worsening global environmental issues, restoration of nature has been desired. In fact, a variety of approaches to restore lost ecosystems have been tried. Unfortunately, it is impossible to restore the lost nature completely. In addition, our ability for ecological restoration against extinction of wildlife is so limited. Our capacity for ecological restoration is limited, however, our limitation is not a justification for “irrestoration” (Choi 2007).

In restoration, we must fundamentally comply with the following three principles: (1) restore the ecosystem consisting of endemic phylogeny that adapts the area to be restored; (2) restore not only one target species but also the ecosystem consisting of biodiversity that evolved with the history in the area to be restored; and (3) pay attention to conserve the genetic variation in each restored species. Seedling transplantation, seed sowing and utilization of a soil seed bank are possible methods to restore the ecosystem consisting of a diversity of plant species. Even in the same native plants in a country, it is common that different phylogenies are established in each region. When individuals were transplanted to

strange regions, introgression (Figure 1) may degrade directly the genetic diversity of the species. In the seedling transplantation and seed sowing, therefore, utilized seedlings or seeds should have the same phylogeny in the area to be restored. However, it is really impossible to prepare seedlings or seeds with genetic diversity from the same phylogeny. If we can prepare such ideal restoration materials from the same phylogeny, what do we restore the plants for? On the other hand, soil seed banks have a potential as more ideal restoration material since it skirts the principles in ecosystem restoration. The use of soil seed banks is thought to be advantageous in conserving and restoring biodiversity because the seed banks of the past and present ecosystem may be expected to contain a variety of species and genetically diverse individuals (e.g., van der Valk & Pederson 1989, Levin 1990). In addition, to restore lost plants from the world, a soil seed bank is the only hope left for us. A seed bank in the soil of an ecosystem can also provide important information as to what species may have existed in the standing vegetation of the past and/or represent a pool of regenerative potential (Hopfensperger 2007). Even a soil seed bank, however, is not a complete restoration material to restore lost vegetation. Since seed banks have some constraints, we should understand the traits and constraints to promote more effective utilization of a seed bank for restoration. In this chapter, I introduce the ecology of how and why plants form a soil seed bank and the constraints of seed banks in restoration. I hope that this chapter contributes to the conservation or restoration of many endangered plants in the world.

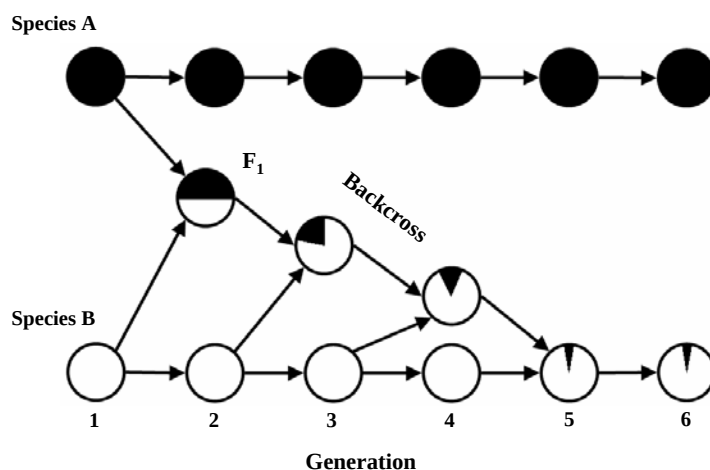


Figure 1. Conceptual diagram of introgression. Genes of species A creep into the genotype of species B in the process of repeated backcrosses.

Soil Seed Bank

A soil seed bank is a seed population living in soil, in plant residue (litter) or on the soil surface. Traditionally, two broad types of seed banks have been designated: transient and persistent. Seeds of species with transient seed banks live for < 1 year and those with persistent seed banks live for ≥ 1 year (e.g., Grime 1981). Although the survival for ≥ 1 year does not mean strictly having multiple germination seasons (Walck et al. 2005), almost persistent seed banks have multiple germination seasons since they survive for ≥ 1 year. On

the other hand, transient seed banks germinate in the first germination season. Thus, only persistent seed banks have an option as to when they germinate to enhance the success in establishment after germination. In this chapter, I focus on the persistent seed banks in the following sections since they may encompass rare or endangered plant species that should be restored.

Germination and Dormancy of Seeds

Although no empirical data are available that indicate a close relationship between seed dormancy and the soil seed bank (Honda 2008), dormancy has been considered essential to the formation of a soil seed bank. Dormant seeds have two discrete phases of ‘dormancy breakage’ and ‘germination’ in seed germination (Figure 2). Dormancy is an innate block of germination in the seeds, but germination of non-dormant seeds is controlled by surrounding physical and chemical conditions. In the germination process of non-dormant seeds, they can germinate until their environmental conditions fill all of the environmental requirements for germination. On the other hand, dormant seeds can not germinate even if their environmental conditions fill all of the environmental requirements for germination because of the innate block of germination in the seeds. Hence, dormant seeds must break their dormancy before the germination process. Note that non-dormant seeds also can not germinate when the surrounding environment does not fill their environmental requirements for germination.

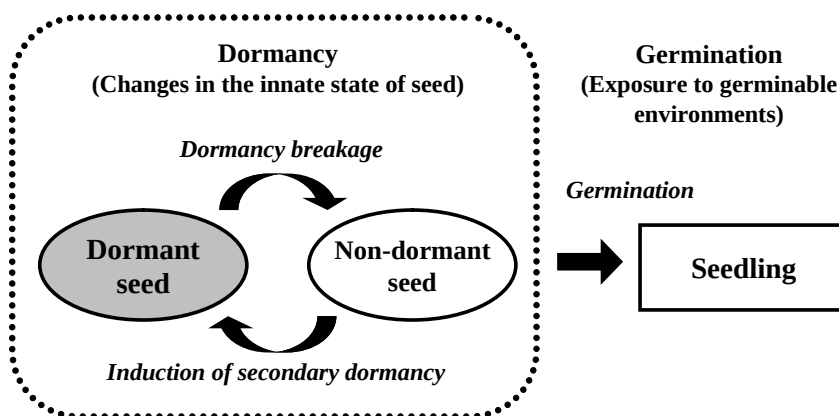


Figure 2. Two discrete phases (dormancy breakage and germination) in the process to produce seedling. Dormancy is changes in the innate state of seed. On the other hand, germination proceeds when seed is exposed to the germinable environments of the seed. Even when the dormancy of a seed is broken, the seed can not germinate until it is exposed to germinable environments for the seed.

Although seeds' failure to germinate in a particular set of environmental conditions is an all-or-nothing property, dormancy is not an all-or-nothing property (Vleeshouwers et al. 1995). When dormant seeds are stimulated by the environmental signal for dormancy breakage, the seeds will be in a non-dormant state. Non-deep physiological dormancy (see the section below) may cycle between dormant state and non-dormant state (Figure 3). Dormancy in many species of spring-germinating plants is broken by moist, low temperature conditions during winter. Then the germinable range will widen gradually and reach the non-dormant

state (i.e., completely extended state in germinable range in Figure 3). Subsequently, germinable range will narrow as surrounding temperature increase and the germinable range will be dormant state (i.e., completely closed state in germinable range in Figure 3). The interval between non-dormant state and dormant state is called 'relative dormancy' or 'conditional dormancy'. Thus, dormancy is sequential property in the allowable range of germination. In an important review focusing on the definition of seed dormancy of Vleeshouwers et al. (1995), they proposed a definition of seed dormancy: dormancy is a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate.

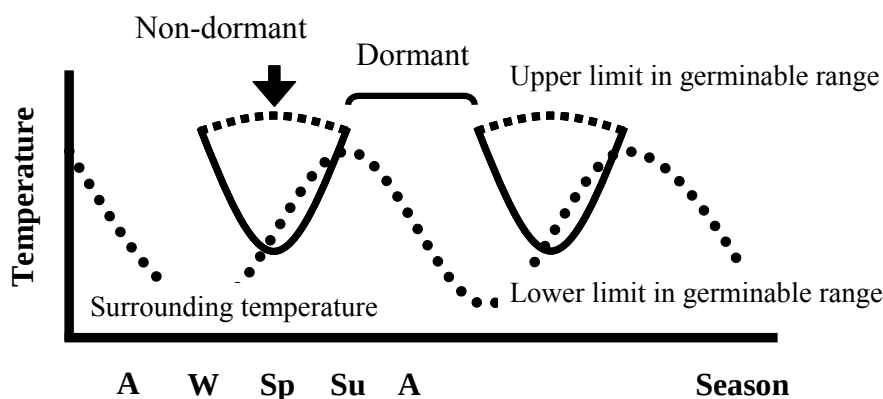


Figure 3. Widening and narrowing of germinable temperature range. Dormancy of many spring-germinating plants is broken by moist, low temperature conditions during winter. Then upper limit in germinable range (square-dotted line) and lower limit in germinable range (solid line) will widen gradually and reach the non-dormant state (i.e., completely extended state in the germinable range). Subsequently, germinable range will narrow as surrounding temperature (circular-dotted line) increase and the germinable range will close (i.e., completely closed state in germinable range). The interval between non-dormant state and dormant state is relative dormancy (conditional dormancy).

Knowledge on phytochrome reaction in seed germination provides insights into seed persistence in soil. Phytochrome, which is a chromoprotein in a soluble form, regulates germination reaction to light. Phytochrome exists in two forms: Pr (inactive form) and Pfr (active form) (Figure 4). Pr absorbs red light (R: 660nm-centered light in light spectrum), then it converts itself to the Pfr form. On the other hand, Pfr form absorbs far-red light (FR: 730nm-centered light in light spectrum), then it converts itself to the Pr form. Thus, reversible conversion of phytochrome is depending on the light that the seed was exposed. The formation of Pfr does not decide seed germination but the ratio of Pfr against total phytochrome (photoequilibrium) decides germination. Photoequilibrium required for germination is different in each plant species (Bewley & Black 1994). In also the R/FR ratio of light, there is a species-specific threshold required for germination (Pearson et al. 2003). The reversion of Pfr to Pr occurs in also dark condition (dark reversion) (Bewley & Black 1994).

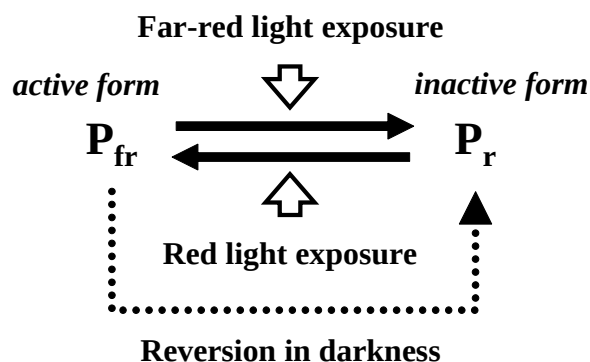


Figure 4. Photoconversion of phytochrome. Two forms of phytochrome exist: P_{fr} (active form accelerating seed germination) and P_r (inactive form). P_r converts itself to P_{fr} form when it was exposed to red light (660nm-centered light in light spectrum) but P_{fr} converts itself to P_r form when it was exposed to far-red light (730nm-centered light in light spectrum). The reversion of P_{fr} to P_r occurs in also dark condition (dark reversion). The formation of P_{fr} against total phytochrome (photoequilibrium) decides germination.

Types of Dormancy

Seed dormancy has wide genetic variation between plant species. Undoubtedly, use of an ‘official’ classification scheme of seed dormancy would facilitate communication among seed scientists by providing a framework for interpretation of results at all layers in the hierarchy of biological organization (Baskin & Baskin 2004). Commonly three fundamentally different types of seed dormancy are recognized, which are physiological dormancy (PD), morphological dormancy (MD) and physical dormancy (PY).

Table 1. Characteristics of dormancy in seeds with deep, intermediate and non-deep physiological dormancy (Baskin & Baskin 2004).

Deep	
	Excised embryo produces abnormal seedling
	GA does not promote germination
	Seeds require c. 3-4 months of cold stratification to germinate
Intermediate	
	Excised embryo produces normal seedling
	GA promotes germination in some (but not all) species
	Seeds require 2-3 months of cold stratification for dormancy break
	Dry storage can shorten the cold stratification period
Non-deep	
	Excised embryo produces normal seedling
	GA promotes germination
	Depending on species, cold (c. 0-10°C) or (warm ≥15°C) stratification breaks dormancy
	Seeds may after-ripen in dry storage
	Scarification may promote germination

Physiological Dormancy (PD)

PD prevents germination until a chemical change takes place in the seed. Baskin & Baskin (2004) recognized three levels of PD: deep, intermediate and non-deep, and characterized each of three dormancy levels as Table 1. PD is common everywhere, although species with no seed dormancy are in the majority in tropical evergreen forest (Fenner & Thompson 2005). The great majority of seeds with PD have non-deep PD (Baskin & Baskin 2004).

Morphological Dormancy (MD)

Seed with MD is immature when shed and a period of growth and/or differentiation is required before germination can take place. In seeds with this type of dormancy, the embryos are small (underdeveloped, not physiologically dormant). They simply need time to grow to full size and then germinate. Under favorable condition for artificial seed stocking, embryos in freshly matured seeds begin to grow within a period of a few days to 1-2 weeks, and seeds germinate within about 30 days (Baskin & Baskin 2004).

Physical Dormancy (PY)

Seeds with PY have impermeable testas or pericarps; the embryo is therefore dry until the seed coat is broken and water enters. The statement is often made in books and review articles in ecology and seed and plant biology that dormancy-break in seeds with water-impermeable seed (or fruit) coats, i.e. PY, is cued to microbial action and/or to abrasion by soil particles (Baskin & Baskin 2000). However, Baskin & Baskin (2000) claimed that they found only weak support in the scientific literature for breakage of PY by soil microbial action and no support for breakage of it by abrasion and that two aspects of the evolutionary biology of PY argue against breakage of dormancy in seeds (or fruits) with water-impermeable coats by these methods. First, several types of anatomically specialized water restriction structures have evolved as part of the seed or fruit coat of taxa with PY. These structures act as 'signal detectors' of physical environmental changes that cause seeds (and fruits) to become water-permeable only at these sites, in seasons and habitats in which there is a good chance that some seedlings will become established. Intriguingly, there is a water gap in the impermeable layer, which is closed at seed maturity, and then opens in response to an appropriate environmental signal (Baskin & Baskin 1998, Baskin 2003). Opening water gap requires commonly high temperatures, large temperature fluctuations or fire (Baskin & Baskin 1998, Baskin 2003). It is therefore common in many habitats with a distinct dry season, including tropical deciduous forests, savannahs, hot deserts, and steppes (Fenner & Thompson 2005). Second, seed (and fruit) coat breakdown by microbial action or by abrasion likely would occur in seasons and habitats in which seedlings could not survive, thus lowering the fitness of the plant taxa in question. Note the crucial distinction between PD, which is reversible, and the other two types, which are not (Fenner & Thompson 2005).

Dormancy types may be combined in the same seed – a combination of morphological and physiological dormancy (morphophysiological: MPD) is very common. Breaking MPD

requires embryo growth and/or differentiation, and the seed must be imbibed for this to happen, although the physiological part of the dormancy can sometimes be broken in the dry seed. MPD is therefore frequent in parts of the world with moist seasonal climates and is particularly common in plants of woodlands or damp grasslands (Fenner & Thompson 2005).

Dormancy and Seed Persistence in Soil

In the ecological literature, it is widely assumed that seeds require some form of dormancy if they are to accumulate a persistent soil seed bank. Indeed, it is clear that many ecologists regard dormancy and persistence as essentially indistinguishable (Thompson et al. 2003). However, no empirical data are available that indicate a close relationship between seed dormancy and the soil seed bank (Honda 2008). Note that many theoretical treatments of the evolution of ‘dormancy’ are actually concerned with seed persistence in soil not dormancy (Thompson et al. 2003). Is there any simple relationship between seed persistence in the soil and dormancy? Thompson et al. (2003) compared longevity indices between species with MPD, PY, PD or non-dormancy. These indices reflect the ability of seeds to survive for more than one year in soil. They concluded that there is no close relationship between dormancy and the persistence in soil over one year.

However, dormancy may contribute to the persistence of seeds for several years as some ecophysiolgists think that the germinability of dormant seed will be sustained for a longer period than non-dormant seed since the metabolism of the dormant seed is suppressed. In addition, other categorizations of dormancy can be proposed, which may reveal a clear relationship between dormancy and the seed bank. Honda (2008) analyzed the relationship between two types of periods (over 1 year or over 5 years) in seed persistence and dormancy categorized with the required stimuli (chilling, dry storage, scarification and fluctuating temperatures) for dormancy breakage. These periods of seed persistence were derived from the definition of a persistent seed bank and a criterion (Thompson et al. 1997) for long-term persistence of seed bank, respectively. Note that it remains controversial whether the requirement for fluctuating temperatures is dormancy (e.g. Vleeshouwers et al. 1995), because the physiological mechanism of the fluctuating temperatures requirement remains to be explained. As shown in Figure 5 and 6, dormancy is not essential for either of the over 1 year persistence and the over 5 years persistence. However, the contribution of dormancy differs slightly between dormancy types. Scarification or dry storage requirements to break dormancy slightly enhanced either of the over 1 year persistence and the over 5 years persistence, whereas chilling requirement decreased the either of the over 1 year persistence and the over 5 years persistence. In contrast, fluctuating temperature requirement clearly contributes to the over 1 year persistence and the over 5 years persistence. Although the analysis of Thompson et al. (2003) could not detect the relationship between the over 1 year persistence and PY, Thompson (2000) noted that ‘the only dormancy type that plays a large part in seed persistence is physical dormancy. Although not all species requiring scarification in the analysis of Honda (2008) are species with PY, PY contributes to over 5 year persistence (Figure 6). Ohga lotus (Picture 1) seeds probably could survive for roughly 3000 years because of its PY.

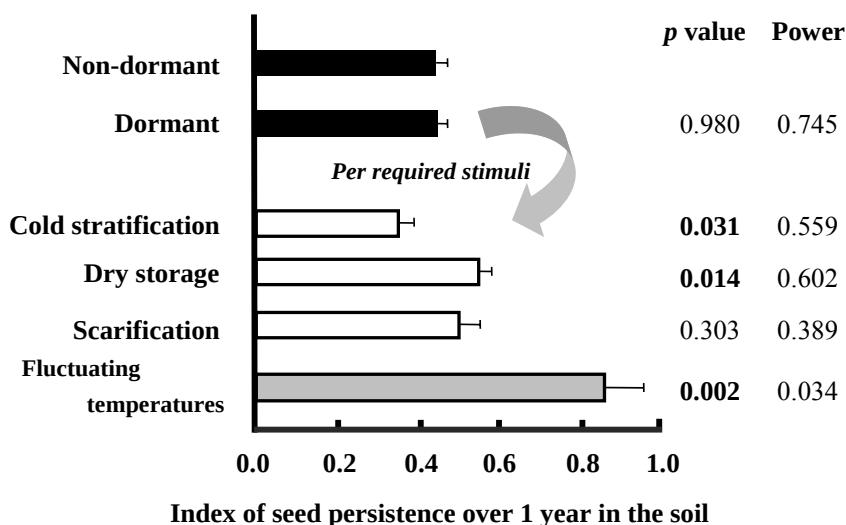


Figure 5. Average in index of seed persistence over 1 year in the soil (Honda 2008). The untransformed index and standard errors are shown. Seed longevity data were derived from Thompson et al. (1997), and the categorization of dormancy followed that of Grime et al. (1988). Dormant (black bar) comprises the lower three categories (white bars), the fluctuating temperatures requirement, and several other minor dormancy types from Grime et al. (1988) such as breaking dormancy with warm stratification. Although physiological mechanisms of the requirement of fluctuating temperatures requirement is unclear, it was categorized in dormant group in Grime et al. (1998). p values indicates the results of two-tailed Student's t-test after arcsine square-root transformation between the associated category of its p value and the non-dormant category. Statistical power was computed for a 10% change in the index under a normal distribution with the observed standard deviation and sample size. Note that not-significant results were not arisen from low statistical powers.

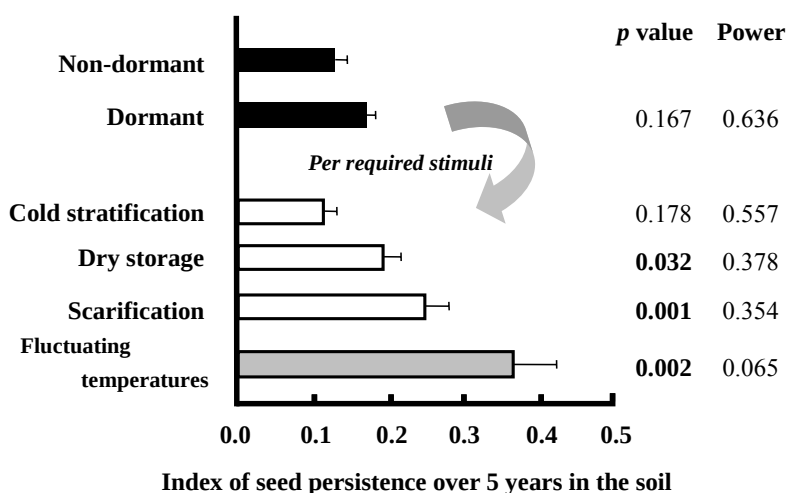


Figure 6. Average in index of seed persistence over 5 year in the soil (Honda 2008). See captions in figure 5. Statistical power was computed for a 5% change in the index under a normal distribution with the observed standard deviation and sample size. Note that not-significant results were not arisen from low statistical powers.

In the mean while, what is the crucial function of seed dormancy? The crucial function of dormancy is to prevent germination when conditions are suitable for germination but the probability of survival and growth of the seedling is low (Vleeshouwers et al. 1995, Fenner & Thompson 2005). Washitani & Masuda (1990) found that in a Japanese tall grassland in which germination was confined to spring, all species that shed their seeds early in the growing season had an absolute requirement for a period of chilling before their seeds would germinate. All species dispersing their seeds in spring, summer or early autumn avoid autumn germination by producing seeds with dormancy that is broken by cold stratification in winter. However, many species that shed their seeds in late autumn lacked dormancy, since by then temperature were already low enough to prevent germination. Dormancy contributes also to avoid germination in favorable condition occurring briefly even in off season when the successful growth is not expected (Hilhorst 1998). Furthermore, dormancy avoids germination on the maternal plants before dispersal (Bewley & Downie 1996). Note that these ecological functions of seed dormancy are included in the concept of germination at the right time. Thus, a large part of dormancy plays successful germination at the right time. It is useful to make a distinction between, short delays, whose primary purpose is to synchronize germination with a season suitable for establishment and growth, and on the other hand, longer delays, measured in years rather than months (Thompson 2000). Probably since temporally favorable conditions always come within a year (e.g., spring for spring germinating plants), dormancy is not essential to persist in soil.

Why Persist in Soil?

An obvious advantage is that it would ensure re-establishment (without immigration) of the population at the same site even if no individuals survived and produced a seed crop in a given year or even in several consecutive years (Baskin & Baskin 1978). Few things more important for plants than ensuring that germination takes place in the right place and at the right time (Fenner & Thompson 2005). Seedlings produced from seeds are remarkably small compared to juveniles produced via vegetative reproduction. Furthermore, they may experience high mortality because they grow independently of the parent plants. Seed germination is therefore an important decision to enter the stage of highest mortality. Although seeds that fail to germinate at the first opportunity may die before they are able to do so, the seeds must avoid germination when germination timing is not adequate spatially and/or temporally. Thus, it is reasonable that seeds equip with various physiological mechanisms to evade fatal germination in this process. Hence seed persistence in years rather than months may be sensitive to spatial unfavorable condition for its subsequent growth. What is spatial unfavorable condition for growth after seed germination? Because of limited nutrient reserves in seeds, they should avoid germination too deep in the soil for the seedlings to reach the surface on the available nutrient reserves. In addition, since the competitive ability of seedlings generated from seeds is quite low, they should avoid germination under dense vegetation. In other words, gap is a common essential environment for growth after germination of many terrestrial plant species. Gap is 'a plant-free space' or, more accurately 'a competitor-free space' (Bullock 2000). Although gap is favorable environment for successful growth in many plants, specific environments are essential for the growth in some species (e.g., a quantity of water for wetland species).

A further process that may contribute to the evolution of seed persistence is sibling competition between seedlings. If most seeds are dispersed only short distance, parent plants may experience strong selection pressure to delay germination of a fraction of their seed output (Thompson 2000). Although few empirical data supports this hypothesis, theoretical works clearly confirm it (Ellner 1986, Nilsson et al. 1994).

Light and Temperature Condition in Soil and under Vegetation

As discussed in more detail below, light and temperature are important gap signal for many plant species. Light permeability through soil is quite low and dramatically decrease within mm level (e.g. Woolley & Stoller 1978, Bliss & Smith 1985, Kasperbauer & Hunt 1988, Benvenuti 1995, Mandoli et al. 1990). Decrease in the light permeability through soil is negatively correlated with the size of soil particles (e.g. Bliss & Smith 1985, Benvenuti 1995, Mandoli et al. 1990). It generally appears that physiologically and ecologically significant amounts of light rarely penetrate more than 4-5 mm through soil and that any penetration beyond 10 mm would generally not be significant (Tester & Morris 1987). In *Datura stramonium* seeds, which have light requirement for germination, germination percentage in soil below 4mm from the surface is equivalent with that in complete darkness (Benvenuti 1995). In addition, soil filter change not only light quantity but light quality. Since the longer wavelengths penetrate into soil more easily, soil filter decrease red/far-red light (R/FR) ratio of daylight (e.g. Woolley & Stoller 1978, Mandoli et al. 1982, 1990, Bliss & Smith 1985, Kasperbauer & Hunt 1988, Benvenuti 1995). Litter also decrease R/FR ratio of light (Bliss & Smith 1985, Pearson et al. 2003). Decrease in R/FR ratio of light is dependent on plant species of the litter (Bliss & Smith 1985, Pearson et al. 2003). Although needle leaf affects uniformly to the spectrum of visible light, broad leaf decrease relatively the R/FR ratio of daylight (Bliss & Smith 1985). However, the effect of soil-induced transformation of light quality for seed germination needs further research..

Vegetation clearly changes light quality of daylight because vegetation absorbs selectively red light (R) in the process of photosynthesis. Hence, selective absorption of R by vegetation decreases R/FR ratio of exposed daylight to the soil surface (Stoutjesdijk 1972, Lee 1987, Smith et al. 1990). In also a gap condition, R/FR ratio of exposed daylight in a small gap is slightly low compared with large gap (Pearson et al. 2003).

In temperature condition in soil, diurnal range in temperature of soil surface is commonly larger in gap environment than under vegetation (e.g. Washitani & Takenaka 1987, Pierson & Wight 1991). At a pasture in southwest Idaho, maximum and minimum temperature in the soil near the surface (below 1 cm from the surface) under the vegetation dominating sagebrush (*Artemisia tridentata tridentata*) is equivalent with that in the gap soil below 10 cm from the surface (Pierson & Wight 1991). The range of temperature fluctuations in soil decreases with the soil depth (e.g. Stoller & Wax 1973, Washitani & Takenaka 1987, Ghersa et al. 1992). The range of temperature fluctuations in soil may be peak in summer in many regions. However, soil temperature at common germination season for many plants (i.e., spring or autumn) fluctuates comparably with that in summer season in some regions (e.g. Stoller & Wax 1973, Washitani & Kabaya 1988).

Gap Detection in Seed Germination

As described above, vegetation obviously affects the light and temperature conditions. Using light and temperature signals, seeds of many plants actually avoid fatal germination under dense vegetation or too deep in soil, in other words, detect gap surface in seed germination. Light requirement for germination (e.g., Wesson & Wareing 1967, 1969a, 1969b, Fenner 1980a, Baskin & Baskin 1985, Pons 1984, Pons 1991), leaf-canopy inhibition (e.g., King 1975, Górski 1975, Fenner 1980b, Silvertown 1980, 1981, Vázquez-Yanes & Smith 1982, Pons 1983, Washitani & Saeki 1984, Washitani 1985), fluctuating temperatures requirement (e.g., Thompson et al. 1977, Thompson & Grime 1983, Benech Arnold et al. 1988), high temperature requirement in germination process (e.g., Washitani & Takenaka 1987), physical dormancy (PY) broken by high temperature (Washitani & Takenaka 1986, Washitani 1988), promotion of germination by soil nitrate (Pons 1989) and increased concentration of soil CO₂ (Yoshioka et al. 1998) are reported as gap-detection mechanisms. The former three properties are important of them all since these three properties were reported in vast plant species in the world. Hence light and temperature are thought as important gap signals for many plant species. In addition, Bouwmeester & Karssen (1989) proposed a hypothesis that dormancy breakage by dry storage may contribute as to detect gap in germination since gap surface may be in dry state comparatively.

Light Requirement for Germination

Light-requiring seeds can germinate when they are exposed to light or natural daylight because exposure to such lights increases the photoequilibrium of phytochromes. Baskin & Baskin (1989) noted that 'a primary reason seeds do not germinate in the soil while non-dormant is that most have a light requirement for germination' (Thompson 2000). The most obvious significance of the requirement is considered as avoidance of germination too deep in soil for the seedlings to reach the surface on the available nutrient reserves (Pons 2000), since light permeability through soil is quite low (e.g. Woolley & Stoller 1978, Bliss & Smith 1985, Kasperbauer & Hunt 1988, Benvenuti 1995, Mandoli et al. 1990). Seeds have pre-existing Pfr before seed dispersal because seeds form Pfr in maturation process of the seed. Germination in the soil may be caused by the pre-existing Pfr in the seed. When the photoequilibrium is low, however, seed may not germinate in darkness. After seed burial, dark reversion may succeed in decreasing photoequilibrium in the soil (Bewley & Black 1994). In *Dactylis glomerata* seeds, germination percentage at 21/11°C fluctuating temperatures condition decreased in proportion to the pre-storage period of the seeds in 16°C darkness (Probert & Smith 1986). Probably due to the effect of dark reversion, even dispersed seeds not requiring light for germination acquire light requirement after they were buried in soil (Wesson & Wareing 1967, 1969b). Prerequisite is that germination is prevented by conditions not conducive to germination. This may be either by forms of dormancy other than germination inhibition (Pons 2000).

Leaf-Canopy Inhibition

As described above, selective absorption of red light by vegetation decreases R/FR ratio of exposed daylight to the soil surface (Stoutjesdijk 1972, Lee 1987, Smith et al. 1990). When seeds were exposed to light with low R/FR ratio, seeds can not germinate since the photoequilibrium of the seeds are decreased. Thus, leaf-canopy inhibition makes seeds detect the presence of canopy cover over the seeds. In *Datura ferox* seeds, whose sensitivity to light after burial is dependent on not only soil depth and but also canopy cover (Botto et al. 1998). However, since light permeability through soil is quite low (e.g. Woolley & Stoller 1978, Bliss & Smith 1985, Kasperbauer & Hunt 1988, Benvenuti 1995, Mandoli et al. 1990), low R/FR light may not affect in germination after seed burial for many plant species. In *Amaranthus patulus* seeds, although germination under vegetation is avoided with leaf-canopy inhibition (Washitani & Saeki 1984), germination is not avoided after burial of the seeds (Washitani 1985). In addition, Pons (2000) advocated that there are two important points of difference in spring as compared with summer: (1) leaf canopies are not so dense in spring as in summer, resulting in higher R/FR ratios; and (2) lower R/FR ratios are required to avoid germination of chilled seeds than of freshly harvested (Pons 1986). The two factors together permit germination in spring under grass of seeds that are at or near the soil surface. Hence, the light condition in spring may not be reliable environmental signal for avoidance of ultimately fatal germination under vegetation (Pons 2000).

Fluctuating-Temperatures Requirements

Temperature fluctuations decrease under vegetation compared with gap and in proportion to soil depth as described above. Unfortunately, although the mechanism of fluctuating temperatures requirements remains unclear, seeds with fluctuating temperatures requirement can actually perceive the range of temperature fluctuations and then avoid fatal germination not only under dense vegetation but also too deep in soil (Ghersa et al. 1992). Note that also the analysis of Honda (2008) (Figure 5 and 6) showed clear contribution of the fluctuating temperatures requirement for seed persistence in soil. Some plants species can germinate in fluctuating temperatures condition even after germination were inhibited with exposure to FR light (e.g., Williams 1983, Pons 1986, Probert & Smith 1986, Benvenuti et al. 2001) or leaf-transmitted light (e.g., Benech Arnold et al. 1988, Honda & Katoh 2007). Thus, temperature fluctuations deny the effect of decrease in the photoequilibrium in such species.

In wetland ecosystem, however, the fluctuating temperatures requirement does not necessarily contribute to the seed persistence in the soil. In *Phragmites australis* seeds, which do not persist in soil, the fluctuating temperatures requirement contributes to detect shallow environment within annual fluctuation of water level (Ekstam et al. 1999).

Interactions between Several Gap-Detection Stimuli

A response to interactions between several gap-detection stimuli may give seeds the ability to determine both the timing and location of germination with some precision (e.g., Hilton 1984, Milberg 1997, Honda & Katoh 2007). Successful targeting of germination on

optimum conditions for establishment makes the evolution of persistence much more likely (Thompson 2000). Although untreated seeds of *Bidens pilosa* germinate well in darkness, the light requirement for germination is induced after they were exposed to leaf-transmitted light (Fenner 1980a). Similar germination behavior is exhibited by *Lactuca sativa*, as though the seeds “remember” the last situation they experienced before burial (Górski 1975). In *Picris hieracioides* var. *japonica* seeds, the experience and timing of receiving leaf-transmitted light affects germination and then the required range of temperature fluctuations will be enhanced (Honda & Katoh 2007). The requirement for gap signals that created high precision of timing in the germination process results in the germination of this species only in gaps.

Predicting Seed Persistence

There are clear tendencies between seed characteristics and persistence in soil. Many studies showed that small and spherical seeds can persist in the soil abundantly compared with large and flattened seeds (e.g. Thompson et al. 1993, 1998, 2001, Bekker et al. 1998, Hodkinson et al. 1998, Honda 2008). Although whole mechanisms that seeds bury themselves passively remain unclear, small and spherical seeds are actually distributed in deep soil (Bekker et al. 1998) since small and spherical seeds can bury themselves more readily into soil compared with large and flattened seeds (Thompson 1987, Benvenuti 2007). In New Zealand, persistent seeds are significantly smaller than transient seeds (Moles et al. 2000), although the relationship is driven entirely by the absence of transient seed banks among species with very small (<0.5mg) seeds. In Australia, however, there is no relationship at all between seed size and seed persistence in the soil (Leishman & Westoby 1998). They considered that the reasons include that seed bank species are dominated by the plants having with physical dormancy (PY) in Australia and that commonly the size of seeds with PY is large. In small-seeded species, not only the ease to bury into soil, they are more dependent on light for germination than large-seeded ones (Milberg et al. 2000). In addition, R/FR ratio required for seed germination decreases in proportion to the seed size (Pearson et al. 2003). Thus, although there are exceptions in Australia, commonly soil seed banks are dominated by small and spherical seeds.

Theoretical (Rees 1994) and empirical (Thompson et al. 1998) studies have suggested also a negative correlation between plant longevity (life history) after germination and seed persistence in the soil. Hence, annual plants tend to accumulate more seeds in seed banks than do perennial plants. It is reasonable that life history has close relationship to the persistence in the soil because annuals without a seed bank would become extinct in the first year when its reproduction failed. Honda (2008) analyzed relationships between 18 types of plant traits that may relate to seed persistence and seed persistence in the soil but he could detect no other relationships except the seed size and life history.

Constraints in Restoration Using Seed Banks

Although seed bank soil seed bank have a potential as more ideal restoration material, it have also some constraints. For utilization in restoration projects, we should understand the traits and constraints to promote more effective utilization of seed bank for restoration.

1. Many Endangered Plants Does not Form a Seed Bank

In the extensive gravelly floodplains of the middle reaches of Japanese rivers, endangered endemic plants *Aster kantoensis* (Washitani et al. 1997) and *Ixeris tamagawaensis* (Honda & Kuramoto 2001) which are important species in conservation (Kuramoto et al. 2000) does not form a soil seed bank unfortunately. Stöcklin & Fischer (1999) investigated whether plant species with longer-lived seeds in the soil had lower rates of local extinction between 1950 and 1985 than species with shorter-lived seeds in 26 intact remnants of extensively used calcareous grasslands. Then they concluded that longer-lived seeds constitute a better buffer against risks of local extinction caused by stochastic process than shorter-lived seeds and that most characteristic species of calcareous grassland do not persist in the seed bank and can not rely on this mechanism as a buffer against local extinction. Similarly, Bakker & Berendse (1999) indicated that there is critical constraints in restoration using seed banks since most seeds present in the seed bank include non-target species with a long-term persistent seed bank. Unfortunately, thus, target species for a restoration project may not be included in soil seed banks. Hence, it is essential that preliminary assessing the species composition of seed banks to select donor soil containing particular target species (e.g., Nishihiro et al. 2006).

2. Low Genetic Differentiation between Seed Bank and Standing Vegetation

Seed banks are expected to contain variety of species and genetically diverse individual in past and present ecosystem (e.g., van der Valk & Pederson 1989, Levin 1990). Honnay et al. (2008) conducted two meta-analyses to find the evidence that 1) a seed bank increase effective population size, and hence whether genetic differentiation (F_{ST}) between subdivided plant populations is lower for species without a seed bank and that 2) population genetic diversity contained in the seed bank can be used as a potential means to restore genetic diversity of the above ground population for a certain plant species. Meta-analysis is the statistical procedure for combining data from multiple studies to earn a reliable general law. To conclude, they showed that seed bank may mitigate the consequences of habitat fragmentation and may protect a species from population genetic differentiation (Honnay et al. 2008). There is no evidence, however, that high levels of genetic diversity are accumulating in the seed bank (Honnay et al. 2008). As they pointed out, however, it might have been due to the smallness of their dataset so that they can not test for the effect of mediating variables such as soil sampling depth on genetic differences between seed bank and vegetation.

3. Polluted Seed Bank with Invasive Exotic Plants Seeds

Once a persistent soil seed bank of an invasive exotic species has been established, either natural or human disturbances will always bring about the domination of the invasive exotic species, which will further replenish the soil seed bank or enlarge the seed sources of the invasive exotic species (Washitani 2004). Honda et al. (2004) analyzed the properties of plants that have the possibility to naturalize to Japan as invasive exotic plants. They concluded that plants with a soil seed bank provide a higher possibility to establish as

invasive exotic plants in Japan than plants without a seed bank. Persistent seed bank strategies of physiological mechanisms to detect gap surface for seedling establishment are common to most invasive exotic species established in Japan (Washitani & Morimoto 1993). Many invasive exotic plants in Japan actually have accumulated their seeds in soil abundantly (Ajima 2001). The use of such soil containing seeds of invasive exotic plants with high density should be avoided in restoration projects. In addition to the preliminary assessing the species composition of seed banks, selective removal of invasive exotics is essential for successful restoration projects using seed banks. However, the establishment of techniques for assessing and managing invasive exotics is one of the most important issues in revegetation using soil seed banks (Nishihiro et al. 2006).

4. Construction of a Safe Site for Target Species at Restoration Site

The favorable conditions in germination and subsequent establishment should be created for sustainable growth of the target species in the restoration projects. Microtopography of the resorted area affects germination of target species since seeds of different species differ in their requirements for conditions suitable for germination (Harper et al. 1965). Restoration projects in plants should target not only environmental conditions favoring germination and establishment, but also growth and reproduction, because the death of emerged individuals before reproduction exhausts soil seed banks and forfeits the potential for vegetation recovery from natural disturbance (Nishihiro et al. 2006). In the conditions favoring establishment after germination, also the abundance of their pollinators should be investigated since pollinators are one of the important environmental factors deciding the reproductive success. Hence, not to waste soil seed banks, it is essential to investigate preliminarily the favorable conditions in germination and the subsequent growth of the target species.

For Effective Restoration Using Seed Banks

Thus, it seems that the underlying problems in restoration using soil seed banks are hostile. Our capacity for ecological restoration is limited, however, our limitation is not a justification for “irrestoration” (Choi 2007). Even in the limitation of restoration using a soil seed bank, the soil seed bank is an environmental-friendly material for restoration. In addition, to restore lost plants from the world, a soil seed bank is the only hope left for us.

Similarity in species composition between soil seed banks and standing vegetation is important information for the restoration using seed banks, since the soil that has low similarity with the associated standing vegetation is naturally valid materials for restoration. The meta-analysis of Hopfensperger (2007) showed standing vegetation and its associated seed bank was the least similar in canopy-closed ecosystems, most similar in canopy-opened ecosystems, and of intermediate similarity in wetlands. These results are consistent with the germination avoidance under dense vegetation described in this chapter. In addition, he showed that the similarity decreased with time since disturbances in forest and wetland ecosystems and increased with time since disturbances in grasslands. Thus, effective timing of soil sampling for restoration may be dependent on ecosystems.

In this chapter, I explained that seed banks prevent germination cleverly in the conditions that the probability of survival and growth of the seedling is low. These insights provide an important suggestion that species composition in the soil favoring the establishment and growth after germination will relatively resemble that for the standing vegetation. On the other hand, when seeds were dispersed to the environment where the growth of individuals of the species is not expected, seeds wait for the favorable condition as the soil seed bank. Hence seeds of wetland species can be excavated from relatively dry soil (van der Valk & Pederson 1989), although the clear physiological mechanism is unknown. The similarity between species composition in the soil where the establishment and growth after germination is not expected and the standing vegetation will be relatively low. Furthermore, at top soil, because of the relatively high speed in the cycle of generational shift (Figure 7), the similarity between species composition at the top soil and the standing vegetation will be relatively high. On the other hand, in the seed in deep soil, because of the relatively low speed in the cycle of generational shift, the similarity between species composition in the deep soil and the standing vegetation will be relatively low. Amazingly, thus, soil sampling for restoration from the deep soil where the establishment and growth after germination is not expected may provide some rare and endangered plants serendipitously. Although small seeds can bury themselves more readily into the soil with compact texture (silt) than into the soil with coarse texture (sand) compared with large seeds, the contribution of physical drop for natural seed burial within a year is recognized only a few millimeters (Benvenuti 2007). Hence, seeds of invasive exotic plants, which naturalized in relatively recent years, must be accumulated in the top soil with high density. Restoration using a seed bank at top soil actually raised invader species rather than endangered plants in some cases. However, soils were sampled from top soil in many restoration projects using soil seed banks, since soil sampling from deep soil increase the cost and labor compared with sampling from top soil. Thus, vertical distribution of soil seed banks provides important information for future restoration using the soil seed bank. Compared with horizontal distribution of seed banks, however, research for the vertical distribution of seed banks are so few. Even many theoretical works on soil seed banks do not consider the vertical distributions of seed banks. More consideration of the vertical distributions in seed banks would bring about the next step in seed bank studies.

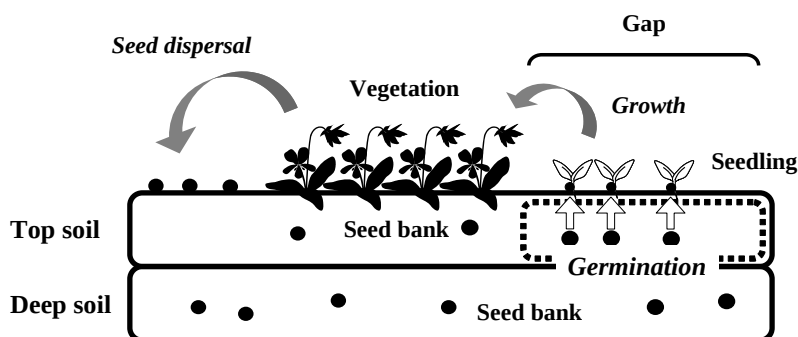


Figure 7. Conceptual diagram of plant life cycle. Seeds with gap-detection mechanism can germinate in gap surface (top soil) and grow successfully. On the other hand, the seeds in deep soil avoid germination and wait for the favorable condition that the successful reproduction is expected. In the seed at the top soil, because of the relatively high speed in the cycle of generational shift, the similarity between species composition at the top soil and the standing vegetation will be relatively high.

I believe that seeds of the endangered or lost plants are buried in the unfavorable environments for the subsequent growth after germination. I hope that soil sampling from such unfavorable environments will restore more species of endangered plants or lost plants.

Acknowledgements

I express my appreciation to Kazuhiro Katoh and Fumiko Ishizuna for their valuable comments and help.

References

- Ajima M. (2001) Accumulation of seeds of exotic species in the soil seed bank in Japan: *Japanese Journal of Conservation Ecology*, **6**, 155-165 (in Japanese)
- Bakker J.P. & Berendse F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities: *Trends in Ecology and Evolution* **14**, 63-68
- Baskin C.C. (2003) Breaking physical dormancy in seeds - focussing on the lens: *New Phytologist* **158**, 279-282
- Baskin C.C. & Baskin J.M. (1989) Physiology of dormancy and germination in relation to seed bank ecology, 53-66 pp., in *Ecology of Soil Seed Banks* (Leck M.A., Parker V.T. & Simpson R.L. ed.), 462 pp., Academic Press, San Diego
- Baskin C.C. & Baskin J.M. (1998) Seeds: *Ecology, Biogeography and Evolution of Dormancy and Germination*, 666 pp., Academic Press, San Diego
- Baskin J.M. & Baskin C.C. (1978) The seed bank in a population of an endemic plant species and its ecological significance: *Biological Conservation* **14**, 125-130
- Baskin J.M. & Baskin C.C. (1985) The light requirement for germination of *Aster pilosus* seeds: Temporal aspects and ecological consequences: *Journal of Ecology* **73**, 765-77
- Baskin J.M. & Baskin C.C. (2000) Evolutionary considerations of claims for physical dormancy break by microbial action and abrasion by soil particles: *Seed Science Research* **10**, 409-416
- Baskin J.M. & Baskin C.C. (2004) A classification system for seed dormancy: *Seed Science Research* **14**, 1-16
- Bekker R.M., Bakker J.P., Grandin U., Kalamees R., Milberg P., Poschlod P., Thompson K. & Willems J.H. (1998) Seed size, shape and vertical distributions in the soil: indicators of seed longevity: *Functional Ecology* **12**, 834-842
- Benech Arnold R.L., Ghera C.M., Sanchez R.A. & Garcia Fernandez A.E. (1988) The role of fluctuating temperatures in the germination and establishment of *Sorghum halepense* (L.) Pers. Regulation of germination under leaf canopies: *Functional Ecology* **2**, 311-318
- Benvenuti S. (1995) Soil light penetration and dormancy of jimsonweed (*Datura stramonium*) seeds: *Weed Science* **43**, 389-393
- Benvenuti S., Macchia M. & Miele S. (2001) Light, temperature and burial depth effects on *Rumex obtusifolius* seed germination and emergence: *Weed Research* **41**, 177-186
- Benvenuti S. (2007) Natural weed seed burial: effect of soil texture, rain and seed characteristics: *Seed Science Research* **17**, 211-219

- Bewley J.D. & Black M. (1994) *Seeds: Physiology of development and germination*, 445 pp., Plenum Press, New York
- Bewley J.D. & Downie B. (1996) Is failure of seeds to germinate during development a dormancy related phenomenon?, 17-27 pp., in *Plant Dormancy: Physiology, Biochemistry and Molecular Biology* (Lang G.A. ed), 386 pp., CABI Publishing, Oxon
- Bliss D. & Smith H. (1985) Penetration of light into soil and its role in the control of seed germination: *Plant, Cell and Environment* **8**, 475-483
- Botto J.F., Sánchez R.A. & Casal J.J. (1998) Burial conditions affect light responses of *Datura ferox* seeds: *Seed Science Research* **8**, 423-429
- Bouwmeester H.J. & Karssen C.M. (1989) Environmental factors influencing the expression of dormancy patterns in weed species: *Annals of Botany* **63**, 113-120
- Bullock J.M. (2000) Gaps and seedling colonization, 375-395 pp., in *Seeds: The ecology of regeneration in plant communities* (Fenner M. ed.), 2nd ed., 410 pp., CABI Publishing, Oxon
- Choi Y.D. (2007) Restoration ecology to the future: a call for new paradigm: *Restoration Ecology* **15**, 351-353
- Ekstam B., Johannesson R. & Milberg P. (1999) The effect of light and number of diurnal temperature fluctuations on germination of *Phragmites australis*: *Seed Science Research* **9**, 165-170
- Ellner S. (1986) Germination dimorphisms and parent-offspring conflict in seed germination: *Journal of Theoretical Biology* **123**, 173-186
- Fenner M. (1980a) The induction of a light requirement in *Bidens pilosa* seeds by leaf canopy shade: *New Phytologist* **84**, 103-106
- Fenner M. (1980b) The inhibition of germination of *Bidens pilosa* seed by leaf canopy shade in some natural vegetation types: *New Phytologist* **84**, 95-101
- Fenner M. & Thompson K. (2005) *The Ecology of Seeds*, 250 pp., Cambridge University Press, Cambridge
- Ghersa C.M., Benech Arnold R.L. & Martinez-Ghersa M.A. (1992) The role of fluctuating temperatures in germination and establishment of *Sorghum halepense*. Regulation of germination at increasing depths: *Functional Ecology* **6**, 460-468
- Górski T. (1975) Germination of seeds in the shadow of plants: *Physiologia Plantarum* **34**, 342-346
- Grime J.P. (1981) The role of seed dormancy in vegetation dynamics: *Annals of Applied Biology* **98**, 555-558
- Grime J.P., Hodgson J.G., Hunt R. (1988) *Comparative Plant Ecology: A Functional Approach to Common British Species*, 742 pp., Unwin Hyman, London
- Harper J.L., Williams J.T. & Sagar G.R. (1965) The behaviour of seeds in soil I. the heterogeneity of soil surfaces and its role in determining the establishment of plants from seed: *Journal of Ecology* **53**, 273-286
- Hilhorst H.W.M. (1998) The regulation of secondary dormancy. The membrane hypothesis revisited: *Seed Science Research* **8**, 77-90
- Hilton J.R. (1984) The influence of light and potassium nitrate on the dormancy and germination of *Avena fatua* L. (wild oat) seed and its ecological significance: *New Phytologist* **96**, 31-34

- Hodkinson D.J., Askew A.P., Thompson K., Hodgson J.G., Bakker J.P. & Bekker R.M. (1998) Ecological correlates of seed size in the British flora: *Functional Ecology* **12**, 762-766
- Honda Y. (2008) Ecological correlations between the persistence of the soil seed bank and several plant traits, including seed dormancy: *Plant Ecology* **196**, 301-309
- Honda Y. & Katoh K. (2007) Strict requirement of fluctuating temperatures as a reliable gap signal in *Picris hieracioides* var. *japonica* seed germination: *Plant Ecology* **193**, 147-156
- Honda Y., Itoh K. & Katoh K. (2004) Plant naturalization possibility to Japan: from a perspective of seed persistence: *Journal of the Japanese Society of Revegetation Technology* **30**, 9-14 (in Japanese with English abstract)
- Honda Y. & Kuramoto K. (2001) Status, dormancy and germination traits of an endangered Plant, *Ixeris tamagawaensis* Kitam. along the Tama River: *Journal of Japanese Institute of Landscape Architecture* **64**, 583-588 (in Japanese with English abstract)
- Honnay O., Bossuyt B., Jacquemyn H., Shimono A. & Uchiyama K. (2008) Can a seed bank maintain the genetic variation in the above ground plant population?: *Oikos* **117**, 1-5
- Hopfensperger K.N. (2007) A review of similarity between seed bank and standing vegetation across ecosystems: *Oikos* **116**, 1438-1448
- Kasperbauer M.J. & Hunt P.G. (1988) Biological and photometric measurement of light transmission through soils of various colors: *Botanical Gazette* **149**, 361-364
- King T.J. (1975) Inhibition of seed germination under leaf canopies in *Arenaria serpyllifolia*, *Veronica arvensis* and *Cerastium holosteoides*: *New Phytologist* **75**, 87-90
- Kuramoto N., Honda Y. & Yagi M. (2000) Endemic plants on shingle river beds and their status in the floodplain of the Tama River: *Bulletin of the Faculty of Agriculture, Meiji University* **123**, 27-32 (in Japanese with English abstract)
- Lee D.W. (1987) The spectral distribution of radiation in two Neotropical rainforests: *Biotropica* **19**, 161-166
- Leishman M.R. & Westoby M. (1998) Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain: *Functional Ecology* **12**, 480-485
- Levin D.A. (1990) The seed bank as a source of genetic novelty in plants: *American Naturalist* **135**, 563-572
- Mandoli D.F., Waldron L.J., Nemson J.A. & Briggs W.R. (1982) Soil light transmission: implications for phytochrome-mediated responses: *Yearbook / Carnegie Institution of Washington* **81**, 32-34
- Mandoli D.F., Ford G.A., Waldron L.J., Nemson J.A. & Briggs W.R. (1990) Some spectral properties of several soil types: implications for photomorphogenesis: *Plant, Cell and Environment* **13**, 287-294
- Milberg P. (1997) Weed seed germination after short-term light exposure: germination rate, photon fluence response and interaction with nitrate: *Weed Research* **37**, 157-164
- Milberg P., Andersson L. & Thompson K. (2000) Large-seeded species are less dependent on light for germination than small-seeded ones: *Seed Science Research* **10**, 99-104
- Moles A.T., Hodson D.W. & Webb C.J. (2000) Seed size and shape and persistence in the soil in the New Zealand flora: *OIKOS* **89**, 541-545
- Nilsson P., Fagerström T., Tuomi J. & Åström M. (1994) Does seed dormancy benefit the mother plant by reducing sib competition?: *Evolutionary Ecology* **8**, 422-430

- Nishihiro J., Nishihiro M.A. & Washitani I. (2006) Restoration of wetland vegetation using soil seed banks: lessons from a project in Lake Kasumigaura, Japan: *Landscape and Ecological Engineering* **2**, 171-176
- Pearson T.R.H., Burslem D.F.R.P., Mullins C.E. & Dalling J.W. (2003) Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view: *Functional Ecology* **17**, 394-402
- Pierson F.B. & Wight J.R. (1991) Variability of near-surface soil temperature on sagebrush rangeland: *Journal of Range Management* **44**, 491-497
- Pons T.L. (1983) Significance of inhibition of seed germination under leaf canopy in ash coppice: *Plant, Cell and Environment* **6**, 385-392
- Pons T.L. (1984) Possible significance of changes in the light requirement of *Cirsium palustre* seeds after dispersal in ash coppice: *Plant, Cell and Environment* **77**, 263-268
- Pons T.L. (1986) Response of *Plantago major* seeds to the red/far-red ratio as influenced by other environmental factors: *Physiologia Plantarum* **68**, 252-258
- Pons T.L. (1989) Breaking of seed dormancy by nitrate as a gap detection mechanism: *Annals of Botany* **63**, 139-143
- Pons T.L. (1991) Induction of dark dormancy in seeds: its importance for the seed bank in the soil: *Functional Ecology* **5**, 669-675
- Pons T.L. (2000) Seed responses to light, 237-260 pp., in *Seeds: The ecology of regeneration in plant communities* (Fenner M. ed.), 2nd ed., 410 pp., CABI Publishing, Oxon
- Probert R.J. & Smith R.D. (1986) The joint action of phytochrome and alternating temperatures in the control of seed germination in *Dactylis glomerata*: *Physiologia Plantarum* **67**, 299-304
- Rees M. (1994) Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure: *American Naturalist* **144**, 43-64
- Silvertown J.W. (1980) Leaf-canopy-induced seed dormancy in a grassland flora: *New Phytologist* **85**, 109-118
- Silvertown J.W. (1981) Micro-spatial heterogeneity and seedling demography in species-rich grassland: *New Phytologist* **88**, 117-128
- Smith H., Casal J.J. & Jackson G.M. (1990) Reflection signals and the perception by phytochrome of the proximity of neighbouring vegetation: *Plant, Cell and Environment* **13**, 73-78
- Stöcklin J. & Fischer M. (1999) Plants with longer-lived seeds have lower local extinction rates in grassland remnants: *Oecologia* **120**, 539-543
- Stoller E.W. & Wax L.M. (1973) Temperature variations in the surface layers on an agricultural soil: *Weed Research* **13**, 273-282
- Stoutjesdijk P.H. (1972) Spectral transmission curves of some types of leaf canopies with a note on seed germination: *Acta Botanica Neerlandica* **21**, 185-191
- Tester M. & Morris C. (1987) The penetration of light through soil: *Plant, Cell and Environment* **10**, 281-286
- Thompson K. (1987) Seeds and seed banks: *New Phytologist* **106** s., 23-34
- Thompson K. (2000) The functional ecology of soil seed banks, 215-235 pp., in *Seeds: The ecology of regeneration in plant communities* (Fenner M. ed.), 2nd ed., 410 pp., CABI Publishing, Oxon

- Thompson K., Bakker J.P. & Bekker R.M. (1997) The Soil Seed Banks of North West Europe: *Methodology, density and longevity*, 276 pp., Cambridge University Press, Cambridge
- Thompson K., Bakker J.P., Bekker R.M. & Hodgson J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora: *Journal of Ecology* **86**, 163-169
- Thompson K., Band S.R. & Hodgson J.G. (1993) Seed size and shape predict persistence in soil: *Functional Ecology* **7**, 236-241
- Thompson K., Ceriani R.M., Bakker J.P. & Bekker R.M. (2003) Are seed dormancy and persistence in soil related?: *Seed Science Research* **13**, 97-100
- Thompson K. & Grime J.P. (1983) A comparative study of germination responses to diurnally fluctuating temperatures: *Journal of Applied Ecology* **20**, 141-156
- Thompson K., Grime J.P. & Mason G. (1977) Seed germination in response to diurnal fluctuations of temperature: *Nature* **267**, 147-149
- Thompson K., Jalili A., Hodgson J.G., Hamzeh'ee B., Asri Y., Shaw S., Shirvany A., Yazdani S., Khoshnevis M., Zarrinkamar F., Ghahramani M.-A. & Safavi R. (2001) Seed size, shape and persistence in the soil in an Iranian flora: *Seed Science Research* **11**, 345-355
- van der Valk A.G. & Pederson R.L. (1989) Seed banks and the management and restoration of natural vegetation, 329-346 pp., in *Ecology of Soil Seed Banks* (Leck M.A., Parker V.T. & Simpson R.L. ed.), 462 pp., Academic Press, San Diego
- Vázquez-Yanes C. & Smith H. (1982) Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance: *New Phytologist* **92**, 477-485
- Vleeshouwers L.M., Bouwmeester H.J. & Karssen C.M. (1995) Redefining seed dormancy: an attempt to integrate physiology and ecology: *Journal of Ecology* **83**, 1031-1037
- Walck J.L., Baskin J.M., Baskin C.C. & Hidayati S.N. (2005) Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns: *Seed Science Research* **15**, 189-196
- Washitani I. (1985) Field fate of *Amaranthus patulus* seeds subjected to leaf-canopy inhibition of germination: *Oecologia* **66**, 338-342
- Washitani I. (1988) Effects of high temperature on the permeability and germinability of the hard seed of *Rhus javanica* L.: *Annals of Botany* **62**, 13-16
- Washitani I. (2004) Invasive exotic species problems in Japan: an introductory ecological essay: *Global Environmental Research* **8**, 1-11
- Washitani I. & Kabaya H. (1988) Germination responses to temperature responsible for the seedling emergence seasonality of *Primula sieboldii* E. Morren in its natural habitat: *Ecological Research* **3**, 9-20
- Washitani I. & Masuda M. (1990) A comparative study of the germination characteristics of seeds from a moist tall grassland community: *Functional Ecology* **4**, 543-557
- Washitani I. & Morimoto N. (1993) Invasive exotic Plants and Animals *Naturalized in Japan*, 191 pp., Hoikusya, Tokyo (in Japanese)
- Washitani I. & Saeki T. (1984) Leaf-canopy inhibition of germination as a mechanism for the disappearance of *Amaranthus patulus* Bertol. in the second year of a secondary succession: *Japanese Journal of Ecology* **34**, 55-61
- Washitani I. & Takenaka A. (1986) 'Safe sites' for the seed germination of *Rhus javanica*: a characterization by responses to temperature and light: *Ecological Research* **1**, 71-82

- Washitani I. & Takenaka A. (1987) Gap-detecting mechanism in the seed germination of *Mallotus japonicus* (Thunb.) Muell. Arg., a common pioneer tree of secondary succession in temperate Japan: *Ecological Research* **2**, 191-201
- Washitani I., Takenaka A., Kuramoto N. & Inoue K. (1997) *Aster kantoensis* Kitam., an endangered flood plain endemic plant in Japan: its ability to form persistent soil seed banks: *Biological Conservation* **82**, 67-72
- Wesson G. & Wareing P.F. (1967) Light requirements of buried seeds: *Nature* **213**, 600-601
- Wesson G. & Wareing P.F. (1969a) The role of light in the germination of naturally occurring populations of buried weed seeds: *Journal of Experimental Botany* **20**, 402-413
- Wesson G. & Wareing P.F. (1969b) The induction of light sensitivity in weed seeds by burial: *Journal of Experimental Botany* **20**, 414-425
- Williams E.D. (1983) Effects of temperature fluctuation, red and far-red light and nitrate on seed germination of five grasses: *Journal of Applied Ecology* **20**, 923-935
- Woolley J.T. & Stoller E.W. (1978) Light penetration and light-induced seed germination in soil: *Plant Physiology* **61**, 597-600
- Yoshioka T., Satoh S. & Yamasue Y. (1998) Effect of increased concentration of soil CO² on intermittent flushes of seed germination in *Echinochloa crus-galli* var. *crus-galli*: *Plant, Cell and Environment* **21**, 1301-1306

Chapter 5

MATHEMATICAL MODELS OF DISEASES SPREADING IN SYMBIOTIC COMMUNITIES

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Abstract

Symbiotic communities are relevant from the biologists' viewpoint. Diseases affecting interacting populations have earlier been considered in ecoepidemic models with interactions of competitive or predational type but also for mutualistic associations. Here the analysis is extended to populations experiencing mutualism, in the more realistic case in which the benefits of the symbiosis cannot exhibit unlimited growth as function of the ecosystem populations. The investigation of some such situations is not only biologically relevant, but it becomes important even from an economic point of view, like for instance the case of chestnut trees affected by chestnut cancer and several mushrooms. We model a symbiotic ecoepidemic system via a dynamical system, assuming that the return coming from positive species interactions has an upper bound. We mathematically analyze its long-term behavior and identify conditions leading to disease eradication. Some new features characteristic of these models with respect to earlier ecoepidemic models with different underlying demographics are highlighted.

Keywords: ecoepidemiology; population models; epidemic models; commensalism; obligate mutualism; facultative mutualism; persistence; local stability; global stability.

1. Introduction

Symbiotic communities are important from the biological point of view, in fact not so long ago, an entire monography has been devoted to these situations, [4]. Relevant examples are for instance the classical cases of the anemone-damselfish and ant-plant interactions

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at extrafloral nectaries leading to pollination, such as moths (of genus *Tegeticula*) pollinating yuccas, [2], but also others involving mycorrhizal fungi, fungus-gardening ants, mixed feeding flocks of birds dispersing seeds of *Casearia corymbosa* in Costa Rica, [24].

In the biomathematic literature great attention has been devoted to competing and predator-prey species interactions, but also the interest toward commensalism and populations living in symbiosis receives quite a bit of consideration. In [25, 26, 27, 43] mutualism is considered within food chains, in which some of the other interactions may be of competitive nature, or in simpler models with three interacting populations, [10, 16, 33]. The effects of variable environments, qualitative analysis of bifurcation and coexistence states are also examined [8, 12, 14, 20, 35]. More recently, diffusion in space [21] and time delays in the context of symbiosis have been investigated, [6, 7, 41, 42].

Diseases affecting a variety of different species living in every possible environment, aquatic, terrestrial or involving birds are listed in [15]. For populations interacting and receiving mutual benefit, but affected by some disease, specific examples are provided by the symbiotic associations of chestnut trees (*Castanea sativa*) and various mushrooms (*Cantharellus cibarius*, *Boletus* spp., *Amanita* spp.) and affected by chestnut cancer (*Endothia parasitica*), or the L-form bacteria forming non-pathogenic symbiosis with a wide range of plants, which are then able to resist further bacterial pathogens [40], or finally the very recently discovered action of the soil nematode *Caenorhabditis elegans*, transferring the rhizobium species *Sinorhizobium melotiti* to the roots of the legume *Medicago truncatula* [1, 23]. Symbiotic associations have been recognized among bacteria, [44] and bacteria and other organisms [5, 34]. Also among plants [31] and plants and mushrooms [30] mutualism plays a relevant role, possibly affecting also other populations in the ecosystem [9].

Ecoepidemiology studies the influence such diseases carry on the underlying demographic situations. The recent literature is rich in papers devoted to ecoepidemic systems in which the basic interactions among the populations entail negative consequences for at least one of them, i.e. they are of competitive or predational nature. Only in [39] a symbiotic situation has been analyzed in the ecoepidemic context. In this Chapter we continue the investigation of ecoepidemic symbiotic systems, as done in [39], where we assumed a Holling type I interaction, i.e. that the benefit one species receives from the intermingling with the other may increase without bounds as a function of the size of the second population. Rather, we assume here that it has an upper limit, as it is indeed common in more advanced models of competing nature. This corresponds to the law of diminishing returns in other sciences, and is usually modeled via a rational function term, of the Michaelis-Menten type.

After presenting the basic demographic and epidemic models on which our system relies, in Section 3 we present the ecoepidemic model and analyze it in Section 4., focusing mainly on the case in which symbiosis is essential for the survival of each involved population. For each equilibrium, stability properties are established. For the disease-free equilibrium the possibility of bifurcations is examined in detail in Section 4.4.. Some particular cases of the model are also examined in Section 4.6., namely the cooperation situation in which each population can thrive also in absence of the other one, the case in which mutualism is facultative only for one of the species and the situation in which one population is entirely infected, 4.6.3.. Results of some numerical simulations are contained in Section 5, a final discussion of the ecological implications of this model is presented in Section 6.

2. The Underlying Models

2.1. Species Demographic Association

We consider a pair of symbiotic species which interact in different ways. At first we consider the situation in which their association is necessary for survival, i.e. in absence of the other species both have no different survival means. In the second case instead, we assume that other food sources are available, so that their association is beneficial, but not crucial for survival. Later we will also consider the mixed cases in which obligate mutualism occurs for one species but for the other one is only facultative. The demographic model reads as follows, see [3],

$$\frac{ds}{dt} = -c_1s + \frac{a_1sp}{1 + d_1p} - e_1s^2, \quad \frac{dp}{dt} = -c_2p + \frac{a_2sp}{1 + d_2s} - e_3p^2, \quad (1)$$

in which all parameters should be taken to be positive unless otherwise specified. Both equations account for net reproduction, first terms, intraspecific logistic-like competition, third terms, and cooperation, second terms. In absence of interactions, for $a_1 = a_2 = 0$, the case $c_1, c_2 > 0$, in which these parameters represent mortalities is not very much interesting as the two populations would be wiped away. For $c_1, c_2 \leq 0$ instead we have (positive) birth rates and in absence of interactions each population would grow toward its respective carrying capacity

$$-\frac{c_1}{e_1} > 0, \quad -\frac{c_2}{e_3} > 0.$$

The interaction terms are Holling type II, or Michaelis-Menten, terms denoting a saturation response mechanism, i.e. as for the law of diminishing returns in operations research relating effort and yield, the larger the population x say, the smaller the value of the response function $f(x)$. Namely, we can write emphasizing the role of the different parameters as follows

$$f(x) = \frac{ax}{1 + dx}, \quad f'(0) = a, \quad f(+\infty) = \frac{a}{d}, \quad (2)$$

so that a is mostly related to the way the response function rises at the origin, and d describes the ultimate value of the return, the larger the latter is the smaller the parameter value. Note that for the two species the saturation level response $f(+\infty)$ and the way these functions initially rise to it, $f'(0)$, could in principle very well be different, since each of the two species p and s by mutual association could perceive the effect of the other one in a different way. In other words, the four parameters a_1, a_2, d_1, d_2 , are taken all to be different, although they relate to the same “physical” association. In view of the previous remarks, in (1) the parameters $c_1, c_2 > 0$ denote thus the case in which the symbiosis is essential for survival, as without it, it is easily seen that the ecosystem collapses, while for $c_1, c_2 < 0$ the converse situation holds, mutualism is facultative.

We now briefly outline the analysis of (1) for each such case, for further comparison with the ecoepidemic model to be introduced later. The two equilibria are easily found: the origin $\check{E}_0$ and $\check{E}_2 = (\check{s}_2, \check{p}_2)$. Letting

$$\begin{aligned} A &= e_1(e_3d_2 - c_2d_2d_1 + a_2d_1), \quad C = a_1c_2 + c_1e_3 - c_1c_2d_1, \quad \Gamma_2 = B^2 - 4AC, \\ B &= c_2d_2a_1 - a_2a_1 + a_2c_1d_1 + e_3d_2c_1 - c_2d_2c_1d_1 - e_1c_2d_1 + e_1e_3, \end{aligned} \quad (3)$$

$\check{s}_2$ solves the quadratic

$$As^2 + Bs + C = 0. \quad (4)$$

Now for $c_1, c_2 > 0$, if $C > 0$ there are either two roots or none if $A > 0$ and for $A < 0$ there is always a unique feasible value of $\check{s}_2$; if $C < 0$ the considerations reverse, always one feasible root for $A > 0$ and either a pair or none for $A < 0$. For the second model with $c_1, c_2 < 0$, only one situation arises, $C < 0$, $A > 0$ in which case there is only one feasible value for $\check{s}_2$. The components of $\check{E}_2$ can be explicitly calculated,

$$\check{s}_2^\pm = \frac{a_2a_1 - c_2d_2a_1 - a_2c_1d_1 - e_3d_2c_1 + c_2d_2c_1d_1 + e_1c_2d_1 - e_1e_3 \pm \sqrt{\Gamma_2}}{2e_1(e_3d_2 - c_2d_2d_1 + a_2d_1)},$$

$$\check{p}_2^\pm = \frac{c_1 + e_1\check{s}_2^\pm}{a_1 - c_1d_1 - e_1d_1\check{s}_2^\pm}. \quad (5)$$

For $c_1, c_2 > 0$ the complete picture for feasibility is then

$$\begin{aligned} &\text{if } A < 0, C > 0 \quad \exists! \text{ root: } \check{s}_2^- \\ &\text{if } A > 0, C > 0, B < 0, \Gamma_2 \geq 0 \quad \exists 2 \text{ roots: } \check{s}_2^\pm \\ &\text{if } A > 0, C < 0 \quad \exists! \text{ root: } \check{s}_2^+ \\ &\text{if } A < 0, C < 0, B > 0, \Gamma_2 \geq 0 \quad \exists 2 \text{ roots: } \check{s}_2^\pm \end{aligned} \quad (6)$$

and for $c_1, c_2 < 0$ there is always the root $\check{s}_2^+$ since unconditionally $A > 0$, $C < 0$, namely from (6) we have

$$A > 0, C < 0 \quad \exists! \text{ root: } \check{s}_2^+. \quad (7)$$

Note however that for feasibility of p_2 , when $c_1 > 0$ the upper bound

$$\check{s}_2 < \frac{a_1 - c_1d_1}{e_1d_1} \quad (8)$$

must be imposed on $\check{s}_2$, while for $c_1 < 0$ the inequalities are required

$$-\frac{c_1}{e_1} \leq \check{s}_2 < \frac{a_1 - c_1d_1}{e_1d_1}. \quad (9)$$

These impose additional constraints on the roots of (4).

The origin has the eigenvalues $-c_1, -c_2$, so that when symbiosis is essential for survival it is always locally asymptotically stable while in the second model, namely for $c_1, c_2 < 0$, it is always unstable.

At $\check{E}_2$ the Jacobian is

$$\check{J}_2 = \begin{bmatrix} -e_1\check{s}_2 & \frac{a_1\check{s}_2}{(1+d_1\check{p}_2)^2} \\ \frac{a_2\check{p}_2}{(1+d_2\check{s}_2)^2} & -e_3\check{p}_2 \end{bmatrix} \quad (10)$$

Easily, we find that

$$\text{tr}(\check{J}_2) < 0, \quad \det(\check{J}_2) = \frac{\check{s}_2\check{p}_2\check{\Delta}}{(1+d_1\check{p}_2)^2(1+d_2\check{s}_2)^2},$$

where

$$\begin{aligned}\tilde{\Delta} = & 2e_3e_1d_1\check{p}_2 + e_3e_1d_2^2\check{s}_2^2 + e_3e_1d_1^2\check{p}_2^2 + 2e_3e_1d_2\check{s}_2 + 4e_3e_1d_1\check{p}_2d_2\check{s}_2 \\ & + 2e_3e_1d_1\check{p}_2d_2^2\check{s}_2^2 + 2e_3e_1d_1^2\check{p}_2^2d_2\check{s}_2 + e_3e_1d_1^2\check{p}_2^2d_2^2\check{s}_2^2 + e_3e_1 - a_1a_2.\end{aligned}$$

For both models the local stability for $\check{E}_2$ reduces to ensuring

$$\tilde{\Delta} > 0. \quad (11)$$

Alternatively one could use the Gershgorin's theorem, in which case sufficient conditions for stability are simply

$$e_1(1 + d_1\check{p}_2)^2 > a_1, \quad e_3(1 + d_2\check{s}_2)^2 > a_2. \quad (12)$$

2.2. Behavior near $\check{E}_2$

The equilibrium $\check{E}_2$ will turn out to be particularly relevant in the ecoepidemic model. We investigate further the system and its dynamics near it. Let us denote by $(\check{J}_2)_{ij}$ the entries of the Jacobian matrix calculated at $\check{E}_2$, (10).

Theorem 1. At the equilibrium $\check{E}_2$ the system has a saddle-node bifurcation for $e_3 = e_3^t$, but neither transcritical nor pitch-fork, nor Hopf bifurcations can occur.

Proof. Recall that $\check{E}_2$ is actually a pair of equilibria, whose characteristic equation is

$$[\tau - (\check{J}_2)_{11}][\tau - (\check{J}_2)_{22}] - (\check{J}_2)_{12}(\check{J}_2)_{21} = 0. \quad (13)$$

One of the eigenvalues of $J(E_2)$ vanishes for $(\check{J}_2)_{11}(\check{J}_2)_{22} = (\check{J}_2)_{21}(\check{J}_2)_{12}$. The latter equation in the parameter e_3 reduces to

$$K(e_3) \equiv e_1[1 + d_1\check{p}_2(e_3)]^2[1 + d_2\check{s}_2(e_3)]^2 = a_1a_2\frac{1}{e_3} \equiv G(e_3), \quad (14)$$

where the notation $\check{s}_2(e_3)$, $\check{p}_2(e_3)$ emphasizes the dependence of the population equilibrium levels on the parameter e_3 . The vanishing of an eigenvalue is then equivalent to an intersection problem. On the right we have the positive branch of a hyperbola, $G(e_3)$, on the left instead the function $K(e_3)$. Note that the function $K(e_3)$ is in fact a continuous function. It can indeed be recast in the form

$$K(e_3) = e_1a_1^2 \left[\frac{1 + d_2\check{s}_2(e_3)}{a_1 - c_1d_1 - d_1e_1\check{s}_2(e_3)} \right]^2 \geq 0.$$

Its only possible discontinuity could occur when the denominator vanishes, for the parameter value $\hat{e}_3 > 0$ say, for which

$$\check{s}_2(\hat{e}_3) = \frac{a_1 - c_1d_1}{d_1e_1},$$

which makes $\check{p}_2(\hat{e}_3) \rightarrow +\infty$. But this is incompatible with the equilibrium condition for $\check{p}_2$, $\frac{d\check{p}}{dt} = 0$ which would imply

$$\hat{e}_3\check{p}_2(\hat{e}_3) = -c_2 + \frac{a_2(a_1 - c_1d_1)}{d_1e_1 + a_1d_2 - c_1d_1d_2},$$

an impossible condition to satisfy, since the left hand side would be infinite and the right hand side is finite. Recalling (3) and (5), as $e_3 \rightarrow +\infty$, the functions $\check{s}_2^\pm(e_3)$ tend to the limits $L_{1,2}$, with

$$L_1 = -\frac{c_1}{e_1}, \quad L_2 = -\frac{1}{d_2},$$

respectively $\check{s}_2^+ \rightarrow L_1$, $\check{s}_2^- \rightarrow L_2$, for $e_1 > c_1 d_2$ and conversely for $e_1 < c_1 d_2$. Consequently, the function K tends therefore to one of the following finite limits as $e_3 \rightarrow +\infty$,

$$K \rightarrow e_1 a_1^2 \left[\frac{1 + d_2 L_{1,2}}{a_1 - c_1 d_1 - d_1 e_1 L_{1,2}} \right]^2 \geq 0, \quad K_1^\infty = 0, \quad K_2^\infty = \frac{1}{e_1} (e_1 - c_1 d_1)^2. \quad (15)$$

On the other hand, $\check{s}_2(0^+)$, $\check{p}_2(0^+)$ can be easily evaluated directly, setting $e_3 = 0$ into (1), to get

$$\check{s}_2(0^+) = \frac{c_2}{a_2 - c_2 d_2}, \quad \check{p}_2(0^+) = \frac{c_1 + e_1 s_2(0^+)}{a_1 - c_1 d_1 - d_1 e_1 s_2(0^+)}.$$

Then using the definition of K , (14), it follows

$$K(0^+) = \frac{a_1^2 a_2^2 e_1}{[(a_1 - c_1 d_1)(a_2 - c_2 d_2) - c_2 d_1 e_1]^2} > 0. \quad (16)$$

If we consider the branch of K leading to K_2^∞ , the function K tends to finite limits at the endpoints of $\mathbf{R}_+$, i.e. its range contains the interval $[\min\{K(0^+), K_2^\infty\}, \max\{K(0^+), K_2^\infty\}]$. For $(e_1 - c_1 d_1)B > 0$ this is the branch related to $\check{s}_2^+$, or conversely the one of $\check{s}_2^-$. The range of the hyperbola $G(e_3)$ on the right of (14) is the whole $\mathbf{R}_+$. By continuity an intersection between the two functions must exist, providing a root e_3^t for (14). But feasibility of $\check{s}_2$ at e_3^t is not guaranteed and must be verified.

Calculating the eigenvectors of $J(\check{E}_2)$ and $J(\check{E}_2)^T$ corresponding to the eigenvalue $\varsigma_1 = 0$, we respectively find

$$\check{\mathbf{U}} = \left(-\frac{(J_2)_{13}\tilde{\theta}_2}{(J_2)_{11}}, \tilde{\theta}_2 \right)^T, \quad \check{\mathbf{Y}} = \left(-\frac{(J_2)_{31}\hbar_2}{(J_2)_{11}}, \hbar_2 \right)^T$$

where $\tilde{\theta}_2$ and $\hbar_2$ denote arbitrary constants. Also, letting F denote the right hand side of the system (1)

$$\frac{\partial F}{\partial e_3} \equiv F_{e_3}(X, e_3) = [0, \check{p}_2^2]^T.$$

Upon evaluation at e_3^t we find $F_{e_3}(\check{E}_2, e_3^t) = (0, -\check{p}_2^2)^T$ and $\check{\mathbf{Y}}^T[F_{e_3}(\check{E}_2, e_3^t)] = -\hbar_2 \check{p}_2^2 \neq 0$. Also $\check{\mathbf{Y}}^T[D^2 F(\check{E}_2, e_3^t)(\check{\mathbf{U}}, \check{\mathbf{U}})] \neq 0$, where $D^2 F(\check{E}_2, e_3^t)$ is the $2 \times 2 \times 2$ tensor of the second partial derivatives of (1) with respect to the system variables (s, p) . Thus the system at least for one of the two equilibria $\check{E}_2$ experiences a saddle-node bifurcation in view of Sotomayor's theorem, [32], Chapter 4.

Since however $\check{\mathbf{Y}}^T[F_{e_3}(\check{E}_2, e_3^t)] = -\hbar_2 \check{p}_2^2 \neq 0$, the system attains neither transcritical nor pitch-fork bifurcations.

For the characteristic equation of (10) to have a pair of complex conjugate roots, we would need $(J_2)_{11} + (J_2)_{22} = -e_1 \check{s}_2 - e_3 \check{p}_2 = 0$, and in view of the feasibility conditions for E_2 this is impossible, unless both $\check{s}_2 \equiv \check{p}_2 = 0$. Hence no Hopf bifurcation can occur at the interior equilibrium.

2.3. Other Variants of the Demographic Model

The system for $c_1, c_2 < 0$ attains two more equilibria namely, $\check{E}_1^a = (\check{s}_1^a, 0)$, $\check{E}_2^a = (0, \check{p}_2^a)$, where

$$\check{s}_1^a = -\frac{c_1}{e_1}, \quad \check{p}_2^a = -\frac{c_2}{e_3}.$$

At $\check{E}_1^a$ the eigenvalues are

$$c_1, \quad \frac{c_2 e_1 - c_1 c_2 d_2 + a_2 c_1}{d_2 c_1 - e_1}, \quad (17)$$

so that this equilibrium is always unstable. The second eigenvalue indeed has a negative denominator, and a negative numerator, $c_2 e_1 - c_1 c_2 d_2 + a_2 c_1 < 0$. Similar considerations show the unconditional instability of $\check{E}_2^a$ in view of the eigenvalues

$$c_2, \quad \frac{c_1 e_3 - c_1 c_2 d_1 + a_1 c_2}{d_1 c_2 - e_3} > 0. \quad (18)$$

We can consider also the mixed cases in which the association is necessary for survival for one population, while for the other one it is not.

For $c_1 > 0$ and $c_2 \leq 0$, since $A > 0$, the original equilibria have the following feasibility conditions

$$\begin{aligned} \text{if } B < 0, C < 0 \quad \exists! \text{ root: } \check{s}_2^+ \\ \text{if } B > 0, C < 0 \quad \exists! \text{ root: } \check{s}_2^+ \\ \text{if } B < 0, C > 0, \Gamma_2 \geq 0 \quad \exists 2 \text{ roots: } \check{s}_2^\pm \end{aligned} \quad (19)$$

Instead E_1^a becomes infeasible, while E_2^a has still the eigenvalues (18) so that it becomes conditionally stable, namely when the second eigenvalue is negative i.e. for

$$a_1 c_2 > c_1 (c_2 d_1 - e_3). \quad (20)$$

For $c_1 \leq 0$ and $c_2 > 0$, the reverse situation holds, $\check{E}_2^a$ is infeasible, and $\check{E}_1^a$ has still the eigenvalues (17) and again it is the second eigenvalue which determines stability, for

$$a_2 c_1 > c_2 (c_1 d_2 - e_1). \quad (21)$$

For the original equilibria in this case feasibility of $s_2^\pm$ holds exactly as given in (6).

We summarize in Table 1 the properties of the equilibria of the demographic model. Note that in Table 1 the conditional feasibility refers always to the same condition, which however in each case takes different solutions sets in the parameter space, in view of the sign changes of the parameters.

2.4. The Disease Model

We will need to introduce a disease in the population system (1) to build the ecoepidemic model. Before doing that, we consider the epidemic model for just one population, since it differs, although slightly, from the classical *SI* epidemic model, the latter denoting the situation in which the disease once contracted, cannot be recovered. Because some vital

Table 1. Equilibria of the demographic model (1)

Case	Equilibrium	Feasibility conditions	Stability conditions	Bifurcations nature
$c_1, c_2 > 0$	$\check{O} \equiv (0, 0)$ $\check{E}_2 \equiv (\check{s}_2, \check{p}_2)$	(6), (8)	stable (11); sufficient: (12)	saddle-node at $e_3 = e_3^t$
$c_1, c_2 < 0$	$\check{O} \equiv (0, 0)$ $\check{E}_2 \equiv (\check{s}_2, \check{p}_2)$ $\check{E}_1^a \equiv (-\frac{c_1}{e_1}, 0)$ $\check{E}_2^a \equiv (0, -\frac{c_2}{e_3})$	(7), (9)	unstable (11); sufficient: (12) unstable unstable	saddle-node at $e_3 = e_3^t$
$c_1 > 0$ $c_2 \leq 0$	$\check{O} \equiv (0, 0)$ $\check{E}_2 \equiv (\check{s}_2, \check{p}_2)$ $\check{E}_1^a \equiv (-\frac{c_1}{e_1}, 0)$ $\check{E}_2^a \equiv (0, -\frac{c_2}{e_3})$	(19), (8) infeasible	unstable (11); sufficient: (12) (20)	saddle-node at $e_3 = e_3^t$
$c_1 \leq 0$ $c_2 > 0$	$\check{O} \equiv (0, 0)$ $\check{E}_2 \equiv (\check{s}_2, \check{p}_2)$ $\check{E}_1^a \equiv (-\frac{c_1}{e_1}, 0)$ $\check{E}_2^a \equiv (0, -\frac{c_2}{e_3})$	(6), (9) infeasible	unstable (11); sufficient: (12) (21)	saddle-node at $e_3 = e_3^t$

dynamics is considered here, the resulting implications are indeed other than the classical ones, like a similar situation that occurred for the first models in which demographic effects in a single population were considered in the context of epidemiology [11, 29]. For a further thorough reference on the classical epidemic models, and more recent developments in epidemiology, see [22]. In fact, let the population be partitioned among susceptibles and infected individuals. Denoting by s and i the members of these respective classes, we have

$$\frac{ds}{dt} = -c_1 s - \lambda i s - e_1 s(s + i), \quad \frac{di}{dt} = \lambda i s - e_2 i(s + i) - \delta i. \quad (22)$$

Here λ represents the disease incidence, modeled in this case via mass action, i.e. by the product term λsi , proportional to each subpopulation size, leading to a homogeneous mixing model. The parameters c_1 and e_1, e_2 retain their meaning as in the previous model, birth or mortality rates and logistic competition, and therefore illustrate the meaning of each term in which they appear, while δ denotes the disease related mortality. Note that the logistic terms contain different coefficients e_1 and e_2 since intraspecific competition is felt in different ways by sound and infected individuals. More specifically, we take $e_2 \neq e_1$, since we could have $e_2 > e_1$ to mean that infected individuals suffer more the intraspecific

competition than sound individuals, or conversely that $e_2 < e_1$, i.e., by the presence of the disease they are impaired and thus the effect of intraspecific competition becomes lower. Upon summation, the whole population would thus grow according to the equation

$$\frac{d(s+i)}{dt} = -c_1 s - e_1 s^2 - (e_1 + e_2) si - e_2 i^2 - \delta i.$$

The equilibria are given by the points $E_0^*(0, 0)$, $E_1^*(s_1^*, i_1^*)$, with

$$s_1^* = \frac{\delta e_1 + \delta \lambda - c_1 e_2}{\lambda (e_1 + \lambda - e_2)}, \quad i_1^* = \frac{c_1 e_2 - c_1 \lambda - \delta e_1}{\lambda (e_1 + \lambda - e_2)}. \quad (23)$$

For $c_1 > 0$ the nullcline for s in (22) does not meet the first quadrant, thus E_1^* is infeasible. Otherwise, for $c_1 < 0$ feasibility of s_1^* requires $e_1 + \lambda > e_2$ and thus for i_1^* it follows $c_1(e_2 - \lambda) > \delta e_1$. The latter cannot be satisfied if $e_2 > \lambda$, and in the opposite case the former is redundant, so that feasibility of E_1^* holds when

$$-c_1(\lambda - e_2) > \delta e_1 \quad (24)$$

Upon evaluating the Jacobian matrix, we easily find the eigenvalues at the origin

$$-c_1, \quad -\delta$$

showing its local asymptotic stability for $c_1 > 0$, and its instability for $c_1 < 0$. Thus in absence of new recruits into the system (22), the whole population is bound to collapse, while with a positive birth rate, disappearance of the population cannot happen. At E_1^* we have the Jacobian

$$J_1^* = \begin{bmatrix} -e_1 s_1^* & -\lambda s_1^* - e_1 s_1^* \\ \lambda i_1^* - e_2 i_1^* & -e_2 i_1^* \end{bmatrix} \quad (25)$$

from which

$$\text{tr}(J_1^*) < 0, \quad \det(J_1^*) = (\lambda - e_2 + e_1) \lambda s_1^* i_1^*.$$

Assuming feasibility, it is then locally asymptotically stable if and only if

$$\lambda - e_2 + e_1 > 0. \quad (26)$$

But (26) is implied by (24), so that E_1^* in this case is unconditionally stable. Thus in this case the population survives, with the endemic level of the disease i_1^* given by (23).

For a positive net birth rate, i.e. $c_1 < 0$, there is an extra equilibrium,

$$E_1^{a*}(s_1^{a*}, 0) \equiv \left(-\frac{c_1}{e_1}, 0 \right).$$

Its eigenvalues are

$$c_1, \quad \frac{1}{e_1} [c_1(e_2 - \lambda) - e_1 \delta]$$

and local stability is then governed by the sign of the latter. Thus for

$$c_1 e_2 < c_1 \lambda + e_1 \delta, \quad (27)$$

Table 2. Equilibria of the epidemic model (22)

Case	Equilibrium	Feasibility conditions	Stability conditions
$c_1 > 0$	$O^* \equiv (0, 0)$		stable
	$E_1^* \equiv (s_1^*, i_1^*)$	infeasible	
$c_1 < 0$	$O^* \equiv (0, 0)$		unstable
	$E_1^* \equiv (s_1^*, i_1^*)$	(24)	stable
	$E_1^{a*} \equiv (-\frac{c_1}{e_1}, 0)$		(27)

the population survives and the disease is eradicated. A sufficient condition for this to occur is provided by $e_2 > \lambda$, i.e. if the mortality rate of the infected due to intraspecific competition is larger than the infected recruitment rate, i.e. the disease incidence.

These considerations show the difference from the classical *SI* epidemic model, in which everyone ultimately gets infected. At most, in this case, the endemicity of the disease reaches the value i_1^* . Moreover, with population mortality explicitly built into the model, the disease vanishes, together with the population itself, if the net birth rate is negative, while if the latter is positive the equilibrium E_1^{a*} states that there is the possibility of eradicating the disease, this occurring when condition (27) holds.

In Table 2 a summarizing scheme of these equilibria is reported.

3. The Ecoepidemic Model

We now merge the above situations. In both models with positive ($c_1, c_2 < 0$) and negative ($c_1, c_2 > 0$) birth rates one of the species is now assumed to be affected by a disease, spreading by contact but not able to cross the species barrier. Let s and i denote the sound and infected subpopulations of the first species, and p the population size of the second one.

