Cambridge Studies in Adaptive Dynamics

Evolutionary Conservation Biology



R. Ferrière, U. Dieckmann, and D. Couvet

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Evolutionary Conservation Biology

As anthropogenic environmental changes spread and intensify across the planet, conservation biologists have to analyze dynamics at large spatial and temporal scales. Ecological and evolutionary processes are then closely intertwined. In particular, evolutionary responses to anthropogenic environmental change can be so fast and pronounced that conservation biology can no longer afford to ignore them. To tackle this challenge, currently disparate areas of conservation biology ought to be integrated into a unified framework. Bringing together conservation genetics, demography, and ecology, this book introduces evolutionary conservation biology as an integrative approach to managing species in conjunction with ecological interactions and evolutionary processes. Which characteristics of species and which features of environmental change foster or hinder evolutionary responses in ecological systems? How do such responses affect population viability, community dynamics, and ecosystem functioning? Under which conditions will evolutionary responses ameliorate, rather than worsen, the impact of environmental change? This book shows that the grand challenge for evolutionary conservation biology is to identify strategies for managing genetic and ecological conditions such as to ensure the continued operation of favorable evolutionary processes in natural systems embedded in a rapidly changing world.

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Cambridge Studies in Adaptive Dynamics

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The modern synthesis of the first half of the twentieth century reconciled Darwinian selection with Mendelian genetics. However, it largely failed to incorporate ecology and hence did not develop into a predictive theory of long-term evolution. It was only in the 1970s that evolutionary game theory put the consequences of frequency-dependent ecological interactions into proper perspective. Adaptive Dynamics extends evolutionary game theory by describing the dynamics of adaptive trait substitutions and by analyzing the evolutionary implications of complex ecological settings.

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CAMBRIDGE UNIVERSITY PRESS Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press The Edinburgh Building, Cambridge CB2 2RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org Information on this title: www.cambridge.org/9780521827003

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First published in print format 2004

ISBN-13 978-0-511-21065-5 eBook (Adobe Reader) ISBN-10 0-511-20705-0 eBook (Adobe Reader) ISBN-13 978-0-521-82700-3 hardback ISBN-10 0-521-82700-0 hardback

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Acknowledgments

Development of this book took place at the International Institute of Applied Systems Analysis (IIASA), Laxenburg, Austria, at which IIASA's former directors Gordon J. MacDonald and Arne B. Jernelöv, and current director Leen Hordijk, have provided critical support. Two workshops at IIASA brought together all the authors to discuss their contributions and thus served as an important element in the strategy to achieve as much continuity across the subject areas as possible.

Financial support toward these workshops given by the European Science Foundation's Theoretical Biology of Adaptation Programme is gratefully acknowledged. Régis Ferrière and Ulf Dieckmann received support from the European Research Training Network *ModLife* (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission.

The success of any edited volume aspiring to textbook standards very much depends on the cooperation of the contributors in dealing with the many points the editors are bound to raise. We are indebted to all our authors for their cooperativeness and patience throughout the resultant rounds of revision. The book has benefited greatly from the support of the Publications Department at IIASA; we are especially grateful to Ewa Delpos, Anka James, Martina Jöstl, Eryl Maedel, John Ormiston, and Lieselotte Roggenland for the excellent work they have put into preparing the camera-ready copy of this volume. Any mistakes that remain are, however, our responsibility.

> Régis Ferrière Ulf Dieckmann Denis Couvet

Notational Standards

To allow for a better focus on the content of chapters and to highlight their interconnections, we have encouraged all the authors of this volume to adhere to the following notational standards:

α	Ecological interaction coefficient
b	Per capita birth rate
d	Per capita death rate
r	Per capita growth rate
R_0	Per capita growth ratio per generation
K	Carrying capacity
Ν	Population size
Ne	Effective population size
<i>x</i> , <i>y</i> , <i>z</i>	Phenotypic or allelic trait values
G	Genetic contribution to phenotype
E	Environmental contribution to phenotype
Р	Phenotype
V_G	Genetic variance(-covariance)
V_E	Environmental variance(-covariance)
V_P	Phenotypic variance(-covariance)
V_A	Additive genetic variance(-covariance)
V_D	Dominance genetic variance(-covariance)
V_I	Epistatic genetic variance(-covariance)
$V_{G \times E}$	Genotype-environment variance(-covariance)
h^2	Heritability
S	Selection coefficient/differential
R	Response to selection
U	Per locus mutation rate
U	Genomic mutation rate
L	Mutation load
F	Inbreeding coefficient
H	Level of heterozygosity
f	Fitness in continuous time ($f = 0$ is neutral)
W	Fitness in discrete time ($W = 1$ is neutral)
t	Time
Т	Duration
τ	Delay time

n	Number of entities other than individuals
p, q	Probability or (dimensionless) frequency
i, j, k	Indices
E ()	Mathematical expectation
Δ	Difference
	Average
·	Equilibrium value

Introduction

Régis Ferrière, Ulf Dieckmann, and Denis Couvet

Evolution has molded the past and paves the future of biodiversity. As anthropogenic damage to the Earth's biota spans unprecedented temporal and spatial scales, it has become urgent to tear down the traditional scientific barriers between conservation studies of populations, communities, and ecosystems from an evolutionary perspective. Acknowledgment that ecological and evolutionary processes closely interact is now mandatory for the development of management strategies aimed at the long-term conservation of biodiversity. The purpose of this book is to set the stage for an integrative approach to conservation biology that aims to manage *species* as well as ecological and evolutionary *processes*.

Human activities have brought the Earth to the brink of biotic crisis. Over the past decades, habitat destruction and fragmentation has been a major cause of population declines and extinctions. Famous examples include the destruction and serious degradation that have swept away over 75% of primary forests worldwide, about the same proportion of the mangrove forests of southern Asia, 98% or more of the dry forests of western Central America, and native grasslands and savannas across the USA. As human impact spreads and intensifies over the whole planet, conservation concerns evolve. Large-scale climatic changes have begun to endanger entire animal communities (Box 1.1). Amphibian populations, for example, have suffered widespread declines and extinctions in many parts of the world as a result of atmospheric change mediated through complex local ecological interactions. The time scale over which such biological consequences of global change unfolds is measured in decades to centuries. The resultant challenge to conservation biologists is to investigate large spatial and temporal scales over which ecological and evolutionary processes become closely intertwined. To tackle this challenge, it has become urgent to integrate currently disparate areas of conservation biology into a unified framework.

1.1 Demography, Genetics, and Ecology in Conservation Biology

For more than 20 years, conservation biology has developed along three rather disconnected lines of fundamental research and practical applications: conservation demography, conservation genetics, and conservation ecology. *Conservation demography* focuses on the likely fate of threatened populations and on identifying the factors that determine or alter that fate, with the aim of maintaining endangered species in the short term. To this end, stochastic models of population dynamics are combined with field data to predict how long a given population of an endangered

Box 1.1 Global warming and biological responses

Increasing greenhouse gas concentrations are expected to have significant impacts on the world's climate on a time scale of decades to centuries. Evidence from longterm monitoring suggests that climatic conditions over the past few decades have been anomalous compared with past climate variations. Recent climatic and atmospheric trends are already affecting the physiologies, life histories, and abundances of many species and have impacted entire communities (Hughes 2000).

Rapid and sometimes dramatic changes in the composition of communities of marine organisms provide evidence of recent climate-induced transformations. A 20-year (1974 to 1993) survey of a Californian reef fish assemblage shows that the proportion of northern, cold-affinity species declined from approximately 50% to about 33%, and the proportion of warm-affinity southern species increased from about 25% to 35%. These changes in species composition were accompanied by substantial (up to 92%) declines in the abundance of most species (Holbrook *et al.* 1997).