The equations of the system below contain standard logistic terms for each population, with net birth rates that can be positive or negative as stated above and interaction terms. The latter determine a positive contribution to the growth of each population, limited above by a maximal possible benefit as illustrated by the last term of (2). The Holling type II terms corresponding to this assumption constitute the major difference with former models, [39]. As in the previous Section, the disease is assumed to be of *SI* type. We model this

situation via the equations

$$\begin{aligned}\frac{ds}{dt} &= -c_1s + \frac{a_1sp}{1+d_1p} - \lambda is - e_1s(s+i), \\ \frac{di}{dt} &= \lambda is + \frac{a_1ip}{1+d_1p} - e_2i(s+i) - \delta i, \\ \frac{dp}{dt} &= -c_2p + \frac{a_2(s+i)p}{1+d_2(s+i)} - e_3p^2.\end{aligned}\tag{28}$$

The parameters retain their meanings, illustrated in the previous Section. Once again, all parameters other than c_1, c_2 are assumed to be nonnegative.

4. Symbiosis Essential for Survival

Consider now (28) for $c_1 > 0, c_2 > 0$. We prove at first that the dynamics is confined to a compact set around the origin, then list the possible equilibria and discuss their stability.

4.1. Boundedness of the System

Theorem 2. The trajectories of the model (28) are uniformly bounded.

Proof. Take the time derivative along the solutions of (28) of the function $\Psi_\alpha = s+i+p$ to get the estimate

$$\begin{aligned}\frac{d\Psi_\alpha}{dt} &= \frac{a_1(s+i)p}{1+d_1p} - c_1s - [e_1s + e_2i](s+i) - \delta i - c_2p + \frac{a_2(s+i)p}{1+d_2(s+i)} - e_3p^2 \\ &\leq -c_1s + \frac{a_1(s+i)}{d_1} - \delta i - c_2p + \frac{a_2p}{d_2} - e_1s^2 - e_2i^2 - e_3p^2 \\ &= \left(\frac{a_1}{d_1} - c_1\right)s - e_1s^2 + \left(\frac{a_1}{d_1} - \delta\right)i - e_2i^2 + \left(\frac{a_2}{d_2} - c_2\right)p - e_3p^2.\end{aligned}$$

If all the brackets in the last term are negative, i.e. if $a_1 < c_1d_1, a_1 < d_1\delta, a_2 < c_2d_2$, then Ψ_α decreases, and since Ψ_α represents a sort of 1-norm in the positive orthant of the *sip* phase space, any plane $s+i+p = \ell$, with $\ell > 0$ in the positive orthant cuts out a simplex with a vertex at the origin, which is a positively invariant set for (28). Conversely, for a suitable $0 < \phi$ with the same estimations, we obtain

$$\begin{aligned}\frac{d\Psi_\alpha}{dt} + \phi\Psi_\alpha &\leq (\phi - c_1)s + \frac{a_1(s+i)}{d_1} + (\phi - \delta)i + (\phi - c_2)p + \frac{a_2p}{d_2} - e_1s^2 - e_2i^2 - e_3p^2 \\ &= \left(\phi + \frac{a_1}{d_1} - c_1\right)s - e_1s^2 + \left(\phi + \frac{a_1}{d_1} - \delta\right)i - e_2i^2 + \left(\phi + \frac{a_2}{d_2} - c_2\right)p - e_3p^2.\end{aligned}$$

By evaluating the maxima of the three parabolas on the right hand side, we can then find $\rho > 0$ such that

$$\frac{d\Psi_\alpha}{dt} + \phi\Psi_\alpha \leq \frac{(\phi + \frac{a_1}{d_1} - c_1)^2}{4e_1} + \frac{(\phi + \frac{a_1}{d_1} - \delta)^2}{4e_2} + \frac{(\phi + \frac{a_2}{d_2} - c_2)^2}{4e_3} \equiv \rho.$$

Note that if some of the conditions $\phi + \frac{a_1}{d_1} \leq c_1$, $\phi + \frac{a_1}{d_1} \leq \delta$, $\phi + \frac{a_2}{d_2} \leq c_2$ hold, the corresponding terms in the definition of ρ could be omitted, thereby obtaining a smaller upper bound. From the above equation it follows anyway

$$\frac{d\Psi_\alpha}{dt} \leq -\phi\Psi_\alpha + \rho$$

implying that

$$\Psi_\alpha(t) \leq e^{-\phi t}\Psi_\alpha(0) + \frac{\rho}{\phi}(1 - e^{-\phi t}) \leq \max(\Psi_\alpha(0), \frac{\rho}{\phi}).$$

Hence, $\limsup \Psi_\alpha(t) \leq \frac{\rho}{\phi}$ as $t \rightarrow \infty$ independently of the initial conditions.

4.2. Equilibria

There are five equilibria, the origin $E_0 \equiv O$ and the four points $E_j = (s_j, i_j, p_j)$, $j = 1, \dots, 4$, of which the first three are boundary points, i.e. where at least one of the populations vanishes. Explicitly, their coordinates are found as follows. First, the endemic equilibrium E_1 in which the second species vanishes, and which coincides with the equilibrium of the purely epidemic system (23), for which then

$$s_1 \equiv s_1^*, \quad i_1 \equiv i_1^*, \quad p_1 = 0.$$

Thus its feasibility has already been discussed, (24) for $c_1 < 0$, recall also Table 2. Then the equilibrium E_2 with both species surviving, and the disease eradicated. Recalling (3) its components are

$$s_2 = \check{s}_2, \quad i_2 = 0, \quad p_2 = \check{p}_2.$$

Again feasibility reduces to the conditions (6) and (8) for $\check{E}_2$. Next we find the equilibrium E_3 with both species surviving, but in the diseased population everyone contracts the disease and no susceptibles are left, namely

$$s_3 = 0, \quad p_3 = \frac{a_2 i_3 - c_2 - c_2 d_2 i_3}{(1 + d_2 i_3) e_3},$$

and where i_3 solves the quadratic $\tilde{A}i^2 + \tilde{B}i + \tilde{C} = 0$, with

$$\begin{aligned} \tilde{A} &= e_2(c_2 d_1 d_2 - a_2 d_1 - d_2 e_3), & \tilde{C} &= c_2 d_1 \delta - a_1 c_2 - e_3 \delta, \\ \tilde{B} &= a_1 a_2 + c_2 d_1 e_2 + c_2 d_1 d_2 \delta - e_2 e_3 - a_1 c_2 d_2 - d_2 e_3 \delta - a_2 d_1 \delta. \end{aligned}$$

Note that these are in general a pair of equilibria, the feasibility of which can be determined with a discussion similar to the one following (4), thus

$$\begin{aligned} \tilde{A} > 0 \quad \tilde{C} < 0 \quad \exists! \text{ root : } i_3^+ & \quad (29) \\ \tilde{\Gamma} \equiv \tilde{B}^2 - 4\tilde{A}\tilde{C} \geq 0, \quad \tilde{A} > 0 \quad \tilde{B} < 0 \quad \tilde{C} > 0 \quad \exists 2 \text{ roots : } i_3^\pm & \\ \tilde{A} < 0 \quad \tilde{C} > 0 \quad \exists! \text{ root : } i_3^- & \\ \tilde{\Gamma} \geq 0, \quad \tilde{A} < 0 \quad \tilde{B} > 0 \quad \tilde{C} < 0 \quad \exists 2 \text{ roots : } i_3^\pm & \end{aligned}$$

Feasibility imposes also a lower bound on i_3 stemming from $p_3 \geq 0$, namely

$$a_2 > c_2 d_2, \quad i_3 \geq \frac{c_2}{a_2 - c_2 d_2}, \quad (30)$$

while E_3 is infeasible for

$$a_2 < c_2 d_2. \quad (31)$$

Finally we have the interior equilibrium E_4 where the whole ecosystem thrives, which has components that can be explicitly calculated, with very complicated algebraic expressions, which must be nonnegative for feasibility. For the analytic expressions of these quantities, we refer the reader to the Appendix.

4.3. Stability

We investigate now the long term performance of the system around the equilibria. The Jacobian matrix J has the following components

$$\begin{aligned} J_{11} &= \frac{a_1 p}{1 + d_1 p} - 2e_1 s - (\lambda + e_1)i - c_1, & J_{12} &= -(\lambda + e_1)s, & J_{13} &= \frac{a_1 s}{(1 + d_1 p)^2}, \\ J_{21} &= (\lambda - e_2)i, & J_{22} &= \frac{a_1 p}{1 + d_1 p} - 2e_2 i + (\lambda - e_2)s - \delta, & J_{23} &= \frac{a_1 i}{(1 + d_1 p)^2}, \\ J_{31} &= \frac{a_2 p}{(1 + d_2(s + i))^2} = J_{32}, & J_{33} &= \frac{a_2(s + i)}{1 + d_2(s + i)} - 2e_3 p - c_2. \end{aligned}$$

It is easily seen that at the origin the Jacobian becomes a diagonal matrix, with eigenvalues

$$-c_1, \quad -\delta, \quad -c_2 \quad (32)$$

so that E_0 is always locally asymptotically stable. In addition we now show its conditional global asymptotic stability.

Theorem 3. Letting $e = \min\{e_1, e_2\}$, E_0 is globally asymptotically stable provided that

$$(a_1 + a_2)^2 < 4ee_3. \quad (33)$$

Proof. To this end, we let $\tilde{\mathbf{R}} = \{(s, i, p) \in \mathbf{R}_+^3, s \geq 0, i \geq 0, p \geq 0\}$ and define the function $L : \tilde{\mathbf{R}} \rightarrow \mathbf{R}$ by $L(t) = s + i + p$. The derivative of the function L along the solutions of the system (28) can be estimated from above as follows

$$\begin{aligned} \frac{dL}{dt} &= -c_1 s + \frac{a_1(s + i)p}{1 + d_1 p} - (e_1 s + e_2 i)(s + i) - \delta i - c_2 p + \frac{a_2(s + i)p}{1 + d_2(s + i)} - e_3 p^2 \\ &\leq -c_1 s + a_1(s + i)p - e(s + i)^2 - \delta i - c_2 p + a_2(s + i)p - e_3 p^2 \\ &\leq -c_1 s - \delta i - c_2 p - e_3 p^2 + [(a_1 + a_2)(s + i)p - e(s + i)^2]. \end{aligned}$$

Evaluating the maximum of the parabola in $s + i$ on the right hand side, we find

$$\frac{dL}{dt} \leq -c_1 s - \delta i - c_2 p - e_3 p^2 + \frac{(a_1 + a_2)^2}{4e} p^2 \leq 0,$$

where the last estimate follows from (33). Moreover, we have $\frac{dL}{dt}(E_0) = 0$. The claim then follows from Lyapunov-Lasalle's invariance principle.

At E_1 the Jacobian matrix factors, and one eigenvalue is immediately available,

$$\frac{a_2\delta - a_2c_1 - c_2e_1 - c_2\lambda + c_2e_2 - c_2d_2\delta + c_2d_2c_1}{e_1 + \lambda - e_2 + d_2\delta - d_2c_1} \quad (34)$$

while the remaining two are the roots of the quadratic characteristic equation stemming from (25). Necessary condition for the local asymptotic stability of equilibrium E_1 is thus (26). We need to require in addition that also the first eigenvalue (34) be negative,

$$\frac{a_2(\delta - c_1)}{e_1 + \lambda - e_2 + d_2\delta - d_2c_1} < c_2. \quad (35)$$

At E_2 again the Jacobian

$$J(E_2) = [b_{ij}] \equiv \begin{bmatrix} -e_1s_2 & -(\lambda + e_1)s_2 & \frac{a_1s_2}{(1+d_1p_2)^2} \\ 0 & c_1 - \delta + (e_1 + \lambda - e_2)s_2 & 0 \\ \frac{a_2p_2}{(1+d_2s_2)^2} & \frac{a_2p_2}{(1+d_2s_2)^2} & -e_3p_2 \end{bmatrix} \quad (36)$$

factors, giving immediately the first eigenvalue

$$c_1 + e_1s_2 + \lambda s_2 - \delta - e_2s_2. \quad (37)$$

The remaining eigenvalues are those arising from (10), so that stability at E_2 is governed by the negativity of (37), i.e.

$$c_1 + e_1s_2 + \lambda s_2 < \delta + e_2s_2. \quad (38)$$

and (11). The latter is then ultimately the condition already found for $\check{E}_2$.

For E_3 we again find a factored Jacobian

$$J(E_3) = \begin{bmatrix} -\lambda i_3 - c_1 - e_1i_3 + e_2i_3 + \delta & 0 & 0 \\ (\lambda - e_2)i_3 & -e_2i_3 & \frac{a_1i_3}{(1+d_1p_3)^2} \\ \frac{a_2p_3}{(1+d_2i_3)^2} & \frac{a_2p_3}{(1+d_2i_3)^2} & -e_3p_3 \end{bmatrix} \quad (39)$$

giving immediately the first eigenvalue, which needs to be negative, otherwise if positive it destabilizes the equilibrium,

$$\delta < c_1 + (\lambda + e_1 - e_2)i_3. \quad (40)$$

In addition, we need the Routh Hurwitz necessary and sufficient conditions for stability which, since $\text{tr}J(E_3) < 0$, reduce to the inequality

$$\det J(E_3) \equiv i_3p_3 \left[e_2e_3 - \frac{a_1a_2}{(1+d_1p_3)^2(1+d_2i_3)^2} \right] > 0. \quad (41)$$

A sufficient condition is obtained by using Gershgorin's theorem,

$$e_2(1+d_1p_3)^2 > a_2, \quad e_3(1+d_2i_3)^2 > a_2. \quad (42)$$

4.4. Behavior near E_2

We devote more time to a deeper analysis of the disease-free equilibrium E_2 , as already done for the pure demographics model, in view of its relevance from the modeling viewpoint. Recall that the entries of the Jacobian matrix calculated at E_2 are denoted by b_{ij} , (36). The following result is in part based on Theorem 1.

Theorem 4. At the equilibrium E_2 the system has a saddle-node bifurcation for some $e_3 = e_3^t$. Taking as bifurcation parameter the disease incidence λ , it possesses a transcritical bifurcation at $\lambda = \lambda_t \equiv \frac{1}{s_2}(\delta + e_2 s_2 - e_1 s_2 - c_1)$, but neither saddle-node, nor pitch-fork, nor Hopf bifurcations can occur.

Proof. Recall that E_2 is actually a pair of equilibria, whose characteristic equation is

$$(\tau - b_{22}) [(\tau - b_{11})(\tau - b_{33}) - b_{13}b_{31}] = 0. \quad (43)$$

One of the eigenvalues of $J(E_2)$ vanishes for either $b_{22} = 0$ or $b_{11}b_{33} = b_{31}b_{13}$.

The latter equation is the same characteristic equation investigated in Theorem 1. The existence of e_3^t is proven here in the same way, with the obvious change of notation of $s_2(e_3)$, $p_2(e_3)$ in place of $\check{s}_2(e_3)$, $\check{p}_2(e_3)$.

For the calculation of the eigenvectors of $J(E_2)$ and $J(E_2)^T$ corresponding to the eigenvalue $\varsigma_1 = 0$, some minor dimensional changes occur. Namely, we find

$$\bar{U} = \left(-\frac{b_{13}\bar{\theta}_3}{b_{11}}, 0, \bar{\theta}_3 \right)^T, \quad \Upsilon = \left(-\frac{b_{31}\bar{h}_3}{b_{11}}, -\frac{b_{32}\bar{h}_3}{b_{22}} + \frac{b_{12}b_{31}\bar{h}_3}{b_{22}b_{11}}, \bar{h}_3 \right)^T$$

where again $\bar{\theta}_3$ and $\bar{h}_3$ stand for arbitrary constants. Also,

$$\frac{\partial F}{\partial e_3} \equiv F_{e_3}(X, e_3) = [0, 0, -p_2^2]^T.$$

Evaluating at e_3^t we have $F_{e_3}(E_2, e_3^t) = (0, 0, -p_2^2)^T$ and $\Upsilon^T[F_{e_3}(E_2, e_3^t)] = -\bar{h}_3 p_2^2 \neq 0$. Moreover $\Upsilon^T[D^2F(E_2, e_3^t)(\bar{U}, \bar{U})] \neq 0$, with $D^2F(E_2, e_3^t)$ now being a $3 \times 3 \times 3$ tensor. Using again Sotomayor's theorem, [32], Chapter 4, at least for one of the two equilibria E_2 the system is then seen to have a saddle-node bifurcation

But at the same time $\Upsilon^T[F_{e_3}(E_2, e_3^t)] = -\bar{h}_3 p_2^2 \neq 0$ forbids the system to attain transcritical or pitch-fork bifurcations.

The other case for which one eigenvalue vanishes is $b_{22} = 0$. Taking as bifurcation parameter the disease incidence, it gives the value $\lambda = \lambda_t \equiv \frac{1}{s_2}(\delta + e_2 s_2 - e_1 s_2 - c_1)$. The other two eigenvalues are

$$\varsigma_{\pm} = \frac{1}{2} \left[b_{33} + b_{11} \pm \sqrt{(b_{11} - b_{33})^2 + 4b_{31}b_{13}} \right].$$

The eigenvectors corresponding to the eigenvalue $\varsigma_1 = 0$ of $J(E_2)$ and $J(E_2)^T$ are respectively $\bar{U} = (0, \theta_1, 0)^T$ and $\bar{\Upsilon} = (0, \bar{h}_1, 0)^T$ where θ_1 and $\bar{h}_1$ represent nonzero constants. Moreover $\frac{\partial F}{\partial \lambda} \equiv F_{\lambda}(X, \lambda) = [-s_i, s_i, 0]^T$. Upon evaluation at λ_t we find $F_{\lambda}(E_2, \lambda_t) = (0, 0, 0)^T$ as well as $\bar{\Upsilon}^T[F_{\lambda}(E_2, \lambda_t)] = (0, \bar{h}_1, 0)(0, 0, 0)^T = 0$. Thus the system at E_2 does not have a saddle-node bifurcation in view once more of Sotomayor's theorem, [32], Chapter 4.

Again we find $\tilde{Y}^T[DF_\lambda(E_2, \lambda_t)\tilde{U}] = (0, \hbar_1, 0)(-s_2\theta_2, s_2\theta_2, 0)^T = \hbar_1 s_2 \theta_2 \neq 0$ as well as $\tilde{Y}^T[D^2F(E_2, \lambda_t)(\tilde{U}, \tilde{U})] \neq 0$, where $D^2F(E_2, \lambda_t)$ is a $3 \times 3 \times 3$ tensor. Thus by the same theorem the system possesses a transcritical bifurcation but no pitch-fork bifurcation.

Finally, since the characteristic equation (43) factors, no Hopf bifurcation arises, the proof follows as in Theorem 1.

4.5. Analysis of the Coexistence Equilibrium E_4

Here the Jacobian is a full matrix. Although the eigenvalues can be determined, their expressions are even more complicated than those found for the other equilibria. To analyse the local stability of this point, we follow a different approach and get a simple set of conditions.

Theorem 5. The solution of system (28) near the interior equilibrium E_4 is locally asymptotically stable if the following inequalities hold

$$\begin{aligned} \frac{a_2 i_4}{(1 + d_2(s_4 + i_4))^2} - e_1 s_4 - e_3 p_4 - \lambda i_4 - e_1 i_4 &< 0 \\ \lambda s_4 - \frac{a_2 s_4}{(1 + d_2(s_4 + i_4))^2} - e_2 s_4 - e_2 i_4 - e_3 p_4 &< 0 \\ e_1 + \lambda - e_2 &< 0. \end{aligned} \quad (44)$$

Conversely, E_4 will be unstable if

$$e_1 + \lambda - e_2 > 0. \quad (45)$$

Proof. To show the first claim on the asymptotic stability of the equilibrium E_4 , we use the method of first approximation. Consider the diagonal matrix $D = \text{diag}(p_4, i_4, s_4)$. The second computed matrix, [28], is

$$J^{[2]}(E_4) = [\bar{b}_{ij}] \equiv \begin{bmatrix} \bar{b}_{11} & J_{23}(E_4) & -J_{13}(E_4) \\ J_{32}(E_4) & \bar{b}_{22} & J_{12}(E_4) \\ -J_{31}(E_4) & J_{21}(E_4) & \bar{b}_{33} \end{bmatrix}.$$

It has the negative diagonal elements, $\bar{b}_{11} = J_{11}(E_4) + J_{22}(E_4) = -(e_1 s_4 + e_2 i_4) < 0$, $\bar{b}_{22} = J_{11}(E_4) + J_{33}(E_4) = -(e_1 s_4 + e_3 p_4) < 0$, $\bar{b}_{33} = J_{22}(E_4) + J_{33}(E_4) = -(e_2 i_4 + e_3 p_4) < 0$. The matrix $J^{[2]}(E_4)$ is similar to $A \equiv DJ^{[2]}(E_4)D^{-1} = (a_{ij})$, with elements

$$\begin{aligned} a_{11} &= \bar{b}_{11}, & a_{12} &= \bar{b}_{12} \frac{p_4}{i_4}, & a_{13} &= \bar{b}_{13} \frac{p_4}{s_4}, \\ a_{21} &= \bar{b}_{21} \frac{i_4}{p_4}, & a_{22} &= \bar{b}_{22}, & a_{23} &= \bar{b}_{23} \frac{i_4}{s_4}, \\ a_{31} &= \bar{b}_{31} \frac{s_4}{p_4}, & a_{32} &= \bar{b}_{32} \frac{s_4}{i_4}, & a_{33} &= \bar{b}_{33}. \end{aligned}$$

Then the matrix $J^{[2]}(E_4)$ is stable if and only if A is stable. Since the diagonal elements of the matrix A are negative, by Gershgorin's theorem it is stable if it is diagonally dominant

in rows. Set

$$\begin{aligned} g_1 &= a_{11} + a_{12} + a_{13} = -(e_1 s_4 + e_2 i_4), \\ g_2 &= a_{21} + a_{22} + a_{23} = \frac{a_2 i_4}{(1 + d_2 (s_4 + i_4))^2} - e_1 s_4 - e_3 p_4 - \lambda i_4 - e_1 i_4, \\ g_3 &= a_{31} + a_{32} + a_{33} = -\frac{a_2 s_4}{(1 + d_2 (s_4 + i_4))^2} + \lambda s_4 - e_2 s_4 - e_2 i_4 - e_3 p_4, \end{aligned}$$

and $\mu^* = \max\{g_1, g_2, g_3\}$. Easily, when the first two conditions (44) are met, then $\mu^* < 0$, implying diagonal dominance. Also note that $\det J_4 = p_4 i_4 s_4 e_3 \lambda (e_1 + \lambda - e_2)$ and in view of the last assumption (44) then $\det J(E_4) < 0$.

The same calculation shows $\det J(E_4) > 0$ if (45) holds, completing the proof.

4.6. Other Ecoepidemic Model Variants

4.6.1. Facultative Mutualism

The formerly found equilibria E_0, E_1, E_2 are found also in this case, $c_1, c_2 < 0$, essentially with the same feasibility analysis. For E_3 however, p_3 becomes here inconditionally feasible, and we have also $\tilde{A} < 0$, so that some of the feasibility conditions (29) disappear. Further, the origin becomes unstable, as two of the eigenvalues (32) are now positive. The other stability results hold, provided the change in sign of c_1, c_2 is taken into account. In this model however there are more equilibria to be considered, namely the boundary points $E_1^a(s_1^a, 0, 0)$ and $E_2^a(0, 0, p_2^a)$. Here

$$s_1^a \equiv s_1^{*a} = -\frac{c_1}{e_1}, \quad p_2^a \equiv -\frac{c_2}{e_3}.$$

For the former, the eigenvalues are given by

$$c_1, \quad \frac{c_1 e_2 - c_1 \lambda - e_1 \delta}{e_1}, \quad \frac{a_2 c_1 + c_2 e_1 - c_1 c_2 d_2}{c_1 d_2 - e_1}$$

and for the latter, they are instead

$$c_2, \quad \frac{c_1 e_3 - c_1 c_2 d_1 + a_1 c_2}{c_2 d_1 - e_3}, \quad \frac{a_1 c_2 + e_3 \delta - c_2 d_1 \delta}{c_2 d_1 - e_3}.$$

But both equilibria are easily seen to be inconditionally unstable, since the last eigenvalue of E_1^a is positive, as $c_1 d_2 - e_1 < 0$ and $a_2 c_1 + c_2 e_1 - c_1 c_2 d_2 < 0$, while for E_2^a conversely it is the second eigenvalue to be positive, since here $c_1 e_3 - c_1 c_2 d_1 + a_1 c_2 < 0$, $c_2 d_1 - e_3 < 0$.

4.6.2. Other Variants

We can consider also the mixed cases in which the association is necessary for survival for one population, while for the other one it is not. The points E_1^a and E_2^a of the purely demographic classical symbiotic model will reappear here in the three dimensional phase space also as new disease-free equilibria, feasible as found in Section 2.3., with respective stability conditions (21) and (27) for E_1^a , while for E_2^a (20) and

$$a_1 c_2 > \delta(c_2 d_1 - e_3). \quad (46)$$

All other equilibria but the origin in these cases retain feasibility and stability conditions, as derived for the original ecoepidemic model, which lead always to conditional feasibility and local asymptotic stability. The origin instead is always unstable.

4.6.3. Absence of Susceptible Population

We now consider a particular case, in which the epidemics-affected species is completely overwhelmed by the disease, so that sound individuals are completely absent. The model (28) with $s = 0$ becomes

$$\frac{di}{dt} = \frac{a_1 i p}{1 + d_1 p} - e_2 i^2 - \delta i, \quad \frac{dp}{dt} = -c_2 p + \frac{a_2 i p}{1 + d_2 i} - e_3 p^2. \quad (47)$$

The equilibria are $\hat{E}_0 = (0, 0)$ and $\hat{E}_3 = (\hat{i}_3, \hat{p}_3) \equiv (i_3, p_3)$. In this case the eigenvalues of the Jacobian at the origin are $-\delta, -c_2$ showing its stability for obligate mutualism and instability when instead it is facultative. At $\hat{E}_3$, the Jacobian matrix $\hat{J}$ is a submatrix of $J(E_3)$, and does not have the eigenvalue (40). The stability conditions then reduce just to (41) and sufficient ones are given by (42).

For the case $c_2 < 0$, as mentioned the origin becomes unstable, and the above system attains also the extra equilibrium

$$\hat{E}_2^a = (0, \hat{p}_2^a) = \left(0, -\frac{c_2}{e_3}\right).$$

The eigenvalues are easily calculated from a triangular Jacobian,

$$\frac{a_1 c_2 + e_3 \delta - \delta d_1 c_2}{-e_3 + d_1 c_2}, \quad c_2, \quad (48)$$

so that stability follows when the former is negative, i.e. if (46) holds

We now consider a further special situation in which the diseased species is entirely infected, and these individuals are so weak so as not to constitute an appreciable population pressure for their similars. This corresponds to taking $s = 0$ and $e_2 = 0$ in (28), or simply setting $e_2 = 0$ in (47) to model this low intraspecific competition. The equilibria are once again $\tilde{E}_0(0, 0)$ and $\tilde{E}_3 = (\tilde{i}_3, \tilde{p}_3)$, but now since $\tilde{A} = 0$,

$$i_3 = -\frac{\tilde{C}}{\tilde{B}},$$

with feasibility condition

$$\tilde{B}\tilde{C} < 0. \quad (49)$$

The origin has the same stability conditions as for (47). $\tilde{E}_3$ is instead always unstable since the Jacobian at this point is

$$\tilde{J}(E_3) = \begin{bmatrix} 0 & \frac{a_1 \tilde{i}_3}{(1 + d_1 \tilde{p}_3)^2} \\ \frac{a_2 \tilde{p}_3}{(1 + d_2 \tilde{i}_3)^2} & -e_3 \tilde{p}_3 \end{bmatrix}$$

so that $\text{tr}(\tilde{J}_3) < 0$ and $\det(\tilde{J}_3) < 0$. For obligate mutualism, $c_2 < 0$, again the extra equilibrium $\tilde{E}_2^a \equiv \hat{E}_2^a$ arises, with the same stability conditions (46).

In these cases Theorem 2 gets modified as follows.

Theorem 6. For $c_2 > 0$ the origin is always globally asymptotically stable.

Proof. In fact, for $s = 0$, $e_2 > 0$, take the time derivative along trajectories of the function $\tilde{\Psi}_\beta = i + p$. The proof follows the one of Theorem 2, but we should exercise some care in deriving the estimate for $\tilde{\Psi}_\beta$. The upper bound indeed in this case is obtained as follows

$$\begin{aligned} \frac{d\tilde{\Psi}_\beta}{dt} &= \frac{a_1 ip}{1 + d_1 p} - e_2 i^2 - \delta i - c_2 p + \frac{a_2 ip}{1 + d_2 i} - e_3 p^2 \\ &\leq \left(\frac{a_1}{d_1} - \delta\right)i - e_2 i^2 + \left(\frac{a_2}{d_2} - c_2\right)p - e_3 p^2 \leq \frac{(a_1 - d_1 \delta)^2}{4e_2 d_1^2} + \frac{(a_2 - d_2 c - 2)^2}{4e_3 d_2^2} = \tilde{\rho} \end{aligned}$$

If instead also $e_2 = 0$, in case $a_1 \leq d_1 \delta$ the first term in the second row of the above estimate can be dropped, as it is nonpositive, and the proof still holds. Should we however have $a_1 > d_1 \delta$, consider

$$\begin{aligned} \frac{d\tilde{\Psi}_\beta}{dt} &\leq (1 + d_2 i) \left[\frac{a_1}{d_1} - \delta - e_2 i \right] i + \left(\frac{a_2}{d_2} - c_2 - e_3 p \right) p \\ &\leq \frac{(a_1 - d_1 \delta)^2}{4d_1^2 e_2} + d_2 i^2 \left[\frac{a_1}{d_1} - \delta - e_2 i \right] + \frac{(a_2 - d_2 c_2)^2}{4d_2^2 e_3} \end{aligned}$$

where the first and third terms are then estimated as in Theorem 2. The last quantity left is the middle term, which is actually the function $g(x) = x^2(A - x)$ having the maximum value $g_{\max} = \frac{4}{27}A^3$ at $x = \frac{2}{3}A$, so that

$$d_2 i^2 \left[\frac{a_1}{d_1} - \delta - e_2 i \right] \leq \frac{4}{27} d_2 \frac{(a_1 - d_1 \delta)^3}{d_1^3 e_2^2}$$

Substituting into the previous estimate, the upper bound $\tilde{\rho}$ can then be determined in this case as well.

We summarize in Table 3 the equilibria of the ecoepidemic model and in Table 4 the ones of particular cases.

5. Analysis of the System Dynamics

Boundedness of the system trajectories has been established for the system for which cooperation is essential for survival. Thus the dynamical behavior is confined to a compact set “sufficiently near” the origin. In view of this result, we perform numerical experiments to ascertain further possible interesting behaviors of the model. We have then run some computer simulations on hypothetical parameter values, to establish also pictorially some of the previous results. Each one of the Figures 1-5 shows that with suitable parameter combinations, the ecoepidemic system (28) settles down to each one of the equilibria E_0 ,

Table 3. Equilibria of the ecoepidemic model (28)

Equilibrium	Feasibility	Stability conditions	Bifurcations conditions
Case $c_1, c_2 > 0$			
O		$\begin{cases} LAS \\ GAS \text{ if (33)} \end{cases}$	
$E_1 \equiv E_1^* \equiv (s_1, i_1, 0)$	infeasible		
$E_2 \equiv \check{E}_2 \equiv (s_2, 0, p_2)$	(6), (8)	$\begin{cases} (11), (38) \\ \text{sufficient: (12)} \end{cases}$	$\begin{cases} \text{saddle-node at } e_3^t \\ \text{transcritical at } \lambda_t \end{cases}$
$E_3 \equiv (0, i_3, p_3)$	(29), (30)	$\begin{cases} (40), (41) \\ \text{sufficient: (42)} \end{cases}$	
E_4	conditional	sufficient: (44)	
Case $c_1, c_2 < 0$			
O		unstable	
$E_1 \equiv E_1^* \equiv (s_1, i_1, 0)$	(24)	(35)	
$E_2 \equiv \check{E}_2 \equiv (s_2, 0, p_2)$	(7), (9)	$\begin{cases} (11), (38) \\ \text{sufficient: (12)} \end{cases}$	$\begin{cases} \text{saddle-node at } e_3^t \\ \text{transcritical at } \lambda_t \end{cases}$
$E_3 \equiv (0, i_3, p_3)$	(29)	$\begin{cases} (40), (41) \\ \text{sufficient: (42)} \end{cases}$	
E_4	conditional	sufficient: (44)	
$E_1^a \equiv (-\frac{c_1}{e_1}, 0, 0)$		unstable	
$E_2^a \equiv (0, 0, -\frac{c_2}{e_3})$		unstable	
Case $c_2 \leq 0 < c_1$			
O		unstable	
$E_1 \equiv E_1^* \equiv (s_1, i_1, 0)$	infeasible		
$E_2 \equiv \check{E}_2 \equiv (s_2, 0, p_2)$	(19), (8)	$\begin{cases} (11), (38) \\ \text{sufficient: (12)} \end{cases}$	$\begin{cases} \text{saddle-node at } e_3^t \\ \text{transcritical at } \lambda_t \end{cases}$
$E_3 \equiv (0, i_3, p_3)$	(29)	$\begin{cases} (40), (41) \\ \text{sufficient: (42)} \end{cases}$	
E_4	conditional	sufficient: (44)	
$E_1^a \equiv (-\frac{c_1}{e_1}, 0, 0)$	infeasible		
$E_2^a \equiv (0, 0, -\frac{c_2}{e_3})$		(20), (46)	
Case $c_1 \leq 0 < c_2$			
O		unstable	
$E_1 \equiv E_1^* \equiv (s_1, i_1, 0)$	(24)	(35)	
$E_2 \equiv \check{E}_2 \equiv (s_2, 0, p_2)$	(6), (8)	$\begin{cases} (11), (38) \\ \text{sufficient: (12)} \end{cases}$	$\begin{cases} \text{saddle-node at } e_3^t \\ \text{transcritical at } \lambda_t \end{cases}$
$E_3 \equiv (0, i_3, p_3)$	(29), (30)	$\begin{cases} (40), (41) \\ \text{sufficient: (42)} \end{cases}$	
E_4	conditional	sufficient: (44)	
$E_1^a \equiv (-\frac{c_1}{e_1}, 0, 0)$		(21), (27)	
$E_2^a \equiv (0, 0, -\frac{c_2}{e_3})$	infeasible		

Table 4. Equilibria of the special ecoepidemic model (47)

Case	Equilibrium	Feasibility conditions	Stability conditions
$s = 0$ $c_2 > 0$	$\hat{O}$ $\hat{E}_3 \equiv (i_3, p_3)$	(29), (30)	GAS (41) sufficient: (42)
$s = 0$ $c_2 < 0$	$\hat{O}$ $\hat{E}_3 \equiv (i_3, p_3)$ $\hat{E}_2^a \equiv (0, \hat{p}_2^a)$	(29)	unstable (41) sufficient: (42) (46)
$s = 0$ $e_2 = 0$ $c_2 > 0$	$\tilde{O}$ $\tilde{E}_3 \equiv (i_3, p_3)$	(49), (30)	GAS unstable
$s = 0$ $e_2 = 0$ $c_2 < 0$	$\tilde{O}$ $\tilde{E}_3 \equiv (i_3, p_3)$ $\tilde{E}_2^a \equiv (0, \hat{p}_2^a)$	(49)	unstable unstable (46)

E_1 (for $c_1 < 0$), E_2 , E_3 and E_4 . The illustrations in Figures 1-5, contain both the solutions as function of time as well as either the three dimensional phase space plots or the pictures of the projection onto the phase plane of sound individuals of the affected species versus the disease unaffected population. Since these are projections of a three dimensional phase space onto a bidimensional subspace, trajectories can and indeed do intersect. Since we have been less able to draw theoretical conclusions on the coexistence equilibrium, we performed a deeper numerical investigation on it, namely we have tried to destabilize E_4 by acting on various parameters of the model, in search of possible bifurcations. Although our experience is certainly not exhaustive, we ran enough simulations to have at least some partial conclusions. With these perturbations we observed only changes in the system trajectories leading to each of the other system's equilibria.

If we compare the underlying demographic system with the ecoepidemic model, we find that the origin behaves in the same way, since $\tilde{E}_0$ and E_0 are equivalent. In fact the origin behaves similarly in all the models we have considered, since for $c_1 > 0$ or $c_2 > 0$ at least for one population, it is always unstable, compare E_0 , $\tilde{E}_0$, $\hat{E}_0$, $\tilde{\tilde{E}}_0$ and E_0^* . All these

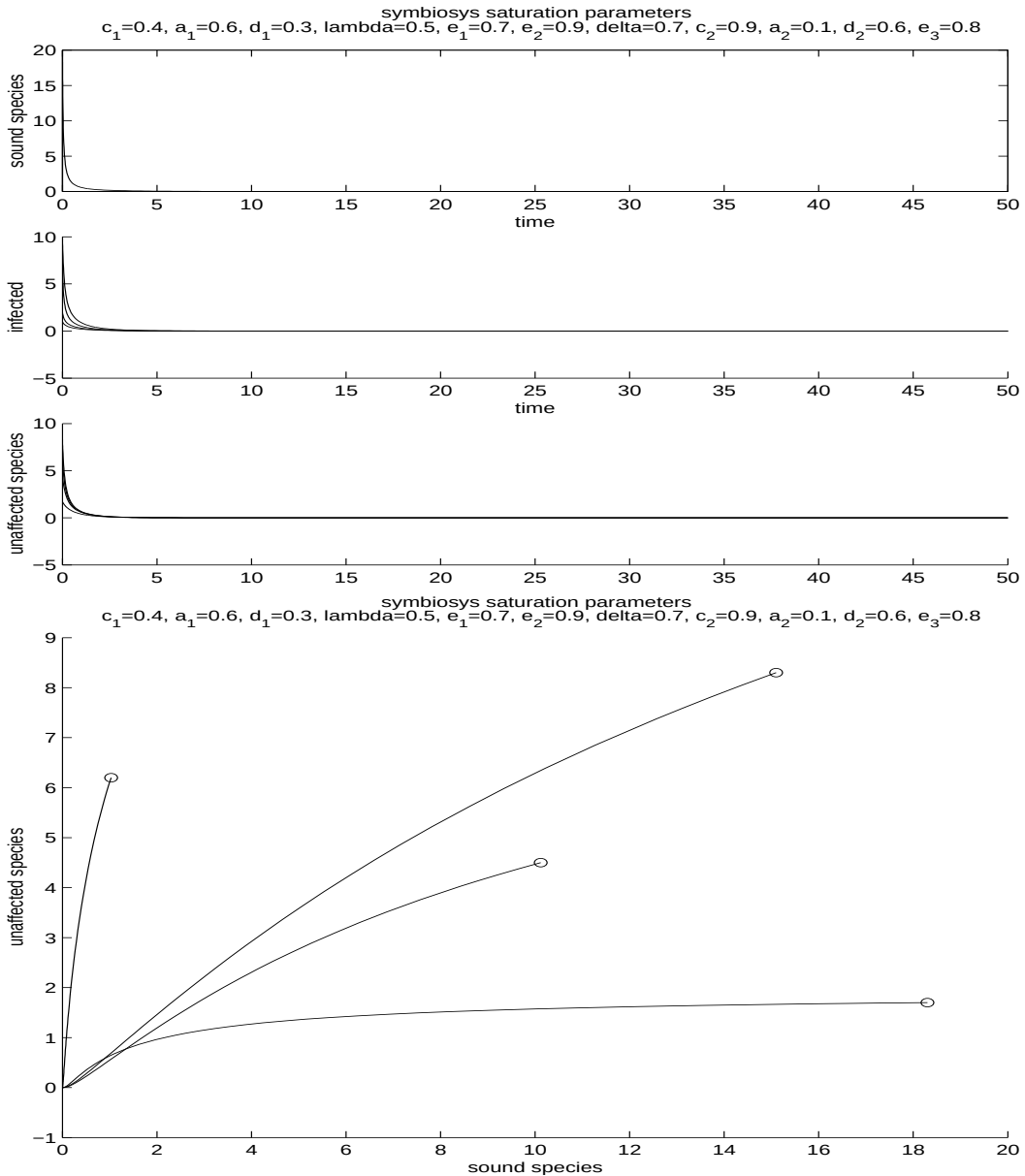


Figure 1. System (28) tends to equilibrium E_0 for the parameter values: $c_1 = 0.4, a_1 = 0.6, d_1 = 0.3, \lambda = 0.5, e_1 = 0.7, e_2 = 0.9, \delta = 0.7, c_2 = 0.9, a_2 = 0.1, d_2 = 0.6, e_3 = 0.8$. The bottom picture shows the sp phase plane projection. Initial conditions are represented by circles.

equilibria become instead stable when symbiosis is essential for survival of the ecosystem, $c_1, c_2 < 0$. Thus in this case of obligate mutualism, the introduction of a disease in either species cannot save the species from their local and global extinction, if the demographic ecosystem is already driven to extinction.

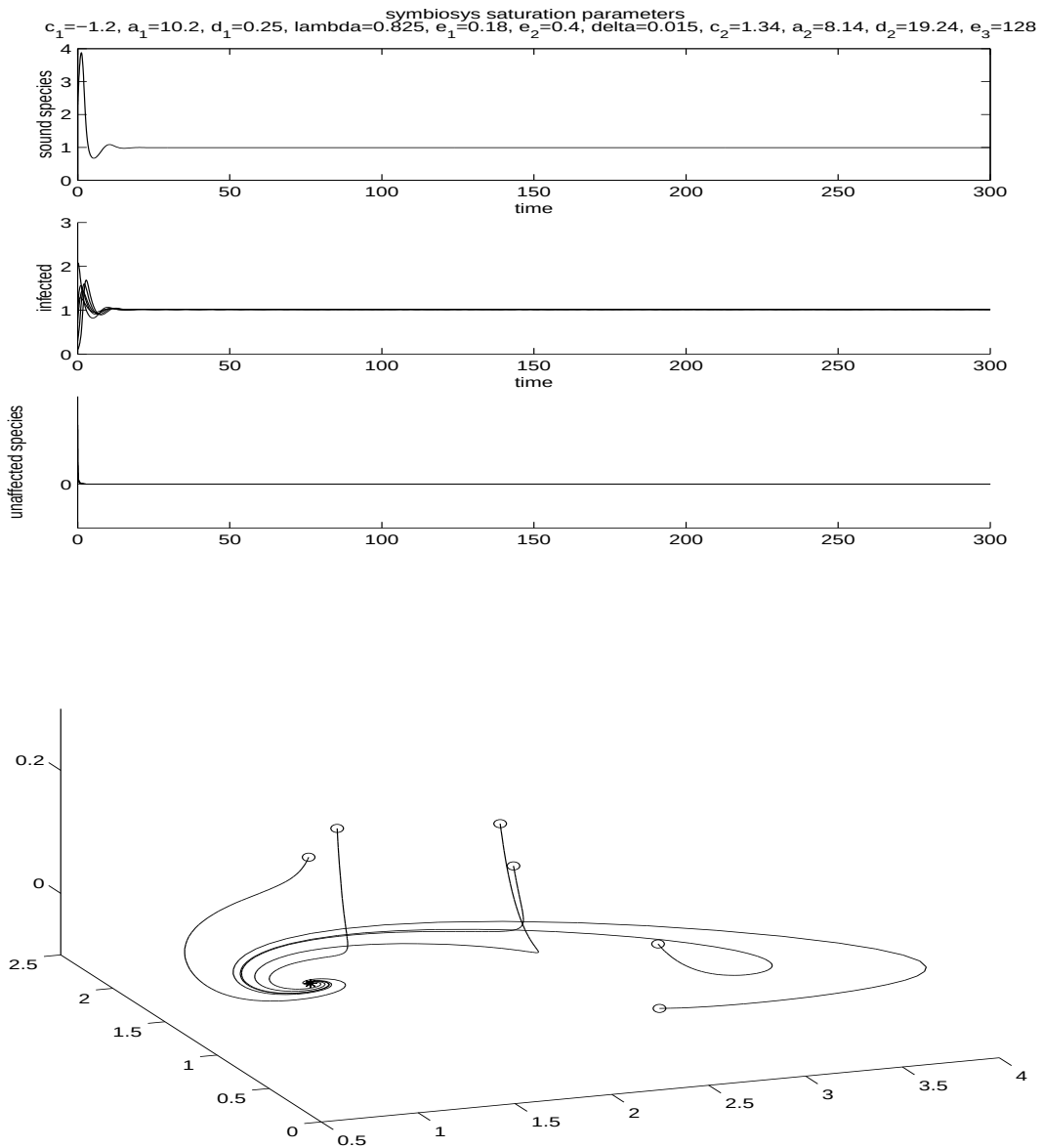


Figure 2. System (28) tends to equilibrium E_1 for the parameter values: $c_1 = -1.2$, $a_1 = 10.2$, $d_1 = 0.25$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.015$, $c_2 = 1.34$, $a_2 = 8.14$, $d_2 = 19.24$, $e_3 = 128$, $\lambda = 0.825$. The bottom pictures shows the three dimensional phase space. Initial conditions are represented by circles.

Further, note that $\check{E}_2$ is independent of the incidence parameter λ , and coincides with E_2 . The eigenvalues of the former are thus also eigenvalues of the latter, which however has a third one (38), depending on λ . By taking the incidence high enough then, it is possible to destabilize E_2 , while maintaining $\check{E}_2$ stable. Indeed above the critical threshold value λ_t the

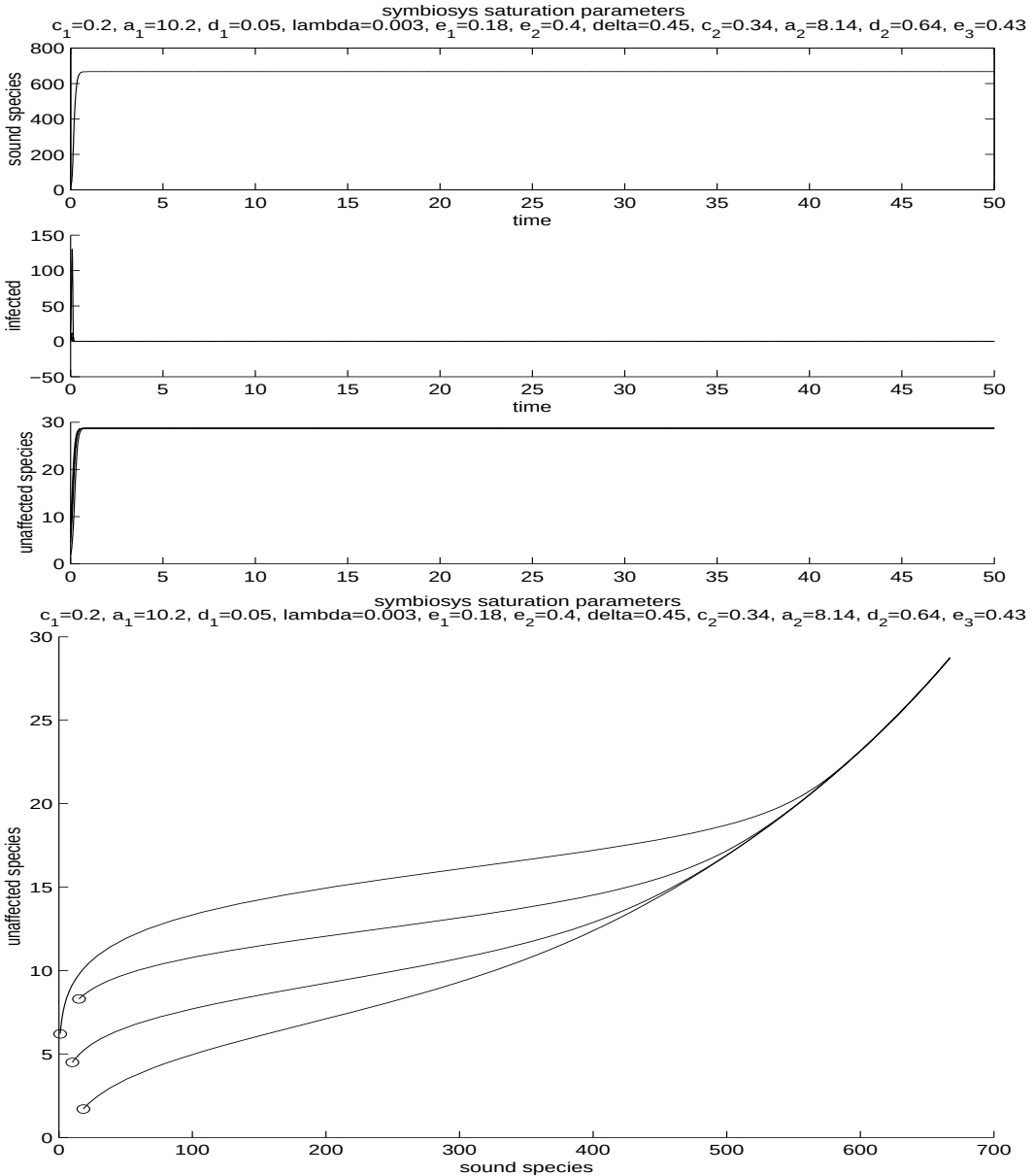


Figure 3. System (28) tends to equilibrium E_2 for the parameter values: $c_1 = 0.2$, $a_1 = 10.2$, $d_1 = 0.05$, $\lambda = 0.003$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.45$, $c_2 = 0.34$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.43$. The bottom picture shows the sp phase plane projection. Initial conditions are represented by circles.

infection-free equilibrium E_2 cannot be kept stable and the disease becomes endemic, while the model without the disease would remain at the level specified by $\tilde{E}_2$. This result holds independently of the fact that species association is necessary for their survival, $c_1, c_2 > 0$, or not $c_1, c_2 < 0$, or only in part $c_1 < 0 < c_2$, $c_2 < 0 < c_1$. For the ecoepidemic

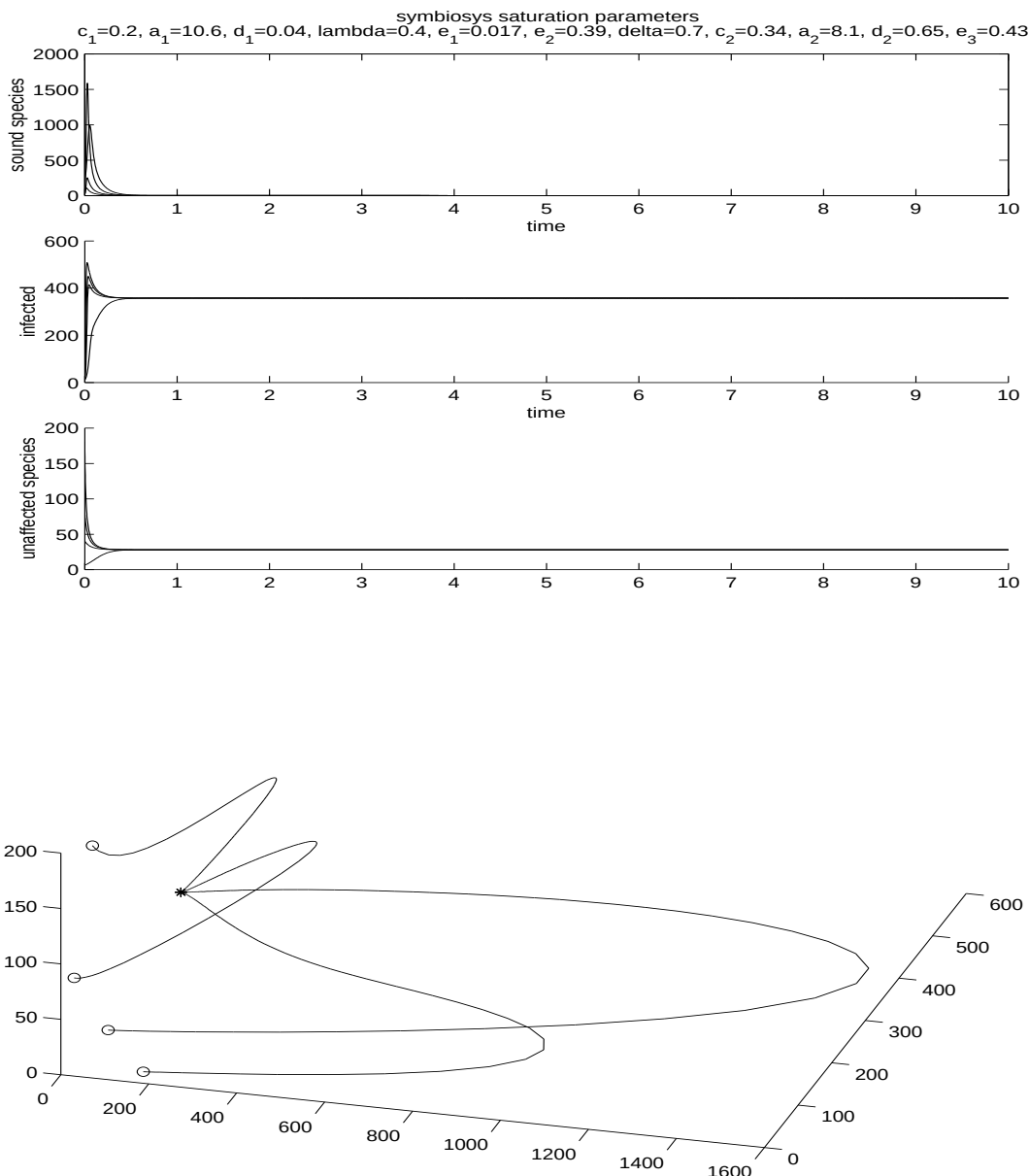


Figure 4. System (28) tends to equilibrium E_3 for the parameter values: $c_1 = 0.2$, $a_1 = 10.6$, $d_1 = 0.04$, $e_1 = 0.017$, $e_2 = 0.39$, $\delta = 0.7$, $c_2 = 0.34$, $a_2 = 8.1$, $d_2 = 0.65$, $e_3 = 0.43$, $\lambda = 0.4$. The bottom picture shows the three dimensional phase space. Initial conditions are represented by circles.

model a transcritical bifurcation at E_2 occurs, when the incidence of the disease crosses the value $\lambda = \lambda_t$, Figure 14. This does not happen for the underlying demographic system. In Figure 15 we plot the sp phase plane just below and above the critical value λ_t to show the radically different behavior of the system's trajectories. Also at $\check{E}_2$ as well at E_2 a saddle-

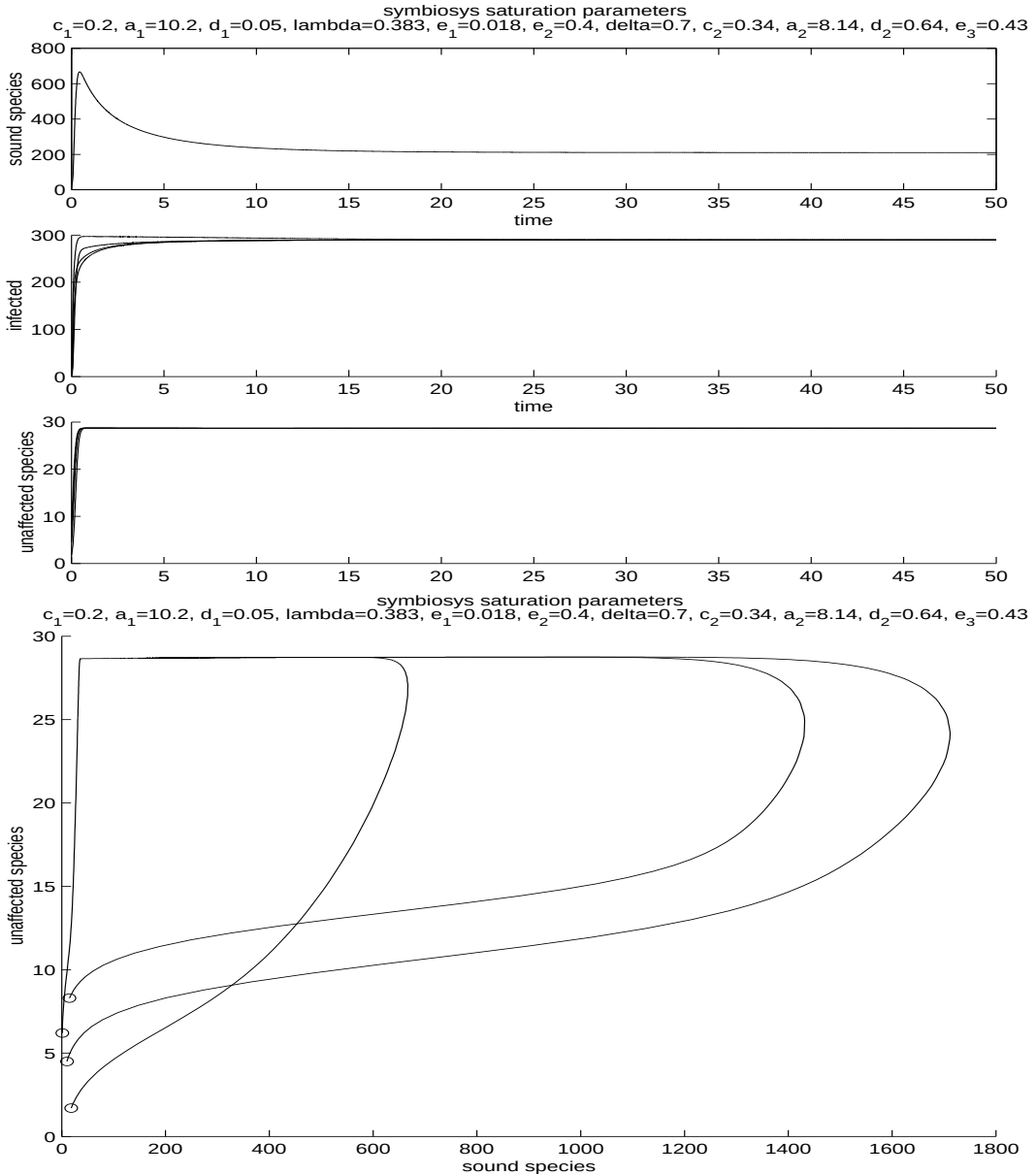


Figure 5. System (28) tends to equilibrium E_4 for the parameter values: $c_1 = 0.2$, $a_1 = 10.2$, $d_1 = 0.05$, $\lambda = 0.383$, $e_1 = 0.018$, $e_2 = 0.4$, $\delta = 0.7$, $c_2 = 0.34$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.43$. The bottom picture shows the sp phase plane projection. Initial conditions are represented by circles.

node bifurcation occurs, see Figure 16. Again in Figures 17 and 18 we plot the system's trajectories in the 3 dimensional phase space, as well as their projections onto the sp phase subspace, below and above the critical value e_3^t . Below e_3^t the system has two coexisting equilibria, the origin and E_2 . There is also the unstable double of E_2 , which has the effect

of partitioning the phase space, so that some trajectories originating in one of these subsets tend to the origin, while some others to E_2 , see Figure 17. However, above e_3^t the two equilibria E_2 have coalesced and disappeared, so that all the system's trajectories now tend to the origin, see Figure 18.

In the case of the disease-subject species being entirely infected and the system thriving also in absence of cooperation ($c_2 < 0$), the disease-free equilibrium $\hat{E}_2^a$ is conditionally stable. Since disease incidence in this condition plays no role, it is rather mainly the disease-related mortality that determines the stability, see the condition (46). However, note that in view of the assumptions, $\hat{E}_2^a$ is desirable only if one wants to get rid of the epidemics, or of the affected species, since here only the unaffected population survives. If the aim is to preserve the ecosystem, $\hat{E}_2^a$ should rather be avoided. This can be obtained with a very low disease related mortality of the affected species δ . A similar situation occurs when the infected are so weak so as not to be able to experience intraspecific competition, namely for $e_2 = 0$. Indeed the equilibrium $\tilde{E}_2^a$ is stable again in the same conditions as for $\hat{E}_2^a$.

At equilibrium E_3 the sound symbiotic species is eliminated from the system, and if for a large enough disease-related mortality condition (40) fails, while still maintaining (41) true, then E_3 becomes unstable while $\hat{E}_3$ with its very same other eigenvalues remains still stable. Conversely destabilizing $\hat{E}_3$ makes also E_3 unstable.

In the basic epidemic model the disease-free equilibrium E_1^{a*} can be attained, for the model in which association is not essential for the system's thriving ($c_1 < 0$), since it is conditionally stable. But the corresponding ecoepidemic equilibrium E_1^a instead is always unstable, i.e. the introduction of the second healthy symbiotic species may not allow disease eradication, with the second population vanishing. Rather, the equilibrium moves toward coexistence among the two healthy species, E_2 , but the latter remains stable only for a low enough value of the disease incidence $\lambda < \lambda_t$. Note also that the stability requirement for E_1^{a*} needs an upper bound on the disease incidence, namely $\lambda < \lambda_1^a \equiv e_2 - \frac{1}{c_1}e_1\delta$. If the disease has a large enough contact rate, in the pure epidemic model the infected cannot be wiped out, so that the disease becomes endemic. Since λ_t is given in terms of s_2 an explicit direct algebraic comparison between the two threshold values λ_t and λ_1^a is in general very difficult or not at all possible. But it is likely that these are different, so that by changes in the contact rate λ one of the two equilibria can be destabilized, while the other one may still remain stable. This again supports the claim that the disease in an ecosystem plays a relevant role.

For $c_1 < 0$, on comparing $\tilde{E}_1^a$ in the purely demographic model, in which only one species survives, the one that possibly can be disease-affected, with the ecoepidemic equilibrium E_1 , in which the same situation occurs, but where the surviving species hosts sound and infected individuals as well, we observe that the former is always unstable, for $c_2 < 0$ or conditionally stable for $c_2 > 0$, (21). The latter instead is conditionally feasible (24) and conditionally stable (35). In the latter, parameters related to the symbiotic population appear. Therefore the symbiotic population affects the outcome of the epidemics. For the pure epidemic model when $c_1 < 0$, E_1^* is conditionally feasible (24) for a high enough contact rate, and stable, while for the ecoepidemic system E_1 has once more the extra eigenvalue depending on parameters related to the symbiotic population. Thus E_1 could be destabilized while E_1^* remains stable, again showing the effects of the mutualistic partner species.

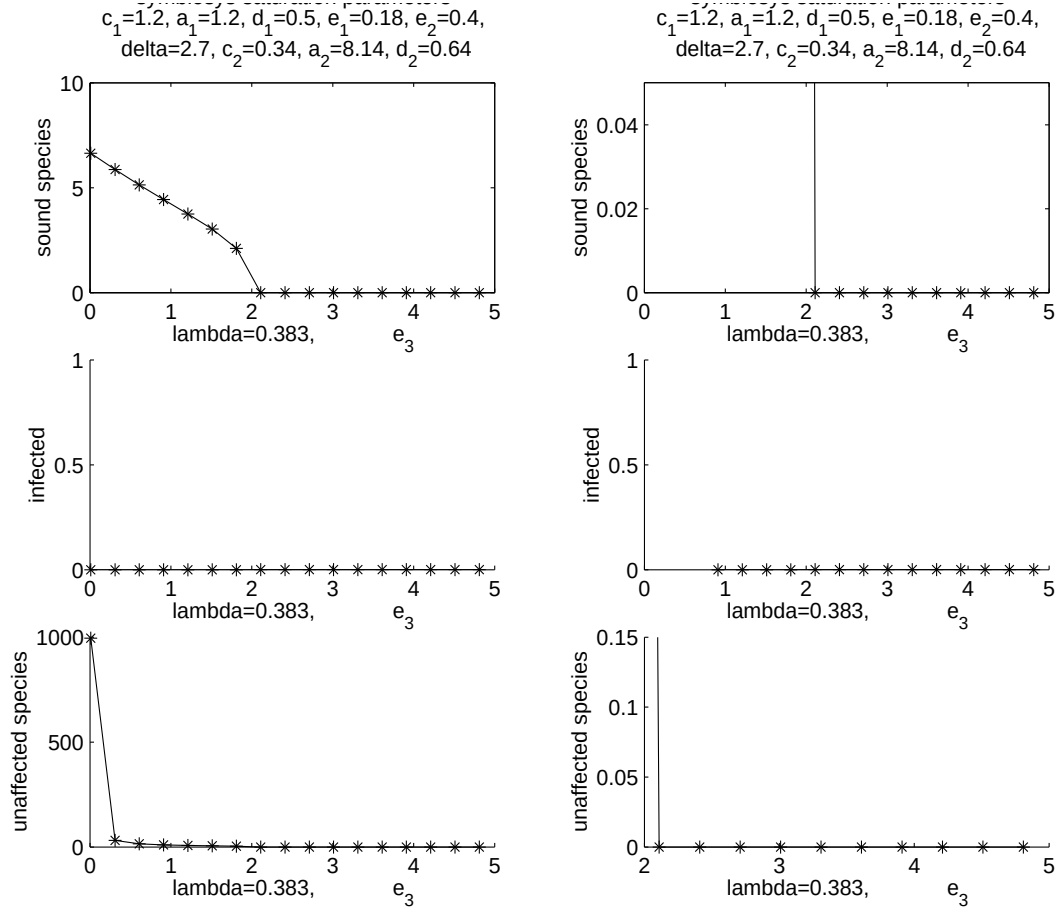


Figure 6. Location of equilibria of (28) as function of the parameter e_3 , for $c_1 = 1.2$, $c_2 = 0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $\lambda = 0.383$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 2.7$, $a_2 = 8.14$, $d_2 = 0.64$. The equilibrium E_2 moves at first toward very low values of the p population, then as shown on the blow up on the right for $e_3 = 1.9$ the system collapses, much earlier than stated by condition (33) which gives the value $e_3 = 121.1606$ as threshold for global asymptotical stability of the origin.

6. Some Ecologic Consequences

Natural systems are in general thought to be finite, in the sense that their growth cannot be beyond bounds, in view of the limited amount of resources available. Thus their mathematical models should mimick this property. Our rigorous result, Theorem 2, shows that this is indeed the case and therefore model (28) is a good starting point for investigations.

Two questions that can be asked are whether in a diseased population the epidemics can be fought by introducing a symbiotic species, for which mutualism however must not be obligate, as we will better see below, and what effects a disease has on symbiotic species. More specifically, we may ask whether a disease can be eradicated from a population using a mutualistic species, and whether it is possible to eradicate an obnoxious pest by a disease,

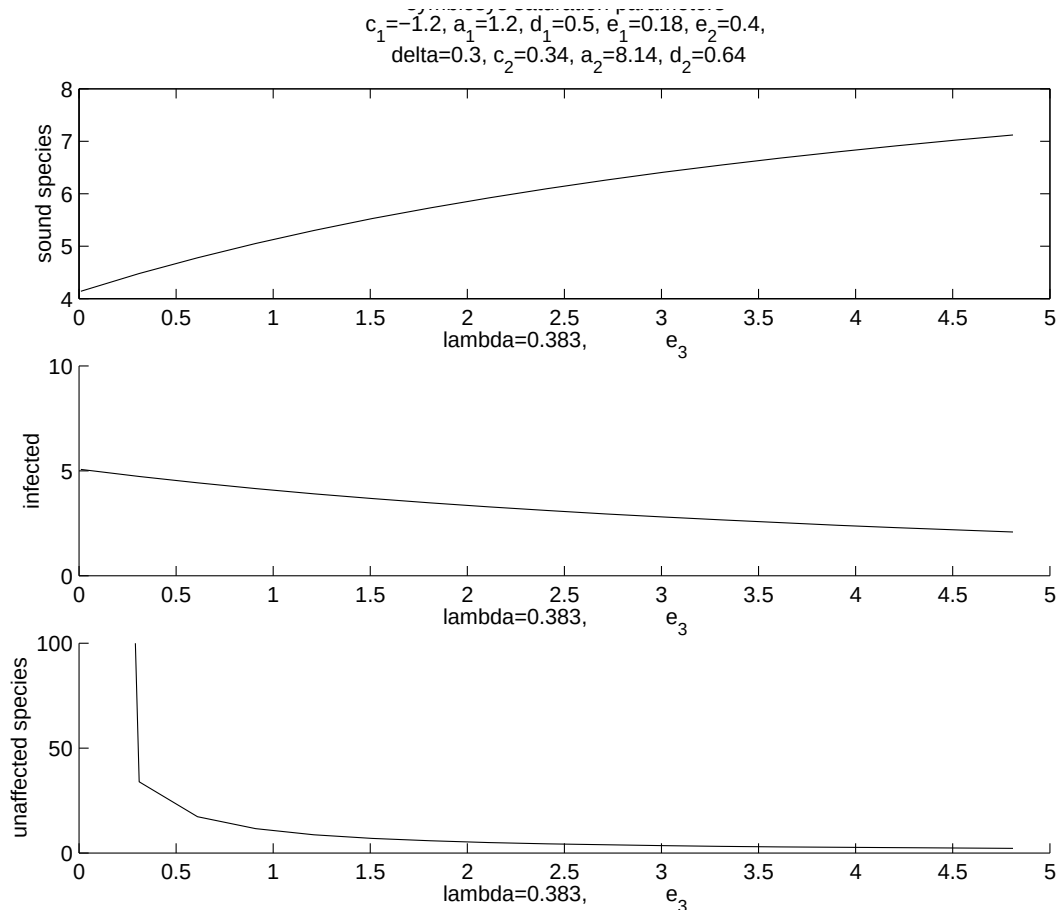


Figure 7. Location of equilibria of (28) as function of the parameter e_3 , for $c_1 = -1.2$, $c_2 = 0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $\lambda = 0.383$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.3$, $a_2 = 8.14$, $d_2 = 0.64$. The point E_3 moves but remains the only equilibrium of the system.

without endangering its symbiotic partner.

Let us start from an endemic disease in a population. In case $c_1 > 0$, the epidemic model states that the diseased population will be wiped out. If we introduce a symbiotic species to rescue it, for which mutualism is facultative, $c_2 > 0$, if the former is already reduced to a few units then the ecosystem will be wiped out anyway. But if for the second species mutualism is obligate, $c_2 < 0$ the origin becomes an unstable equilibrium and therefore also the first species will be saved from extinction. In case model (22) is instead at equilibrium E_1^* , when $c_1 < 0$, the introduction of the symbiotic species results useless if the net reproduction rate of the new species c_2 is “large enough” so as to satisfy (35), equilibrium E_1 will remain stable, i.e. the first species will thrive, with an endemic disease, and the newly introduced one will disappear. The result seems to be somewhat counterintuitive, but we should recall that the parameters describing the return for the second species

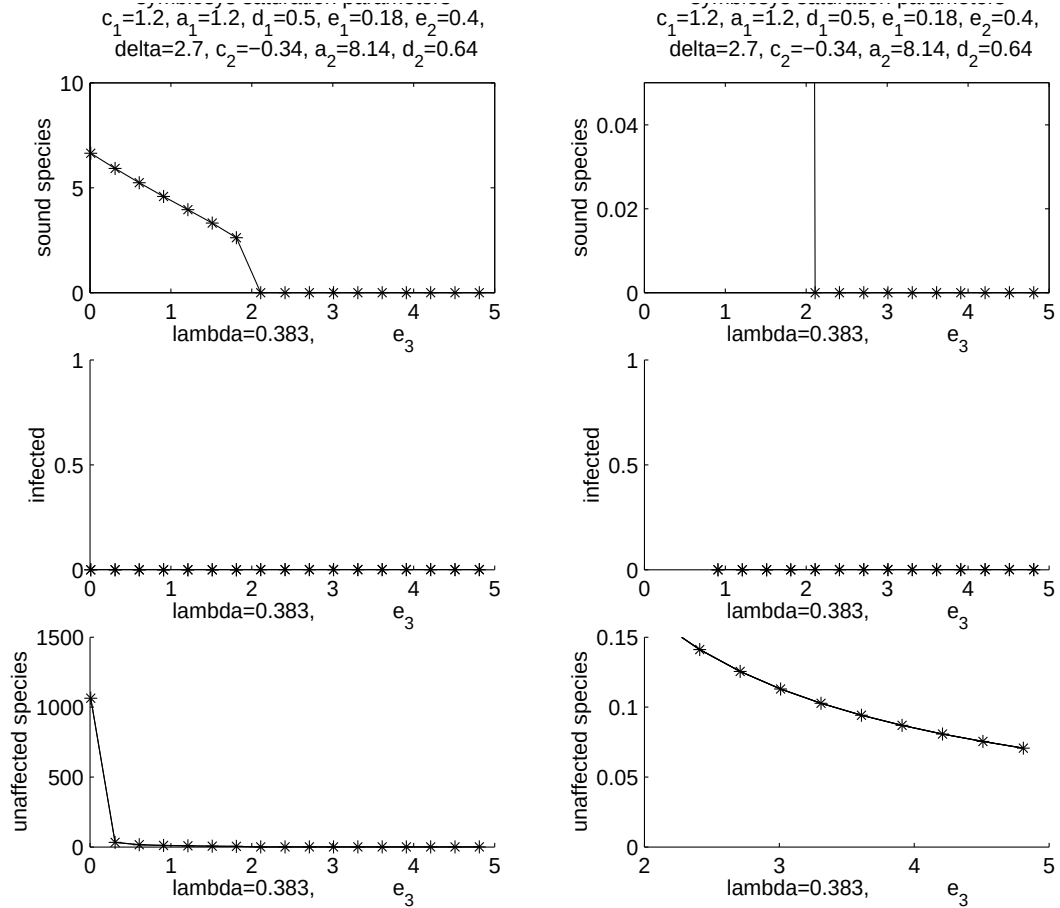


Figure 8. Location of equilibria of (28) as function of the parameter e_3 , for $c_1 = 1.2$, $c_2 = -0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $\lambda = 0.383$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 2.7$, $a_2 = 8.14$, $d_2 = 0.64$. The equilibrium E_2 moves toward E_2^a and merges into it about the value $e_3 = 2.2$. The blow up on the right shows that the p population is not vanishing like the other ones.

also play a role, a_2 large and d_2 small will indeed favor the violation of condition (35) and therefore help instead in destabilizing E_1^* . In case (35) is not satisfied the system will be driven to another equilibrium where the newly introduced species thrives, if (21) does not hold. It is however hard to determine whether the disease will be eradicated or still remain endemic. But for a large c_2 it is likely that together with (35) also (21) is violated and in such case the disease would indeed be eradicated. When the net birth rate of the newly introduced species is positive and large enough to destabilize E_1^* , and in particular also larger than the long term benefit it gets from the mutualism with the former species, (2), E_3 is infeasible, since (31) is satisfied. Theoretically, if the parameters of the new species can also be adjusted so as to violate either the feasibility or the stability conditions of both equilibria E_2 , and E_4 , then in this case the ecosystem will move toward E_1^a , which would

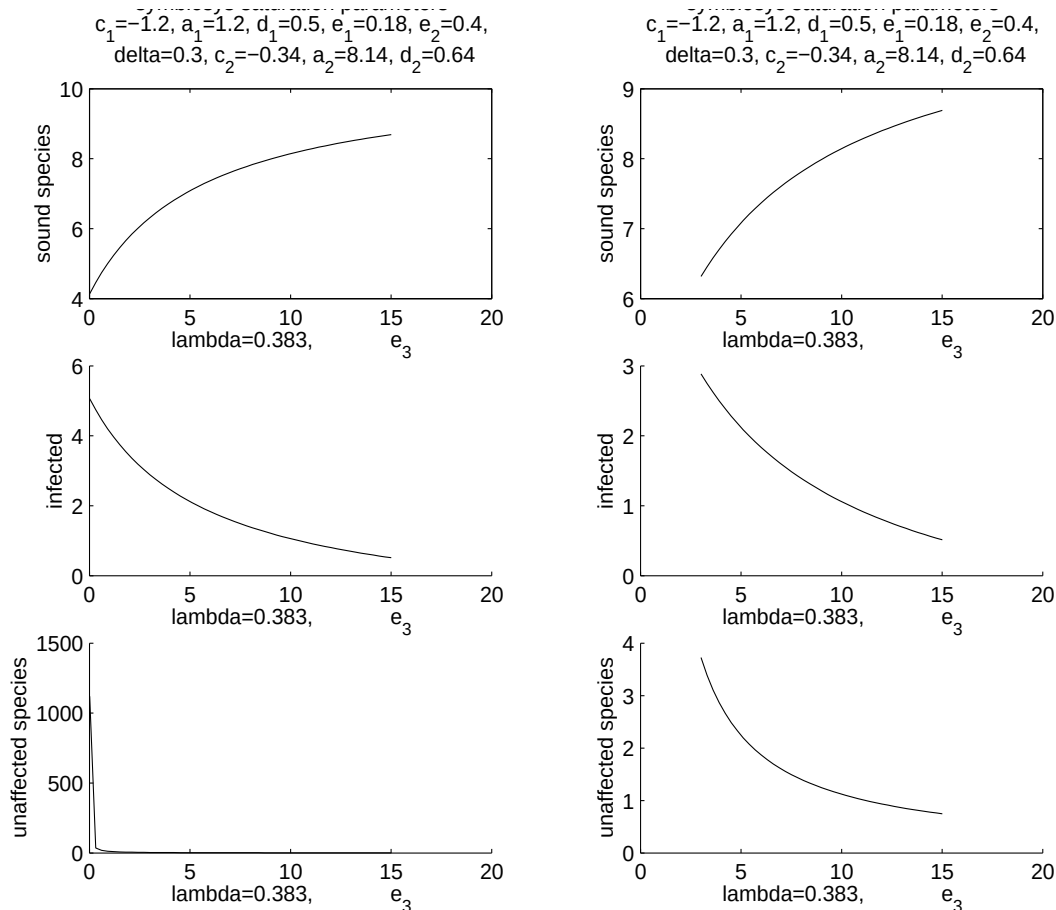


Figure 9. Location of equilibria of (28) as function of the parameter e_3 , for $c_1 = -1.2$, $c_2 = -0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $\lambda = 0.383$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.3$, $a_2 = 8.14$, $d_2 = 0.64$. The point E_3 moves but as the blow up on the right shows, it remains always the only equilibrium of the system.

thus be the only stable equilibrium of the system; note indeed that (21) is compatible with (31). Thus the disease present originally in the first species would be eradicated; the second species would also disappear, but it would have played an essential role, since without it, it would not have been possible to destabilize the endemicity of the disease.

If the epidemic model instead is at equilibrium E_1^{a*} , for $c_1 < 0$, i.e. when the population exhibits logistic growth, this population survives in a disease-free environment, “accidentally” introducing a symbiotic species, the outcome depends on the kind of association for the newly introduced population. Indeed if the latter shows obligate mutualism, $c_2 < 0$, then it destabilizes the equilibrium, thereby making either p itself establish in the ecosystem or the disease endemic in the first population. Conversely, if symbiosis is facultative, $c_2 > 0$, the equilibrium E_1^{a*} could remain stable if (21) holds, i.e. in this case introducing the new species p has no effects, as p itself will ultimately be washed out of the system.

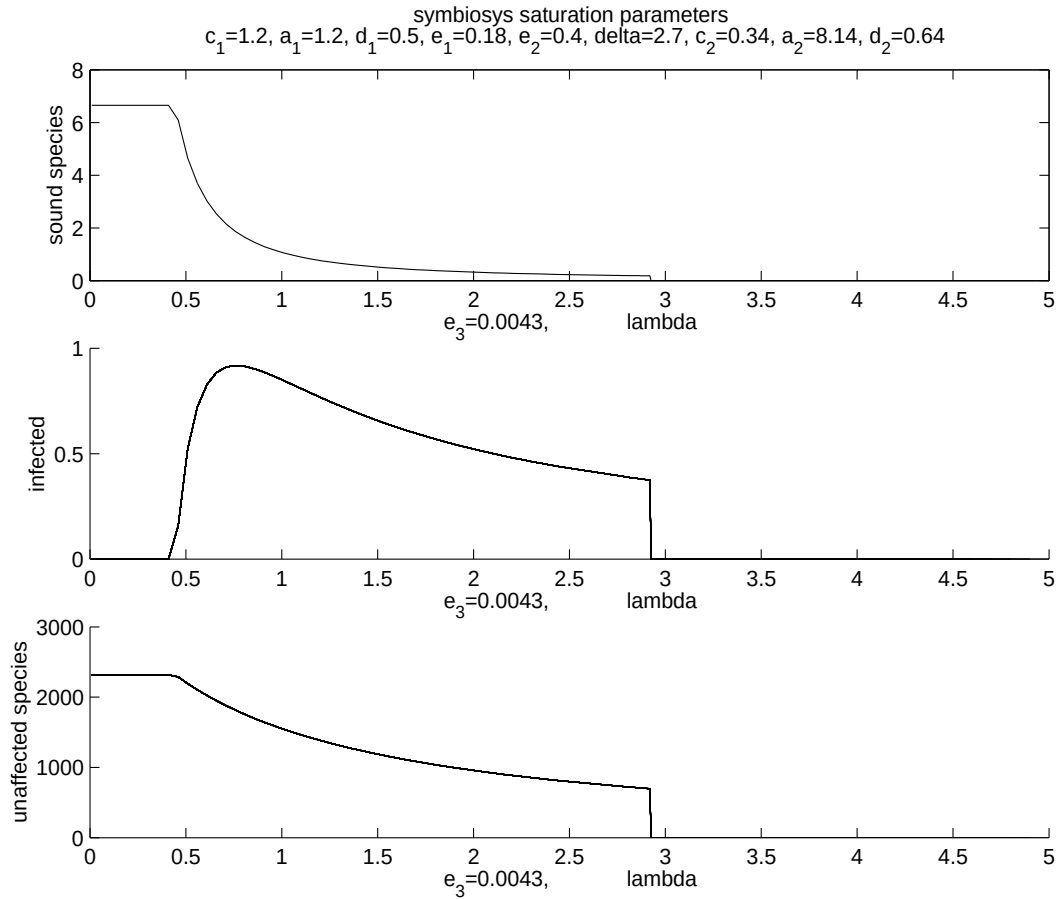


Figure 10. Location of equilibria of (28) as function of the parameter λ , for $c_1 = 1.2$, $c_2 = 0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 2.7$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.0043$. Initially there is E_2 , then for $\lambda = 0.4$ we find E_4 , then at $\lambda = 2.9$ the system collapses to the origin.

We consider now the ecosystem in which the symbiotic species are present (1) and look at the influence a disease has on it. If one of the species catches a transmissible disease, the model gets modified into (28).

Suppose at first that in the obligate mutualism case $c_1, c_2 > 0$ the demographic model is not able to sustain the ecosystem so that it tends to the origin. The introduction of the disease is however not able to destabilize this equilibrium, so that it cannot avoid that an obligate mutualistic environment already having difficulties in thriving would be wiped out. Thus in the case of obligate mutualism, the introduction of a disease in one of the two species cannot save either one from extinction, if the ecosystem is driven to that outcome. But in the case of other types of interactions, such as predator-prey ecosystems, species preservation can be insured by allowing a disease in the predators, [19]. Thus the action of the disease on a demographic interacting populations model depends also on the type of intermixing

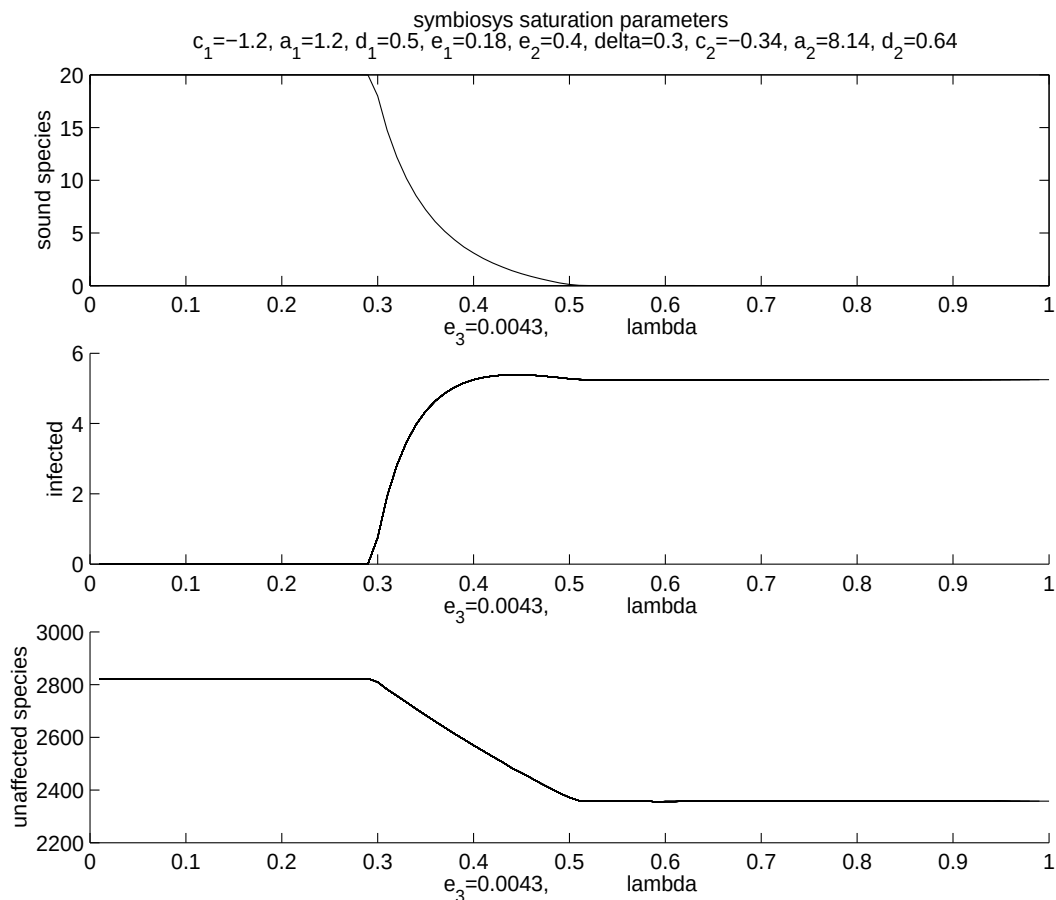


Figure 11. Location of equilibria of (28) as function of the parameter λ , for $c_1 = -1.2$, $c_2 = -0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.3$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.0043$. Initially there is E_2 , then for $\lambda = 0.3$ we find E_4 , then at $\lambda = 0.5$ the system moves to E_3 .

the species share. For all the other types of symbiotic interactions, where mutualism is facultative at least for one of the species involved, the populations in the demographic model cannot both disappear, and this characteristic is inherited by the corresponding ecoepidemic systems.

Assume now instead that the demographics is able to sustain the two populations both at nonzero levels, $\tilde{E}_2 = (s_2, p_2)$. To remain stable with the introduction of the disease, this equilibrium needs the extra condition (38) to be satisfied. Now an epidemics with a large incidence λ or low disease-related mortality δ is likely to invalidate (38) so that the disease-free coexistence equilibrium is destroyed. Thus, like in many other ecoepidemic situations, in the case of symbiotic epidemic models too, the disease has a relevant influence since with a high incidence it may destabilize a purely demographic stable equilibrium.

The question is now what will happen to the ecosystem, upon introduction of the disease

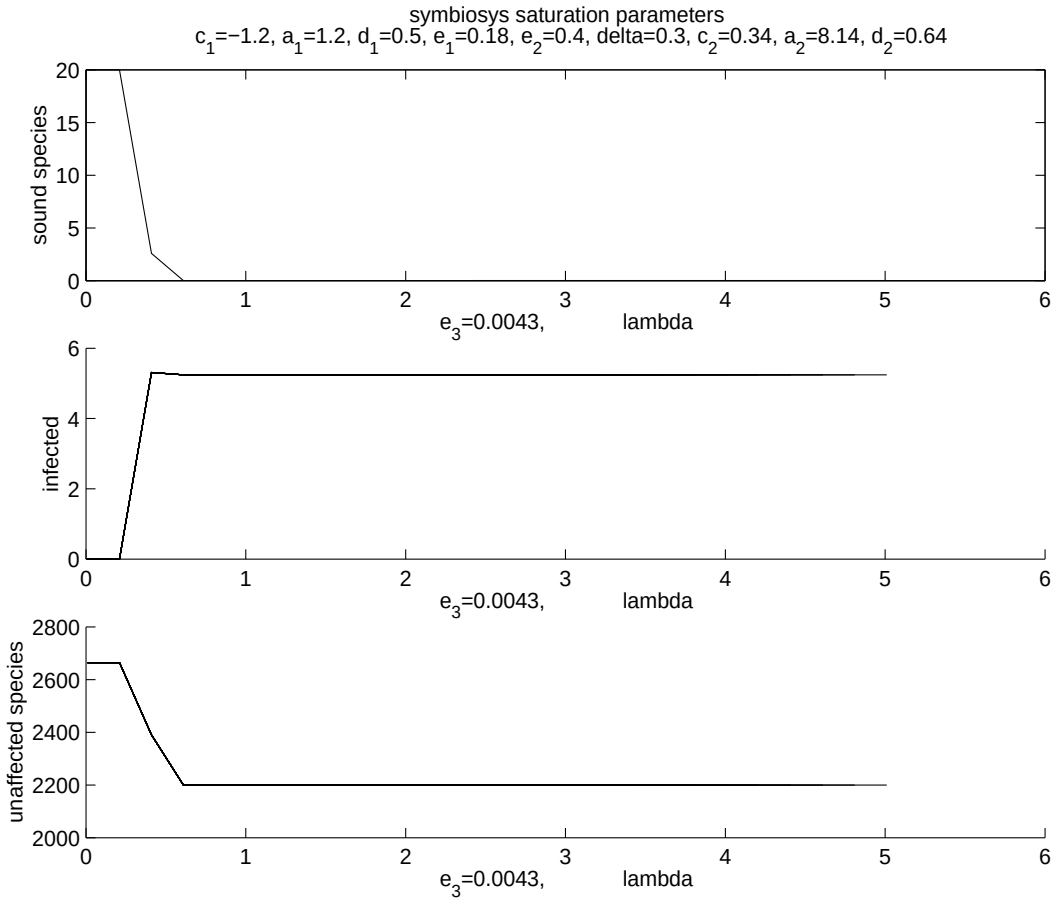


Figure 12. Location of equilibria of (28) as function of the parameter λ , for $c_1 = -1.2$, $c_2 = 0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.3$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.0043$. Initially there is E_2 , then for about $\lambda = 0.3$ we find E_4 , then near $\lambda = 0.8$ the system moves to E_3 .

destabilizing the coexistence of the symbiotic species. One possibility is clearly that the ecosystem thrives in the new situation, with both species still present and the disease at an endemic level, equilibrium E_4 . But other outcomes are that the affected species only survives, if it has a positive net birth rate and high enough intraspecific competition for the infected, since conditions (24), (35) hold, although together with the endemic disease. This would be a way of eliminating a pest p from the environment, at the price of having the disease remaining in the other species. Similar conclusions can be obtained in other types of demographic models, of predator-prey or competition types, [36, 37, 38]. Alternatively, both species can survive, but at the price of the diseased one to be completely invaded by the epidemics, at equilibrium E_3 . For this to occur, a large disease incidence, a low disease mortality and a low enough interaction term a_2 between the two species are conditions likely to satisfy (40) and (42) and to drive the ecosystem to this outcome.