Ocean warming, especially in the tropics, may also affect terrestrial species. Increased evaporation levels generate large amounts of water vapor, which accelerates atmospheric warming through the release of latent heat as the moisture condenses. In tropical regions, such as the cloud forests of Monteverde, Costa Rica, this process results in an elevated cloud base and a decline in the frequency of mist days, a trend that has been associated strongly with synchronous declines in the populations of birds, reptiles, and amphibians (Pounds *et al.* 1999).

Since the mid-1980s, dramatic declines in amphibian populations have occurred in many parts of the world, including a number of apparent extinctions. Kiesecker *et al.* (2001) presented evidence that climate change may be the underlying cause of this global deterioration. In extremely dry years, reductions in the water depth of sites used by amphibians for egg laying increase the exposure of their embryos to damaging ultraviolet B radiation, which allows lethal skin infection by pathogens. Kiesecker *et al.* (2001) link the dry conditions in their study sites in western North America to sea-surface warming in the Pacific, and so identify a chain of events through which large-scale climate change causes wholesale mortality in an amphibian population.

species is likely to persist *under given circumstances*. Conservation demography can advertise some notable achievements, such as devising measures to boost emblematic species like the grizzly bear in Yellowstone National Park, planning the rescue of Californian condors, or recommending legal action to protect tigers in India and China.

A different stance is taken by *conservation genetics*, which focuses on the issue of preserving genetic diversity. Although the practical relevance of population genetics in conservation planning has been heatedly disputed over the past 15 years, empirical studies have lent much weight to the view that the loss of genetic diversity can have short-term effects, like inbreeding depression, that account for a significant fraction of a population's risk of extinction (Saccheri *et al.* 1998). There



Figure 1.1 The integrative scope of evolutionary conservation biology (b) reconciles the three traditional approaches to the management of biodiversity (a).

is even experimental support for the contention that restoring genetic variation (to reduce inbreeding depression) can reverse population trajectories that would otherwise have headed toward extinction (Madsen *et al.* 1999).

The third branch of conservation biology, *conservation ecology*, relies on utilizing, for ecosystem management, the extensive knowledge developed by community ecologists and ecosystem theorists, in particular of the complicated webs of biotic and abiotic interactions that shape patterns of biodiversity and productivity. All the species in a given ecosystem are linked together, and when disturbances – such as biological invasions, disease outbreaks, or human overexploitation – cause one species to rise or fall in numbers, the effects may cascade throughout these webs. From a conservation perspective, one of the central questions for community and ecosystem ecologists is how the diversity and complexity of ecological interactions influence the resilience of ecosystems to disturbances.

All ecologists and population geneticists agree that evolutionary processes are of paramount importance to understand the genetic composition, community structure, and ecological functioning of natural ecosystems. However, relatively little integration of demographic, genetic, and ecological processes into a unified approach has actually been achieved to enable a better understanding of patterns of biodiversity and their response to environmental change (Figure 1.1). This book demonstrates why such an integrative stance is increasingly necessary, and offers theoretical and empirical avenues for progress in this direction.

1.2 Toward an Evolutionary Conservation Biology

All patterns of biodiversity that we observe in nature reflect a long evolutionary history, molded by a variety of evolutionary processes that have unfolded since life appeared on our planet. In this context, should we be content with safeguarding as much as we can of the current planetary stock of species? Or should we pay equal, if not greater, attention to fostering ecological and evolutionary processes that are responsible for the generation and maintenance of biodiversity? Evolutionary responses to environmental changes can, indeed, be so fast and so strong that researchers are able to witness them, both in the laboratory and in the wild. Some striking instances (Box 1.2) include:

- Laboratory experiments on fruit flies that illuminate the role of intraspecific competition in driving fast, adaptive responses to pollution;
- Experiments on Caribbean lizards under natural conditions that demonstrate rapid morphological differentiation in response to their introduction into a new habitat; and
- Statistical analysis of extensive data on harvested fish stocks, from which we learn that the overexploitation of these natural resources can induce a rapid life-history evolution that must not be ignored when the status of harvested populations is assessed.

From their review of the studies of microevolutionary rates, Hendry and Kinnison (1999) concluded that rapid microevolution perhaps represents the norm in contemporary populations confronted with environmental change.