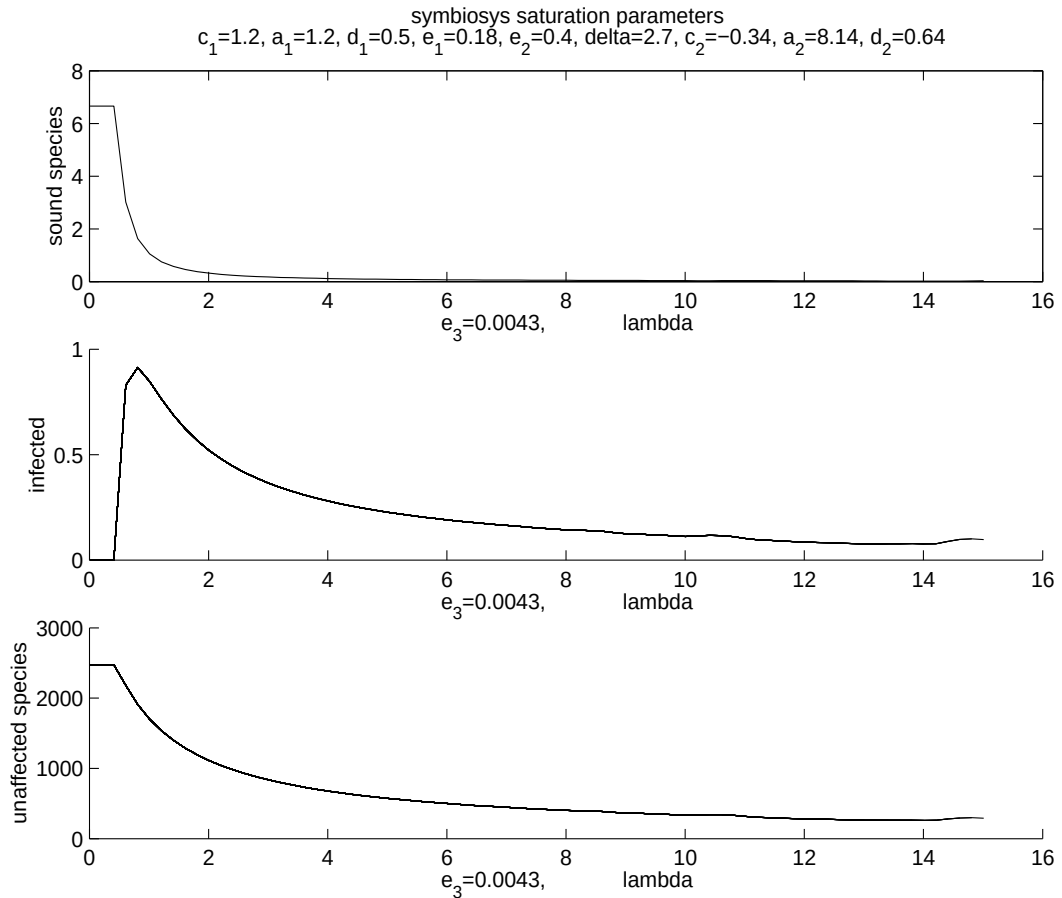


Figure 13. Location of equilibria of (28) as function of the parameter λ , for $c_1 = 1.2$, $c_2 = -0.34$. The other parameter values are $a_1 = 1.2$, $d_1 = 0.5$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 2.7$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.0043$. Initially there is E_2 , then for $\lambda = 0.4$ we find E_4 , then at around $\lambda = 5.0$ the system moves to E_3 .

The particular situations in which only one population survives in a disease-free environment could also be attained, at equilibria E_2^a , E_1^a , if the mutualistic association is vital only for one of the two species. In such case the only surviving species will be the one not needing the symbiosis. Clearly conditions (20) and (21) ensuring the stability of these outcomes are satisfied for large enough interaction terms a_1 , a_2 between the populations, but we need also (46) and (27), i.e. a large disease related mortality.

Note that both equilibria E_3 and $\hat{E}_3$ could be acceptable since the infected species and the unaffected population both thrive, but not desirable since the disease remains endemic. Then our aim would be to try to make them unstable. As remarked earlier, E_3 can be destabilized by a large disease-related mortality δ , while instead $\hat{E}_3$ would be less affected, although δ appears also implicitly in the remaining eigenvalues common to both equilibria. If the affected population is not yet overwhelmed by the disease, a larger disease incidence

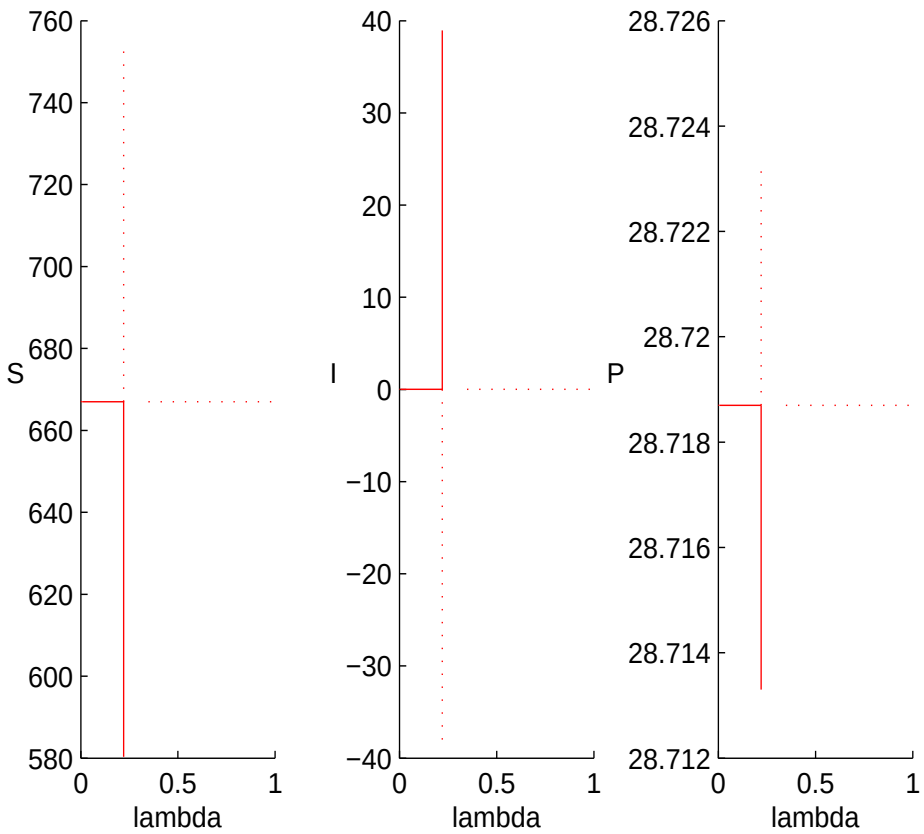


Figure 14. Transcritical bifurcation of (28) at $\lambda = \lambda_t \equiv 0.2204$. The other parameter values $c_1 = 0.2$, $a_1 = 10.2$, $d_1 = 0.05$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.45$, $c_2 = 0.34$, $a_2 = 8.14$, $d_2 = 0.64$, $e_3 = 0.43$.

might prevent the total disappearance of the susceptibles violating (40); but the outcome is not certain, in the sense that if all other equilibria are also destabilized, for an obligated mutualistic environment, the system might very well be driven even to extinction. This cannot happen if at least one of the associations is facultative, i.e. at least one of c_1 and c_2 is positive. In such cases however some other “boundary” equilibrium might be attained, where some other subpopulation disappears. When mutualism is facultative for both species, and the net birth rate c_2 of the unaffected species is low enough, then (35) fails and the system cannot reach E_1 , so that either the disease is eradicated, E_2 or the endemic coexistence equilibrium is reached, E_4 .

When the infected population is overwhelmed by the disease, i.e. susceptibles are absent, and $e_2 = 0$, i.e. no intraspecific competition is possible, the equilibrium $\tilde{E}_3$ is always unstable, a desirable situation. But as already remarked, the stability of $\tilde{E}_3$ is conditional. So the absence of the susceptible population plays a more positive role when the individuals

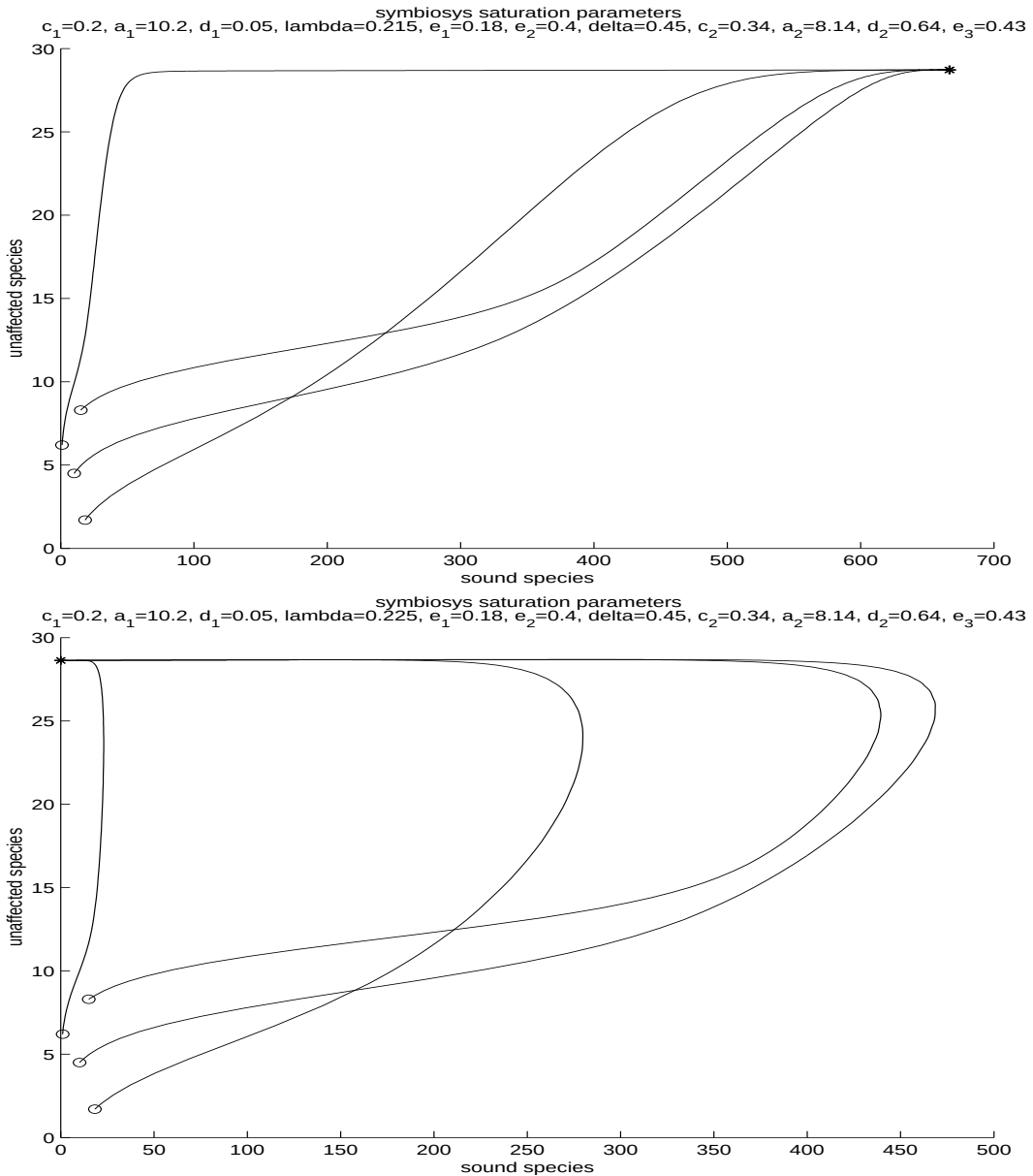


Figure 15. The sp phase plane of (28) just below $\lambda = 0.215$ (upper picture) and above (lower picture) $\lambda = 0.225$ of the value of the transcritical bifurcation $\lambda = \lambda_t \equiv 0.2204$. The other parameter values are $c_1 = 0.2, a_1 = 10.2, d_1 = 0.05, e_1 = 0.18, e_2 = 0.4, \delta = 0.45, c_2 = 0.34, a_2 = 8.14, d_2 = 0.64, e_3 = 0.43$.

of the infected population are so weak that they are unable to compete with their fellows. Therefore a weakening disease on an entirely infected population may have a desirable effect on the system, destabilizing the endemic equilibrium. In such case the system would be driven toward the only remaining stable equilibrium $\tilde{E}_2^a$, which is disease free. How-

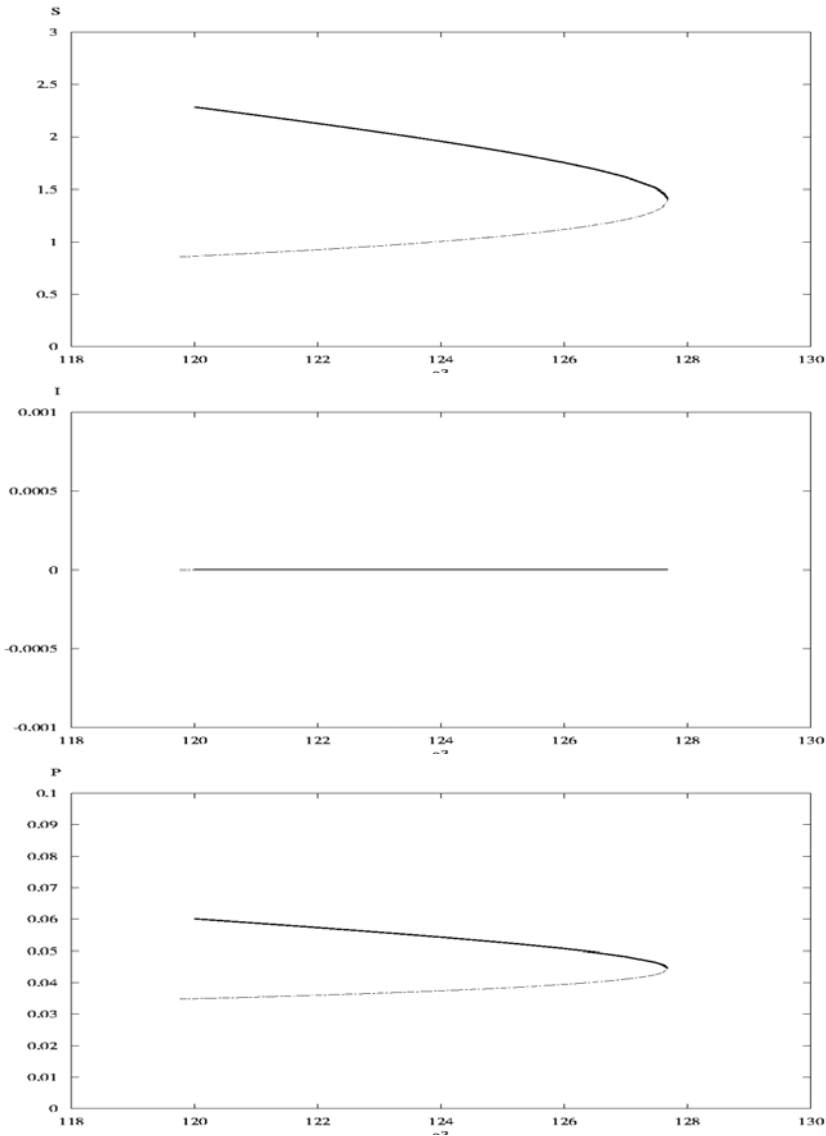


Figure 16. Bifurcation diagram of (28) near the disease-free equilibrium $E_2 = (2.2852, 0, 0.06011)$. The saddle-node bifurcation occurs for $e_3 = e_3^t \equiv 127.7$. The other parameter values are $c_1 = 0.2$, $a_1 = 10.2$, $d_1 = 0.05$, $\lambda = 0.003$, $e_1 = 0.18$, $e_2 = 0.4$, $\delta = 0.45$, $c_2 = 0.34$, $a_2 = 8.14$, $d_2 = 0.64$. Top to bottom are the equilibria for s , i , p as functions of e_3 . The thick line represents the loci of the stable equilibria, the dotted line the unstable ones.

ever, in this case, this implies that only the unaffected population survives. Thus the disease eradication can be obtained at the price of wiping out of the ecosystem its very hosts.

A similar conclusion holds for E_2^a , when the species association is not necessary for their survival, $c_1, c_2 < 0$ and $\hat{E}_2^a$. In fact the latter can be kept stable by a large disease-

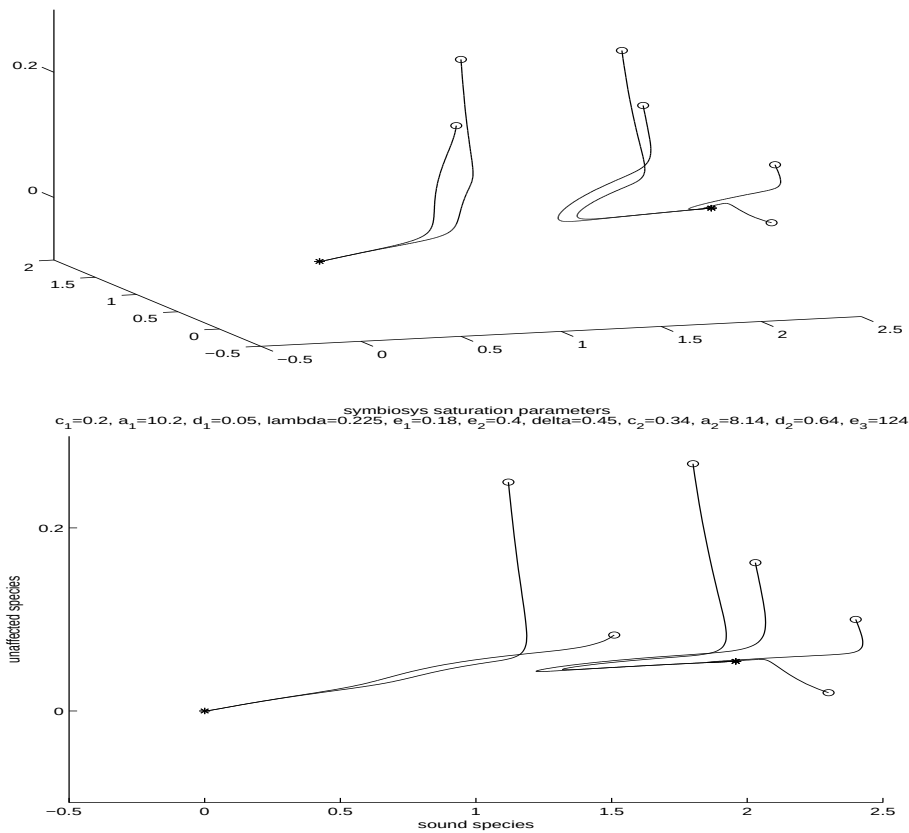


Figure 17. Top: the phase space of (28) near the saddle-node bifurcation at $e_3 = e_3^t \equiv 127.7$, at the disease-free equilibrium $E_2 = (2.2852, 0, 0.06011)$. The bifurcation parameter is $e_3 = 124$. The other parameter values are $c_1 = 0.2, a_1 = 10.2, d_1 = 0.05, \lambda = 0.003, e_1 = 0.18, e_2 = 0.4, \delta = 0.45, c_2 = 0.34, a_2 = 8.14, d_2 = 0.64$. Clearly the origin and the disease free E_2 are both stable equilibria, as is visible also from the two dimensional projection in the sp phase subspace, bottom.

related mortality, see (46), while the former is always unstable. In this case the absence of the susceptible population from the original system would allow the possibility of eradicating the disease, and with it the affected species, while its presence would prevent the stability of E_2^a . In presence of the sound population the disease however could still be controlled via the stability of the equilibrium E_2 .

If the disease-unaffected population p represents a nuisance, it would be possible to fight it by introducing a disease in its symbiotic species s , for which mutualism is facultative, $c_1 < 0$, at the same time striving to attain the stability conditions for E_1 . To this end, compare the stability conditions (21) of $\tilde{E}_1^a$ for the case $c_2 > 0 > c_1$, since otherwise $\tilde{E}_1^a$ is unstable, that require a large return a_2 for the association, with those of E_1 namely (24),

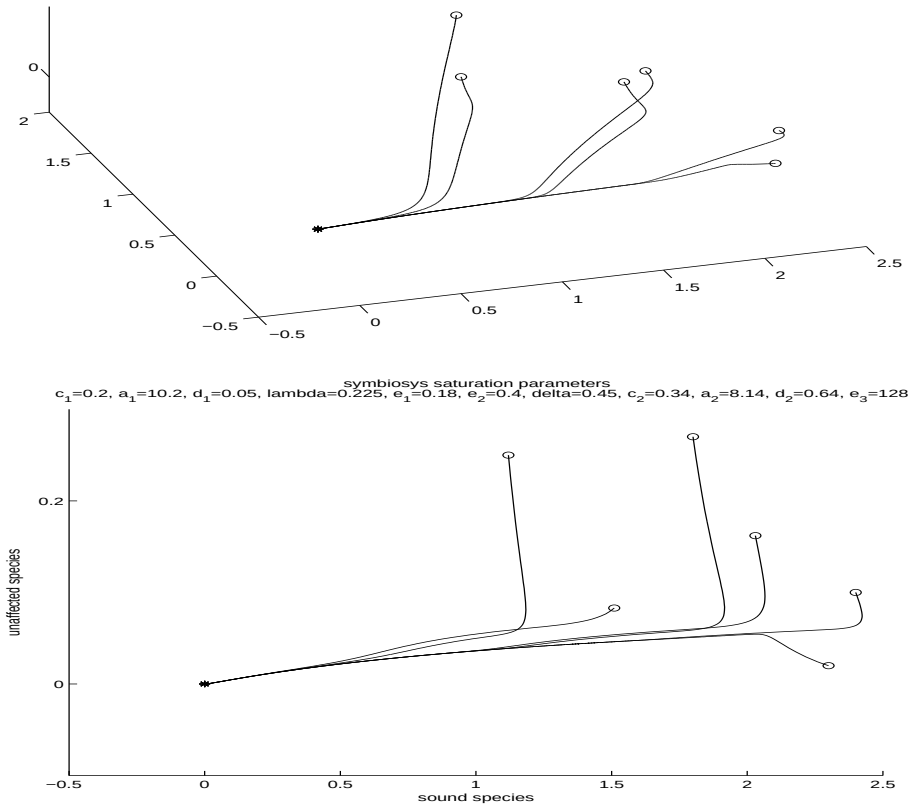


Figure 18. Top: the phase space of (28) near the saddle-node bifurcation at $e_3 = e_3^t \equiv 127.7$, at the disease-free equilibrium $E_2 = (2.2852, 0, 0.06011)$. The bifurcation parameter is $e_3 = 128$. The other parameter values are $c_1 = 0.2, a_1 = 10.2, d_1 = 0.05, \lambda = 0.003, e_1 = 0.18, e_2 = 0.4, \delta = 0.45, c_2 = 0.34, a_2 = 8.14, d_2 = 0.64$. Initial conditions as in Figure 17. Clearly the origin has become the only stable equilibrium. The equilibrium E_2 has now disappeared, as it is visible also from the two dimensional projection in the sp phase subspace, bottom.

(35), for which a large disease incidence λ or a large net birth rate of the disease free species c_2 are needed.

Note that when the disease incidence is above the difference between the intraspecific competition terms of susceptible and infected individuals $\lambda > e_2 - e_1$, then E_1 is feasible and E_4 becomes unstable. If the incidence is large enough, then, coexistence and the situation in which the unaffected species is wiped out of the ecosystem are mutually exclusive.

7. Conclusion

The aim of this Chapter has been the mathematical investigation of an ecoepidemic model in which the basic demographics represent mutual association of two populations with limited benefits for both species coming from the interaction. Several such cases have been considered, focusing mostly on the obligatory mutualism and secondly on the facultative symbiotic association. The introduction of a disease in one of the species is seen to produce relevant effects on the model, as it had already been observed in other ecoepidemic systems where the underlying demographic relationship were of competitive or predator-prey nature, but also some new findings have been outlined.

Appendix

The interior equilibrium of the ecoepidemic model E_4 has the following components

$$s_4 = -\frac{\Theta_4}{\Lambda_4}, \quad i_4 = \frac{\Xi_4}{\Pi_4}, \quad p_4 = \frac{c_2 e_1 - c_2 e_2 - a_2 \delta - c_2 d_2 c_1 + c_2 \lambda + a_2 c_1 + c_2 d_2 \delta}{(-e_1 - \delta d_2 - \lambda + e_2 + d_2 c_1) e_3},$$

where the explicit expressions of the above quantities are given below.

$$\begin{aligned} \Theta_4 = & e_3 \delta e_1^2 + e_3 e_2^2 c_1 + c_2 a_1 e_2^2 + c_2 a_1 e_1^2 - a_2 c_1 a_1 e_2 + a_2 c_1 a_1 \lambda \\ & + a_2 c_1 a_1 e_1 + a_2 e_2 d_1 c_1^2 - a_2 \delta a_1 e_1 + c_2 a_1 \lambda^2 - a_2 \delta a_1 \lambda - 2 c_2 e_1 \delta d_1 \lambda \\ & + c_2 d_2 c_1 \delta d_1 e_1 + c_2 d_2 c_1 \delta d_1 \lambda + c_2 d_2 \delta e_2 d_1 c_1 - e_3 \delta e_1 d_2 c_1 + c_2 d_2 c_1 a_1 e_2 \\ & - c_2 d_2 c_1^2 e_2 d_1 + c_2 d_2 \delta a_1 e_1 + c_2 d_2 \delta a_1 \lambda - c_2 d_2 \delta a_1 e_2 - c_2 d_2 \delta^2 d_1 e_1 \\ & + c_2 \lambda e_2 d_1 c_1 + e_3 \delta \lambda^2 + c_2 e_2 \delta d_1 e_1 + c_2 e_2 \delta d_1 \lambda - e_3 \delta \lambda d_2 c_1 - e_3 e_2 c_1 d_2 \delta \\ & + a_2 \delta^2 d_1 e_1 + a_2 \delta^2 d_1 \lambda - a_2 c_1 \delta d_1 e_1 - a_2 c_1 \delta d_1 \lambda - c_2 d_2 \delta^2 d_1 \lambda + c_2 e_1 e_2 d_1 c_1 \\ & - a_2 \delta e_2 d_1 c_1 - c_2 d_2 c_1 a_1 e_1 - c_2 d_2 c_1 a_1 \lambda - c_2 \delta d_1 \lambda^2 - c_2 e_2^2 d_1 c_1 - c_2 \delta d_1 e_1^2 \\ & + e_3 \delta^2 e_1 d_2 + e_3 e_2 c_1^2 d_2 - e_3 \delta \lambda e_2 - e_3 \delta e_1 e_2 + e_3 \delta^2 \lambda d_2 - e_3 e_2 c_1 e_1 \\ & - e_3 e_2 c_1 \lambda - 2 c_2 \lambda a_1 e_2 - 2 c_2 e_1 a_1 e_2 + 2 e_3 \delta e_1 \lambda + 2 c_2 e_1 a_1 \lambda + a_2 \delta a_1 e_2, \end{aligned}$$

$$\begin{aligned} \Lambda_4 = & \lambda (c_2 d_1 e_1^2 - 2 e_3 \lambda e_1 + 2 e_3 e_2 e_1 + c_2 \lambda^2 d_1 + 2 c_2 e_1 \lambda d_1 - e_3 e_2^2 \\ & + c_2 d_2 \delta d_1 e_1 - e_3 \lambda^2 + c_2 e_2^2 d_1 - e_3 e_1^2 + a_2 \delta e_2 d_1 - a_2 \delta d_1 \lambda - a_2 \delta d_1 e_1 \\ & - e_3 \delta e_1 d_2 - e_3 \delta \lambda d_2 + e_3 e_2 d_2 \delta + a_2 c_1 \lambda d_1 + e_3 \lambda d_2 c_1 + a_2 c_1 d_1 e_1 \\ & - a_2 c_1 d_1 e_2 - e_3 e_2 d_2 c_1 + c_2 d_2 \delta d_1 \lambda - c_2 d_2 \delta e_2 d_1 - 2 c_2 e_1 e_2 d_1 - 2 c_2 \lambda e_2 d_1 \\ & - c_2 d_2 c_1 d_1 e_1 - c_2 d_2 c_1 \lambda d_1 + c_2 d_2 c_1 d_1 e_2 + e_3 e_1 d_2 c_1 + 2 e_3 e_2 \lambda), \end{aligned}$$

$$\begin{aligned}
\Xi_4 = & e_3\delta e_1^2 + e_3e_2^2c_1 + c_1\lambda^2e_3 + c_2a_1e_2^2 + c_2a_1e_1^2 - a_2c_1a_1e_2 + a_2c_1a_1\lambda \\
& + a_2c_1a_1e_1 + a_2e_2d_1c_1^2 - a_2\delta a_1e_1 + c_2a_1\lambda^2 - a_2\delta a_1\lambda - c_2e_1\delta d_1\lambda \\
& + c_2d_2c_1\delta d_1e_1 - c_2d_2c_1\delta d_1\lambda + c_2d_2\delta e_2d_1c_1 - e_3\delta e_1d_2c_1 + c_2d_2c_1a_1e_2 \\
& - c_2d_2c_1^2e_2d_1 + c_2d_2\delta a_1e_1 + c_2d_2\delta a_1\lambda - c_2d_2\delta a_1e_2 - c_2d_2\delta^2d_1e_1 \\
& + 2c_2\lambda e_2d_1c_1 - e_1c_1\lambda c_2d_1 + c_1^2\lambda c_2d_2d_1 + e_1c_1\lambda e_3 - c_1^2\lambda e_3d_2 - c_1\lambda^2c_2d_1 \\
& - c_1^2\lambda a_2d_1 + c_2e_2\delta d_1e_1 + e_3\delta \lambda d_2c_1 - e_3e_2c_1d_2\delta + a_2\delta^2d_1e_1 - a_2c_1\delta d_1e_1 \\
& + a_2c_1\delta d_1\lambda + c_2e_1e_2d_1c_1 - a_2\delta e_2d_1c_1 - c_2d_2c_1a_1e_1 - c_2d_2c_1a_1\lambda \\
& - c_2e_2^2d_1c_1 - c_2\delta d_1e_1^2 + e_3\delta^2e_1d_2 + e_3e_2c_1^2d_2 - e_3\delta e_1e_2 - e_3e_2c_1e_1 \\
& - 2e_3e_2c_1\lambda - 2c_2\lambda a_1e_2 - 2c_2e_1a_1e_2 + e_3\delta e_1\lambda + 2c_2e_1a_1\lambda + a_2\delta a_1e_2,
\end{aligned}$$

$$\begin{aligned}
\Pi_4 = & \lambda(e_1 + \lambda - e_2)(e_1c_2d_1 - e_3e_1 - c_2e_2d_1 - a_2\delta d_1 - e_3\delta d_2 \\
& - c_2d_2c_1d_1 - e_3\lambda + e_3e_2 + c_2\lambda d_1 + e_3d_2c_1 + a_2c_1d_1 + c_2d_2\delta d_1).
\end{aligned}$$

References

- [1] Adams, B. J., Fodor, A., Koppenhöfer, H. S., Stackebrandt, E., Stock, S. P., Klein, M. G. (2006) Biodiversity and systematics of nematode-bacterium entomopathogens, *Biological Control*, **37**, 32–49.
- [2] Addicott, J.F. (1985) Competition in mutualistic systems, in D.H. Boucher (Editor), *The Biology of Mutualism: Ecology and Evolution*, Croom Helm, London, 217–247.
- [3] Bazykin, A. D. (1998) Nonlinear dynamics of interacting populations, *Series on non-linear science*, Chua, L.O. (Ed), Series A, vol. 11. World Scientific; (original in Russian, Nauka, Moscow (1985)).
- [4] Boucher, D.H. (1985) *The Biology of Mutualism: Ecology and Evolution*, Croom Helm, London.
- [5] Boursaux-Eude, C., Gross, R. (2000) New insights into symbiotic associations between ants and bacteria, *Res. Microbiol.* **151**, 513–519.
- [6] Chen, F. (2008) Permanence for the discrete mutualism model with time delays, *Math. Comput. Modelling* **47**, 431–435.
- [7] Chen, F., Shi, J., Chen, X. (2004) Periodicity in a Lotka-Volterra facultative mutualism system with several delays, *Gongcheng Shuxue Xuebao* **21**, 403–409.
- [8] Feng, P. (2008) Global and blow-up solutions for a mutualistic model, *Nonlinear Anal.* **68**, 1898–1908.
- [9] Finkes, L. K., Cady, A. B., Mulroy, J. C., Clay, K., Rudgers, J. A. (2006) Plant-fungus mutualism affects spider composition in successional fields, *Ecology Letters* **9**, 347–356.

- [10] Gan, W., Lin, Z. (2008) Coexistence and asymptotic periodicity in a competitor-competitor-mutualist model, *J. Math. Anal. Appl.* **337**, 1089–1099.
- [11] Gao, L.Q., Hethcote, H.W. (1992) Disease transmission models with density-dependent demographics, *J. of Math. Biology* **30**, 717–731.
- [12] Graves, W. G., Peckham, B., Pastor, J. (2006) A bifurcation analysis of a differential equations model for mutualism, *Bull. Math. Biol.* **68**, 1851–1872.
- [13] Greenhalgh, D., Haque, M. (2006) A predator-prey model with disease in the prey species only, *Mathematical Methods in the Applied Sciences*, **30**, 911–929.
- [14] Guo, Z. (2005) Coexistence states for systems of mutualist species, *J. Math. Anal. Appl.* **303**, 61–80.
- [15] Gulland, F.M.D. (1995) The impact of infectious diseases on wild animal populations - a review, in B.T. Grenfell, A.P. Dobson (Editors) *Ecology of infectious diseases in natural populations*, Cambridge Univ. Press.
- [16] Gyllenberg, M., Yan, P., Wang, Y. (2006) Limit cycles for competitor-competitor-mutualist Lotka-Volterra systems, *Phys. D* **221**, 135–145.
- [17] Haque, M., Venturino, E. (2006) Increase of the prey may decrease the healthy predator population in presence of a disease in the predator, *HERMIS* **7**, 39–60.
- [18] Haque, M., Venturino, E. (2006) The role of transmissible diseases in Holling-Tanner predator-prey model, *J. of Theoretical Population Biology* **70**, 273–288.
- [19] Haque, M., Venturino, E. (2007) An ecoepidemiological model with disease in the predator: the ratio-dependent case, *Math. Meth. Appl. Sci.* **30**, 1791–1809.
- [20] He, X. Z., Gopalsamy, K. (1994) Dynamics of Lotka-Volterra mutualism in changing environments, *Nonlinear World* **1**, 173–185.
- [21] Hei, L. (2007) Global bifurcation of co-existence states for a predator-prey-mutualist model with diffusion, *Nonlinear Anal. Real World Appl.* **8**, 619–635.
- [22] Hethcote, H. W. (2000) The Mathematics of Infectious Diseases, *SIAM Review* **42**, 599–653.
- [23] Horiuchi, J.I., Prithiviraj, B., Bais, H.P., Kimball, B.A., Vivanco, J.M. (2005) Soil nematodes mediate positive interactions between legume plants and *Rhizobium bacteria*, *Planta* **222**, 848–857.
- [24] Jantzen, D.H., De Vries, P., Gladstone, D.E., Higgins, M.L., Levinsohn, T.M. (1980) Self- and cross-pollination of *Encyclia cordigera* (Orchidaceae) in Santa Rosa National Park, Costa Rica, *Biotropica* **12**, 1398–1406.
- [25] Kooi, B. W.; Kuijper, L. D. J.; Kooijman, S. A. L. M. (2004) Consequences of symbiosis for food web dynamics, *J. Math. Biol.* **49**, 227–271.

- [26] Kumar, R.; Freedman, H. I. (2002) Mathematical analysis in a model of obligate mutualism with food chain population, *Nonlinear Dyn. Syst. Theory* **2**, 25–44.
- [27] Kumar, R., Freedman, H. I. (1989) A mathematical model of facultative mutualism with populations interacting in a food chain, *Math. Biosci.* **97**, 235–261.
- [28] Li, Y.M., Graef, J.R., Wang, L., Karsai, J. (2000) Global dynamics of a SEIR model with varying total population size, *Math. Biosci.* **160**, 191–213.
- [29] Mena-Lorca, J., Hethcote, H.W. (1992), Dynamic models of infectious diseases as regulator of population sizes, *J. Math. Biology* **30**, p. 693-716.
- [30] Muller, C. B., Krauss, J. (2005) Symbiosis between grasses and asexual fungal endophytes, *Current Opinion in Plant Biology* **8**, 450–456.
- [31] Paszkowski, U. (2006) Mutualism and parasitism: the yin and yang of plant symbioses, *Current Opinion in Plant Biology* **9**, 364–370.
- [32] Perko, L. (2000) *Differential Equations and Dynamical Systems*, third Edition, Springer Verlag, Berlin.
- [33] Rai, B., Freedman, H. I., Addicott, J. F. (1983) Analysis of three-species models of mutualism in predator-prey and competitive systems, *Math. Biosci.* **65**, 13–50.
- [34] Stewart, F. J., Cavanaugh, C. M. (2006) Bacterial endosymbioses in *Solemya* (Mollusca: Bivalvia)—Model system for studies of symbiont-host adaptation, *Antonie van Leeuwenhoek* **90**, 343–360.
- [35] Sun, G., Wei, W. (2003) The qualitative analysis of commensal symbiosis model of two populations, *Math. Theory Appl. (Changsha)* **23**, 65–68.
- [36] Venturino, E. (1995) Epidemics in predator-prey models: disease among the prey, in O. Arino, D. Axelrod, M. Kimmel, M. Langlais (Editors) *Mathematical Population Dynamics: Analysis of Heterogeneity*, Vol. one: *Theory of Epidemics*, Wuerzt Publishing Ltd, Winnipeg, Canada, 381-393.
- [37] Venturino, E. (2001) The effects of diseases on competing species, *Math. Biosci.*, **174**, 111-131.
- [38] Venturino, E. (2002) Epidemics in predator-prey models: disease in the predators, *IMA Journal of Mathematics Applied in Medicine and Biology*, **19**, 185-205.
- [39] Venturino, E. (2007) How diseases affect symbiotic communities, *Math. Biosci.* **206**, 11-30.
- [40] Walker, R., Ferguson, C.M.J., Booth, N.A., Allan, E.J. (2002) The symbiosis of *Bacillus subtilis* L-forms with Chinese cabbage seedlings inhibits conidial germination of *Botrytis cinerea*, *Letters in Applied Microbiology* **34**, 42-45.
- [41] Wu, H. Xia, Y., Lin, M. (2008) Existence of positive periodic solution of mutualism system with several delays, *Chaos Solitons Fractals* **36**, 487–493.

- [42] Yan, X.-P., Li, W.-T., (2007) Bifurcation and global periodic solutions in a delayed facultative mutualism system, *Phys. D* **227**, 51–69.
- [43] Zaghrout, A. A. S. (1991) Stability and persistence of facultative mutualism with populations interacting in a food chain, *Appl. Math. Comput.* **45**, part I, 1–15.
- [44] Zhao, B. G., Lin F. (2005) Mutualistic symbiosis between *Bursaphelenchus xylophilus* and bacteria of the genus *Pseudomonas*, *For. Path.* **35**, 339–345.

Chapter 6

EFFECTS OF CHEMICAL CONTAMINANTS ON WILDLIFE: IDENTIFICATION OF BIOMARKERS IN A SENTINEL SPECIES

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Abstract

Current agriculture activities worldwide imply extended used of chemical complex mixtures. Roughly 85–90% of pesticides applied in agriculture never reaches target organisms, but disperse through the air, soil and water. Therefore, wildlife living in habitats adjoining heavily treated croplands is likely to be exposed to complex pesticide mixtures over extended periods. One of the main challenges of the Environmental Toxicology is to relate the presence of a chemical in the environment with a valid prediction of the resultant hazards for those organisms potentially receptors. Alterations or malfunction of organism normal vital functions can be identified using *Biomarkers*, considered as measurable biochemical, histological, physiological, and morphological changes in response to xenobiotic undesirable action. Environmental pollution may interfere with growth and development of organisms, but the induction of genetic damage due to long-term, low level chronic exposure to chemicals is perhaps the most relevant biological effect. It can cause a decrease in wildlife populations fitness by the effects of somatic and heritable mutations, that is, an increase in genomic instability. Therefore, the evaluation of the potential genotoxicity of a chemical product is

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essential for environmental hazard assessment and biodiversity conservation. Genotoxic biomarkers, specially non-destructive short term tests, provide a particularly promising alternative of increasing interest and relevance for measuring the potential effects in vertebrate species in both, laboratory and field studies. Moreover, if this assessment is done in species of particular ecological value, the information can be used to assess the impact of xenobiotics on both the species and the ecosystem. The identification of sentinel species as well as sensitive biomarkers of chronic genotoxicity represents an early warning system to detect adverse effects in natural environments.

Crocodylians are integral components of wetlands all around the world. Taking into account the agricultural frontiers expansion during the last years, many crocodilian populations live nowadays in habitats under a high contaminant pressure. Due to their biological characteristics they can be exposed to contaminants in all life stages. As a consequence, crocodylians world-wide appear as excellent model species of environmental pesticide contamination.

1. Introduction

At present, there are several factors involved in the loss of the world's biodiversity. Among them, chemical contamination of the environment, including the effects of long-term, low-level chronic exposure of organisms, has been implicated in the decline or disappearance of many populations [1].

Since the early 1990s, the concern about the impacts of toxic chemicals on biodiversity has been increasing. Wildlife, people, and entire ecosystems around the world are threatened by chemicals that can endanger survival and physiology of the organisms. Even though there is considerable and growing scientific evidence of damage to wildlife from chemical exposures, researchers are only just beginning to disentangle the questions about the effects of chronic low-level exposure (as opposed to brief high doses of chemicals), combinations of chemicals, and interactions between chemicals and other physiological and environmental factors [2].

Environmental Risk Associated to Increasing Use of Pesticides

Pesticides is a general term, which comprises chemical and biological products used to kill or control pests. Pesticides include products designed to act as insecticides, herbicides, fungicides, and rodenticides [3].

As a consequence of world demand, during the '90s, there was a significant agriculture transformation in developing countries, motorized by the adoption of transgenic crops (soy, corn, cotton) and no-tillage system, a model directly associated with the high consume of very specific pesticides [4]. Roughly 10-15% of pesticides applied agriculturally reach target organisms directly, while the rest disperse through the environment (air, soil and water) [5].

While cultivated lands are constantly expanding over neighboring ecosystems in regions monopolized by intensive agriculture [5-7], the maintenance of biodiversity depends on the preservation of remnant wildlife habitat [8]. However, constant exposure to toxic chemicals over the life span of the organisms living in such areas has been speculated to have cumulative deleterious effects [9,10]. Pesticides may produce deep consequences in ecosystems, including death of organisms and lesions on animals, suppression of immune system, disruption of endocrine system, reproductive inhibition or failure, teratogenic and

carcinogenic effects, cellular and molecular alterations including DNA damage, etc. [11]. Moreover, when present in low concentrations, pesticides may not cause acute detectable effects in organisms, but may induce other kind of damage, like genetic disorders and physiologic alterations, and in the long run anyway, reduce their life span [12]. Both laboratory and field studies have shown that sub-lethal and sub-organismal level effects, such as DNA damage, small turnover rate for proteins, etc., influence energy metabolism, fitness and reproductive success, leading to population level effects. Indeed, increase genomic instability has been suggested to play important roles in decreased fitness of the populations [1,13,14]. In view of this, habitats adjoining croplands are under a high pressure and the impact of pesticides into the wildlife associated is, in most of the cases, unknown [15,8,16].

The benefits of herbicide use in agriculture are relatively well known. However, serious concerns continue to be voiced about potential effects from recurrent exposure to low levels of herbicides, and differential sensitivity of animals and humans in relation to age, sex or size [15].

Risk Assessment of Pesticide Formulations: Chemical Mixtures.

A fundamental problem in the assessment of environmental effects of pollutants is the question of mixtures [17]. Not uncommonly, organisms are exposed to complex mixtures of pollutants, albeit at low concentrations. Chemical mixtures are an ever present problem as synergistic or antagonistic effects may result because of such mixtures in the environment, making the assessment of their toxic effects extremely difficult. In this way, effects which may sometimes be negligible when individual chemicals are considered, can become significant when integrated into these mixtures [9,18,14].

Virtually every pesticide product contains ingredients other than what is called the "active" ingredient(s), the one designed to provide killing action. These ingredients are misleadingly called "inert" and have the purpose to act as coadjuvants and surfactants, making the product easier to use or more efficient. In general, they are not identified on the labels of pesticide products because manufacturers claim that such information constitutes trade secrets [19].

During the approval of pesticides, active ingredients are generally assessed singly for their potential impact on animal and human health and safety standards are set for individual chemicals. In the field, however, pesticides are commonly applied as mixtures, or 'tank-mixes'. As crop pests may appear simultaneously, pesticides are commonly spray for a number of different weed, insect or disease pests on the same occasion. A number of different active and coadjuvant ingredients are used formulated into one product, and also several different formulated products are tank-mixed for application in order to satisfy these varying requirements for pest control. In view of this, in order to accurately assess pesticide hazards, the evaluation of the product must be done as it is actually used and introduced into the environment, that is as a chemical mixture [20].

Formulated Products Based on Glyphosate: An Herbicide Widely Used.

Glyphosate [N-phosphonomethyl glycine (GLY)] is a systemic herbicide widely used on agriculture and nonagricultural activities for non-selective weed control [21,22]. It inhibits plant growth through interference with the production of certain essential aromatic amino acids [23,24]. This biosynthetic pathway is not shared by members of the animal kingdom, so it is claimed to be selectively toxic to plants and relatively nontoxic to animals [25,26].

Current agriculture activities imply the use of commercial GLY-based formulations, which are complex and variable chemical mixtures, rather than the use of the active chemical ingredient (GLY) alone. Coadjuvants and surfactants are included in formulations to increase the adsorption of GLY and improve the effectiveness of the herbicide action. Surfactants may have a toxicity several times higher than GLY itself, making the formulated product of greater toxicity than the active ingredient (a.i.) [21,22].

One of the most widely used GLY commercial formulation is Roundup® (RU), first introduced in 1974 [27]. During the last 25 years it has been increasingly used in agriculture and it continues expanding, particularly in applications involving plant varieties that are genetically modified to tolerate GLY treatment, such as soy [26,28].

Crocodylians (*Caiman latirostris*) as Sentinel Organisms of Pesticide Contamination.

It has become increasingly obvious in recent years that environmental contaminants can significantly affect many species of reptiles and among them, crocodylians [29]. However, these animals are often excluded from environmental contamination studies and ecological risk assessments, even though they are important elements of the ecosystem. Crocodylians (alligators, caimans, crocodiles, gharials) are integral components of wetland ecosystems; they are long-lived, top-level carnivores with fairly restricted home ranges, necessarily associated to water, inhabiting tropical and sub-tropical habitats throughout the world [30]. It is considered that they are likely to show any effects associated with environmental contamination [29]. Regarding their biological and ecological characteristics, these animals can be exposed to contaminants in all life stages. Contaminants accumulated by females can be transferred to the embryos through the egg yolk, affecting embryo development in ovo. In the same way, embryos might be directly affected by contaminants that pass through the eggshell from the surrounding environment during incubation. Juveniles or adults may be exposed to contaminant by the food web, water and sediments typical of the natural environment where they live [31]. Many studies have been made in order to assess exposure to pesticides in different crocodylian species at different life stages, including viable and nonviable eggs [32,33], juveniles [34,35] and adults [36].

Of the living 23 species of the order Crocodylia, two inhabit Argentina, *Caiman latirostris* (Broad-snouted caiman) and *Caiman yacare* (Yacare caiman), both of them occurring in the northeastern region of the country. *C. latirostris* inhabits Jujuy, Salta, Formosa, Santiago del Estero, Entre Ríos, Santa Fe, Corrientes, Chaco and Misiones provinces (Fig. 1) [37]. This species shows a well defined seasonal cycle that depends on climatic factors (temperature, rain). In Argentina, their breeding season takes place during spring-summer, from late October - December (mating and copulation season) to March,

when hatching occurs after an incubation period of 65-80 days approximately, depending on temperature [38].

As a consequence of agricultural frontiers expansion during the last years, nowadays several areas of *C. latirostris* geographic distribution are in the proximity of regions with intense agricultural activity. In addition, the breeding season of this species coincides with the period in which pesticides are applied extensively in these areas, as a requirement of agricultural system success. Therefore, a potential contamination risk exists for this species that could be particularly significant for developing embryos.



Figure 1. Geographic distribution map of *C. latirostris* and *C. yacare* in Argentina.

Conservation Status of *C. latirostris*

One of the most realistic approaches for natural ecosystem conservation is the sustainable use of wild animals and plants of commercial interest, since economic benefits may act as a stimulus for *in situ* conservation [38].

As many crocodilian species, broad-snouted caiman has recovered from an endangered or threatened status, thanks to the stimuli generated by sustainable use programs and international controls. There are nowadays four ongoing projects in Argentina involving sustainable use of the two caiman species present in the country by means of the ranching technique. The first one begun in Santa Fe, Argentina, in 1990 with the "*Caiman latirostris* Experimental Ranching Program" [39], known as Proyecto Yacaré (PY). This program involves sustainable use of *C. latirostris* based on ranching technique, which consists of eggs harvesting from natural environments, artificial incubation and captive rearing of the

hatchling under controlled conditions. Then, a percentage of the hatchlings are reintroduced into the wild approximately at ten months old, and the remaining animals are used for commercial utilization [38]. As a consequence of the implementation of this program, *C. latirostris* population status in Argentina evidenced an important recovery that led CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) to transferred this species from Appendix I to II in 1997, allowing the commercialization of those products coming only from entitled ranching programs in Argentina and without affecting survival of the managed species [38]. The existence of the PY sustainable used program allows the development of experimental studies with great availability of animals of different age, from eggs to adults, a great knowledge of the species biology in its natural environment and the possibility to follow animals by captive rearing after experiments, without exerting negative effects in this protected species.

Evaluation of Environmental Agent Effects: Biomarkers

The term "biomarker" is used in a broad sense to include almost any measurement reflecting an interaction between a biological system and an environmental agent, which may be chemical, physical or biological. However, in this context we consider particularly chemical agents [40]. Three classes of biomarkers are identified while recognising that clear distinction of category is often not possible:

- * biomarker of exposure: an exogenous substance or its metabolite or the product of an interaction between a xenobiotic agent and some target molecule or cell that is measured in a compartment within an organism;
- * biomarker of effect: a measurable biochemical, physiological, behavioural or other alteration within an organism that, depending upon the magnitude, can be recognized as associated with an established or possible health impairment or disease;
- * biomarker of susceptibility - an indicator of an inherent or acquired ability of an organism to respond to the challenge of exposure to a specific xenobiotic substance.

Biomarkers of exposure can be used to confirm and assess the exposure of individuals or populations to a particular substance. Biomarkers of effect can be used to document adverse health effects elicited by external exposure and absorption of a chemical. Thus the linkage of biomarkers between exposure and effect contributes to the definition of dose-response relationships. Biomarkers of susceptibility help elucidate the degree of the response to exposure elicited in individuals [40].

Biological Effect Monitoring: From Laboratory to Field

One of the main challenges of the Environmental Toxicology is to relate the presence of a chemical in the environment with a valid prediction of the resultant hazards for those organisms potentially receptors. Alterations or malfunction of organism normal vital functions can be identified using Biomarkers of effect, considered as biological responses (biochemical, histological, physiological, and morphological changes) to an environmental

xenobiotic at the individual level or below which demonstrates a departure from normal status. Changes at the level of population, community, or ecosystem are not included in this definition, although they are the ultimate concern of ecologists when applying the biomarker concept [40,41].

Biological effect monitoring can be an important component of studies of interactive pesticides effects and related compounds. At a practical and operational level one of the most desirable characteristics of a biomarker assay is sensitivity. An assay should be sensitive enough to detect early stages of the process of toxicity, before the organism reaches the disease state. Such an assay can give early warning of the harmful effects of a xenobiotic on individuals. Sensitive biomarkers of effect offer considerable potential to be used in studies of organisms exposed to low levels of pesticides mixtures, especially because detection of pesticide exposure is frequently extremely difficult [40,42].

Of immediate interest and relevance are nondestructive assays that provide a measure of toxic effect in vertebrate species and that can be used in both laboratory and parallel field studies. Nondestructive assays can be performed on blood, skin, excreta, and eggs of birds, fish, reptiles, and amphibians. Also, nondestructive sampling is generally preferable to destructive sampling, as it permits serial sampling of individuals and minimizes the direct influence of the experimenter on populations under investigation in the field. The development of biomarker strategies could be part of a movement toward more ecologic endpoints in the safety evaluation of chemicals [42].

Dose-response relationships between concentrations (doses) of pollutants and biomarker responses can be established under closely controlled conditions in the laboratory. The important question is whether the same or similar responses are observed in the field. First, there are serious practical difficulties in measuring dose and response in the field. Second, the field situation is likely to be complicated by other factors that are not under the control of the experimenter. The presence of other chemicals and other organisms and changes in temperature, pH, wind speed, and rate of flow of water may all have effects on a dose-response relationship. Thus, knowledge and/or control of environmental factors are important when making comparisons between laboratory and field [42]. The use of artificial or simulated real situations may provide a halfway point between the two extremes where dose-response relationships may be tested [43]. Here, to a considerable extent, environmental factors are under the control of the experimenter and studies may be designed to model real environmental conditions more closely.

On the other hand, harmful effects of contaminants on individuals can be measured in the field and attributed to a particular chemical, or combination of chemicals, in a dose-dependent manner. There is already a promising collection of assays that can be used in blood, which is relatively easy to obtain from certain species in the field.

In conclusion, nondestructive biomarker assays on vertebrates that make appropriate comparisons between laboratory and field provide a logical approach to the assessment of the environmental effects of contaminants, which has already proved its worth [42].

Developmental Toxicity

Considerable scientific evidence demonstrates that early life stages of oviparous organisms often exhibit a greater toxicological sensitivity to chemical contaminants than adult

life stages. Metabolic transformation of contaminants in eggs is expected to be low as critical enzyme systems are poorly developed in embryonic tissues [44].

Developmental toxicity is taken in its widest sense to include any effect interfering with normal development both before and after birth. It has now become clear that exposure to chemicals can cause many different effects on the embryo in addition to gross structural anomalies. This definition is very broad and includes any interference with development of the embryo before birth or interference with postnatal development. Effects can manifest themselves either prenatally or postnatally; examples include reduced body weight, growth and developmental retardation, organ toxicity, death, abortion, structural (teratogenic) defects, functional defects, latent onset of adult disease including cancer, early reproductive senescence and shortened life span [45].

Each structure in the embryo develops at a different time and at a different rate. These organ-specific periods of extreme susceptibility have termed critical periods or critical windows of susceptibility. Critical periods for functional deficit are longer than those for structural maturation and may extend postnatally [46,47].

Chemicals produce adverse effects in the developing embryo by a variety of mechanisms. These may involve interactions of the exogenous agent with endogenous receptors, adduction of reactive intermediates to DNA or proteins, lipid peroxidation, enzyme inhibition, cell membrane alterations and others [48].

Biomarkers of Developmental Toxicity

The knowledge of contaminant exposure during embryonic development is considered a crucial prerequisite for toxicological risk assessment. Biomarkers indicative of developmental toxicity could include measurements of detrimental effects produced by chemical or other exposures during embryonic stages of development. Irreversible lesions can be embryo-lethal or result in functional anomalies in the offspring. Examples of biomarkers of developmental toxicity include low birth weight, chromosome anomalies, and delayed growth of specific organ systems. Growth and survival are important indicators of normal function. From the point of view of screening, body weight gain and deviations from a normal range of body weight at a given time in development may be significant indications of developmental toxicity [49,45].

The eggs of birds, amphibians, and reptiles are readily obtained and could be widely used for biomarker studies in developmental toxicity, a practice that is usually regarded as nondestructive [45].

Biomarkers of Genotoxicity

From the ecotoxicological point of view, the evaluation of genotoxicity has a particular importance for environmental hazard assessment and biodiversity conservation, due to the fact that genotoxic effects of chemicals or complex mixtures may be crucially important at the population and community levels. Chemical pollutants can cause a decrease in wildlife populations fitness by the effects of somatic and heritable mutations that increase genomic instability and can have a selective effect against sensitive phenotypes [50,51]. Genotoxic

biomarkers, specially non-destructive short term tests, provide a particularly promising alternative of increasing interest and relevance for measuring the potential effects in vertebrate species in both, laboratory and field studies.

Among the variety of short term tests developed for detecting DNA damage, the Comet assay or Single Cell Gel Electrophoresis (SCGE) assay and the Micronucleus (MN) test are often used since they are fast, convenient and of easy application, particularly interesting as methods to undertake *in vivo* monitoring studies [52,53]. The MN assay is a cytogenetic method that has been widely used as a biological monitor of contaminated areas and in the screening of compounds to determine their genotoxicity after direct or indirect exposure *in vivo*. This test detects the effects of mutagenic agents on chromosomes by the identification of lagging chromosomes and acentric fragments that remain separate from the nucleus [52]. Thus, spindle poisons (aneugenic agents) and clastogenic compounds both lead to an increase in the number of micronucleated cells. This test can be applied to many proliferating cell population regardless of its karyotype, which makes it an appropriate test system for the monitoring of genotoxic effects in wild living species [54,55]. The SCGE assay detects DNA single strand breaks and alkali labile sites in various cells types and offers the possibility to measure DNA integrity at cellular level [53,56]. Cells with DNA damage display increased migration of DNA fragments from the nucleus, forming a “comet tail”.

Pesticide Genotoxicity

Studies on the biological effects of currently used pesticides have increased in recent years, however, there are often incomplete, and sometimes contradictory data on their genotoxicity. Pesticides tend to be very reactive compounds that can form covalent bonds with various nucleophilic centres of cellular biomolecules, including DNA. Besides, it was also showed that several pesticides induce reactive oxygen species (ROS) formation which may be involved in the production of DNA-single strand breaks [57,25]. Some studies have suggested that concentrations of such compounds at or below the levels which may occur environmentally may produce genotoxic effects when tested as combined mixtures [20].

Different pesticides were found to caused genotoxic effects evidenced by the SCGE assay and the MN test *in vitro* [58-59] and *in vivo* in different organisms such as fishes [60,61,12] amphibians [62-64] and mammals [58,25,65] including humans [66,67]. However, studies on reptiles species are rather scarce or do not exist, at our knowledge.

Genotoxicity of Glyphosate Formulation

Regarding genotoxic effect of GLY and its commercial formulation RU, several studies in different test systems have been conducted over the past years, reporting inconsistent results. Usually, studies have tested either the a.i. GLY or its commercial formulation RU, and only a few have investigated both compounds simultaneously. Li and Long [68] reported negative results for GLY genotoxic evaluation *in vitro* and *in vivo* in rat. In the same way, other studies found that neither the a.i. [69] nor the formulation RU induced an increment in the frequency of micronuclei [69-71] or chromosomal aberration [71] after *in vivo* exposure.

Contrary to these results, Bolognesi et al [25] observed that both GLY and RU produced positive genotoxic effects *in vitro* and *in vivo* in mouse. Similarly, Clements et al [62] reported positive DNA damage for RU and its active agent in *Rana catesbeiana* tadpoles. The formulation induced an increment of DNA damage on freshwater goldfish *Carassius auratus* [72] and in the fish *Tilapia rendalli*, but not in mice [73]. *In vivo* positive results for DNA adducts in mice were demonstrated with RU, while it was not the case with GLY alone [74]. Other authors reported contradictory findings *in vitro* after exposure to RU [75].

2. Effects of Pesticides on *Caiman Latirostris* Embryos: Developmental Toxicity and Genetic Alterations.

During the last years we have been developing studies in order to assess pesticide environmental contamination risk in *C. latirostris*. Considering that no previous studies had been made yet in this species, at the beginning we had to standardize two widely used genotoxic biomarker techniques, the Comet assay and the MN test, introducing different modifications to the protocols for their application in erythrocytes of *C. latirostris*. In the same way, we determined MN and damage index (Comet assay) baseline values in this species, in order to establish its suitability as a sentinel organism for genotoxic monitoring of environmental pollutants [76].

The baseline level of DNA damage varies depending on the species and the cell type used and this will influence the sensitivity of the assay to detect genotoxic effects [77]. The baseline MN levels of *C. latirostris* determined in our study was higher than those informed previously for the little amount of reptiles species studied [78,79] and was a value comparable to those reported for mammals and birds species considered good sentinel organisms for genotoxic evaluation [77]. Data referring to the application of the Comet assay was the first reported for all reptile species.

On the other hand, MN and Comet assay baseline values were found to be independent of the clutch of origin, sex and size of the animals, showing that they are quite stable among juvenile caimans, and demonstrating thereby the suitability of these techniques as accurate monitoring tools for the evaluation of genotoxic agents in *C. latirostris*, as well as the suitability of this species as a sentinel organism of genotoxic effects. This was the first reference to the application of genotoxic techniques in *C. latirostris* and the second for all crocodilians. Moreover, the possibility to apply them in peripheral blood erythrocytes and the fact that blood collection in this species does not imply any damage for the animals, represent great advantages as non-destructive monitoring techniques [76].

Then, with the aim to evaluate the potential risk associated to *in ovo* pesticide exposure undergoing in the natural environments of broad-snouted caiman, different *in vivo* toxicological assays were carried out. First, we conducted an experiment in which we exposed caiman eggs under controlled conditions to increasing concentrations of the glyphosate formulation Roundup (from RU50 to RU1750) by topication (chemical applied directly to the eggshell) at the beginning of the incubation period. We evaluate embryonic and post-natal development and genotoxic effects analysing hatching success, size of the animals at birth and later (3 and 12 months) and applying the MN test and Comet assay in erythrocytes of the newborn caimans.

The results revealed genotoxic effects of RU evidenced by the MN test and Comet assay in erythrocytes of *C. latirostris* exposed *in ovo* (Figs. 2 and 3). Moreover, differences in the percentage of DNA damage increment related to negative control observed between the highest concentration of Roundup applied (RU1750) and a widely known genotoxic agent used as positive control (Ciclophosphamide) was fairly slight (Figs. 4 and 5) [80]. This findings agree with those that reported positive genotoxic results with Roundup formulation using the MN test and/or Comet assay *in vivo* and confirm which have been concluded in other researches [62,60,72] that this herbicide may not be as safe as previously thought, at least as a formulated product, because surfactants added to the active ingredient may considerably increase its toxicity.

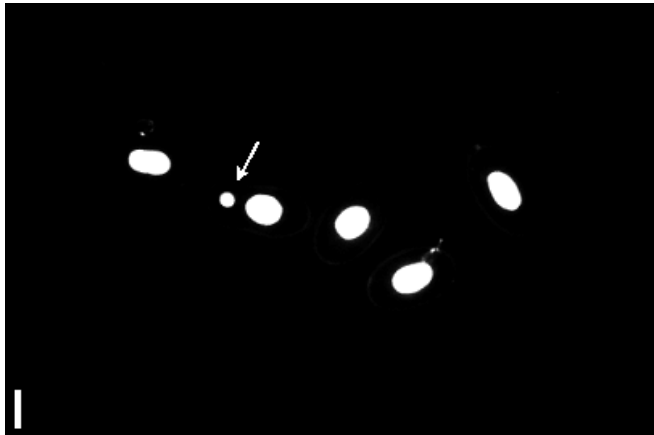


Figure 2. *C. latirostris* erythrocytes showing MN (arrow) as a result of pesticide exposure. Bar = 10 μ .

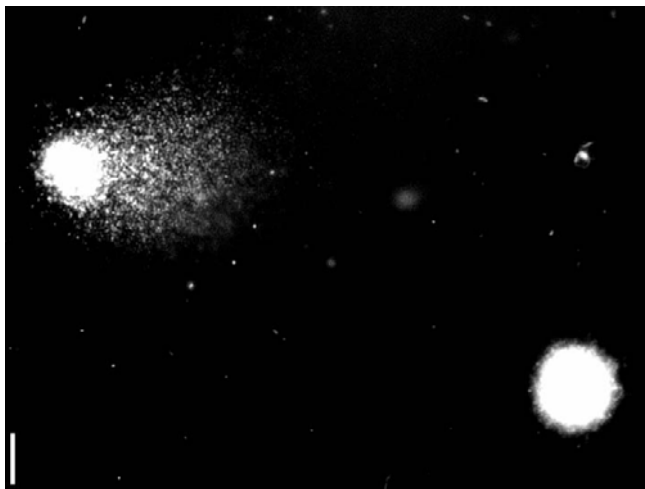


Figure 3. Comet images of two different damage classes obtained from peripheral blood erythrocytes after pesticide exposure. Bottom right: class 1, minimum damage; top left: class 3, high damage. Bar = 10 μ .

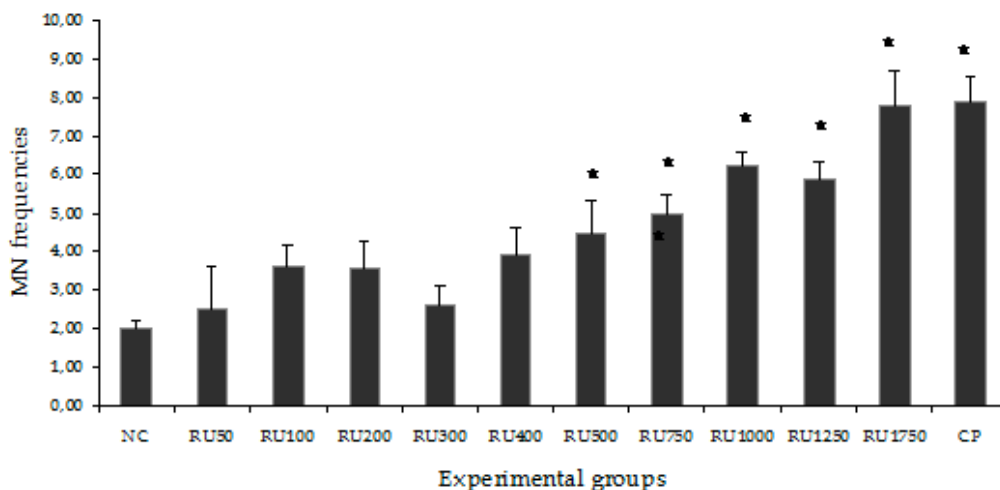


Figure 4. MN frequencies (mean $\pm$ S.E.) observed in *C. latirostris* hatchlings after *in ovo* exposure in the different experimental groups. NC: negative control; RU: groups exposed to increasing concentrations of Roundup; CP: positive control exposed to Ciclophosphamide. *Statistically different compared to NC.

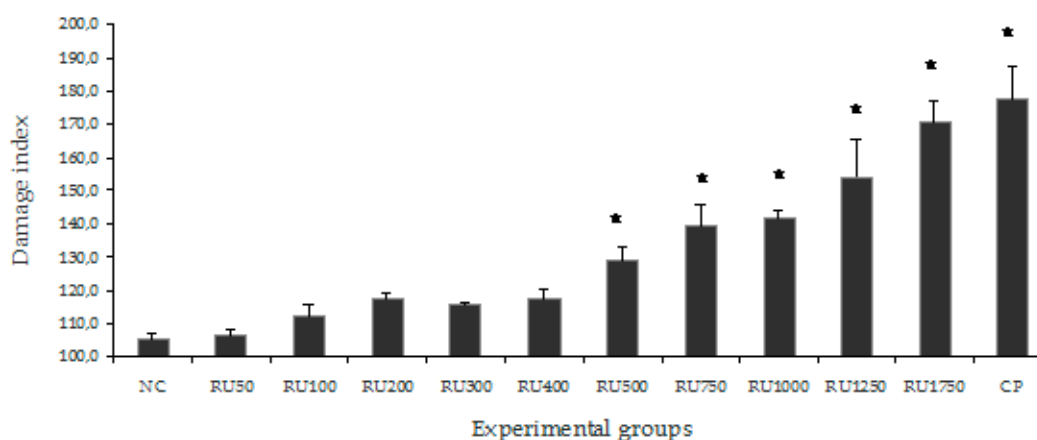


Figure 5. Damage index (comet assay) (mean $\pm$ S.E.) observed in *C. latirostris* hatchlings after *in ovo* exposure in the different experimental groups. NC: negative control; RU: groups exposed to increasing concentrations of Roundup; CP: positive control exposed to Ciclophosphamide. *Statistically different compared to NC.

On the other hand a clear concentration-effect relation was observed for MN frequencies and DI mean values as RU concentration increased, in accordance with other studies [25,62,72]. We also determined that the genotoxic effect produced by the formulation was independent of both the clutch of origin and body size of the animals.

Data on the size of animals demonstrated that no effect was observed at the moment of hatching but the increment in weight of animals exposed to the herbicide formulation was less

in comparison to the controls in the first months of caimans life, showing detrimental effect on post-natal development of the caimans exposed *in ovo*.

In a second study, we tried to simulate a possible situation of direct exposure of caiman nests in environments surrounding crops in order to model real environmental conditions more closely. We constructed artificial nests, put eggs inside and then spread them with pesticides. Two groups of nests were spread with pesticide formulations at the concentrations agriculturally recommended in two different moment of the incubation period: at the beginning and a month later, following the pesticide application schedule used in agriculture practices. The first group (T1) received a glyphosate formulation in the two applications and the second one (T2) received the glyphosate formulation in the first application and a mixture of glyphosate, endosulfan and cypermethryn in the second. A thrid group of nests remained as control. At birth, we evaluated again embryonic and post-natal development and genotoxic effects using the same endpoints than in the previous study.

None of the treatment applied produced any effect on size of the animals at birth, or in the subsequent growth evaluated after 3 or 12 months. However, the results obtained from both genotoxic endpoints, the Comet assay and the MN test, demonstrated that both T1 and T2 induced an increase in DNA damage (Figs. 6 and 7) [81].

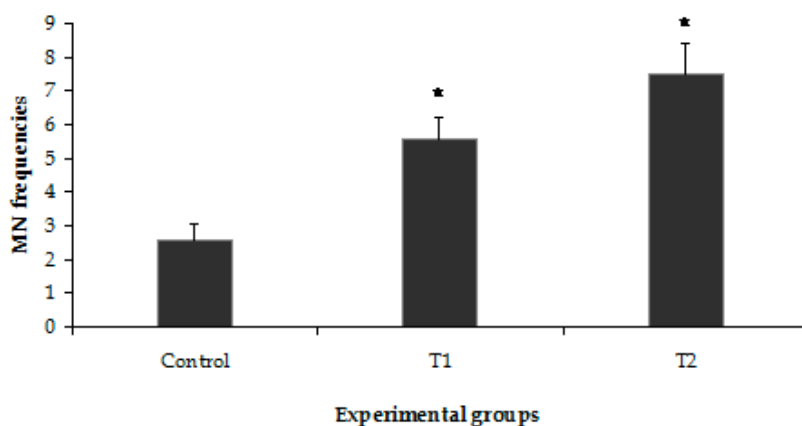


Figure 6. MN frequencies (mean $\pm$ S.E.) in different experimental groups after application of pesticides over nests. T1: treated with GLY formulation only; T2: treated with GLY formulation and then with the mixture GLY-endosulfan-cypermethryn formulations. *Statistically different compared to control.

In this experiment we demonstrated genotoxic effects of glyphosate formulation alone as well as in combination with endosulfan and cipermethryn commercial formulations on *C. latirostris* embryos in exposure circumstances similar to those possibly happening nowadays in natural environments near to crops, where this and other important species live. Even when this experimental design could be considered extreme or unreal taking into account that direct pesticide spray over caiman nests rarely happens, it is a fact that neighbouring cropland habitats receive recurrent and continuous exposure to low levels of pesticides, that could have cumulative deleterious effects on animals living there, specially considering the differential sensitivities that exist among them [10].

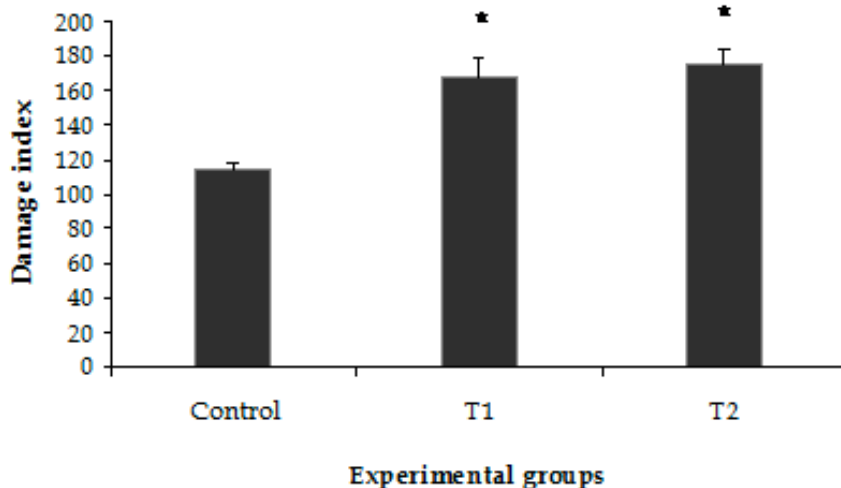


Figure 7. Damage index (Comet assay) (mean $\pm$ S.E.) in different experimental groups after application of pesticides over nests. T1: treated with GLY formulation only; T2: treated with GLY formulation and then with the mixture GLY-endosulfan-cypermethryn formulations. *Statistically different compared to control.

3. Conclusion

The identification of sensitive biomarkers in sentinel species among the natural biota is imperative to thoroughly evaluate genetic damage, which has significant consequences for short- and long-term survival of the natural species [82]. While rapid progress has been made in the last few decades to determine the impact of environmental factors on the induction of genetic damage in human populations, there has been relatively limited progress to determine the impact of such factors in wild or natural species [14]. The results obtained in our studies with *C. latirostris* demonstrated that this species is a useful sentinel for genotoxic monitoring of environmental contamination and that the Comet assay and the MN test are sensitive tools in determining the potential genotoxicity of pesticides *in vivo*. Furthermore, our studies also showed detrimental genotoxic and developmental effects in caimans after *in ovo* exposure to pesticides commonly and increasingly used in agriculture. Any damage induced in essential portions of the DNA, if not correctly repaired, can become particularly pronounced when the lesions are produced during embryogenesis, when rapid organogenesis is taking place [83].

Data provided here will be useful for future work involving the biomonitoring of natural regions where *C. latirostris* can be under increasing contaminant pressure, mainly taking into account the increasing ecological and economic value that this species have.

In our study, the herbicides were tested as the complex commercial mixtures due to this is the form in which they are routinely applied in agriculture and introduced into the environment. Considering the wide use of this pesticides mainly for agricultural activities, risk assessment of commercial technical formulations regarding its potential in promoting damage in the genetic material of natural species, has to be considered of primary importance.

Acknowledgements

Our studies are supported by Proyecto Yacaré and Yacarés Santafesinos (Con. Gob. Sta. Fe/MUPCN), Universidad de Buenos Aires (MDM PIP 5012- CONICET, UBACyT X107-UBA, Bs. As., Argentina) and Universidad Nacional del Litoral (UNL-Sta. Fe, Argentina). We would like to thank other members of Proyecto Yacaré (www.mupcn.com.ar/yacare).

References

- [1] Bickham, J.W.; Sandhu, S.; Hebert, P.D.N.; Chikhi, L.; Athwal, R. Effects of chemical contaminants on genetic diversity in natural populations: implications for biomonitoring and ecotoxicology. *Mutat. Res.*, 2000, 463, 33–51.
- [2] Brown, V. WWF, *Detox Campaign*. Causes for concern: chemicals and wildlife, 2003.
- [3] EPA Office of Pesticide Programs. *What is a Pesticide?*. 2006. Available from: <http://www.epa.gov/pesticides/about/>.
- [4] Pengue, W.A. Transgenic crops in Argentina and its hidden costs, in: E. Ortega and S. Ulgiati (Eds.), *Proceedings of IV Biennial International Workshop "Advances in Energy Studies"*, Campinas, SP, Brazil, 2004, pp. 91-101.
- [5] Moses, M.; Johnson, E.S.; Anger, W.K.; Buse, V.W.; Horstman, S.W.; Jackson, R.J.; Lewis, R.G.; Maddy, K.T.; McConnell, R.; Meggs, W.T.; Zahm, S.H. Environmental equity and pesticide exposure. *Toxicol. Ind. Health*, 1993, 9, 913-959.
- [6] Lehmann, V.; Pengue, W.A. Herbicide tolerant soybean: Just another step in a technology treadmill?. *Biotech. Develop. Mon.*, 2000, 43, 11-14.
- [7] Larriera, A.; Siroski, P.; Cardozo, M. Caiman yacare and Caiman latirostris ranching program in Corrientes, Argentina: YACARÉ PORÁ, in: *Proceedings of the 18th Working Meeting of the Crocodile Specialist Group of the Species Survival Commission of IUCN - The World Conservation Union*, Montelimar, France, 2006, pp. 374–378.
- [8] McLaughlin, A.; Mineau, P. The impact of agricultural practices on biodiversity. *Agric. Ecos. Environ.*, 1995, 55, 201-212.
- [9] Vrzoc, M.; Petras, M.L. Comparison of alkaline single cell gel -Comet- and peripheral blood micronucleus assays in detecting DNA damage caused by direct and indirect acting mutagens. *Mutat. Res.*, 1997, 381, 31–40.
- [10] Freeman, J.L.; Rayburn, A.L. In vivo genotoxicity of atrazine to anuran larvae. *Mutat. Res.*, 2004, 560, 69–78.
- [11] Islam, S.; Tanaka, M. Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. *Marine Pollut. Bull.*, 2004, 48, 624–649.
- [12] de Campos Ventura, B.; de Fransceschi de Angelis, D.; Marin-Morales, M.A. Mutagenic and genotoxic effects of the Atrazine herbicide in *Oreochromis niloticus* (Perciformes, Cichlidae) detected by the micronuclei test and the comet assay. *Pest. Biochem. Physiol.*, 2008, 90, 42–51.
- [13] Saura-Mas, S.; Boone, M.D.; Bridges, C.M. Evaluation of direct effects of an insecticide on Gray Treefrogs: laboratory and fields trials. *J. Herpetol.* 2002, 36, 715-719.

- [14] Jha, A.N. Ecotoxicological applications and significance of the comet assay. *Mutag.*, 2008, 1–15. doi:10.1093/mutage/gen014.
- [15] Freemark, K.; Boutin, C. Impacts of agricultural herbicide use on terrestrial wildlife in temperate landscapes: *A review with special reference to North America. Agric. Ecosys. Environm.*, 1995, 52, 67–91.
- [16] Tsui, M.T.K.; Chu, L.M. Aquatic toxicity of glyphosate-based formulations: comparison between different organisms and the effects of environmental factors. *Chemosph.*, 2003, 52, 1189–1197.
- [17] Walker, C.H.; Hopkin, S.P.; Sibly, R.M.; Peakall, D.B. *Principles of Ecotoxicology*, London, Taylor & Francis, 1996.
- [18] Pimentel, D.; Greiner, A.; Bashore, T. Economic and environmental costs of pesticide use. In: Rose, J. (ed.) *Environmental Toxicology: Current Developments*, Gordon and Breach Science Publishers, UK, 1998, pp. 121–187.
- [19] Cox, C. Inert ingredients in pesticides: *Who's keeping secrets?*. *J. Pestic. Reform*, 1999, 19, 2–7.
- [20] Committee on Toxicity. Committee on Toxicity of Chemicals in Food, Consumer Products and the Environment. *Risk Assessment of Mixtures of Pesticides and Similar Substances*, © Crown Copyright, 2002.
- [21] U.S. EPA. Pesticide Fact Sheet: Glyphosate, Office of Pesticide Programs, EPA Publication No. 540/FS-88-124, Washington, DC, 1986.
- [22] WHO. Environmental Health Criteria 159: *Glyphosate*, Geneva, 1994.
- [23] Amrhein, N.; Deus, B.; Gehrke, P.; Steinrücken, H.C. The site of the inhibition of the Shikimate pathway by glyphosate. *Plant Physiol.*, 1980, 66, 830–834.
- [24] Atkinson, D. Toxicological properties of glyphosate, in: Grossbard, E.; Atkinson, D. (eds.), *The Herbicide Glyphosate, Butterworth and Co. Ltd.*, Toronto, Canada, 1985, pp. 127–133.
- [25] Bolognesi, C.; Bonatti, S.; Degan, P.; Gallerani, E.; Peluso, M.; Rabboni, R.; Roggieri, P.; Abbondandolo, A. Genotoxic activity of glyphosate and its technical formulation Roundup. *J. Agric. Food Chem.*, 1997, 45, 1957–1962.
- [26] Williams, G.M.; Kroes, R.; Munro, I.C. Safety Evaluation and Risk Assessment of the Herbicide Roundup and Its Active Ingredient, Glyphosate, for Humans, *Regul. Toxicol. Pharmacol.*, 2000, 31, 117–165.
- [27] Franz, J.E.; Mao, M.K.; Sikorski, J.A. Glyphosate: A Unique Global Herbicide, ACS Monograph No. 189. *Am. Chem. Soc. (ACS)*, Washington, DC, 1997.
- [28] Bradberry, S.M.; Proudfoot, A.T.; Vale, J.A. Glyphosate Poisoning, *Toxicol. Rev.*, 2004, 23.
- [29] Brisbin Jr., I.L.; Jagoe, C.H.; Gaines, K.F.; Gariboldi, J.C. Environmental contaminants as concerns for the conservation biology of crocodilians, in: *Crocodiles: Proceedings of the 14th Working Meeting of the Crocodile Specialist Group of the Species Survival Commission of IUCN - The World Conservation Union*, Singapore, Japan, 1998, pp. 155–173.
- [30] Campbell, K.R. Ecotoxicology of crocodilians. *Appl. Herpetol.*, 2003, 1, 45–163.
- [31] Hall, R.J.; Henry, P.F.P. Assessing effects of pesticides on amphibians and reptiles: status and needs. *Herpetol. J.*, 1992, 2, 65–71.

- [32] Crain, D.A.; Spiteri, I.D.; Guillette Jr., L.J. The functional and structural observations of the neonatal reproductive system of alligators exposed in ovo to atrazine, 2,4-D, or estradiol. *Toxicol. Indust. Health*, 1999, 15, 180-185.
- [33] Milnes, M.R.; Allen, D.; Bryan, T.; Sedacca, C.; Guillette Jr., L.J. Developmental effects of embryonic exposure to toxaphene in the American alligator (*Alligator mississippiensis*), *Comp. Bioch. Phys. Part C: Toxicol. Pharmacol.*, 2004, 138, 81-87.
- [34] Guillette Jr., L.J.; Brock, J.W.; Rooney, A.A.; Woodward, A.R. Serum concentration of various environmental contaminants and their relationship to sex steroid concentrations and phallus size in juvenile american alligators. *Arch. Environ. Contam. Toxicol.*, 1999, 36, 447-455.
- [35] Lind, P.M.; Milnes, M.R.; Lundberg, R.; Bermudez, D.; Örborg, J.; Guillette Jr., L.J. Pesticide-Polluted Lake (Lake Apopka, Florida). *Environ. Health Persp.*, 2004, 112, 359-372.
- [36] Crain, D.A.; Noriega, N.; Vonier, P.M.; Arnold, S.F.; McLachlan, J.A.; Gillette Jr., L.J. Cellular bioavailability of natural hormones and environmental contaminants as a function of serum and cytosolic binding factors. *Toxicol. Indust. Health*, 1998, 14, 261-273.
- [37] Yanosky, A.A. Histoire naturelle du Caïman à museau large (*Caiman latirostris*), un Alligatoriné mal connu, *Rev. Fr. Aquariol. Herpetol.*, 1990, 17, 19-31.
- [38] Larriera, A.L.; Imhof, A.; Siroski, P. Estado actual de los programas de conservación y manejo del género Caiman en Argentina, in: Castroviejo, J.; Ayarzagüena, J.; Velasco, A. (eds.), *Contribución al conocimiento del Género Caiman de Suramerica*, Public. Asoc. Amigos de Doña Ana 18, Sevilla, España, 2008, pp. 294.
- [39] Larriera, A. A program of monitoring and recovering of caimans populations in Argentina with the aim of management, in: *Crocodiles. Proceedings of the 10th Working Meeting of the Crocodile Specialist Group of the Species Survival Commission of IUCN - The World Conservation Union*, Vol 2, Gland, Switzerland, 1990, pp. 1-5.
- [40] IPCS Environmental Health Criteria 155. Biomarkers and Risk Assessment: Concepts and Principles, Geneva, World Health Organization, *International Programme on Chemical Safety*, 1993.
- [41] Peakall, D.B.; Walker, C.H. The role of biomarkers in environmental risk assessment. 3: Vertebrates. *Ecotoxicol.*, 1994, 3, 173-179.
- [42] Biomarker Strategies to Evaluate the Environmental Effects of Chemicals, *Environ. Health Perspect.*, 1998, 106 (Suppl 2), 613-620.
- [43] Crossland, N.O. Extrapolating from mesocosms to the real world. *Toxicol Ecotoxicol News* 1994, 1, 15-22.
- [44] Russel, R.W.; Gobas, F.A.P.; Haffner, G.D. Maternal transfer and in ovo exposure of organochlorines in oviparus organisms: a model and field verification. *Environ. Sci. Technol.*, 1999, 33, 416-420.
- [45] IPCS Environmental Health Criteria 225. Principles For Evaluating Health Risks To Reproduction Associated With Exposure To Chemicals, Geneva, World Health Organization, *International Programme on Chemical Safety*, 2001.
- [46] Daston, G.P.; Manson, J.M. Critical periods of exposure and developmental outcome. *Inhal Toxicol*, 1995, 7, 863-871.

- [47] Daston, G.P. Other functional abnormalities: methods and data evaluation. In: Hood RD (ed.), *Handbook of developmental toxicology*. Boca Raton, Florida, CRC Press, 1996, pp 357–381.
- [48] US NRC. Scientific frontiers in developmental toxicology and risk assessment. Washington, DC, US *National Research Council, National Academy Press*, 2000.
- [49] Adams, J.; Buelke-Sam, J. Behavioral assessment of the postnatal animal: Testing and methods development. In: Kimmel CA & Buelke-Sam J (ed.), *Developm. Toxicol.* New York, Raven Press, 1981, pp 233–258.
- [50] [51] Rajaguru, P.; Vidya, L.; Baskarasethupathi, B.; Kumar, P.A.; Palanivel, M.; Kalaiselvi, K. Genotoxicity evaluation of polluted ground water in human peripheral blood lymphocytes using the comet assay. *Mutat. Res.*, 2002, 517, 29–37.
- [51] Castaño, A.; Bols, N.; Braunbeck, T.; Diericks, P.; Halder, M.; Isomaa, B.; Kawahara, K.; Lee, L.E.; Mothersill, C.; Part, P.; Repetto, G.; Rieogo Sintes, J.; Rufli, H.; Smith, R.; Wood, C.; Segner, H. The use of fish cells in ecotoxicology. *Alt. Lab. Anim.*, 2003, 31, 317–351.
- [52] Schmid, W. The micronucleus test. *Mutat. Res.*, 1975, 31, 9–15.
- [53] Singh, N.P.; McCoy, M.T.; Tice, R.R.; Schneider, E.L. A simple technique for quantitation of low levels of DNA damage in individuals cells. *Exp. Cell. Res.*, 1988, 175, 184–191.
- [54] Ueda, T.; Hayashi, M.; Ohtsuka, Y.; Nakamura, T.; Kobayashi, J.; Sofuni, T. A preliminary study of the micronucleus test by acridine orange fluorescent staining compared with cromosomal aberration test using fish erythropoietic and embrionic cells. *Water Sci. Technol.*, 1992, 25, 235–240.
- [55] Hayashi, M.; Ueda, T.; Uyeno, K.; Wada, K.; Kinae, N.; Saotome, K.; Tanaka, N.; Takai, A.; Sasaki, Y.F.; Asano, N.; Sofuni, T.; Ojima, Y. Development of genotoxicity assay systems that use aquatic organisms. *Mutat. Res.*, 1998, 399, 125–133.
- [56] Hartmann, A.; Agurell, E.; Beevers, C.; Brendler-Schwaab, S.; Burlinson, B.; Clay, P.; Collins, A.; Smith, A.; Speit, G.; Thybaud, V.; Tice, R.R. Recomendations for conducting the in vivo alkaline Comet assay. *Mutag.*, 2003, 18, 45–51.
- [57] Bagchi, D.; Bagchi, M.; Hassoun, E.A.; Stohs, S.J. In vitro and in vivo generation of reactive oxygen species, DNA damage and lactate dehydrogenase leakage by selected pesticides. *Toxicol.*, 1995, 140, 129–140.
- [58] Zuyao, N.; Shouqi, L.; Yuqing, L.; Ying, T.; Dinguo, P. Induction of micronucleus by organophosphorus pesticides in vivo and in vitro. *J. West China Univ. Med. Sci.*, 1993, 24, 82–86.
- [59] Mattiuzzo, M.; Fiore, M.; Ricordy, R.; Degrassi, F. Aneuploidy-inducing capacity of two widely used pesticides. *Carcinog.*, 2006, 27, 2511–2518.
- [60] Grisolia, C.K. A comparison between mouse and fish micronucleus test using cyclophosphamide, mitomycin C and various pesticides. *Mutat. Res.*, 2002, 518, 145–150.
- [61] Ateeq, B.; Farah, M.A.; Ahmad, W. Detection of DNA damage by alkaline single cell gel electrophoresis in 2,4-dichlorophenoxyacetic-acid- and butachlor-exposed erythrocytes of *Clarias batrachus*. *Ecotoxicol. Environm. Saf.*, 2005, 62, 348–354.
- [62] Clements, C.; Ralph, S.; Petras, M. Genotoxicity of select herbicides in *Rana catesbeiana* tadpoles using the alkaline single-cell gel DNA electrophoresis (comet) assay. *Environ. Mol. Mutagen.*, 1997, 29, 277–288.