Looking much further back, analysis of macroevolutionary patterns suggests further evidence that the interplay of ecological and evolutionary processes is essential in securing the diversity and stability of entire communities challenged by environmental disturbances. Striking patterns of ecological and morphological stability observed in some paleontological records (e.g., from the Paleozoic Appalachian basin) are now explained in terms of "ecological locking": in this view, selection enables populations to respond swiftly to high-frequency disturbances, but is constrained by ecological conditions that change on an altogether slower time scale (Morris *et al.* 1995). Rapid microevolutionary processes driven and constrained by ecological interactions are therefore believed to be critical for the resilience of ecosystems challenged by environmental disturbances on a wide range of temporal and spatial scales.

Such empirical evidence for a close interaction of ecological and evolutionary processes in shaping patterns of biodiversity prompts a series of important questions that should feature prominently on the research agenda of evolutionary conservation biologists:

- How do adaptive responses to environmental threats affect population persistence?
- What are the key demographic, genetic, and ecological determinants of a species' evolutionary potential for adaptation to environmental challenges?
- Which characteristics of environmental change foster or hinder the adaptation of populations?
- How should the evolutionary past of ecological communities influence contemporary decisions about their management?
- How should we prioritize conservation measures to account for the immediate, local effects of anthropogenic threats and for the long-term, large-scale responses of ecosystems?

Box 1.2 Fast evolutionary responses to environmental change



Pollution raises threats that permeate entire food webs. Ecological and evolutionary mechanisms can interact to determine the response of a particular population to the pollution of its environment. This has been shown by Bolnick (2001), who conducted a series of experiments on fruit flies (*Drosophila melanogaster*). By introducing cadmium-intolerant populations to environments that contained both cadmium-free and cadmium-

laced resources, he showed that populations experiencing high competition adapted to cadmium more rapidly, in no more than four generations, than low-competition populations. The ecological process of intraspecific competitive interaction can therefore act as a potent evolutionary force to drive rapid niche expansion.

Reintroduction of locally extinct species and reinforcement of threatened populations are important tools for conservation managers. A study by Losos *et al.* (1997) investigated, through a replicated experiment, how the characteristics of isolated habitats and the sizes of founder populations affected the ecological success and evolutionary differentiation of morphological characters. To this end, founder populations of 5–10 lizards (*Anolis sagrei*) from a large island were introduced into 14 much smaller islands that did



not contain lizards naturally, probably because of periodic hurricanes. The study indicates that founding populations of lizards, despite their small initial size, can survive and rapidly adapt over a 10–14 year period (about 15 generations) to the new environmental conditions they encounter.

Overexploitation of natural ecosystems is a major concern to conservation biologists. Heavy exploitation can exert strong selective pressures on harvested populations, as in the case of the Northeast Arctic cod (*Gadus morhua*). The exploitation pattern of this stock was changed drastically in the early 20th century with the widespread introduction of motor trawling in the Barents Sea. Over the



past 50 years, a period that corresponds to 5–7 generations, the life history of Northeast Arctic cod has exhibited a dramatic evolutionary shift toward earlier maturation (Jørgensen 1990; Godø 2000; Heino *et al.* 2000, 2002). The viability of a fish stock is therefore not just a matter of how many fish are removed

each year; to predict the stock's fate, the concomitant evolutionary changes in the fish life-history induced by exploitation must also be accounted for. These adaptive responses are even likely to cascade, both ecologically and evolutionarily, to other species in the food chain and have the potential to impact the whole marine Arctic ecosystem.

Tackling these questions will require a variety of complementary approaches that are based on a solid theoretical framework. In Box 1.3, we outline the concept of the "environment feedback loop" that has been proposed as a suitable tool to link the joint operation of ecological and evolutionary processes to the dynamics of populations.