- [63] Campana, M.A.; Panzeri, A.M.; Moreno, V.J.; Dulout, F.N. Micronuclei induction in *Rana catesbeiana* tadpoles by the pyrethroid insecticide lambda-cyhalothrin. *Genet. Mol. Biol.*, 2003, 26, 99–103.
- [64] Lajmanovich, R.C.; Cabagna, M.; Peltzer, P.M.; Stringhini, G.A.; Attademo, A.M. Micronucleus induction in erythrocytes of the *Hyla pulchella* tadpoles (Amphibia: Hylidae) exposed to insecticide endosulfan. *Mutat. Res.*, 2005, 587, 67–72.
- [65] Knopper, L.; Mineau, P.; McNamee, J.P.; Lean, D.S. Use of Comet and Micronucleus Assays to Measure Genotoxicity in Meadow Voles (*Microtus pennsylvanicus*) Living in Golf Course Ecosystems Exposed to Pesticides. *Ecotoxicol.*, 2005, 14, 323–335.
- [66] Garaj-Vhrovac, V.; Zeljezic, D. Evaluation of DNA damage in workers occupationally exposed to pesticides using single-cell gell electrophoresis (SCGE) assay. Pesticide genotoxicity revealed by the comet assay. *Mutat. Res.*, 2000, 469, 279–285.
- [67] Simoniello, M.F.; Kleinsorge, E.C.; Scagnetti, J.A.; Grigolato, R.A.; Poletta, G.L.; Carballo, M.A. DNA damage in workers occupationally exposed to pesticides mixtures, *J. Appl. Toxicol.*, 2008. DOI: 10.1002/jat.1361.
- [68] Li, A.P.; Long, T.J. An evaluation of the genotoxic potential of glyphosate. *Fundam. Appl. Toxicol.* 1988, 10, 537–546.
- [69] Rank, J.; Jensen, A.G.; Skov, B.; Pedersen, L.H.; Jensen, K. Genotoxicity testing of the herbicide Roundup and its active ingredient glyphosate isopropylamine using the mouse bone marrow micronucleus test, Salmonella mutagenicity test, and allium anaphase–telophase test. *Mutat. Res.*, 1993, 300, 29–36.
- [70] Kier, L.D.; Stegeman, S.D.; Dudek, S.; McAdams, J.G.; Flowers, F.J.; Huffman, M.B.; Heydens, W.F. Genotoxicity studies of glyphosate, alachlor and butachlor herbicide formulations. *Fundam. Appl. Toxicol.*, 1997, 36, 1, 305.
- [71] Dimitrov, B.D.; Gadeval, P.G.; Benova, D.K.; Bineva, M.V. Comparative genotoxicity of the herbicides Roundup, Stomp and Reglone in plant and mammalian test systems. *Mutag.*, 2006, 21, 375–382.
- [72] Cavas, T.; Könen, S. Detection of cytogenetic and DNA damage in peripheral erythrocytes of goldfish (*Carassius auratus*) exposed to a glyphosate formulation using the micronucleus test and the comet assay, *Mutag.*, 2007, 22, 263–268.
- [73] Grisolia, C.K. A comparison between mouse and fish micronucleus test using cyclophosphamide, mitomycin C and various pesticides. *Mutat. Res.*, 2002, 518, 145–150.
- [74] Peluso, M.; Munnia, A.; Bolognesi, C.; Parodi, S. 32Ppostlabeling detection of DNA adducts in mice treated with the herbicide Roundup. *Environ. Mol. Mutagen.*, 1998, 31, 55–59.
- [75] Šiviková, K.; Dianovský, J. Cytogenetic effect of technical glyphosate on cultivated bovine peripheral lymphocytes. *Inter. J. Hyg. Environm. Health*, 2006, 209, 15–20.
- [76] Poletta, G.L.; Larriera, A.; Kleinsorge, E.; Mudry, M.D. Caiman latirostris (broad-snouted caiman) as a sentinel organism for genotoxic monitoring: Basal values determination of micronucleus and comet assay. *Mutat. Res.*, 2008, 650, 202–209.
- [77] Kirsch-Volders, M.; Sofuni, T.; Aardema, M.; Albertini, S.; Eastmond, D.; Fenech, M.; Ishidate Jr., M.; Kirchner, S.; Lorge, E.; Morita, T.; Norppa, H.; Surralés, J.; Vanhauwaert, A.; Wakata, A. Report from the in vitro micronucleus assay working group. *Mutat. Res.*, 2003, 540, 153–163.

- [78] Zúniga-González, G.; Torres-Bugarín, O.; Luna-Aguirre, J.; González-Rodríguez, A.; Zamora-Perez, A.; Gómez-Meda, B.C.; Ventura-Aguilar, A.J.; Ramos-Ibarra, M.L.; Ramos-Mora, A.; Ortiz, G.G.; Gallegos-Arreola, M.P. Spontaneous micronuclei in peripheral blood erythrocytes from 54 animal species (mammals, reptiles and birds): Part two. *Mutat. Res.*, 2000, 467, 99-103.
- [79] Zúniga-González, G.; Torres-Bugarín, O.; Zamora-Perez, A.; Gómez-Meda, B.C.; Ramos-Ibarra, M.L.; Martinez-González, S.; González-Rodríguez, A.; Luna-Aguirre, J.; Ramos-Mora, A.; Ontiveros-Lira, D.; Gallegos-Arreola, M.P. Differences in the number of micronucleated erythrocytes among young and adult animals including humans Spontaneous micronuclei in 43 species. *Mutat. Res.*, 2001, 494, 161-167.
- [80] Poletta, G.; Larriera, A.; Kleinsorge, E.; Mudry, M.D. Genotoxicity of the herbicide formulation Roundup® (glyphosate) in *Caiman latirostris* evidenced by the Comet assay and the Micronucleus test. 19th *Working Meeting of the Crocodile Specialist Group*, IUCN-SSC, 2008, Santa Cruz de la Sierra, Bolivia.
- [81] Poletta, G.L.; Kleinsorge, E.; Mudry, M.D.; Larriera, A.; Siroski, P.A. *Caiman latirostris* embryos exposed to pesticides in a field experiment simulating agrochemical application practices. 19th *Working Meeting of the Crocodile Specialist Group*, IUCN-SSC, 2008, Santa Cruz de la Sierra, Bolivia.
- [82] Moore, M.N.; Depledge, M.N.; Readman, J.W.; Leonard, D.R.P. An integrated biomarker-based strategy for ecotoxicological evaluation of risk in environmental management. *Mutat. Res.*, 2004, 552, 247-268.
- [83] Lee, R.F.; Steinert, S.. Use of the single cell gel electrophoresis/comet assay for detecting DNA damage in aquatic (marine and freshwater) animals. *Mutat. Res.*, 2003, 544, 43-64.

Chapter 7

EVIDENCE OF ANTIMICROBIAL RESISTANCE IN EURASIAN OTTER (*LUTRA LUTRA* LINNAEUS, 1758) FECAL BACTERIA IN PORTUGAL

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Abstract

Bacterial antimicrobial resistance is a well recognized problem for human and animal health. Evaluation of antimicrobial resistance in enteric microbiota is a powerful tool to monitor selective pressure from drugs used for treating animal and human infectious diseases, or from compounds used in farming practices for prophylaxis. Screening antibiotic susceptibility patterns of wildlife animal isolates provides useful information on environmental contamination by resistant strains, deriving from contaminated effluents or from free-ranging animals that are potential vectors of resistance determinants.

Recently, we examined the antimicrobial resistance of *Escherichia coli* (n=7) and *Enterococcus* spp. (n=26) isolates obtained from 35 fecal samples from Eurasian otter (*Lutra lutra* Linnaeus, 1758) free-living in Pego do Altar and Monte Novo reservoirs and associated river stretches in Alentejo region, South Portugal. The 12 antimicrobials, tested as recommended in the Clinical and Laboratory Standards Institute guidelines, belonged to different antimicrobial drug classes, acting through inhibition of transduction (n=6), cell wall synthesis (n=4), DNA gyrase (n=1) and folate synthesis (n=1).

Levels of resistance were different for the two bacterial genera considered. All *E. coli* isolates were susceptible to 5 of the antimicrobials tested, while none of *Enterococcus* spp. isolates was susceptible to all compounds. All enterococci were resistant to cephalexin, cephotaxim, enrofloxacin and streptomycin. With exception of one *E. coli* isolate, all bacteria presented a multiresistant profile, being resistant to more than one antimicrobial drug class.

The animals sampled were not likely to have been subject to antibiotherapy. Therefore, low resistance levels were expected, since antimicrobial treatment exposure is still considered the major reason for emergence, selection, and dissemination of resistant bacteria. The multiresistant profile found in most isolates supports the hypothesis that environmental exposure of intestinal microbiota to antimicrobial agents may select for resistant bacterial strains, but the occurrence of point mutations or acquisition of transmissible mobile DNA elements responsible for antimicrobial resistance must also be taken into consideration.

The antimicrobial resistance profile of *E. coli* and *Enterococcus* spp. isolates from otters' fecal samples may provide useful information to assess the potential of antimicrobial resistance transmission from the environment contaminated by humans and domestic and wild animals, being particularly relevant in dams and rivers where human activities, such as farming or outdoor recreational activities, occur near or in the water. Resistance profiles should be taken upon consideration in future plans regarding management and conservation of otters, particularly in environments where cattle density near aquatic systems is high.

Introduction

Eurasian otters (*Lutra lutra* Linnaeus, 1758) are medium size mustelids, with approximately 60 to 90 cm long, 6 to 10 kg weight, short legs and a fusiform body ending in a long tail, usually 35 to 47 cm long. These free-range otters have interdigital membranes that allow them to actively swim and forage in water. They are territorial, solitary and nocturnal animals. They breed all year, although births of one to five cubs are most common in spring, after a two months gestation. They may live up to 9 years in the wild and up to 12 years in captivity. They eat mainly fish, but their diet may also include crustaceans, amphibians, birds and small rodents (Carnivora, 2008).

Eurasian otters are classified as "Near Threatened" mammals. In Europe, they are one of the main animal species under protection, and their capture and habitat destruction are interdicted by the Bern and Washington Conventions (IUCN, 2006). Their distribution extended across Europe and Asia, but after the 1950s it declined in Western Europe, and otters became absent from large areas of their former range (Foster-Turley et al., 1990; Mason & MacDonald, 1986). There has been a species recovery in most of Europe due to natural conditions, conservation projects and reintroduction programs (Cortés et al., 1998; IUCN, 2006; Kranz & Toman, 2000).

Otters can be found in a wide variety of aquatic habitats, including highland and lowland lakes, rivers, streams, marshes, swamp forests and coastal areas. They are easily adaptable, being able to live in salt and freshwater habitats and in sewerage systems from urban areas. Generally, otter distribution is correlated with the presence of freshwater and bank side vegetation (Reuther & Hilton-Taylor, 2004), and their habitats are extremely vulnerable to man-made changes. Populations' densities are affected by rivers canalisation, removal of bank side vegetation, dam construction, wetlands draining, aquaculture activities and associated man-made impacts on aquatic systems. Pollution is a major threat to otters in western and central Europe, where the main pollutants are the organochlorines dieldrin and DDT/DDE, polychlorinated biphenyls and mercury, since rivers and lakes acidification results in the decline of fish biomass, reducing the otter's food resources. This reduction can also be due to organic pollution from nitrate fertilisers, untreated sewage, or farm slurry (Reuther & Hilton-Taylor, 2004). Other major causes of otters' mortality are drowning, due to

the presence of fyke nets set for eels or fish as well as creels set for marine crustaceans, road kills, and poaching.

Contrasting the apparent pattern of decline in Eurasian otter populations until the 1990s (Mason & MacDonald, 1986; Foster-Turley et al., 1990; MacDonald and Mason, 1994; Romanowski et al., 1997; Cortés et al., 1998; Ruiz-Olmo & Delibes, 1998; Kranz & Toman, 2000; Conroy & Chanin, 2002), otters in Portugal have always been considered one of the most viable populations from Europe (Macdonald & Mason, 1982; Mason & MacDonald, 1986; Santos-Reis, 1983; Santos-Reis et al., 1995; Trindade et al., 1998). Although not well known, otter densities are suspected to be high in Portugal (Santos-Reis et al., 2003). They are distributed throughout the country, inhabiting all types of river and wetland systems, including coastal areas (Beja, 1995; Santos-Reis et al., 1995; Trindade et al., 1998), which may result from the large diversity of preys' and favourable habitat found (MacDonald & Mason, 1982; Farinha & Trindade, 1994; Santos-Reis et al., 1995). Some populations cross the boundary between Portugal and Spain.

In Portugal, otters' status was recently changed from "Insufficiently Known" to "Least Concerned" (Cabral et al., 2005). Otters' conservation in this country is a vital issue and their conservation is mandatory by the "Habitats" Directive and Natura 2000 Network, since populations are stable, representing a biodiversity "hotspot".

Dams can adversely influence Eurasian otters' distribution and are frequently suggested as a contributing factor to the decline of this species in Europe (MacDonald & Mason, 1984; Ruiz-Olmo, 2001). However, otters can use these man-made habitats under some circumstances, such as the ones occurring in Portugal. The favorable status of otter populations in Portugal may lead them to occupy, especially during the dry season, habitats like dams, which are suboptimal in terms of refuge but offer profitable prey (Pedroso & Santos Reis, 2006). Sales-Luís et al. (2007) suggested that otters using tributaries near dams feed predominantly in the dam, and results by these authors indicate that otter populations make use of these conjoint systems to ensure their survival. These infra-structures offer plenty of water and suitable preys, attracting otters during the recurrent periods of dryness suffered by Mediterranean water systems (Prenda et al., 2001; Pedroso & Santos Reis, 2006). In addition, dams are used by humans for recreational activities, like bathing, camping and water sports.

The accurate determination of otter populations is extremely difficult, and capture, telemetry and other invasive methods are being questioned. Studies can rely on direct observation, but this method only allows to determine otters numbers in specific habitats and regions where the animals are diurnal (Kruuk, 1995). Direct observation requires experienced observers and special habitat features (Ruiz-Olmo et al., 2001), which is also true for quantification methods based on footprints identification. The urge for information regarding genetic, demographic and life-history data from this species made the development of molecular identification methods essential (Kohn & Wayne, 1997; Kruuk, 2006). Individual identification can now be performed by fecal DNA analysis obtained from fresh scats collected from surveys conducted at sunrise in consecutive days, which allows the determination of otter's abundance and territory range (Dallas et al., 2003; Arrendall et al., 2004; Selkoe & Toonen, 2006).

Regarding river-otters health status, these animals can suffer from viral, bacterial, fungal and parasitic diseases (Kimber & Kollias II, 2000), but valid microflora characterization studies are scarce and little is known about the clinical significance of isolates and

environmental contaminant-related diseases, or about their potential role as reservoirs of antimicrobial resistant bacteria.

There are several studies that describe the difficulties experienced in the treatment of human-related infections promoted by antimicrobial resistant bacteria (Monroe & Polk, 2000). It has also been observed that human and animal infections are increasingly related, making studies on identification of animal and environmental reservoirs of antimicrobial resistant bacteria a matter of public health importance (Cole et al., 2005; Sayah et al., 2005).

Until recently, it was assumed that the emergence, selection, and dissemination of antimicrobial resistant bacteria were mainly caused by selective pressure related to antibiotic misuse and abuse (Monroe & Polk, 2000; Sayah et al., 2005). Antimicrobial resistance characteristics may be due to intrinsic mechanisms that promote the inactivation or modification of antimicrobial compounds, the decrease of bacterial cell wall or membrane permeability, the activation of efflux pump mechanisms that actively expel antimicrobials, or the modification of target receptors (Sayah et al., 2005). Resistance characteristics may also be explained by the ability of expression of acquired resistance mechanisms that some bacterial strains demonstrate. Examples of these mechanisms comprise the occurrence of chromosomal gene mutations or the expression of resistance genes present in plasmids, transposons, bacteriophages or other mobile elements acquired from other bacteria. These elements are known to be responsible for the transfer of multiresistant profiles, characterized by the phenotypic resistance to more than one antimicrobial drug class (Sayah et al., 2005).

Antimicrobial resistance characteristics presented by the normal enteric microbiota can be used to infer on the extent of selective pressure caused by antimicrobial use in human and animal populations (SWARM, 2007). Commensal intestinal bacteria, such as *Escherichia coli* and *Enterococcus* spp., may act as reservoirs for resistance genes and are able to disseminate bacterial resistant determinants to animal or human pathogens (Skurnik et al., 2006; SWARM, 2007). Therefore, the evaluation of antimicrobial resistance profiles of bacteria belonging to the normal enteric microbiota of healthy animals can be used as an indicator of antimicrobial resistance dispersion in the environment (SWARM, 2007).

E. coli is a facultative anaerobic non-spore forming Gram-negative bacteria. Their pleomorphic rods are often mobile by peritrichous flagella (Bettelheim, 1992; ICMSE, 1996). This commensal bacterium is commonly found in the digestive tract of humans and warm blood animals, being isolated from feces from humans and domestic and wild animals (Bettelheim, 1992; ICMSE, 1996). *E. coli* is mainly transmitted by fecal-oral route, but dissemination through contaminated water has also been described (Bettelheim, 1992; Blackburn & McCarthy, 2000; Bertin et al., 2001). In fact, since *E. coli* represents 1% of the total fecal microbiota of humans and warm blood animals, it is likely for sewers to always contain high levels of this microorganism.

E. coli may present stable plasmids that can harbor antimicrobial resistance genes or other virulence factors (Bettelheim, 1992; Kimura et al., 2000). The ability of this microorganism to survive in adverse conditions facilitates the potential transmission of antimicrobial resistance genes or other virulence factors (Paton & Paton, 1998; Blackburn & McCarthy, 2000; Natvig et al., 2002).

Enterococci are facultative anaerobes and catalase-negative Gram-positive bacteria, with a coccoid shape, and presenting the Lancefield D group antigen (Sneath et al., 1986; Giraffa, 2002; Giraffa, 2003; Klein, 2003). They are also commensal microorganisms, representing a major percentage of the bacteria associated with the gastrointestinal tract of mammals

(Aarestrup et al., 2000; Giraffa, 2002; Giraffa, 2003; Klein, 2003). After fecal elimination to the environment, they may colonize several ecosystems due to their exceptional capacity to resist and multiply in hostile environments. Consequently, enterococci are not only associated to warm blood animals, but also to soils, water and vegetables (Giraffa, 2002; Giraffa, 2003; Klein, 2003). Nevertheless, it should be noticed that enterococci distribution varies according to the species, due to host specificity (Vancanneyt et al., 2002). *E. faecalis* usually occurs in human intestines, although it can also be found in other mammals feces. On the other hand, *E. faecium* and *E. durans* are more common in swine feces, and the last one can also be found in birds (Sneath et al., 1986; Giraffa, 2002; Klein, 2003).

Generally these microorganisms present low virulence, but the emergence of *E. faecium* and *E. faecalis* strains resistant to antimicrobial compounds is becoming a serious problem. This resistance can be intrinsic or acquired, by mutation or by transfer of mobile elements such as plasmids or transposons (Sneath et al., 1986; van den Boggard et al., 1997; Jensen, 1998; Jensen et al., 1998; Aarestrup et al., 2000; Borgen et al., 2000; Aarestrup et al., 2002; Vancanneyt et al., 2002; van den Bogaard et al., 2002; Domig et al., 2003). Epidemiologic studies indicate that *E. faecium* constitutes a major threat in terms of antimicrobial resistance (Knudtson & Hartman, 1992; Giraffa, 2002).

These are several studies that describe the occurrence and distribution of antimicrobial resistant bacteria isolated from domestic and farm animals, but little is known about the presence of antimicrobial resistant determinants in the microbiota of wild animals (Caprioli et al., 1991; Sayah et al., 2005). This information is extremely relevant to establish the accurate prevalence and distribution of antimicrobial resistant determinants, and to evaluate the potential role of wild animals in environmental contamination with resistant bacterial strains (Cole et al., 2005).

In this work we have shown the presence of resistant *Enterococcus* spp. and *E. coli* in fecal samples of free-ranging Portuguese otters. Bacteria were isolated from stool swabs collected in September 2007 and March 2008, from the river and reservoir stretches from Pego do Altar and Monte Novo, two dams located in Alentejo region, South Portugal. Bacterial isolates were identified on the basis of their morphology and metabolic pathways, and their antimicrobial resistance profile regarding 12 antimicrobial drugs was evaluated by the standard disk diffusion method, according to the Clinical and Laboratory Standards Institute (CLSI) guidelines.

Material and Methods

Study Area

The study was conducted in two large dams and associated river stretches, located in Alentejo region, in the South of Portugal. Pego do Altar Dam is located in the Sado River Basin and Monte Novo Dam is located in the Guadiana River Basin (Fig. 1).

Guadiana and Sado rivers are two of the most important rivers in Portugal. Alentejo region is characterized by its vast plains and a relatively uniform climate. However, because of the sea influence, aridity increases towards the southeast, with higher temperatures and lower air humidity. Annual precipitation ranges from 800mm in the north and west to less than 500mm in the southeast. The landscape, typically Mediterranean, is characterized by

large cereal fields and holm/cork oak woods, with cork oaks (*Quercus suber*) dominating in the west and holm oaks (*Quercus faginea*) in the east. Considerable areas of pine (*Pinus* spp.) and eucalyptus (*Eucalyptus globules*) trees can also be found. Many of the small streams in Alentejo do not have a permanent water regime, drying up partially or completely in summer.

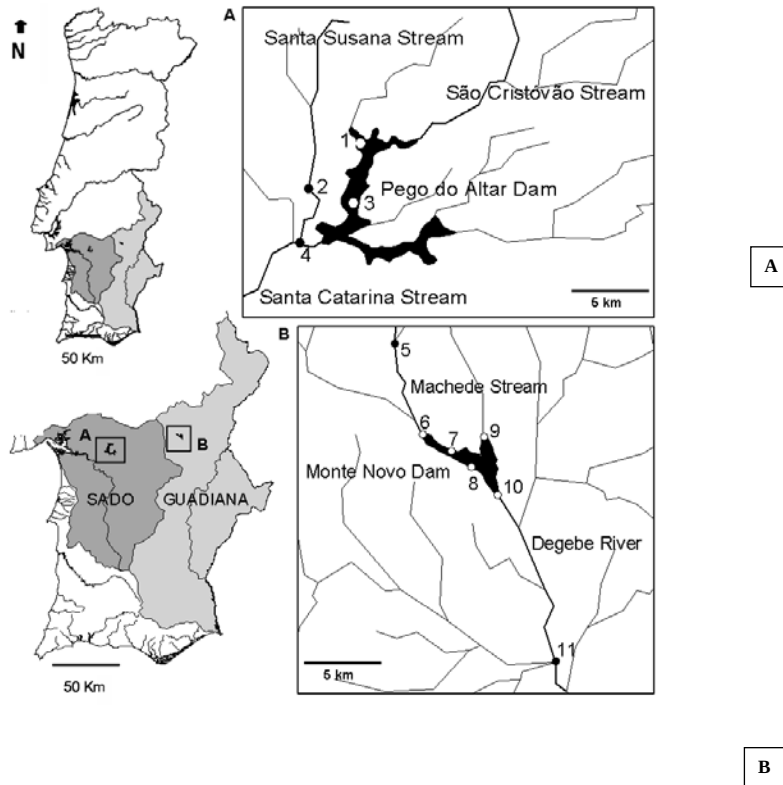


Figure 1. Location of the sampled stretches in Sado (A) and Guadiana (B) Basins in South Portugal: 1 - Pego do Altar Dam (north) 2 - Santa Susana Stream (north); 3 - Pego do Altar Dam (center); 4 - Santa Susana Stream (south); 5 - Machede Stream (upstream); 6 - Machede Stream (near dam); 7 - Monte Novo Dam (west); 8 - Monte Novo Dam (center); 9 - Monte Novo Dam (North); 10 - Monte Novo Dam (dam wall); 11- Degebe River (Downstream).

In general, Alentejo basins are located in semi-dry regions where the lack of water availability promoted an increased human intervention in the water courses, namely with construction of water reserves for human and agriculture consumption. As a result, aquatic ecosystems have been suffering changes that endanger fauna and flora, specially the aquatic species, such as autochthonous fish species. Pego do Altar Dam is the oldest dam (1949), with a volume of 37100 m³ and Monte Novo Dam the more recent one (1982), with a volume of 31000 m³. Both dams were essentially created for irrigation and water reserve. In general, water quality in both basins is degraded, but it hasn't been established yet if this characteristic is associated with intense local pollution of urban and agro-industrial origin or with diffuse pollution sources, mainly caused by agricultural practices (Ferreira et al., 2004; INAG, 2007).

Scat Sampling

Otters are free-living and mostly nocturnal. To assure the collection of fresh scats that were deposited by the otter within less than 15h, surveys were conducted at sunrise, for seven consecutive days. Scat collection in Pego do Altar Dam and adjacent river-stretches was conducted in September 2007, and in Monte Novo Dam and adjacent river-stretches was performed in March 2008. Otter scats are easily recognizable to the trained eye and are usually deposited by the otter in prominent places as marking activity for territory defense. The surveyed streams included common otter deposition sites, in order to increase the probability of collecting fresh scats. Survey length in each sampling site was 600m (Pedroso et al., 2007). Scats collected at one sampling site may be deposited by the same individual, but scats from different sampling sites probably are not, since sampling sites are distant.

In Pego do Altar Dam were selected for survey seven transects in streams adjacent to the dam (São Cristovão, Santa Catarina and Santa Susana streams) and four dam transects. In Monte Novo Dam were surveyed six transects in streams adjacent to the dam (3 in Machede Stream and 3 in Degebe River) and four dam transects.

Thirty-five scats were collected and processed for microflora analysis and antimicrobial resistance determination (Table 1). For each scat sample analysed, an AMIES swab (FL medical) was immediately performed for bacteria identification, and kept refrigerated until further processing.

Table 1. Fecal otter (*Lutra lutra*) samples collected at surveyed sampling sites of Pego do Altar and Monte Novo Dams and adjacent streams.

Sample Nº
Sample Code
Location
Pego do Altar Dam
1
L3/07
Santa Susana Stream (North)
2
L4/07
Pego do Altar Dam (North)
3
L5/07
Pego do Altar Dam (North)
4
L6/07
Pego do Altar Dam (North)
5
L7/07
Pego do Altar Dam (North)
6
L8/07
Santa Susana Stream (South)

Table 1. Continued

7
L9/07
Santa Susana Stream (South)
8
L10/07
Santa Susana Stream (South)
9
L11/07
Santa Susana Stream (South)
10
L12/07
Santa Susana Stream (South)
11
L13/07
Pego do Altar Dam (center)
12
L14/07
Pego do Altar Dam (North)
14
L16/07
Pego do Altar Dam (North)
15
L17/07
Pego do Altar Dam (North)
Monte Novo Dam
16
L1/08
Machede Stream (near dam)
17
L2/08
Monte Novo Dam (North)
18
L3/08
Degebe River (Downstream)
19
L4/08
Degebe River (Downstream)
20
L5/08
Monte Novo Dam (dam wall)
21
L6/08
Machede Stream (upstream)

Table 1. Continued

22
L7/08
Monte Novo Dam (center)
23
L8/08
Machede Stream (near dam)
24
L9/08
Monte Novo Dam (dam wall)
25
L10/08
Degebe River (Downstream)
26
L11/08
Monte Novo Dam (West)
27
L12/08
Monte Novo Dam (dam wall)
28
L13/08
Monte Novo Dam (center)
29
L14/08
Degebe River (Downstream)
30
L15/08
Monte Novo Dam (center)
31
L16/08
Degebe River (Downstream)
32
L17/08
Monte Novo Dam (center)
33
L18/08
Monte Novo Dam (West)
34
L19/08
Monte Novo Dam (dam wall)
35
L20/08
Degebe River (Downstream)

Bacteria Identification and Antimicrobial Resistance Determination

The isolation of *E. coli* and *Enterococcus* spp. from the otters fecal AMIES swab samples was performed using specific bacteriological protocols.

E. coli isolation was carried out in MacConkey agar plates (Oxoid), incubated at 37°C for 24h. This selective medium includes bile salts and crystal violet to inhibit the growth of Gram-positive bacteria. It also includes lactose and neutral red, and lactose positive *E. coli* colonies are easily recognized due to their bright pink coloration (Biokar Diagnostics, 2008; Quinn et al., 1994).

Enterococcus spp. isolation was performed using Slanetz and Barley agar (Oxoid), incubated at 37°C for 24h. This selective medium includes sodium azide that inhibits the growth of Gram-negative bacteria, and triphenyltetrazolium chloride, an indicator that it is reduced to an insoluble formazan inside the cells, turning enterococci colonies red to maroon (Biokar Diagnostics, 2008).

Identification of isolates was performed through their macro and microscopic morphology, staining characteristics and biochemical profiles using the identification systems API 20E for *E. coli* identification and API Strep for *Enterococcus* spp., according to manufacturer's instructions (bioMérieux).

Antimicrobial susceptibility testing was performed by the disk diffusion method recommended in the CLSI guidelines, using Mueller-Hinton agar plates (Biokar Diagnostics). Antimicrobial drugs tested were as follows: amoxycillin/clavulanate (AMC, 30 µg), ampicillin (AMP, 10 µg), chloramphenicol (C, 30 µg), cephalexin (CL, 30 µg), gentamicin (CN, 10 µg), cephotaxim (CTX, 30 µg), enrofloxacin (ENR, 5 µg), nalidixic acid (NA, 30 µg), penicillin G (P, 10 units), streptomycin (S, 10 µg), sulphamethoxazole/trimethoprim (SXT, 19:1, 25 µg) and tetracycline (TE, 30 µg). Antimicrobial disks were purchased from Oxoid.

Results

Thirty-five fresh scats (Table 1) were collected in 13 of the 21 surveyed sites (Fig. 1 and Table 1) and a total of 26 *Enterococcus* spp. isolates (Table 2), and seven *E. coli* isolates were obtained (Table 3).

The antimicrobial resistance profile of the isolates under study is shown in Tables 2 and 3. For analysis purpose, isolates with intermediate susceptibility were considered as resistant. None of the 33 isolates tested was susceptible to all antimicrobial agents tested.

All the 26 enterococci isolates were resistant to CL, CTX, ENR and S. Five of these isolates were resistant to all antimicrobials tested. High levels of resistance were observed for CN (N=21, 80.77%) and NA (N=25, 96.15%). Intermediate levels of resistance were observed for AMP (N=12, 46.15%), SXT (N=13, 50.0%) and TE (N=18, 69.23%). Lower levels of resistance were observed for AMC (N=9, 34.62%), and C and P (N=10, 38.46%). All enterococci isolates presented a multiresistant profile. Similar antimicrobial resistance patterns were observed in enterococci isolates from fecal samples L3 and L4/2007, from samples L11 and L16/2007, from samples L4, L6 and L9/2008, and from samples L3 and L19/2008 (Table 2 and 3).

E. coli isolates presented lower levels of resistance. All seven isolates were susceptible to C, CN, CTX, ENR and SXT. None of the isolates was resistant to all antimicrobials testes. High levels of resistance were observed for TE (N=8, 71.43%) and P (N=6, 85.71%). Intermediate levels of resistance were observed for AMP (N=4, 57.143%) and NA and S (N=3, 42.86%). Lower levels of resistance were observed for AMC and CL (N=2, 28.57%). Only one *E. coli* isolate did not present a multiresistant profile, and similar patterns of resistance were observed in *E. coli* isolates from fecal samples 14/2007 and 16/2007 (Table 2 and 4).

Table 2. Levels of resistance observed for *Enterococcus* spp. and *E. coli* isolates from otter (*Lutra lutra*) scat samples.

Antimicrobial compounds	<i>Enterococcus</i> spp. (N=26)	<i>E. coli</i> (N=7)
	Resistant bacterial isolates	
AMC	9 (34.62%)	2 (28.57%)
AMP	12 (46.15%)	4 (57.14%)
C	10 (38.46%)	0
CL	26 (100%)	2 (28.57%)
CN	21 (80.77%)	0
CTX	26 (100%)	0
ENR	26 (100%)	0
NA	25 (96.15%)	3 (42.86%)
P	10 (38.46%)	6 (85.71%)
S	26 (100%)	3 (42.86%)
SXT	13 (50.0%)	0
TE	18 (69.23%)	5 (71.43%)

Table 3. Antimicrobial resistance profile of enterococci isolated from otter (*Lutra lutra*) scat samples.

Isolate N°	Sample code	Isolate identification	Antimicrobial resistance profile
1	L3 / 2007	<i>E. faecium</i>	AMC-AMP-C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
2	L3 / 2007	<i>E. durans</i>	CL-CTX-ENR-NA-S
3	L4 / 2007	<i>E. faecalis</i>	CL-CTX-ENR-NA-S
4	L5 / 2007	<i>E. durans</i>	CL-CTX-ENR-NA-S-SXT-TE
5	L7 / 2007	<i>E. faecalis</i>	CL-CTX-ENR-NA-S-TE
6	L8 / 2007	<i>E. faecium</i>	AMP-CL-CTX-ENR-NA-S-SXT
7	L9 / 2007	<i>E. faecium</i>	AMC-AMP-CL-CN-CTX-ENR-NA-S

Table 3. Continued

Isolate N°	Sample code	Isolate identification	Antimicrobial resistance profile
8	L10 / 2007	<i>E. faecium</i>	AMC-AMP-CL-CN-CTX-ENR-NA-S-SXT-TE
9	L11 / 2007	<i>E. fecalis</i>	C-CL-CN-CTX-ENR-NA-S-SXT-TE
12	L16 / 2007	<i>E. fecalis</i>	C-CL-CN-CTX-ENR-NA-S-SXT-TE
14	L1 / 2008	<i>E. faecium</i>	CL-CN-CTX-ENR-NA-P-S-TE
15	L3 / 2008	<i>E. faecium</i>	CL-CN-CTX-ENR-NA-S-TE
18	L4 / 2008	<i>E. faecium</i>	CL-CN-CTX-ENR-NA-S
19	L6 / 2008	<i>E. faecium</i>	CL-CN-CTX-ENR-NA-S
20	L8 / 2008	<i>E. faecium</i>	AMP-C-CL-CN-CTX-ENR-NA-S-TE
21	L9 / 2008	<i>E. faecium</i>	CL-CN-CTX-ENR-NA-S
22	L10 / 2008	<i>E. faecium</i>	AMC-AMP-C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
24	L11 / 2008	<i>Ent. sp.</i>	AMC-AMP-CL-CN-CTX-ENR-P-S-SXT
25	L12 / 2008	<i>E. faecium</i>	AMC-AMP-CL-CN-CTX-ENR-NA-P-S-TE
26	L13 / 2008	<i>E. faecium</i>	AMC-AMP-C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
27	L15 / 2008	<i>E. faecium</i>	AMC-AMP-C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
28	L16 / 2008	<i>E. faecium</i>	AMC-AMP-C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
30	L18 / 2008	<i>E. faecium</i>	AMP-C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
31	L18 / 2008	<i>E. fecalis</i>	C-CL-CN-CTX-ENR-NA-P-S-SXT-TE
32	L19 / 2008	<i>E. durans</i>	CL-CN-CTX-ENR-NA-S-TE
33	L19 / 2008	<i>E. durans</i>	CL-CN-CTX-ENR-NA-S-TE

Table 4. Antimicrobial resistance profile of *E. coli* isolated from otter (*Lutra lutra*) scat samples.

Isolate N°	Sample code	Antimicrobial resistance profile
10	L14 / 2007	AMC-AMP-CL-NA-P-TE
11	L16 / 2007	AMC-AMP-CL-NA-P-TE
13	L17 / 2007	NA-P-TE
16	L4/2008	S-TE
17	L4/2008	AMP-P-TE
23	L11 / 2008	P-S
29	L17 / 2008	AMP-P-S

Discussion

Public interest in wildlife animals' welfare and conservation has grown in the last years. Studies have focused on aspects related wildlife health status, diseases and causes of mortality, since researchers have realized that these animals can be used as potential environmental pollution monitors, while being, simultaneously, potential vehicles of zoonoses, diseases transmission to farm and companion animals, and antimicrobial resistant bacteria (Simpson, 2000; Salyers and Shoemaker, 2006). In fact, Cole et al. (2005) already established the role of wild birds in pathogenic bacteria and antimicrobial resistance gene transmission to humans, through the contamination of agricultural fields and water used for human consumption.

Free-range river otters are well spread in Portugal, in a wide variety of aquatic environments, therefore being ideal vectors from the transmission of fecal bacteria and antimicrobial resistance factors.

The evaluation of antimicrobial resistant *E. coli* and *Enterococcus* spp. present in fecal samples from free-ranging river otters is an important tool for monitoring the spread of antimicrobial resistance. These bacteria belong to the normal enteric microbiota of healthy animals, and may be responsible for spreading transferable resistance genes located in mobile elements to pathogenic or commensal human and animal bacteria (SWARM, 2007).

Cultured-based methods for *E. coli* and *Enterococcus* spp. isolation from the fecal samples may present several limitations for fecal microflora characterization (Leser et al., 2002). In fact, although some authors suggested the use of molecular biology methods for the characterization of fecal bacteria (Kohn & Wayne, 1997), these methods can also be insufficient (Harmsen et al., 1999), as they provide no information on viability of microorganisms. Culture-based methods have proven adequate to verify if viable *E. coli* and *Enterococcus* spp. isolated from the fecal samples carried antimicrobial resistance determinants, since these bacteria are extremely resistant and can survive in adverse conditions for long periods of time (Waterman & Small, 1998). The use of appropriated medium to transport the samples to the laboratory and the bacterial survival ability are a guarantee of a successful recovery by culture-based methods. The use of selective procedures for target bacteria isolation, as recommended by Nikolova et al., 2001, helps eliminating the background microflora that sometimes is observed during bacteriological examinations.

From the 35 fecal samples tested in this study, it was possible to identify seven *E. coli* isolates and 26 *Enterococcus* spp isolates. The low frequency of *E. coli* isolates was not expected, since *E. coli* strains usually correspond to 1% of the total number of intestinal bacteria of warm blood animals (Bettelheim, 1992). *E. coli* low frequency suggests the occurrence of variations in fecal mammals' microbiota, and that otters' intestine could have been colonized during evolution by other *Enterobacteriaceae* and related bacteria, such as *Citrobacter* spp., *Enterobacter* spp., *Klebsiella* spp., *Morganella morganii*, *Pantoea* spp., *Salmonella* spp., *Serratia* spp., *Shigella* sp., and *Enterobacter* spp. Another hypothesis is that these others diet may have changed, since it is known that sudden diet changes may affect the bacteria ratio in intestinal microbiota (Bettelheim, 1992).

Regarding *E. coli* antimicrobial resistance, none of the isolates was susceptible to all the antimicrobial agents tested, and all except one isolate presented a multiresistant profile. No obvious differences on resistance to antimicrobials with different action mechanisms were

observed. All *E. coli* isolates were susceptible to antimicrobials that inhibit translation (C, CN), cell wall synthesis (CTX), folate synthesis (SXT) and replication, by impairing DNA gyrase action (ENR). Lower levels of resistance were observed for antimicrobials that inhibit translation (AMC), and also cell wall synthesis (CL). Intermediate levels of resistance were observed for drugs that impair cell wall synthesis (AMP) and translation by ribosomes (NA, S). Higher levels of resistance were observed for antimicrobials that affect cell wall synthesis (P) and translation (TE) (Koolman & Roehm, 2005).

In spite of the recognized geno and phenotypic differences between *E. coli* and *Enterococcus* spp., analogous results were obtained for enterococci isolates. None of the isolates was susceptible to all antimicrobial agents tested, all presenting a multiresistant profile, with no evident differences in resistance to antimicrobials with different action mechanisms. Lower levels of resistance were observed for antimicrobials that inhibit translation (AMC, C), and cell wall synthesis (P). Intermediate levels of resistance were observed for drugs that impair cell wall synthesis (AMP), translation by ribosomes (TE) and folate synthesis (SXT). Higher levels of resistance were observed for antimicrobials that affect cell translation (CN, NA) (Koolman and Roehm, 2005).

The major difference between the antimicrobial resistance characteristics of the two bacterial species was related to the number of antimicrobial compounds to which each specie was resistant to. While *E. coli* isolates were resistant to a maximum of 5 antimicrobial drugs, a profile presented by only two isolates, all enterococci tested were resistant to a minimum of 5 compounds, with 5 isolates (19.23%) resistant to all antimicrobials tested. These data are supported by the fact that enterococci are able to present not only acquired resistance mechanisms but also intrinsic resistance to antimicrobial drugs, and suggest that *Enterococcus* spp. might be a more serious problem regarding antimicrobial resistance transmission than *E. coli*.

Antimicrobial resistant bacteria have already been isolated from wild animals (Caprioli et al., 1991; Cole et al., 2005; Skurnik et al., 2006). It is generally believed that the main reason for the emergence, selection, and dissemination of antimicrobial resistant determinants is excessive exposure to antimicrobial drugs. In fact, Sayah et al. (2005) stated that wildlife that has not been deliberately exposed to high concentrations of antimicrobial compounds shows low antimicrobial resistance. However, our results contradict this hypothesis. The fecal samples analyzed in this study were obtained from free-ranging otters that are extremely unlikely to have been submitted to antibiotherapy. The isolation of high antimicrobial resistant bacteria isolated from animals that had never been exposed to drugs has also been described in a previous study on Timorese River Buffalos (Oliveira et al., 2007), suggesting that environmental exposure of commensal microorganisms to antimicrobial agents may contribute for the selection of resistant bacterial strains. Considering the location of the sampling sites, these otters were probably exposed to antimicrobial compounds present in ground water contaminated by animal and human wastes (Cole et al., 2005; Salyers & Shoemaker, 2006; Sayah et al., 2005; Skurnik et al., 2006). The indirect contact with livestock fecal material that may bear antimicrobial resistant bacteria could be involved in the transmission of resistant determinants from commensal microorganisms to free-ranging wildlife, turning them into new environmental reservoirs of resistant microorganisms (Cole et al., 2005). River Sado Basin pollution is mainly due to agriculture practices (Ferreira et al., 2004). No water pollution sampling stations are present near the surveyed sites and so it is not possible to correlate the presence of pathogenic and antimicrobial resistant bacteria with

specific pollution sources (Ferreira et al., 2004). However, no intensive agriculture is present neither in Pego do Altar Dam nor in its adjacent streams and contamination is only likely to occur upstream. Regarding Monte Novo Dam and its surroundings, the water quality is considered bad, probably due to direct discharges from small villages (INAG, 2007). It is also important to point out that some sampling sites, such as Santa Susana and Machede Streams, are located near small villages and present bad quality eutrophic water probably due to lack of stream current and the presence of cattle. In other parts of the reservoir, the water is also eutrophic due to the presence of cattle and human activities. The presence of cattle is continuous in all sampling sites, sometimes very high, not only in number of individuals but also in the occurrence of cattle droppings in the dam and stream margins.

Non-antibiotic selection pressure due to the presence of heavy metals or disinfectants used in agricultural practices may also select for antibiotic resistance genes (Harbottle et al., 2006). This hypothesis must also be taken into consideration. Although the sampling sites near the Sado Basin are far from agricultural fields, agriculture practices along this river basin may originate chemical compounds that reach the sampled areas, and therefore may contribute for the occurrence of non-antibiotic selection pressure. On the contrary, agricultural levels in the Guadiana Basin are low. However, some level of agricultural practices is observed near the Guadiana sampling sites, which may explain the similarity in the antimicrobial resistance levels of the bacteria isolated from seats obtained in the two river Basins.

Chloramphenicol resistance was observed in enterococci isolates, suggesting that another mechanism of resistance transmission has occurred, since the administration of this drug in cattle therapeutic is legally forbidden, and its use for the treatment of human infection is not frequent. Resistance to quinolones and cephalosporins has been attributed to the occurrence of point mutations in *Enterococcus* spp. and *E. coli* (Harbottle et al., 2006; Sayah et al., 2005), and these stable mutations can persist in bacteria, even in the absence of selective pressure (Sayah et al., 2005). These two bacterial species can also acquire antimicrobial resistance determinants from environmental bacteria via genome integration of mobile DNA elements, as described by Harbottle et al. (2006), Rice (2006) and Sayah et al. (2005). These authors have described the association of the acquisition of cassette-associated genes present in integrons to aminoglycosides, phenicols and sulfonamides resistance, and the relation of plasmids integration with β -lactams, tetracycline, cephalosporines and sulphonamides resistance. The multiresistance profiles could be due to co-selection or co-transfer phenomena that may originate the simultaneous development of resistance traits to antimicrobial drugs with different modes of action (Sayah et al., 2005).

Antimicrobial resistance is not always related to antimicrobial administration, since the isolation of antimicrobial resistant bacteria and the detection of resistance genes and transfer mechanisms are previous to the application of modern antimicrobial drugs in human and animal therapeutics (Harbottle et al., 2006). This hypothesis is supported by the fact that resistant bacteria were found in historic culture collections. Therefore, these intrinsic resistance mechanisms may have evolved in antibiotic-producing microorganisms presenting characteristic physiological or biochemical features, such as soil bacteria, to protect them against their own antimicrobial compounds. Antibiotic-producing microorganisms have been extensively used in antibiotic preparations, which might have influenced the transmission and dissemination of resistant determinants and the establishment of multiple resistant profiles (Harbottle et al., 2006).

Antimicrobial resistance profiles of multiresistant bacteria can be used to differentiate between distinct resistant strains populations, and to identify the resistance source (Kaszanyitzky et al., 2003; Sayah et al., 2005). In this study, similar patterns of resistance were found in two *E. durans* isolates from the one sample (L19/2008) obtained in Monte Novo Dam, suggesting that they are probably the same strain. Similar patterns of resistance were also found in two *E. coli* isolates from fecal samples L14/2007 and L16/2007 obtained in the same sampling site (Pego do Altar dam), suggesting that these fecal samples may be originated from the same individual. However, similar patterns were observed in *E. fecalis* from samples L11/2007 and L16/2007, and in *E. faecium* from samples L4/2008, L6/2008 and L9/2008, collected from different sampling sites. As the probability of scats collected in distant sampling sites belonging to the same individual is low, these results point out to the probability of dissemination of specific antimicrobial resistance patterns between different animals and/or to the probability that these patterns are originated from a common source. This probability is further enhanced by the fact that the same antimicrobial profile is observed in scats from the two sampling sites, and also in different bacterial species. In this study, an *E. durans* isolate from sample L3/2007 and an *E. fecalis* isolate from sample L4/2007 showed the same antimicrobial resistance profile, as well as an *E. faecium* isolate from L3/2008 and an *E. durans* isolate from L19/2008. For the accurate identification of the contamination source, fingerprinting of these isolates is suggested. These new data would also contribute for the development of effective management plans to minimize environmental contaminations (Smith et al., 2002).

The present study presents strong evidence of antimicrobial resistance occurrence in *Lutra lutra* fecal bacteria in Portugal. Characterization of the antimicrobial resistance profile of otters' fecal bacteria can be useful to evaluate the potential of these animals to act as reservoirs for resistance genetic determinants and to contribute for environmental contamination, which could be responsible for the transmission of resistant bacteria from humans and animals to autochthon wildlife and vice-versa. It could also contribute for the geographic localization of the contamination source, and for the strategic management and conservation of otters'. This is especially relevant in sites near water where cattle density is high or where human recreational activities such as bathing, water sport practice or camping occur with high frequency, as observed for the dams sampled in this study.

The collection a wider set of otter fecal samples will allow to perform genetic characterization and clonality studies on the bacterial isolates, which may elucidate on the origin of the high antimicrobial resistance frequency observed, on the environmental routes of antibiotic resistance dissemination and also on the potential role of wildlife as vectors of antimicrobial resistance.

Acknowledgements

This study was conducted with the financial support of the "Centro de Investigação Interdisciplinar em Sanidade Animal" (CIISA/FMV) from Faculdade de Medicina Veterinária (Faculty of Veterinary Medicine, Technical University of Lisbon) and of the European Union (contract number EVK2-CT-2002-00142-FRAP). M. Oliveira, N. Pedroso and T. Sales-Luís hold scholarships from "Fundação para a Ciência e Tecnologia" (SFRHBDP/23226/05, SFRH/BD/17495/2004 and SFRH/BD/5163/2001).

References

- Aarestrup, F.M., Agerso, Y., Gerner-Smidt, P., Madsen, M. & Jensen, L.B. (2000). Comparison of antimicrobial resistance phenotypes and resistance genes in *Enterococcus faecalis* and *Enterococcus faecium* from humans in the community, broilers, and pigs in Denmark. *Diagnostic Microbiology and Infectious Disease*, **37**, 127-137.
- Aarestrup, F.M. & McNicholas, P.M. (2002). Incidence of high-level evermicin resistance in *Enterococcus faecium* among food animals and humans. *Antimicrobial Agents and Chemotherapy*, **46**, 3088-3090.
- Arrendal, J., Walker, C.W., Sundqvist, A.K., Hellborg, L. & Vilal, C. (2004). Genetic evaluation of an otter translocation program. *Conservation Genetics*, **5**, 79-88.
- Beja, P.R. (1995). *Patterns of availability and use of resources by otters (Lutra lutra L.) in southwest Portugal* (Ph.D. Dissertation). Aberdeen, Scotland: Aberdeen University, 171.
- Bettelheim, K.A. (1992). *The prokaryotes: The genus Escherichia*. (Balows, A., Trüper, H.G., Dworkn, M., Harder, W. & Schleifer, K.-H.). New York, USA: Springer-Verlag, 2696-2736.
- Bertin, Y., Boukhors, K., Pradel, N., Livrelli, V. & Martin, C. (2001). Stx2 subtyping of shiga toxin-producing *Escherichia coli* isolated from cattle in France: detection of a new Stx2 subtype and correlation with additional virulence factors. *Journal of Clinical Microbiology*, **39**, 3060-3065.
- Biokar Diagnostics. Products for Microbiology [online]. 2008 [cited 2008 July 31]. Available from: http://www.pvl.pt/images/stories/pdf/catalogo_biokar.pdf
- Blackburn, C.W. & McCarthy, J.D. (2000). Modifications to methods for the enumeration and detection of injured *Escherichia coli* O157:H7 in foods. *International Journal of Food Microbiology*, **55**, 285-290.
- Borgen, K., Sominsen, G.S., Sundsfjord, A., Wasteson, Y., Olsvik, Ø. & Kruse, H. (2000). Continuing high prevalence of Van-A type vancomycin-resistant enterococci on Norwegian poultry farms three years after avoparcin was banned. *Journal of Applied Microbiology*, **89**, 478-485.
- Cabral, M.J. (2005). *Livro Vermelho dos Vertebrados de Portugal* (Almeida, J., Almeida, P.R., Dellinger, T., Ferrand d'Almeida, N., Oliveira, M.E., Palmeirim, J.M., Queiroz, AL., Rogado, L. & Santos-Reis, M.). Lisbon, Portugal: Instituto da Conservação da Natureza.
- Caprioli, A., Donelli, G., Falbo, V., Passi, C., Pagano, A. & Mantovani, A. (1991). Antimicrobial resistance and production of toxins in *Escherichia coli* strains from wild ruminants and the Alpine marmot. *Journal of Wildlife Diseases*, **27**, 324 - 327.
- Carnivora. Lontra (*Lutra lutra* LINNAEUS, 1758). [online]. 2008 [cited 2008 July 29]. Available from: <http://carnivora.fc.ul.pt/lontra.htm>.
- Cole, D., Drum, D.J.V., Stallknecht, D.E., White, D.G., Lee, M., Ayers, S., Sobsey, M. & Maurer, J.J. (2005). Free-living Canada Geese and Antimicrobial Resistance. *Emerging Infectious Diseases*, **11**, 935 - 938.
- Conroy, J.W.H. & Chanin, P.R.F. (2002). The status of the Eurasian otter (*Lutra lutra*). *IUCN Otter Specialist Group Bulletin*, **19A**, 24 - 48.

- Cortés, Y., Fernández-Salvador, R., Garcia, F., Virgós, E. & Llorente, M. (1998). Changes in otter *Lutra lutra* distribution in Central Spain in the 1964-1995 period. *Biological Conservation*, **86**, 179 - 183.
- Dallas, J.F., Coxon, K.E., Sykes, T., Chanin, P.R.F., Marshall, F.M., Carss, D.N., Bacon, P.J., Piernney, S.B. & Racey, P.A. (2003). Similar estimates of population genetic composition and sex ratio derived from carcasses and faeces of Eurasian otter *Lutra lutra*. *Molecular Ecology*, **12**, 275-282.
- Domig, K.J., Mayer, H.K. & Kneifel, W. (2003). Methods used for the isolation, enumeration, characterization and identification of *Enterococcus* spp. 2. Pheno- and genotypic criteria. *International Journal of Food Microbiology*, **88**, 165-188.
- Farinha J.C. & Trindade A. (1994). *Contribuição para o inventário e caracterização de zonas húmidas em Portugal continental*. (Publicação MedWet). Lisbon, Portugal: Instituto de Conservação da Natureza.
- Ferreira, M.T., Alves, M.H., Aguiar, F. & Moreira, I. (2004). *Gestão ambiental de sistemas fluviais: aplicação à bacia hidrográfica do rio Sado: Qualidade abiótica da água e fontes poluidoras na bacia do Sado* (Moreira, I., Saraiva, M.G., Correia, F.N.). Lisbon, Portugal: ISA press, 173 - 225.
- Foster-Turley, P., MacDonald, S. & Mason, C. (1990). *Otters: an action plan for their conservation* (IUCN Species Survival Commission). Gland, Switzerland: IUCN.
- Giraffa, G. (2002). Enterococci from foods. *FEMS Microbiology Reviews*, **26**, 163-171.
- Giraffa, G. (2003). Functionality of enterococci in dairy products. *International Journal of Food Microbiology*, **88**, 215-222.
- Hanni, K.D., Mazet, J.A.K., Gulland, F.M.D., Estes, J., Staedler, M., Murray, M.J., Miller, M. & Jessup, D.A. (2003). Clinical pathology and assessment of pathogen exposure in southern and Alaskan sea otter. *Journal of Wildlife Diseases*, **39**, 837-850.
- Harbottle, H., Thakur, S., Zhao, S. & White, D.G. (2006). Genetics of antimicrobial resistance. *Animal Biotechnology*, **17**, 111 - 124.
- Harmsen, H.J.M., Gibson, G.R., Elfferich, P., Raangs, G.C., Wildeboer-Veloo, A.C.M., Argaz, A., Roberfroid, M.B. & Welling, G.W. (1999). Comparison of viable cell counts and fluorescence *in situ* hybridization using specific rRNA-based probes for the quantification of human fecal bacteria. *FEMS Microbiology Letters*, **183**, 125-129.
- ICMSF (International Commission On Microbiological Specifications For Foods). (1996). *Microorganismos de los alimentos: Características de los patógenos microbianos: Escherichia coli patógeno intestinal*. (Roberts, T.A., Baird-Parker, A.C. & Tompkin, R.B.). Zaragoza, España: Editorial Acribia, S. A., 147-164.
- INAG. Meteorologia em Tempo Real: Análise Global para 2007 [Online]. 2007 [cited 2008 July27]. Available from: http://snirh.pt/snirh.php?main_id=1&item=4.1.1&objlink=&objrede.
- IUCN. 2006 IUCN Red List of Threatened Species [Online]. 2006 [cited 2008 January day]. Available from: <http://www.iucnredlist.org>.
- Jensen, L.B. (1998). Differences in the occurrence of two base pair variants of Tn1546 from vancomycin-resistant enterococci from humans, pigs, and poultry. *Antimicrobial Agents and Chemotherapy*, **42**, 2463-2464.
- Jensen, L.B. & Van Den Bogaard, A. (1998). Occurrence of *satA* and *vgb* genes in streptogramin-resistant *Enterococcus faecium* isolates of animal and human origins in The Netherlands. *Antimicrobial Agents and Chemotherapy*, **42**, 3330-3331.

- Kaszanyitzky, E.J., Jánosi, S., Egyed, Z., Ágost, G. & Semjén, G. (2003). Antibiotic resistance of staphylococci from humans, food and different animal species according to data of the Hungarian resistance monitoring system in 2001. *Acta Veterinaria Hungarica*, **51**, 451 – 464.
- Kimber, K.R. & Kollias II, G.V. (2000). Infectious and parasitic diseases and contaminant-related problems of North American river otters (*Lontra canadensis*): a review. *Journal of Zoo and Wildlife Medicine*, **31**, 452-472.
- Kimber, K.R., Kollias II, G.V. & Dubovi, E.J. (2000). Serologic survey of selected viral agents in recently captured wild North American river otters (*Lontra canadensis*). *Journal of Zoo and Wildlife Medicine*, **31**, 168-175.
- Kimura, R., Mandrell, R.E., Galland, J.C., Hyatt, D. & Riley, L.W. (2000). Restriction-site-specific PCR as a rapid test to detect enterohemorrhagic *Escherichia coli* O157:H7 strains in environmental samples. *Applied and Environmental Microbiology*, **66**, 2513-2519.
- Klein, G. (2003). Taxonomy, ecology and antibiotic resistance of enterococci from food and the gastro-intestinal tract. *International Journal of Food Microbiology*, **88**, 123-131.
- Knudtson, L.M. & Hartman, P.A. (1992). Routine procedures for isolation and identification of enterococci and fecal streptococci. *Applied and Environmental Microbiology*, **58**, 3027-3031.
- Kohn, M.H. & Wayne, R.K. (1997). Facts from feces revisited. *TREE*, **12**, 223-227.
- Koolman, J. & Roehm, K.-H. (2005). *Color Atlas of Biochemistry*. (Second edition). New York, USA: Thieme Stuttgart, 254 – 255.
- Kranz, A. & Toman, A. (2000). *Mustelids in a Modern World: Management and Conservation Aspects of Small Carnivore/ Human Interactions*. Leide: Backhuys Publishers, 163 - 184.
- Kruuk, H. (1995). *Wild otters predation and populations*. Oxford, UK: Oxford University Press, 290.
- Kruuk H (2006) *Otters: ecology, behaviour and conservation*. Oxford, UK: Oxford University Press, 265.
- Leser, T.D., Amenuvor, J.Z., Jensen, T.K., Lindecrona, R.H., Boye, M. & Møller, K. (2002). Culture-Independent Analysis of Gut Bacteria: the Pig Gastrointestinal Tract Microbiota Revisited. *Applied and Environmental Microbiology*, **68**, 673-690.
- MacDonald, S.M. & Mason, C.F. (1982). The otter *Lutra lutra* in central Portugal. *Biological Conservation*, **22**, 207-215.
- MacDonald, S.M. & Mason, C.F. (1984). Otters in Morocco. *Oryx*, **18**, 157-159.
- MacDonald S.M. & Mason C.F. (1994). Status and conservation needs of the otter (*Lutra lutra*) in the western Palaearctic. *Council of Europe Press. Nature and Environment*, **67**, 1-54.
- Mason, C. & MacDonald, S. (1986). *Otters: ecology and Conservation*. Cambridge: Cambridge University Press, 236.
- Monroe, S. & Polk, R. (2000). Antimicrobial use and bacterial resistance. *Current Opinion in Microbiology*, **3**, 496-501.
- Natvig, E.E., Ingham, S.C., Ingham, B.H., Cooperband, L.R. & Roper, T.R. (2002). *Salmonella enterica* serovar Typhimurium and *Escherichia coli* contamination of root and leaf vegetables grown in soils with incorporated bovine manure. *Applied and Environmental Microbiology*, **68**, 2737-2744.

- Nikolova, S., Tzevetkov, Y., Najdenski, H. & Vesselinova, A.V. (2001). Isolation of pathogenic yersiniae from wild animals in Bulgaria. *Journal of Veterinary Medicine Series B*, **48**, 203-209.
- Oliveira, M., Monteiro, J.L., Santos, V., Carneiro, C., Nunes, S.F. & Vilela, C.L. (2007). Identification and antimicrobial resistance profile of gram-positive cocci from skin microbiota of timorese river buffalo (*Bubalus bubalis*). In *Proceedings of the Leibniz Institute for Zoo and Wildlife Research*. (7, 25 – 36). Berlin, Germany.
- Paton, J.C. & Paton, A.W. (1998). Pathogenesis and diagnosis of Shiga toxin-producing *Escherichia coli* infections. *Clinical Microbiology Reviews*, **11**, 450-479.
- Pedroso, N.M. & Santos-Reis, M. (2006). Summer Diet of Eurasian Otters in Large Dams of South Portugal. *Hystrix*, **17**, 117-128.
- Pedroso, N.M., Sales-Luís, T. & Santos-Reis, M. (2007). Use of Aguieira Dam by Eurasian otters in Central Portugal. *Folia Zoologica*, **56**(4), 365–377.
- Prenda, J., López-Nieves, P. & Bravo, R. (2001). Conservation of otter (*Lutra lutra*) in Mediterranean area: the importance of habitat quality and temporal variation in water availability. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **11**, 343-255.
- Reuther, C. & Hilton-Taylor, C. (2004). *Lutra lutra*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 26 July 2008.
- Quinn, P.J., Carter, M.E., Markey, B. & Carter, G.R. (1994). *Clinical Veterinary Microbiology* (Mosby). Edinburgh, UK: Elsevier.
- Rice, L.B. (2006). Antimicrobial resistance in gram-positive bacteria. *The American Journal of Medicine*, **119**, S11 - S19.
- Romanowski, J., Gruber, B. & Brzezinski, M. (1997). The recovering otter population of central Poland. *Otter Specialist Group Bulletin*, **14**, 24-25.
- Ruiz-Olmo, J. & Delibes, M. (1998). *La nutria en España ante el horizonte del año 2000*. Málaga, Spain: SECEM.
- Ruiz-Olmo, J., Saavedra, D. & Jiménez, J. (2001). Testing the surveys and visual and track censuses of eurasian otters (*Lutra lutra*). *Journal of Zoology, London*, **253**, 359-369.
- Sales-Luís, T., Pedroso, N.M. & Santos-Reis, M. (2007). Prey availability and diet of the Eurasian otter (*Lutra lutra*) on a large reservoir and associated tributaries. *Canadian Journal of Zoology*, **85**, 11.
- Salyers, A. & Shoemaker, N.B. (2006). Reservoirs of antibiotic resistance genes. *Animal Biotechnology*, **17**, 137 – 146.
- Santos-Reis, M. (1983). Status and distribution of the Portuguese mustelids. *Acta Zoologica Fennica*, **174**, 213-216.
- Santos-Reis, M., Trindade, A. & Beja, P.R. (1995). Situation et état des recherches sur la loutre au Portugal. *Cahiers d’Ethnologie*, **15**, 1-14.
- Santos-Reis, M., Ferreira, J.P., Pedroso, N., Baltazar, C., Matos, H., Pereira, I., Grilo, C., Sales-Luís, T., Santos, M.J., Cândido, A.T., Sousa, I. & Rodrigues, M. (2003). *Projectos de Monitorização de Mamíferos. Monitorização de Carnívoros. Relatório Final. 2ª Fase de Monitorização. Programa de Minimização para o Património Natural da área de regolfo de Alqueva e Pedrógão*. Lisboa, Portugal: Centro de Biologia Ambiental (FCUL)/Centro de Estudos da Avifauna Ibérica (CEAI), 207.
- Sayah, R.S., Kaneene, J.B., Johnson, Y. & Miller, R. (2005). Patterns of Antimicrobial Resistance Observed in *Escherichia coli* Isolates Obtained from Domestic- and Wild-

- Animal Fecal Samples, Human Septage, and Surface Water. *Applied and Environmental Microbiology*, **71**, 1394 – 1404.
- Selkoe, K.A. & Toonen, R.J. (2006). Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecology letters*, **9**, 615-629.
- Simpson, V.R. (2000). Veterinary advances in the investigation of wildlife diseases in Britain. *Research in Veterinary Science*, **69**, 11 - 16.
- Skurnik, D., Ruimy, R., Andremon, A., Amorin, C., Rouquet, P., Picard, B. & Denamur, E. (2006). Effect of human vicinity on antimicrobial resistance and integrons in animal fecal *Escherichia coli*. *Journal of Antimicrobial Chemotherapy*, **57**, 1215 – 1219.
- Smith, W.A., Mazet, J.A.K. & Hirsh, D.C. (2002). *Salmonella* in California wildlife species: prevalence in rehabilitation centers and characterization of isolates. *Journal of Zoo and Wildlife Medicine*, **33**, 228-235.
- Sneath, H.A., Mair, N.S., Sharpe, M.E. & Holt, J.G. (1986). *Bergey's Manual of Systematic Bacteriology*. Baltimore, USA: William & Wilkins.
- SWARM (2007). *SWARM 2006: Swedish Veterinary Antimicrobial Resistance Monitoring*. Uppsala, Sweden: The National Veterinary Institute (SVA), 44.
- Trindade, A. Farinha, N. & Florêncio, E. (1998). A distribuição da lontra *Lutra lutra* em Portugal: situação em 1995. In *Estudos de Biologia e Conservação da Natureza do Instituto para a Conservação da Natureza* (**28**, 1–121). Lisboa, Portugal.
- Vancanneyt, M., Lombardi, A., Andrighetto, C., Knijff, E., Torriani, S., Björkroth, K.J., Franz, C.M.A.P., Moreno, M.R.F., Revets, H., De Vuyst, L., Swings, J., Kersters, K., Dellaglio, F. & Holzapfel, W.H. (2002). Intraspecies genomic groups in *Enterococcus faecium* and their correlation with origin and pathogenicity. *Applied and Environmental Microbiology*, **68**, 1381-1391.
- Van Den Bogaard, A.E., Jensen, L.B. & Stobberingh, E.E. (1997). Vancomycin-resistant enterococci in turkeys and farmers. *The New England Journal of Medicine*, **337**, 1558-1559.
- Van Den Bogaard, A.E., Willems, R., London, N., Top, J. & Stobberingh, E.E. (2002). Antibiotic resistance of fecal enterococci in poultry, poultry farmers and poultry slaughterers. *The Journal of Antimicrobial Chemotherapy*, **49**, 497-505.
- Waterman, S.R. & Small, P.L.C. 1998. Acid-sensitive enteric pathogens are protected from killing under extremely acidic conditions of pH 2.5 when they are inoculated onto certain solid food sources. *Applied and Environmental Microbiology*, **64**, 3882-3886.
- Whitton, B.A. & Lucas M.C. (1997). Biology of the Humber rivers. *Science of the Total Environment*, **194/195**, 247-262.

Chapter 8

**BEHAVIOR OF WILD ANIMALS AGAINST HUMANS
IN RESERVATIONS, SANCTUARIES,
AND HUNTED AREAS – REVIEW AND THEORETICAL
APPROACH**

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Abstract

In nearly all hunted areas, game animals fly from humans, avoid being seen by seeking shelter during the day, and have a preference for nocturnal activity. This behavior has widely been assumed to be normal and shyness of all wild animals against humans has been accepted as natural behavior of these species, especially between hunters. On the other hand, in all non-hunted reserves wild animals display a behavior against humans very different from animals under human hunting pressure. This has been described as “national park effect”. It consists of astonishing tolerance of potential prey animals towards humans, substantially reduced or even completely lacking flight behavior, and distinct daylight activity on open terrains. A general explanation of these effects is given based on the emotions of animals as well as on their learning behavior.

The response of inexperienced animals towards humans is based on general anxiety for unpredictable and possibly dangerous events. The emotion of general anxiety has to be distinguished from specific fear. Both processes can be modified by learning from experiences with humans. As hunting is the main cause for mortality in many game populations, hunting strategies will be the key factor to understand the learned behavior of deer towards hunters and tourists in a certain area. Theoretical learning curves are developed for different conditions. They support the importance of game sanctuaries and the development of drawback-free strategies for population regulation.

Additionally, the behavior of large predators towards humans can be interpreted based on general anxiety, specific fear, and learning. Recommendations are developed under these aspects for convenient strategies towards these species and to avoid conflicts.

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To better understand human-wildlife conflicts, more experimental investigations on the learning behavior of the different species are required. Such investigations will open new ways to solve human – wildlife conflicts regarding ethical aspects.

Key words: disturbance, anxiety, fear, learning, human-wildlife conflicts

Introduction

It has been suggested that the impact of humans on populations of wild animals has endangered species or even brought them to extinction since humans were able to construct effective hunting weapons like bows and arrows, organize cooperative hunts, and construct effective traps (overkill-hypothesis, Martin 1984; Owen-Smith 1989, Beutler 1996). As one of several options against this tendency, different civilizations have created wildlife reservations to preserve endangered populations and species. The first European reserve was declared as early as 1487 in Switzerland out of the religious motivation that the eradication of game species like red deer and chamois would offend God's order (Thürer 1979). The need for game meat was often an additional motive to preserve wild animals and to restrict uncontrolled hunting. For example, this need for game led to the protection of the New Forest in southern England as a Royal Hunting Forest as early as in the eleventh century.

In all non-hunted reserves, wild animals display a behavior towards humans different from animals under human hunting pressure. This has been described as "national park effect" (Bergmann and Wille 2001, Borkowski 2001). It consists of an astonishing tolerance of potential prey animals of humans, substantially reduced or even completely lacking flight behavior, and clear daylight activity on open terrains. This behavior is one reason for the high attraction of such reserves for many visitors. The possibility to observe animals like chamois and ibex is a motivation to visit these areas for many people. A similar behavior was reported from animals of island populations where no predators or humans have been present for a long time (Berger 1999, or as found 1835 by Darwin on islands of the Galapagos archipelago, Schaumann 2002).

On the other hand, large predators normally do not avoid humans, human settlements, or domestic animals. This may cause conflicts between human interests and even endanger persons and domestic animals especially in reservations, where wild animals are protected (Conover et al. 1995, Gunther et al. 2004, Bargali et al. 2005, Wilson et al. 2005). Such conflicts require adequate solutions based on the animal's behavior to protect domestic animals and humans as well as to enable the observation of these species by tourists (Smith et al. 2005, Rondinini and Boitani 2007).

In nearly all European forests, game animals fly from humans, avoid being seen by seeking shelter during the day, and have a preference for nocturnal activity. This behavior has widely been assumed as normal and shyness of all wild animals towards humans has been accepted as the natural behavior of these species, especially between hunters. Some hunters even assume lacking flight behavior from humans as unnatural for game species like wild boar, red deer, and fallow deer. For predators like wolves and bears, natural shyness from humans has often been expected. Nevertheless, in many wild parks the same species can be seen as day-active and not at all impressed by the close presence of humans. This discrepancy was pinpointed for example by Scherzinger (1992), who called for larger protected areas

where wild animals should be able to develop their natural spatial preferences undisturbed. Only if large mammals, prey species as well as predators, can develop their natural spatial behavior uninfluenced by humans the real objective of national parks or other regions devoted for natural development can be achieved. Their behavior against humans is in so far a key factor for their natural ecological function.

Within normally hunted areas in Germany and other European countries, game sanctuaries have been created. These areas are supposed to give game animals a possibility to avoid disturbances, build up a normal social structure and reproduce undisturbed, develop their species-specific activity- and feeding rhythms, and use open places like meadows or clearings. In such zones, a behavior of game animals equivalent to the “national park effect” is expected and as a result a reduction of damage of tree vegetation too. The possibility to declare such zones has been mentioned in some hunting laws but there is not a single assumption about the impact of hunting and tourism on the animal’s flight and vigilance behavior. While some groups estimate tourists as the main disturbing factors, others estimate hunting as the reason for high vigilance, flight, and preference for thickets in wild animals.

What may be the background of these behaviors, how can they be interpreted on a general biological background and which consequences should humans draw for their own behavior towards these animals?

General Vigilance and Shyness Towards Humans

It must be assumed that nearly all animals including humans have a certain carefulness against natural, unpredictable, and possibly dangerous events. It must have been developed during evolution as a meaningful reaction to avoid damage and must be presented by specific emotional states (Matthen 1998). Such a central nervous state has been defined as emotion of general anxiety and is distinguished from clue specific fear in animals (Stamm 1967, Boissy 1995, Misslin 2003). General anxiety is based on a certain degree of basic vigilance as sustained attention or tonic alertness. It is modified by the sleep-wake cycle and the actual level of cognitive performance (Oken et al. 2006). This general tonic alertness has a specific central neuronal basis that is related to the central basis of the daily rhythm, the suprachiasmatic nucleus (SCN, Aston-Jones 2005). Thalamic neurons regulate natural functional states such as sleep and alertness. The similarity in electrophysiological properties indicates that the thalamocortical system must be as ancient as the vertebrates itself (Llinas and Steriade 2006). Accordingly, non-specific anxiety or tonic alertness should be a very basic and evolutionary old adaptation of vertebrates against all possibly dangerous situations. General anxiety as well as fear are both emotional functions, based on neural circuits, neuromodulators and neurotransmitters and closely related to the neuroendocrine system (Boissy 1995).

The more specific fear of predators or otherwise potentially dangerous animals like conspecifics is usually called vigilance and has to be regarded as a different system or as a specific subsystem form the general alertness system. It includes special adaptations of surveillance behavior to predator strategies, special attention to and reactions against predator key stimuli, and social components. Anti-predatory behavior has been classified into predator-species-specific vigilance and into non-specific vigilance against all predators, the latter resembling the concept of general anxiety (Lima 1992). Vigilance behavior in its more

restricted sense has received much attention from behavior ecologists (e.g. Ylönen and Magnhagen 1992, Krebs and Davis 1996).

Anti-predator vigilance (watching out for predators) is regarded as one of two often mutually exclusive tasks: to feed and to avoid being fed (Kie 1999, Proctor et al. 2003). Many theoretical and empirical studies investigate this trade-off, especially in birds. Vigilance models and field investigations include flock spacing and vigilance rate (Blumstein et al. 2002, Fritz et al. 2002, Ragusa-Netto 2002, Dominguez 2003). The vigilance state of parents has been found to depend on many factors like availability of cover, behavior and state of the juveniles, presence of mates and sex (Artiss et al. 1999, Toigo 1999, White and Berger 2001, Treves 2003).

The degree of expression of vigilance behavior is not independent from experience, since it may be reduced during long periods without predation (Sand et al. 2006, Blumstein et al. 2006). Training of anti-predatory behavior is possible and may be effective for reintroductions into areas where predators are present (de Azevedo and Young 2006). In cows, vigilance decreased in successive test sessions. It was found to be higher towards dogs than towards humans and higher towards persons with whom the animals previously had negative experience (Welp et al. 2004). This means that even domestic bovids have not only fixed reactions against predator species, but are able to learn to modify their vigilance behavior towards humans depending on positive respectively negative experience.

Large mammals have behavioral mechanisms against specific natural predators. They react towards key stimuli without previous experience. This has been demonstrated for example for equids by the so called "Quadrupede - test" (Zeeb 1959, Scheibe et al. 2000). In many species of artiodactyls, auditory and visual signals, defensive behavior, and group-related behaviors against natural enemies have been found (Caro et al. 2004). Mouflon's (*Ovis gmelini musimon*) escape distance increased very significantly in the presence of a dog compared to humans without dogs, indicating an innate predator scheme for canids (Martinetto and Cugnasse 2001). Chamois (*Rupicapra rupicapra*) reaction differed against hikers and paragliders (Enggist-Dublin and Ingold 2003). This may be due to a fixed reaction pattern against the sound produced by low flying paragliders, resembling the warning signals of the species.

Anti-predatory behavior furthermore includes strategies like hiding in cover, choice of feeding and resting sites, modification of feeding and activity times, sociality, and direct defense (Lima and Dill 1990). Even in closely related species like white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) these components can be expressed differently as a result of slightly different evolutionary adaptations (Lingle and Wilson 2001). These different elements of the natural anti-predator behavior of animals have been declared as the key factors for the understanding of all forms of human disturbance (Frid and Dill 2002).

On the other hand, it cannot be assumed that the large mammals submitted to human hunting pressure were able to develop an innate fear or a specific enemy scheme against humans or even a releasing mechanism and a specific anti-predatory behavior during evolution. The duration of this specific human selection factor has been much too short and human hunting behavior not consistent at least in the temperate regions since the start of human hunting. The flight behavior of wild animals against humans therefore must be in so far a learned behavior only (Scherzinger 1991).

The Importance of Hunting

The reason for wild animals to learn to flight from humans can only be the lethal threat of hunting (Petrak 1996). This is sometimes denied by hunters, with critical tests lacking. A lot of direct and indirect indications and even anecdotal reports support this assumption.

White tailed deer change their spatial behavior depending on the hunting periods as they change from hunted to non-hunted areas generally or only during the daylight hours, or move farther into escape cover and develop crepuscular activity patterns (Kilgo et al 1968, Naugle et al. 1997, Kilpatrick and Lima 1999). Mule deer did not change their home ranges but hunts caused them to prefer areas with more cover (Kufeld et al. 1988).

Red deer (*Cervus elaphus*) reacted on hunts with changes in spatial behavior like avoiding open terrains or changing to non-hunted areas (Schmidt 1992, Conner et al. 2001, Burcham et al. 1999, Baumann et al. 1999). Even short hunting periods increased the flight distance by about 25% (Bender et al. 1999). Red deer in the Rocky Mountains shifted the timing of their movements to private land in response to the beginning of archery hunting season (Vieira et al. 2003). Space-use sharing between red deer and hunters was decreased depending on the hunting seasons on bulls and cows separately. High vegetative cover allowed higher degrees of space-use sharing than open woods (Millspaugh et al. 2000). After shooting 25 red deer for the first and only time in an area previously excepted from hunting in a Swiss National Park, only 20 of previously 200 animals were visible (Filli and Nievergelt 1996). It took two years after cessation of hunting until red deer and chamois were visible again on open terrains during the day, but the animals changed their behavior immediately as hunting increased at the boundaries of the area (Douglas 1971). Female red deer in a hunted area behaved generally more carefully than males which can be explained by the experience of loosing juveniles to hunting (Petrak 1996).

Wild boar (*Sus scrofa*) dung pellets were found less frequently in hunted than in non-hunted areas (Rosenfeld 2000). Some wild boar groups left their home area as a result of drive hunts and changed to areas as far as 6 km for 4 to 6 weeks, while others stayed in their territory (Sodeikat and Pohlmeier 2002).

Impalas (*Aepyceros melampus*) spent more time being vigilant and flight distances at the approach of humans were significantly greater at an area where more impalas were hunted compared to a less hunted area (Matson et al. 2005).

Roe deer (*Capreolus capreolus*) were influenced by hunting dogs and forced into refuge zones (Maillard et al 1999). Prior to the hunting season roe deer were often observed in a touristic intensively used area on open terrain, but not any more after the onset of the hunting season (Büker et al. 1999). During the progress of the hunting season, hunting success dropped due to increased avoidance behavior of white-tailed deer (Grau and Grau 1980). Flight distances in roe deer were the shortest in a reserve without hunting compared to gradually hunted areas while fallow deer showed no changed flight behavior (de Boer et al. 2004).

This short overview demonstrates how variable and fine-tuned the reaction of deer on hunting may be. This is an additional indication for the importance of learning in this animal-human interrelation. Therefore, the behavioral mechanism described by Fig. 1 must be assumed as a reaction on normal human hunting tactics. Animals learn to react on humans like on natural predators but with a lack of innate key stimuli. Instead, they develop a newly

learned anti-predatory scheme for humans, which may but must not be restricted to hunters. This often leads to avoidance and flight behavior against all humans in deer.

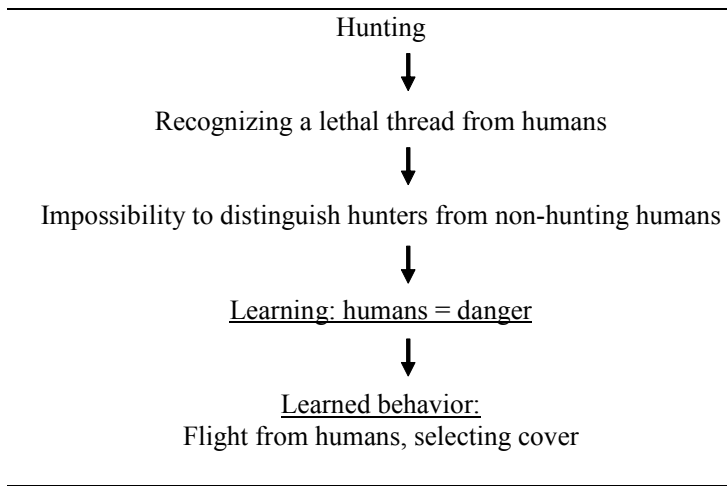


Figure 1. Behavioral reaction of wild animals on normal hunting practice.

On the other hand, hunters strive to stay unperceived by the animals and have developed a series of rules to avoid exactly this learning procedure. This includes rules as never to shoot on young animals in the presence of the mother, to keep a resting period after a kill, and never approach a killed animal on the direct way from the hide (Petrak 1999). They often also camouflage hiding places and high seats and generally try to walk quiet and inconspicuous while hunting. If animals are submitted to such a stealth hunting practice, they will perceive an anonymous danger, and a different learning procedure may result (Fig. 2).

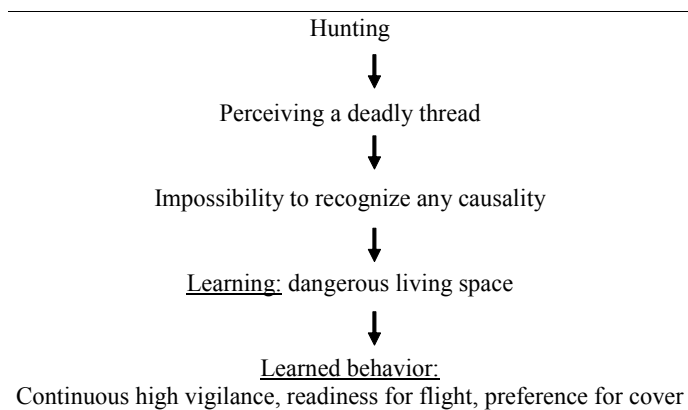


Figure 2. Behavioral reaction of wild animals on stealth hunting.

Stealth hunting practice will, if of sufficient frequency or duration, increase the general anxiety level mentioned above in the animals, which is different from predator-specific fear. This learning process may require a longer time but will finally be an even deeper impairment than clue-specific fear. It may be related to the whole area, not temporarily restricted and

universal against all stimuli not certainly classified as harmless. The two different mechanisms general anxiety and clue-specific fear with the related species-specific learning capabilities on hunting and non hunting humans and natural predators may explain the wide variety of reactions on human disturbance (Taylor and Knight 2003).

Reaction Towards Non-hunting Humans

The learning processes on the two different human hunting strategies can be inverted such as other learning processes too. In inexperienced animals one may assume that based on a basic carefulness the reaction on humans will decrease as more non-hunting and non-dangerous persons are perceived by the animals. This can be interpreted as a desensibilisation process (Fig. 3). Accordingly, these learning processes lead to a different valuation of humans and determine the behavior of wild animals fundamentally.

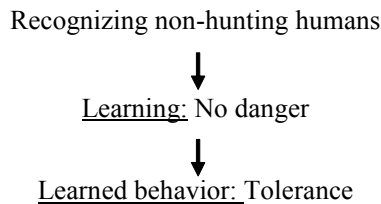


Figure 3. Behavioral reaction of wild animals on non-hunting humans.

Such a partial desensibilisation or habituation process has been observed in roe deer after repeated disturbance of the same type (e.g. passing of an unleashed dog on forest routes). After 15 repeated disturbances, habituation reduced the increase of energy consumption calculated from heart rate reaction by only 10% (Olesen et al. 1998). It is not possible to decide if the learning process was already finished and the remaining reaction expressed the special and fixed fear against an animal corresponding to the specific predator scheme of wolves or if further reduction would occur following repeated exposition. Flight response of fallow deer (*Dama dama*) towards human observers in an enclosure was reduced in areas where frequent, regular and predictable human activity occurred. The reaction was determined by the security provided by the immediate environment and the habituation to human presence (Recarte et al. 1998). Chamois showed the highest flight distances towards humans in rarely frequented areas but reduced reaction distances against visitors on frequently used trails in highly frequented areas. Persons on infrequently used paths or positions caused flight even in frequently visited areas (Bögel and Lotz 2000). Chamois were able to adapt to people in frequently visited areas (Patterson 1988). These observations illustrate that game animals are able to learn that humans at certain places are harmless. Instead, spotting humans at unusual places causes flight based on general anxiety against novel and uncertain situations.

Red deer showed clear signs of habituation towards a human in an experimental situation after only six test sessions. The highest degree of habituation occurred in a situation where the person remained at the entrance of the pen, while lower habituation occurred against a

situation where the person entered the pen partially or crossed it totally (Pollard and Littlejohn 1995).

The behavior of elk in the Rocky Mountain National Park showed clear signs of adaptation to human disturbance as neither the types of behavior nor the visibility were influenced by visitor frequency. The effect has been discussed as resulting from cessation of hunting (Schultz and Bailey 1978). There are even indications that mammals may use humans to shield against carnivores (Berger 2007).

Learning Capabilities and Learning Curves

To develop predictions about the behavior of game in real situations the frequency of hunters and non-hunting persons have to be taken into account as well as the learning capabilities of the species. As learning curves of these species are not known and the memory capabilities are also not experimentally investigated, hypothetical learning curves are given in fig. 4 and fig. 5. The valuation of humans depends on the probability to get negative experiences from humans. The values indicated on the abscissa in fig. 4 and fig. 5 can be interpreted as accumulated over the successive time periods during a learning process but also as a function of the long lasting hunting probabilities in different areas. In so far, these theoretical curves can be regarded as classical learning curves but can also be used to determine the reaction of animals under different hunting pressure in different areas.

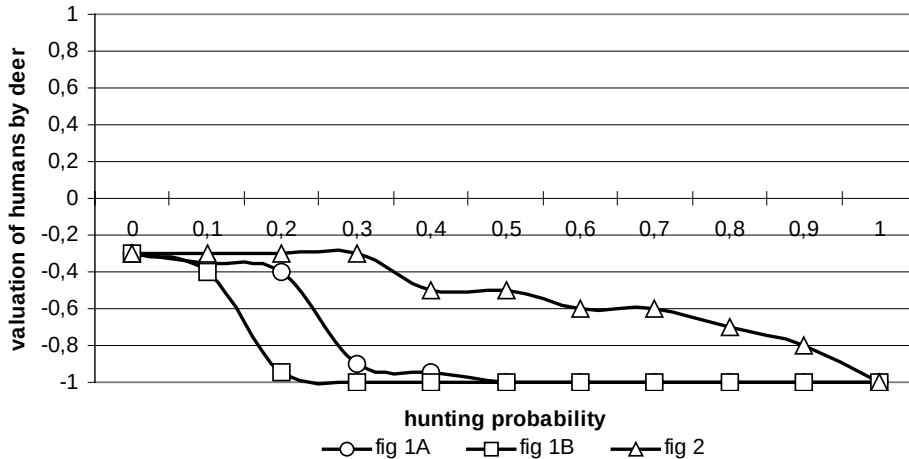


Figure 4. Valuation of humans by deer, schematic learning curves. Hunting probability can be regarded as accumulating in the individual memory. The valuation of humans can be interpreted as expression of a learning process with accumulating hunting experience by an individual or as the result of a learning process from a long-lasting learning process from the constant hunting probability at a place. The different curves symbolize two different hunting intensities (A and B) following a “normal” hunting as assumed in fig 1 and a “stealth” hunting strategy following fig. 2.

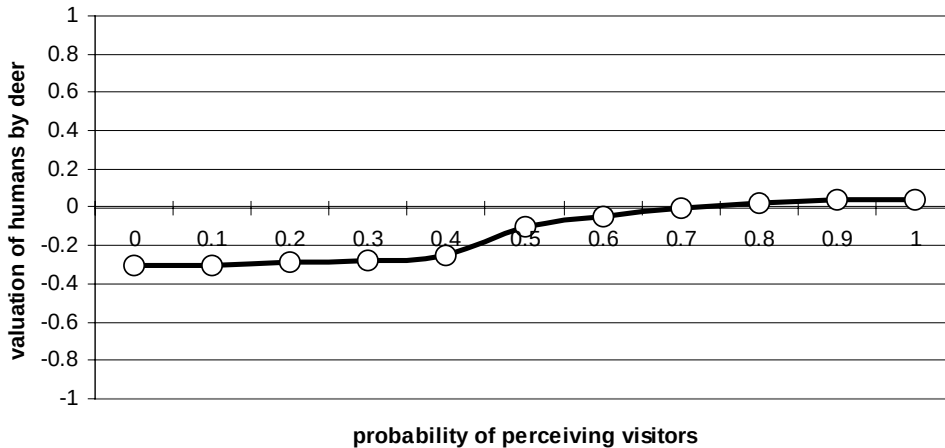


Figure 5. Valuation of non - hunting humans by deer. Schematic learning curve following the situation characterized by fig. 3.

For Fig. 4 it is assumed that the animals react stronger the better they perceive the hunting pressure which increases the specific fear. The animals learn to treat humans like their natural predators. But also “stealth” hunting strategies over a long time will change the behavior based on a good memory by increasing general anxiety.

All these hypothetical learning curves express the assumption of a certain basic carefulness which is changed into avoidance by negative experience. This basic carefulness may be reduced on the other hand by the repeated experience of humans being not dangerous and finally even changes into a positive reaction. Such a slightly positive reaction may result from the experience of security or the availability of preferred food close to humans on open terrain or even the lack of competitors. If humans use paths and places regularly their occurrence and behavior can be predicted by the animals and so fulfill the general requirement for security and may be as such positively valued. Independently, the predator-specific fear of prey-species may be increased by experience.

The behavior of game at a certain place will always be a summation of these diverging tendencies and depend on the relative frequencies of negative and positive experience from humans.

A similar learning process has to be assumed for large predators. These animals have a certain basic carefulness towards unknown events as well as specific fear of other large animals too. They may learn to correlate the specific fear reaction to humans or on symbols of human presence if these are correlated to negative experience. If not negatively affected by humans they will perceive the neutral value or even an advantage in approaching humans, or areas regularly frequented by humans as well as domestic flocks. Brown bears (*Ursus arctos*) tolerated the experimentally introduced tourism in Alaska very well, and did not generally reduce their food intake. Only adult males at a viewing area reduced food intake resulting from a 15% decline in foraging time when viewers were present. Salmon intake did not differ between pre-treatment and treatment years despite a 10% decline in time spent fishing when viewers were present (Rode et al. 2006).

Learned aversion may be a strategy independent from fear to reduce damage or exclude the utilization of special areas by some species of wild animals. For example, foxes are able

to develop negative reactions against certain tastes (Macdonald and Baker 2004) as well as Black and Polar bears (Wooldridge 1980). For avoidance training of black bears (*Ursus americanus*), automatic electric shock devices have been found to be very effective (Breck et al. 2006). Conditioning badgers with a combination of an aversive agent and a novel odor produced learned aversion towards untreated food in the presence of the odor cue (Baker et al. 2007). These effects have been described as secondary repellents, meaning that a link is established by aversive conditioning between a negative stimulus and a specific behavior, a specific area, or a specific prey item (Shivik et al. 2003).

Conclusions for Human Behavior

Humans should accordingly take care to deliver the convenient stimuli against the different animal species. Normal hunting practice must be assumed to be a general key factor and one important reason for forest damage. Excluding game animals from grazing on open meadows or grassland forces them to use dense vegetation, where they have only trees to browse. If deer populations shall be used or regulated, a discussion about alternative forms and strategies to remove animals should be opened. Such strategies should be developed to strictly prevent any negative experience against humans spreading out in a population. Since many species seem to be able to distinguish between dangerous and safe areas, a systematic differentiation between hunted and non-hunted areas may also be a valuable approach. Game sanctuaries which include both cover and attractive vegetation may contribute to reduce the impact of hunting and compensate the drawbacks on forest regeneration. Such measures may improve visibility of deer for tourists and therefore increase the attraction of natural landscapes if basic regulations for tourists such as restriction on paths and tracks are followed.

It may be required to not give positive stimuli against dangerous predatory species like wolves and bears even in reservations but to train these species systematically to avoid approaching human individuals, domestic animals, or settlements. Such negative experiences should better not be directly connected to humans but to well perceivable symbols of human presence like clearly visible electric fences, specific smells, or noises. The same principle may be applied against other wild animal species e.g. to prevent wild boars from entering villages, gardens, or fields. This will focus the avoidance learning of animals on specific clues and restricted places, as well as on specific situations, but not generally on humans. On the other hand, the effectiveness of negative conditioning depends in all species on really negative experiences, simple light- and sound-emitting frightening devices alone proved ineffective against deer and elk (VerCauteren et al. 2005). It required aversive conditioning treatments using either humans or dogs to create sequences resembling chases by predators to temporarily modify the behavior of elk (Kloppers et al. 2005). A systematic negative training using well perceivable non-human symbols will prevent the establishment of negative experience and prevent flight from visitors in the field and wood, with the undesired drawbacks on visibility or tree regeneration by concentrating browsing in the cover of thickets. It may be suggested that the concept of secondary repellents will be useful for protecting resources of human concern in a much broader sense as assumed until now. As an alternative, non-lethal methods for solving the growing number of conflicts between humans and wildlife will meet ethical requirements of growing importance (Fall and Jackson 2002).

As a conclusion, the behavior of wild animals towards humans should not be regarded as innate and fixed but as a result of the sum of experiences which an animal as individual, or member of a family, or social group has experienced in the past. As it may be assumed that experiences can be learned at least from the mother or other adults of the same social group, the behavior of wild animals reflect widely the long-term strategy of humans towards these animals. Accordingly, humans should be much more aware to arrange their behavior in respect to the desired behavior of the different wild animal species in an area. To better understand these interrelations, more experimental investigations on the learning behavior of the different species in respect to positive and negative experiences, interrelation between signal strength or factor importance and memory duration or on the capability to learn from con-species will be very valuable.

References

- Artiss, T., Hochachka, W.M., and Martin, K. 1999. Female foraging and male vigilance in white-tailed ptarmigan (*Lagopus leucurus*): opportunism or behavioural coordination? *Behavioral Ecology and Sociobiology* **46**: 429-434
- Aston-Jones, G. 2005. Brain structures and receptors involved in alertness. *Sleep Medicine Suppl.* **1**: 3-7.
- Baker, S.E., Johnson P.J., Slater, D., Watkins, R.W., Macdonald, D.W. 2007. Learned food aversion with and without an odour cue for protecting untreated baits from wild mammal foraging. *Applied Animal Behaviour Science* **102**: 410-428
- Bargali, H.S., Akhtar, N., and Chauhan, N.P.S. 2005. Characteristics of sloth bear attacks and human casualties in North Bilaspur forest division, Chhattisgarh, India. *Ursus* **16**: 263-267
- Baumann, P.J., Jenks, J.A., and Roddy, D.E. 1999. Evaluating techniques to monitor elk movements across fence lines. *Wildlife Society Bulletin* **27**: 344-352
- Bender, L.C., Beyer, D.E., and Haufler, J.B. 1999. Effect of short-duration, high intensity hunting on elk wariness in Michigan. *Wildlife Society Bulletin* **27**: 441-445
- Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proceedings of the Royal Society of London, Series B, Biological Sciences* **266**: 2261-2267
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* **3**: 620-623
- Bergmann, H.H., and Wille, V. 2001. Flüchten oder Gewöhnen - Feindabwehrstrategien wildlebender Tiere als Reaktion auf Störungen. *Laufener Seminarbeiträge* **1/ 2001**: 17-22
- Beutler, A. 1996. Die Großtierfauna Europas und ihr Einfluß auf Vegetation und Landschaft. Pages 51-106 in: B. Gerken, and Meyer, C., editors, Wo lebten Pflanzen und Tiere in der Naturlandschaft und der frühen Kulturlandschaft Europas? *Natur- und Kulturlandschaft* **1**, Höxter 1996
- Blumstein, D.T., Daniel, J.C., Schnell, M.R., Ardron, J.G., and Evans C.S. 2002. Antipredator behaviour of red-necked pademelons: a factor contributing to species survival? *Animal Conservation* **5**: 325-331

- Blumstein, D.T., Bitton, A., and DaVeiga, J. 2006. How does the presence of predators influence the persistence of antipredator behavior? *Journal of Theoretical Biology* **239**: 460-468
- Bögel, R., and Lotz, A. 2000. Lebensraumansprüche der Gemse in Wechselwirkung zu Waldentwicklung und Tourismus im Nationalpark Berchtesgaden. BfN-Schriftenreihe "Angewandte Landschaftsökologie" Nr. 35
- Boissy, A. 1995. Fear and fearfulness in animals. *Quarterly Revue of Biology* **70**: 165-191
- Borkowski, J. 2001. Flight behaviour and observability in human-disturbed sika deer. *Acta Theriologica* **46**: 195-206
- Breck, S.W., Lance, N., and Callahan, P. 2006. A shocking device for protection of concentrated food sources from black bears. *Wildlife Society Bulletin* **34**: 23-26
- Büker, A., Scheibe, K.M., Streich, J., Eichhorn, K., and Scheibe, A. 1999. Reaktion von freilebenden Rehen (*Capreolus capreolus*) auf anthropogene Aktivitäten in Abhängigkeit von der Landschaftsstruktur. Pages 298-309 in: B. Gerken and Görner, M., editors, Europäische Landschaftsentwicklung mit großen Weidetieren Geschichte, Modelle und Perspektiven. *Natur- und Kulturlandschaft* **3**, Höxter/Jena 1999
- Burcham, M., Edge, W.D., and Marcum, C.L. 1999. *Elk use of private land Wildlife Society Bulletin* **27**: 833-839.
- Caro, T.M., Graham, C.M., Stoner, C.J., and Vargas, J.K. 2004. Adaptive significance of antipredator behaviour in artiodactyls. *Animal Behaviour* **67**: 205-228
- Conner, M.M., White, G.C., and Freddy, D.J. 2001. Elk movement in response to early-season hunting in northwest Colorado. *Journal of Wildlife Management* **65**: 926-940.
- Conover, M.R., Pitt, W.C., Kessler, K.K., DuBow, T.J. and Sanborn, W.A., 1995. Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin* **23**, pp. 407-414
- De Azevedo, C.S., and Young, R.J. 2006. Do captive-born greater rheas *Rhea americana* Linnaeus (Rheiformes, Rheidae) remember antipredator training? *Behavioral Ecology and Sociobiology* **23**: 194-201
- De Boer, H.Y., van Breukelen, L., Hootsmans, M.J.M., and van Wieren, S.E. 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology* **10**: 35-41
- Dominguez, J. 2003. Sleeping and vigilance in Black-tailed Godwit. *Journal of Ethology* **21**: 57-60
- Douglas, M.J.W. 1971. Behaviour responses of red deer and chamois to cessation of hunting. *New Zealand Journal of Science* **14**: 507-518
- Enggist-Düblin, P., and Ingold, P. 2003. Modelling the impact of different form of wildlife harassment, exemplified by a quantitative comparison of the effects of hikers and paragliders on feeding and space use of chamois *Rupicapra rupicapra*. *Wildlife Biology* **9**: 37-45
- Fall, M.W., Jackson, W.B. 2002. The tools and techniques of wildlife damage management - changing needs: an introduction. *International Biodeterioration & Biodegradation* **49**: Issue: 87-91
- Filli, F., and Nievergelt, B. 1996. The effect of a one time hunting of red deer in an area of the Swiss National Park. *Zeitschrift für Jagdwissenschaften* **42**: 249-255
- Frid, A., and Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6** (1): art. no. 11

- Fritz, H., Guillemain, M., and Durant, D. 2002. The cost of vigilance for intake rate in the mallard (*Anas platyrhynchos*): an approach through foraging experiments. *Ethology, Ecology & Evolution* **14**: 91-97
- Grau, G.A., and Grau, B.L. 1980. Effects of hunting on hunting effort and white-tailed deer behaviour. *Ohio Journal of Science* **80**: 150-156
- Gunther, K.A., Haroldson, M.A., Frey, K., Cain, S.L., Copeland, J., and Schwartz, C.C. 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992-2000. *Ursus* **15**: 10-22
- Kie, J.G. 1999. Optimal foraging and risk of predation: Effects on behavior and social structure in ungulates. *Journal of Mammology* **80**: 1114-1129
- Kilgo, J.C., Labisky, R., and Fritzen, D.E. 1998. Influences of hunting on the behaviour of white-tailed deer: Implications for conservation of the Florida Panther. *Conservation Biology* **12**: 1359
- Kilpatrick, H.J., Lima, K. 1999. Effects of archery hunting on movement and activity of female white-tailed deer in an urban landscape. *Wildlife Society Bulletin* **27**: 433-440.
- Kloppers, E.L., St Clair, C.C., Hurd, T.E. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society* **10**: 1 Article Number: 31
- Krebs, J. R., and Davis, N. B. 1996. Einführung in die Verhaltensökologie. Blackwell, Berlin
- Kufeld, R.C., Bowden, D.C., and Schrupp, D.L. 1988. Influence of hunting on movements of female mule deer. *Journal of Range Management* **41**: 70-72
- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**: 619-640
- Lima, S.L. 1992. Life in a multi-predator environment: some considerations for anti-predatory vigilance. *Annales zoologici Fennici* **29**, 217-226
- Lingle, S., and Wilson, W.F. 2001. Detection and avoidance of predators in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O-hemionus*) *Ethology* **107** (2): 125-147
- Llinas, R.R., and Steriade, M. 2006. Bursting of thalamic neurons and states of vigilance. *Journal of Neurophysiology* **95**: 3297-3308
- Macdonald, D.W., Baker, S.E. 2004. Non-lethal control of fox predation: the potential of generalised aversion. *Animal Welfare* **13**: 77-85
- Martinetto, K., and Cugnasse, J.M. 2001. Reaction distance in Mediterranean Mouflon (*Ovis gmelini musimon* x *Ovis* sp.) in the presence of hikers with a dog on the Caroux plateau (Herault, France) *Revue d'Ecologie Terre et Vie* **56**: 231-242
- Maillard, D., Morellet, N., and Gaudin, J.C. 1999. Seasonal variation of home range domaine vital and habitat selection of the roe deer in a Mediterranean habitat: The case of adult female and male. *Revue d'Ecologie Terre et Vie* **54**: 71-87
- Martin, P.S. 1984. Prehistoric overkill: the global model. In: Martin PS, Klein RG (eds.) *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press., Tucson: pp. 354-403
- Matson, T.K., Goldizen, A.W., and Putland, D.A. 2005. Factors affecting the vigilance and flight behaviour of impalas. *South African Journal of Wildlife Research* **35**: 1-11
- Matthen, M. 1998. Biological universals and the nature of fear. *The Journal of Philology* **95**: 105- 132
- Millsaugh, J.J., Brundige, G.C., Gitzen, R.A., and Raedeke, K.J. 2000. Elk and hunter space-use sharing in South Dakota. *Journal of Wildlife Management* **64**: 994-1003

- Misslin, R. 2003. The defense system of fear: behavior and neurocircuitry. *Clinical Neurophysiology* **33**: 55-66
- Naugle, D.E., Jenks, J.A., Kernohan, B.J., and Johnson, R.R. 1997. Effects of hunting and loss of escape cover on movements and activity of female white-tailed deer, *Odocoileus virginianus*. *The Canadian Field-Naturalist* **111**: 595- 600
- Oken, B.S., Salinsky, M.C., and Elsas, S.M. 2006. Vigilance, alertness, or sustained attention: physiological basis and measurement. *Clinical Neurophysiology* **117**: 1885–1901.
- Olesen, C.R., Theil, P.K., and Coutant, A.E. 1998. Ravildt og forstyrrelser. Faglig rapport fra DMU, nr. 237, Miljø- og Energiministeriet Danmarks Miljøundersøgelser, Ronde, DK
- Owen-Smith, N. 1989. Megafaunal extinctions: The conservational message from 11,000 years b.p. *Conservation Biology* **3**: 405 – 412
- Patterson, I.J. 1988. Responses of Apennine Chamois to human disturbance. *Zeitschrift für Säugetierkunde* **53**: 245-252
- Petrak, M. 1996. Der Mensch als Störgröße in der Umwelt des Rothirsches. *Zeitschrift für Jagdwissenschaften* **42**: 180-194
- Petrak, M. 1999. Feindverhalten des Rehwildes - Herausforderungen für den Jaeger. *Schriftenreihe des Landesjagdverbandes Bayern* **7**: 15-36
- Pollard, L.C., Littlejohn, R.P. 1995. Consistency in avoidance of humans by individual red deer. *Applied Animal Behaviour Science*, **45**: 165-174
- Proctor, C.J., Broom, M., and Ruxton, G.D. 2003. A communication-based spatial model of antipredator vigilance. *Journal of Theoretical Biology* **220**: 123-137
- Ragusa-Netto, J. 2002. Vigilance towards raptors by nuclear species in bird mixed flocks in a Brazilian savannah. *Studies on Neotropical Fauna and Environment* **37**: 219-226
- Recarte, J.M., Vincent, J.P., and Hewison, A.J.M. 1998. Flight responses of park fallow deer to the human observer. *Behavioural Processes* **44**: 65-72
- Rode, K.D., Farley, S.D., Robbins, C.T. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* **133**: 70-80
- Rondinini, C., Boitani, L. 2007. Systematic conservation planning and the cost of tackling conservation conflicts with large carnivores in Italy. *Conservation Biology* **21**: 1455-1462
- Rosenfeld, A. 2000. Wild boar habitat preference: a case of human influence. *Israel Journal of Zoology* **46**: 171
- Sand, H., Wikenros, C., Wabakken, P., and Liberg, O. 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society B-Biological Sciences* **273**: 1421-1427
- Schaumann, W. 2002. Charles Darwin, Leben und Werk. Ecomed, Landsberg/Lech
- Scheibe, K.M., Berger, A., Budras, K., Bull, J., Eichhorn, K., Dehnhard, M., Kalz, A., Sieling, C., Weber, S., and Zimmermann, W. 2000. Research on Przewlaski horses in the semireserve Schorfheide. Pages 31-39 in V.S. Havrylenko, editor. *New biosphere reserve „Askania Nova“: protection and preservation of rare species*. Ukrain's'ka Mis'ka Drukarnja, Cherson.
- Schultz, R.D., Bailey, A.J. 1978. Responses of national park elk to human activity. *Journal of Wildlife Management* **42**: 91-100
- Scherzinger, W. 1992. Die “ethologische Nische”, ein Schlüsselproblem im Biotop- und Artenschutz. *Seevögel, Zeitschrift des Vereins Jordsand, Hamburg*. **12/1992**, SH1, 93-98

- Schmidt, K. 1992. On the influence of feeding and hunting on the space-time behaviour of alpine red deer. *Zeitschrift für Jagdwissenschaften* **38**: 88-100
- Shivik, J.A., Treves, A., Callahan, P. 2003. Nonlethal Techniques for Managing Predation: Primary and Secondary Repellents. *Conservation Biology* **17** : 1531–1537
- Smith, T.S., Herrero, S., DeBruyn, T.D. 2005. Alaskan brown bears, humans, and habituation *URSUS* **16**: 1-10
- Sodeikat, G., and Pohlmeier, K. 2002. Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). *Zeitschrift für Jagdwissenschaften* **48** Suppl.: 161-166
- Stamm, R.A. 1967. Furcht und Angst bei Tieren. Pages 127- 141 in: P. Kielholz, editor, *Angst, Psychische und somatische Aspekte*. Huber, Bern
- Taylor, A.R., and Knight, R.L. 2003. Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications* **13**: 951-963
- Thürer, E. 1979. Geschichte des Jagdwesens und der Jagdbanngebiete im Kanton Glarus. Dissertation University Zürich
- Toigo, C. 1999. Vigilance behavior in lactating female Alpine ibex. *Canadian Journal of Zoology* **77**: 1060-1063
- Treves, A., Drescher, A., and Snowdon, C.T. 2003. Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology* **109**: 135-146
- VerCauteren, K.C., Shivik, J.A., Lavelle, M.J. 2005. Efficacy of an animal-activated frightening device on urban elk and mule deer. *Wildlife Society Bulletin* **33**: 1282-1287
- Vieira, M.E.P., Conner, M.M., White, G.C., and Freddy, D.J. 2003. Effects of archery hunter numbers and opening dates on elk movement *Journal of Wildlife Management* **67**: 717-728
- Welp, T., Rushen, J., Kramer, D.L., Festa-Bianchet, M., and de Passille, A.M. 2004: Vigilance as a measure of fear in dairy cattle. *Applied Animal Behaviour Science* **87**: 1-13
- White, K.S., Berger, J. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* **79**: 2055-2062
- Wilson, S.M., Madel, M.J., Mattson, D.J., Graham, J.M., Burchfield, J.A., Belsky, J.M. 2005. Natural landscape features, human-related attractants, and conflict hotspots: a spatial analysis of human-grizzly bear conflicts. *URSUS* **16**: 117-129
- Wooldridge, D.R. 1980. Chemical aversion conditioning of polar and black bears. *Bear Biology Association Conference Series* Supplement: No. 3: 167-173
- Ylönen, H. and Magnhagen, C. 1992 : Antipredatory behaviour : a "hot spot" of evolutionary ecology of the nineties. *Annales zoologici Fennici* **29**, 179-182
- Zeeb, K. 1959. Das Verhalten des Pferdes bei der Auseinandersetzung mit dem Menschen. *Säugetierkundliche Mitteilungen* **7** SH 142

Chapter 9

CLIMATE CHANGE EFFECTS ON WILDLIFE POPULATIONS

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Abstract

It is now widely accepted that many wildlife species are under imminent threat as a result of climate change. Climate change effects on the demography of populations (i.e., changes in fecundity or survival rates) can be direct (i.e., abiotic through factors such as rainfall or temperature) or indirect through species interactions (i.e., through consumers, resources or competitors). Over time these processes and dynamics can result in positive, negative or neutral net effects with increasing, declining or stable population trends. For certain species groups it has been argued that shorter-lived species with higher fecundity might have a life span too short to develop behavioral adaptation to directional changes in their environment and are thus more sensitive to global change ('behavioral adaptation hypothesis'). In contrast, it has been postulated that short-lived and small-bodied species have a higher adaptation potential because (in the long term) shorter generation times allow higher rates of evolutionary adaptation ('structural adaptation hypothesis'). To evaluate these two hypotheses and to assess if and under which conditions net effects of climate change on species' demography are primarily positive or negative, we analyzed a selection of 47 peer-reviewed, empirical wildlife studies for the time period 1990-2007. Among all studies analyzed 73% reported negative climate change effects of which 60% were caused by biotic effects, i.e., indirect effects. There was an increased likelihood of positive effects amongst animals with shorter longevity (mean longevity = 13.3 and 5.7 years for negative and positive population

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effects, respectively). This suggests there may be an advantage to being shorter lived during periods of climatic change, and provides some support for the structural adaptation hypothesis. Mean number of generations studied was 4.1 ($n=34$, $SD=8.2$) and 9.3 ($n=12$, $SD=10.1$) among studies that reported negative and positive population effects, respectively. To our knowledge the results from this meta-analysis represent the first general assessment of climate change-induced demographic effects on wildlife populations.

Keywords: global warming, biodiversity, body size, population demography, life history, adaptation, evolution

1. Introduction

Climate change has evolved as one of the major foci in debates on the environmental future of our planet. Rapid changes in global and regional climates are now felt in the everyday lives of most people on earth and are widely recognized as a major threat to global biodiversity with the potential to vastly alter species ranges (Root et al. 2003) and accelerate negative effects of global land use change and habitat destruction.

Wildlife populations can be affected through direct, abiotic effects such as changes in precipitation, temperature or disturbance regimes. These direct, demographic effects can be felt through changes in survival rates and/or reproductive output. For example, in the past four decades population dynamics of High Arctic Peary caribou have been subject to several population die-offs due to warmer spring weather with ice coating on the ground or thicker-than-usual snow cover. These biotic disturbances result in temporary inaccessibility of forage resources and unusually high mortality rates (Tews et al. 2007).

Direct effects at the species level can lead to further indirect effects via inter-specific interactions including predation, competition and resource availability (Barbraud & Weimerskirch 2001, Durant et al. 2003, Pounds et al. 2006). To illustrate this, a change in a climate variable may directly increase mortality rates of juveniles and decrease overall population abundance of one species. If this species is preyed upon by another species and the predator has to face reduced resource availability (assuming that it is not capable of switching prey species) this would result in indirect or biotic effects. Hence, the indirect consequences of climate change have the potential to vastly increase (or decrease) the proportion of species that may become extinct due to climate change beyond the numbers predicted by direct effects. Over time both direct (i.e., abiotic) and indirect (i.e., biotic) effects of climate change can lead to positive, negative or neutral net effects resulting in increasing, declining or stable population trends, respectively.

For example, climate change has decreased fecundity and survival in some polar bear (*Ursus maritimus*) populations. Higher temperatures have reduced the extent of sea ice and resulted in earlier annual thaws and delayed freezing which limits the bears' access to seals, their main prey (Stirling et al. 1999, Derocher et al. 2004). However, there is evidence that climate warming may also lead to positive changes in some species' vital rates. Chamaille-Jammes et al. (2006) reported that regional warming in southern France resulted in a positive fitness response in mountain populations of the common lizard (*Lacerta vivipar*); individual body size increased dramatically for four populations studied over nearly two decades, resulting in increased reproductive output.

Examples of biotic, indirect effects are also numerous. For example, climate change has been shown to decrease survival rates in Emperor Penguins (*Aptenodytes forsteri*) in the Antarctic; an increase in sea surface temperatures reduced krill availability which are consumed by fish and squid, the main prey of Emperor penguins (Barbraud & Weimerskirch 2001). Durant et al. (2003) found that breeding success of Atlantic puffins (*Fratercula arctica*) increased under climate change as it was positively affected by higher sea temperatures, which impacted the size and abundance of the puffins' main prey, the Norwegian spring-spawning herring (*Clupea harengus*).

How well wildlife populations are able to cope with rapid climatic changes and whether overall effects are primarily positive or negative depend on the adaptation potential of a species. Following its principle the outcome of natural selection can result in behavioral and/or physical (or structural) adaptation over ecological and evolutionary time scales.

One theory suggests that larger-bodied species (usually species at higher trophic levels) may be more sensitive to unfavorable changes in climatic conditions than smaller-bodied species due to longer generation times (e.g., Raffaelli 2004). Thus, shorter generation times allow higher rates of evolutionary (here physical or structural) adaptation and, hence, over time such species may show positive climate change effects at the population level. We will coin this the 'structural adaptation hypothesis.' Another hypothesis suggests that shorter-lived species with higher fecundity might have life spans too short to develop behavioral adaptations to directional changes in their environment and are thus more sensitive to global change (Jiguet et al. 2007). In other words, longer-lived species are more resilient to unfavorable climatic changes because they are better able to develop strategies of behavioral adaptation. We will coin this the 'behavioral adaptation hypothesis'.

Thus, according to these two hypotheses, shorter generation times may imply lower behavioral adaptation potential but higher evolutionary adaptation potential. In contrast, species with longer generation times would benefit from potentially higher rates of behavioral adaptation but lower potential to adapt phenotypically. In other words, under climatic change there may be both advantages and disadvantages to being short-lived (and usually smaller bodied) versus long-lived (and usually larger bodied).

In order to test both hypotheses and analyze which species and life history traits are more likely to show positive vs. negative and biotic vs. abiotic (i.e., direct vs. indirect) responses we conducted a literature analysis on climate change effects on wildlife populations. The central question that we intend to discuss is: if global warming continues its rapid development, is there a general trend that may allow us to predict which species are more likely to go extinct as a result of climate change?

2. Methods

The literature survey and analysis was conducted for the time period 1990-2008 using the ISI Web of Science® and searching with the keywords 'climate change', 'climate', or 'global warming' with any combination of the keywords 'growth rate', 'population', 'species', 'fecundity', and 'survival'. Further criteria were developed to filter the most relevant marine and terrestrial vertebrate and invertebrate studies. We excluded the

following studies: (i) vertebrate studies of less than 3 years, (ii) laboratory experiments, (iii) comparative or ‘space-for-time’ substitute studies (e.g., low versus high temperature regimes for two different study locations as a climate warming surrogate), (iv) simulation studies, (v) long-distance migratory bird studies, and (vi) species’ range studies. We explicitly searched for longer term empirical studies that monitored changes in demographic rates (e.g., fecundity, survival, or abundance) for wildlife populations and which reported significant changes as a result of one or more climate variables. Based on the above criteria and constraints we selected a total of 42 peer-reviewed studies for the purpose of our analysis.

We then developed different categories for our meta-analysis where we recorded the species group (e.g., mammal, bird, fish), the effect type (i.e., biotic or abiotic), climate change net effect (i.e., positive or negative), demographic parameter measured (i.e., reproduction, survival, abundance), and total study years. Based on the MPI longevity records database (Carey & Judge 2002) we further added the maximum reported age (years) for each study species. We used longevity as a proxy to investigate whether positive or negative effects of climate change are correlated with life span and whether the ‘behavioral adaptation’ or the ‘structural adaptation’ hypothesis prevails.

We assumed that trophic position co-varies with body mass, allowing us to use mass to evaluate how indirect (i.e., biotic) and direct (i.e., abiotic) population responses were distributed across all study species with respect to their trophic position. Body mass data (expressed in grams) were obtained primarily from Silva and Downing (1995; mammals) and Dunning (2008; birds). In cases where multiple measurements were reported per species, mean, minimum and maximum body sizes were averaged (or for each sex, if applicable) following Mattila and Bokma (2008); if only a range of body sizes was available, the value selected was the range midpoint. Subsequently, if available the average of both sexes was used, otherwise the average of whatever data available was used. Other masses were obtained from the literature for collared pikas (*Ochotona collaris*; Smith 1974), common toad (*Bufo bufo*; Vioturon & Lengagne 2008), reindeer (*Rangifer tarandus*; Holand et al. 2006), sardines (*Sardina pilchardus*; Sinovčić et al. 2004) and anchovies (*Engraulis encrasicolus*; Sinovčić et al. 2004).

3. Results

Based on 44 species analyzed from 39 long-term marine and terrestrial studies we identified 47 ‘study species’ as four studies had multiple species, and three species were each the subject of two studies. Positive climate change effects on species’ demography (i.e., increase in survival and/or fecundity or increase in abundance either via direct/biotic or indirect/abiotic effects) occurred in ~27% of all studies. Of these, ~54% were caused by biotic (i.e., indirect) effects, whereas ~46% were caused through direct, abiotic effects. Of all studies, ~73% reported negative effects (i.e., decrease in survival and/or fecundity or abundance) in which 60% were caused by biotic effects (e.g., through another species in the food web). Although the majority of studies showed negative effects, positive effects were commonly found, especially for thermally constrained species or species in high latitude and high altitude ecosystems where considerable warming has been reported (Table 1). In total we found 6 insect, 1 amphibian, 1 reptile, 5 fish, 21 bird and 10 mammal species. In all of these

species groups (except the amphibian and reptile study species) we found both positive and negative population responses.

Binomial logistic regression was used to assess the relationship between species longevity (years), and positive or negative demographic effects (PROC LOGISTIC, SAS Institute 1990; dichotomous dependent variable; Figure 1). There was an increased likelihood of positive effects amongst animals with shorter longevity (binomial logistic regression; $\chi^2 = 11.89$, $df = 1$, $p = 0.0006$, $n = 46$; Alpine grasshopper (*Paprides nitidus*) excluded because both positive and negative effects reported). Mean longevity was 13.3 years among studies that reported negative population effects ($n = 34$, $SD = 8.5$). Mean longevity was 5.7 years among studies with positive population effects ($n = 12$, $SD = 3.8$). For species with positive demographic effects the large majority (~83%) were shorter lived with longevity of <10 years. This was the opposite for species with negative effects where only ~29% had longevity of <10 years.

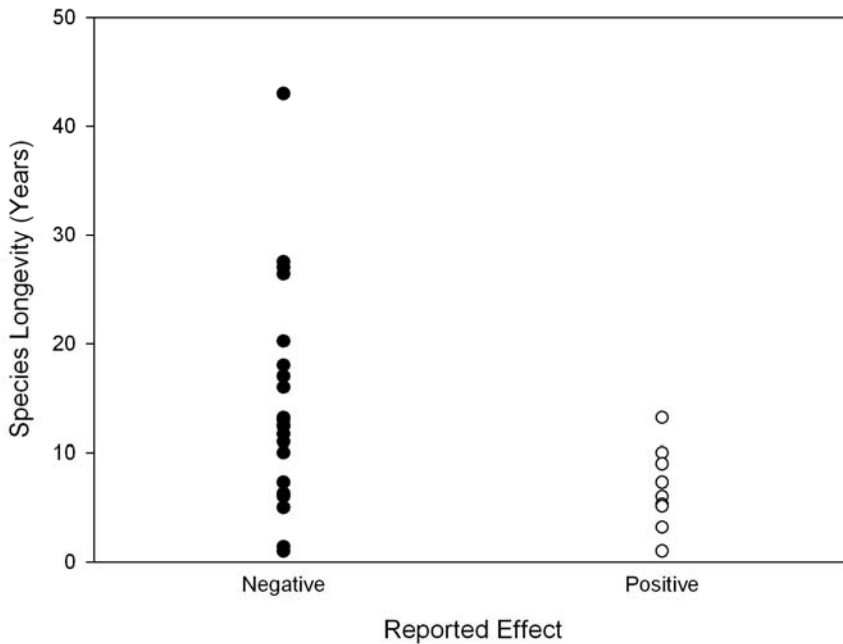


Figure 1. Mean species longevity for studies where positive ($n = 12$) and negative ($n = 34$) demographic responses were reported (binomial logistic regression; $\chi^2 = 11.89$, $df = 1$, $p = 0.0006$, $n = 46$).

Table 1. List of study species with scientific name, species group, body mass ('BM'), longevity in years ('Long'), number of generations studied ('# Gen'), demographic effects reported with changes in survival rate ('S'), fecundity/reproductive rate ('R'), abundance ('A'), abiotic effects ('Ab'), biotic effects ('Bi'), study length ('Yrs'), study location and reference (first author and publication year). For further details see main text and references. Studies were ranked by longevity (years).

Species:						Effects reported:					Study:		
Common name	Scientific name	Group	BM (g)	Long (yr)	# Gen	S	R	A	Ab	Bi	Yrs	Location	Reference (first author)
Aphid	<i>Acyrtosiphon svalbardicum</i>	Insect	-	1	1.0	+	+		Y	Y	1	Spitsbergen, Norway	Strathdee (1993)
Alpine Grasshopper	<i>Paprides nitidus</i>	Insect	-	1	20.0	-/+			Y		20	Alpine Grasslands, NZ	White (1991)
Skipper Butterfly	<i>Hesperia comma</i>	Insect	-	1	20.0		+			Y	20	Grassland, UK	Davies (2006)
Tiger Moth	<i>Arctia caja</i>	Insect	-	1	31.0	-			Y		31	United Kingdom	Conrad (2003)
Skipper Butterfly	<i>Atalopedes campestris</i>	Insect	-	1	35.0	+			Y		35	Northern USA	Crozier (2004)
Checkerspot Butterfly	<i>Euphydryas editha bayensis</i>	Insect	-	1	39.0	-				Y	39	Grassland, Canada	McLaughlin (2002)
Tundra Vole	<i>Microtus oeconomus</i>	Mammal	3.85	1.4	2.9	-			Y		4	Norway	Aars (2002)
Common Lizard	<i>Lacerta vivipara</i>	Reptile	-	3.2	5.6	+	+		Y		18	Southern France	Chamaille-Jammes (2006)
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	Bird	64	5	7.4			-	Y	Y	37	North America	Anders (2006)
Dipper	<i>Cinclus cinclus</i>	Bird	59.8	5.1	3.9		+		Y	Y	20	Southern Norway	Saether (2000)
Anchovy	<i>Engraulis encrasicolus</i>	Fish	17.1	5.3	14.9			+	Y	Y	79	North Sea	Beare (2004)
Collared Pikas	<i>Ochotona collaris</i>	Mammal	130	6	1.2		+		Y		7	Yukon, Canada	Franken (2004)
Collared Pikas	<i>Ochotona collaris</i>	Mammal	130	6	2.0	-	-		Y		12	Rocky Mountains	Morrison (2007)
Black-legged Kittiwakes	<i>Rissa tridactyla</i>	Bird	408	6	2.7		-			Y	16	North Sea	Frederiksen (2004)
Snake Pipefish	<i>Entelurus aequoreus</i>	Fish	-	6	12.5	+	+		Y		75	Northeastern Atlantic	Kirby (2006)
Lesser Kestrel	<i>Falco naumanni</i>	Bird	153	6.2	1.9		-			Y	12	Spain	Rodriguez (2003)
Razorbill	<i>Alca torda</i>	Bird	726	6.3	1.4	-				Y	9	Northern Norway	Sandvik (2005)
Pied Flycatcher	<i>Ficedula hypoleuca</i>	Bird	13.9	7.3	2.5		-			Y	18	Central Europe	Both (2006)
Pied Flycatcher	<i>Ficedula hypoleuca</i>	Bird	13.9	7.3	3.4		+			Y	25	Central Europe	Winkel (1997)
Sardine	<i>Sardina pilchardus</i>	Fish	23.7	9	8.8			+	Y	Y	79	North Sea	Beare (2004)
Gentoo Penguin	<i>Pygoscelis papua</i>	Bird	5,950	10	2.6			+	Y		26	Antarctic	Forcada (2006)

Table 1. Continued

Species:						Effects reported:					Study:		
Common name	Scientific name	Group	BM (g)	Long (yr)	# Gen	S	R	A	Ab	Bi	Yrs	Location	Reference (first author)
Adelie Penguin	<i>Pygoscelis adeliae</i>	Bird	4,850	10	2.6			-	Y		26	Antarctic	Forcada (2006)
Chinstrap Penguin	<i>Pygoscelis antarcticus</i>	Bird	4,156	10	2.6			-	Y		26	Antarctic	Forcada (2006)
Common Guillemot	<i>Uria aalge</i>	Bird	993	11	1.3	-				Y	14	Northern Norway	Sandvik (2005)
Bruennich's Guillemot	<i>Uria lomvia</i>	Bird	964	11	1.3	-				Y	14	Northern Norway	Sandvik (2005)
Reindeer	<i>Rangifer tarandus</i>	Mammal	78,300	11	1.3	-			Y		14	Central Norway	Weladji (2003)
Peary Caribou	<i>Rangifer tarandus pearyi</i>	Mammal	86,000	11	3.6	-	-		Y		40	Arctic	Miller (2003)
Rockhopper Penguin	<i>Eudyptes chrysocome</i>	Bird	2330	11	12.7			-		Y	140	Antarctic	Hilton (2006)
Pigeon Guillemot	<i>Cephus columba</i>	Bird	530	11.7	2.4		-			Y	28	California, USA	Sydeman (2001)
Xantus's Murrelet	<i>Synthliboramphus hypoleucos</i>	Bird	167	12.4	2.3		-			Y	28	California, USA	Sydeman (2001)
Brown Trout	<i>Salmo trutta</i>	Fish	-	12.5	2.0			-	Y		25	Mountains, Alps	Hari (2006)
Harbour Porpoise	<i>Phocoena phocoena</i>	Mammal	61,000	13	0.8	-				Y	10	North Sea	MacLeod (2007)
White-tailed Ptarmigan	<i>Lagopus leucurus</i>	Bird	355	13	1.9			-	Y	Y	25	Colorado, USA	Wang (2002)
Atlantic Puffin	<i>Fratercula arctica</i>	Bird	381	13.2	1.0	-				Y	13	Northern Norway	Sandvik (2005)
Atlantic Puffin	<i>Fratercula arctica</i>	Bird	381	13.2	2.0		+			Y	27	Norway	Durnat (2003)
Common Toad	<i>Bufo bufo</i>	Amphibian	94.2	16	1.4	-	-		Y		22	United Kingdom	Reading (2007)
Gray Jay	<i>Perisoreus canadensis</i>	Bird	71.7	16	1.6		-		Y		26	Boreal Forest, Canada	Waite (2006)
Emperor Penguin	<i>Aptenodytes forsteri</i>	Bird	33,850	16	3.1	-	-		Y	Y	50	Antarctic	Barbraud (2001)
Northern Spotted Owl	<i>Strix occidentalis caurina</i>	Bird	621	17	0.8	-	-			Y	14	Northern California, USA	Franklin (2000)
Southern Gemfish	<i>Rexea solandri</i>	Fish	-	17	0.9		-		Y		15	Marine, New Zealand	Remwick (1998)
Beaver	<i>Castor fiber</i>	Mammal	17,000	17	0.9		-			Y	15	Central Europe	Nolet (2005)
Capercaillie	<i>Tetrao urogallus</i>	Bird	2,950	18	1.3		-		Y	Y	24	Scotland	Moss (2001)
Elephant Seal	<i>Mirounga leonina</i>	Mammal	1,900,000	20.25	0.4	-				Y	8	Antarctic	McMahon (2005)
Western Gull	<i>Larus occidentalis</i>	Bird	932	26.4	1.1		-			Y	28	California, USA	Sydeman (2001)
Moose	<i>Alces alces</i>	Mammal	304,000	27	1.5		-		Y		40	Northwest Minnesota, USA	Murray (2006)
Polar Bear	<i>Ursus maritimus</i>	Mammal	315,000	27.5	0.9		-		Y		25	Arctic	Derocher (2004)
Ringed Seal	<i>Phoca hispida</i>	Mammal	81,000	43	0.2		-		Y	Y	10	Hudson Bay, Canada	Ferguson (2005)

Binomial logistic regression was also used to assess the relationship between longevity and the duration of the study (ratio of study length to longevity; i.e., number of generations studied) and positive or negative demographic effects (Figure 2). A ratio of >1 indicates that more than one generation was investigated over the course of the study whereas a value of <1 indicates a study with a lower level of confidence when the study length covered less than the maximum reported age. When analyzing the relationship between study length and longevity we found a general trend (Figure 2) similar to the previous results (Figure 1). However, the relationship was not statistically significant (binomial logistic regression; $\chi^2 = 2.62$, $df = 1$, $p = 0.105$, $n = 46$). Mean number of generations studied was 4.1 ($n = 34$, $SD = 8.2$) and 9.3 ($n = 12$, $SD = 10.1$) among studies that reported negative and positive population effects, respectively. When only studies with a ratio larger than 1 were considered ($n = 35$) mean ratio was 5.9 and 11.7, respectively.

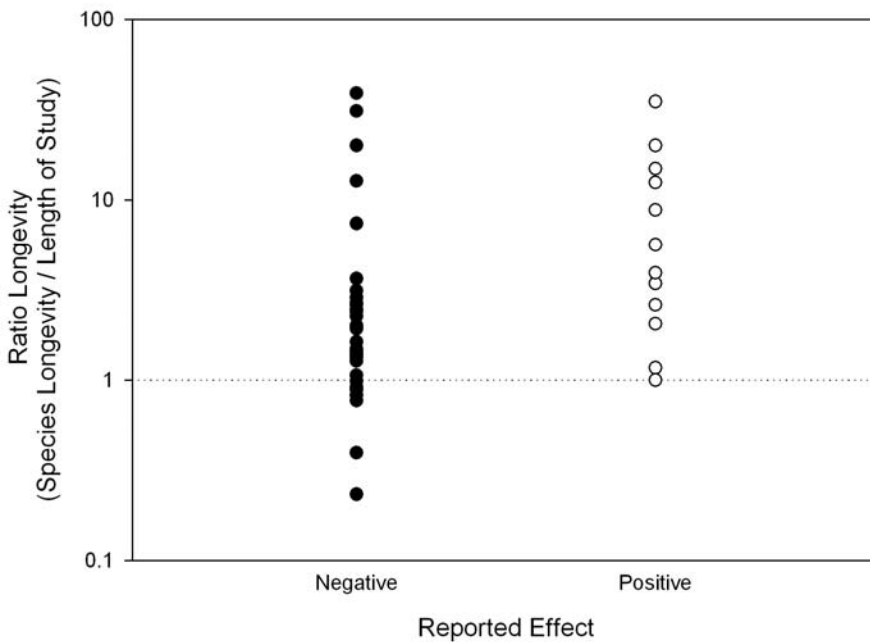


Figure 2. Species longevity ratio (ratio of study length to species longevity; i.e., number of generations studied) for studies where positive ($n = 12$) and negative ($n = 34$) demographic responses were reported (binomial logistic regression; $\chi^2 = 2.62$, $df = 1$, $p = 0.105$, $n = 46$).

We then analyzed how indirect (i.e., biotic) and direct (i.e., abiotic) population responses were distributed across all study species with respect to their trophic position. We used two-way ANOVA (PROC GLM, SAS Institute 1990) to compare body masses among the groups of studies that reported abiotic (direct) effects, biotic (indirect) effects, or both abiotic & biotic effects (see Table 1). No statistical differences in body mass were detected between groups (two-way ANOVA; $F_{df=2,34} = 0.28$, $p = 0.8$). Mean body mass of species for which abiotic effects were reported was 66,600 grams (118,000 SD, $n = 12$), 117,000 grams (460,000 SD, $n = 17$) for species for which biotic effects were reported, and 14,800 grams

(29,200 SD, $n = 8$; numbers rounded due to significant figures) for species for which both abiotic and biotic effects were reported (Figure 3).

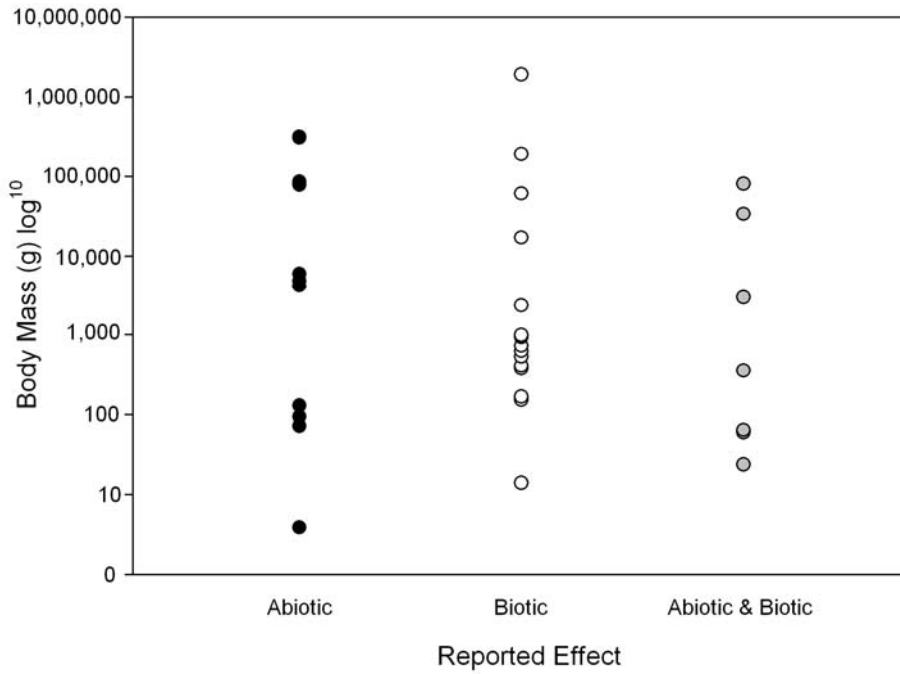


Figure 3. Distribution of log-transformed body mass (g) for 37 study species for abiotic ($n=12$), biotic ($n=17$), and both abiotic and biotic ($n=8$) effects. Abiotic effects refer to direct climate change-induced demographic effects (e.g., changes in juvenile mortality through weather conditions during breeding), biotic effects represent effects on the species' demography via consumer or resource species (e.g., predator or prey abundance directly effected by climate change).

4. Discussion

Although climate change effects on wildlife populations are often perceived as largely negative, especially in the public domain, our review showed a surprisingly large proportion of positive climate change effects on species' demography (~27%), either via indirect (i.e., biotic) or direct (i.e., abiotic) effects. However, whether the general prevalence of negative climate change effects on species' demography (~73%) is globally representative cannot be answered with such a study.

According to the studies in our literature review, species with shorter life spans were more likely to have positive demographic responses to climate change. This suggests there may be an advantage to being shorter lived during periods of climatic change, and provides some support for the structural adaptation hypothesis. However, it has also been shown that species with short generation times, such as insects, are also able to develop strategies of behavioral adaptation under rapid environmental change (e.g., Dennis & Sparks 2005) and we therefore suggest that evolutionary advantages of short-lived species cannot be attributed to structural adaptation processes alone.

Although we were unable to report a statistically significant relationship between the number of generations studied (ratio of longevity to study length) and positive or negative study outcomes, it is interesting to note that all studies which documented positive effects encompassed at least one full generation. Species with positive effects tended to be found among studies where a larger number of generations have been studied (compared to studies which reported negative effects). This result may indicate that species' responses to climate change may shift over time and could change from negative to positive depending on how many generations are studied.

There are many empirical examples demonstrating that both adaptation processes can take place over relatively short ecological time scales. For example, Indian tree frogs (*Polypedates maculatus*) showed behavioral differences that depend on their level of hydration (Lillywhite et al. 1998). In warmer years painted turtles (*Chrysemys picta*) grew larger and turtles reached sexual maturity faster (Frazer et al. 1993). Physiological effects of temperature, primarily sex determination, also can occur while reptiles are still within their eggs (Gutzke & Crews 1988). The body weight of North American wood rat (*Neotoma spp.*) has shown a significant decline that is inversely correlated with a significant increase in temperature (Smith et al. 1998). Juvenile red deer (*Cervus elaphus*) in Scotland grew faster in warm springs, leading to increases in adult body size (Albon & Clutton-Brock 1988), and thus higher reproduction potential.

However, we are aware of the fact that ecological time frames cannot fully provide the scale at which evolutionary processes of physical or structural adaptation may take place. Yet, despite the higher potential of behavioral adaptation for longer lived species our analysis shows that across all studies and species groups short-lived species appear to be better able to adapt under climatic changes. For plant species the importance of structural adaptation and generation time is particularly striking. For example, some annuals may be able to develop types that can adapt to climate warming whereas very long-lived species such as trees with a life span of several hundred years will not be capable of adapting quickly (Franks et al. 2007).

Empirical research on population-level consequences of climate change is a complex and challenging endeavor. Evidence on the dynamic interplay of direct, biotic effects and resulting changes in the interactions of species depend on how long population-level responses are monitored. Short-term studies may not be able to capture significant changes in demographic rates, especially for k-selected species or species with long generation times. Evidence of climate change effects depend on where a wildlife population is studied; at a receding range margin where environmental conditions are less favorable, demographic changes may be more severe whereas a population at the centre of its range with less pronounced environmental changes may be still thriving. In addition, the studies analyzed here may be hampered by methodological problems such as the length of time-series data of observed impacts in relation to the life cycle length of a species and the availability of climate data to which demographic changes are compared. Finally, another challenge is that the pace of climatic change (and how fast this change is 'perceived' by a species) has to be seen in the context of a species' life cycle relative to the environmental variable measured and ecological niche studied. For example, changes and 'perceptions' of average water temperatures over years or decades may vary spatially among local freshwater systems and different life history stages of a species. This, in turn can translate to very different behavioral and structural adaptation processes.

The Earth's biodiversity and climate are ever-changing. Over evolutionary time scales speciation and extinction have often resulted from long-term, 'natural' environmental changes. Now we are seeing short to mid-term climatic changes as a result of human industrialization. We are still far away of being able to make any predictions about where this will lead to in the long term. However, what we know is that climatic change in concert with anthropogenic habitat destruction, conversion, and fragmentation, as well invasive species are all contributing to a deadly cocktail for the integrity and intactness of current ecological systems on earth.

Acknowledgements

JT was supported through a Natural Sciences and Engineering Research Council (NSERC) Postdoctoral Fellowship. PLFF and MF gratefully acknowledge support from Université du Québec à Rimouski, NSERC, Centre d'études Nordiques, and Canada's ArcticNet research group. Many thanks also to Kevin Dufour for helpful discussions and suggestions.

References

- Aars, J. & Ims, R.A. (2002) Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. *Ecology* **83**: 3449-3456.
- Albon, S.D. & Clutton-Brock, T.H. (1988) Climate and population dynamics of red deer in Scotland. In: *Ecological Change in Uplands*, Usher M.B. & Thompson, D.B.A. (eds.) Blackwell Scientific Publications, Oxford, pp. 93-107.
- Anders, A.D. & Post, E. (2006) Distribution-wide effects of climate on population densities of a declining migratory landbird. *Journal of Animal Ecology* **75**: 221-227.
- Barbraud, C. & Weimerskirch, H. (2001) Emperor penguins and climate change. *Nature* **411**: 183-186.
- Beare, D., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E. & Reid, D. (2004) An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology* **10**: 1209 – 1213.
- Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E., (2006) Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81-83.
- Carey, J.R. & Judge, D.S. (2002) *Longevity Records: Life Spans of Mammals, Birds, Amphibians, Reptiles, and Fish*. Odense Univ. Press, Odense, Denmark. [online: <http://www.demogr.mpg.de/>].
- Chamaille-Jammes S., Massot, M., Aragon, P. & Clobert, J. (2006) Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* **12**: 392-402.
- Conrad, K.F., Woiod, I.P. & Perry, J. (2003) East Atlantic teleconnection pattern and the decline of a common arctiid moth. *Global Change Biology* **9**: 125-130.
- Crozier, L. (2001) Climate Change and Its Effect on Species Range Boundaries: A Case Study of the Sachem Skipper Butterfly In: Schneider, S.H. & Root, T.L. (Ed.) *Wildlife*

- Responses to Climate Change: North American Case Studies*, Pages 57-92, Island Press, Washington.
- Davies, Z.G.**, Wilson, R.J., Coles, S. & Thomas, C.D. (2006) Changing habitat associations in response to climate, in a thermally constrained species, the silver-spotted skipper butterfly. *Journal of Animal Ecology* **75**: 247-256.
- Dennis, R.L.H. & Sparks, T.H. (2005) Landscape Resources for the Territorial Nymphalid Butterfly *Inachis io*: Microsite Landform Selection and Behavioral Responses to Environmental Conditions. *Journal of Insect Behavior* **18**: 725-742.
- Derocher, A.E., Lunn, N.J. & Stirling, I. (2004) Polar Bears in a Warming Climate. *Integrative and Comparative Biology* **44**: 163-176.
- Dunning, J.B., Jr. (2008) CRC Handbook of Avian Body Masses. 2nd Edition. Boca Raton: CRC Press.
- Durant, J.M., Anker-Nilssen, T. & Stenseth, N.Chr. (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc. R. Soc. Lond. B* **270**: 1461-1466.
- Ferguson, S.H., Stirling, I. & McLoughlin, P. (2006) Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* **21**: 121 – 135.
- Forcada, J.P.N., Trathan, K.R., Murphy, E.J. & Croxall, J.P. (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* **12**: 411 – 423.
- Franken, R.J. & Hik, D.S. (2004) Interannual Variation in Timing of Parturition and Growth of Collared Pikas (*Ochotona collaris*) in the Southwest Yukon. *Integrative and Comparative Biology* **44**: 186-193.
- Franklin, A.B., Anderson, D.R., Gutierrez, R.J. & Burnham, K.P. (2000) Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* **70**: 539-590.
- Franks, S.J., Sim, S. & Weis, A.E. (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *PNAS* **104**: 1278-1282.
- Frazer, N.B., Greene, J.L. & Gibbons, J.W. (1993) Temporal variation in growth rate and age at maturity of male painted turtles, *Chrysemys picta*. *American Midland Naturalist* **130**: 314-324.
- Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. & Wilson, L.J. (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology* **41**: 1129-1139.
- Gutzke, W.H.N. & Crews, D. (1988) Embryonic temperature determines adult sexuality in a reptile. *Nature* **332**: 832-834.
- Hari, R.E., Livingstone, D.M., Siber, R., Burkhardt-Holm, P., Guettinger, H. (2006) Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. *Global Change Biology* **12**: 10-26.
- Hilton, G.M., Thompson, D.R., Sagar, P.M., Cuthbert, R.J., Cherel, Y. & Bury, S.J. (2006) A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. *Global Change Biology* **12**: 611-625.
- Holand, Ø., Weladji, R.B., Røed, K.H., Gjøsæter, H., Kumpula, J., Gaillard, J.-M., Smith, M.E. & Nieminen, M. (2006) Male age structure influences females' mass change during rut in a polygynous ungulate: the reindeer (*Rangifer tarandus*). *Behavioral Ecology and Sociobiology* **59**: 682-688.

- Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E. & Couvet, D. (2007) Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology* **13**: 1672-1684.
- Kirby, R.R., Johns, D.G. & Lindley, J.A. (2006) Fathers in hot water: rising sea temperatures and a Northeastern Atlantic pipefish baby boom. *Biology Letters* **2**: 597-600.
- Lillywhite, H.B., Mittal, A.K., Garg, T.K. & Das, I. (1998) Basking behavior, sweating and thermal ecology of the Indian tree frog *Polypedates maculatus*. *Journal of Herpetology* **32**: 169-175.
- MacLeod, C.D., Santos, M.B. Reid, R.J., Scott, B.E. & Pierce, G.J. (2007) Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? *Biology Letters* **3**: 185-188.
- Mattila, T.M. & Bokma, F. (2008) Extant mammal body masses suggest punctuated equilibrium. *Proc. Roy. Soc. B* **275**: 2195-2199.
- McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002) Climate change hastens population extinction. *PNAS* **99**: 6070-6074.
- McMahon, C.R., Bester, M.N., Burton, H.R., Hindell, M.A. & Bradshaw, C.J.A. (2005) Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonine*. *Mammal Review* **35**: 82-100.
- Miller, F.L. & Gunn, A. (2003) Catastrophic die-off of Peary caribou on the western Queen Elizabeth Islands, Canadian High Arctic. *Arctic* **56**: 381-390.
- Morrison, S.F. & Hik, D.S. (2007) Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. *Journal of Animal Ecology* **76**: 899-907.
- Moss, R., Oswald, J. & Baines, D. (2001) Climate change and breeding success: decline of the capercaillie in Scotland. *Journal of Animal Ecology* **70**: 47-61.
- Murray, D.L., Cox, E.W., Ballard, W.B., Whitlaw, H.A., Lenarz, M.S., Custer, T.W., Barnett, T. & Fuller, T.K. (2006) Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs* **166**: 1-29.
- Nolet, B.A., Broftovd, L., Heitkoenig, I.M.A., Vorel, A. & Kostkan V. (2005) Slow growth of a translocated beaver population partly due to a climatic shift in food quality. *Oikos* **111**: 632-640.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J., & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**: 161-167.
- Raffaelli, D.G. (2004) How extinction patterns affect ecosystems. *Science* **306**: 1141-1142.
- Reading, C.J. & Clarke, R.T. (1995) The effects of density, rainfall and environmental temperature on body condition and fecundity in the common toad, *Bufo bufo*. *Oecologia* **102**: 453-459.
- Renwick, J.A., Hurst, R.J. & Kidson, J.W. (1998) Climatic influences on the survival of southern Gemfish (*Rexea solandri*, *Gempylidae*) in New Zealand waters. *International Journal of Climatology* **18**: 1655-1667.
- Rodríguez, C. & Bustamante, J. (2003) The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? *Journal of Animal Ecology* **72**: 793-810.

- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57-60.
- Sæther, B.E., Tufto, J. Engen, S., Jerstad, K., Røstad, O.W. & Skåtan, J.E. (2000) Population Dynamical Consequences of Climate Change for a Small Temperate Songbird. *Science* **287**: 854–856.
- Sandvik, H., Erikstad, K.E., Barrett, R.T. & Yoccoz, N.G. (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology* **74**: 817–831.
- SAS Institute Inc. (1990) SAS/STAT user's guide. Version 6. SAS Institute Inc., Cary, NC.
- Silva, M. & Downing, J. CRC Handbook of Mammalian Body Masses. Boca Raton: CRC Press; 1995.
- Sinovčić, G., Franičević, M., Zorica, B. & Čikeš-Keč, V. (2004) Length-weight and length-length relationships for 10 pelagic fish species from the Adriatic Sea (Croatia). *Journal of Applied Ichthyology* **20**: 156–158.
- Smith, A.T. (1974) The distribution and dispersal of Pikas: influences of behavior and climate. *Ecology* **55**: 1368-1376.
- Smith, F.A., Browning, H. & Shepherd, U.L. (1998) The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico. *Ecography* **21**: 140-148.
- Stirling, I., Lunn, N.J. & Iacozza, J. (1999) Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climate change. *Arctic* **52**: 294-306.
- Strathdee, A.T., Bale, J.S., Block, W.C., Coulson, S.J., Hodkinson, I.D. & Webb, N.R. (1993) Effects of temperature elevation on a field population of *Acyrtosiphon svalbardicum* (Hemiptera : Aphididae) on Spitsbergen. *Oecologia* **96**: 457-465.
- Sydeman, W.J., Hestera, M.M., Thayera, J.A., Gressb, F., Martinc, P. & Buffad, J. (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress In Oceanography* **49**: 309-329.
- Tews, J., Ferguson, M.A.D. & Fahrig, L. (2007) Potential net effects of climate change on High Arctic Peary caribou: lessons from a spatial-explicit simulation model. *Ecological Modelling* **207**: 85-98.
- Vioturon, Y. & Lengagne, T. (2008) Freezing before mating severely affects the fitness of a capital breeder. *Physiological and Biochemical Biology* **81**: 204-210.
- Waite, T.A. & Strickland, D. (2006) Climate change and the demographic demise of a hoarding bird living on the edge. *Proc Biol Sci.* **273**: 2809–2813.
- Wang, G., Hobbs, N.T., Giesen, K.M., Galbraith, H., Ojima, D.S. & Braun, C.E. (2002) Relationships between climate and population dynamics of white-tailed ptarmigan *Lagopus leucurus* in Rocky Mountain National Park, Colorado, USA. *Climate Research* **23**: 81-87.
- Weladji, R.B. & Holand, Ø. (2003) Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. *Oecologia* **136**: 317-323.
- White, E.G. & Sedcole, J.R. (1991) A 20-year record of alpine grasshopper abundance with interpretations for climate change. *New Zealand Journal of Ecology* **15**: 139-152.
- Winkel, W. & Hudde, H. (1997) Long-Term Trends in Reproductive Traits of Tits (*Parus major*, *P. caeruleus*) and Pied Flycatchers (*Ficedula hypoleuca*). *Journal of Avian Biology* **28**: 187-190.

Chapter 10

**A SRI LANKAN ELEPHANT ORPHANAGE:
DOES IT INCREASE WILLINGNESS
TO CONSERVE ELEPHANTS?
HOW DO VISITORS REACT TO IT?**

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Abstract

Pinnawala Elephant Orphanage (PEO) was established in Sri Lanka in 1975 to provide a refuge for elephants that were injured, orphaned, abandoned or separated from their families/herds in the wild. The orphanage cares for such animals and it was hoped that after their rehabilitation, some would be successfully returned to the wild. It is mainly used as a facility for viewing elephants and providing visitors with elephant-based recreation. It attracts over 35,000 visitors (both local and foreign) per month on average. However, little or no attempt has been made to examine the reaction of visitors to its activities and its impact on their willingness to support the conservation of elephants. This paper after providing background on the PEO, reports findings from two visitor surveys (one of local visitors and one of foreign visitors) conducted at the PEO. It provides information on the characteristics of visitors, the satisfaction they gained from the visit, their attitudes towards the conservation of the elephant and the impact of their visit to the PEO on this, their reactions to the current facilities available at the orphanage, and their maximum willingness to pay (WTP) to enter the PEO. Some differences are evident between these two samples in relation to satisfaction received, responses to the WTP elicitation, and attitudes towards the information and interpretive facilities. For example, a higher percentage of Sri Lankan respondents compared to foreign correspondents said that their experience at the PEO had increased their support for the conservation of the Asian elephants, and while nearly all respondents thought that more should be done to conserve the Asian elephant, a larger percentage of Sri Lankans compared

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to foreigners thought that high income countries should help to pay for this. Nevertheless, the majority of the respondents (in both samples) indicated that their support for the conservation of the Asian elephant had increased with their visit to the Orphanage. This indicates that a considerable unrecorded and as yet unutilized amount of support could be generated both financially and otherwise to conserve endangered species through wildlife-based refuges (combined with recreational facilities) such as those at the PEO in Sri Lanka. A particular feature of this article is its discussion of the role which wildlife refuges play in practice compared to the role they could play in the conservation of endangered species.

1. Introduction

With increased concern about nature conservation, people both in developed and less developing countries (LDCs) have become more environmentally sensitive (Boyd and Butler, 1996). As a result, nature conservation and wildlife-based recreation have received increased attention both from tourists and recreationists (Lee, 1997). Furthermore, Reynolds and Braithwaite (2001) point out that within the overall context of tourism, wildlife-based tourism has experienced rapid growth over the past few decades. Harrison (2001) predicts that in LDCs, this sector will be able to attract more economic opportunities than conventional sectors in the future. The analysis of Tosun (2001) provides a useful insight into the challenges and the obstacles facing countries in the developing world in achieving economic stability of their tourism industry (see also Sinclair and Tsegaye, 1990; Tisdell, 2000). However, it is clear from the literature (see for instance, Obua and Harding, 1996; Akama and Kieti, 2003) that one of the keys to economic stability and effective management of recreation sites is the availability of accurate information about visitors, about the resources that attract them as well as their reaction to the available facilities.

As Harrison (2001) states, the managers of most recreation sites in LDCs either do not seem interested in integrating such information about visitors into their development planning or they do not have the capability financially and otherwise to explore this information. The situation in Sri Lanka is no exception. Our investigation into the research studies undertaken on outdoor recreational sites in Sri Lanka reveals that, although a few studies have been completed, none has focused on the issues involved from the perspective of visitors. For example, Abeygunawardena and Kodituwakku (1992) and Gunathilaka and Vieth (1998) estimated the scenic value of Peradeniya Royal Botanical Garden and the elephants in the Pinnawala Elephant Orphanage respectively. Similarly, Silva and Kotagama (1997) estimated optimal entry fees for the Udawalawe National Park. On the other hand, Rajaratne and Walker (2001), and Thilakaratne and Santiapillai (2002) in their analyses discuss the issues involved respectively in captive breeding and the management of elephants in the Pinnawala Elephant Orphanage.

The purpose of this study is to present the findings of two sample surveys conducted at the Pinnawala Elephant Orphanage (PEO) in Sri Lanka in early 2003 and to supplement this with recent secondary information collected in 2007. One survey was of visitors from foreign countries to the PEO, and the other was of local Sri Lankan visitors. The aims were to assess the characteristics of visitors, the satisfaction they gained from the visit, their attitudes towards conservation of the elephant, their reactions to the current facilities available at the orphanage, and their maximum willingness to pay (WTP) to enter the PEO. Responses to

questions about whether the visit of respondents to the PEO had increased their support for the conservation of the Asian elephant are given particular attention.

The paper first briefly describes the background of the PEO and identifies some of its main management issues. Then the survey method and data collection procedure are outlined. Next follows an empirical analysis of results from the visitor surveys. First the attributes of those surveyed are presented; second, enjoyment of visits and willingness to pay for the improvement of the PEO by visitors are analysed; third, the attitudes of visitors to conserving the Asian elephant and their reaction to information and interpretive facilities are assessed; fourth the visitors' suggestions for improving the PEO are presented. The results are reported, analysed and compared between local and foreign visitors. There is then a general discussion of the role that wildlife refuges, such as that at Pinnawala play, or can play in the conservation of endangered species.

2. Pinnawala Elephant Orphanage: Background

The PEO in Sri Lanka is a captive elephant-based outdoor recreation facility that was initially established in 1975 by the Department of Wildlife Conservation (DWC). Initially this orphanage was started in 1972 at the Wilpattu National Park, then shifted to the tourist complex at Bentota and then to the Dehiwala Zoological Garden. From the Zoological Garden, it was moved in 1975 to Pinnawala, the current location. At that time, the orphanage had five baby elephants which formed the nucleus for the orphanage at Pinnawala. The PEO covers an area of nine hectares of a former coconut plantation in the Kegalle District, some 90km northeast of Colombo, the capital of Sri Lanka. It is not far from the main road between Colombo and Kandy. At present, the PEO is managed by the Department of National Zoological Gardens (DNZG) of the Ministry of Environmental and Natural Resources Management. Apart from the volunteers, casual workers and people who work for the contract suppliers of fodder for the elephants, a full-time workforce consists of 65 people. This includes two veterinary surgeons working at the PEO. In addition, some young individuals from higher income countries work at the Orphanage as volunteers and pay for a working holiday there. The elephants' day at the orphanage begins as early as 7.00 am and visitors are allowed to enter the facility after 8.30 am. It remains open until 6.00 pm every day including public holidays. DNZG (2007) provides a detailed account of the daily events and the other activities of the PEO as well as the entry fee.

The initial objectives of establishing the PEO included provision of a place of refuge and care for elephants that were injured, orphaned, abandoned or separated from their families or herds in the wild. Although the PEO was started with five such animals, at present the PEO provides shelter for 83 captive elephants: 26 of these animals are less than 10 years old, 37 animals are between 10 and 20 years in age, and 22 animals are older than 20 years. About 50% of the total elephants in the orphanage are comprised of females. According to DNZG (2007), this is the largest captive herd of elephants in the world belonging to the subspecies *Elephas maximus maximus*, the Sri Lankan sub species of Asian elephant (*Elephas maximus*). Most of the young elephants in this herd, aged less than 20 years, were born in the PEO after the captive breeding programme was started in the early 1980s (Lair, 1997).

Thilakaratne and Santiapillai (2002) provide a detailed account of the captive breeding programme undertaken at the PEO. With the success of this breeding programme, the PEO

has also become an important place for elephant education and research as well as the main centre in the country for releasing domesticated elephants. However, it should be noted that most of these activities at present seem to be operating below capacity; for instance, the number of elephants released by the PEO over the last ten years is far from adequate to meet the current demand for domesticated elephants in Sri Lanka. This situation was clearly demonstrated by a public protest that was held in Colombo in early 2003 demanding that wildlife authorities in the country release more elephants for domestic use (see Wijewardana, 2003). The numbers of domestic elephants in Asia have been declining, partly because there are fewer elephants in the wild. It is becoming rare to see domesticated working elephants like the one shown in Figure 1.



Figure 1. Domesticated elephants are now becoming rarer in Asia. The domesticated elephant in this photograph is loading logs onto a truck in rural Sri Lanka. (Photo: C. Tisdell)

However, with the increase in the elephant population inside the orphanage, over the years the PEO has become an attractive outdoor attraction for both local and foreign visitors (see Figure 2). Our analysis of secondary data on tourist arrivals at the PEO between 1993-2002 reveals 39,765 visitors to the orphanage per month on average, of which 97.3 % were the local visitors. The number of tourist arrivals at the PEO increases seasonally every year between August and September, when they peak. This is linked with the local school holidays, the well known religious pageant (*Esala prahara*) in Kandy and the increase in foreign tourist arrivals due to the summer holidays in the Europe. The PEO charges two different admission fees to visitors: locals pay less than the foreign visitors. These entry fees

alone generate Rs. 11, 56 606 worth of income per month for the PEO amounting to Rs. 138, 79272 per annum on average.



Figure 2. Elephants enjoying their visit to the river in Pinnawala Elephant Orphanage. This sight is a major attraction for visitors to the Orphanage. (Photo C. Tisdell)



Figure 3. A view of some shops within Pinnawala Elephant Orphanage which sell souvenirs and other items to visitors. These shops contribute to economic activity in the local economy and in rural Sri Lanka as a result of their purchases. The shopkeepers are keen on expanding the number of visitors to the Orphanage. (Photo: C. Tisdell)

The actual economic impact of PEO on the local and regional economies is considerable as has been demonstrated by Tisdell and Bandara (2005). As a result of a survey of vendors of souvenirs and other products in or near the PEO, Tisdell and Bandara (2005) found that the major source of their supplies was either from the local area or from outside the metropolitan

area of the capital city of Sri Lanka, Colombo. It was concluded that the orphanage contributed significantly to economic decentralisation in Sri Lanka and that it had promoted regional economic development. According to the local government authority in Pinnawala, during this period 152 new businesses were started up in the vicinity of the PEO and along the road to it from the Colombo-Kandy main road junction. Moreover, the discussions that we had with locals and the business community while undertaking this research study reveals that most of these businesses around the Pinnawala area and all those in the PEO came into existence after the PEO was established (see Figure 3). Now they seem to be dependent heavily on the tourists visiting the orphanage. Thus, many local people recognise the PEO as an economic centre and would not like to see it disappear from Pinnawala. The assurance of the continued existence of the PEO is, therefore, quite important for ensuring the stability of local and regional economies in and around the PEO.

Policy makers at the DNZG and the local government authorities in Pinnawala seem to be confronting at least four major challenges as far as the PEO is concerned:

- a) achieving the initial objectives of setting up of the PEO;
- b) obtaining the visitors' support for the long-term objectives of conserving the elephant in Sri Lanka;
- c) the assurance of the economic stability of local and regional economies in and around the PEO; and
- d) providing a visitor friendly environment in and outside the PEO.

In facing these challenges, it is essential to look first at the feasible options that could be utilised to maintain a continuous flow of visitors to the PEO, at least at the current level in the short run until new strategies are formulated to attract additional visitors in the long run. This is because the PEO, as any other outdoor recreation facility, may lose its popularity over time unless its existing structure is continuously revitalised. Visitors to any such facility always search for high quality services and products that correspond to the changing life styles, tastes, needs and wants.

According to Akama and Kieti (2003) most visitors, particularly Western and affluent local tourists are influenced by 'push-and-pull' motivational factors when they make their initial decision to visit a tourist destination in an LDC. The push factors may include the urge to escape from the pressure of the workplace and the stress associated with the urban life while the pull factors may include the ambition to travel to different places in search of novelty and exploration in a natural setting. Thus, the key to the success of any recreational venture, such as the PEO, is found only when it meets with the initial expectations of the tourists. Such expectations can be stimulated through information provided via advertisements, commercials, brochures, mass media and informal information from friends and relatives, but understanding what exactly tourists would like to have is an empirical issue that requires more research and discussion. Jayawardena (2002) points out that this has become a salient issue in most service industries.

3. The Survey

3.1. Samples

Sampling data presented in this paper were collected from two sub-samples of visitors to the PEO between 20 March and 10 April, 2003. One sample consisted of local adult visitors and the other of foreign adult visitors. A hundred and fifty visitors were chosen from each of these samples so as to provide a stratified sample. In this process, we also kept in mind the potential differences between these two visitor groups, in their preferences and values both in the preparation of questionnaires and the administration of the survey. The main purpose of these two samples is to help identify the precise reactions to the PEO by specific social segments of visitors who may have different perceptions about wildlife-based recreation facilities such as the PEO and also to assess the establishment of such facilities as an effective means to promote public support for the conservation of endangered species such as the Asian elephant.

According to Akama, (1996) the support of tourists from the Western world to conserve wildlife and natural areas, particularly in LDCs, has increased greatly in recent years for three reasons:

- a) the postmodern social and economic changes;
- b) the emergence of a new paradigm to enhance environmental ethics and values; and
- c) the experiences of the degradation of pristine natural areas since the advent of the Industrial Revolution.

Often tourists from the Western countries pledge both financial and other support to improve the facilities of the wildlife-based recreation facilities in LDCs. Furthermore, if they are satisfied with the existing facilities in those places, they are more likely to recommend them to others as recreation spots that should be visited (Akama and Kieti, 2003). Söderlund (1998) describes this as the cheapest and most effective form of marketing and promotion of the tourist destination in the LDC.

Locals, particularly urban dwellers and nature-lovers (including students) who visit the PEO provide a strong local market base for the continuity of the PEO. They also spread the message among other locals that conservation of the elephant in Sri Lanka is a common responsibility which should be shared with others, particularly the economic losses incurred by the farmers in the areas where human-elephant conflict prevails in the country. As Bandara and Tisdell (2003) observe, there is considerable unrecorded and as yet unutilised support among the majority of Sri Lankans for conservation of wild elephants. This analysis of locals visitors' reactions to the PEO could be used to investigate further the local support both financially and otherwise to conserve this endangered species in the long run. This would provide policy-makers with more information about people's reaction to the wildlife based-recreation facilities in general and the PEO in particular. This is necessary to improve the facilities in these places and sustain their long-term economic viability.

3.2. Interviewers and the Data Collection Procedure

Deriving accurate information from field surveys is highly dependent upon the survey methods employed. The direct face-to-face interview method is the most commonly used approach at recreation sties, such as PEO, to obtain information from visitors (Lee and Han, 2002) and was used in this study. FAO (2000) describes the value of this method compared to the mailed and self-administered questionnaire formats in developing country contexts. Mail surveys yield a low response rate and self-administered questionnaires suffer from self-selection biases. Further, face-to-face surveys have the advantage that trained interviewers can actually interact with respondents, and can clarify respondents' doubts thereby minimising non-response rates. Direct interviews also have the added advantage that trained interviewers may judge the sincerity of respondents. Consequently, the quality of the data generated can be expected to improve.

In the present study, two separate questionnaires were used to conduct the interviews: One was intended for the local visitors and the other for the tourists from foreign countries. Both questionnaires were designed to focus on four major areas: (1) visitors' socio-economic characteristics, (2) willingness to pay, (3) conservation attitudes, and (4) perception of the current facilities and their future development. In these questionnaires, the respondents were presented with seven common sets of questions:

1. questions to establish conversational rapport with the respondents;
2. to identify their origin and their travel arrangement;
3. to evaluate their satisfaction with their visit and the change in their conservation attitudes after their visit to the PEO;
4. to assess the maximum willingness of visitors to pay to enter the PEO;
5. to evaluate visitors' views about the present status of interpretive facilities available in the PEO;
6. to canvass the respondents' opinions and suggestions to improve the PEO, and
7. to relate the respondents' responses to their socio-economic background.

Six graduate research students from the University of Kalaniya were used as interviewers to administer the questionnaires. Interviews were conducted both in *Sinhala* and English. The supplementary information, particularly about existing facilities available in the PEO for visitors and historical data in relation to the establishment of the PEO, tourist arrivals and other information were obtained from the unpublished official documents of the DNZG and informal interviews held with the officials at both PEO and DNZG. We also undertook a number of informal interviews with local people and the business community around the PEO area to gather supplementary information, in particular to understand the impact of the PEO on the local economy.

4. Attributes of Those Surveyed

Haefen and Phaneul (2003) point out that it is important to understand visitor attributes or characteristics in order to manage outdoor recreation in a sustainable manner. This is because the planning of new developments, management of visitors, monitoring trends and predicting

recreation demands all require adequate information on visitor characteristics. Furthermore, provision of good quality services and facilities being demanded by visitors would depend to a large extent on sound management and will also require such knowledge of visitors. While recreational sites, such as the PEO, have the potential to yield a large amount of information, in this study we collected only the information on visitor characteristics that seemed to have immediate policy relevance.

We found that one third of the respondents in the sample had visited the PEO before. This was marked in the sub-sample of local visitors, with 56% having visited the PEO previously. This indicates that the PEO has become a popular recreational destination worth visiting more than once at least for the majority of local visitors. Kozak (2002) provides insights into tourist motivation for visiting the same destination repeatedly, suggesting that such a habit of visitation is influenced by the following motivational categories: ‘culture’, ‘pleasure-seeking/fantasy’, ‘relaxation, or ‘physical’ factors. Although in this study we did not specifically investigate the factors that influenced the respondents’ repeated visits to the PEO, the informal discussions which we had with them revealed that a mixture of all these factors were responsible for their decisions. Survey data reveals that the majority of the respondents (about 83% of the aggregate sample) had visited the PEO either with their family or friends (see Table 1). The PEO is a popular destination for both local and foreign tourists.

It can be observed from Table 1 that overseas visitors were more likely than locals to visit the PEO as individuals. Nevertheless, the majority of visitors (whether local or foreign ones) visited the PEO with family members or friends, thereby adding a socializing dimension to their visit.

Table 1. Distribution of sampled visitors to the PEO according to whether they were individual visitors, visited with a family group or came with friends

Type of visit	Sample		
	Local	Foreign	Aggregate
As an individual visitor	7 (4.7)	41 (27.3)	48 (16.0)
Part of a family group	74 (49.3)	47 (31.3)	121 (40.3)
With friends	69 (46.0)	62 (41.3)	131 (43.6)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of the totals in the respective samples

Table 2. The sampled distribution of foreign visitors to the PEO according to their country of permanent settlement

Country	Number	Country	Number	Country	Number
England	51 (34.0)	Sweden	5 (3.1)	Japan	1 (0.6)
Germany	29 (19.3)	India	3 (1.8)	Hungary	1 (0.6)
Holland	11 (7.3)	Austria	2 (1.2)	Malaysia	1 (0.6)
France	8 (5.3)	USA	2 (1.2)	Slovenia	1 (0.6)
Australia	8 (5.3)	Pakistan	2 (1.2)	Ireland	1 (0.6)
Switzerland	8 (5.0)	Spain	2 (1.2)	Canada	1 (0.6)
Denmark	6 (3.7)	China	2 (1.2)	Czech Republic	1 (0.6)

Note: Values in parentheses are percentages of total number of respondents in the samples

Data on origin of the visitors to the orphanage were examined separately: local visitors in relation to the area (district) where they have settled in Sri Lanka; visitors from overseas were analyzed in relation to the country where they had permanently settled. It was found that 80.6% of foreign visitors sampled were from Europe, and the rest were from Asia and Pacific countries. Table 2 presents the sampled distribution of foreign visitors to the PEO according to their country of permanent settlement. The data gathered about the travel arrangement of these foreign visitors reveals that 57% of respondents travelled to the PEO as part of a package tour and the rest came as independent travellers.

Consideration of the origin of the local visitors to the PEO reveals that majority were from urban and semi-urban areas in Sri Lanka. About 55% were from areas located within a 60km radiance of the PEO such as Kagalle, Kandy, Kurunagalla, Matale and Gampha. Table 3 gives the distribution of local visitors to the PEO in relation to the area (district) where they were settled in Sri Lanka. Thus it can be concluded that relative frequency of visits by locals increases the closer is their proximity to the PEO. This is to be expected because travel costs are higher for visitors who live further away from the PEO. These results accord with the basic economic theory of demand because travel costs add to the cost of visiting the site and therefore one expects a downward sloping demand curve in terms of the relative frequency of visits as the required distances for travel increases (Tisdell, 2005, p.160).

Table 3. The distribution of sampled local visitors to the PEO according to the area (district) where they are settled in Sri Lanka

District	Number	District	Number	District	Number
Kandy	34 (22.7)	Gampha	11 (7.3)	Anurathpura	2 (1.3)
Colombo	28 (18.7)	Ratnapura	9 (6.0)	Matara	1(0.7)
Nuweraeliya	20 (13.3)	Kagalle	8 (5.3)	Puttalam	1(0.7)
Kurunagala	16 (10.7)	Galle	3 (2.0)		
Matale	14 (9.3)	Kalutara	3 (2.0)		

Note: Values in parentheses are percentages of the total number of local respondents

Given the nature of the survey, it was impractical to ask detailed questions about the socio-economic background of the respondents and there was a concern that asking too many personal details would lead to non-cooperation by those approached for responses. Therefore, it was decided to limit socio-economic questions to general ones relating to the level of income of respondents and their level of educational attainment. Previous studies have found that those who engage in nature-based recreational activities tend to have higher incomes than the average for their relevant population, and tend to have a higher level of educational attainment than others in their country. In relation to their level of income, respondents were asked: *Do you consider your level of income to be above the average in your country?* Responses were recorded as 'yes' or 'no'. The responses to this question could be used to find out whether visits to this recreational facility are dominated by those who are affluent. Our analysis of the responses to this question reveals that overall about 55% of visitors surveyed earned above average income in their home country both at aggregate and sub-sample levels (see Table 4 for details). The stated information indicates that the majority of visitors both from Sri Lanka and from overseas have above average levels of income. It is

usually found that those who have an above average level of income are more inclined to observe nature than those who do not.

Table 4. Responses for the question: “Do you consider your level of income to be above the average in your country?”

Response	Sample		
	Local	Foreign	Aggregate
Yes	85 (56.7)	81 (54)	166 (55.3)
No	65 (43.3)	69 (46)	134 (44.7)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentage of the totals in the respective samples

Visitors were also asked about their level of education. Respondents were asked: ‘*Have you had any tertiary education, for example, university or technical college education?*’ and their responses were recorded as ‘yes’ or ‘no’. About 65% of the foreign visitors surveyed had tertiary education qualifications. This is well above the average in most Western countries. However, this figure was only 12% for the local visitors surveyed. This is quite understandable because the annual placements offered by the tertiary education institutions (both universities and technical colleges) in Sri Lanka to those who gain the General Certificate of Education Advanced Level, known as GCE A/L, is still less than 5% of the total number of students who sit for this exam every year. Consequently, few Sri Lankans have an opportunity to obtain tertiary qualifications. Thus, the percentage of Sri Lankan visitors with tertiary education appears to be above the Sri Lankan average. Most studies find the interest in viewing nature and in supporting nature conservation rises with the level of educational attainment of individuals. The results from this study are consistent with this relationship.

5. Enjoyment of Visits and Willingness to Pay

Akama and Kieti (2003) point out that tourists, like other customers, usually have prior expectations about the type and quality of tourist services to be offered in a particular destination they visit. Thus, it is important to assess the level of satisfaction or enjoyment that visitors have received from their visit to any tourist attraction (such as the PEO) from a policy point of view. In this study, we asked respondents ‘*Have you enjoyed your visit to the PEO?*’ This was precursor to asking interviewees to state the maximum entry fee that they would be prepared to pay to visit the PEO.

Respondents’ opinions of the level of satisfaction they received from their visit to the PEO were recorded on a three-point-scale: ‘a lot or very much’, ‘a little’ or ‘not at all’. The majority of respondents (87.6%) in the aggregate sample indicated that they enjoyed their visit to the PEO very much. This was higher in the foreign visitor sub-sample (95.3%) than in the Sri Lankan sub-sample (80%). None of the respondents in either of the sub-samples indicated that they did not enjoy their visit to the orphanage at all. Table 5 summarises the levels of satisfaction at the aggregate and sub-sample levels.

Table 5. Stated level of enjoyment received by the sampled visitors to the PEO

Level of enjoyment	Sample		
	Local	Foreign	Aggregate
A lot or very much	120 (80.0)	143 (95.3)	263 (87.6)
A little	30 (20.0)	7 (4.6)	37 (12.3)
Not at all	---	--	--
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of the totals in the respective samples

Interviewees were asked what is the maximum entry fee they would have been willing to pay to enter the orphanage. This provides an economic measure of the consumers' surplus (or visitors' surplus) which they obtained (or expected to obtain) from visiting the orphanage. While 28 per cent of those interviewed said they were unwilling to pay more than the current entry fee, 72 per cent responded that they would have been prepared to pay a higher fee. The distribution of responses is shown in Table 6. It can be seen that on the whole, foreign visitors indicated that they would have been prepared to pay more to enter the orphanage than domestic visitors. This implies that their demand for visiting this attraction is more inelastic for foreign visitors than it is for domestic visitors.

Table 6. The distribution of the willingness of those interviewed to pay a higher entry fee to the orphanage than the existing one.

Sample	Unwilling to change or offered a lower amount	Number of respondents				
		Willingness to increase by up to 25%	Willingness to increase by 25 to 50%	Willingness to increase by 50 to 75%	Willingness to increase by 75 to 100%	Willingness to increase by more than 100%
Local	46 (30.7)	21 (14.0)	3 (2.0)	7 (4.7)	54 (36.0)	19 (12.7)
Foreign	38 (25.3)	19 (12.6)	11 (7.3)	4 (2.7)	18 (12.0)	60 (40.0)
Aggregate	84 (28.0)	40 (13.3)	14 (4.7)	11 (3.7)	72 (24.0)	79 (26.3)

Note: Values in parentheses are percentages of the totals in the respective samples

The results indicate that if entry fees to the PEO were to be increased by just under 25 per cent, visitor numbers would fall by 41.3 per cent. This would result in a fall in revenue from entry fees for the PEO. Receipts from both domestic and foreign visitors would decrease but to a greater extent from locals than from foreigners. On the other hand, it should be borne in mind that these results relate to values stated by those interviewed. To some extent, these may reflect strategic bias. In other words, some respondents may have understated their willingness to pay in the hope that this would keep entry fees down. Also, respondents were already at the PEO when interviewed. Therefore, the values stated by some may refer to their willingness to pay for an additional visit in the future. Normally, one would expect this to be a smaller sum than for their initial visit or earlier visits due to diminishing marginal utility.

Ecotourism is usually regarded as tourism that takes place in a natural environment is careful of this environment and which also includes an educational element (Tisdell, 1996).



Figure 4. Visitors watching elephants assembled in the river flowing through Pinnawala Elephant Orphanage. Some visitors complained that viewing facilities are primitive. (Photo: C. Tisdell)



Figure 5. A large blind elephant guided by a mahout carries a heavy concrete weight at Pinnawala Elephant Orphanage. (Photo: C. Tisdell)

The tourism that occurs at the PEO takes place in an environment that has been greatly modified. From this point of view, it cannot be regarded as an example of ecotourism. The PEO is more like an open zoo in which the elephants have become domesticated or at least, semi-domesticated. Furthermore, at the time of our survey, there were no educational and

interpretative facilities at the orphanage. The main attraction was to watch the elephants (accompanied by mahouts) bathing in a river which runs through the grounds of the PEO (Figure 4). Another attraction was to see a large blind elephant, accompanied by a mahout, carry a very heavy concrete slab, thereby demonstrating the mighty strength of the elephant (Figure 5). The lack of educational and interpretative facilities about the plight of the Asian elephant meant that the PEO was failing to do as much as it could have done to provide political and social support for the conservation of wild Asian elephants.

In order to assess the amount of information that visitors obtained as a result of their visit to the PEO, we asked those interviewed whether they had obtained a lot of information, not much information or no information about the Asian elephant and about the role of the orphanage. The results are summarised in Table 7. Both the majority of domestic visitors and most of the foreign visitors said that they had obtained little or no information about the Asian elephant and its predicament. In fact, all of the locals said this and only about a third of the foreigners interviewed said that they obtained a lot of information. In the latter case, however, it seems likely that the information was provided by the guides who accompanied many foreign visitors.

Table 7. The distribution of responses obtained as to how much information about the Asian elephant, its status and the role of the PEO interviewees had obtained from their visit to the PEO.

Response	Sample		
	Local	Foreign	Aggregate
A lot of information	0 (0.0)	52 (34.7)	52 (17.0)
Not much information	33 (22.0)	75 (50.0)	108 (36.0)
No information	117 (78.0)	23 (15.0)	140 (46.7)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of the total in the respective samples

Table 8. Distribution of the responses of those interviewed about whether they would have liked more information about the role of the PEO during their visit

Response	Sample		
	Local	Foreign	Aggregate
Yes	149 (99.3)	132 (88.0)	281 (93.6)
No	1 (0.7)	18 (12.0)	19 (6.3)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of the total in the respective samples

Even though most respondents said that they had obtained little or no information at the PEO about the status of the Asian elephant and the role of the PEO in its conservation, it is possible that they might be satisfied by this and did not have a demand for more information. However, this proved not to be the case. The overwhelming majority of respondents said that they would have liked to have received more information about the role of the PEO and about the Asian elephant. This was especially marked in the case of domestic visitors but less so in relation to foreign visitors, many of whom may have obtained information from guides accompanying them and for their own reading. The distribution of the responses of those

interviewed as to whether they would have liked to have received more information about the role of the PEO during their visit is shown in Table 8.

5. Changes in Attitudes Towards the Conservation of the Asian Elephant and Related Issues

One of the original reasons for establishing the PEO was to foster public support for the conservation of the Asian elephant which is an endangered species (IUON, 1996). In order to determine whether their visit to the PEO had increased their support for the conservation of the Asian elephant, those interviewed were asked: *Has your experience at the PEO increased your support for the conservation of the Asian elephant?* They responded ‘a lot’, ‘a little’ or ‘not at all’. The majority of respondents (see Table 9) responded that their visit to the PEO had increased their support for the conservation of the Asian elephant a lot. This was so for both domestic and foreign visitors. However, as can be seen from Table 9, the stated increase in support for the conservation of the Asian elephant is stronger relatively speaking for domestic respondents than for foreign respondents. This may be because more foreign visitors were, prior to their visit, already strongly in favour of the conservation of the Asian elephant. However, the reason for the difference would require more investigation. Thus, despite the lack of information provided about the status of the Asian elephant at the PEO (Table 8), on the whole, the experience of the sampled visitors at the PEO substantially increased their support for the conservation of the Asian elephant. This is probably because it increased their **empathy** with the species – the experience had emotional appeal for the visitors (Tisdell and Wilson, 2005). For how long the initial reaction would be retained and with what intensity is unknown but things suggest that with the passage of time the intensity is likely to decline (Tisdell et al., 2008). The results also indicate that support for animal conservation can be promoted by emotional factors even in the absence of the provision of information about it. However, it could be that there is less decay (with the passage of time) in support for the conservation of a wildlife species when experiences with endangered wildlife are accompanied by the provision of relevant information about it.

Table 9. Respondents’ support towards conservation of the Asian elephant in relation to their experience at the PEO

Response	Sample		
	Local	Foreign	Aggregate
A lot	118 (78.7)	94 (62.7)	212 (70.6)
A little	32 (21.3)	50 (33.3)	82 (27.3)
Not at all	--	6 (4.0)	6 (2.0)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of the totals in respective samples

As a further indicator of the support of visitors to the PEO for the conservation of the Asian elephants, respondents were asked: *Do you agree with the view that much more should be done to conserve the Asian elephant?* The distribution of their responses is shown in Table 10. The overwhelming majority responded ‘Yes’. However, it is easy for respondents to say

this because the respondents were under no obligation to back up their 'Yes' statement with any economic contribution or sacrifices of their own.

Table 10. Distribution of responses of those interviewed as to whether they agree with the view that much more should be done to conserve the Asian elephant

Response	Sample		Total
	Local	Foreign	
Yes	148(98.6)	144 (96.0)	292 (97.3)
No	02 (1.3)	2 (1.3)	4(1.3)
Unsure	--	4 (2.6)	4 (1.3)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of totals in the respective samples

Conserving the Asian elephant in the wild involves economic costs and sacrifices. This raises the question of who should meet these costs. To what extent is there an obligation on high income countries to assist with the conservation of endangered wildlife in less developed countries? These issues are discussed to some extent in Tisdell (2005, Ch.4, 1999). In the present study, the respondents were asked: *Do you think high income countries should help pay for conserving the Asian elephant?* Table 11 presents a summary of the respondents' responses to this question. It can be sure that there was much more support for this view amongst the Sri Lankans interviewed than amongst foreigners. Nevertheless, in both cases the majority of the respondents thought that high income countries should contribute towards the cost of conserving the Asian elephant. The question of how much they should contribute was not asked.