1.3 Environmental Challenges and Evolutionary Responses

Complex selective pressures on phenotypic traits arise from the interaction of individuals with their local environment, which consists of abiotic factors as well as conspecifics, preys and predators, mutualists, and parasites. Phenotypic traits respond to these pressures under the constraints imposed by the organism's genetic architecture, and this response in turn affects how individuals shape their environment. This two-way causal relationship – from the environment to the individuals, and back – defines the environment feedback loop that intimately links ecological and evolutionary processes.

The structure of this feedback loop is decisive in determining how ecological and evolutionary processes jointly mediate the effects of biotic and abiotic environmental changes on species' persistence and community structure (Box 1.4). Three kinds of phenomena may ensue:

- Genetic constraints and environmental feedback can result in "evolutionary trapping", a situation in which a population is incapable of escaping to an alternative fitness peak that would ensure its persistence in the face of mounting environmental stress.
- Frequency-dependent selection may sometimes hasten extinction by promoting adaptations that are beneficial from the perspective of individuals and yet detrimental to the population as a whole, leading to processes of "evolutionary suicide".
- By contrast, "evolutionary rescue" may occur when a population's persistence is critically improved by adaptive changes in response to environmental degradation.

The relevance of evolutionary trapping, suicide, and rescue was first pointed out in the realm of verbal or mathematically simplified models (Wright 1931, Haldane 1932, Simpson 1944). Now, however, these concepts help to explain a wide range of evolutionary patterns in realistic models and, even more importantly, have also been documented in natural systems (Box 1.5). Among the most remarkable examples, the study of a narrow endemic plant species, *Centaurea corymbosa*, provides a clear-cut illustration of evolutionary trapping. The collection and analysis of rich demographic and genetic data sets led to the conclusion that *C. corymbosa* is stuck by its limited dispersal strategy in an evolutionary dead-end toward extinction: while variant dispersal strategies could promote persistence of the plant, they turn out to be adaptively unreachable from the population's current phenotypic state. In general, the possibility of evolutionary suicide should not come as a surprise in species that evolve lower basal metabolic rates to cope with the stress imposed

Box 1.3 The environmental feedback loop

Populations alter the environments they inhabit. The environmental feedback loop characterizes these interactions of populations with their environments and thus plays a key role in describing their demographic, ecological, and adaptive dynamics.



The environmental feedback loop goes beyond the self-evident interaction between a population and its environment. In fact, the concept aims to capture the pathways along which the characteristics of a resident population affect the variables that describe the state of its environment and how these, in turn, influence the demographic properties of resident or variant phenotypes in the population (Metz *et al.* 1996a; Heino *et al.* 1998). Some illustrative examples of variables that belong to these three fundamental sets are given below.

- Population characteristics: mean phenotype, abundance, or biomass, number of newborns, spatial clumping index, sex ratio, temporal variance in population size, etc. All these variables may be measured, either for the population as a whole or for stage- or age-specific subpopulations.
- Environmental variables: resource density, frequency of intraspecific fights, density of predators, helpers, or heterospecific competitors, etc.
- Demographic properties: rate of growth, fecundity, mortality, probability of maturation, dispersal propensity, etc.

The resultant loop structure involves precisely those environmental variables that are both affected by population characteristics and also impact relevant demographic properties. Specifying the environmental feedback loop therefore enables a description of all density- and/or frequency-dependent demographic mechanisms and selection pressures that operate in a considered population.

The minimal number of environmental variables or population characteristics that are sufficient to determine the demographic properties of resident and variant phenotypes is known as the dimension of the environmental feedback loop (Metz *et al.* 1996a; Heino *et al.* 1998; see also Chapter 11). This dimension has two important implications. First, it acts as an upper bound for the number of phenotypes that can stably coexist in the population (Meszéna and Metz 1999). Second, adaptive evolution can operate as an optimizing process and maximize population viability, under the constraints imposed by the underlying genetic system, only if the environmental feedback loop is one-dimensional (Metz *et al.* 1996a).