Table 11. Distribution of responses to the view that high income countries help pay for the conservation of the Asian elephant

Response	Sample		Total
	Local	Foreign	
Yes	147(98.0)	115 (76.7)	262 (87.3)
No	03 (2.0)	7 (4.6)	10 (3.3)
Unsure	--	28 (18.6)	28 (9.3)
Total	150 (100)	150 (100)	300 (100)

Note: Values in parentheses are percentages of the totals in respective samples

6. Visitors' Suggestions for Improving Pinnawala Elephant Orphanage

Those interviewed were asked whether they had any suggestions for improving the PEO. If they said 'Yes', they were then asked to give their suggestions. Sixty eight per cent of respondents did this. The percentage of visitors who had suggestions was higher amongst the foreign visitors interviewed compared to locals. The suggestions received are set out in Table 12 and have been organized under the following headings.

- a) improvement of current services and facilities at the orphanage;
- b) safety and security;
- c) elephant care and welfare;
- d) information and interpretive facilities;
- e) improvement of services and facilities outside the orphanage; and
- f) improvement of revenue status and encouragement of spending by visitors.

Table 12. List of suggestions for improving the PEO given by the visitors surveyed

Improvement of the current service and facilities at the orphanage
• Construct resting huts for public. • Relocate existing car park near the orphanage gate. • Build more public toilets. • Develop cafeteria facilities. • Establish a camping site • Expand the size of the orphanage. • Construct walking tracks. • Provide public drinking water facility. • Establish regular system to collect garbage. • Hire a professional manager and a curator.
Safety and security of the visitors
• Construct observation platform for public along the river bank. • Set up a first aid or medical centre. • Tighten security along the road from the orphanage to the river when elephants take their usual bath in the morning and afternoon. • Use appropriate safety standards.
The elephant care and welfare
• Plant more shade trees. • Increase the space available for the elephants inside the orphanage. • Begin a public sponsorship program for elephants. • Encourage more volunteers. • Construct a proper pond inside the orphanage for elephants. • Grant more freedom to the elephants. • Free some elephants into the wild or keep them in natural habitat. • Encourage visitor involvement with the orphanage activities such as feeding. • Do not fully domesticate elephants in the orphanage.
Information and interpretive facilities
• Provide an information booklet at the gate. • Employ professional guides. • Display more information about elephants and their way of life. • Encourage lectures, public talks and educational demonstrations. • Set up an elephant museum to display more information about human-elephant relationships and conflict. • Employ interpreters.

Table 12. Continued

Improvement of services and facilities outside the orphanage;
• Construct wider roads. • Provide a shuttle bus service at least from Colombo-Kandy main road junction. • Regulate activities of the business people along the road to orphanage. • Construct a public car park.
Improvement of revenue status and encouragement of visitor spending
• Begin elephant- based extra activities such as elephant dances. • Amalgamate other public entertainment activities such as carnivals, fairs and exhibitions with the orphanage. • Encourage visitors to spend more time inside the orphanage by providing more entertainment opportunities. • Promote local business people to pay a certain percentage of their income to improve the facilities in the orphanage. • Increase the entry fee. • Encourage public donations. • Use trained elephants for elephant rides. • Sell the excess stock of elephants as domesticated elephants.

The comments received are quite varied. It can also be seen that some of the suggestions conflict. For instance, several suggestions for improving the receipts of the PEO and for encouraging spending by visitors appear to conflict with those that relate to elephant care and welfare. For example, the proposal to have elephant dances would conflict with the view expressed by some visitors that elephants in the orphanage should not be fully domesticated and ought to be kept under more natural conditions.

7. Discussion – What Role Do and Should Wildlife Orphanages and Refuges (Such as the PEO) Play in the Conservation of Endangered Wildlife Species?

The results from this study raise the following question: What role do and should wildlife orphanages and refuges, such as the one at Pinnawala, play in the conservation of endangered species? Some of their desirable functions in relation to animal welfare and the conservation of species would most likely include the following:

- a) Saving individual wild animals that have been injured, orphaned or others disabled from suffering and an early death.
- b) Returning to the wild those animals that have recovered from their ordeal and which have a reasonable chance of surviving in the wild.
- c) When visitors (tourists) are permitted to enter the refuges they should learn about the plight of the species involved and be involved in education that builds support for the conservation of the species involved in the wild. If possible practical ways in which

visitors can contribute to the conservation of the species should be brought to their attention.

- d) The facilities of the refuge should be used to add to scientific knowledge about the biology and ecology of the species involved. This knowledge may help contribute to its conservation.

Nevertheless, it has to be recognized that caring for animals in refuges is expensive and particularly in developing countries, it is necessary for refuges to generate funds to cover these costs. Consequently, in most wildlife refuges the task of caring for resident animals requires funds to be collected from visitors. This may be necessary even in cases where the presence of visitors can have some negative impact on the rehabilitation of animals in the refuge, as has been claimed to be the case in refuges for orangutans (*Pongo pygmaeus*). Nevertheless, in some cases, there is a danger that commercial gain can become the prime rationale for the operation of the refuge. This may result in the slow return of the animals to the wild, if they are released at all, and semi-captive breeding may occur to maintain the stock of the species in the refuge for viewing purposes.

The lure of increased income may result in the conservation objectives of wildlife refuges being lost sight of. There is a particular risk of this happening when members of local community (including merchants) become economically very dependent on the commercial activities of the refuge, as at the PEO. This interest group is likely to exert political pressure for the adoption of policies by the refuge which will maximize their income. For example, Tisdell and Bandara (2005) found from a survey of stallholders based in the PEO and nearby local shopkeepers that they were keen to see visitor numbers to the PEO increase to this end they thought the elephant dances should be provided at the PEO as well as elephant rides and that festivals ought to be staged in the PEO to attract more visitors. Such activities seem, however, as though they would be at odds with original conservational objectives of the PEO. They would appear to transform the PEO into a large outdoor circus.

On the other hand, the reality is that many wild animals held in orphanages or in refuges cannot be successfully returned to the wild. Usually Asian elephants that have been held in refuges fail to survive when they are returned to the wild. If they are young and come to the refuge as orphans, they have had little chance to learn from their mother the skills of survival in the wild. This appears to be a particular problem for more intelligent wild mammals. Such animals have several years of dependence on their mothers. Secondly, elephants in the wild belong to family groups and outside elephants are excluded from these groups. This makes it likely that elephants released to the wild from refuges will not survive. This maybe one of the reasons why the PEO has released no elephants to the wild since its foundation.

In recent years another Asian elephant refuge has been established in Sri Lanka namely at Udawalawe National Park (see Figure 6). The elephants in this refuge are able to travel into the Park and return to the refuge for feeding. Therefore, the conditions in which they are kept are more natural than at the PEO. It is possible that these elephants may form groups. The plan of the refuge is that when rehabilitated elephants are released back to the wild, this be done in groups. Whether this will be successful remains to be seen.



Figure 6. A group of orphaned elephants being fed milk by attendants at Udawalawe National Park. These elephants have free entry to this national park but come back from the park to this feeding area at feeding time. (Photo: C. Tisdell)

Another case of intelligent mammal which it is difficult to return to the wild once it has been held in a wildlife refuge is the orangutan (Rijksen and Meijeard, 1999). This endangered species continues to exist only in Borneo and Sumatra. Its habitat is disappearing fast as a result of deforestation and the spread of agriculture, especially the expansion in oil palm plantations, a source (amongst other things) of biodiesel. Forest fires, particularly in Indonesia, are an additional threat to the continuing survival of the orangutan, and these fires have become more frequent as land is cleared for the extension of agriculture following its logging (Singleton et al., 2004; Tisdell and Swarna Nantha, 2007). Several refuges and rehabilitation centres for orangutans have been established in Borneo to care for orphaned, injured and displaced orangutans which are tourist attractions and which obtain income from visitors.

However, as in the case of the Asian elephant, their success in returning orangutans to the wild is limited. This is particularly so for orphaned orangutans. Young orangutans depend on their mothers for many years. During this period, they learn from their mother skills and obtain information about how to survive in the wild on their own. They learn, for example, which foods are safe to eat, those that are poisonous, where to find their edible foods at what time of the year. They do not have the same opportunity in an orphanage and when returned to the wild, lack many survival skills and are unlikely to survive. Older orangutans may also have difficulty in re-adjusting to the wild if they have been kept in captivity for long enough to become habituated to it. Also in some cases, it is difficult to find wild habitats with **under utilized carry capacity** to which animals from refuges can be released. If the carrying capacity of particular area is fully utilized by a species, the release of additional population can only result in the death of some of the resulting population.

Thus, for several species of wildlife, refuges and orphanages do not provide a suitable base for returning endangered wildlife successfully to the wild. In some cases, refuges may even hasten the disappearance of species. This is because they can become palliative for the

disappearance of endangered species in the wild. Their presence may ease human conscience or guilt about extinction of the species because some individuals of the affected species are being cared for in refuges. Yet in most cases, it seems that the presence of refuges does little or nothing to prevent the eventual extinction of the species concerned.

Overall wildlife refuges and orphanages appear to be a weak mechanism for saving endangered species from extinction in the wild, for the reasons just outlined. They can, however, be used as an effective way to make visitors aware of the threat to endangered species provided that appropriate information is given to visitors. They can, become a vehicle for increasing the public's political support for the conservation of endangered species. However, some pro-development governments may oppose this emphasis.

Despite the limited value of wildlife refuges and orphanages as conservation mechanisms, many people would still believe that they are worthwhile supporting because of the compassionate care that they give to orphaned, injured and displaced wildlife. Nevertheless, they do not seem to be a suitable substitute for other measures to save endangered wildlife from extinction.

8. Concluding Comments

It was found from our survey that visits to Pinnawala Elephant Orphanage increased the support of most visitors for the conservation of the Asian elephant. However, most visitors learnt little about the reason for the existence of the PEO, the status of the Asian elephant, threats to the continuing existence of the Asian elephant, aspects of its biology and ecology and its cultural significance. Nor were any practical suggestions made about how visitors might contribute to efforts to save the species from extinction. If information were provided about such aspects, the PEO might have a more effective impact on the conservation of the Asian elephant. At present, the positive support for conservation which it evokes from visitors might be an emotional flash-in-the-pan. A longer lasting and more positive impact on the conservation of the Asian elephant might be achieved if some of the positive suggestions made by visitors to the PEO (see Table 12) were implemented, such as the provision by the PEO of information about the status of the Asian elephant. The building and refurbishing of a first-class museum concentrating on all aspects of the elephant, including its cultural and historical relevance to human beings in Sri Lanka and elsewhere (see Tisdell and Bandara, 2004; Tisdell, 2005) could make a major contribution to the conservation of the Asian elephant via its impact on public opinion.

Acknowledgements

We would like to thank M.G Kuleratne and his team for their assistance with the interviews with visitors at Pinnawala Elephant Orphanage and the assistance extended to us by its staff. The usual caveat applies.

References

- Akama, J.S., (1996). Western environmental values and nature-based tourism in Kenya. *Tourism Management*, **17**:567-574.
- Akama, J.S. and Kieti, D.M., (2003). Measuring tourist satisfaction with Kenya's wildlife safari: A case study of Tsavo West National Park. *Tourism Management*, **24**:73-81.
- Abeygunawardena, P. and Kodituwakku, K.A.S.S. (1992). Economics of recreation value of Peradeniya Royal Botanical Garden in the *Proceedings of 3rd Regional Workshop on Multipurpose Trees*, Kandy, Sri Lanka.
- Bandara, R. and Tisdell, C. (2003) Comparison of rural and urban attitudes to the conservation of Asian elephants in Sri Lanka: *Biological Conservation*, **110**: 327-342.
- Department of National Zoological Gardens (2000). Pinnawala Elephant Orphanage (Brochure). Department of National Zoological Gardens Dehiwala, Sri Lanka.
- FAO, (2000). *Application of the Contingent Valuation Method in Developing Countries: A Survey*. Information Division, Food and Agricultural Organization of the United Nations, Via delle Terme di Caracalla, Rome, Italy.
- Gunathilaka, H.M. and Vieth, G.R. (1998). An assessment of scenic value of Sri Lankan elephants: the case of Pinnawala Orphanage. *Sri Lanka Journal of Social Science*, **21**: 37-51.
- Haefen, R.H. and Phaneul, D.J., (2003). Estimating Preferences for outdoor recreation: a comparison of continuous and count data demand system frameworks. *Tourism Management*, **45**:612-630.
- Harrison, D. (2001). *Tourism and the Less Developed World: Issues and Case Studies*, CABI Publishing, Wallingford, U.K.
- Jayawardena, C., (2002). Future challenges for tourism in the Caribbean. *Social and Economic Studies*, **51**:1-23.
- Kozak, M., (2002). Comparative analysis of tourist motivation by nationality and destination. *Tourism Management*, **23**:221-232.
- Lair, R. (1997). Gone astray: the care and management of the Asian elephant in domesticity, FAO, Thailand, RAP Publication: 1997/16.
- Lee, C. (1997). Valuation of nature based tourism resources using dichotomous choice contingent valuation method. *Tourism Management*, **18**:587-591.
- Lee, C. and Han, S.Y., (2002). Estimating the use and preservation values of national parks' tourism resource using a contingent valuation method. *Tourism Management*, **23**:531-540.
- Obua, J. and Harding, D.M. (1996). Visitor characteristics and attitudes towards Kibale National Park, Uganda. *Tourism Management*, **17**:495-505.
- Rajaratne, A.A.J. and Walker, B. (2001). The Elephant Orphanage (Pinnawala): a proposal for development. *Gajah*, **20**:20-29.
- Rijksen, H.D. and Meijer, E. (1999). *Our Vanishing Relative: The Status of Wild Orangutans at the Close of the Twentieth Century*. Kluwer Academic Publishers, Dordrecht.
- Silva, K. A. I. D. and Kotagama, H. B., (1997). An optimal fee for entrance to Udawalawa National Park: an assessment. *Tropical Agricultural Research*, **9**: 317-329.

- Sinclair, M.T. and Tsegaye, A. (1990). International tourism and export instability. *Journal of Development Studies*, **26**: 487-503
- Singleton, I., Wich, S., Stephens, S., Admoko, S., Leighton, M., Rosen, N., Taylor-Holzer, K., Lacy, R. and Byers, O. (eds.) (2004). *Orangutan Population and Habitat Viability Assessment: Final Report*. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA.
- Söderlund, M., (1998). Customer satisfaction and its consequences of customer behaviour revisited: the impact of different levels of satisfaction on word of mouth, feedback to the supplier and loyalty. *International Journal of Service Industry Management*, **9**:169-188.
- Thilakaratne, N. and Santhiapillai, C., (2002). The status of domesticated elephants at the Pinnawala Elephant Orphanage, Sri Lanka. *Gajah*, **21**:41-52.
- Tisdell, C., (1996). Ecotourism, economics and the environment: observations from China. *Journal of Travel Research* 34(4):11-19. Reprinted in C. Tisdell (2001) *Tourism Economics, the Environment and Development*. Edward Elgar, Cheltenham, UK, Northampton, MA, USA.
- Tisdell, C., (1999). *Biodiversity, Conservation and Sustainable Development: Principles and Practices with Asian Examples*. Edward Elgar, Cheltenham, UK; Northampton, MA, USA.
- Tisdell, C. (2000). *The Economics of Tourism*. Edward Elgar, Cheltenham, UK, Northampton, MA, USA.
- Tisdell, C. (2005). Elephants and polity in ancient India as exemplified by Kautilya's *Arthashastra (Science of Polity)*. *Economics, Ecology and the Environment* Working Paper No. 120, School of Economics, The University of Queensland, Brisbane, Australia.
- Tisdell, C. (2005). *Economics of Environmental Conservation* 2nd Edn. Edward Elgar, Cheltenham, UK and Northampton, MA, USA
- Tisdell, C. and Bandara, R. (2004). Human societies, economics and the fate of the Asian elephant. *Science India* **7** (9 & 10): 67-72.
- Tisdell, C. and Bandara R. (2005). Wildlife-based recreation and local economic development: the case of Pinnawala Elephant Orphanage in Sri Lanka. *Sri Lankan Journal of Social Sciences*, **28**(1&2);65-96.
- Tisdell, C. and Swarna Nantha, H. (2007). Conservation of the proboscis monkey and the orangutan in Borneo: comparative issues and economic considerations. *Economics, Ecology and the Environment, Working Paper* No.82, The School of Economics, The University of Queensland, Brisbane, Australia.
- Tisdell, C. and Wilson, C. (2005). Perceived impacts of ecotourism on environmental learning and conservation: turtle watching as a case study. *Environment Development and Sustainability*, **7**: 291-302.
- Tisdell, C., Wilson, C. and Swarna Nantha, H. (2008). Contingent valuation as a dynamic process. *The Journal of Socio-Economics*, **37**:1443-1458.
- Tosun, C. (2001). Challenges of sustainable tourism development in developing world: the case of Turkey. *Tourism Management*, **22**:289-303.
- Wijewardana, S. (2003). Decrease in domestic elephant population in Sri Lanka. *Diviyina* (Sunday Edition), 8th February 2003, News Section, p.3.

Chapter 11

WILDLIFE CONSERVATION AND THE VALUE OF NEW ZEALAND'S OTAGO PENINSULA: ECONOMIC IMPACTS AND OTHER CONSIDERATIONS

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Abstract

Valuing objects is a distinctive human trait. It is necessary for rational behaviour. Factors that are likely to influence valuations, the difficulties of getting agreements about valuations and the limited perspective of economics as a basis for valuation are discussed generally in this article. Attributes of Otago Peninsula that seem to be valuable and worth conserving are listed and discussed, taking into account possible conflicts in getting maximum value from these attributes. Particular attention is given to the economic value of conserving wildlife species on the Otago Peninsula. As a result of the presence of these species and their use for tourism, expenditure of over \$100 million NZ is generated annually in the Dunedin regional economy (directly or indirectly) and 800-1000 full-time equivalent jobs are created. The economic opportunity cost of this wildlife conservation on the Peninsula is low and the economic benefits from this conservation are well in excess of the costs involved. When non-use economic values and the social values associated with Otago Peninsula are taken into account, this further adds to the value of conserving this wildlife. While there has been remarkable expansion in wildlife tourism on the Otago Peninsula and its economic impact in the Dunedin region in the last two decades, (especially in the viewing of Yellow-eyed Penguins), difficulties and constraints are emerging that are likely to hamper its future expansion. However, wildlife tourism on the Otago Peninsula will still have a huge economic impact on Dunedin's regional economy in the future. Consequently, even if assessed solely in terms of their economic value, the wildlife attractions of the Otago Peninsula are well worth conserving. Furthermore, the value of conserving biodiversity on the Peninsula exceeds its touristic and its economic value. Some conservation organizations (such as the Yellow-eyed Penguin Trust), even though not directly involved in tourism, add to its economic value as well as to its social value and promote the highly desired goal of conserving biodiversity.

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1. Introduction and Background

The purpose of this article is to identify a number of factors that are important in determining the value of New Zealand's Otago Peninsula and to highlight the importance of wildlife conservation as a contributor to its economic value. Two species of wildlife, the Southern Royal Albatross (*Diomedea epomophora*) and the Yellow-eyed Penguin (*Megadytes antipodes*) add substantially to the economic value of the Otago Peninsula mainly by their significance as tourist attractions. However, other wildlife present on the peninsula also make a contribution to its overall economic value.

It should be noted that many of the issues raise in this exposition are not specific to the Otago Peninsula. They are relevant to many geographical areas that have attractive environmental features, particularly natural attractions, and competing uses.

The Otago Peninsula is located on the South Island of New Zealand close to the centre of the city of Dunedin and although it is mainly rural, it falls within the boundaries of Dunedin City Council. It contains some villages, farms (which mostly graze cattle and sheep) and conservation areas. It is in fact almost an island being surrounded on one side by Otago Harbour and on the other side by the southern Pacific Ocean. It is located more than 45° south of the Equator and some of its wildlife species are frequently associated with the sub-Antarctic. Useful background on the geography of the Peninsula, the history of its human settlement and its biodiversity can be found in Kai Tiahu Ki Otago (2006). A generalised map of the Otago Peninsula is shown in Figure 1.

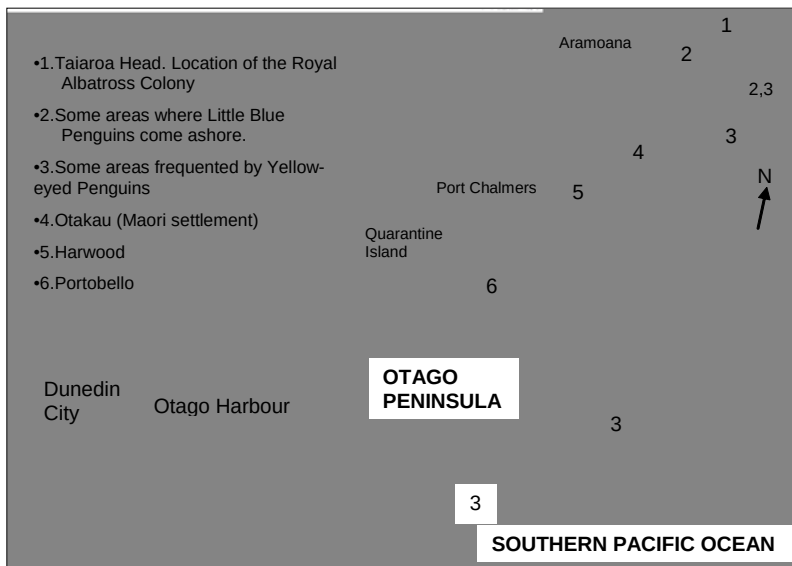


Figure 1. A generalised map of the Otago Peninsula showing some areas frequented by its wildlife attractions.

2. The Process of Valuing Objects

The valuation of objects, including their economic valuation, is usually controversial and is probably imperfect. Nevertheless, valuing objects is a major preoccupation of human beings; one that seems to distinguish human beings from other species. Values provide a guide to individuals about how they should act, and are essential for engaging in rational behaviour.

In this article, I shall discuss the process of valuing objects (such as geographical features of the Otago Peninsula), outline the valuable attributes of the Otago Peninsula, provide information on the economic impacts (benefits) of wildlife conservation on the Peninsula, and discuss non-use economic values and social values which are not captured by economic impact analysis, and then conclude.

How, why and to what extent individuals come to value objects is a little explored but a fascinating subject. It is not usually a matter examined by economists because they normally take people's wants and values as given. This seems to be the source of the jibe that "economists know the price of everything and the value of nothing". While that is an unfair assessment, it is true that economic values give a limited perspective on the value of objects. They are not a complete measure of value because they only measure what can be assessed in terms of money. For example, the economic value of an object is often assessed in terms of the maximum amount of money that people are willing to pay for it or the maximum amount they would pay if it is an object requiring conservation to ensure that it is conserved. Economic value is not a measure of the 'ultimate' value of an object even though it is often an important factor to take into account in deciding on the ultimate value of an object. Thus, the role of economic valuation should be seen in this perspective. The importance of doing this was already stressed by Arthur Pigou (1932) (the founder of welfare economics and social cost-benefit analysis) early in the last century. He stressed that economics could not be the ultimate arbiter of what is valuable.

Valuation of objects is complicated by the fact that many values are culturally determined and alter historically as societies change and as ethical standards develop. For example, as John Passmore (1974) has pointed out, in Western countries, social attitudes towards nature and animals have altered substantially in recent times. There is, for instance, greater recognition of the rights of other species to exist and greater objection to cruelty to animals now than in the past. Conserving other species has become a valued objective in itself and those who contribute to saving other species obtain moral satisfaction from doing it when the socially accepted 'correctness' of such behaviour increases. These trends have undoubtedly added to the perceived value of nature conservation, including nature conservation on the Otago Peninsula.

To some extent what is valued by individuals depends on their experiences and perceptions. These are partly shaped by the society in which they live and by the educational processes that have helped to shape their values and their perceptions of the world. Just as it is sometimes said that 'beauty is in the eye of the beholder', up to a point what is valued and by how much is determined by personal factors. Therefore, it is little wonder that there is so much controversy about what should be valued and by how much.

Given the personal aspect of valuing objects, it is not surprising that individuals' valuations of objects have been a subject of psychological research. Individuals' capacities to

value items are restricted by their limited ability to obtain information, retain it and process it, that is by what has been described as their bounded rationality (Simon 1957, Tisdell, 1996). Personal valuations may be altered by the type of information provided to individuals (Tisdell, 2007b) and by advertising and promotion. The psychology of valuation deserves more study (Tisdell et al., 2008).

Economists are aware that the amount of money one pays for a commodity or object is frequently not a complete measure of its economic benefit. The economic value of an object is often greater than the amount paid for it. There are even some commodities for which nothing is paid but which nevertheless, have economic value. For example, individual New Zealanders may pay nothing for the continuing existence of the kiwi (the national bird emblem of New Zealand) but many would be willing to pay to ensure its continuing existence and would give this a high priority. However, as I mentioned before, economic value is just one dimension of value and considerable room exists for controversy about what should be valued and by how much.

The values expressed by individuals are often culturally or institutionally influenced. Many Australians, for example, may consider the kiwi to be a scruffy, insignificant animal of little value but not New Zealanders. These views would, however, be most likely reversed when it comes to valuing the conservation of the flightless emu, the bird symbol on the Australian coat-of-arms. The choice of these birds as avian emblems of New Zealand and Australia respectively help shape these valuations. Similarly, Americans are likely to be willing to pay a considerable sum to keep the bald eagle (*Haliaeetus leucocephalus*), a symbol of the United States, in existence, but as individuals they need pay nothing for this.

Despite differences of opinions about values, in most societies a degree of consensus emerges about what should be valued. Without some agreement on values and social goals, social action would be paralysed. Economic considerations are almost invariably factors that are taken into account in setting social goals, including those relating to the state of the environment.

3. The Valuable Attributes of Otago Peninsula Worth Conserving

What is valuable or should be valued on the Otago Peninsula? Not being a local and not having had an opportunity to survey locals for their views, my list of what might be regarded as valuable on the Peninsula is likely to be incomplete. A useful overview of features of the Otago Peninsula which are believed to be valuable is contained in Kai Tahu ki Otago Ltd. (2006). An important aspect of this Peninsula, is that it includes many diverse features or attributes in a relatively small area. The following are some of the attributes that I consider to be of value and which are worth conserving. These are not necessarily in order of importance.

1. European heritage sites. Some are on private land, such as battery placements built for defence during World War II. Scope exists to develop these further as tourist attractions.
2. Maori heritage. This has been little developed for tourism purposes.
3. Impressive landscapes and seascapes with panoramic views.
4. Relatively rare and unique wildlife species which are comparatively easy to see. The rarity of the species from a global perspective and their vulnerable conservation

status adds to the value of these species, such as the Royal Albatross and the Yellow-eyed Penguin.

5. A high degree of natural biodiversity within a small geographical area. This biodiversity is being sustained and increased by programmes of Yellow-eyed Penguin Trust. Apart from conserving the Yellow-eyed Penguin, it is restoring natural vegetation in areas under its control with the help of volunteers. Some other NGOs (such as STOP, the Save the Otago Peninsula organization), as well as some private landholders, are doing likewise.
6. Much of the land on the Peninsula is used for livestock (sheep and cattle) and therefore, has some economic value for grazing, even though it is not rich agricultural land. In some portions also plantation forestry involving the planting of conifers has developed. Up to a point, these land uses may add to the scenic value of the Peninsula. They are a part of the scenic mosaic. Europeans have accepted the view that some types of agriculture enhance the scenic qualities (or values) of some landscapes and provide subsidies to agriculture as part of the EU's Common Agricultural Policy (CAP) to conserve these landscapes (Tisdell and Hartley, 2008, Ch. 4).

Another use of the land on the Peninsula is for residential purposes. Residential clusters have developed on the Peninsula and presumably pressures exist to allow further residential development in the area given the scenic views available and the demand for rural or semi-rural living within relatively easy reach of the centre of Dunedin. However, significant residential development of the area is likely to destroy the Peninsula's current attractive environment and endanger other valuable environmental qualities of the Peninsula. Often residential developments are up to a point self-destructive; they destroy the environment that originally attracted settlers to the area.

Negative environmental impacts of residential development usually include (1) destruction of landscape values; (2) loss of natural habitat and species dependent on such habitat; (3) development of infrastructure such as roads, which often result in further destruction of natural habitat (roadside areas often contain important remnant vegetation, as is evident on the Otago Peninsula) and roads may result in road-kills of wanted wildlife; (4) various weeds may spread from domestic gardens and (5) domestic animals, such as cats, may pose serious risks to nearby wildlife. It is also important to note that development of infrastructure to serve tourism demands, such as the widening of roads, can have adverse environmental impacts on landscape values and on biodiversity.

The above raises a number of questions: To what extent are these conservation possibilities and uses in conflict with one another? To what extent are they compatible? What is the comparative value of each use? What is the most valuable or best combination of land use on the Peninsula? These are all questions that could be discussed if there happened to be enough time to do so. For example, measures to develop ecotourism (and other forms of tourism) can conflict with the conservation of Maori heritage on the Peninsula (Higham, 2001) and agricultural activities can conflict with nature conservation. When such conflicts exist, the big issue is how to get the right balance between nature conservation and land use. This is an important question for land-use planners. The best economic balance (or set of balances) can in principle be determined. To do so, however, will not necessarily settle social conflict because, for one thing, economic values are not ultimate values.

It is likely that conserving a mosaic or mixture of land uses on the Peninsula has the most value. While nature conservation and restoration on the Peninsula have a high economic value, restoring the whole Peninsula to the 'natural' state that existed prior to European settlement (even if possible) is unlikely to be the most highly valued option. For example, in many cases, open agricultural land adds to scenic values and there is some evidence that most individuals like mosaic patterns of land use. This is not to say that further restoration of natural vegetation on the Peninsula will not add to its value. It will do so by adding to biodiversity, reducing soil erosion and providing other ecosystem services. Often the areas targeted for such restoration have limited alternative uses, for example, for agriculture.

4. The Contribution of Wildlife Conservation to the Economic Value of the Otago Peninsula – Economic Impact Analysis

The presence of wildlife, particularly of two species (the Royal Albatross and the Yellow-eyed Penguin), on the Peninsula, add greatly to its economic value and generate much needed income and employment for Dunedin's regional economy. In the year ended September 2006, from the data which I collected from wildlife establishments on the Peninsula, over a quarter of a million visits were made to wildlife attractions on the Peninsula. The annual turnover of the establishments directly utilizing wildlife as attractions was estimated to be of the order of NZ\$6.5 million. [Note that all dollar values reported in this article are for New Zealand dollars]. Four of the enterprises involved had an annual turnover in excess of one million dollars. The equivalent if 70 full-time persons were employed directly in the industry at wildlife viewing sites.

The economic impact on Dunedin's regional economy of wildlife tourism on the Peninsula in terms of its generation of income and employment was much greater than that at wildlife sites because of multiplier or flow-on economic effects. Furthermore, the presence of wildlife on the Peninsula brought visitors to the Dunedin region who would not have come in the absence of the special wildlife species on the Peninsula and induced some visitors (who would have come to Dunedin anyway) to stay longer. As a result, there was extra local expenditure on accommodation, food, drink, entertainment and travel and so on. My conservative estimates (Tisdell, 2007a) suggest that this would have directly contributed an extra \$60 million in expenditure to the local economy, and with multiplier effects (which result from further spending on the local commodities by recipients of this money) the net economic contribution can be predicted to be well in excess of \$100 million. Furthermore, the total employment generated locally as a result of the wildlife species on the Peninsula will be well in excess of the 70 full-time equivalent persons directly employed by wildlife enterprises on the Peninsula. The exact figures are not available but the total local employment generated is bound to run into the hundreds. I have estimated (Tisdell, 2007a) that it results in the equivalent of 800-1000 extra full-time equivalent jobs in the Dunedin region.

An interesting feature of the use of wildlife on the Otago Peninsula for tourism is that the amount of land (space) that has to be forgone to preserve the terrestrial habitat of the current focal species (which are mainly marine-based) is very little. These wildlife species generate a very high economic impact on the local economy and the economic benefit per hectare of land set aside for them is huge. The agricultural returns forgone from conserving those

wildlife species are minimal. In the case of sheep, some landowners who combine sheep farming with the use of Yellow-eyed Penguins as tourist attractions claim that the presence of the two species is compatible. The fact that two graziers on the Peninsula willingly combine sheep grazing with the conservation and commercial viewing of wildlife (including the Yellow-eyed Penguins) indicates that they are not sacrificing income to engage in wildlife tourism. The economic opportunity cost to landowners of engaging in wildlife tourism on the Peninsula appears to be relatively low.

The site of the Royal Albatross Colony at Taiaroa Heads on the Peninsula occupies only 8 hectares. The recent annual turnover of the Royal Albatross Centre was around \$1.6 million. Therefore, its average turnover per hectare is \$200,000 annually. When the direct and indirect economic impact of the existence of the Royal Albatross Colony on Dunedin's regional economy is taken into account, this might amount to one-third to a half the regional economic impact of wildlife on the Peninsula as a result of the local tourism generated. This would result in an average economic impact of \$4-6 million annually per hectare. Although similar figures are not available for the Yellow-eyed Penguin, their economic impact in relation to the land area they use is undoubtedly very high.

The economic impact of individual members of the key tourist species on the Peninsula is also very high. For example, there are about 30 breeding pairs of albatross at the Royal Albatross Colony. Therefore, the average annual turnover per pair of the Royal Albatross Centre is about \$50,000 and the economic impact on Dunedin's regional economy is \$1-2 million annually. Each pair of Yellow-eyed Penguins on the Peninsula would also have a very high impact. There are estimated to be about 200-250 Yellow-eyed Penguins nesting on Otago Peninsula (see Figure 2). This suggests that the average economic impact of each pair of these Yellow-eyed Penguins on the Dunedin regional economy is about a quarter of a million dollars annually assuming that about \$60 million annually is the economic impact locally from the presence of these penguins. This assumption is reasonable because visits to sites on the Peninsula that have the Yellow-eyed Penguin as an attraction now generate about twice the revenue obtained by the Royal Albatross Centre (Tisdell, 2007a). It is now the premier wildlife attraction in economic terms (Figures 3 and 4). However, only a small proportion of Yellow-eyed Penguins on the Peninsula is available for viewing by tourists. The economic impact of those utilized for viewing is clearly much higher on average than a quarter of a million dollars.

The economic benefits forgone (these are opportunity cost and should be compared with the economic benefits gained) of conserving wildlife vary with the wildlife species involved. On the Peninsula, the main species used for tourism are those that find their food in marine areas but come ashore to rest and reproduce. Seals and sea lions use mainly shoreline areas for this latter purpose whereas Yellow-eyed Penguins and Little Blue Penguins (*Eudyptula minor*) venture further afield but do not go far from the shore, and the Royal Albatross uses a small area of a headland for this purpose. Overall the terrestrial area used by these wildlife species is quite small, the species do not compete with livestock for food or predate on them, and most of the areas used by them do not seem to be of high value for livestock grazing. Hence, the economic benefits forgone by graziers in conserving these species seems to be low. Some, however, such as seals and sea lions could have adverse impact on human fishing activities (see Wright, 1998) and in some cases mariculture. It has also been suggested that they could create water pollution problems which could adversely affect sales of littlenecked

clams from Papanui Inlet (personal communication on August 16, 2007, from Lala Frazer based on advice from Roger Belton of Southern Clams).



Figure 2. A Yellow-eyed Penguin with its juvenile at its nest on the Otago Peninsula [Photograph kindly supplied by the Yellow-eyed Penguin Trust, Dunedin, New Zealand].



Figure 3. A close-up view of the head of a Yellow-eyed Penguin.[Photograph kindly supplied by the Yellow-eyed Penguin Trust, Dunedin, New Zealand].

Furthermore, the return of Hooker's Sea Lion (*Phocarctos hookeri*) to the Otago Peninsula (Wright, 1988) has created a new challenge for the conservation of the Yellow-eyed Penguin because some of these sea lions predate on Yellow-eyed Penguins. Therefore,

their presence is not welcomed by all of those who are trying to conserve the Yellow-eyed Penguin on the Otago Peninsula.



Figure 4. Yellow-eyed Penguins engaged in preening on the Otago Peninsula. This species is now the premier tourist attraction on the Otago Peninsula.[Photograph kindly supplied by the Yellow-eyed Penguin Trust, Dunedin, New Zealand].

One of the reasons why the presence of wildlife on the Otago Peninsula has a high economic impact on the local economy is that most accessible sites for viewing the main species used for wildlife tourism can only be reached by way of privately owned land or land under the control of a Trust. This means that in most cases, landholders have the right of exclusion of visitors and can charge a fee for access. This results in a larger appropriation of outside money for the local economy than if there were open-access to the viewing of the focal wildlife species. It may also result in their more effective protection and conservation than otherwise would occur with open-access because landholders are able to profit or obtain income from wildlife tourists. This provides them with an economic incentive to conserve those species which provide them with income. In fact, in one area on the Otago Peninsula where there is public access for viewing the Yellow-eyed Penguin, significant conservation problems have emerged because unsupervised visitors have been disturbing Yellow-eyed Penguins at their nesting sites and the number nesting at this site (Sandfly Bay, the most southerly site on the Peninsula for Yellow-eyed Penguins indicated in Figure 1) have declined. Significant adverse visitor impacts on these penguins have reduced their numbers in this area and could see them eventually disappear there (Fouts, 2008). It has been suggested that public volunteers be recruited to control visitors at Sandfly Bay as has been done at Pilots Beach, a public beach just inside the entrance to Otago Harbour, where Little Blue Penguins come ashore (Fouts and Harwood, 2008).

The above observations imply that economically important wildlife species on the Otago Peninsula have a higher chance of surviving and adding sustainably to the economic value of the Otago Peninsula if they are in areas under the control of New Zealand Trusts (which are

in effect, government empowered NGOs) or the species are on land areas under private control. Areas in which there is public access (open-access) jeopardize the long-run survival of those species when visitor numbers increase because visitors interact negatively with these species (Tisdell, 2001, Ch.2) unless visitors are subject to community control, for example, by volunteers in conjunction with the New Zealand Department of Conservation as at Pilots Beach. Also, as mentioned above, open-access wildlife tourism is likely to have a smaller economic impact on local communities than in cases where access-fees are charged for wildlife viewing.

Another feature that adds to the economic impact of wildlife on the Otago Peninsula is that this wildlife is not located far from a major city, Dunedin. This means that it is relatively accessible and the cost of travelling to it once in Dunedin is low. The comparative location of the Otago Peninsula adds to its economic value for tourism and other purposes.

Several examples exist of commercial wildlife tourism being combined with livestock grazing on the Peninsula. Nevertheless, views differ about how desirable this combination is because there is usually some loss in natural biodiversity as a result of grazing by livestock. In this regard, the efforts of the Yellow-eyed Penguin Trust are important because it is not only trying to conserve the Yellow-eyed Penguin but to restore the natural habitats associated with it. Consequently, its activities add value by enriching natural biodiversity and its revegetation programme in many areas reduces soil erosion. It makes an important contribution to the land use mosaic on the Otago Peninsula, and generates environmental value beyond its contribution to conserving the Yellow-eyed Penguin. Its strategies also help to reduce the risk that the Yellow-eyed Penguin will disappear from the Otago Peninsula prematurely.

There has been remarkable expansion in the economic importance of wildlife tourism on the Peninsula in the last two decades. For example, in 1987 there appear to have been no more than 14,000-15,000 persons engaging in wildlife tourism on the Peninsula (Tisdell, 1988). By 2006, this number had swelled to an estimated 200,000. It had increased by more than 13 times the 1987 figure and its local economic impact in all probability increased by much more than this. The fastest growth was in visitor participation in viewing Yellow-eyed Penguins. Whereas this was minimal in 1987 (and was dwarfed by the viewing of the albatross), viewing Yellow-eyed Penguins was the major tourist wildlife activity on the Peninsula in 2006. More visitors to the Otago Peninsula participated in the viewing of Yellow-eyed Penguins in 2006 than participated in gazing at the Royal Albatross (Tisdell, 2007a). However, the rapid and significant growth in wildlife tourism on the Peninsula is creating some capacity problems and difficulties for the wildlife tourism (Tisdell, 2007a). For example, during peak tourist periods, many visitors to the Royal Albatross Colony do not get a chance to view albatross from its hide because it is not large enough to cope with the demand.

There are of course other wildlife on the Peninsula that are a part of the wildlife tourism mix and which use the foreshores. These include Hooker's Sea Lion, New Zealand Fur Seals (*Arctocophalus forsteri*), Little Blue Penguins and others (Kai Tahu ki Otago, p.49) even though they are not the main wildlife tourist attractions at present.

5. Non-use Economic Values and Social Values Associated with the Otago Peninsula Add to the Value of Conserving its Wildlife

The economic benefits and the value of the Otago Peninsula are not just confined to the Dunedin region. It is drawcard for visitors to New Zealand and to the South Island. Available data indicate that the majority of persons viewing wildlife on the Otago Peninsula are from overseas. Such visitors have a positive economic impact on the whole of New Zealand's economy. Thus, the presence of the Otago Peninsula with its particular attractions has a positive economic impact in New Zealand generally.

Tourism provides an economic incentive for conserving wildlife on the Otago Peninsula but it is not the only (economic) reason for conserving wildlife there. Efforts by bodies such as the Yellow-eyed Penguin Trust help satisfy public demands for conserving wildlife and biodiversity and provide a safety back-up to the local wildlife tourism industry. In addition, expenditure by such bodies adds to local employment and incomes. These are all extra economic benefits. Furthermore, there are social benefits to the local community via voluntary contributions to such conservation efforts. The results should also add to community pride in these conservation achievements.

Economists recognize that even when individuals do not use a facility or commodity, they may still place an economic value on it. These values are referred to as non-use economic values (Tisdell, 2005, pp.110-113). Some individuals who do not visit Otago Peninsula may value its continuing existence and will want to conserve its existing attributes, such as its wildlife. They might, in principle, be willing to pay for this conservation even though they have little intention of visiting it. This is described as *existence value*. Or some may wish to pay for its conservation because they want to keep open the opportunity of visiting it in the future. This is called *option value*. Furthermore, some non-users may want to conserve the Peninsula for the benefit of future generations and be prepared to pay to do so. This is called *bequest value*. In addition, it is possible that those who actually visited the Peninsula would be willing to contribute more than they paid for the visit (or even more than the maximum they would have been willing to pay for the visit) to ensure the future existence of the Peninsula in a desired state, retain the option of visiting it again, or to ensure that it is conserved in a desired state for the benefit of future generations. These non-use values are difficult to estimate but can still be very important. There are, however, no reliable estimates of the existence, option and bequest values for the attractions of the Otago Peninsula.

As mentioned above, economics is unable to capture or measure all values. This is true for example, of social or sociological values. Conservation activities on the Otago Peninsula have provided a basis for significant social cooperation involving non-government organizations, trusts and government bodies. This has social value because it helps to empower local communities, promotes social cohesion, provides individuals with a sense of belonging, and enhances their social purpose. Social benefits of this type have been well documented by Dianne Buchan (2007).

6. Concluding Observations

Valuing geographical assets, such as the Otago Peninsula with all of its associated attributes, is likely to result in a variety of estimates depending on one's point of view. There can be no doubt, however, that the Otago Peninsula is a very valuable asset from varied points of view. Its economic value for wildlife tourism alone is large. I have estimated that wildlife tourism on the Peninsula pumps more than \$100 million per year into Dunedin regional economy, ensures the employment of several hundred (800-1000) people locally and has some wider positive economic impacts on New Zealand's economy. Moreover, existence, option and bequest benefits from wildlife on the Peninsula further add to its economic value. In addition, community-led conservation initiatives on the Peninsula (often involving NGOs, trusts and the Department of Conservation) increase the social value of conservation on the Peninsula even though this cooperative aspect is not captured by economic measures of value. While the full economic potential of conservation on the Peninsula has not yet been realized, continuing growth in wildlife tourism on the Peninsula is facing some capacity constraints, environmental and economic challenges which are outlined in Tisdell (2007a). Nevertheless, even if the rate of growth in wildlife tourism on the Otago Peninsula slows, the value of this Peninsula for wildlife tourism and nature conservation will still remain huge. It is an asset well worth conserving.

In concluding, let me stress that wildlife need not be used commercially to be of economic value nor need it be a tourist attraction. The Yellow-eyed Penguin Trust does not utilize the Yellow-eyed Penguin for tourism. Yet the Trust's efforts to conserve the Yellow-eyed Penguin and restore its natural habitats and associated biodiversity on the Otago Peninsula (and elsewhere) have economic value, according to modern concepts of economic value. Apart from the Trust creating local employment and incomes by its expenditure, the Trust supplies conservation services that have non-use economic value. It caters for the demand of those who would like to see the continuing *existence* of the Yellow-eyed Penguin on the Otago Peninsula in a natural state, who want to retain the *option* of interacting with it in the future and who would wish to make it available to future generations as a *bequest* for them to enjoy. In addition, habitat restoration and predator control by the Trust provide general environmental services and side-benefits of economic value. Furthermore, the activities of the Yellow-eyed Penguin Trust and other conservation organizations focusing on the Otago Peninsula generate important social and sociological values (Buchan, 2007). These cannot be satisfactorily measured in terms of economics but nevertheless, add to the value of the Otago Peninsula.

Economics cannot be the final arbiter of what is valuable but it can be a very useful input into deciding what is valuable. Even if the economic benefits from conservation on the Otago Peninsula happened to be low, many might believe it to be important to conserve the current attractions of the Peninsula. The case for putting a high priority on conservation on the Otago Peninsula is strengthened by the fact that this also yields high economic benefits.

The survival of key wildlife species used on the Peninsula for tourism is by no means guaranteed. Continuing conservation effort is needed to safeguard the species there. The loss of the key species would be a major economic blow to Dunedin's regional economy, to its social activities, and result in a significant loss of biodiversity. At the present time, wildlife conservation effort is concentrated on shorelines and nearby land areas on the Peninsula.

However, the importance of offshore areas (as feeding grounds) for the key wildlife species also needs to be kept in mind.

The public needs to be kept aware of the importance of conserving wildlife on the Otago Peninsula and how it adds value to the Peninsula. The support given by Mainland (a New Zealand manufacturer of cheese and other dairy products) to the Yellow-eyed Penguin Trust has played a very positive role in that regard and the new initiative by Vodafone (a supplier of mobile telephone services) to provide support to the Yellow-eyed Penguin Trust will help further. The effort to keep the public informed needs to continue and to be adequately funded. Otherwise, the public is likely to lose sight of the value of conservation on the Peninsula and political support for wildlife conservation there may falter.

Acknowledgements

This is a revised paper prepared for a Public Lecture given on October 12, 2007 at the St. David Street Lecture Theatre, The University of Otago, Dunedin on the occasion of the Yellow-eyed Penguin Trust's 20th Anniversary Conference, "Almost an Island: Valuing Otago Peninsula". This lecture was sponsored by the Department of Tourism, School of Business, Otago University and The Yellow-Eyed Penguin Trust. I am grateful to the Yellow-eyed Penguin Trust and its donors for their support to me which has enabled me to complete the research for this paper. I thank all those in the Dunedin area who gave of their time to answer my questions and follow up my queries. In particular, I would like to thank David McFarlane for the assistance he has given to me with this project and Dr. Dorian Owen of the Department of Economics, Otago University, for assistance in gathering relevant secondary economic data for this project and his Department for providing me with facilities during my visit to Dunedin. Comments by David McFarlane and Hemanath Swarna Nantha on the original draft of this paper are appreciated. Margaret Suman's help in supplying photographs of the Yellow-eyed Penguins on behalf of the Yellow-eyed Penguin Trust is gratefully acknowledged. The usual caveat applies.

References

- Buchan, D. (2007). *Not Just Trees in the Ground: The Social and Economic Benefits of Community-led Conservation Projects*. WWF-New Zealand, Wellington.
- Fouts, M. (2008). As public give penguins the push at Sandfly Bay, expert says it's time to do something now. *The Star*, May 8, p.1, Dunedin, New Zealand.
- Fouts, M. and Harwood, B. (2008). Volunteers invaluable. *The Star*, May 8, pp.1-2, Dunedin, New Zealand.
- Higham, J.E.S. (2001). *Managing ecotourism at Taiaroa Head Royal Albatross Colony* Pp. 17-29 in M. Shackley (ed.) *Flagship Species: Case Studies in Wildlife Tourism Management*, The International Tourism Society, Burlington, Vermont, USA.
- Kai Tahu ki Otago Ltd (2006). *Biodiversity Management on Otago Peninsula: A Community Perspective*, Dunedin, NZ.
- Passmore, J.A. (1974). *Man's Responsibility for Nature: Ecological Problems and Western Traditions*. Duckworth, London.

- Pigou, A.C. (1932). *The Economics of Welfare*, 4th ed. Macmillan, London
- Simon, H. (1957). *Models of Man*. Wiley, New York.
- Tisdell, C. (1988). The economic potential of wildlife on the Otago Peninsula especially the Yellow-eyed Penguin for tourism. *Economics Discussion Papers* No. **8818**, August. University of Otago, Dunedin, NZ.
- Tisdell, C. (1996). *Bounded Rationality and Economic Evolution*. Edward Elgar, Cheltenham, UK and Northampton, MA, USA.
- Tisdell, C. (2005). *Economics of Environmental Conservation*, 2nd ed. Edward Elgar, Cheltenham, UK and Northampton, MA, USA.
- Tisdell, C. (2007a). The Economic Importance of Wildlife on the Otago Peninsula – 20 Years On. Economics, Ecology and the Environment, *Working Paper* No. **153**. School of Economics, The University of Queensland, Brisbane, Australia.
- Tisdell, C. (2007b). Knowledge and the valuation of public good and experiential commodities: information provision and acquisition. *Global Business and Economic Review*, **9**(2/3), 170-182.
- Tisdell, C. (2001). *Tourism Economics, the Environment and Development*. Edward Elgar, Cheltenham, UK, and Northampton, MA, USA.
- Tisdell, C. and Hartley, K. (2008). *Microeconomic Policy: A New Perspective*, Edward Elgar, Cheltenham, UK and Northampton, MA, USA.
- Tisdell, C., Wilson, C. and Swarna Nantha, H. (2008). Contingent valuations as a dynamic process. *The Journal of Socio-Economics*, **37**, 1443-1458.
- Wright, M. (1988). *Ecotourism on Otago Peninsula: Preliminary Studies of Yellow-eyed Penguin (*Megadyptes antipodes*) and Hooker's Sea Lion (*Phocarctos hookeri*)*. Department of Conservation, Wellington, NZ.

SHORT COMMUNICATIONS

BIOLOGICAL MONITORING USING A NEW TECHNIQUE

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1. Background

Data obtained from wildlife are useful for the evaluation of risks to human health, including those to the next generation. In this study, various environmental pollutants were investigated using samples from wildlife. We have previously investigated the degree of contamination with toxic elements, such as cadmium (Cd), chromium (Cr), molybdenum (Mo), thallium (Tl) and vanadium (V), in kidney and liver samples obtained from wild birds (Mochizuki et al., 1998, Mochizuki et al., 1999, Mochizuki et al., 2002 a, b, Mochizuki et al., 2005, Ueda et al., 1998). Studies that use wildlife are prone to problems (Krimsky, 2000), although the importance of biological monitoring has been pointed out in many studies that have investigated environmental pollution (Colborn et al., 1996). It is known that the levels of several elements, such as Cd, nickel (Ni) and selenium (Se), increase and decrease depending on the age of the animal (Elinder et al., 1981), and detailed analysis of the age of wildlife specimens is usually difficult. Another problem is that it is difficult to draw inferences from the degree of pollution of the habitat of wildlife such as migratory birds.

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Carnivores are frequently used for studies involving wildlife because they are positioned at the top of the food chain. The greater scaup (*Aythya marila*) is generally classified as a carnivorous bird that eats animals such as shellfish. However, it is known that this bird also uses feed of vegetable origin, depending on the environments in which it rests during migration. The often narrow classification of feeding habits is a daunting problem for studies of wildlife. To obtain a detailed understanding of the actual migratory flight path and the degree of contamination of the environment inhabited by migratory species is even more difficult. Thus, the data obtained from wildlife are usually distributed over a wide range, and outliers are often obtained. We investigated these problems using the data obtained in our studies of wildlife, and suggest the possibility of a new index for biological monitoring.

2. Example from Our Study

The Cd content of kidney and liver isolated from a total of 80 wild ducks was investigated in the present study (Table 1). The data were analyzed using Lotus 2001 (Lotus Development Corporation), Excel 2003 (Microsoft Corporation) and JMP 7 (SAS Institute Japan). The Cd content of kidney and liver samples was not detection (ND)-67.44 and ND-21.15 $\mu\text{g/g}$ dry weight (wt.), respectively. The data obtained from dabbling and diving ducks had a wide distribution (Fig.1 a,b). Previous studies of biological monitoring using wildlife have performed comparisons using mean values, and the comparisons have been made among

Table 1. The wild birds used in the present study. The sample from wood duck was obtained from a zoo in Japan.

Species	Scientific name	n	Classification
Dabbling ducks			
Spot-billed duck	<i>Anas poecilorhyncha</i>	19	Resident
Mallard	<i>Anas platyrhynchos</i>	7	Winter visitor
Northern pintail	<i>Anas acuta</i>	11	Winter visitor
Eurasian wigeon	<i>Anas penelope</i>	15	Winter visitor
Common teal	<i>Anas crecca</i>	6	Winter visitor
Wood duck	<i>Aix sponsa</i>	1	(Zoo)**
Gadwall	<i>Anas strepera</i>	2	Winter visitor
Northern shoveler	<i>Anas clypeata</i>	2	Winter visitor
Garganey	<i>Anas querquedula</i>	1	Winter visitor
	Subtotal	64	
Diving ducks			
Greater scaup	<i>Aythya marila</i>	6	Winter visitor
Tufted duck	<i>Aythya fuligula</i>	6	Winter visitor
Common pochard	<i>Aythya ferina</i>	3	Winter visitor
Common scoter	<i>Melanitta nigra</i>	1	Winter visitor
	Subtotal	16	
	Total	80	

different species. It is difficult to compare data from different species because the distributions of the data varied greatly with species, as shown in Fig.2 a,b. The data obtained in our studies show that biological monitoring using the comparison only of mean values is not appropriate.

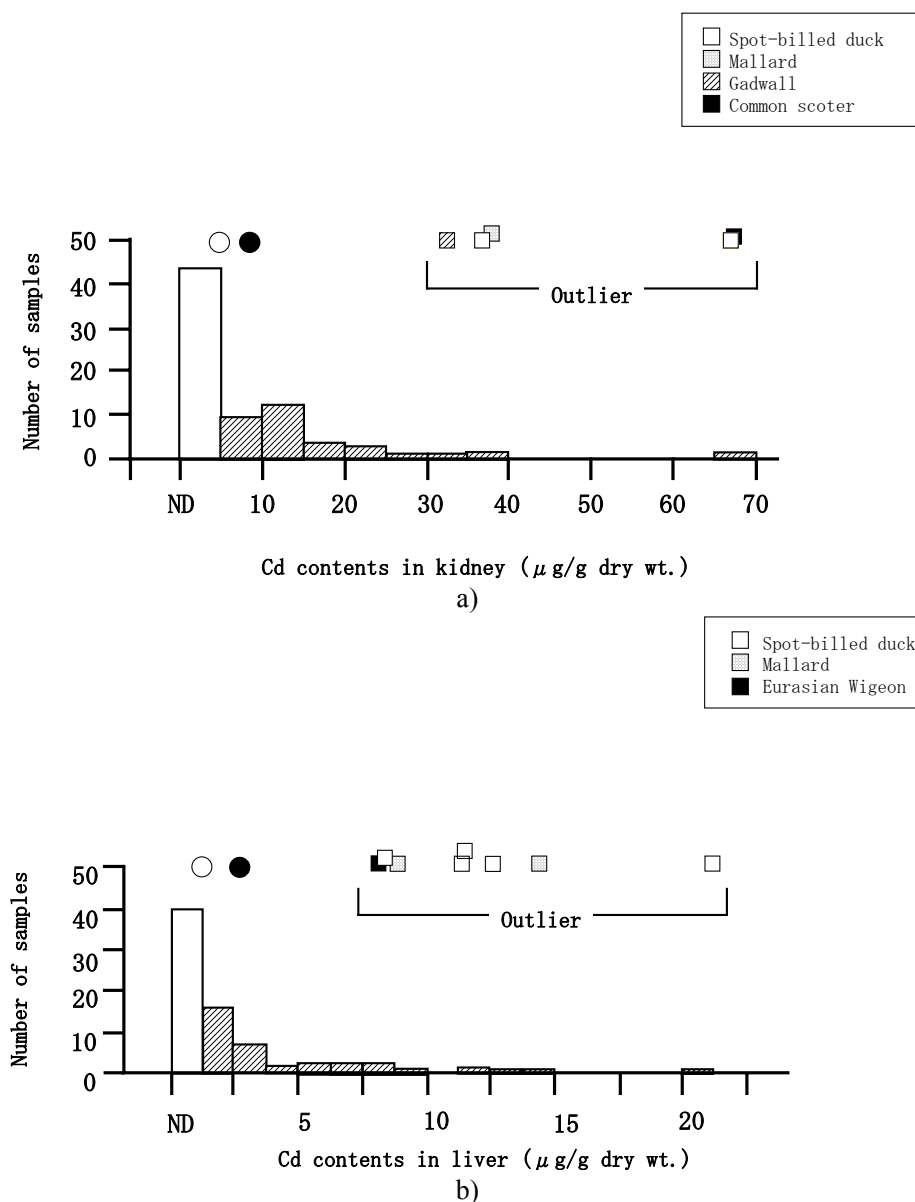


Figure 1. The distribution of Cd content ($\mu\text{g/g dry wt.}$) in kidney (Fig 1 –a) and liver (Fig 1-b) of 80 wild birds. White bar included not detectable data (kidney $n=24$, liver $n=19$), ● ; Mean, ○:Median

The presence of outliers was observed in our study, as shown in Fig1. The outliers may be excluded by statistical data processing in studies that use experimental animals. However,

outliers should be not excluded in studies of wildlife because the outliers may indicate potential contamination of the animals.

Various problems in the measurement of Cd contamination of animal specimens have been solved using a new index, the cadmium standard regression line (CSRL) (Mochizuki et al., 2008 a,b). The degree of oil contamination in diving ducks was analyzed using CSRL in a previous study (Mochizuki et al., 2008 b). In that study, acute Cd poisoning of oiled diving ducks was clearly demonstrated, although the degree of Cd contamination was not made clear by the comparison of mean values.

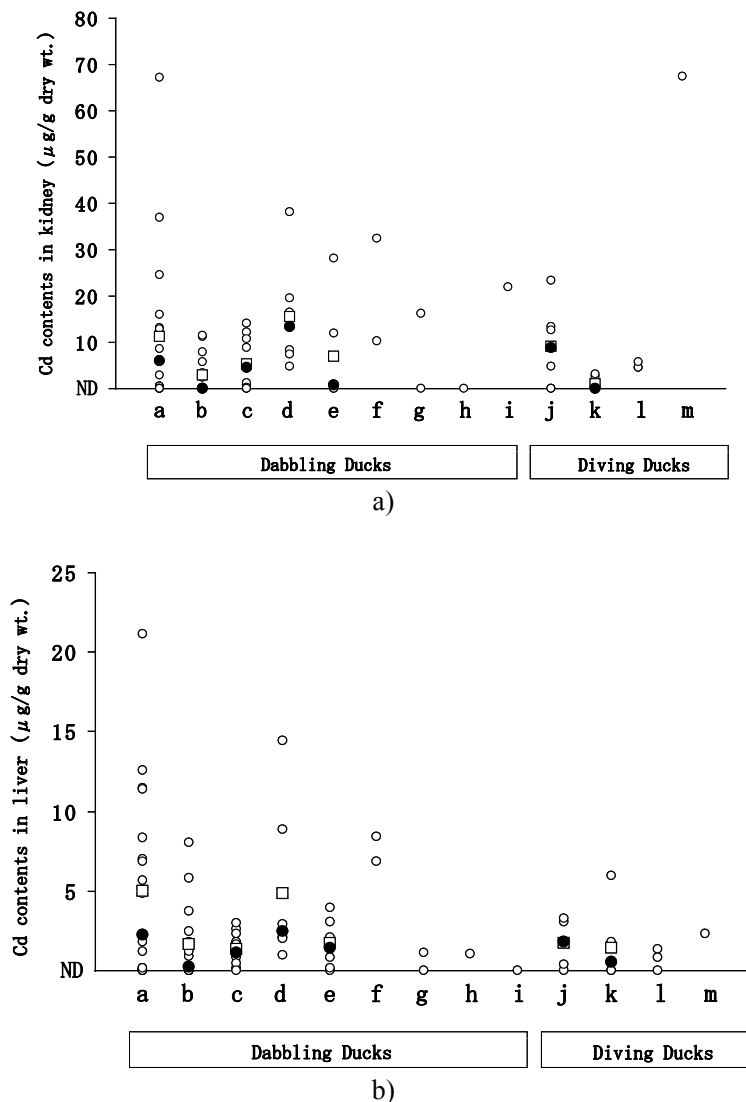


Figure 2. The distribution of Cd content (μg/g dry wt.) in kidney (Fig 2-a) and liver (Fig 2-b) of each species. Dabbling ducks, a: Spot-billed duck, b: Eurasian wigeon, c: Northern pintail, d: Mallard, e: Common teal, f: Northern shoveler, g: Gadwall, h: Garganey, i: Wood duck, Diving ducks, j: Greater scaup, k: Tufted duck, l: Common pochard, m: Common scoter, □: Mean value, ●: Median

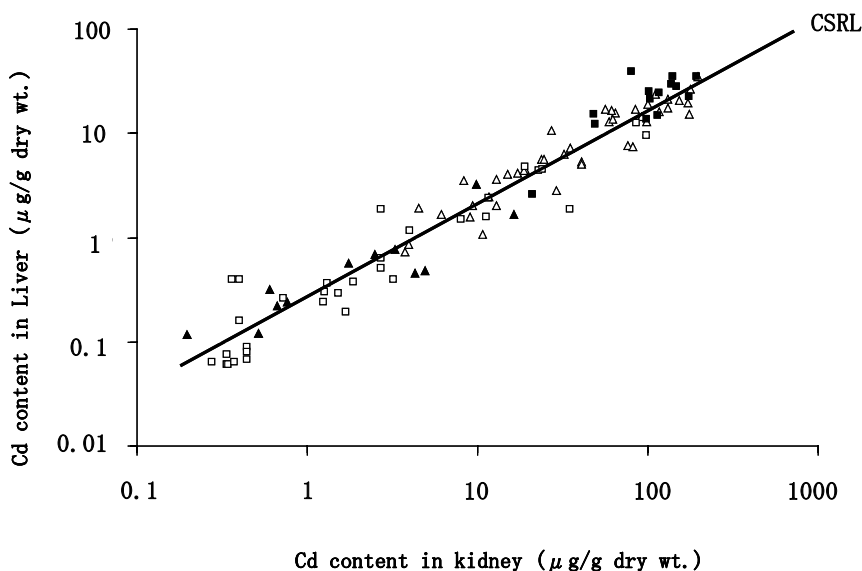


Figure 3. The relationship between the Cd contents of kidney and liver based on 101 data points from different wildlife (original data, Mochizuki et al., 2008 a). Filled triangles: land birds and waterfowl; empty triangles: seabirds; empty squares: terrestrial mammals; filled squares: marine mammals.

3. What is the CSRL?

The 101 points obtained from previous publications that reported Cd levels in wildlife as arithmetic means were plotted on a graph and a straight line (the CSRL) was obtained, as shown in Fig. 3. After logarithmic transformation, the parameters of the CSRL were: $Y=0.902X-1.334$, $Y=\log(y)$, $X=\log(x)$, $R^2=0.943$, $p<0.01$. The regression line obtained was thought to be an indicator of non-polluted animals, because any contamination of the wildlife was not indicated by this analysis. The CSRL was compared with data obtained from polluted animals of various species, including humans (Mochizuki et al., 2008 a, b) (Fig.4&5). Data from rats were used for the model of acute Cd poisoning, and data from polluted humans and monkeys were used for the model of chronic Cd poisoning. The monkeys were poisoned by a low concentration of Cd in their drinking water over several years (Otaki and Kimura, 1992), and the rats were administered 0.1, 1 or 2 mM CdCl₂ over a 2-hr period at a diminishing rate by infusion into a vein and then perfusion of organs (Mochizuki et al., 2008 a). Data from patients with Itai-itai disease and humans living in a polluted area (Friberg et al., 1974; Kuzuhara et al., 1992; Yamada et al., 1992) were also compared with the CSRL. Although data from humans living in non-polluted areas (Bem et al., 1993; Piotrowski et al., 1996; Takács and Tatár 1987; Teranishi et al., 1999) still fitted the CSRL, the data from Cd contaminated humans did not fit the regression line. In contrast, interesting information was obtained when data from experimental animals were compared with the CSRL regression line. The data from rats were positioned on the upper part of the CSRL, and those from monkeys were located at the bottom section of the regression line. These results suggest that data from cases of acute Cd poisoning are located on the upper part of the CSRL regression line, as a result of the relatively high Cd content of the liver in such

cases. It is known that the distribution of Cd in various organs depends on the number of doses, the dose applied and the period during which Cd is administered. A higher Cd level in the kidney has been reported in animals in the early stage of Cd contamination. It is known that the Cd content of the liver gradually decreases, while the Cd content of the kidney is increased. In the final stages, the Cd content of the liver becomes higher than that of the kidney because Cd accumulation in the kidney ceases as a result of renal lesions. The position of the data from humans exposed to pollution on the regression line may indicate that they were in the final stages of Cd poisoning.

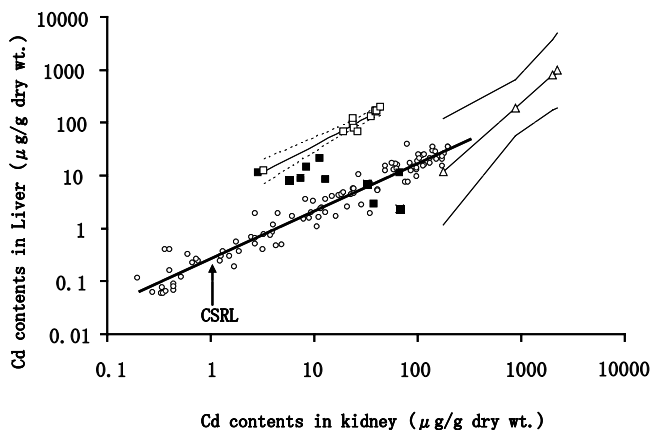


Figure 4. The relation between the CSRL and the values obtained from experimental animals and wild birds. Empty circles: 101 data points from wildlife; filled squares: data from rats; empty triangles: data from monkeys; filled squares: outliers from wild birds.

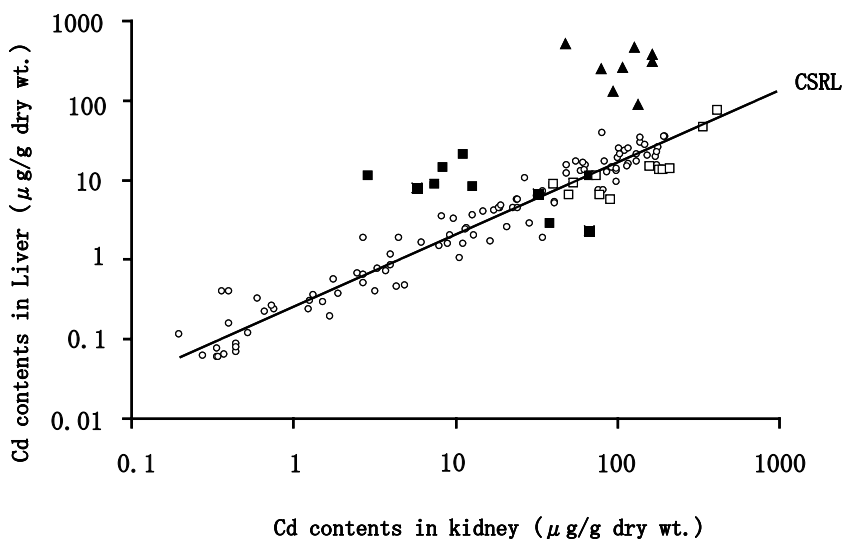


Figure 5. The relation between the CSRL and the values obtained from humans and wild birds. Empty circles: 101 data points from wildlife; filled squares: data from humans (not contaminated); filled triangles: data from patients with itai-itai disease and humans living in polluted areas; filled squares: outliers from wild birds.

4. The Analysis of Outliers Using the CSRL

We have previously stressed the importance of outliers in studies involving wildlife; therefore the significance of outliers was analyzed using the CSRL. The outliers obtained from the analysis of 80 wild ducks were compared with the CSRL, as shown in Fig.4&5. The Cd content of Kidney or that of liver, whichever was ND were excluded from this analysis. Although two data points from the outliers obtained from wild ducks fitted on to the CSRL, the others divided from the regression line. The results obtained from experimental animals and those from wild birds showed different characteristics, as shown in Fig 4. However, the distribution of outliers from wild birds (after log transformation: $Y=-0.35X+3.04$, $Y=\log(y)$, $X=\log(x)$) was similar to that of the data from humans living in a polluted area (after log transformation: $Y=-0.30X+1.32$ $Y=\log(y)$, $X=\log(x)$) (Fig.5). There was no significant difference between the slopes of the outlier data and those obtained from humans exposed to pollution ($p<0.01$). The outliers consisted of data from spot-billed ducks, mallard, Eurasian wigeon, gadwall and northern shoveler ducks. The spot-billed duck is a residential bird in Japan and this species can be observed throughout the year, although the other ducks used in the present study have breeding areas outside Japan (Brazil, 1991). It has recently been pointed out that many mallard breed in Japan, although mallard is also classified as a winter visitor. Higher Cd contents, from a global perspective, have been reported in various environmental samples from Japan, including soil (Asami, 2001), air (Friberg et al., 1974), stream water (WHO, 1992), and lake water (WHO, 1992). The higher Cd content and outliers observed in spot-billed ducks and mallard may indicate contamination of the environment in Japan. This result is supported by reports that describe high Cd levels in Japanese agricultural products and in the organs of Japanese human (Asami,2001 ; Friberg et al., 1974; WHO, 1992).

In conclusion, we suggest that biological monitoring using the CSRL can make full use of the characteristics of all data, including outliers. Therefore, we propose that this index will be useful for studies that involve the biological monitoring of wildlife.

References

- Asami T (2001). *Toxic metal pollution in soil in Japanese soil*, AGNE Gijyutu Center, Tokyo, pp3-174. (in Japanese).
- Brazil MA (1991). *The birds of Japan*. Christopher Helm, A&C Black, London.
- Bem EM, Kaszper BW, Orlowski C, Piotrowski JK, Wojcik G, Zolnowska E(1993). Cadmium, zinc, copper and metallothionein levels in the kidney and liver of humans from central Poland. *Environ Monitor Assess*, **25**: 1-13.
- Colborn T, Dumanoski D, Myers JP (1996). *Our stolen future*. trans. into Japanese: Shoeisya, Japanese translation rights arranged with Colborn T, Dumanoski D, Myers JP c/o The Spieler Agency, New York through Tuttle-Mori Agency, Inc., Tokyo.
- Elinder CG, Jonsson L, Piscator M, Rahnster B (1981). Histopathological changes in relation to cadmium concentration in horse kidneys. *Environ Res*, **26**: 1-22.
- Friberg L, Piscator M, Nordberg ,GF, Kjellström T(1974). *Cadmium in the environment*, 2 nd ed. CRC press, Ohio, pp1-400 (trans. into Japanese: Ishiyaku Publisher)

- Kuzuhara Y, Sano K, Hayashi C, Kitanura S (1992). The concentration of heavy metals in autopsy samples: humans lived in cadmium polluted and non-polluted areas, in: Japanese Society of Public Health (eds), *Kankyo Hoken Reports* No 59, Japanese Society of Public Health, Tokyo, pp 154-155. (in Japanese)
- Krimsky S (2000). *Hormonal chaos*, trans. into Japanese: Fujiwara shoten, the translation published by arrangement with the Johns Hopkins University Press through The English Agency (Japan) Ltd.
- Mochizuki M, Hondo R, Kumon K, Sasaki R, Matsuba H, Ueda F(2002a). Cadmium contamination in wild birds as an indicator of environmental pollution. *Environ Monit Assess*, **73**:229-235.
- Mochizuki M, Sasaki R, Yamashita Y, Akinaga M, Anan N, Sasaki S, Hondo R, Ueda F. (2002b). The distribution of molybdenum in the tissues of wild ducks. *Environ Monit Assess*, **77**:155-61.
- Mochizuki M, Ueda F, Hondo R (1998). Vanadium contents in organs of wild birds. *J Trace Elem Exp Med*, **11**:431.
- Mochizuki M, Mori M, Akinaga M, Yugami K, Oya C, Hondo R, Ueda F(2005). Thallium contamination in wild ducks in Japan. *J Wildl Dis*, **41**:664-668.
- Mochizuki M, Mori M, Hondo R, Ueda F (2008a). A new index for evaluation of cadmium pollution in birds and mammals. *Environ Monit Assess*, **137**:35-49.
- Mochizuki M, Mori M, Hondo R, Ueda F (2008b). "A cadmium standard regression line" A possible new index for biological monitoring, in: Ahmed El Nemr (eds), *New Developments in Environmental Pollution and Climate Change*, Research Signpost (Submitted)
- Mochizuki M, Ueda F, Sasaki S, Hondo R (1999). Vanadium contamination and the relation between vanadium and other elements in wild birds. *Environ Pollut*, **106**:249-51.
- Otaki N, Kimura M (1992). *Experimental studies on the chronic effect of cadmium* - 5. The analysis of heavy metals and specific protein, in: Japanese Society of Public Health (eds), *Kankyo Hoken Reports* No 59, Japanese Society of Public Health, Tokyo, pp. 34-42. (in Japanese)
- Piotrowski JK, Orlowski C, Bem EM, Brys M, Baran E (1996). The monitoring of cadmium, zinc and copper in the kidneys and liver of humans deceased in the region of Cracow (Poland). *Environ Monitor Assess*, **43**: 227-236.
- Takács S, Tatár A (1987). Trace elements in the environment and in human organs. *Environ Res*, **42**:312-320.
- Teranishi A, Ninomiya R, Koizumi N (1999). *Relationship of metallothionein to cadmium and to zinc in human liver and kidney*. in: C. Klaassen (eds), *Metallothionein IV*: Birkhäuser Verlag, Basel, pp. 485-488.
- Ueda F, Mochizuki M, Hondo R (1998). Cadmium contamination in liver and kidney in Japanese wild birds. *J Trace Elem Exp Med*, **11**:258.
- Yamada Y, Honda R, Tsuritani I, Ishizaki M, Kido T, Nogawa, K (1992). Exposure for environmental cadmium and calcium concentration in human organs, in: Japanese Society of Public Health (eds), *Kankyo Hoken Reports* No 59, Japanese Society of Public Health, Tokyo, pp127-130. (in Japanese)
- WHO (1992). *Environmental health criteria 134 cadmium*.
<http://www.inchem.org/documents/ehc/ehc/ehc134.htm>.

GIS-BASED HABITAT MODEL OF JAVAN HAWK-EAGLE (*SPIZAETUS BARTELSI*) USING INDUCTIVE APPROACH IN JAVA ISLAND, INDONESIA

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Abstract

The Javan Hawk-Eagle (JHE) is categorized in the IUCN Red List of Threatened Species (CITES Appendix 2) as one of the world's rarest and most endangered raptors in the remaining original natural forests of Java, Indonesia. Since it is not feasible to conduct complete field surveys for a landscape-scale, this paper proposes a GIS-based extrapolation model based on local-scale model in order to generate a map of potential and present habitat suitability for JHE in the entire landscape. Using autologistic regression, we developed a GIS-based habitat model for JHE in Java Island and subsequently estimated the population number of JHE. The obtained model will be the most useful for the wildlife management conservation planning process in order to help identify "hot spots" that are most likely to harbor JHE. Most of the predicted suitable habitats in Java Island are distributed in the mountainous area. The area with the largest proportion of suitable habitat for JHE is located in East Java, and then followed by West Java and the last in Central Java. Totally, about 41

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locations (85%) of 48 historical localities recorded were recognized as suitable habitat. The estimated number of JHE pairs based on model extrapolation would place the population size about 108-542 (median = 325) pairs. Although this estimated population is higher compared to other studies, JHE had always been described as either rare or very rare. The apparent discrepancy between this estimated population and others, which might not suggest an increase in present JHE, may be explained by several reasons such as increased accessibility to formerly unexplored habitat and more recent satellite imageries and GIS techniques application used in estimation of suitable habitat of JHE and finally will allow a better population estimate.

1. Introduction

The Javan Hawk-Eagle (*Spizaetus bartelsi*) is an endemic raptor and evergreen-forest specialist in the remaining original natural forests of Java, Indonesia [1]. The Javan Hawk-Eagle (JHE) is categorized in the IUCN Red List of Threatened Species (CITES Appendix 2) as one of the world's rarest and most endangered raptors. Small population size, severe habitat loss, forest fragmentation, and illegal hunting have all contributed to the "endangered" status of this species [2, 3]. However, population estimates until very recently have been very low, based on the amount of suitable habitat remaining divided into the estimated size of individual territories. Various authors have estimated the population size differently; "Not more than 60 breeding pairs" [4], "67–81 pairs" [5], "81–108 pairs" [6], "270–600 (median = 435) pairs" [7].

Predictive modeling commonly uses deductive and inductive approaches. Deductive models are based on theories about the behavior of the prehistoric population. Inductive models, which are more commonly used, are based on observed patterns in ground surveys or other data. One of the more powerful and widely used inductive techniques coupled with Geographic Information Systems (GIS) in habitat modeling is logistic regression [8, 9, 10]. Preliminary predictive habitat models were developed for a restricted portion of the JHE distribution in Gunung Gede-Pangrango National Park (TNGP) and its surrounding areas using logistic and autologistic regression model and successfully validated in the Southern part of West Java [11]. This method provided a useful quantitative "first step" for modeling endangered species distributions where specific habitat requirements are difficult to obtain.

Large-scale conservation planning requires the identification of priority areas in which species have a high likelihood of long-term persistence. This typically requires high spatial resolution data on species and their habitat. Such data are rarely available at a large geographical scale, so habitat distribution modelling is often required to identify the locations of suitable habitat. GIS can be used to construct spatially explicit habitat models for both common and rare wildlife species especially for a large geographical scale based on inductive approach [12, 13]. GIS technology provides the ability to construct models of habitat that rely on existing or readily obtained information (e.g., remotely sensed images, digital elevation models, topographic maps, etc.). With adequate data collection, such models often can analytically identify specific habitat characteristics across wider landscapes with high predictive power and therefore provide considerable utility. Such models offer the possibility of being able to minimize field work, and GIS-based models are easily updated as new information becomes available.

However, to be effective in the long term, JHE habitat management should not be confined only to the local and regional scale, but must also address the landscape-scale, i.e. the scale at which population processes occur. Therefore, a method is needed that allows identification of probability model of JHE habitat distribution efficiently over large areas. In addition, the method must be able to produce spatially explicit habitat suitability maps at the landscape level, which will be an important tool for the habitat management of this species. Since it is not feasible to conduct complete field surveys for a landscape-scale, GIS-based extrapolation models using an inductive approach can be used to generate maps of potential and present habitat suitability for JHE in the entire landscape.

Therefore, our primary objective was to extrapolate the predicted probability model of JHE habitat distribution from the local-scale model to landscape-scale model in order to generate maps of potential and present habitat suitability for JHE in the entire landscape. Subsequently, population number of JHE will be estimated.

2. Method of Analysis

In order to generate the present habitat suitability of JHE in Java Island, we extrapolated the best model that was developed in nest-site scale (Gunung Gede-Pangrango National Park (TNGP) and validated in regional-scale (southern parts of West Java) [11]. Subsequently, the result was compared with the historical localities record of JHE for model accuracy. Afterward, predicted suitable habitat was used for calculating the population estimation of JHE in whole Java Island.

2.1. Study Area

Java Island of about 132,000 km² is administratively divided into four provinces (Banten, West Java, Central Java, and East Java), one special region (DI Yogyakarta), and one special capital district (Jakarta) (Figure 1). The population of Java Island in 2007 was estimated to be about 130 million with a density of 985 inhabitants/km² [14]. Java is almost entirely of volcanic origin (about 43 mountains) that formed an east-west spine which has at one time or another been active volcanoes. The highest volcano in Java is Mount Semeru (3,676 m) in East Java and the most active volcano in Java and also in Indonesia is Mount Merapi (2,914 m) in Central Java [15]. Further mountains and highlands help to split the interior into a series of relatively isolated regions suitable for wet-rice cultivation. The average annual temperature varies between 22°C and 27.5°C and the annual mean rainfall ranges from 1,000 mm up to 6,000 mm. We obtained climate data courtesy of the Meteorological and Geophysical Agency of Indonesia (BMG) for 1993–2002.

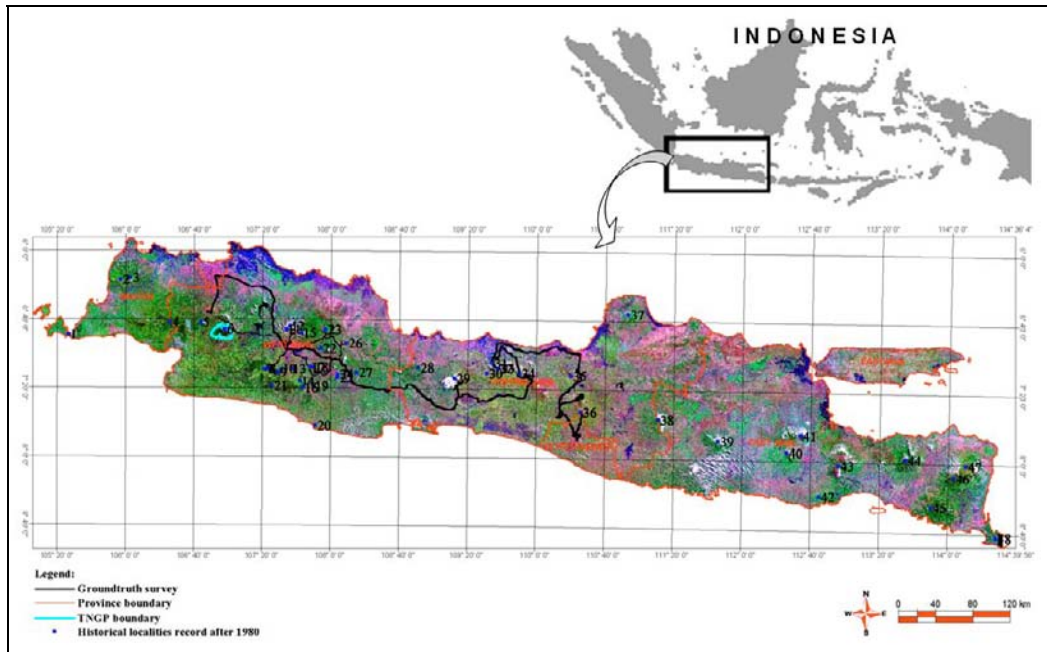


Figure 1. Study area: Java Island (Source: GeoCover Landsat mosaic, S-48-05_2000, S-50-05_2000).

2.2. Model Extrapolation

GIS-based landscape model was developed to evaluate habitat suitability of JHE in Java Island because it was not possible to conduct nest-site scale field surveys for the entire Java Island. This landscape-scale model was developed based on extrapolation of the best model obtained from the previous study [11] that was an autologistic regression model which calculated 1,500m of neighborhood size (ALR_50). This model accounted spatial autocorrelation through the addition of autocovariate variable. The best model retained the explanatory environmental variables, i.e. slope (SLP), elevation (ELV), normalized different vegetation index (NDVI) and autocovariate (AUTOCOV).

Probability of the JHE habitat (P_i) is explained by the equation below.

$$P_i = \frac{1}{1 + \exp[-(0.2371SLP - 0.0070ELV + 0.0189NDVI + 19.8063AUTOCOV - 6.8592)]}$$

SLP and ELV data were derived from Shuttle Radar Topography Mission (SRTM) Digital terrain elevation data of 2000. While, NDVI data obtained from MODIS NDVI 250m of 2002. For model extrapolation, 250*250 m pixel size was used.

Then, threshold the probability value at 0.5 is performed in order to produce the habitat suitability model. Subsequently, this model was compared with the historical localities record after 1980 (Table 1) [3, 16, 17, 18] for model accuracy.

2.3. Population Estimation

The number of breeding pairs of this species has been estimated by dividing the area of presumed suitable habitat by assumed home-range size. Suitable habitat was obtained from thresholding the predicted probability of JHE habitat at probability value of 0.5. In order to avoid the overestimate of the population size, we excluded the habitat patches with area below the 50 km². In this study, the population size was estimated using minimum and maximum home range size. Minimum home range size was based on result of the best model of habitat distribution in TNGP and its surrounding areas [11] which assumed to have a high quality habitat and also agreed with the current approximate distance between nests in TNGP [19] and the median home range size in Java [7]. Even though the exact minimum home range size obtained was 225 ha, but we used 400 ha for population estimation. Home range size of 2,000 ha was selected as maximum home range size in this study, since several researchers had been used it for estimating population number of JHE [17, 18, 20, 21].

Table 1. Historical localities of JHE record in Java Island after 1980

No.	Location	Prov.	No.	Location	Prov.
1	Ujung Kulon National Park	WJ	25	Mt. Galunggung	WJ
2	Mt. Asepun	WJ	26	Mt. Jagat	WJ
3	Mt. Karang	WJ	27	Mt.Sawal	CJ
4	Gunung Halimun National Park	WJ	28	Mt. Segara	CJ
5	Mt. Salak	WJ	29	Mt. Slamet	CJ
6	Gunung Gede-Pangrango National Park	WJ	30	Mt.Cupu/Simembut	CJ
7	Situ Patengan	WJ	31	Linggoasri	CJ
8	Cimanggu	WJ	32	Mt. Lumping	CJ
9	Mt. Patuha	WJ	33	Lebakbarang	CJ
10	Mt. Tilu	WJ	34	Mt. Kemulan	CJ
11	Mt. Burangrang	WJ	35	Mt. Ungaran	CJ
12	Mt. Tangkuban Perahu	WJ	36	Mt. Merapi-Merbabu	CJ
13	Mt. Malabar	WJ	37	Mt. Muria	CJ
14	Mt. Puntang	WJ	38	Mt. Lawu	CJ
15	Bukit Tunggul	WJ	39	Mt. Liman-Wilis	EJ
16	Mt. Papandayan	WJ	40	Mt. Kawi	EJ
17	Kawah Kamojang	WJ	41	Mt. Arjuno	EJ
18	Mt. Guntur	WJ	42	Lebakharjo	EJ
19	Mt.Cikuray	WJ	43	Mt. Bromo Tengger Semeru	EJ
20	Leuweung Sancang Wildlife Reserve	WJ	44	Yang highland	EJ
21	Mt. Simpang	WJ	45	Meru Betiri National Park	EJ
22	Mt. Masigit Kareumbi Hunting Park	WJ	46	Mt. Raung	EJ
23	Mt. Tampomas	WJ	47	Mt. Ijen	EJ
24	Mt. Talaga Bodas	WJ	48	Alas Purwo National Park	EJ

Note: Prov, Province; WJ, West Java; CJ, Central Java; EJ, East Java.

Source: BirdLife International (2001); Setiadi et al. (2000); van Balen et al. (1999; 2001).

3. Results

3.1. Model Extrapolation of JHE Habitat Distribution

JHE habitat distribution in entire Java Island based on ALR_50 model (Figure 2) was obtained from extrapolation of predicted probability model in TNGP and its surrounding areas which was successfully validated in Southern parts of West Java.

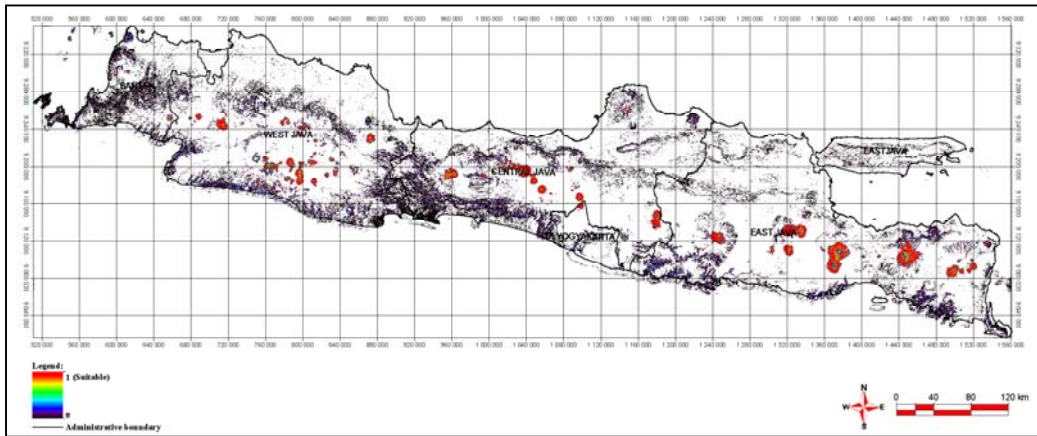


Figure 2. Predicted probability of JHE distribution in Java Island (extrapolation) based on ALR_50 model.

Subsequently, a habitat suitability model (Figure 3) was obtained from thresholding the predicted probability of JHE distribution at 0.5, and then the historical localities record after 1980 was overlaid to this model. Suitable habitat based on ALR_50 model covered about 3,107 km² and distributed in entire Java Island.

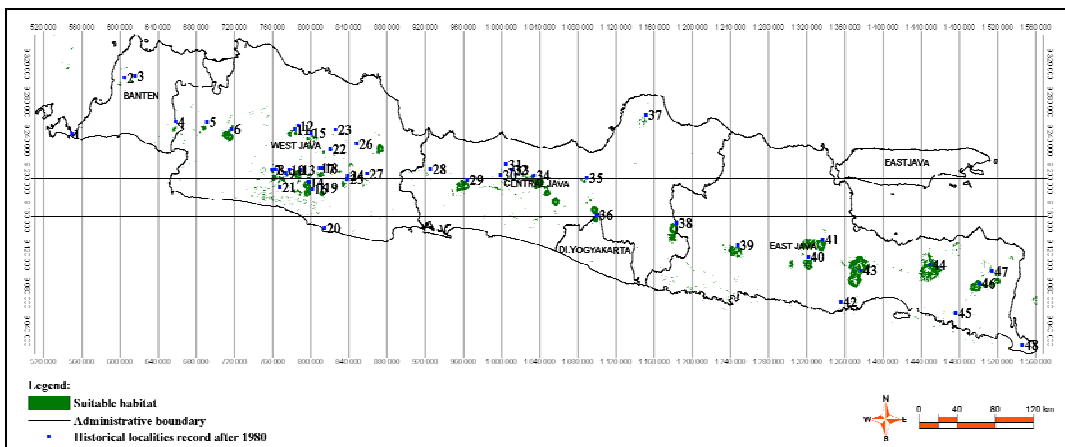


Figure 3. Habitat suitability model of JHE in Java Island (extrapolation) based on threshold of ALR_50 model at 0.5.

Totally, about 41 locations (85%) of 48 historical localities record were recognized as suitable habitat in this model and the rest of the locations (15%) were recognized as omission error, when the model predicts as an unsuitable habitat even though the species has indeed been found in that location that were Ujung Kulon National Park (locality number: 1), Leuweung Sancang Wildlife Reserve (No. 20), Mt. Tampomas (No. 23), Mt. Jagat (No. 26), Mt. Cupu/Simembut (No. 30), Meru Betiri National Park (No. 45), and Alas Purwo National Park (No. 48).

3.2. Population Estimation

Totally about 16 patches (2,166 km²) with a predicted probability of JHE presence > 0.5 and area > 50 km² were identified as habitat patch in our model, and then we used them for calculating the population of JHE (Figure 4).

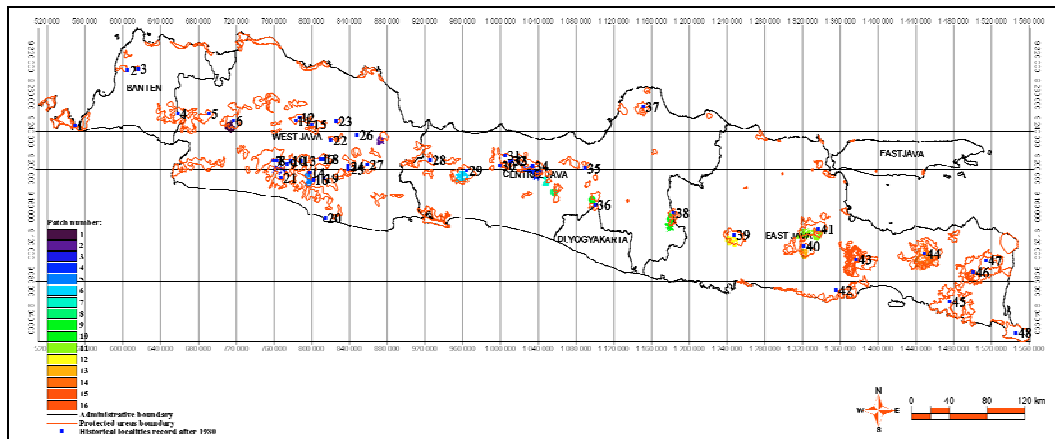


Figure 4. Distribution of habitat patches of JHE in Java Island.

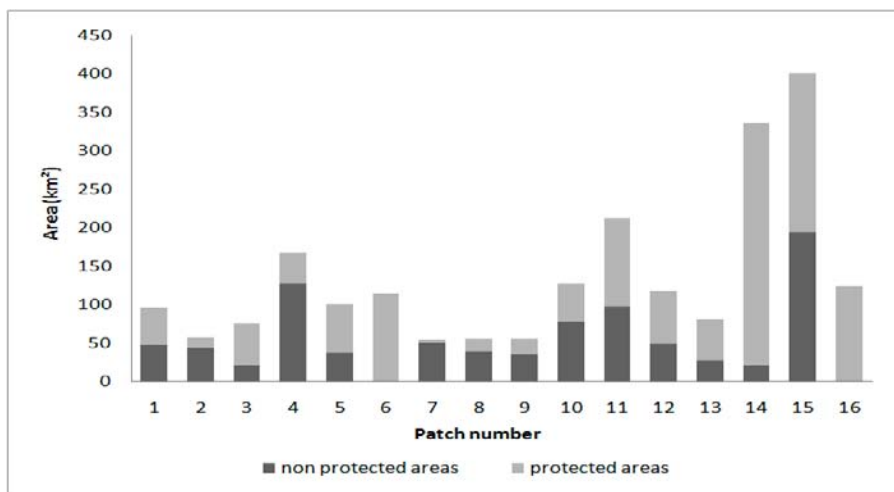


Figure 5. Proportion area of habitat patches which located inside and outside protected area network.

Comparing this to the protected area network which is produced by World Conservation Monitoring Centre in 1996, we found that 60.4% (1,309 km²) of the habitat patches already existed inside the protected area network (Figure 5).

The estimated number of pairs per habitat patch based on ALR_50 model is presented in Table 2. In this study, the estimated number of JHE pairs using ALR_50 model extrapolation would place the population size about 108-542 (median = 325) pairs. Estimated population was obtained in this study compare to other studies is presented in Table 3.

Table 2. Habitat patches and population estimation of JHE in Java Island

Patch number	Location	Prov.	Area (km ²)	Edge (km)	Estimated population (pair)	
					Minimum homerange	Maximum homerange
1	Mt. Gede-Pangrango	WJ	95	128	24	5
2	Mt. Cireme	WJ	56	73	14	3
3	Mt. Simpang-Mt.Tilu	WJ	75	180	19	4
4	Mts. Dieng (Mt.Kemulan)	WJ	167	218	42	8
5	Mt. Papandayan	WJ	100	108	25	5
6	Mt. Slamet	CJ	112	137	28	6
7	Mts Dieng(Mt.Sumbing)	CJ	54	62	14	3
8	Mts Dieng (Mt.Sindoro)	CJ	55	55	14	3
9	Mts Merapi-Merbabu	CJ	55	54	14	3
10	Mt. Lawu	CJ	127	165	32	6
11	Mt. Arjuno-Welirang	EJ	212	312	53	11
12	Mt. Liman-Wilis	EJ	117	193	29	6
13	Mt. Kawi	EJ	81	89	20	4
14	Yang highlands	EJ	336	666	84	17
15	Mts. Bromo Tengger Semeru National Park	EJ	401	577	100	20
16	Mt. Raung	EJ	123	168	31	6
Sum			2166	3185	542	108
Mean			135			
Median						325

Note: Prov, Province; WJ, West Java; CJ, Central Java; EJ, East Java.

Table 3. Estimated population of JHE in Java Island based on ALR_50 model and other studies

Source	Estimated population	
	Pairs	Median
ALR_50 model (this study)	108-542	325
Gjershaug et al. (2004)	270-600	435
van Balen et al. (1999, 2000, 2001)	137-188	-
Sözer and Nijman (1995)	81-108	-
van Balen and Meyburg (1994)	67-81	-
Meyburg et al. (1989)	60	-

4. Discussions

For conservation and development planning, it is often necessary to evaluate a large area for possible alternatives/strategies. Landscape-scale models are effective for generating spatial distributions of potential and present habitat suitability for JHE over a large area using GIS and remote sensing-based data. The predicted probability of habitat suitability may not always be accurate at specific locations because probability itself does not mean present existence. However, they will provide critical information for research, planning, and management needs at landscape scales [22, 23]. Compared to corresponding nest-site scale models, landscape-scale models use coarser information that is acquired from satellite remote sensed data such as MODIS NDVI 250 m of data resolution.

Habitat suitability model of JHE in Java island obtained in this study may be the most useful in the conservation planning process to help identify “hot spots” that are most likely to harbor JHE. A general trend in the habitat distribution of JHE can be seen with this model. Most of the predicted suitable habitats in Java Island are distributed in the mountainous area. The area with the largest proportion of encountering suitable habitat for JHE is located in East Java, and then followed by West Java and the last in Central Java.

Three locations (Leuweung Sancang Wildlife Reserve (locality number: 20), Mt. Tampomas (No. 23), and Mt. Jagat (No. 26) located in southern parts of West Java were also recognized as omission error in model validation. The other three locations (Ujung Kulon National Park (No.1), Meru Betiri National Park (No.45), and Alas Purwo National Park (No.48)) are known as the relatively large remaining lowland forest area in Java Island [1]. Before World War II, the forest area in Meru Betiri National Park was continuous with those in Alas Purwo National Park to the east, but agricultural developments have now severed this link [1]. The last location, Mt. Cupu/Simembut (No.30) where the small fragments of natural forest remain is located at 350–1,000 m elevation and surrounded by either open ground or pine plantation [17]. The last observation in seven locations mentioned above was conducted in 1997, and undoubtedly all these locations have experienced similar threats, including forest conversion (illegal logging and agricultural expansion), illegal hunting, and isolation from other patches.

In recent years, the wide recognition of the effects that both threatening processes and climate change have on biological diversity, has enhanced the importance of acquiring knowledge on the patterns of species diversity [24]. Moreover, an understanding of the environmental factors that favor key species can guide the management of protected areas [25]. The categorization of habitat quality displayed in the spatial model can be used to prioritise areas requiring protection based on their value. This statement is made on the premise that the probability of species presence is positively correlated with the quality of the habitat [12]. Our model showed that 60.4% of habitat patches existed inside the protected areas and the remaining area extends far outside protected areas. The role of this area for the expansion of the JHE population is likely important. More attention should be paid to this evidence by several agencies (i.e. ministries, national parks, NGOs) to formulate a JHE conservation plan and to identify urgent conservation actions. Therefore, the result of this study may help to proactively manage habitat for JHE, providing the impact of harmful activities within the area to JHE habitat is assessed on a multi-level management scale.

These habitat distribution models were developed based on currently available and thus limited information. New knowledge gained in the future on the habitat requirements for this species may alter the assumptions for the habitat models. Efforts need to be made to update these models whenever new information on the habitat requirements of JHE becomes available. These models and associated documentation that synthesize the biology and ecology of the JHE provide a framework that will make the effort to update the knowledge and models effective.

Based on our habitat patches model of JHE, our population estimation is comparable to those of Gjershaug et al. [7] who reported the extrapolation to the entire forest habitat in Java would place the JHE population size about 270–600 (median = 435) pairs. However, other studies did not estimate similar population numbers [4, 5, 6, 17, 18, 21]. Although this estimated population is higher compared to other studies, the JHE had always been described as either rare or very rare. The apparent discrepancy between this estimated population and others, might not suggest an increase in present JHE. The increased accessibility to formerly unexplored habitat also undoubtedly contributed to more birds having been observed. Finally, more sophisticated field identification techniques have contributed to a larger number of positive identifications. At the same time, more recent satellite imageries and GIS techniques application used in this study will allow a more precise estimate of the extent of natural forest cover in Java and finally will allow a better estimate of its population number of JHE.

The landscape-scale models based on extrapolation of the site-scale model provide spatial explicit assessment of the potential and present habitat suitability at the scales of the greatest practical needs. These models provide effective tools for conservation and development planning as well as monitoring and management of JHE habitat.

Acknowledgements

The authors wish to express sincere thanks to the directors and staff of Gunung Gede-Pangrango National Park (TNGP) for granting permission to carry out surveys in TNGP. We are grateful to the Raptor Conservation Society (RCS) and Indigenous Nature Conservation Society (YPAL), especially to Mr. Usep Suparman, Mr. Zaini Rakhman for sharing information on breeding data and their guidance during field surveys. This study was partially

supported by The JSPS-DGHE Core University Program on Applied Biosciences between Bogor Agricultural University (IPB)/The University of Tokyo.

References

- [1] Whitten, T., Soeriaatmadja, R.E., Afiff, S.A. (1996). *The ecology of Java and Bali: the ecology of Indonesia series*, Vol. 2. Singapore: Periplus Editions.
- [2] BirdLife International. (2000). *Threatened birds of the world*. Barcelona Spain: Lynx Edicions and BirdLife International.
- [3] BirdLife International. (2001). *Threatened birds of Asia: the BirdLife International red data book*. Cambridge, U.K: BirdLife International.
- [4] Meyburg, B-U., van Balen, S., Thiollay, J-M., Chancellor, R.D. (1989). Observations on the endangered Javan Hawk Eagle *Spizaetus bartelsi*. In Meyburg, B-U., & Chancellor, R.D. (Eds.), *Raptors in the modern world* (pp. 279-299). Berlin, London and Paris: WWGBP.
- [5] van Balen, S., & Meyburg, B-U. (1994). The Javan Hawk Eagle *Spizaetus bartelsi*: results of recent research on distribution, status and ecology. In Meyburg, B-U., & Chancellor, R.D. (Eds.) *Raptor Conservation Today* (pp. 89-92). Berlin, London and Paris: WWGBP and The Pica Press.
- [6] Sözer, R., & Nijman, V. (1995). Behavioral ecology, distribution and conservation of the Javan Hawk Eagle *Spizaetus bartelsi* Stresemann, 1924. *Versl. Techn. Gegev.*, **62**, 1-122.
- [7] Gjershaug, J.O., Røv, N., Nygård, T. (2004). Home-range size of the Javan Hawk-Eagle (*Spizaetus bartelsi*) estimated from direct observations and radiotelemetry. *Journal of Raptor Research*, **38**, 343-349.
- [8] Osborne, P.E., Alonso, J.C., Bryant, R.G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, **38**, 458-471.
- [9] Bailey, S.-A., Haines-Young, R.H., Watkins, C. (2002). Species presence in fragmented landscape: modeling of species requirements at the national level. *Biological Conservation*, **108**, 307-316.
- [10] Engler, R., Guisan, A., Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence. *Journal of Applied Ecology*, **41**, 263-274.
- [11] Syartinilia, & Tsuyuki, S. (2008). GIS-based modeling of Javan Hawk-Eagle distribution using logistic and autologistic regression models. *Biological Conservation*, **141**, 756-769.
- [12] Gibson, L.A., Wilson, B.A., Aberton, J.G. (2004). Landscape characteristics associated with species richness and occurrence of small native mammals inhabiting a coastal heathland: a spatial modeling approach. *Biological Conservation*, **120**, 75-89.
- [13] Posillico, M., Meriggi, A., Pagnin, E., Lovari, S., Russo, L. (2004). A habitat model for brown bear conservation and land use planning in the central Apennines. *Biological Conservation*, **118**, 141-150.
- [14] BPS, Bappenas, UNFPA. (2005). *Indonesia population projection 2000-2025*. Indonesia: BPS, Bappenas, and UNFPA.

- [15] Siebert, L., & Simkin, T. (2002). *Volcanoes of the World: an Illustrated Catalog of Holocene Volcanoes and their Eruptions*. 2002 [May, 2005]. Available from: URL: <http://www.volcano.si.edu/world/>.
- [16] Setiadi, A.P., Rakhman, Z., Nurwatha, P.F., Muchtar, M., Raharjaningtrah, W., 2000. Status, distribution, population, ecology and conservation Javan Hawk-eagle *Spizaetus bartelsi* Stresemann, 1924 on southern part of west Java. Final Report BP/FFI/*BirdLife International*/YPAL-HIMBIO UNPAD, Bandung.
- [17] van Balen, S., Nijman, V., Sözer, R. (1999). Distribution and conservation of the Javan Hawk-eagle *Spizaetus bartelsi*. *Bird Conservation International*, **9**, 333-349.
- [18] van Balen, S., Nijman, V., Sözer, R. (2001). Conservation of the endemic Javan hawk-eagle *Spizaetus bartelsi* Stresemann, 1924 (Aves: Falconiformes): density, age-structure and population numbers. *Contributions to Zoology*, **70**, 161-173.
- [19] Suparman, U. (2005). Konservasi Elang Jawa *Spizaetus bartelsi* Stresemann, 1924 di cagar alam Telaga Warna, Puncak 2000-2005: status, distribusi, ekologi dan aksi konservasi. Cianjur, Indonesia: *Raptor Conservation Society*.
- [20] Thiollay, J.-M., & Meyburg, B.-U. (1988). Forest fragmentation and conservation of raptors: survey on the Island of Java. *Biological Conservation*, **44**, 229-250.
- [21] van Balen, S., Nijman, V., Prins, H.H.T. (2000). The javan hawk-eagle: misconceptions about rareness and threat. *Biological Conservation*, **96**, 297-304.
- [22] Lindenmayer, D.B., & Possingham, H.P. (1996). Modeling the inter-relationship between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum in south-eastern Australia. *Landscape ecology*, **11**(2), 79-105.
- [23] Wu, X.B., Smeins, F.E. (2000). Multiple-scale habitat modeling approach for rare plant conservation. *Landscape and Urban Planning*, **51**, 11-28.
- [24] Heaney, L.R. (2001). Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, **10**, 15-39.
- [25] Manel, S., Williams, H.C., Ormerod, S.J. (2001). Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921-931.

CONFLICTS WITH HUMANS AND CONSERVATION OF LARGE CATS IN BRAZILIAN RANCHES

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Abstract

Cattle depredations by large cats were recorded by ranch-hands for six years (1998 – 2003) in the *Ouro Branco* ranch, central-western Brazil. The mean annual depredation by these large cats represented about 18.9% of the cattle mortality and 0.4% of the cattle stock. Depredation was not occurred at random and was mainly associated with cattle's age class, calving seasons, and spatial location. Some of the large cats depredation (22.3%; $n = 69$) were checked in the field and distinguished between puma (*Puma concolor*) and jaguar (*Panthera onca*) kills, from October 2002 to May 2003. Most of the depredation was caused by pumas (92.75%; $n = 64$) and few ones were caused by jaguars (7.25%; $n = 5$). In contrast, jaguars were the main victims of persecution by local poachers. In six years (1998 – 2003), three pumas and five jaguars were killed in the ranch and in three neighboring ranches. In addition, ranchers have offered three cows (USD\$ 365) as a reward for each large cat killed by local poachers. This control has become the main reason for the extermination of these large cats, particularly in areas not legally protected. Based on these results, non-lethal techniques should be encouraged to avoid depredations and, calves should be kept as far as possible from forest fragments. Also, it is necessary to have a scientific approach that comprises bio-ecological, socio-economic and cultural aspects to reduce the human-wildlife conflicts caused by depredation. Due to the great complexity of these interactions, a great effort must be made to guarantee large cats' conservation in Brazilian ranches.

Introduction

Conflicts between livestock owners and predators have probably appeared since human beings started to raise livestock around 9000 years ago (Nowell & Jackson, 1996). Domestic livestock lack virtually all of their ancestor's anti-predator behaviors, and represent a

relatively easily killed prey when compared to wild prey species of similar size (Linnell *et al.*, 1999a).

Large cats are considered as potential domestic livestock predators across different regions of the world (Anderson, 1981; Schaller *et al.*, 1988; Mizutani, 1993; Seidensticker *et al.*, 1993; Oli *et al.*, 1994). Also, livestock depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) has frequently been reported in most of the American continent (Ackerman *et al.*, 1984; Rabinowitz, 1986; Yañez *et al.*, 1986; Hoogesteijn *et al.*, 1993; Mazzolli *et al.*, 2002). Livestock depredation by puma and jaguar may be influenced by innate and learned behavior; health and status of individual cats; division of space and resources among these two cat species; livestock husbandry practices; and abundance and distribution of natural preys (Polisar *et al.*, 2003). When the density of prey species such as capybaras, peccaries, deer and armadillos decrease, both the puma and jaguar are forced to look for food in the domestic stocks (Crawshaw, 2004).

In Brazil, ranchers usually use livestock depredation as a reason to justify pumas and jaguars persecution (Quigley & Crawshaw, 1992; Silva, 1994), which are threatened in several regions of the country (Fonseca *et al.*, 1994). The control exerted by local people as a way to avoid livestock depredation has become the main reason for the disappearance of the large cats, especially in the areas not legally protected (Jackson & Nowell, 1996; Linnell *et al.*, 1999a). Consequently, a huge conservation effort must be promoted for coexistence of large cats with humans, especially in private lands.

Felids are **important** to the ecological health of the natural environments because they play a crucial **ecological** role as the top predator of the food chain (Terborgh, 1990). Thus, the **presence of these species should** indicate a good environmental quality of the ecosystems. In addition, felids are considered flagship species that serve as symbols to stimulate conservation awareness and action.

In this chapter, data on cattle depredation by large cats were recorded for six years (1998 – 2003) in the *Ouro Branco* ranch in Central-western Brazil. The distinction between puma and jaguar kills was only possible during the field work, from October 2002 to May 2003. Also, persecution of pumas and jaguars by local poachers was recorded in the ranch and in three neighboring ranches. Therefore, it is extremely necessary so that appropriate management strategies can be found to reduce the attacks' rate and the conflict with local people.

Methods

Study Area

The study area is located at the *Ouro Branco*, *Pintado*, *Rio Vermelho* and *Lagoa da Prata* ranches, in the Municipality of Bonópolis, State of Goiás, Central-western Brazil (Figure 1).

The study area is in a transitional area between the Cerrado and the Amazon Forest biomes (Dinerstein *et al.*, 1995). The climate is hot, semi-humid, and with a distinct dry season during four months of the year (May to August). The mean annual precipitation of 1874 mm occurs from September to April. The mean annual temperature is 25°C and the

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mean altitude is 290 m (IBGE, 2002). The vegetation mosaic is characterized by agriculture and permanent pastures, with gallery forests, dense deciduous forest and bush savanna (Miranda & Guimarães, 2002).

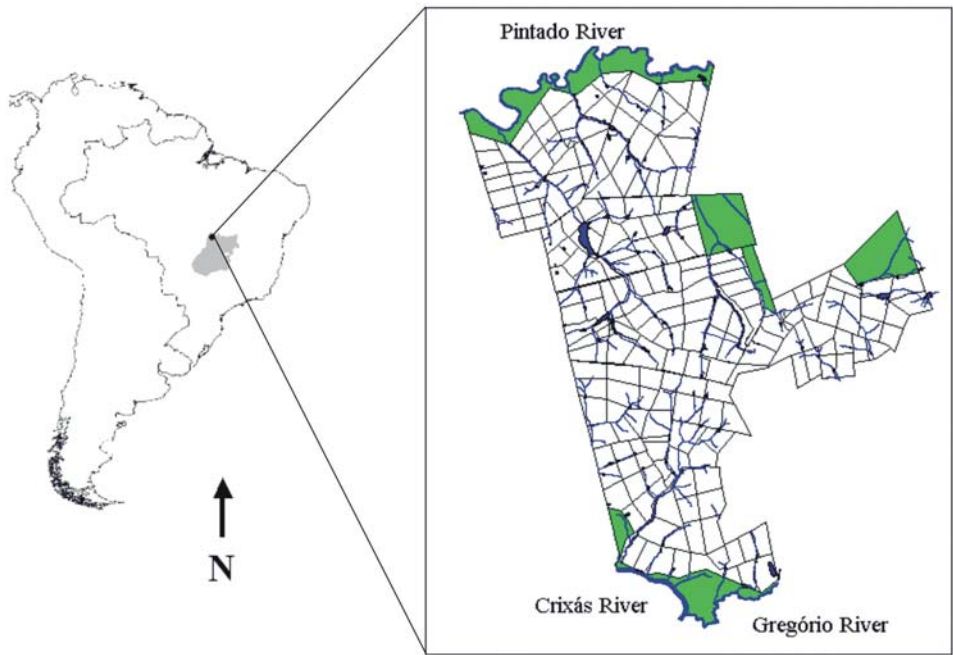


Figure 1. Location of the *Ouro Branco* ranch in Central-western Brazil.



Figure 2. Partial view of a pasture surrounded by riparian forest in the study area.

In general, the study area has approximately 80% of disturbed areas (exotic pastures, dams and roads) and at least 20% of permanent protected areas (forest patches and riparian forests). The most important natural reserves are the riparian forests of three important rivers, located on the limits of the *Ouro Branco* ranch. Pintado and Gregório rivers discharge in Crixás River, one of the main effluents on the right bank of Araguaia River in the Araguaia river basin. Some disturbed areas were partially surrounded by forest patches or riparian forests (Figure 2).

The Cerrado ecosystem was considered as one of the priority areas for jaguar study and conservation, due to the lack of knowledge on the species' geographic range and population status (Sanderson *et al.*, 1999). In addition, the Cerrado is severely treated and most of its natural areas were replaced to cultivate exotic pastures. Currently, soybean and cattle are the main economic activities in the region.

Depredation by Large Cats

Data on cattle depredation were recorded by experienced ranch-hands at the *Ouro Branco* ranch, from January 1998 to December 2003. The cattle mortality was determined in the field by ranch-hands through of peculiar characteristics of bovine carcasses (e.g.: diseases, malnutrition, ingestion of toxic plants, lightning, malpractice during vaccination, diastolic parturition, snake bites and depredation by large cats).

Data about precipitation (mm), cattle stock fluctuation, monetary values and biomass (kg) of each bovine category were taken Monthly Cattle Bulletin of the *Ouro Branco* ranch, from January 1998 to December 2003. Bovine were grouped into five categories: calves (0-12 months old), heifers and "garrotes" (12-24 months old), cows, oxen and bulls (older than 24 months). To estimate the total bovine biomass (kg/km²), the individual mean body mass was multiplied by the total number of animals and divided by the area (km²), as suggested by Schaller (1983), Crawshaw & Quigley (1984) and Polisar *et al.* (2003).

Values were expressed as mean $\pm$ SD. Statistical significance was measured at $p < 0.05$. The Spearman (r_s) correlation coefficient was used to test the relationship between depredation (total killed) and the age (in months) of the bovine killed, monthly total depredation and monthly births of calves, monthly total depredation and monthly rainfall (mm), and monthly rainfall (mm) and monthly births of calves.

The Chi-square test (χ^2) was used to verify the existence of significant differences between the genders of the bovines killed by large cats.

The pastures where depredation occurred were plotted on a digital map in order to identify the areas of higher incidence of attacks and their distance to the nearest forest patches. The Pearson (r) correlation coefficient was used to test the relationship between total depredation on each pasture and the distance from the center of the pasture to forest cover.

The ranch-hands were not able to routinely distinguish between puma and jaguar kills. This distinction was only possible during the field work, from October 2002 to May 2003, whenever depredations occurred and the killed or wounded animals were found. The carcasses were examined to determine the cause of death. In addition to age and sex of the kill, we also looked for external or internal lesions caused by bites or claw marks, especially in the head, neck and legs, in order to identify the predator.

Pumas kill their preys by suffocation, biting their throat and also leaving marks of their claws in the shoulders and back of their preys. They start eating their prey through the ventral part, reaching the ribs and the muscles of the posterior legs. Also, after pumas have eaten, they may cover the carcass with vegetation (Pitman *et al.*, 2002). In contrast, jaguar attacks result in dislocated or broken cervical vertebrae, either due to the impact of the animal fall on the ground or to a bite on the base of the skull or on the neck. Usually the jaguar starts eating the head, neck and pectoral area, frequently leaving the posterior parts intact (Schaller & Crawshaw, 1980; Mondolfi & Hoogesteijn, 1986; Guix, 1992; Hoogesteijn *et al.*, 1993).

Conflict with Humans

From October 2002 to May 2003, several informal interviews were made with ranch-hands and other employees at *Ouro Branco*, *Pintado*, *Rio Vermelho* and *Lagoa da Prata* ranches. The routine cattle management, from artificial insemination, birth, weaning, feeding, vaccination, stamping, delivering and slaughtering was accompanied and regularly monitored to better understand the functioning and the work dynamic in the ranches. Also, the key-informants talked about their perspective and attitude towards large cats during informal conversations at work, meals, parties or celebrations, car rides downtown, at the bakery, at the gas station and at school. Whenever possible, data on large cats mortality resulting from illegal hunting were recorded, as for example, the gender and approximate weight (kg) of the animal, place, date and reason for the hunting. In addition, hunting reports, skulls, leather and pictures of large cats hunted were recorded from local people. Because this study had a great impact on local people, several places were quite receptive to assessing data and to observing the attitude of the population towards the presence of large cats in the region.

Results

Depredation by Large Cats

Cattle mortality was classified into two major categories: (1) depredation by large cats and (2) other causes. Mortality by other causes included diseases, malnutrition, ingestion of toxic plants, lightning, malpractice during vaccination, diastolic parturition, and snake bites.

From January 1998 to December 2003, the total depredation by large cats was 309 heads (Table 1). The mean annual depredation was 51.5 ± 18.4 heads, equivalent to 0.4% of the mean annual stock of the cattle in the ranch. The economic loss caused by depredation was US\$ 25 865, with a mean of US\$ 4310.89 per year (US\$ 11.97 per day), representing an economic loss of 0.3% of the estimated cattle stock value.

Calves were the most vulnerable age category to all causes of mortality ($n = 722$; 56.3% of all deaths). Depredation by large cats had a negative correlation with age of the killed animals ($p < 0.05$; $r_s = -0.80$), being more frequent in newborns (0-2 months) and practically absent in calves older than 12 months. The mean annual depredation of calves was 51 ± 23 , equivalent to 1.2% of the mean annual number of births (4296 ± 958) during the study period.

Table 1. Age class (month) and estimated biomass (kg) of killed bovine by large cats, from January 1998 to December 2003.

Age class (months)	Depredation (n)	Mean body mass (kg)	Estimated biomass (kg)
0-3	170	50	8 500
3-6	89	120	10 680
6-9	41	180	7 380
9-12	6	275	1 650
12-24	0	350	0 000
>24	3	420	1 260
Total	309	-	29 470

Most of the biomass preyed upon was from animals 4 to 6 months old (36.2%; 10 680 kg), followed by calves younger than 3 months (28.8%; 8500 kg), and 7 to 9 months old (25%; 7380 kg). The mean annual depredation resulted in an estimated biomass loss of 63.8 kg/km², equivalent to 0.4% of the bovine mean annual biomass.

Cattle depredation increased from October to May, soon after the births occurred (September through December), and then decreased from June to September, after the births ceased (May to June). Depredation rates were proportional to the seasonal number of births: 23.8% ($n = 6\ 135$) of the births and 28.2% ($n = 87$) of the kills during the dry season (May to September); and 76.2% ($n = 19\ 644$) of the births and 71.8% ($n = 222$) of the kills during the rainy season (October to April). Depredation had no direct association with the births of calves ($p > 0.05$) which was associated to the monthly rain precipitation (mm) ($p < 0.01$; $r_s = 0.43$).

The sex ratio at birth of calves was approximately 1:1 (50.1%:49.9%). However, males were more frequently killed by large cats ($n = 183$; 59.2%) than females ($n = 126$; 40.8%) ($\chi^2 = 10.51$, $df = 1$; $p < 0.01$).

Depredation occurred only in 31.2% ($n = 68$) of the pastures of the ranch. The proportion of pastures next to forest with depredation represented 54% ($n = 33$) of the 61 total pastures that were at least partially surrounded by forest patches or riparian forests. The number of depredation on pastures bordering forest that had depredation ($n = 150$, 48.5%) was also not distinguished to the number of depredation on pastures not bordering forest that suffered depredation ($n = 159$, 51.5%). No kills occurred in the central portion (main house) of the farm, close to the headquarters. The distance from the center of the pasture in relation to areas of native forest was 1317.48 ± 941.03 meters. There was a marginally significant correlation between the total depredation on each pasture and the distance from the center of the pasture to forest cover ($p < 0.05$; $r = -0.23$).

From October 2002 to May 2003, some of the kills ($n = 69$; 22.3%) were checked to distinguish between puma and jaguar kills. The majority of the kills checked ($n = 64$; 92.7%) were confirmed to have been by puma tended to kill smaller calves than jaguars. The mean weight of calves lost to pumas and to jaguars was 74 kg (0- to 6-months old) and 144 kg (3- to 9-months old), respectively. The total cattle biomass damaged by pumas and jaguars during this period were 4740 kg and 720 kg, respectively.

Conflict with Humans

Persecution of pumas and jaguars as a way to control the species was frequently recorded (Figure 3). Local poachers reported that some ranchers offer three cows (USD\$ 365) as a reward for each large cat killed.



Figure 3. Adult male jaguar killed by local poacher because cattle depredation in the study area.

Several large cats were exterminated with hunting methods that used dogs or ambushing with an artificial jaguar calling device called *esturrador* (e.g.: a device made by the hunter to attract jaguars by reproducing their roaring). Poachers made it quite clear his preference for hunting jaguars. An important local poacher had killed 40 jaguars but only two pumas in different cattle ranches of the region. Also, a total of three pumas and five jaguars were killed in the study area (Table 2).

Table 2. Puma (*Puma concolor*) and jaguar (*Panthera onca*) killed in the *Ouro Branco* ranch and in three neighboring ranches (*Pintado*, *Rio Vermelho* and *Lagoa da Prata* ranches), from January 1998 to December 2003.

Gender (Sex)	Puma	Jaguar	Total
Male	3	2	5
Female	0	3	3
Total	3	5	8

Conclusion

Although jaguars attacked less cattle than pumas, they were the main victims of persecution by local poachers in the study area. A similar situation was observed in the Argentine Chaco where jaguar persecution did not follow depredation but was a continuous process. Jaguars were persecuted as soon as their tracks have been observed in the forest. In contrast, pumas were persecuted only after they have attacked domestic livestock (Altrichter, *et al.*, 2006). Also, the preference shown by jaguars for riparian environments, where they can find their main prey species, exposes them to more frequent contact with humans, since local people use rivers to access even the most secluded areas (Crawshaw, 2003).

Management strategies used to reduce human-wildlife conflicts are important tools for wild cats' conservation (Nowell & Jackson, 1996). Moreover, using several strategies combined should increase their global efficiency (Manzatti, 1999). These strategies would include translocation (Rabinowitz, 1986; Linnell *et al.*, 1999b), economic compensation (Verdade & Campos, 2004; Bulte & Rondeau, 2005), prohibition of hunting and also the suggestion of several preventive measures (Pitman *et al.*, 2002). However, the strategies to reduce depredation by large cats are still quite controversial among diverse interest groups. It is believed that it is necessary to reduce conflicts between groups of interest to make it viable to define a management policy of public interest so that predators might co-exist with humans (Laundré & Clark, 2003).

In some parts of the world, the landowner must require the presence of a government official to verify the degree of depredation before the extermination of the predator is authorized (Jackson & Nowell, 1996). In Brazil, according to article 37 of the Law of Crimes Against the Environment, "it is not a crime to kill an animal when it is done, among other cases, to protect crops, orchards, and herds of the predatory or destructive actions of a wild animal once it has been legally authorized by the competent government authority" (MMA, 2000). In 1994, to mediate the huge conflict caused by depredation, to answer to ranchers reports on depredation and, to develop activities of research and management, among other things, was created (Decree n° 78/94 and n° 101/95) the National Center for Research and Conservation of Natural Predators of the Brazilian Institute of Environment and Renewed Natural Resources (CENAP/IBAMA). Since then, national and local official authorities have received a great number of calls related to depredation of domestic animals. The lack of trained professionals though and the flaws in the records of occurrences have prevented efficient actions on this matter (Pitman *et al.*, 2002; Verdade & Campos, 2004).

It is necessary to qualify professionals to evaluate the damages caused by wildlife, including depredation. It is fundamental to offer special training since graduation to biologists, agronomists and professionals of related areas, in special to specialists in domestic livestock breeding. These specialists could draw projects of animal production considering the presence of the large cats in cattle ranches thus reducing the depredation by a set of breeding management techniques. They could also develop budgets for annual expenditure forecasting the amount of money to be set aside for probable losses resulting from large cats depredation. In Brazil, a few manuals have been written to guide professionals in farm work and to suggest preventive measures to reduce large cats depredation (Pitman *et al.*, 2002). It is also necessary to write guides to rural producers and to the local population focused on environmental education (Leite & Crawshaw, 1999; Marchini & Luciano, 2008).

A great incentive to reduce loss caused by depredation would be a partial reduction in the Rural and Territorial Taxes (ITR) for ranchers with large properties that could provide evidence of loss by depredation. According to Hoogesteijn & Chapman (1997), the inclusion of cattle ranches in conservation programs would require government and conservation agencies to help landowners to develop a system that would assure that the regulations for conservation of their property would effectively be put into effect. At long run, an official net of ranch-reserves would stand a better chance of being sustainable. This net might be comprised of landowners that would be willing to receive tax incentives, protection for land exploiting and, a prestigious and officially recognized social status besides having in their land the potential to significantly contribute to conservation efforts.

Therefore, it is necessary to have a scientific approach that comprises bio-ecological, socio-economic and cultural aspects to reduce the conflict caused by depredation. Due to the great complexity of these interactions, a great effort must be made to guarantee large cats conservation in Brazilian ranches.

Acknowledgements

I thank the World Wildlife Fund - Brazil (WWF – Brazil) and the Ford Foundation (grant # CSR 268-2002), the Idea Wild (grant # 676), *Ouro Branco* ranch, and Benvinda Belem Lopes for their support. I also thank Bruna C.R. de Carvalho, Rodrigo D. Amato, Fernando A. Haddad, Bento C.A. Neto and all employees of *Ouro Branco* ranch who provided invaluable assistance during the field work. In addition, I would like to extend my grateful thanks to Peter G. Crawshaw Jr, Claudio M. Haddad, Katia Maria P.M.B. Ferraz, Luciano M. Verdade, Cristiano T. Trinca, Olga Z. Zumstein and Antonio Zumstein for their help, suggestions and comments.

References

- Ackerman, B.B.; Lindzey, F.G. & Hemker, T.P. (1984). Cougar food habits in southern Utah. *Journal of Wildlife Management*, **48**, 147-155.
- Altrichter, M.; Boaglio, G. & Perovic, P. (2006). The decline of jaguars *Panthera onça* in the Argentine Chaco. *Oryx*, **40**, 302-309.
- Anderson, J.L. (1981). The re-establishment and management of a lion *Panthera leo* population in Zululand, South Africa. *Biological Conservation*, **19**, 107-117.
- Bulte, E.H. & Rondeau, D. (2005). Why compensating wildlife damages may be bad for conservation. *Journal of Wildlife Management*, **69**, 14-19.
- Crawshaw Junior, P.G. (2003). A personal view on the depredation of domestic animals by large cats in Brazil. *Natureza & Conservação*, **1**, 71-73.
- Crawshaw Junior, P.G. (2004). Depredation of domestic animals by large cats in Brazil. *Human Dimensions of Wildlife*, **9**, 329-330.
- Crawshaw Junior, P.G. & Quigley, H.B. (1984). *A ecologia do jaguar ou onça-pintada no Pantanal: Estudos bioecológicos do Pantanal, Parte I*. Brasília, DF: Instituto Brasileiro de Desenvolvimento Florestal (IBDF).

- Dinerstein, E.; Olson, D.M.; Graham, D.J.; Webster, A.L.; Primm, S.A.; Bookbinder, M.P. & Ledec, G. (1995). *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean*. Washington (DC): The World Bank.
- Fonseca, G.A.B.; Rylands, A.B.; Costa, C.M.R.; Machado, R.B. & Leite, Y.L.R. (1994). *Livro vermelho dos mamíferos brasileiros ameaçados de extinção* (2.ed.). Belo Horizonte, MG: Fundação Biodiversistas.
- Guix, J.C. (1992). El jaguar en la pluvisilva atlántica de Brasil. *Vida Silvestre*, **71**, 32-37.
- Hoogesteijn, R.; Hoogesteijn, A. & Mondolfi, E. (1993). Jaguar predation vs. conservation: cattle mortality by felines on three ranches in the Venezuelan Llanos. In N. Dunstone & M.L. Gorman (Eds.), *Mammals as predators, Proceeding Symposium Zoological Society of London*, **65**, 391-407.
- Hoogesteijn, R. & Chapman, C.A. (1997). Large ranches as conservation tools in the Venezuelan Llanos. *Oryx*, **31**, 274-284.
- (IBGE) Instituto Brasileiro de Geografia e Estatística. (2002). *Mapa da Série Brasil Geográfico*, (2.ed.). Brasília, DF.
- Jackson, P. & Nowell, K. (1996). Problems and possible solutions in management of felid predators. *Journal Wildlife Research*, **1**, 304-314.
- Laundré, J. & Clark, T.W. (2003). Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation*, **6**, 159-170.
- Leite, M.R.P. & Crawshaw Junior, P.G. (1999). *Toizinho e a onça*. São Paulo, SP: Editora Lake.
- Linnell, J.D.C.; Odden, J.; Smith, M.E.; Aanes, R. & Swenson, J.E. (1999a). Large carnivores that kill livestock: do “problem individuals” really exist? *Wildlife Society Bulletin*, **27**, 698-705.
- Linnell, J.D.C.; Aanes, R.; Swenson, J.E.; Odden, J. & Smith, M.E. (1999b). Translocation of carnivores as a method for managing problem animals: a review. *Biodiversity and Conservation*, **6**, 1245-1257.
- Manzatti, L. (1999). *Predação de animais domésticos e plantações no entorno do Parque Nacional do Iguazú (PR) – Análise da percepção de fazendeiros e alternativas de manejo*. Piracicaba, SP: Dissertação (Mestrado) - Escola Superior de Agricultura “Luiz de Queiroz”, Universidade de São Paulo.
- Marchini, S. & Luciano, R. (2008). *Guia de convivência gente e onças*. Alta Floresta: MT: Editora Amazonarium Ltda.
- Mazzolli, M.; Graipel, M.E. & Dunstone, N. (2002). Mountain lion depredation in southern Brazil. *Biological Conservation*, **105**, 43-51.
- (MMA) Ministério do Meio Ambiente (2000). *Lei da vida: a lei dos crimes ambientais*. Lei nº. 9.605 de 12 de fevereiro de 1998 e Decreto nº 3.179 de 21 de outubro de 1999. Brasília, DF: Gráficos Charbel.
- Miranda, E.E. & Guimarães, M. (2002). *GeoGoiás 2002: Mapa da cobertura vegetal do Estado*. Brasília, DF.
- Mizutani, F. (1993). Home range of leopards and their impact on livestock on Kenya ranches. In N. Dunstone & M.L. Gorman (Eds.), *Mammals as predators, Proceeding Symposium Zoological Society of London*, **65**, 425-439.
- Mondolfi, E. & Hoogesteijn, R. (1986). Notes on the biology and status of the jaguar in Venezuela. In S.D. Miller & D.D. Everett (Eds.), *Cats of the world: biology*,

- conservation and management (pp. 85-124). Washington, DC: National Wildlife Federation.
- Nowell, K. & Jackson, P. (1996). *Wild cats: status survey and conservation action plan*. Gland, VD: International Union for Conservation of Natural Resources.
- Oli, M.K.; Taylor, I.R. & Rogers, M.E. (1994). Snow leopard *Panthera uncia* predation of livestock: an assessment of local perceptions in the Annapurna Conservation Area, Nepal. *Biological Conservation*, **68**, 63-68.
- Pitman, M.R.P.L.; Oliveira, T.G.; Cavalcanti, S.M.C.; Paula, R.C. & Indrusiak, C. (2002). *Manual de identificação, prevenção e controle de predação por carnívoros*. Brasília, DF: Edições IBAMA.
- Polisar, J.; Maxit, I.; Scognamillo, D.; Farrell, L.; Sunquist, M.E. & Eisenberg, J.F. (2003). Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation*, **109**, 297-310.
- Quigley, H.B. & Schaller, G.B. (1988). *Ecology and conservation of the jaguar in the Pantanal region of Brazil*. Final Report to National Geographic Society, Brasília, DF.
- Quigley, H.B. & Crawshaw Junior, P.G. (1992). A conservation plan for the jaguar (*Panthera onca*) in the Pantanal region of Brazil. *Biological Conservation*, **61**, 149-157.
- Rabinowitz, A.R. (1986). Jaguar predation on domestic livestock in Belize. *Wildlife Society Bulletin*, **14**, 170-174.
- Sanderson, E.W.; Chetkiewicz, C.L.B.; Rabinowitz, A.; Redford, K.H.; Robinson, J.G. & Taber, A.B. (1999). A geographic analysis of the status and distribution of jaguars across the range. In R.A. Medellin, C.L.B. Chetkiewicz, A. Rabinowitz, K.H. Redford, J.G. Robinson, E.W. Sanderson & A.B. Taber (Eds.), *El jaguar en el nuevo milenio: Una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguares en América*. Mexico, DF: Universidad Nacional Autónoma de México/Wildlife Conservation Society.
- Schaller, G.B. (1983). Mammals and their biomass on a Brazilian ranch. *Arquivos de Zoologia, São Paulo*, **31**, 1-36.
- Schaller, G.B. & Crawshaw Junior, P.G. (1980). Movement patterns of jaguar. *Biotropica*, **12**, 161-168.
- Schaller, G.B.; Junrang, R. & Mingjiang, Q. (1988). Status of the snow leopard *Panthera uncia* in Qinghai and Gansu Provinces, China. *Biological Conservation*, **45**, 179-194.
- Seidensticker, J. & McDougal, C. (1993). Tiger predatory behaviour, ecology and conservation. In N. Dunstone & M.L. Gorman (Eds.), *Mammals as predators, Proceeding Symposium Zoological Society of London*, **65**, 105-125.
- Silva, F. (1994). *Mamíferos silvestres: Rio Grande do Sul* (2.ed.). Porto Alegre, RS: Fundação Zoobotânica do Rio Grande do Sul.
- Terborgh, J. (1990). The role of felid predators in neotropical forests. *Vida Silvestre Neotropical*, **2**, 3-5.
- Verdade, L.M. & Campos, C.B. (2004). How much is a puma worth? Economic compensation as an alternative for the conflict between wildlife conservation and livestock production in Brazil. *Biota Neotropica* **4** (2), <http://www.biotaneotropica.org.br/v4n2/pt/abstract?short-communication+BN02204022004>.
- Yáñez, J.L.; Cárdenas, J.C.; Gezelle, P. & Jaksic, F.M. (1986). Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestock ranges. *Journal of Mammalogy*, **67**, 604-606.

FROM ACCEPTANCE TO SUPPORT: WHEN DAMAGE COMPENSATION TURNS INTO PERFORMANCE PAYMENTS

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Abstract

Damage compensation schemes are widely used as tools for the reconciliation of human-wildlife-conflicts. Two forms of compensation schemes exist: *ex ante* and *ex post*. While the latter is commonly used to compensate wildlife damages in many parts of the world, it is also often criticized for several reasons. Arguments against its use include the associated high transaction costs and the lack of those schemes to provide positive incentives for wildlife conservation. The importance of integrating positive incentives into conservation activities is not only highlighted by many economists, but also mentioned in the CBD. As a result, increasing attention has to be paid to the second form of compensation: *ex ante* compensation schemes. Changing compensation from one scheme to the other provides a high potential to increase public support for wildlife conservation. Instead of only distributing the damage costs more fair in the society as under *ex post* schemes, payments under *ex ante* compensation are directly linked to the number of animals including offspring. The aim of both instruments is therefore fundamentally different: Whereas the first scheme seeks only to gain acceptance for damage-causing species, strives the latter for an active support. In that respect, *ex ante* compensations are payments for environmental services (PES). PES imply the need to address complex trade-offs between the “provider” and the “consumer” of an environmental good through compensations. Many scholars have assessed the advantages of PES over indirect approaches, but its application still remains “under-construction”.

A large amount of literature deals with the relevance of such payments for conservation activities, but the relation between *ex ante* compensation and payments for environmental services has not yet been mentioned in the literature. This study aims to fill this gap by systematically looking at damage compensation schemes and payments for environmental

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services, arguing that an increased use of the latter will support wildlife conservation by shifting the focus from acceptance to support.

Introduction

Human-wildlife conflicts have a long history and are probably as old as humankind itself. Predatory species such as large carnivores were perceived as a direct threat to humans and their livestock or as competitors for game. Consequently, the eradication of species like bears, wolves or otters was a categorical objective in agricultural societies (Breitenmoser 1997). From an economic point of view, human-wildlife conflicts which result from competition over limited resources such as game, fish, livestock or habitat are resource-conflicts. They sharpen with increasing resource scarcity; but they are also influenced by a variety of other factors such as legal framework, the socio-economic conditions of people concerned and their general perceptions towards predators. This chapter looks at resource-conflicts as the most common example of human-wildlife conflicts, with a focus on predatory species.

In the last decades, human-wildlife conflicts evoked an increasing interest. Two aspects have played a major role thereby. The first was the implementation of conservation instruments that provide strong protection for most predatory species. This has enabled the successful recovery of some of them, for example the European otter. What conservationists have named “a success story of conservation” (Kruuk 2002) was accompanied by a revival of conflicts. Especially ponds with their artificially high fish densities suffer from otter damages. Consequently, conflicts were reported from traditional fish pond areas such as South Bohemia in the Czech Republic or the Upper Lusatia in Germany (Mysiak et al. 2004). Similar patterns are also noticeable for other species, such as for grey seals in the Baltic Sea (Varjopuro 2005). A strong protection status restricts the possibility of lethal control for damage-causing species. In this respect, it eliminates the rights of the persons concerned to protect themselves from these damages (de Klemm 1996). Legal protection of predators can therefore impose considerable costs on certain people, especially on land users who share a habitat with them. Quite obvious, this leads to a more negative attitude towards the respective species and may in turn be contradictory for conservation.

The second aspect with far-reaching influence on human-wildlife conflicts is a shift in the perception of predators. In many urban-shaped societies, they are no longer seen as “pests” or competitors but instead recognized as symbols of nature and wilderness which may experience great sympathy. An extreme example was the case of the bear “Bruno” in Europe in 2006. The animal was shot after a series of livestock killings in Germany and Austria, causing a great emotional response in both countries including notifications and funeral services.

Effective solutions for human-wildlife conflicts need to take the aspects of increasing costs and perception changes into account. A major role in this process is played by damage compensation schemes. They distribute the costs of predation between those in favour of predator conservation and those who must suffer the costs thereof. More equal cost distribution is not only an argument of fairness but aims to raise acceptance of the respective species. Effective compensation is therefore expected to reduce revenge killing and poaching (Nyhus et al. 2005).

However, damage compensation schemes have also been criticized as cost-intensive measures that fail to reach their aim. Farmers may continue to kill wildlife even when

compensated (Naughton-Treves 2003). I see another major shortcoming in the fact that such payments are of a passive nature and provide no incentive for species protection. Because conservation funding is usually very limited, the efficient use of the available funds is highly important. This holds as well true for damage compensation schemes, which can require a considerable amount of money, also for their associated administrative costs (Schwerdtner & Gruber 2007).

In this chapter, I look at the prospects and challenges of damage compensation schemes to mitigate human-wildlife conflicts. In a second step, I introduce payments for environmental services and explain their potential to provide incentives for active conservation support. Based on this, I suggest a shift from the traditional “pure compensation” approach in species conservation towards the use of payments for environmental services.

Damage Compensation Schemes in Their Most Common Form

Simply speaking, damage compensation schemes aim at reimbursing people who have experienced a kind of wildlife damage for their occurring costs. The compensation can take a monetary form or is provided as allowance in kind. The first is more common, whereas the amount of money paid can vary greatly from only a fraction of the value lost over the market value to additional payments for indirect losses such as the time needed to readjust things after an incident (Nyhus et al. 2005, Fourli 1999). The compensating body is usually the federal or the state government; in this case the money is raised through taxes. If state programmes are not available, conservation organisations or even hunting associations occasionally undertake this task. Money is then raised by membership fees or donations.

A large number of countries employ damage compensation schemes, but information on their effectiveness is still limited. Nyhus et al. (2003) and Nyhus et al. (2005) provide the first comprehensive overviews on the challenges and shortcomings of damage compensation schemes; however there is still a need to carry out more and detailed on-the-ground-studies. Despite the limited information available, there is agreement on the fact that compensation for wildlife damages forms an important part of a comprehensive approach for the mitigation of human-wildlife conflicts (Nyhus et al. 2005, Schwerdtner & Gruber 2007).

Compensation is usually carried out in an ex-post form. Requests for payments are made after the damage has occurred; the amount of compensation is based on an estimation of actually arising costs. Type and level of damages are therefore monitored directly. Ex-post compensation is intuitively the most straightforward method, because affected people get compensated for their loss. But it has some serious disadvantages. Firstly, there is information asymmetry between the injured person and the compensating body. In most cases, the claimant knows more or less exactly the amount of damage that has occurred. In order to get as much compensation as possible, including the option of additional income, claimants have an incentive to overstate the damages. The compensating body is therefore faced with the problem that the information provided by the claimant might be wrong. To limit this information asymmetry, most schemes include personal controls by a trained inspector whose confirmation of damages is a precondition for payments. But personal controls on the site are a time-consuming and therefore costly activity. There is evidence that administrative costs can be higher than the costs of the damage itself (Karanth & Madhusudan 2002). However, administrative costs do not arise on one side only. Depending on the requirements, the

making of a claim can also be a very time-consuming activity. To receive compensation for otter damages in the German State of Saxony under the “Regulation for Cases of Hardship”, fishermen have to calculate their marginal return for each pond to prove the difference between the expected and the actual production. In some cases, people refused to claim for compensation because of the high effort involved.

Another problem arises if there is a longer period until payments are made, because this forces the claimants to initially bear the costs by themselves. In Portugal, compensation for damages by wolves may take one year or longer until it is disbursed. Not surprisingly, the acceptance of wolves among farmers is quite low, and illegal killing is an important source of wolf mortality in Portugal.

But the crucial disadvantage of ex-post compensation scheme is the fact that they have no positive influence on the perception of predators. Predator presence in an area is not rewarded, but can lead to damages. Depending on the scheme, compensation may only cover a certain amount of the actual damage, making a claim needs effort, damages may not be confirmed and any longer period between the damage and the payment additionally intensifies the economic hardship. Thus, there is good reason to look for alternative to ex-post compensation.

Payments for Environmental Services

Payments for environmental services are an instrument which offers economic incentives for conservation activities. They honour the creation of environmental goods, including the preservation and the management of different species habitats. In cultural landscapes, these services were originally a “by-product” of traditional land-use forms. For example, the management of extensively used fish ponds also maintains habitats for a large number of aquatic and semi-aquatic species, including the otter. Changing cultivation practices and the abandonment of less-productive areas stopped the random provision of such services in many areas. Because a lot of these environmental goods are considered as beneficial to the society, a mechanism was created to assure their continuity: payments for environmental services (PES). PES imply the need to address the trade-offs between the “provider” and the “consumer” of environmental goods through monetary compensations. Therefore, they offer positive incentives for active conservation because services that used to be outside of market transactions are now included. Thus, the provision of environmental goods becomes part of the normal production cycle. Usually, payments for environmental services are implemented in the form of voluntary contracts between land users and a governmental authority or conservation association. Quite often they are embedded in so-called agri-environment schemes (AES) and run for several years.

Payments for environmental services can be either action-orientated or result-orientated. At present, most schemes use the first approach, where the providers of environmental goods receive money for adopting measures that are prescribed. The amount of money paid is fixed; it is calculated according to the average costs which arise when the measures are carried out. Often a kind of additional “premium payment” is included as an incentive for participation. Land user will participate if the payments provided at least cover their costs for adopting certain measures or even provide an additional profit. Payments are also made for leaving

certain activities undone, such as fertilisation or regular mowing. In these cases, the money is understood as a compensation for the income loss due to the less intensive production.

Action-orientated payments guarantee the service provider an income. Land users have the security that their monetary losses are actually covered, which positively influences their participation. On the other hand, serious disadvantages are associated with this approach. Because the payment is not linked to the intended results, it is uncertain that they are actually reached. However, the money is also spent if the measures fail to reach their aim. Action-orientated payments have therefore been criticised for their limited effectiveness (Kleijn et al. 2001, Kleijn et al. 2006). Against this background, increasing interest has arisen on the practicability of result-orientated payments.

Under the result-orientated approach, payments are tight to a defined outcome, such as the number of certain plant species in a meadow. How the results are reached is not of interest, relevant for paying is only the question if the intended results are actually obtained. This enables more freedom: Every participant can decide according to her or his individual production and costs structures how to act. Different possibilities exist how the amount of payment is calculated. If information on the costs of measures which need to be carried out is available, this can serve as an indicator. Alternatively one can use peoples willingness to pay for a certain outcome as a basis; this needs however an adequate study. Another possibility is to take available funds as given and let potential service providers make their bids. The benefits of the result-orientated approach are obvious: no money is spent for fruitless measures; and instead of being forced to follow pre-defined measures, land users can decide how to obtain the results. But this approach is not without criticism. The results do not entirely depend on the land user; factors such as weather or seed potential can play an important role in the case of plant species. Even more difficult is the case of animal species: fragmentation or disturbance might avoid the colonisation of new created habitats. Thus, in fear of having costs for habitat creation which are not compensated, land users may refuse to participate in result-orientated schemes. But we are convinced that result-orientated payments provide a promising potential to be used for predator conservation and the mitigation of human-wildlife conflicts.

Predator Conservation as an Environmental Service?

When comparing ex-post damage compensation schemes and payments for environmental services, the rationale behind both instruments seems fundamentally different. In the first case, people are compensated for costs without having an influence if they arise or not. In the second case, people are paid for the supply of environmental goods which they can choose to create or not. Thus, we shall call the first a passive instrument and the second an active one. Whereas damage compensation schemes can at best only reach acceptance, PES provide incentives for active conservation support. Why not using this potential to mitigate human-wildlife conflicts?

We have already mentioned that the changed attitudes towards predatory species as well as their conservation status have had an influence on human-wildlife conflicts and their possible solutions. Not only conservationists but a majority of people perceives the occurrence of species likes otters and wolves as an enrichment of today's species composition and therefore beneficial. In this case, predator conservation including the maintenance of their

habitats and the provision of food sources can be seen as an environmental service. Instead of compensating damages, payments are made conditional on wildlife abundance (Ferraro & Kiss 2002). Land users or communities who share their territory with certain species receive a payment for every animal on their property respectively for the successful reproduction of the species. This approach is called performance payments (Nyhus et al. 2005) or compensation in advance (Schwerdtner & Gruber 2007).

The best known example of performance payments comes from Northern Sweden, where Sami reindeer herders receive money for successful wolverine reproduction on their territories (Zabel & Holm-Müller 2007). Similarly, the German State of Saxony employs a measure called “Support of feeding habitats for endangered species”. Mostly used for otters, the “otter bonus” provides payments for fishermen in order to stock ponds with additional fish which is directly understood as otter food. The amount of compensation is based on the potential consumption of resources. The number and distribution of predators is monitored and payments are calculated according to statistical data on consumption. The actual amount of damage has no influence on the payments; it’s the predicted amount that matters.

Thus, compensation in advance avoids the problem of information asymmetry and requires no controls of the individual cases. Precondition is a good data basis; including a species monitoring as well as data on consumption. Collection and updating of such data can evoke significant administrative costs, depending on the methods used. In the long run, the associated costs of such a scheme may still be considerably lower than under ex-post compensation (Schwerdtner & Gruber 2007). Of main importance is the fact that the presence of predators in an area is rewarded; the compensation may even turn into an income if the payments exceed the damages. However, a careful consideration of some factors is crucial for the implementation of performance payments. Firstly, an overlap between the species habitat and a private or common property is important. In cases where the attendance of animals is attached to certain, rather small areas with a single owner, payments can be made to individual beneficiaries. In the example of otters hunting in fish ponds, payments are attached to the pond owner. This is used for the performance payments for otters in Germany. In the case of wide-ranging animals, the question who shall get the reward is far more complicated to answer (Nyhus et al. 2005). In the example of wolverines in Sweden, the reindeer herds consist of animals with different owners and graze on common land. The Swedish government makes payments to the Sami communities, who either distribute the money among individual herders or use it for community purposes. Secondly, a disadvantage of performance payments is that the actual damage costs are not visible. If damages exceed the compensation paid, the system loses its conservation incentives. Thus, a constant population monitoring is needed. Thirdly, compensation in advance makes only sense if damages can be predicted. Species causing damages which vary in time and / or space may therefore not be suitable for performance payments (Schwerdtner & Gruber 2007).

Conclusion

Damage compensation schemes are an important instrument for the mitigation of human-wildlife conflicts. By distributing arising costs more equally in the society, they aim at raising acceptance for predatory species. But despite their extensive use, there is evidence of limited effectiveness of damage compensation schemes. I argue that this is mainly due to their

passive nature. If carried out in an ex-post form, damage compensation schemes lack incentives for an active conservation support. A promising alternative is the use of payments for environmental services. Instead of being compensated for occurring losses, participants receive payments for the existence or successful reproduction of predators on their land. Because these payments are made independently of damages, predator conservation is rewarded as an environmental service.

References

- Ferraro, P. J. & Kiss, A. (2002). Direct payments to conserve biodiversity. *Science*, **298**, 1718-1719.
- Karanth, K. U. & Madhusudan, M. D. (2002). *Mitigating human-wildlife conflicts in Southern Asia*. In Terborgh, J., van Schaik, C., Davenport, L. C. & Rao, M. (Eds.), *Making Parks work: Identifying Key Factors to Implementing Parks in the Tropics* (250-264). Covelo, CA: Island Press.
- Kleijn, D., Berendse, F., Smit, R., Gilissen, N., (2001). Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, **413**, 723–725.
- Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E. J. P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T. M., Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243-254.
- Kruuk, H. 2002. *Hunters and Hunted. Relationships between Carnivores and People*. Cambridge: Cambridge University Press.
- Myšiak, J.; Schwerdtner, K.; Ring, I. (2004). *Comparative analysis of the conflicts between carp pond farming and the protection of otters (Lutra lutra) in Upper Lusatia and South Bohemia*. UFZ-Diskussionspapier, Leipzig: Helmholtz-Centre for Environmental Research.
- Naughton-Treves, L.; Grossberg, R. & Treves, A. (2003). Paying for tolerance: Rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, **17**, 6, 1500-1511.
- Nyhus, P. J., Osofsky, S. A., Ferraro, P., Madden, F. & Fischer, H. (2005). Bearing the costs of human-wildlife conflict: the challenges of compensation schemes. In: Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds.), *People and Wildlife: Conflict or Coexistence?* (106-121). Cambridge: Cambridge University Press.
- Varjopuro, R. (2005). *Grey Seal Conservation and Coastal Fishing in Finland*. In: Jones P. S., Young, J. & Watt, A. D. (Eds.), *Biodiversity conflict management, a report of the BIOFORM project*, 68-69. http://www.maposda.net/bioforum/CMWGV_4.pdf
- Zabel, A. & Holm-Müller, K. 2007. Conservation Performance Payments for Carnivore Conservation in Sweden. *Conservation Biology*, **22**, 2, 247-251.

THE SIGNIFICANCE OF ANTHROPOGENIC IMPACT ON FORAGE PLANT SPECIES RICHNESS IN STRUCTURE OF RUMINANT GUILDS: FOOD BENEFITS OF PASTURES WITH TWO FOREST TYPES

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Abstract

The paper deals with the relationship between species diversity of forage plants and structure of ruminant guilds at different stages of the disturbed communities. A general approach based on comparison of two systems of ruminant ranking, by their forage species richness and by abundance of ruminant species in a community. The number of plant species was considered as several variables regarding to forage value in diet of ruminants. It was found that species structure of the vegetation is at least a one of the conditions which determines the structure of the ruminant guilds. Population density of ruminants whose forage plant sets are more diverse is larger. The total number of forage plant species has a decisive significance, but not number

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of the most significant species. Anthropogenic disturbance of vegetation and change of plant species richness support change in structure of ruminant guilds.

Key words: species diversity, plant-animal interaction, ruminants, community

The Significance of Anthropogenic Impact

The species abundance distribution is in top ten questions of community ecology (Chesson, 2000; Adler et al., 2007; McGill et al., 2007; Alonso et al., 2008). One of the important and actively investigated topics in this field is why similar species in the space of apparently unseparated environment are different in abundance? We support common tendency to consider the community structure by simpler examples, i.e. one trophic level communities, which were most studied (Giljarov, 2007). Functionally similar species that are regarded as guilds after Root (1967) are especially interesting. But the polyphony of hypotheses, neutral-niche dilemma, and absence of the conventional view about community structure provide only one way of the question improving for the present. It is selection of several widest distributed and carefully investigated kinds of community whose pattern of the species distribution can shape at least our own view. Associated with vegetation ruminant guild is the most prominent example of such communities (Illius, O'Connor, 2000).

Quantitative parameters of trophic resource, i.e. mass and energy content, has a primary significance for consumer (Wecker, 1994; Bergman et al., 2001; Barancekova, 2004), but initially necessary that qualitative data should be accessible. Species diversity is a one of the most important qualitative parameters of resource (Picasso et al. 2008).

Evidences of the dependence of consumer population on resource diversity are numerous (Bardgett, Shine, 1999; Wilsey, Potvin, 2000; Watkinson, Ormerod, 2001; Tracy, Sanderson, 2000; Tracy, Faulkner, 2006; Griggs, 2007), and the positive correlation between diversity and stability of communities was accepted as axiom (Frank, McNaughton, 1991; Brummer, 1998; Onoprienko, 1998). Why data about resource diversity can not be used for explanation of structure of consumer guilds? Choice of the approach is essential to the success. Plant species diversity usually refers to the number of species (richness) and their relative abundance (evenness) within a defined area (Sanderson et al., 2004). But attention to the evenness after richness is the attempt to be focused on the structure of resource by another formal criterion which again ignores the forage value of plant species in the ruminant species diets.

Technological progress is accompanied by disturbance of wildlife environment and, eventually, of human environment. On the one hand, this causes urgency of the investigation of action mechanism and effect of transforming factor (Bailey et al., 1996; Focardi et al., 1996; Fortin et al., 2003), on the other hand, anthropogenic impact provide us by live experimental data, i.e. chronological consequences of vegetation and ruminant guild modifications.

The goal of the study is to assess the dependence of the ruminant species abundance on the structured by forage value species richness of forage vegetation in the process of anthropogenic disturbance. We initially follow the resource hypothesis framework (McKane et al., 2002) and a priori believe that even unseparated resource can be structured in the consumption aspect.

Materials and Methods

Habitat with the oak and Korean pine forests in the east end of Temperate Asia are selected as an object of study. These forests are dominant vegetation types of habitats of ruminants at the joints of Russian Far East, Korea, and northeastern China (Kurentsova, 1973; Dobrynin, 2000). There are three associated with these habitat types ruminant species: Siberian roe deer *Capreolus pigargus* Pall., red deer *Cervus elaphus* L., and sika deer *Cervus nippon* Temm. (Ellerman, Morrison-Scott, 1951; Danilkin, 1999; 2005). Common check list of forage plants include 805 species (Sheremetyev, Prokopenko, 2005; 2006). Three stages of habitat disturbance were studied: 1 – with partly felled main tree species; 2 – with completely felled main trees, but with saved accompanying tree species; 3 – open habitats (Kurentsova, 1973). Fire (oak forest) and tree felling (Korean pine forest) are considered as main factors of habitat disturbance.

General Approach

Principal way of analysis consists in comparison of two ranking systems of ruminant species. On the one hand, ruminants are ranked in order of increasing species richness of forage vegetation, and, on the other hand, in order of increasing abundance. It is proposed that if population density increases together with their food benefits the structure of ruminant guilds is formed by the structure of vegetation. The comparison of habitats on different stage of vegetation disturbance with undisturbed ones (references) reflects of anthropogenic impact, i.e. changes of ruminant population that occurring on our eyes may be explained by the effect of vegetation transformation in aspect of species richness change.

Measurements and Statistical Procedure

Data set of population density (individuals per 10 sq km) was applied for ranking of ruminant species by abundance. The data was provided by the Far Eastern Branch of the B.M. Zhitkov Russian Hunt and Animal Breeding Research and Development Institute, Khabarovsk. Relevés of forage plant species from 2000 sq m plots in every habitat type were used for second ranking, which was made thought the annotated diets of ruminant species, i.e. the numbers of plant species were calculated according to their forage significance for every ruminant species. A most detailed five-grade scale of forage value was presented (Prisjagruk, Prisjagruk, 1974; Bromley, Kucherenko, 1983; Sheremetyev, Prokopenko, 2006): 1st grade - ballast food plants, which actually do not provide even small forage needs; 2nd grade - plant species with small nutritive value; 3rd grade - plant species with influential nutritive value, but without full supply of routine needs; 4th grade - plant species, which actually do provide routine needs; 5th grade - most significant plant species, which did promote fat accumulation. Assuming that ruminants utilize plants according to forage value grades we believe that 5th grade plants will be utilized in the first place, then 4th grade plants, and so on. Therefore the numbers of plant species in every habitat type were calculated using this method: number of 5th grade plant species, summary

number of species in 4th and 5th grades, summary number of species in 3rd, 4th, and 5th grades, and so on.

The matrices with data set were formed as well as Levins's community matrixes (Levins, 1968). Spearman correlation coefficient was used to estimate degree of correspondence of two rankings. All statistical procedures were performed using the Statistica 8.0 software for Windows StatSoft, Inc. (2007).

Results

Structure of Ruminant Guilds

Population density of ruminant species in reference habitats is in Fig. 1. The anthropogenic disturbance resulted in an increase in the population density of the sika deer to 141 individuals per 10 sq km in habitats with pine forests and to 146 individuals in habitats with oak forests. The population density of the red and roe deer is decreased. In the interpenetration zone of the red, roe, and sika deer, the former two species disappeared. Thus, in both undisturbed and transformed habitats, the sika deer, roe deer, and red deer were ranked #3, #2, and #1, respectively. Red deer has greater rank than roe deer though zero-order population density of both species in habitats with disturbed vegetation because it is known that roe deer was excluded firstly (Sheremetyev, Prokopenko, 2005).

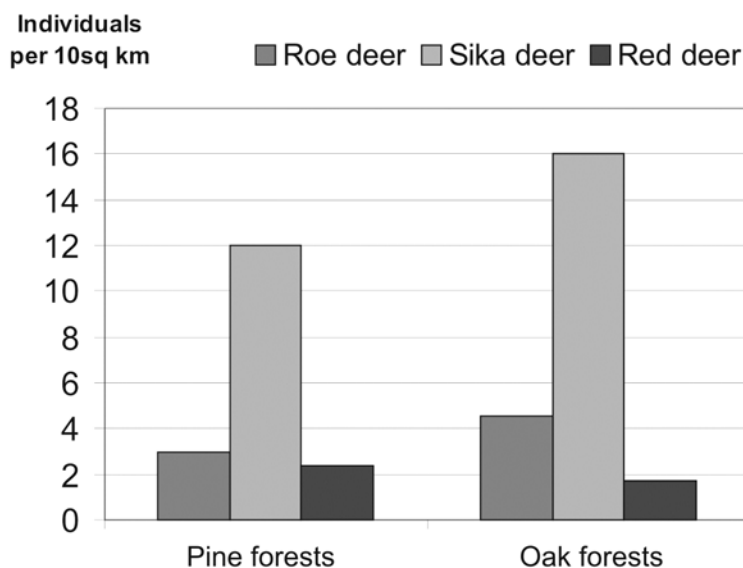


Figure 1. Population density of ruminant species in undisturbed habitats

The number of forage plant species.

An essential decrease of numbers plant species is a common trait of all ruminant/grade cases in 1st stage of disturbance with respect to reference. General difference between both

types of habitat arise on second stage, when the number of plant species may even exceed some reference values or decrease with lesser rate (oak and pine forest, Fig. 2 and 3 consequently).

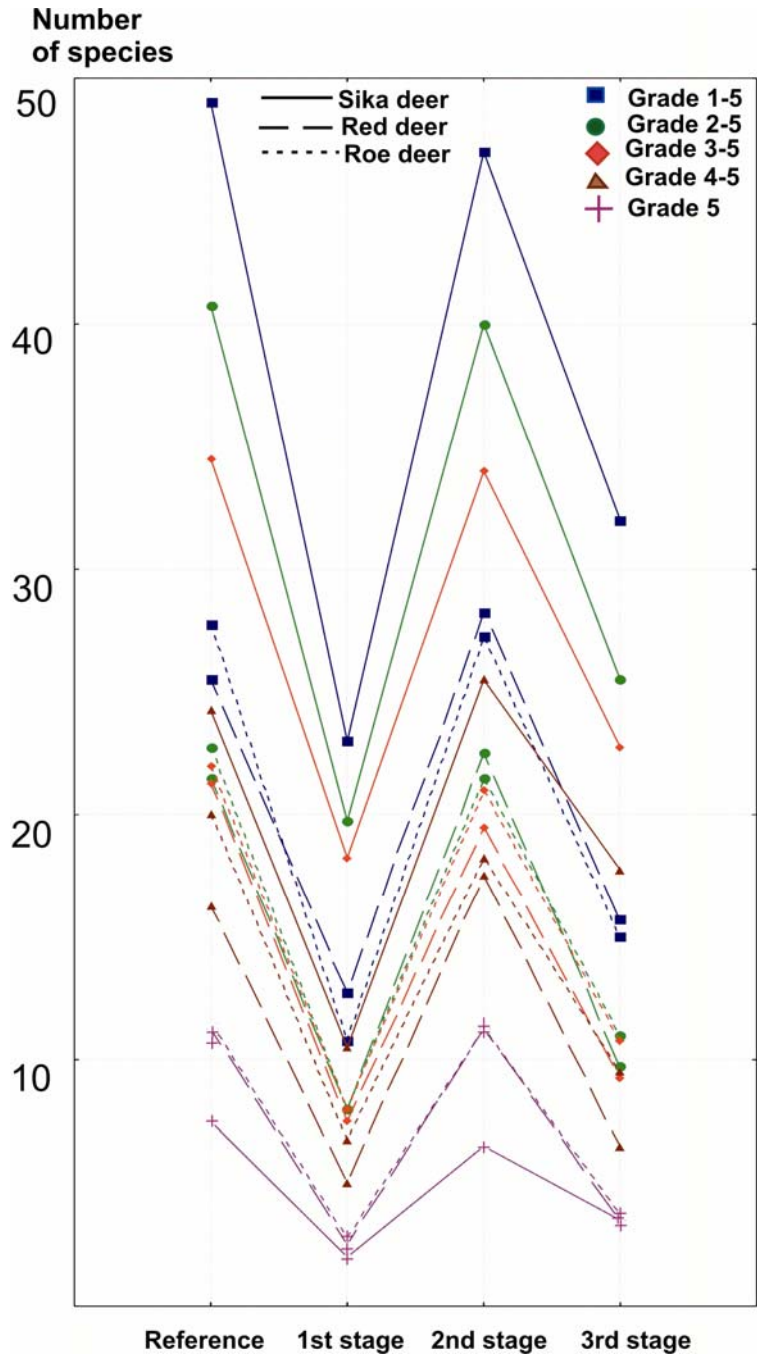


Figure 2. Anthropogenic impact on number of forage plant species in habitats with the oak forests.

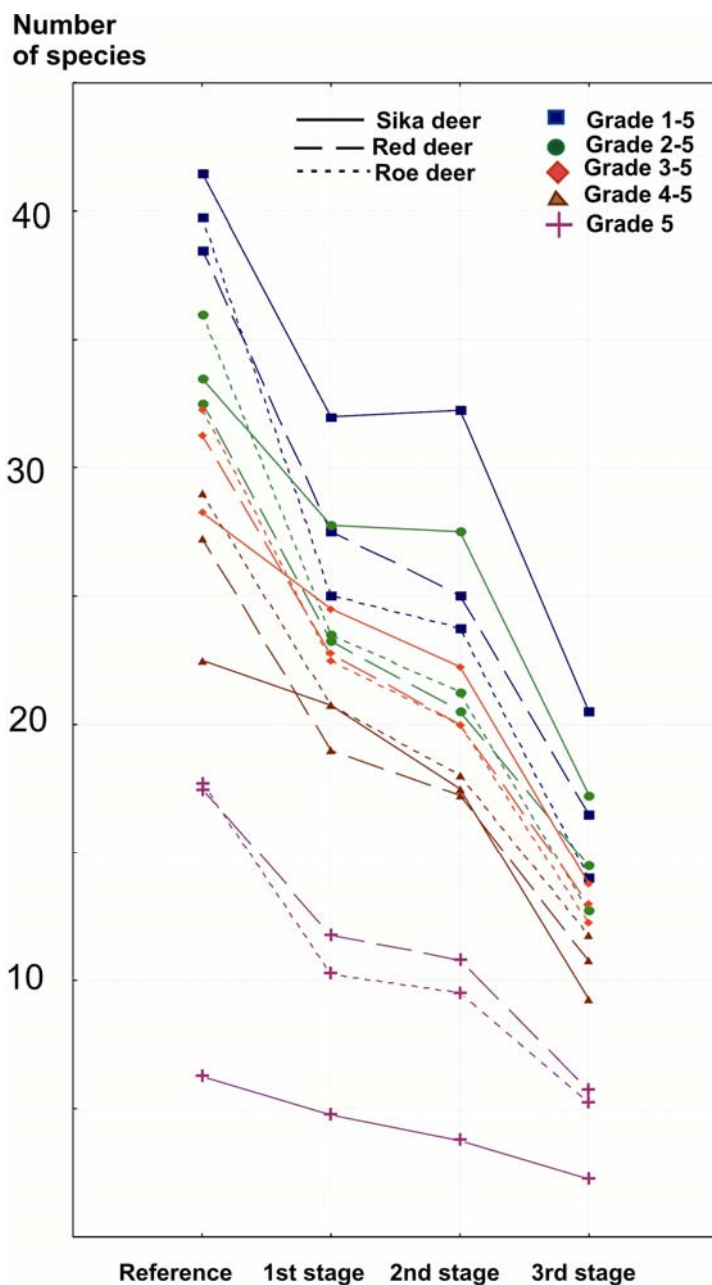


Figure 3. Anthropogenic impact on number of forage plant species in habitats with the Korean pine forests.

Ranks of Ruminants in Order of Plant Species Richness.

Rankings of ruminant species by their forage plant species richness are in table 1. Sika deer have benefice in respect of the total number of plant species in both reference habitat

Table 1. Ranks of ruminant species in order of increasing species richness of forage vegetation

	Pine forest			Oak forest		
	Roe deer	Sika deer	Red deer	Roe deer	Sika deer	Red deer
Reference	1-5	2	3	1	2	3
habitats	2-5	3	2	1	2	3
	3-5	3	1	2	2	3
	4-5	3	1	2	2	3
	5	3	1	2	3	1
1st stage	1-5	1	3	2	1	3
	2-5	2	3	1	2	3
	3-5	1	3	2	2	3
	4-5	2	3	1	2	3
	5	2	1	3	3	1
2nd stage	1-5	1	3	2	1	3
	2-5	2	3	1	1	3
	3-5	1	3	2	2	3
	4-5	3	2	1	2	3
	5	2	1	3	2	1
3rd stage	1-5	1	3	2	1	3
	2-5	2	3	1	2	3
	3-5	1	3	2	2	3
	4-5	3	1	2	2	3
	5	2	1	3	3	2

types, but roe deer prevail by the number of most significant plants. As disturbance is increased sika deer gain the benefice in respect of the number of species at others forage value grades, but no in most significant species. Roe deer have a smallest rank in respect of the total number of plant species in habitats with disturbed vegetation.

Spearman correlation coefficient. A common trait of both habitat types is a decrease of correlation coefficient (almost without exclusion) to the statistically significant negative values along the increase of forage value grade. Habitats with undisturbed Korean pine forest are characterized by absence of significant positive correlation between ruminant population density and number of plant species at all forage value grades excluding last with the total number (table 2).

Table 2. Spearman correlation between ruminant population density and number of plant species

Pine forest				
	Reference habitats	1 stage	2 stage	3 stage
Grade 1-5	0,503953	0,875000***	0,750000**	0,944911***
Grade 2-5	0,355023	0,750000**	0,692935*	0,645689*
Grade 3-5	-0,472456	0,625000*	0,267725	-0,417016
Grade 4-5	-0,472456	0,000000	-0,096825	-0,519701
Grade 5	-0,875000***	-0,500000	-0,288675	-0,614192*

Oak forest				
	Reference habitats	1 stage	2 stage	3 stage
Grade 1-5	0,875000***	0,903696***	0,875000***	0,755929**
Grade 2-5	0,818923**	0,692935*	0,875000***	0,409462
Grade 3-5	0,750000**	0,692935*	0,645497*	0,409462
Grade 4-5	0,944911***	0,283473	0,692935*	0,425210
Grade 5	-0,640490*	-0,649519*	-0,414039	0,204124

*Statistical significance $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Discussion

Main point of change in structure of ruminant guilds which accompany with anthropogenic vegetation disturbance is that guild from three consumers with comparatively moderate population density eventually turn into guild with one consumer, which increased many times.

Trends of changes of species richness at all forage value grades suggest that in spite of lesser anthropogenic impact 1st stage of the oak forest disturbance has a more significant influence for pasture then the following stages. The falling of richness in 1st stage of the pine forest disturbance is a smaller than one in the oak forest, but differences between 1st and 2nd stage at any grade/ruminant cases are smaller than between 1st stage and reference. Some stabilization of the number of species in the pine forest and increase one in the oak forest in 2nd stage relatively 1st stage are probably explained by the immigration of new plant species. Probably these differences may be explained by the matter of the anthropogenic factor (fire vs. tree felling), locality of the pine forest in further north latitudinal zone, and neighborhood

with the oak forests of resource of the new plant species, which successfully occupy the disturbed fragments. A priori, we don't know precisely in which stage ruminant guilds were changed, but in accordance with these data this may be already in 1st stage. If it is does so any attempts of ruminant population restoration even at initial stage of habitat disturbance will have fatal error, i.e. original structure of guilds is non-renewable or may be kept only artificially until original structure of the vegetation is unrenewed for at least these habitat types.

Sika deer in habitats with original Korean pine forests are in preference only in respect of the total number of plant species. This may explain why population density of this species in this habitat type is lesser than in other. Number of plant species at all stages in both disturbed habitat types provide preference to sika deer at all grades excluding one or two with most forage value. Red deer are in preference over roe deer in respect of the total number of plant species (table 1), i.e. this parameter must signify more than another.

The results of correlation analysis suggest that influence of the number of plant species on population density of ruminants commonly increase with the addition of the little value plants, and the number of most significant plants makes no difference to structure of guild (tabl. 2).

Sika deer gain considerable advantage such as more diverse pastures in habitats with the pine forest only after vegetation disturbance. These advantages in habitats with the oak forest occur ad origin, and disturbance impact is expressed in terms of decrease of the plant species number especially for others ruminants, but no ranking change.

Finally, it may be asserted that structure of resource is at least one of the circumstances, which determine structure of consumer guilds. Population density of species, which are provided by more diverse forage, is more. Species richness of most valuable forage has not the decisive influence on guilds, but the total number of forage species is important.

Acknowledgements

We thank to Dr. S.V. Prokopenko of the Institute of Biology and Soil Science of FEB RAS (Vladivostok, Russia) for his helpful contribution in this topic.

References

- Adler P.B., HilleRisLambers J., Levine J.M. 2007. A niche for neutrality. *Ecol. Let.* **10** (2): 95-104
- Alonso D., Ostling A., Etienne R.S., 2008. The implicit assumption of symmetry and species abundance distribution. *Ecol. Let.* **11**(2): 93-105.
- Bailey D.W., Gross J.E., Laca E.A., Rittenhouse L.R., Coughenour M.B., Swift D.M., Sims P.L., 1996. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manage.* **49**: 386-400.
- Barancekova M., 2004. The roe deer diet: Is floodplain forest optimal habitat? *Folia Zool.* **53**: 285-292.
- Bardgett R.D., Shine A., 1999. Linkages between plant diversity, soil microbial biomass, and ecosystem function in temperate grasslands. *Soil Biol Biochem.* **31**: 317-321.

- Bergman C.M., Fryxell J.M., Gates C.C., Fortin D., 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* **70** (2): 289-300.
- Bromley G.F., Kucherenko S.P., 1983. Ungulate animals of USSR Far East. *Moscow: FESC AS of USSR.*
- Brummer E.C., 1998. Diversity, stability, and sustainable American agriculture. *Agron J.* **90**: 1-2.
- Chesson P., 2000. Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.* **31**: 343-366.
- Danilkin A.A., 1999. *Deer (Cervidae)*. Moscow: GEOS.
- Danilkin A.A., 2005. *Hollow-horned ruminants (Bovidae)*. Moscow: KMK Press.
- Dobrynin A.P., 2000. *Oak forests of Russian Far East*. Vladivostok: Dalnauka Press.
- Ellerman J.R., Morrison-Scott T.C.S., 1951. Checklist of Palearctic and Indian mammals 1758 to 1946. *London: British Museum.*
- Focardi S., Marcellini P., Montanaro P., 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *J. Anim. Ecol.* **65**: 606-620.
- Fortin D., Fryxell J.M., O'Brodovich L., Frandsen D., 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. *Oecologia*. **134**: 219-227.
- Frank D.A., McNaughton S.J., 1991. Stability increases with diversity in plant communities: Empirical evidence from the 1988 Yellowstone drought. *Oikos*. **62**: 360-362.
- Giljarov A.M., 2007. From niches to neutrality in biological community. *Priroda*, **11**: 29-37.
- Griggs T. C., 2007. Introduction to the CSSA Symposium - Beyond the Plant: Biodiversity Impacts on the Grazing Animal. *Crop Sci.* **47**: 380-381.
- Illius A.W., O'Connor T.G., 2000. Resource heterogeneity and ungulate population dynamics. *Oikos*. **89**: 283-294.
- Kurentsova G.E., 1973. Natural and anthropogenic changes of vegetation in Primorie and Southern Priamurie. *Novosibirsk: Nauka Press.*
- Levins R., 1968. *Evolution in changing environment*. Princeton: Princeton University Press.
- McKane R.B., Johnson L.C., Shaver G.R., Nadelhoffer K.J., Rastetter E.B., Fry B., Giblin A.E., Kielland K., Kwiatkowski B.L., Laundre J.A., Murray G., 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*. **415**: 68-71.
- McGill B.J., Etienne R.S., Gray J.S. et al., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework // *Ecol. Let.* **10**(10): 995-1015.
- Onoprienko Y.I., 1998. *Biological informational systems*. Vladivostok: Dalnauka.
- Picasso V.D., Brummer E.C., Liebman M., Dixon P.M., Wilsey B.J., 2008. Crop Species Diversity Affects Productivity and Weed Suppression in Perennial Polycultures under Two Management Strategies. *Crop Sci.* **48**: 331-342.
- Prisjagruk N.P., Prisjagruk V.E., 1974. Forage plants through taxa, life forms, and seasons. *Frunze: Kyrgyzstan Press.*
- Root R.B., 1967. The niche exploitation pattern of the blue-gray gnatcatcher // *Ecol. Monogr.* **37**: 317-350.
- Sanderson M.A., Skinner R.H., Barker D.J., Edwards G.R., Tracy B.F., Wedin D.A., 2004. Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Sci.* **44**: 1132-1144.

- Sheremetyev I.S., Prokopenko S.V., 2005. Feeding ecology of Far Eastern ungulates. *Vladivostok: Dalnauka Press*.
- Sheremetyev I.S., Prokopenko S.V., 2006. General analysis of forest vegetation in the south of the Far East with regard to the feeding of wild ruminants (*Artiodactyla*, *Ruminantia*). *Russ. J. Ecol.* **37**: 217-224.
- Tracy B.F., Sanderson M.A., 2000. Patterns of plant species richness in pasture lands of the Northeast United States. *Plant Ecol.* **149**: 169-180.
- Tracy B.F., Faulkner D.B., 2006. Pasture and Cattle Responses in Rotationally Stocked Grazing Systems Sown with Differing Levels of Species Richness. *Crop Sci.* **46**: 2062 - 2068
- Watkinson A.R., Ormerod S.J., 2001. *Grasslands, grazing and biodiversity*: Editors' introduction. *J Appl. Ecol.* **38**: 233-237.
- Wecker F.W., 1994. *Selective feeding by black-tailed deer - forage quality or abundance*. *J. Mamm.* **75**: 905-913.
- Wilsey B.J., Potvin C., 2000. Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology.* **81**: 887-892.

INDEX

A

- Abies alba*, 5, 36
abiotic, xii, 5, 12, 239, 240, 241, 242, 244, 246, 247
Abiotic, 247
abnormalities, 198
abortion, 44, 188
absorption, 31, 121, 123, 186
Abundance, 75
Academic Search Premier, 108
access, 21, 51, 53, 69, 78, 82, 83, 84, 85, 86, 87, 101, 102, 108, 240, 285, 286, 320
accessibility, 302
accidental, 81, 103
accommodation, 282
accuracy, 303, 304
achievement, 95
acid, 41, 210
acidic, 221
acidification, 202
acidophilic, 17
ACS, 196
activation, 204
acute, 16, 183, 296, 297
Adams, 52, 90, 176, 198
adaptation, xii, 23, 24, 178, 225, 230, 239, 240, 241, 242, 247, 248
adduction, 188
adducts, 190, 199
administration, 215, 259
administrative, 327, 330
adsorption, 184
adult, 7, 8, 11, 19, 22, 26, 37, 131, 187, 188, 200, 231, 235, 248, 250, 252, 259
adults, 8, 79, 184, 186, 233
advertisements, 258
advertising, 280
Africa, viii, 53, 54, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 106, 107, 108, 109, 321
afternoon, 269
agar, 210
age, ix, xiv, 8, 10, 18, 19, 21, 22, 23, 30, 46, 50, 112, 131, 183, 186, 234, 242, 246, 250, 255, 293, 313, 316, 317, 327
agent, 24, 26, 186, 188, 190, 191, 232
agents, viii, xi, 4, 16, 17, 24, 25, 26, 189, 190, 202, 210, 213, 214, 219
aggression, 19, 21, 22, 37
aggressive behavior, 18, 19, 21
agricultural, x, 7, 8, 14, 35, 37, 41, 54, 55, 59, 63, 68, 70, 72, 77, 78, 84, 85, 94, 106, 131, 182, 185, 194, 195, 196, 206, 213, 215, 281, 282, 299, 309, 326, 331
agricultural crop, 14
agriculture, x, 50, 52, 53, 57, 59, 62, 63, 64, 66, 68, 77, 78, 79, 82, 83, 84, 85, 86, 87, 95, 181, 182, 183, 184, 193, 194, 206, 214, 215, 272, 281, 282, 315, 342
aid, 103, 269
air, x, 5, 15, 55, 181, 182, 205, 299
air pollution, 5
Alaska, 231
Alberta, 37
alertness, 225, 233, 236
alkali, 189
alkaline, 55, 195, 198
allies, 103
Alps, 245
alternative, x, 29, 38, 50, 51, 82, 182, 189, 232, 282, 323, 328, 331
alternatives, 85, 309
Amazon, 314
amino, 184
aminoglycosides, 215
amphibia, 242, 243, 251
amphibians, 187, 188, 189, 196, 202
anaerobes, 204
anaerobic, 204
androgen, 19
Angola, 100, 104
animal health, x, 201
animal welfare, 270
animals, vii, x, xi, xii, xiii, xiv, 3, 4, 7, 8, 11, 12, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 26, 29, 39, 50, 59, 65, 78, 81, 82, 86, 132, 182, 183, 184, 185,

186, 190, 192, 193, 200, 201, 202, 203, 204, 205, 213, 214, 216, 217, 220, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 234, 235, 237, 239, 243, 252, 253, 255, 270, 271, 272, 279, 281, 294, 295, 296, 297, 298, 299, 316, 317, 318, 320, 321, 322, 325, 330, 342

annuals, 124, 248

ANOVA, 246

antagonistic, 183

Antarctic, 241, 244, 245, 278

anthropogenic, 249, 334, 335, 336, 340, 342

antibiotic, x, 201, 204, 215, 216, 219, 220

antibiotic resistance, 215, 216, 219, 220

antibody, 25, 30

anticoagulant, 16, 33

anticoagulants, 16, 17, 28, 30, 38

antigen, 204

ants, 136, 176, 327

anxiety, xi, 223, 224, 225, 228, 229, 231

API, 210

application, xiv, xv, 16, 88, 183, 189, 190, 193, 194, 200, 215, 302, 310, 325

aquaculture, 202

aquatic habitat, 202

aquatic habitats, 202

aquatic systems, xi, 202

Arctic, 240, 245, 251, 252

Argentina, 181, 184, 185, 186, 195, 197

argument, 326

arid, 55, 79, 96, 252

arithmetic, 297

Arizona, 92, 97, 109, 235

Arizona State University, 97, 109

armed conflict, viii, 97, 98, 101, 102, 103, 104, 106, 108, 109

asexual, 178

ash, 9, 10, 131

Asia, 202, 256, 262, 311, 331, 335

Asian, xii, 253, 254, 255, 259, 266, 267, 268, 271, 272, 273, 274, 275

assessment, x, xii, 54, 93, 94, 98, 109, 182, 183, 187, 188, 198, 218, 240, 274, 279, 310, 312, 322, 323

assets, 288

assimilation, 31

assumptions, 161, 310

asymmetry, 327, 330

asymptotic, 143, 147, 148, 150, 152, 177

asymptotically, 138, 143, 147, 150, 153

Atlantic, 241, 244, 245, 249, 250, 251

Atlas, 93, 219

atrocities, 104

attacks, 10, 233, 314, 316, 317

attitudes, xii, 90, 92, 253, 254, 255, 260, 274, 329, 331

Australia, 92, 124, 130, 253, 261, 275, 277, 280, 290, 312

Austria, 43, 261, 326

authority, 105, 258, 320, 328

autocorrelation, 29, 304

autopsy, 300

availability, 19, 22, 28, 86, 93, 96, 100, 186, 206, 217, 220, 226, 231, 241, 248, 254

average costs, 328

aversion, 17, 231, 232, 233, 235, 237

avoidance, 19, 21, 84, 122, 123, 126, 227, 228, 231, 232, 235, 236

avoidance behavior, 227

awareness, 104, 105, 314

B

baby boom, 251

Bacillus, 178

Bacillus subtilis, 178

bacteria, xi, 25, 30, 136, 176, 177, 179, 201, 202, 204, 205, 207, 210, 213, 214, 215, 216, 218, 220

bacterial, x, xi, 16, 136, 201, 202, 203, 204, 205, 211, 213, 214, 215, 216, 219

bacterial strains, 204, 205, 214

bacteriophages, 204

bacterium, 204

Bali, 311

ballast, 335

banks, ix, 111, 113, 114, 124, 125, 126, 127, 131, 132, 133

barrier, 62, 144

barriers, 79

base pair, 218

battery, 280

beef, 51, 79, 80, 82

beetles, 42

behavior, x, xi, 9, 13, 15, 16, 17, 18, 19, 21, 22, 35, 39, 124, 135, 153, 159, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 234, 235, 236, 237, 251, 252, 302, 314

Belgium, 35

bell, 51

benefits, ix, xiii, 51, 52, 77, 79, 83, 85, 88, 95, 98, 99, 101, 102, 104, 135, 175, 183, 185, 277, 279, 283, 287, 288, 329, 331, 335

bias, 82, 264

bifurcation, 136, 139, 140, 149, 150, 159, 160, 170, 171, 172, 173, 174, 177

bile, 210

binding, 87, 197

biodiesel, 272

biodiversity, vii, viii, x, xiii, 17, 52, 53, 54, 87, 92, 94, 95, 97, 98, 99, 100, 102, 103, 104, 107, 108, 109, 112, 113, 182, 188, 195, 203, 240, 249, 277, 278, 281, 282, 286, 287, 288, 331, 343

biogeography, 53, 54

biological control, 12

biological responses, 186

biomarker, 186, 187, 188, 190

biomarkers, x, 182, 186, 187, 188, 189, 194, 197

biomass, 12, 13, 202, 316, 318, 323, 341

biomolecules, 189

biomonitoring, 194, 195
 biosphere, 236
 biota, 194
 biotic, xii, 4, 5, 12, 23, 239, 240, 241, 242, 244, 246, 247, 248
 biotic factor, 4, 5, 12
 birds, 14, 28, 136, 187, 188, 190, 200, 202, 205, 213, 226, 242, 251, 252, 280, 293, 294, 295, 297, 298, 299, 300, 310, 311
 birth, 100, 137, 142, 143, 144, 164, 168, 170, 174, 188, 190, 193, 317, 318
 birth rate, 100, 137, 143, 144, 164, 168, 170, 174
 birth weight, 188
 births, 202, 316, 317, 318
 bison, 342
 bleeding, 16
 blocks, 53, 83, 88
 blood, 16, 26, 35, 45, 187, 190, 191, 195, 198, 200, 204, 205, 213
 blood collection, 190
 blood vessels, 16
 body size, 192, 240, 242, 248
 body weight, 20, 188, 248
 Bolivia, 200
 bone marrow, 199
 bonus, 330
 Borneo, 272, 275
 Borrelia infection, 27
 borreliosis, vii, viii, 3, 4, 24, 26, 27, 33, 35, 41, 43, 44, 45
 Bosnia, 39
 Botanical Garden, 254
 Botswana, 83
 bounds, 136, 162
 bovine, 199, 219, 316, 318
 Brazil, xiv, 195, 299, 313, 314, 315, 320, 321, 322, 323
 Brazilian, xiv, 236, 313, 315, 317, 319, 320, 321, 323
 breakdown, 101, 117
 breeder, 252
 breeding, 8, 9, 10, 11, 12, 14, 15, 17, 18, 19, 20, 21, 24, 43, 45, 46, 184, 185, 241, 247, 251, 254, 255, 271, 283, 299, 302, 305, 310, 320
 Britain, 46, 130, 221
 broilers, 217
 browsing, 232
 Buenos Aires, 195
 buffer, 125
 Bulgaria, 7, 220
 bushes, 8, 9
 bushmeat, 51, 78, 101, 105, 106, 108
 butterfly, 250

C

cabbage, 178
 cadmium, 293, 296, 299, 300

Caenorhabditis elegans, 136
 calcium, 300
 calving, xiv, 313
 Canada, 178, 196, 217, 239, 244, 245, 249, 261
 cancer, ix, 135, 136, 188
 CAP, 281
 capacity, 85, 102, 106, 112, 126, 137, 198, 205, 256, 272, 286, 288
 Capacity, 39
 carcinogenic, 183
 carefulness, 225, 229, 231
 Caribbean, 274, 322
 case study, 93, 94, 274, 275, 311
 castration, 33
 categorization, 119, 310
 cats, xiv, 281, 313, 314, 316, 317, 318, 319, 320, 321, 323
 cattle, xi, xiv, 50, 59, 64, 74, 80, 202, 215, 216, 217, 237, 278, 281, 313, 314, 316, 317, 318, 319, 320, 321, 322, 323
 causality, 228
 cell, xi, 186, 188, 189, 190, 195, 198, 200, 201, 204, 214, 218
 Census, 95
 Central Europe, 26, 244, 245
 Chad, 99
 changing environment, 342
 chaos, 300
 charcoal, 78, 79
 chemical agents, 16, 17, 186
 chemical composition, 9
 chemicals, x, 78, 181, 182, 183, 187, 188, 195
 Chemotherapy, 217, 218, 221
 children, 50, 53, 56
 China, 198, 261, 275, 323, 335
 Chi-square, 64, 316
 chloride, 210
 chromium, 293
 chromosome, 188
 chromosomes, 189
 circulation, 12
 citizens, 331
 civil society, viii, 97, 109
 civil war, 99, 100, 101, 105, 109
 clams, 284
 classes, xi, 142, 186, 191, 201
 classical, 135, 141, 142, 144, 151, 230
 classification, xiii, 116, 128, 294
 clay, 9
 climate change, xii, 239, 240, 241, 242, 247, 248, 249, 251, 252, 310
 climate warming, 240, 242, 248, 250
 climatic factors, 184
 clinics, 51
 clonality, 216
 clouds, 55
Clupea harengus, 241
 clusters, viii, 49, 59, 62, 64, 68, 72, 76, 83, 84, 85, 86, 87, 89, 281

- CO₂, 122, 133
 coagulation, 16
 coastal areas, 202, 203
 coconut, 255
 cocoons, 12
 co-existence, 177
 cognitive, 225
 cognitive performance, 225
 cohesion, 287
 Coke, 74, 75
 collaboration, 27, 105
 collateral, 53, 82, 108
 collateral damage, 108
 colleges, 263
 colonisation, 129, 329
 Colorado, 234, 245, 252
 colors, 130
 commensalism, 135, 136
 commercialization, 186
 commercials, 258
 commodity, 280, 287
 communication, 32, 39, 52, 105, 116, 284
 communities, ix, xv, 29, 32, 34, 37, 47, 51, 52, 53, 77, 82, 88, 94, 107, 128, 129, 131, 135, 178, 286, 287, 330, 333, 334, 342
 community, vii, xv, 3, 4, 23, 34, 35, 38, 52, 53, 65, 79, 84, 85, 86, 87, 88, 90, 91, 95, 96, 107, 132, 187, 188, 217, 258, 260, 271, 286, 287, 330, 333, 334, 336, 342
 compaction, 81
 compensation, xiv, xv, 52, 88, 105, 323, 325, 326, 327, 328, 329, 330, 331
 competence, 16
 competition, 11, 13, 28, 31, 32, 51, 78, 80, 81, 83, 121, 130, 137, 142, 143, 144, 152, 161, 168, 170, 174, 240, 326
 competitiveness, 22
 competitor, 77, 177
 complexity, xiv, 313, 321
 components, x, 138, 146, 147, 175, 182, 184, 225, 226
 composition, 9, 79, 80, 125, 126, 127, 176, 218, 329
 compounds, x, xi, 16, 17, 187, 189, 201, 204, 205, 211, 214, 215
 computer simulations, 153
 concentration, 17, 50, 53, 55, 57, 61, 68, 79, 82, 83, 122, 133, 191, 192, 197, 297, 299, 300
 concrete, 24, 65, 98, 265, 266
 conditioning, 232, 235, 237
 conductive, 122
 confidence, 246
 confinement, 64
 conflict, 88, 95, 98, 100, 101, 102, 103, 105, 107, 108, 109, 129, 237, 259, 269, 270, 281, 314, 320, 321, 323, 331
 confrontation, 19
 conifer, 37, 42, 45
 coniferous, 9, 29, 30, 39
 consensus, 83, 86, 280
 conservation, vii, viii, ix, x, xi, xii, xiii, xiv, xv, 5, 34, 37, 49, 50, 51, 52, 53, 77, 78, 83, 84, 85, 86, 88, 89, 90, 91, 92, 94, 95, 96, 97, 98, 99, 102, 103, 104, 105, 106, 107, 108, 109, 111, 113, 125, 182, 185, 188, 196, 202, 203, 213, 216, 218, 219, 235, 236, 253, 254, 255, 259, 260, 266, 267, 268, 270, 271, 273, 274, 275, 277, 278, 279, 280, 281, 283, 284, 285, 287, 288, 289, 301, 302, 309, 310, 311, 312, 313, 314, 316, 320, 321, 322, 323, 325, 326, 327, 328, 329, 330, 331
 constraints, xiii, 57, 78, 113, 124, 125, 138, 242, 277, 288
 construction, 79, 80, 81, 202, 206
 construction materials, 79
 consumers, xii, 103, 104, 239, 264, 340
 consumption, 16, 22, 23, 35, 45, 206, 213, 229, 251, 330, 334
 contaminant, x, 182, 184, 188, 194, 219
 contaminants, x, 182, 184, 187, 188, 195, 196
 contamination, x, xiii, 182, 184, 185, 190, 194, 201, 205, 213, 215, 216, 219, 293, 294, 296, 297, 298, 299, 300
 continuity, 140, 259, 328
 contracts, 83, 146, 328
 control, xiv, 22, 23, 28, 33, 35, 40, 41, 86, 87, 101, 102, 105, 106, 129, 131, 132, 182, 183, 184, 187, 191, 192, 193, 194, 235, 281, 285, 286, 288, 313, 314, 319, 326
 Convention on International Trade in Endangered Species, xiii, 186, 301, 302
 conversion, 77, 83, 115, 249, 309
 cooling, 55
 coordination, 233
 copper, 299, 300
 copulation, 17, 184
 corn, 182
 correlation, 13, 21, 22, 25, 64, 74, 103, 124, 217, 221, 316, 317, 318, 336, 339, 340, 341
 correlation analysis, 341
 correlation coefficient, 316, 336, 339
 correlations, 64, 102, 103, 130
 corridors, 8, 10, 17, 49, 53, 55, 79, 82, 84, 85, 86, 87, 88, 93
 corruption, 98
 Costa Rica, 136, 177
 cost-benefit analysis, 279
 costs, xiii, xiv, 50, 51, 52, 85, 94, 102, 195, 196, 262, 268, 271, 277, 325, 326, 327, 328, 329, 330, 331
 cotton, 182
 Council of Europe, 219
 covalent, 189
 covalent bond, 189
 coverage, 54, 64
 covering, viii, 14, 49, 68
 cows, xiv, 226, 227, 313, 316, 319
 CRC, 30, 39, 198, 250, 252, 299
 credit, 82
 creep, 113
 crime, 320

crimes, 322
 critical habitat, 78
 critical period, 188
 critical value, 159, 160
 criticism, 329
 Croatia, viii, 3, 4, 10, 15, 25, 26, 27, 31, 33, 34, 36, 38, 39, 40, 41, 42, 43, 45, 252
 crop residues, 106
 croplands, x, 181, 183, 193
 crops, 14, 40, 68, 77, 78, 82, 85, 99, 182, 193, 195, 320
 crude oil, 42
 crustaceans, 202, 203
 crying, 16
 CSR, 321
 cultivation, 16, 50, 51, 54, 57, 64, 78, 303, 328
 cultural values, 104
 culture, vii, 79, 83, 89, 104, 107, 215, 261
 curiosity, 28
 customers, 263
 cycles, 8, 26, 35, 37, 38, 177
 cyclophosphamide, 198, 199
 cytochrome, 6, 39
 cytosolic, 197
 Czech Republic, 14, 29, 261, 326

D

dairy, 218, 237, 289
 dairy products, 218, 289
 Dallas, 203, 218
 danger, 81, 98, 102, 228, 229, 271
 data collection, 73, 255, 302
 data processing, 295
 data set, 336
 database, 108, 242
 dating, ix, 112
 death, 11, 16, 32, 126, 182, 188, 270, 272, 316
 deaths, 81, 102, 317
 decay, 267
 decentralisation, 258
 deciduous, 9, 11, 13, 22, 26, 33, 36, 43, 117, 315
 decisions, 107, 235, 261
 decoupling, 233
 defects, 188
 defense, 207, 226, 236
 deficiency, 101, 251
 deficit, 188
 definition, 56, 115, 118, 140, 146, 186, 187, 188
 deforestation, 29, 98, 272
 degradation, 32, 51, 78, 79, 80, 81, 88, 98, 100, 102, 103, 104, 106, 259
 dehydrogenase, 198
 demand, 56, 102, 182, 256, 262, 264, 266, 274, 281, 286, 288
 demand curve, 262
 Democratic Republic of Congo, 99, 101, 105, 107, 108
 demographic change, 248
 demographics, x, 135, 149, 167, 175, 177
 demography, xii, 131, 239, 240, 242, 247, 249
 Denmark, 20, 41, 217, 249, 261
 density, xi, xv, 13, 14, 18, 19, 21, 23, 24, 35, 36, 37, 38, 46, 56, 57, 78, 79, 85, 87, 88, 94, 100, 126, 127, 132, 177, 202, 216, 251, 303, 312, 314, 333, 336, 339, 341, 342
 dependent variable, 243
 deposition, 207
 deprivation, 45, 46
 derivatives, 140
 desire, 51, 77, 82
 destruction, vii, 17, 78, 100, 104, 108, 202, 240, 249, 281
 detection, vii, ix, 3, 4, 111, 131, 187, 199, 215, 217, 294
 developed countries, 104
 developed nations, 104
 developing countries, 182, 254, 271
 dew, 17
 diamonds, 100, 102, 104
 diet, xv, 7, 8, 12, 15, 22, 23, 24, 27, 35, 42, 43, 46, 202, 213, 220, 252, 333, 341
 diet composition, 27, 252
 diets, 22, 23, 31, 334, 335
 differentiation, 117, 118, 125, 232
 diffusion, 136, 177, 205, 210
 digestive tract, 204
 diminishing returns, 136, 137
 direct observation, 19, 311
 disabled, 270
 discharges, 215
 discontinuity, 139
 diseases, 4, 24, 27, 50, 136, 177, 178, 203, 213, 219, 221
 dispersion, 204
 displaced persons, 99
 displacement, viii, 49, 53, 57, 60, 61, 62, 63, 64, 65, 66, 67, 68, 70, 72, 78, 79, 80, 81, 82, 84, 85, 87, 89, 97, 109
 disposition, 25
 disseminate, 204
 distribution, vii, viii, 3, 4, 9, 12, 15, 17, 23, 24, 29, 30, 38, 39, 40, 41, 46, 49, 57, 60, 76, 79, 87, 119, 127, 130, 185, 202, 203, 205, 218, 220, 252, 261, 262, 264, 266, 267, 294, 295, 296, 298, 299, 300, 302, 303, 305, 306, 309, 310, 311, 312, 314, 323, 326, 330, 334, 341
 diversification, 82
 diversity, viii, ix, xv, 4, 29, 41, 53, 82, 87, 88, 91, 103, 111, 112, 113, 125, 128, 195, 203, 310, 312, 333, 334, 341, 342
 diving, 294, 296
 division, 53, 81, 82, 83, 84, 92, 233, 314
 DNA, xi, 183, 188, 189, 190, 191, 193, 194, 195, 198, 199, 200, 201, 202, 203, 214, 215
 DNA damage, 183, 189, 190, 191, 193, 195, 198, 199, 200

dogs, 226, 227, 232, 319
 dominance, 33, 36, 37, 43, 151, 342
 donations, 270, 327
 donkey, 74
 donor, 125
 donors, 102, 289
 double counting, 66
 draft, 289
 drainage, 80
 drinking, 17, 77, 269, 297
 drinking water, 269, 297
 drought, 77, 99, 106, 342
 droughts, 80, 81, 82, 83, 84, 86, 88, 106
 drowning, 202
 drugs, x, 201, 205, 210, 214, 215
 drying, 206
 dung, 65, 79, 227
 duration, 16, 18, 21, 99, 226, 228, 233, 246
 dynamical system, ix, 135

E

early warning, x, 182, 187
 ears, 7, 9, 11
 earth, 240, 249
 eating, 88, 317
 ecological, x, 12, 13, 43, 47, 57, 78, 80, 84, 85, 86, 87, 92, 96, 98, 103, 112, 118, 120, 126, 128, 129, 132, 136, 182, 184, 194, 225, 241, 248, 249, 314, 323, 342
 Ecological Economics, 94
 ecological restoration, 112, 126
 ecologists, 118, 187, 221, 226
 ecology, 12, 19, 22, 27, 31, 36, 41, 42, 45, 77, 89, 96, 113, 117, 128, 129, 131, 132, 219, 237, 251, 252, 271, 273, 310, 311, 312, 323, 334, 342, 343
 economic activity, 257
 economic change, 51, 56, 259
 economic development, 52, 258
 economic growth, 52
 economic incentives, 79, 328
 economic losses, 234, 259
 economic stability, 254, 258
 economic status, 58
 economic theory, 262
 economics, xiii, 100, 253, 275, 277, 279, 287, 288
 ecosystem, ix, x, 52, 53, 54, 55, 57, 77, 78, 80, 81, 83, 84, 86, 87, 91, 95, 97, 100, 101, 107, 112, 113, 123, 125, 135, 136, 137, 147, 156, 161, 163, 164, 165, 166, 167, 168, 172, 174, 182, 184, 185, 187, 235, 282, 316, 341, 343
 ecosystem restoration, 113
 ecosystems, vii, viii, 3, 4, 5, 6, 12, 92, 96, 98, 99, 107, 112, 126, 130, 166, 182, 184, 195, 205, 206, 242, 251, 314, 342
 ecotoxicology, 195, 198
 ectoparasites, 24, 25
 Education, 96, 263
 educational attainment, 262
 effluents, x, 201, 316
 egg, 184
 electromagnetic, 16
 electromagnetic wave, 16
 electromagnetic waves, 16
 electrophoresis, 198, 199, 200
 electrophysiological properties, 225
 elephant, xii, 50, 74, 102, 251, 253, 254, 255, 256, 258, 259, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275
 elk, 230, 232, 233, 236, 237
 embryo, 17, 116, 117, 118, 184, 188
 embryogenesis, 194
 embryonic development, 188
 embryos, 117, 184, 185, 193, 200
 emigration, 53
 emission, 34
 emotion, xi, 223, 225
 emotional, 225, 267, 273, 326
 emotional state, 225
 emotions, xi, 223
 empathy, 267
 employees, 317, 321
 employment, 100, 282, 287, 288
 empowered, 286
 empowerment, 51, 82
 encephalitis, 24
 encouragement, 85, 269, 270
 endangered plant species, 114
 endocrine, 182
 endocrine system, 182
 endothelial cell, 28
 endothelial cells, 28
 energy, 20, 23, 42, 85, 183, 229, 334, 342
 energy consumption, 229
 England, 9, 34, 224, 261
 enlargement, 11
 enterococci, xi, 201, 205, 210, 211, 214, 215, 217, 218, 219, 221
 enterprise, 84
 entertainment, 270, 282
 environment, vii, ix, x, xi, xii, xiii, 3, 4, 17, 24, 43, 46, 78, 87, 88, 94, 96, 98, 99, 100, 101, 103, 106, 108, 109, 111, 114, 120, 121, 123, 127, 136, 165, 166, 168, 169, 170, 181, 182, 183, 184, 186, 194, 202, 204, 205, 229, 235, 239, 241, 258, 264, 265, 275, 280, 281, 294, 299, 300, 334
 environmental change, 53, 247, 248
 environmental conditions, 107, 114, 126, 187, 193, 248
 environmental contaminants, 184, 197
 environmental contamination, x, 184, 190, 194, 205, 216
 environmental degradation, 98, 102, 106
 environmental effects, 109, 183, 187
 environmental factors, 21, 126, 131, 187, 194, 196, 310

environmental impact, 85, 93, 98, 99, 101, 102, 106, 109, 281
 environmental issues, 112
 EPA, 195, 196
 epidemic, 135, 136, 141, 142, 144, 146, 161, 163, 165, 167, 251
 epidemics, viii, 4, 161, 162, 167, 168
 epidemiology, 24, 31, 142
 equilibrium, 136, 139, 140, 141, 143, 144, 146, 147, 148, 149, 150, 152, 153, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 170, 171, 172, 173, 174, 175, 251
 equipment, 59
 equity, 195
 erosion, 81, 100, 102
 erythrocytes, 190, 191, 198, 199, 200
Escherichia coli, x, xi, 201, 204, 205, 210, 211, 212, 213, 214, 215, 216
 estimating, 101, 305, 217, 218, 219, 220, 221
 estimating, 101, 305
 Estonia, 33
 estradiol, 197
 ethical standards, 279
 ethics, 51, 259
 eucalyptus, 206
 Europe, 6, 7, 8, 9, 11, 13, 14, 18, 22, 26, 34, 39, 40, 41, 45, 132, 202, 203, 256, 262, 326
 European Union, 216
 Europeans, 281
 evolution, 7, 20, 24, 29, 41, 52, 88, 118, 121, 124, 213, 225, 226, 240, 250
 evolutionary process, 248
 examinations, 213
 exchange relationship, 106
 exclusion, 95, 98, 285, 339
 exercise, 153
 expert, 20, 289
 expertise, 84
 exploitation, 51, 101, 102, 342
 explosives, 100
 exposure, x, xi, 30, 103, 114, 116, 122, 123, 130, 181, 182, 183, 184, 186, 187, 188, 189, 190, 191, 192, 193, 194, 195, 197, 202, 214, 218, 300
 extinction, 53, 112, 125, 131, 156, 163, 166, 170, 224, 233, 249, 251, 273
 extraction, 99, 103, 104
 extrapolation, xiii, xiv, 301, 302, 303, 304, 306, 308, 310
 eyes, 7, 9, 11, 335

F

fabric, 52
Fagus sylvatica, 17, 20, 37, 39, 40, 44
 failure, 52, 107, 114, 129, 182
 fairness, 326
 family, 4, 6, 105, 233, 237, 261, 271
 family members, 105, 261

FAO, 35, 41, 260, 274
 Far East, 335, 342, 343
 farmers, 57, 87, 106, 221, 259, 328
 farming, x, xi, 78, 201, 202, 283, 331
 farmland, 27, 44, 100
 farms, 78, 85, 95, 217, 278
 fat, 27, 45, 335
 fauna, 54, 206
 fear, xi, 28, 52, 223, 224, 225, 226, 228, 229, 231, 235, 236, 237, 329
 February, 8, 11, 275
 feces, 15, 204, 205, 219
 fee, 83, 255, 263, 264, 270, 274, 285
 feedback, 101, 275
 feeding, vii, xiii, 3, 4, 9, 13, 17, 19, 20, 22, 23, 24, 34, 35, 38, 47, 56, 80, 136, 225, 226, 234, 237, 269, 271, 272, 289, 294, 317, 330, 343
 fees, 11, 254, 256, 264, 327
 females, 8, 9, 14, 15, 18, 19, 20, 21, 37, 38, 43, 46, 184, 250, 255, 318
 fencing, 53
 fertility, 11, 15, 27, 46
 fertilization, 17
 fertilizers, 78
 fever, vii, viii, 3, 4, 25, 26, 38, 40
 fiber, 10, 245
 fiber content, 10
 finance, 102, 104
 financial resources, viii, 97
 financial support, 90, 216
 fingerprinting, 216
 Finland, 7, 8, 9, 12, 29, 40, 331
 fire, 34, 85, 117, 340
 fires, 272
 firewood, 85, 99, 101
 first aid, 269
 first generation, 16
 fish, 187, 190, 198, 199, 202, 203, 206, 241, 242, 252, 326, 328, 330
 fisheries, 195, 250
 fishing, 231, 283
 fitness, x, 9, 117, 181, 183, 188, 240, 249, 250, 252
 flexibility, 103
 flight, xi, xiii, 57, 223, 224, 225, 226, 227, 228, 229, 232, 235, 294
 flood, 133
 flora, 130, 131, 132, 206
 flow, 12, 32, 51, 77, 104, 187, 258
 fluctuations, ix, 46, 111, 117, 121, 123, 124, 129, 132, 250
 fluorescence, 218
 fluorescence in situ hybridization, 218
 flushing, 46
 focusing, 115, 136, 175, 288
 folate, xi, 201, 214
 follicle, 32
 food, vii, xiii, 3, 8, 9, 11, 12, 13, 14, 15, 16, 17, 19, 20, 21, 22, 23, 24, 28, 29, 31, 32, 34, 35, 36, 38, 41, 45, 46, 50, 77, 82, 99, 100, 106, 136, 137, 177,

178, 179, 184, 202, 217, 219, 221, 231, 232, 233, 234, 242, 251, 282, 283, 294, 314, 321, 330, 335, 342
 food intake, 231
 food production, 100
 Ford, 130, 321
 forecasting, 320
 foreigners, xii, 254, 264, 266, 268
 forest ecosystem, viii, 4, 5, 6, 12, 24
 forest fragments, xiv
 forest habitats, 22
 forest management, 17
 forest resources, 101
 forestry, 3, 5, 16, 28, 34, 36, 45, 281
 forests, vii, viii, xiii, 3, 4, 5, 7, 9, 10, 13, 14, 15, 17, 22, 26, 30, 31, 36, 39, 42, 44, 117, 202, 224, 301, 302, 315, 316, 318, 323, 335, 336, 337, 338, 341, 342
 fragmentation, 53, 81, 82, 83, 95, 125, 249, 302, 312, 329
 France, 31, 195, 217, 235, 240, 244, 261
 freedom, 269, 329
 freezing, 9, 240
 freshwater, 190, 200, 202, 248
 frog, 251
 fruits, ix, 82, 112, 117
 frustration, 50
 fuel, 79, 99, 101
 fumigation, 17
 funding, 105, 107, 327
 funds, 84, 99, 271, 327, 329
 fungal, 5, 17, 178, 203
 fungi, 136
 fungicides, 182
 Fur, 286
 fusiform, 202

G

garbage, 39, 269
 gas, 317
 gastrointestinal, 204
 gastrointestinal tract, 204
 GCE, 263
 gel, 28, 195, 198, 200
 gender, 317
 gene, 6, 32, 136, 204, 213
 generation, xii, 82, 198, 239, 241, 246, 247, 248, 282
 genes, 204, 213, 215, 217, 218, 220
 genetic disorders, 183
 genetic diversity, viii, ix, 4, 53, 111, 113, 125, 195
 genetics, 17, 333
 Geneva, 100, 196, 197
 Geneva Convention, 100
 genocide, 103
 genome, 28, 215
 genomic, x, 43, 181, 183, 188, 221

genotoxic, 188, 189, 190, 191, 192, 193, 194, 195, 199
 genotype, 112, 113
 genotypes, ix, 111
 gentamicin, 210
 Geographic Information System, xiv, 58, 59, 60, 90, 302, 309, 310, 311
 geography, 278
 Germany, 11, 14, 22, 32, 41, 45, 220, 225, 237, 261, 325, 326, 330
 germination, ix, 5, 15, 16, 111, 113, 114, 115, 116, 117, 120, 121, 122, 123, 124, 126, 127, 128, 129, 130, 131, 132, 133, 178
 gestation, 202
 Global Positioning System, 57, 58, 59, 60
 global warming, 240, 241, 251, 252
 Globalization, 91
 glycine, 184
 glyphosate, 190, 193, 196, 199, 200
 goals, 106, 280
 God, 224
 gold, 100
 governance, 99
 government, viii, 50, 51, 52, 53, 56, 59, 77, 82, 83, 85, 90, 97, 99, 100, 101, 103, 105, 258, 273, 286, 287, 320, 321, 327, 330
 grades, 335, 336, 339, 340, 341
 grain, 50, 106
 Gram-negative, 204, 210
 Gram-positive, 204, 210
 gram-positive bacteria, 220
 graph, 297
 grass, 10, 11, 25, 79, 82, 123
 grasses, 133, 178
 grassland, 55, 59, 68, 76, 120, 125, 128, 131, 132, 232
 grasslands, 55, 118, 125, 126, 341
 grazing, 55, 79, 80, 82, 85, 86, 87, 93, 232, 281, 283, 286, 341, 342, 343
 Great Britain, 11
 Greece, 43
 gross domestic product, 103
 ground water, 198, 214
 group size, 60, 64, 65, 68, 69, 74, 76, 80, 82
 grouping, 20, 82
 groups, vii, xii, 3, 12, 13, 20, 25, 39, 43, 80, 103, 104, 192, 193, 194, 221, 225, 227, 237, 239, 243, 246, 248, 259, 271, 320
 growth, viii, ix, x, 4, 9, 10, 11, 13, 15, 16, 23, 24, 27, 32, 44, 52, 54, 56, 57, 83, 84, 86, 98, 99, 112, 117, 118, 120, 126, 127, 128, 135, 144, 162, 165, 181, 184, 188, 193, 210, 241, 250, 251, 252, 254, 286, 288
 growth rate, 241, 250
 guidance, 310
 guidelines, x, 91, 106, 201, 205, 210
 guilt, 273
 Guinea, 100, 108, 109
 guns, 104

gut, 29, 31

H

habitat, vii, ix, xiii, xiv, 3, 4, 6, 7, 8, 10, 11, 12, 14, 17, 18, 19, 20, 24, 32, 35, 36, 54, 55, 59, 60, 63, 64, 66, 68, 70, 75, 76, 77, 78, 81, 82, 87, 88, 98, 100, 103, 111, 125, 132, 182, 202, 203, 220, 235, 236, 240, 249, 250, 269, 272, 281, 282, 288, 293, 301, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 326, 329, 330, 335, 337, 338, 339, 341
 habitat quality, 87, 88, 220, 310
 habituation, 229, 237
 hands, 317
 hantavirus, 26, 30, 35, 37, 40, 41
 harassment, 78, 234
 harbour, 251
 harm, 78, 81
 harmful effects, 12, 187
 harvest, 5, 8, 11, 104
 harvesting, 34, 82, 88, 91, 185
 hazards, x, 181, 183, 186
 health, x, 4, 12, 24, 25, 59, 98, 100, 183, 186, 201, 203, 213, 293, 300, 314
 health effects, 186
 health status, 203, 213
 hearing, 15
 heart, 229
 heart rate, 229
 heavy metal, 215, 300
 heavy metals, 215, 300
 height, 10, 20
 Hemiptera, 252
 herbicide, 183, 184, 191, 192, 195, 196, 199, 200
 herbicides, 78, 182, 183, 194, 198, 199
 herbivores, 12, 22, 56, 87, 91
 herbivorous, 34
 herring, 241
 heterogeneity, 82, 129, 131, 342
 heterogeneous, 25, 82
 Higgs, 24, 36
 high pressure, 183
 high risk, 43
 high temperature, 117, 122, 132, 242
 high-fat, 42
 highlands, 303, 308
 high-level, 217
 histological, x, 181, 186
 HIV, 103
 Holland, 261
 Holocene, 312
 Honda, 112, 114, 116, 118, 119, 120, 122, 123, 124, 125, 126, 128, 130, 132, 300
 hormonal control, 32
 hormone, 15, 19
 hormones, 18, 19, 197
 horse, 299
 horses, 236

host, 24, 25, 27, 41, 43, 45, 109, 205
 hostile environment, 205
 hostility, 51
 hot spots, xiv, 301, 309
 hot water, 251
 House, 28
 household, 79
 housing, 57, 58, 65
 hub, 79
 human, vii, viii, x, xi, xiii, xiv, 4, 16, 24, 25, 26, 33, 49, 50, 51, 53, 54, 57, 59, 60, 61, 62, 64, 65, 66, 68, 70, 71, 72, 73, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 93, 94, 95, 101, 103, 104, 105, 106, 107, 125, 183, 194, 198, 201, 202, 204, 205, 206, 213, 214, 215, 216, 218, 221, 223, 224, 226, 227, 229, 230, 231, 232, 233, 234, 236, 249, 273, 277, 278, 279, 283, 293, 299, 300, 313, 325, 330, 334
 human activity, 49, 61, 229
 human interactions, 57
 human welfare, 106
 humanitarian, viii, 97, 103, 104, 105, 106, 107
 humans, vii, xi, 3, 4, 12, 16, 24, 25, 26, 50, 76, 79, 80, 82, 87, 88, 98, 100, 102, 183, 189, 200, 202, 203, 204, 213, 216, 217, 218, 219, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 236, 237, 297, 298, 299, 300, 314, 320, 326
 humidity, 13, 26, 205
 humus, 9
 Hungarian, 219
 Hungary, 261
 hunting, xi, 51, 77, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 234, 235, 236, 237, 302, 309, 317, 319, 320, 322, 327, 330
 husbandry, 314
 hybrids, 32
 hydration, 248
 hypothesis, xi, xii, 33, 38, 121, 122, 129, 202, 213, 214, 215, 239, 240, 241, 242, 247, 334

I

ice, 13, 240
 Idaho, 121
 identification, x, 30, 182, 189, 194, 203, 204, 207, 210, 211, 212, 216, 218, 219, 302, 303, 310
 identity, 59
 IMA, 178
 images, 54, 191, 217, 302
 immigration, 51, 53, 86, 89, 120, 340
impact analysis, 279
 implementation, 51, 98, 106, 186, 326, 330
 imports, 104
 in situ, 185
 in situ hybridization, 218
 in vitro, 44, 189, 190, 198, 199
 in vivo, 189, 190, 191, 194, 198
 inactivation, 204

- inactive, 14, 115, 116
incentive, 285, 287, 321, 327, 328
incentives, xiv, 92, 325, 327, 328, 329, 330, 331
incidence, 26, 36, 46, 142, 144, 149, 157, 159, 161, 167, 168, 169, 174, 316
inclusion, 321
income, xii, 50, 51, 77, 100, 102, 106, 254, 255, 257, 262, 263, 268, 270, 271, 272, 282, 283, 285, 327, 329, 330
incomes, 262, 287, 288
increased access, xiv, 310
increased competition, 82
incubation, 184, 185, 190, 193
incubation period, 185, 190, 193
India, 233, 261, 275
Indian, 248, 251, 342
indication, 227
indicators, 128, 188
indices, 103, 118
indigenous, 99, 104, 310
indirect effect, xii, 78, 102, 239, 240, 241
Indonesia, xiii, 272, 301, 302, 303, 311, 312
induction, x, 129, 133, 181, 194, 199
industrial, 250
industrialization, 249
industry, 54, 87, 88, 99, 254, 282, 287
inelastic, 264
inequality, 148
inert, 183
infection, vii, viii, 3, 4, 12, 16, 24, 25, 26, 27, 28, 215
infections, vii, 3, 4, 21, 26, 31, 37, 45, 204, 220
infectious, vii, x, 3, 4, 24, 25, 26, 27, 177, 178, 201
infectious disease, vii, x, 3, 4, 24, 25, 27, 177, 178, 201
infectious diseases, x, 4, 24, 27, 177, 178, 201
inferences, 293
infestations, 38
infinite, 140
information asymmetry, 327, 330
Information System, 60
infrastructure, 81, 100, 281
ingestion, 16, 316, 317
inherited, 167
inhibition, xi, 32, 122, 123, 129, 131, 132, 182, 188, 196, 201
inhibitor, 39
injuries, 234
injury, 18
Innovation, 92
inorganic, 12
insecticide, 195, 199
insecticides, 182
insects, 5, 11, 12, 22, 247
insecurity, 98
insemination, 317
insight, 254
instability, x, 44, 99, 108, 141, 143, 152, 181, 183, 188, 275
institutions, 59, 65, 66, 68, 70, 72, 73, 85, 90, 263
instruments, xiv, 85, 325, 326, 329
integration, 109, 215, 342
integrity, 52, 80, 82, 86, 87, 88, 189, 249
intensity, vii, 3, 4, 10, 15, 19, 24, 103, 233, 267
interaction, 19, 20, 25, 34, 106, 130, 136, 137, 144, 168, 169, 175, 186, 334
interactions, ix, x, xii, xiv, 19, 36, 37, 57, 91, 123, 135, 136, 137, 166, 167, 177, 182, 188, 239, 240, 248, 250, 313, 321
interdisciplinary, viii, 3
interest groups, 320
interference, 184, 188
interpretation, 116
interrelations, 233
interrelationships, 39
interval, 10, 115, 140
intervention, 103, 206
interview, 260
interviews, 260, 273, 317
intestine, 213
intrinsic, 204, 205, 214, 215
invasive, ix, 111, 112, 125, 126, 127, 132, 203, 249
invasive species, ix, 111, 112, 249
invertebrates, 22, 31
investment, 51
investors, 51, 52, 77, 84, 85, 88
ions, 18, 19, 215, 224, 286
Ireland, 38, 43, 261
irrigation, 51, 57, 59, 77, 78, 206
Islam, 195
island, 33, 38, 54, 224, 278, 309
isolation, 54, 210, 213, 214, 215, 218, 219, 309
Israel, 236
Italy, 28, 30, 135, 236, 274
IUCN, xiii, 88, 91, 93, 195, 196, 197, 202, 217, 218, 220, 275, 301, 302
ivory, 100, 102

J

- Jacobian, 138, 139, 143, 147, 148, 149, 150, 152
Jacobian matrix, 139, 143, 147, 148, 149, 152
January, 12, 103, 218, 316, 317, 318, 319
Japan, ix, 111, 112, 125, 126, 128, 130, 131, 132, 133, 196, 261, 293, 294, 299, 300, 301
Japanese, 12, 120, 125, 128, 130, 132, 299, 300, 301
Java, xiii, xiv, 301, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312
jobs, xiii, 277, 282
joints, 335
judge, 260
Jung, 301, 302, 304, 306, 308, 310, 312
justification, 112, 126
juveniles, 120, 184, 226, 227, 240

K

karyotype, 189
 Kenya, viii, 49, 50, 51, 52, 53, 54, 55, 56, 77, 78, 81, 88, 90, 91, 92, 93, 94, 95, 96, 104, 109, 274, 322
 kernel, 29
 kidney, 27, 293, 294, 295, 296, 297, 298, 299, 300
 kidneys, 299, 300
 killing, 51, 78, 84, 99, 100, 183, 221, 326, 328
 King, 14, 20, 37, 122, 130
 Korea, 301, 335
 Korean, 335, 338, 339, 341
 krill, 241

L

labor, 127
 lack of control, 101
 lactate dehydrogenase, 198
 lactating, 237
 lactose, 210
 lakes, 11, 202
 lambda, 156, 157, 158, 159, 160, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 173, 174
 land, viii, 5, 10, 15, 43, 49, 50, 51, 52, 53, 54, 56, 57, 59, 60, 62, 64, 65, 77, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88, 89, 91, 92, 93, 94, 100, 106, 109, 227, 234, 240, 272, 280, 281, 282, 283, 285, 286, 288, 297, 311, 321, 326, 328, 329, 330, 331, 342
 land tenure, 50, 52, 57
 land use, viii, 49, 50, 51, 52, 53, 54, 77, 81, 83, 84, 85, 86, 87, 88, 89, 91, 92, 93, 94, 106, 109, 240, 281, 282, 286, 311, 326, 328, 329
 Land Use Policy, 91, 93, 109
 landscapes, 83, 91, 107, 109, 196, 232, 280, 281, 302, 328, 331
 land-use, 88, 281, 328
 larvae, 8, 22, 26, 195
 law, 99, 101, 102, 103, 125, 136, 137
 law enforcement, 99, 101
 laws, 225
 LDCs, 254, 259
 lead, 53, 54, 79, 82, 152, 189, 203, 229, 240, 249, 262, 328
 leadership, 88
 leakage, 198
 learning, xi, 43, 57, 223, 224, 227, 228, 229, 230, 231, 232, 233, 275
 learning behavior, xi, 223, 224, 233
 learning process, 228, 229, 230, 231
 leather, 317
 legume, 136, 177
 Leibniz, 220, 223
 lens, 128
 Lepidoptera, 22, 31
 lesions, 182, 188, 194, 298, 316
 Liberia, 100, 104

life cycle, ix, 111, 127, 248
 life forms, 342
 life span, xii, , 8 182, 183, 188, 241, 242, 247, 248
 lifestyle, 79, 83, 85, 258
 lifetime, 10, 11
 light conditions, 18
 light transmission, 130
 likelihood, xii, 54, 239, 243, 251, 302
 limitation, ix, 24, 111, 112, 126
 limitations, 213
 linear, 15
 linkage, 186
 links, 88, 107
 lipid, 188
 lipid peroxidation, 188
 liver, 293, 294, 295, 296, 297, 298, 299, 300
 livestock, 50, 52, 53, 55, 56, 57, 59, 60, 64, 65, 66, 67, 68, 74, 76, 77, 78, 79, 80, 81, 82, 84, 86, 87, 88, 91, 92, 93, 94, 95, 96, 106, 214, 281, 283, 286, 313, 314, 320, 322, 323, 326
 living conditions, 3, 4
 loans, 53
 local community, 79, 86, 287
 local government, 258
 localization, 216
 location, viii, xiv, 49, 54, 55, 57, 58, 59, 67, 69, 80, 84, 85, 123, 214, 244, 255, 286, 307, 309, 313
 logging, 40, 272, 309
 London, 27, 31, 32, 36, 46, 96, 129, 176, 196, 220, 221, 233, 289, 290, 299, 311, 322, 323, 342
 long period, 213, 226
 long-distance, 242, 249
 longevity, xii, 118, 119, 124, 128, 131, 132, 239, 242, 243, 244, 246, 248
 long-term, ix, x, 23, 99, 102, 106, 107, 111, 112, 118, 125, 135, 181, 182, 194, 233, 242, 249, 258, 259, 302
 loss of control, 106
 losses, 16, 21, 50, 88, 320, 327, 329, 331
 low-level, 182
 loyalty, 275
 lungs, 29
 lymphocytes, 198, 199

M

maintenance, 12, 29, 43, 85, 88, 112, 182, 329, 342
 maize, 78
 Malaysia, 30, 261
 males, 14, 18, 19, 21, 22, 33, 36, 227, 231, 318
 malnutrition, 316, 317
 malpractice, 316, 317
 mammal, 6, 12, 29, 31, 32, 37, 39, 40, 44, 45, 47, 54, 59, 63, 64, 72, 74, 75, 94, 96, 233, 242, 251, 272, 312
 Mammalian, 39, 252
 mammals, 5, 7, 9, 12, 13, 14, 16, 28, 29, 34, 35, 43, 45, 46, 54, 55, 59, 63, 64, 68, 75, 76, 78, 100, 189,

- 190, 200, 202, 204, 205, 213, 225, 226, 230, 242, 271, 297, 300, 311, 342
- management, viii, xi, xiv, 17, 30, 40, 52, 83, 84, 85, 91, 94, 95, 97, 103, 105, 107, 132, 195, 197, 200, 202, 216, 234, 254, 255, 260, 261, 274, 301, 303, 309, 310, 314, 317, 320, 321, 322, 323, 328, 331, 342
- mandibular, 37
- man-made, 202, 203
- manufacturer, 210, 289
- manure, 219
- Maori, 278, 280, 281
- mapping, viii, 49
- marginal utility, 264
- marine mammals, 297
- market, 58, 68, 82, 83, 85, 87, 259, 327, 328
- market prices, 87
- marketing, 104, 259
- markets, 51, 57, 66, 67, 68, 79, 83, 85, 86, 92
- marsh, 7
- marshes, 9, 202
- Maryland, 30
- mass media, 258
- Massachusetts, 93
- maternal, 120, 237
- Mathematical Methods, 177
- matrix, 139, 143, 147, 148, 149, 150, 152
- maturation, 24, 34, 122, 188
- maturation process, 122
- Mauritania, 98
- meals, 317
- meanings, 145
- measure of value, 279
- measurement, 130, 186, 236, 296
- measures, viii, 4, 11, 97, 232, 273, 281, 288, 320, 326, 328, 329
- meat, 53, 83, 85, 91, 100, 106, 224
- media, 258
- median, xiv, 302, 305, 308, 310
- Medicago truncatula*, 136
- medicinal plants, 88
- medicine, 26
- Mediterranean, 9, 11, 31, 34, 35, 41, 203, 205, 220, 235
- melt, 13
- membership, 52, 327
- membranes, 202
- memory, 43, 230, 231, 233
- meningoencephalitis, vii, 3, 4
- mercury, 202
- meta-analysis, xii, 126, 240, 242
- metabolic, 8, 205
- metabolic pathways, 205
- metabolism, 44, 118, 183
- metabolite, 186
- Metallothionein, 300
- meteorological, vii, 3, 13
- Mexico, 252, 323
- mice, 4, 6, 7, 9, 12, 14, 15, 19, 20, 21, 22, 23, 24, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 40, 41, 43, 44, 45, 46, 190, 199
- microbial, 117, 128, 341
- microbiota, x, xi, 201, 202, 204, 205, 213, 219, 220
- microclimate, 12
- microflora, 203, 207, 213
- micronucleus, 195, 198, 199
- microorganism, 204
- microorganisms, 12, 16, 24, 25, 205, 213, 214, 215
- Microsoft, 60, 294
- Middle East, 40
- migrant, 57, 108
- migration, viii, xiii, 24, 49, 53, 61, 64, 70, 78, 79, 80, 82, 83, 84, 85, 86, 87, 88, 100, 107, 189, 294
- migratory birds, 293
- militant, 98, 100
- military, 98, 99, 102, 104, 105, 109
- militias, 101, 104
- milk, 80, 272
- Ministry of Environment, 255
- Minnesota, 245
- misconceptions, 312
- mites, 42
- mitochondrial, 6
- mixing, 142
- MMA, 320, 322
- mobility, vii, 3, 4, 18, 24, 25
- modeling, 15, 149, 302, 311, 312
- models, ix, x, 30, 31, 44, 135, 136, 139, 142, 144, 155, 162, 167, 168, 177, 178, 226, 302, 303, 309, 310, 311, 312
- moisture, 55
- molecular biology, 213
- Møller, 219
- mollusks, 8
- molybdenum, 293, 300
- money, 50, 85, 88, 279, 280, 282, 285, 320, 327, 328, 329, 330
- monkeys, 63, 78, 95, 237, 297, 298
- Monroe, 204, 219
- morning, 269
- Morocco, 219
- morphological, x, 35, 116, 117, 181, 186
- morphology, 7, 22, 24, 29, 205, 210
- morphometric, 28
- mortality, xi, xiv, 10, 13, 37, 41, 102, 120, 142, 144, 161, 167, 168, 169, 173, 202, 213, 223, 240, 247, 313, 316, 317, 322, 328
- mortality rate, 10, 13, 142, 144, 240
- mosaic, 87, 281, 282, 286, 304, 315
- Moscow, 176, 342
- mothers, 271, 272
- moths, 136
- motivation, 224, 261, 274
- mountains, 303
- mouse, vii, 3, 7, 8, 11, 20, 22, 23, 30, 31, 32, 33, 34, 36, 37, 40, 42, 43, 45, 46, 47, 190, 198, 199
- mouth, 26

movement, 14, 18, 20, 52, 64, 76, 81, 86, 187, 234, 235, 237, 342
 MPI, 242
 multiple sclerosis, 43
 multiplier, 282
 multiplier effect, 282
 muscles, 33, 317
 mushrooms, ix, 23, 135, 136
 mutagenic, 189
 mutation, 205
 mutations, x, xi, 181, 188, 202, 204, 215

N

Namibia, 94
national, xi, 50, 51, 54, 56, 84, 88, 89, 101, 103, 105, 223, 224, 225, 236, 272, 274, 280, 310, 311, 320
 national parks, 50, 54, 56, 89, 101, 225, 274, 310
 National Research Council, 198
 nationality, 274
 native plant, 112
 NATO, 39
 Natura 2000, 203
 natural, vii, viii, x, xi, xiii, 3, 4, 5, 8, 9, 12, 18, 23, 26, 31, 32, 38, 39, 40, 41, 43, 80, 82, 87, 88, 89, 94, 99, 100, 101, 102, 104, 107, 109, 122, 125, 126, 127, 129, 132, 177, 182, 184, 185, 186, 190, 193, 194, 195, 197, 202, 223, 224, 225, 226, 227, 229, 231, 232, 241, 249, 258, 259, 264, 269, 270, 271, 278, 281, 282, 286, 288, 301, 302, 309, 310, 314, 316, 323
 natural enemies, vii, 3, 18, 226
 natural environment, vii, x, 3, 4, 182, 184, 185, 190, 193, 264, 314
 natural food, 23, 31, 32
 natural habitats, 82, 87, 286, 288
 natural resource management, 94
 natural resources, 99, 102, 104
 natural selection, 241
 naturalization, 130
 nature conservation, 254, 263, 279, 281, 282, 288
 Nebraska, 37
 neck, 8, 316, 317
 negative attitudes, 84
 negative consequences, 98, 100, 136
 negative experiences, 232, 233
 negative stimulus, 232
 negativity, 148
 neglect, 85, 95
 nematode, 136
 nematodes, 21, 177
 neonatal, 197
 Nepal, 323
 nesting, 20, 82, 283, 285
 Netherlands, 107, 108, 109, 218
 network, 58, 65, 70, 81, 103, 307, 308
 neuroendocrine, 225
 neuroendocrine system, 225

neurons, 225, 235
 neurotransmitters, 225
 New England, 221
 New Jersey, 91, 96
 New Mexico, 252
 New York, 60, 92, 96, 109, 129, 217, 290, 299
 New Zealand, 130, 234, 245, 251, 252, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 288, 289
 next generation, 293
 NGO, 83
 NGOs, 103, 281, 286, 288, 310
 nickel (Ni), 293
 Nielsen, 20
 Nile, 100
 nitrate, 122, 129, 130, 131, 133, 202
 nitrogen, 30
 noise, 20, 79, 80, 81, 85
 non-destructive, x, 182, 189, 190
 nongovernmental, 105
 nongovernmental organization, 105
 non-human, 232
 nonlinear, 176
 nonparametric, 27
 non-renewable, 341
 nontoxic, 184
 normal, x, xi, 18, 80, 100, 116, 119, 181, 186, 187, 188, 204, 213, 223, 224, 225, 227, 228, 230, 328
 normal conditions, 18
 normal development, 188
 normal distribution, 119
 North America, 14, 22, 26, 196, 219, 244, 248, 250
 North Atlantic, 252
 Northeast, 343
 Norway, 33, 34, 39, 45, 244, 245
 novelty, 130, 258
 nuclear, 236
 nuclei, 44
 nucleus, 189, 225, 255
 nutrient, ix, 111, 120, 122
 nutrients, 10, 23
 nutrition, 17, 23, 42
 nuts, 24, 39
 nymphs, 26

O

oat, 117, 129
 obligate, 135, 137, 152, 153, 156, 162, 163, 165, 166, 178
 obligation, 268
 observations, 197, 229, 275, 285
 obstruction, 17
 oedema, 44
 offshore, 289
 Ohio, 235, 299
 oil, 42, 124, 272, 296
 olfaction, 46
 olfactory, 37

omission, 307, 309
 one dimension, 280
 online, 217, 249
 operations research, 137
 opportunism, 233
 opportunity costs, 50, 94
 Oregon, 39, 44, 109
 organ, 188
 organic, 12, 202
 organic matter, 12
 organism, x, 181, 186, 187, 190, 199
 organization, 40, 45, 46, 102, 105, 116, 281
 organizations, viii, xiii, 97, 103, 104, 105, 107, 277, 287, 288
 orientation, viii, 18, 49, 88, 89
 oscillation, 14
 otters, xi, 202, 203, 205, 210, 213, 214, 216, 217, 219, 220, 326, 329, 330, 331
 outliers, xiii, 294, 295, 296, 298, 299
 ovaries, 27, 32
 overexploitation, viii, 97, 99, 101, 102, 104, 107
 overgrazing, 81, 82
 ownership, 50, 51, 52, 53, 56, 79, 81, 82, 85, 87, 88, 102
 oxygen, 12, 20

P

Pacific, 262, 278
 Pakistan, 261
 palliative, 272
 Paper, xiii, 54, 90, 91, 92, 93, 94, 96, 253, 255, 259, 275, 289, 290, 301, 333
 parameter, 137, 139, 141, 149, 153, 156, 157, 158, 159, 160, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 242, 341
 parasite, 11, 21
 parasites, 12, 16, 24, 35, 38, 43, 87
 parents, 226
 Paris, 311
 particles, 117, 121, 128
 partnership, 52, 107
 partnerships, 95, 103, 105
 passive, 51, 327, 329, 331
 pastoral, 52, 77, 85, 87, 92, 106
 pasture, 7, 68, 77, 80, 81, 82, 83, 84, 100, 121, 315, 316, 318, 340, 343
 pastures, 315, 316, 318, 341
 pathogenic, 16, 25, 213, 214, 220
 pathogens, vii, 3, 4, 26, 27, 87, 136, 204, 221
 pathology, 218
 pathways, 30, 205
 patients, 25, 44, 297, 298
 PCR, 219
 peat, ix, 112
 peer, xii
 penguins, 241, 249, 283, 285, 289
 penicillin, 210
 per capita, 103
 perception, 131, 260, 326, 328
 perceptions, 237, 248, 259, 279, 323, 326
 performance, 27, 29, 147, 225, 252, 330
 perfusion, 297
 periodic, 178, 179
 periodicity, 5, 32, 177
 peripheral blood, 190, 191, 200
 permeability, 121, 122, 123, 132, 204
 permit, 123
Peromyscus maniculatus, 22, 30
 personal, 52, 262, 279, 284, 321, 327
 personal communication, 52, 284
 personal control, 327
 Perth, 92
 perturbations, 155
 pest control, 35, 183
 pesticide, x, 181, 182, 183, 187, 190, 191, 193, 195, 196
 pesticides, x, 78, 181, 182, 183, 184, 185, 187, 189, 193, 194, 195, 196, 198, 199, 200
 pests, 28, 182, 183, 326
 petroleum, 100
 pH, 187, 221
 phase space, 145, 155, 157, 159, 160, 161, 173, 174
 phenotypes, 188, 217
 phenotypic, 44, 204, 214
 Philippines, 312
 photographs, 289
 photometric measurement, 130
 photon, 130
 photoperiod, 44
 photosynthesis, 121
Phragmites australis, 123, 129
 phylogenetic, 6
 phylogeny, 39, 112, 113
 physical environment, 117
 physiological, vii, x, 3, 19, 114, 116, 117, 118, 119, 120, 126, 127, 181, 182, 186, 215, 236
 physiology, 13, 24, 132, 182
 pigs, 217, 218
 plague, 26
 planning, viii, xiv, 4, 103, 106, 236, 254, 260, 301, 302, 309, 310, 311
 plants, vii, viii, ix, xv, 4, 8, 9, 10, 12, 13, 15, 20, 22, 23, 40, 77, 88, 111, 112, 113, 114, 115, 118, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 136, 177, 184, 185, 252, 316, 317, 333, 335, 339, 341, 342
 plasmids, 204, 205, 215
 plastic, 65
 play, xiii, 18, 24, 164, 183, 254, 255, 270, 314, 329
 point mutation, xi, 202, 215
 poisoning, 16, 296, 297, 298
 poisonous, 272
 poisons, 189
 Poland, 10, 13, 16, 29, 36, 220, 299, 300
 polar bears, 252
 police, 14, 103

- political instability, 105, 107
 politics, 108
 pollination, 136
 pollutants, 183, 187, 188, 190, 202, 293
 pollution, x, 5, 42, 78, 102, 181, 195, 202, 206, 213, 214, 215, 283, 293, 298, 299, 300
 pond, 269, 326, 328, 330, 331
 pools, ix, 111
 poor, 11, 23, 50, 51, 77, 79, 81, 82, 86, 100, 101, 104
 population, vii, viii, xi, xii, xiv, 3, 4, 8, 10, 11, 12, 13, 14, 15, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 39, 41, 42, 43, 44, 45, 46, 47, 50, 51, 53, 54, 56, 79, 81, 86, 87, 88, 89, 98, 101, 102, 103, 105, 106, 113, 120, 125, 128, 130, 131, 135, 136, 137, 139, 141, 142, 143, 144, 146, 151, 152, 155, 161, 162, 163, 165, 169, 170, 171, 172, 173, 177, 178, 183, 186, 187, 188, 189, 218, 220, 223, 232, 239, 240, 241, 242, 243, 246, 248, 249, 250, 251, 252, 256, 262, 272, 275, 301, 302, 303, 305, 307, 308, 309, 310, 311, 312, 316, 317, 320, 321, 330, 334, 335, 336, 339, 340, 341, 342
 population density, 11, 12, 15, 18, 21, 22, 23, 24, 46, 103, 335, 336, 340, 341
 population growth, 10, 54, 56, 98
 population size, xiv, 3, 12, 13, 35, 56, 125, 144, 178, 302, 305, 308, 310
 pores, 29
 Portugal, x, 201, 203, 205, 206, 213, 216, 217, 218, 219, 220, 221, 328
 positive correlation, 13, 74, 334, 339
 positive feedback, 101
 positive interactions, 177
 posttraumatic stress, 103
 potassium, 129
 poultry, 217, 218, 221
 poverty, 51, 88, 98, 103, 106
 poverty reduction, 88
 power, 11, 58, 119, 302
 powers, 119
 PPO, 34
 practical knowledge, 103
 precipitation, 10, 13, 14, 205, 240, 314, 316, 318
 predators, xi, 12, 16, 17, 19, 20, 37, 166, 178, 223, 224, 225, 226, 227, 229, 231, 232, 233, 234, 235, 313, 314, 320, 322, 323, 326, 328, 330, 331
 prediction, x, 181, 186, 342
 predictive model, 95
 pre-existing, 122
 preference, xi, 223, 224, 225, 228, 236, 319, 320, 341
 pregnancy, 29
 premium, 328
 pressure, x, xi, 56, 78, 121, 152, 182, 183, 194, 201, 204, 215, 223, 224, 226, 230, 231, 258, 271
 prevention, 12, 19, 25, 104
 preventive, 320
 prices, 87
 primate, 68
 primates, 59, 68, 82
 priming, 29
 priorities, 102
 pristine, 259
 private, 52, 56, 57, 83, 87, 88, 94, 227, 234, 280, 281, 286, 314, 330
 private ownership, 57, 83
 private property, 94
 privatization, 92
 probability, 120, 127, 207, 216, 230, 231, 286, 303, 304, 305, 306, 307, 309, 310
 producers, 12, 320
 production, 5, 34, 36, 46, 52, 78, 79, 184, 189, 217, 320, 323, 328, 329
 productivity, 32, 42, 87, 100
 professional management, 52
 profit, 285, 328
 profits, 85
 progesterone, 46
 prognosis, 38
 program, 12, 59, 88, 106, 185, 186, 195, 197, 217, 269
 prokaryotes, 217
 prolactin, 46
 promote, xiii, 50, 104, 113, 116, 124, 204, 259, 277, 335
 property, 50, 59, 77, 114, 115, 162, 321, 330
 prophylaxis, x, 201
 protected area, 53, 54, 55, 81, 85, 87, 88, 89, 91, 92, 94, 98, 101, 103, 105, 107, 108, 109, 224, 307, 308, 310, 316
 protected areas, 53, 54, 55, 81, 85, 87, 88, 89, 91, 92, 94, 107, 108, 224, 310, 316
 protection, 11, 17, 20, 22, 32, 34, 79, 87, 88, 92, 104, 108, 202, 224, 234, 236, 285, 310, 321, 326, 327, 331
 protein, 106, 300
 proteins, 183, 188
 protocol, 37
 protocols, 190, 210
 protozoa, 43, 45
 proximal, 30
 proxy, 242
Pseudomonas, 179
 psychology, 280
 public, xiv, 25, 27, 35, 41, 52, 59, 65, 105, 204, 247, 255, 256, 259, 267, 269, 270, 273, 285, 286, 287, 289, 290, 320, 325
 public awareness, 105
 public domain, 247
 public health, 27, 35, 41, 204
 public interest, 320
 public opinion, 273
 public support, xiv, 259, 267, 325
 pumps, 288
 pupae, 12, 22, 31

Q

qualifications, 263
Quercus, 5, 16, 23, 29, 32, 206
 questionnaire, 260
 questionnaires, 259, 260

R

radiation, 130
 radio, 18, 19
 radius, 14, 18, 58, 60, 61, 73
 rain, vii, 19, 55, 57, 63, 64, 128, 132, 184, 318
 rain forest, vii, 132
 rainfall, xii, 55, 63, 78, 79, 239, 251, 303, 316
 random, xiv, 53, 313, 328
 range, xiii, 4, 8, 18, 20, 23, 27, 29, 36, 42, 50, 51, 52, 53, 54, 56, 79, 80, 81, 83, 84, 87, 88, 93, 114, 115, 121, 123, 124, 136, 140, 188, 202, 203, 235, 237, 242, 248, 294, 305, 316, 322, 323
 rangeland, 55, 79, 87, 131
 rape, 103
 RAS, 333, 341
 rat, 30, 31, 33, 44, 189, 248
 rationality, 280
 rats, 32, 34, 35, 39, 297, 298
 reactive oxygen, 189, 198
 reactive oxygen species (ROS), 189, 198
 reading, 58, 266
 reality, 89, 271
 rebel, 103, 104
 recall, 146, 163
 receptors, x, 181, 186, 188, 204, 233
 recession, 11
 reclamation, 5
 recognition, 43, 46, 279, 310
 reconciliation, xiv, 325
 recovery, ix, 34, 112, 126, 186, 202, 213, 326
 recreation, xii, 237, 253, 254, 255, 258, 259, 260, 261, 274, 275
 recreational, xi, xiii, 202, 203, 216, 254, 258, 261, 262
 Red Cross, 105
 red light, 115, 116, 121, 123
 redistribution, 233
 reduction, 8, 23, 31, 88, 102, 202, 225, 229, 321
 refuge, xii, 203, 227, 253, 255, 271, 272
 refugee camps, 100, 103, 106
 refugees, viii, 97, 99, 100, 101, 103, 104, 106, 107, 109
 regeneration, 9, 39, 129, 131, 232
 regional, xiii, 108, 240, 257, 258, 277, 282, 283, 288, 303
 regional economies, 257, 258
 regression, xiv, 32, 243, 246, 296, 297, 298, 299, 300, 301, 302, 304, 311
 regression line, 296, 297, 298, 299, 300

regular, 5, 17, 106, 229, 269, 329
 regulation, xi, 34, 35, 38, 44, 45, 129, 223
 regulations, 232, 321
 rehabilitation, xii, 221, 253, 271, 272
 rejection, 32
 relationship, xv, 6, 9, 13, 21, 30, 32, 54, 60, 64, 114, 118, 124, 175, 187, 197, 243, 246, 248, 263, 297, 316, 333
 relationships, 31, 60, 106, 124, 186, 187, 252, 269
 relatives, 258
 relaxation, 261
 relevance, x, xv, 34, 149, 182, 187, 189, 261, 273, 325
 remission, 105
 remote sensing, 309, 311
 renal, vii, viii, 3, 4, 25, 26, 38, 40, 298
 renewable resource, 101, 108
 repair, 85
 replication, 214
 reproduction, vii, 3, 4, 7, 10, 13, 15, 19, 21, 37, 41, 42, 46, 82, 120, 124, 126, 127, 131, 137, 163, 242, 248, 330, 331
 reptile, 190, 242, 243, 250
 reptile species, 190
 reptiles, 184, 187, 188, 189, 190, 196, 200, 248
 research, 18, 20, 26, 27, 57, 90, 103, 105, 107, 121, 127, 137, 248, 249, 254, 256, 258, 260, 279, 289, 309, 311, 320
 Research and Development, 335
 researchers, 18, 54, 57, 182, 213, 305
 reserves, ix, xi, 95, 111, 120, 122, 206, 223, 224, 316
 reservoir, vii, 3, 4, 24, 25, 26, 27, 30, 39, 40, 43, 45, 205, 215, 220
 reservoirs, viii, x, 4, 25, 26, 201, 204, 214, 216
 resettlement, 106, 109
 residential, 58, 281, 299
 residuals, 42
 residues, 106
 resilience, 251
 resin, 10
 resistance, x, xi, 16, 33, 201, 202, 204, 205, 207, 210, 211, 212, 213, 214, 215, 216, 217, 218, 219, 220, 221
 resistance, 217
 resolution, 302, 309
 resource availability, 240
 resources, viii, xii, 46, 50, 51, 52, 56, 57, 72, 77, 78, 79, 80, 81, 82, 83, 86, 87, 93, 97, 99, 100, 101, 102, 104, 105, 107, 108, 162, 202, 217, 232, 239, 240, 254, 274, 314, 326, 330
 restructuring, 79
 retaliation, 50
 retardation, 188
 returns, 282
 revenue, 51, 54, 84, 87, 264, 269, 270, 283
 Reynolds, 254
 rhetoric, 109
Rhizobium, 177
 rhythm, 18, 225

rhythms, 225
 ribosomes, 214
 rice, 33
 rice field, 33
 risk, 16, 26, 43, 184, 185, 188, 190, 194, 197, 198,
 200, 234, 235, 271, 286
 risk assessment, 184, 188, 194, 197, 198
 risks, 125, 281, 293
 river systems, 78
 rivers, xi, 7, 11, 63, 68, 77, 78, 79, 85, 100, 125, 202,
 205, 221, 250, 316, 320
 Roads, 58, 61, 62, 70, 72, 81
 Rocky Mountain National Park, 230, 252
 rodent, vii, viii, 3, 4, 9, 11, 12, 13, 14, 15, 16, 17, 22,
 23, 24, 25, 26, 28, 29, 30, 32, 33, 34, 35, 36, 37,
 38, 41, 43, 45
 rodenticides, 16, 17, 33, 38, 39, 182
 rodents, vii, viii, 3, 4, 5, 6, 7, 10, 11, 12, 13, 14, 15,
 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 28, 30,
 31, 32, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44,
 45, 46, 47, 202
 rods, 204
 Rome, 274
 Royal Society, 233, 236
 ruminant, xv, 333, 334, 335, 336, 338, 339, 340, 341
 rural, 51, 88, 96, 100, 102, 105, 106, 256, 257, 274,
 278, 281, 320
 rural areas, 105
 rural development, 96
 Russia, 333, 341
 Russian, 176, 335, 342
 Rwanda, 100, 101, 102, 103, 106, 108, 109

S

sacred, 104
 safeguard, 87, 288
 safety, 183, 187, 269, 287
 salaries, 105
 sales, 106, 283
 saline, 55
 Salmonella, 199, 213, 219, 221
 salt, 202
 salts, 210
 sample, 9, 18, 20, 29, 119, 207, 216, 254, 259, 261,
 262, 263, 294
 sample survey, 254
 sampling, ix, 15, 23, 37, 44, 46, 47, 82, 112, 125,
 126, 127, 128, 187, 207, 214, 215, 216
 sand, 22, 127
 SAS, 243, 246, 252, 294
 satellite, xiv, 302, 309, 310
 satisfaction, xii, 253, 254, 260, 263, 274, 275, 279
 saturation, 137, 156, 157, 158, 159, 160, 162, 163,
 164, 165, 166, 167, 168, 169, 171, 173, 174
 savannah, 96, 236
 Scandinavia, 11, 44, 236
 scarcity, 51, 101, 326

Schmid, 198
 scholarships, 216
 school, 51, 59, 66, 256, 317
 scientific knowledge, 271
 scientists, vii, 16, 27, 116
 SCN, 225
 sea ice, 240
 seabirds, 252, 297
 seals, 240, 283, 326
 search, 155, 258
 searching, 19, 81, 241
 seasonal variations, 9
 seasonality, 132
 second generation, 17
 secondary data, 256
 secretion, 44
 secrets, 183, 196
 security, 90, 100, 229, 231, 269, 329
 sedentary, 81
 sediments, 184
 seed, ix, 5, 9, 10, 12, 13, 16, 20, 23, 34, 36, 43, 45,
 111, 112, 113, 114, 115, 116, 117, 118, 119, 120,
 121, 122, 123, 124, 125, 126, 127, 128, 129, 130,
 131, 132, 133, 329
 seeding, 41
 seedlings, ix, 4, 5, 12, 29, 39, 42, 111, 113, 117, 120,
 121, 122, 178
 seeds, ix, 4, 5, 8, 9, 10, 11, 12, 15, 17, 20, 21, 22, 23,
 24, 42, 45, 111, 112, 113, 114, 116, 117, 118, 120,
 121, 122, 123, 124, 125, 126, 127, 128, 129, 131,
 132, 133, 136
 selecting, 228
 selenium, 293
 semi-arid, 50, 55, 91
 senescence, 188
 sensing, 311
 sensitivity, 29, 123, 133, 183, 187, 190
 separation, 10, 36
 series, 42, 228, 303, 311, 326
 serology, 25
 serum, 197
 service provider, 329
 services, xv, 51, 79, 82, 258, 261, 263, 269, 270,
 282, 288, 289, 325, 326, 327, 328, 329, 331
 settlements, 57, 61, 62, 63, 72, 73, 82, 83, 85, 86, 89,
 224, 232
 settlers, 281
 sewage, 202
 sex, 15, 17, 18, 19, 183, 190, 197, 218, 226, 242,
 248, 316, 318
 sex hormones, 19
 sex ratio, 218, 318
 sex steroid, 197
 sexuality, 250
 SFS, 66, 95
 shade, 129, 269
 shape, 60, 128, 130, 132, 204, 279, 280, 334
 shaping, 33
 shares, 53, 79, 83

- sharing, 50, 51, 52, 53, 95, 227, 235, 310
 sheep, 59, 64, 66, 67, 68, 80, 98, 278, 281, 283
 shellfish, xiii, 294
 shelter, xi, 18, 20, 82, 223, 224, 255
 Shigella, 213
 shock, 232
 shoot, 99, 228
 shores, 11
 short run, 258
 shortage, 78
 short-term, 99, 130, 248
 Short-term, 248
 shoulders, 317
 shrubland, 55, 59, 64, 68, 69, 70, 76, 80, 82
 shrublands, 82
 shyness, xi, 223, 224
 sibling, 121
 Sierra Leone, 100, 104
 sign, 141, 143, 151
 signals, ix, 38, 44, 111, 122, 124, 131, 226
 signs, 16, 68, 229, 230
 silver, 36
 similarity, 56, 126, 127, 130, 215, 225
 simulation, 242, 252
 simulations, 136, 153, 155
 Singapore, 196, 311
 sites, vii, 79, 105, 117, 132, 189, 207, 210, 214, 215, 216, 226, 254, 261, 280, 282, 283, 285
 skills, 271, 272
 skin, 25, 187, 220
 sleep, 225
 sleep-wake cycle, 225
 Slovakia, 15
 Slovenia, 31, 261
 small intestine, 8
 small mammals, 7, 25, 26, 29, 30, 31, 33, 34, 36, 37, 38, 42, 44, 45
 Smithsonian, 46
 Smithsonian Institution, 46
 smoothing, 29
 social activities, 288
 social attitudes, 279
 social behavior, 21, 22
 social behaviour, 30
 social benefits, 287
 social cohesion, 287
 social conflicts, 83, 98, 102
 social factors, 39, 103
 social group, 233
 social institutions, 57, 101
 social organization, 46
 social problems, 100
 social regulation, 34
 social relations, 13, 21
 social status, 321
 social structure, 14, 21, 225
 social support, 266
 socioeconomic, 102, 103
 socioeconomic conditions, 102
 sociological, 287, 288
 sodium, 210
 software, 60, 336
 soil, ix, x, 5, 9, 11, 12, 17, 25, 30, 35, 37, 42, 45, 55, 79, 80, 81, 100, 111, 112, 113, 114, 115, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133, 136, 181, 182, 215, 282, 286, 299, 341
 soil erosion, 79, 282, 286
 soil particles, 117, 121, 128
 soil seed bank, ix, 111, 112, 113, 114, 118, 124, 125, 126, 127, 128, 130, 131
 soils, ix, 10, 55, 79, 111, 127, 130, 205, 219
 solar, 85
 solar panels, 85
 solutions, 141, 145, 147, 155, 176, 179, 224, 322, 326, 329
 Sorghum, 128, 129
 South Africa, 93, 95, 99, 100, 235, 321
 South America, 323
 South Dakota, 235
 soy, 182, 184
 soybean, 195, 316
 space-time, 237
 Spain, 17, 203, 218, 220, 244, 261, 311
 spatial, viii, xiv, 30, 33, 49, 54, 58, 59, 60, 62, 83, 84, 85, 86, 88, 89, 90, 91, 95, 120, 225, 227, 236, 237, 302, 304, 309, 310, 311, 313
 spatial analysis, viii, 49, 59, 60, 90, 95
 spatial location, viii, xiv, 49, 54, 58, 84, 85, 313
 speciation, 249
 species, vii, ix, x, xi, xii, xiii, xv, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, 28, 31, 34, 35, 38, 40, 45, 46, 50, 52, 53, 54, 55, 59, 60, 63, 64, 66, 68, 72, 74, 75, 76, 77, 78, 79, 80, 82, 84, 86, 88, 96, 98, 100, 105, 106, 111, 112, 113, 114, 115, 116, 117, 118, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 132, 135, 136, 137, 144, 146, 152, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 177, 178, 182, 184, 185, 186, 187, 189, 190, 193, 194, 198, 200, 202, 203, 205, 206, 214, 215, 216, 219, 221, 223, 224, 225, 226, 230, 231, 232, 233, 236, 239, 240, 241, 242, 243, 244, 246, 247, 248, 249, 250, 252, 254, 255, 259, 267, 270, 271, 272, 273, 277, 278, 279, 280, 281, 282, 283, 285, 286, 288, 289, 294, 295, 296, 297, 299, 302, 303, 305, 307, 310, 311, 312, 314, 316, 319, 320, 325, 326, 327, 328, 329, 330, 333, 334, 335, 336, 337, 338, 339, 340, 341, 342, 343
 species richness, xv, 311, 333, 334, 335, 338, 339, 340, 343
 specificity, 205
 spectrum, 23, 115, 116, 121
 speed, 127, 187
 spindle, 189
 spine, 303
 spiritual, 104

- spleen, 11, 27
 sports, 203
 springs, vii, 3, 78, 248
 sprouting, 39
 Sri Lanka, xii, xiii, 253, 254, 255, 256, 257, 258, 259, 261, 262, 263, 265, 267, 268, 269, 271, 273, 274, 275
 stability, 44, 135, 136, 139, 141, 143, 145, 147, 148, 150, 151, 152, 153, 161, 162, 164, 169, 170, 173, 254, 258, 334, 342
 stabilization, 340
 stabilize, 53, 103
 stages, x, xv, 17, 26, 53, 182, 184, 187, 188, 248, 298, 333, 335, 340, 341
 stakeholders, viii, 77, 87, 88, 97, 103, 104, 105, 107, 108
 standard deviation, 119
 standard error, 119
 standards, x, 183, 201, 205, 269, 279
 staphylococci, 219
 starvation, 251
 statistics, 29, 57
 steroid, 17, 44, 197
 steroidogenesis, 44
 Stimuli, 123
 stimulus, 185, 232
 stochastic, 125
 stock, xiv, 270, 271, 313, 316, 317, 330
 stock value, 317
 stomach, 23
 storage, 116, 118, 119, 122
 strain, 44, 216
 strains, x, xi, 25, 26, 201, 202, 204, 205, 213, 214, 216, 217, 219
 strategic, 107, 216, 264
 strategic management, 216
 strategies, viii, xi, 29, 51, 52, 56, 80, 97, 102, 103, 104, 107, 126, 187, 223, 225, 226, 229, 231, 232, 237, 241, 247, 258, 286, 309, 314, 320, 342
 stratification, 116, 119, 120
 streams, 11, 202, 206, 207, 215, 250
 strength, 233, 266
 streptococci, 219
 stress, 21, 32, 39, 51, 103, 258, 288
 STRUCTURE, 333
 students, 259, 260, 263
 Styria, 43
 sub-Saharan Africa, viii, 97, 108
 subsidies, 281
 subsistence, 100, 102
 substances, 22, 23
 success rate, 17
 suffering, 206, 270
 sulfonamides, 215
 Sumatra, 272
 summer, 11, 13, 15, 18, 19, 20, 21, 22, 23, 120, 121, 123, 206, 256
 Sun, 178
 Sunday, 275
 sunflower, 22
 supervisors, 105
 supplemental, 38
 suppliers, 255
 supply, 14, 32, 58, 82, 85, 102, 106, 329, 335
 suppression, 16, 17, 25, 182
 suprachiasmatic, 225
 suprachiasmatic nucleus, 225
 surface area, 8, 12, 14
 surface layer, 131
 surface water, 25
 surfactants, 183, 184, 191
 surgeons, 255
 surplus, 39, 264
 surveillance, 225
 survival, xii, 5, 13, 17, 18, 19, 24, 32, 37, 42, 81, 90, 102, 113, 120, 127, 136, 137, 138, 141, 151, 153, 156, 158, 172, 182, 186, 188, 194, 203, 213, 233, 239, 240, 241, 242, 244, 251, 252, 271, 272, 286, 288
 survival rate, xii, 13, 239, 240, 241, 244
 surviving, 146, 161, 169, 270, 285
 susceptibility, x, 9, 95, 186, 188, 201, 210
 sustainability, 92
 sustainable growth, 126
 sustainable tourism, 275
 swamps, 45, 77, 78, 79, 86, 96
 Sweden, 8, 9, 10, 35, 221, 261, 330, 331
 switching, 41, 240
 Switzerland, 91, 93, 197, 218, 224, 261
 symbioses, 178
 symbiosis, ix, 135, 136, 137, 138, 156, 165, 169, 177, 178, 179
 symbiotic, ix, 135, 136, 137, 151, 161, 162, 163, 165, 166, 167, 168, 173, 175, 176, 178
 symbolic, ix, 112
 symbols, 231, 232, 314, 326
 symmetry, 341
 sympathy, 326
 syndrome, vii, viii, 3, 4, 25, 26, 38, 40, 103
 synergistic, 183
 synthesis, xi, 40, 195, 201, 214
 systematics, 31, 176
 systems, xv, 20, 83, 94, 136, 162, 167, 175, 176, 177, 178, 188, 189, 198, 199, 202, 203, 210, 248, 249, 333, 335, 342

T

- tactics, viii, 97, 99, 104, 227
 taiga, 35
 tall trees, 29
 tangible, 51
 tangible benefits, 51
 tanks, 71
 Tanzania, 55, 83, 93, 94, 100, 101, 103, 104, 109
 taste, 15, 17
 tax incentive, 321

- tax incentives, 321
 taxa, 117, 342
 taxes, 327
 taxonomic, 98
 technology, 99, 195, 302
 teeth, 5
 telephone, 289
 telophase, 199
 temperature, xii, 13, 14, 15, 46, 114, 115, 117, 118, 120, 121, 122, 123, 124, 128, 129, 131, 132, 133, 184, 185, 187, 239, 240, 242, 248, 250, 251, 252, 303, 314
 temporal, ix, 111, 220
 tenure, 94
 teratogenic, 182, 188
 territorial, 9, 202
 territory, 9, 14, 17, 18, 19, 20, 21, 203, 207, 227, 330
 territory defense, 207
 tertiary education, 263
 testes, 211
 tetracycline, 210, 215
 Thailand, 274
 thalamocortical system, 225
 thallium, 293
 theory, 53, 54, 103, 241
 therapeutics, 215
 Thomson, 63, 65, 69, 74, 75
 threat, viii, xii, 13, 16, 39, 49, 50, 53, 54, 83, 84, 85, 87, 89, 202, 205, 239, 240, 272, 273, 312, 326
 threatened, viii, 49, 182, 185, 314
 threatening, 82, 310
 threats, 53, 57, 78, 87, 273, 309
 threshold, 32, 115, 157, 161, 162, 304, 306, 342
 throat, 317
 ticks, 26, 43
 Tilapia, 190
 timber, 5, 58, 99, 100, 102, 104
 time, viii, xii, 4, 11, 12, 15, 16, 17, 18, 21, 22, 23, 25, 26, 56, 59, 85, 101, 103, 117, 120, 126, 136, 145, 149, 153, 155, 156, 157, 158, 159, 160, 173, 176, 188, 213, 224, 227, 228, 230, 231, 234, 239, 240, 241, 248, 249, 250, 255, 258, 265, 267, 270, 272, 281, 288, 289, 303, 310, 327, 330, 342
 time frame, 248
 time periods, 230
 timing, ix, 111, 120, 123, 124, 126, 131, 227
 tin, 58, 59, 65
 tissue, 43
 Tokyo, 111, 132, 293, 299, 300, 301, 311
 tolerance, xi, 80, 223, 224, 331
 tomato, 78
 tonic, 225
 topographic, 302
 total employment, 282
 tourism, xiii, 51, 52, 54, 77, 84, 85, 87, 88, 91, 105, 225, 231, 236, 254, 264, 265, 274, 275, 277, 280, 281, 282, 283, 285, 286, 287, 288, 290
 tourist, 79, 255, 256, 258, 259, 260, 261, 263, 272, 274, 278, 280, 283, 285, 286, 288
 toxic, 16, 17, 22, 23, 182, 183, 184, 187, 293, 316, 317
 toxic effect, 16, 17, 183, 187
 toxic substances, 22, 23
 toxicity, 184, 187, 188, 191, 196
 toxicological, 187, 188, 190
 toxicology, 198
 toxins, 217
 tracking, 29
 trade, 51, 55, 101, 104, 105, 106, 107, 108, 183
 trade-off, 226
 trading, 106
 tradition, 27
 traffic, 81, 85, 89
 training, 232, 234, 320
 traits, 113, 124, 130, 215, 241, 251
trans, 149, 299, 300
 transaction costs, xiv, 325
 transactions, 328
 transduction, xi, 201
 transfer, 197, 204, 205, 215
 transformation, 119, 121, 182, 188, 297, 299, 335
 transgenic, 182, 195
 transition, 105
 translation, 214, 299, 300
 translocation, 217, 320
 transmission, xi, 25, 39, 43, 50, 130, 131, 177, 202, 204, 213, 214, 215, 216
 transplantation, 112, 113
 transport, vii, 3, 4, 213
 transposons, 204, 205
 traps, 11, 12, 15, 18, 19, 23, 46, 224
 travel, 258, 260, 262, 271, 282
 trees, ix, 4, 5, 8, 9, 10, 11, 20, 21, 30, 40, 42, 79, 100, 131, 132, 135, 136, 206, 232, 248, 269, 335
 trend, ix, 111, 241, 246, 309
 trial, 34
 tribes, 50, 56
 trigeminal, 44
 tropical forest, 109
 tropical forests, 109
 trout, 250
 trucks, 99
 trust, 94
 trusts, 287, 288
 tularemia, 26
 tundra, 249, 342
 Turkey, 275
 turkeys, 221
 turnover, 30, 183, 282, 283
 turtle, 275
 turtles, 248, 250
 two-way, 246

U

Uganda, 274
 Ukraine, 24

ultrasound, 16, 34
 unclassified, 72
 UNESCO, 108
 UNFPA, 311
 uniform, 205
 United Kingdom, 107, 109, 135, 244, 245
 United Nations, 109
 United Nations Environmental Programme, 106, 109
 United States, 30, 34, 40, 234, 280, 322, 343
 universities, 263
 updating, 330
 urban areas, 105, 106, 202
 urbanization, 53
 urine, 25
 USSR, 342
 Utah, 321

V

vaccination, 316, 317
 valence, 12
 validation, 309
 values, xiii, 14, 98, 104, 106, 119, 153, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 190, 192, 199, 230, 259, 264, 274, 277, 279, 280, 281, 282, 287, 288, 294, 295, 298, 316, 337, 339
 vanadium, 293, 300
 variability, 32
 variable, 21, 136, 184, 227, 240, 243, 248, 304
 variables, xv, 33, 125, 140, 242, 304, 333
 variation, 6, 8, 28, 32, 35, 41, 45, 112, 116, 130, 220, 235, 250
 vector, 26
 vegetables, 205, 219
 vegetation, ix, xv, 10, 11, 13, 14, 20, 23, 26, 55, 79, 81, 84, 99, 111, 112, 113, 120, 121, 122, 123, 125, 126, 127, 129, 130, 131, 132, 202, 225, 232, 281, 282, 304, 315, 317, 333, 334, 335, 336, 339, 340, 341, 342, 343
 vegetative reproduction, 120
 vehicles, 213
 vein, 297
 Venezuela, 322
 Vermont, 289
 vertebrae, 7, 317
 vertebrates, 44, 187, 225
 veterinarians, 27
 victims, xiv, 103, 313, 320
 village, 105
 violence, 104, 106
 violent, 98, 102, 105, 108, 109
 virulence, 25, 204, 205, 217
 virus, 26, 28, 30, 31
 virus infection, 28
 viruses, 26, 30
 visible, 8, 10, 121, 173, 174, 227, 232, 330
 vision, 107

W

volcanic activity, 55
 voles, 4, 6, 7, 8, 9, 10, 11, 12, 15, 18, 19, 22, 23, 24, 27, 28, 29, 31, 33, 34, 35, 36, 37, 38, 39, 40, 43, 44, 45, 46, 249
 vulnerability, 101
 walking, 58, 59, 269
 war, viii, 97, 98, 99, 100, 101, 102, 103, 104, 105, 107, 108, 109
 warfare, 99, 102, 103, 104, 106, 107, 109
 warfarin, 33, 38
 warlord, 100
 Warsaw, 32
 warts, 9
 waste disposal, 102
 wastes, 214
 water, vii, x, xi, 3, 5, 11, 17, 19, 20, 25, 45, 50, 51, 53, 55, 56, 57, 63, 64, 68, 70, 72, 77, 78, 79, 80, 82, 83, 84, 85, 86, 87, 89, 100, 101, 117, 120, 123, 181, 182, 184, 187, 202, 203, 204, 205, 206, 213, 214, 215, 216, 220, 248, 250, 269, 283, 297, 299
 water quality, 100, 206, 215
 water resources, 51, 72, 78, 79, 86, 87
 water supplies, 50
 waterfowl, 297
 wavelengths, 121
 wealth, vii, 3, 4, 56
 weapons, 85, 105, 224
 web, 177, 184, 233, 242
 weight changes, 37
 weight loss, 11
 welfare, 98, 213, 269, 270, 279
 welfare economics, 279
 West Africa, 99
 Western countries, 259, 279
 Western Europe, 202
 wetlands, ix, x, 77, 111, 126, 182, 202
 wild ducks, 294, 299, 300
 wild meat, 91
 wilderness, 326
 wildlife, vii, viii, x, xi, xii, xiii, xiv, xv, 4, 49, 50, 51, 52, 53, 54, 55, 56, 57, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 100, 108, 112, 181, 182, 183, 188, 195, 196, 201, 213, 214, 216, 221, 224, 232, 234, 235, 239, 240, 241, 242, 247, 248, 254, 255, 256, 259, 267, 268, 270, 271, 272, 273, 274, 277, 278, 279, 280, 281, 282, 283, 285, 286, 287, 288, 289, 290, 293, 294, 296, 297, 298, 299, 301, 302, 320, 321, 323, 325, 326, 327, 330, 334
 wildlife conservation, viii, xiii, xiv, 49, 50, 51, 52, 54, 57, 77, 78, 84, 87, 93, 95, 277, 278, 279, 289, 323, 325, 326
 wind, 55, 187
 windows, 188

winter, 8, 10, 11, 13, 14, 15, 19, 20, 35, 41, 46, 114, 115, 120, 249, 252, 299
wires, 85
wood, vii, ix, 3, 8, 9, 12, 18, 22, 23, 24, 28, 30, 31, 32, 33, 34, 35, 36, 37, 40, 42, 43, 44, 45, 46, 59, 79, 112, 232, 248, 294
woods, 22, 43, 206, 227
word of mouth, 275
workers, viii, 4, 27, 105, 199, 255
workforce, 255
workplace, 258
World Bank, 322
World Health Organization, 35, 41, 196, 197, 299, 300
World War, 41, 280, 309
World War I, 41, 280, 309
World War II, 41, 280, 309
worms, 8
WTP, xii, 253, 254

X

xenobiotic, x, 181, 186, 187

xenobiotics, x, 182

Y

yang, 178
yield, 13, 23, 24, 137, 260, 261
yin, 178
yolk, 184
Yugoslavia, 38

Z

Zimbabwe, 93, 95
zinc, 299, 300
zoology, 333
zoonosis, 25
zoonotic, 4, 45
zoonotic diseases, 4