Box 1.4 Evolutionary rescue, trapping, and suicide

Populations that evolve under frequency-dependent selection have a rich repertoire of responses to environmental change. In general, such change affects, on the one hand, the range of phenotypes for which a population is not viable (gray regions in the panels below) and, on the other hand, the selection pressures (arrows) that, in turn, influence the actual phenotypic state of the population (thick curves).



Three prototypical response patterns can be distinguished:

- Evolutionary rescue (left panel) occurs when environmental deterioration reduces the viability range of a population to such an extent that, in the absence of evolution, the population would go extinct, but simultaneously induces directional selection pressures that allow the population to escape extinction through evolutionary adaptation.
- Evolutionary trapping (middle panel) happens when stabilizing selection pressures prevent a population from responding evolutionarily to environmental deterioration. A particularly intriguing case of evolutionary trapping results from the existence of a second evolutionary attractor on which the population could persist: unable to attain this safe haven through gradual evolutionary change, the population maintains its phenotypic state until it ceases to be viable.
- Evolutionary suicide (right panel) amounts to a gradual decline, driven by directional selection, of a population's phenotypic state toward extinction. Such a tendency can be triggered and/or exacerbated by environmental change and is the clearest illustration that evolution cannot always be expected to act in the "interest" of threatened populations.

by an extreme environment, as exemplified by many animals living in deserts. A species that undergoes a reduction in metabolic rates must often divert resources away from growth and reproduction to invest in maintenance and survival. In consequence, reproductive rates fall and population densities decline, while the species' range may shrink. These adaptations confer a selective advantage to particular individuals, but run against the best interest of the species as a whole (Dobson 1996). Evolutionary rescue, on the other hand, is thought to be ubiquitous to maintain the diversity of communities. One example has recently been worked out in detail: the persistence of metapopulations of checkerspot butterflies (*Melitaea cinxia*) in degrading landscapes has been shown to depend critically on the potential for dispersal strategies to respond adaptively to environmental change.

Box 1.5 Evolutionary trapping, suicide, and rescue in the wild

Centaurea corymbosa (Asteraceae) is endemic to a small geographic area (less than 3 km²) in southeastern France. Combining demographic and genetic analysis, Colas *et al.* (1997) concluded that the scarcity of long-range dispersal events associated with the particular lifehistory of this species precludes establishment of new populations and thus evolution toward colonization ability, even though nearby unoccupied sites would offer suitable habitats for the species. Thus, *C. corymbosa* seems to be trapped in a life-history pattern that will lead to its ultimate extinction.



Evolution of lower basal metabolic rates in response to environmental stress seems to pave the way for evolutionary suicide. Exposing *Drosophila* to dry conditions in the laboratory for several generations leads to the evolution of a strain



of fruit fly with lowered metabolic rates and an increased resistance to dessication; incidentally, this also leads to a greater tolerance to a range of other stresses (starvation, heat shock, organic pollutants). These individuals, however, exhibit a reduction in their average birth rate, and thereby place their whole population at a high risk of extinction.

Evolutionary rescue can occur in a realistic metapopulation model of checkerspot butterflies (*Melitaea cinxia*) subject to habitat deterioration (Heino and Hanski 2001). In these simulations, which have been calibrated to an outstanding wealth of field data, habitat quality deteriorates gradually. In the absence of metapopulation evolution, habitat change leads to extinction as habitat occupation falls to zero. By contrast, the adaptive response of migration propensity results in evolutionary rescue.



Evidently, current communities must have gone through a series of environmental challenges throughout their history. Evolutionary trapping and suicide must thus have eliminated many species that lacked the ecological and genetic abilities to adapt successfully, and current species assemblages are expected to comprise those species that are endowed with a relatively high potential for evolutionary rescue (Balmford 1996). This cannot but strengthen the view that to maintain the ecological and genetic conditions required for the operation of evolutionary processes should rank among the top priorities of conservation programs.

1.4 Evolutionary Conservation Biology in Practice

In a few remarkable instances, management actions have already been undertaken with the primary aim of maintaining the potential for evolutionary responses to environmental change.

One such example is provided by the conservation plan devised for the Florida panther (Felis concolor coryi). Management of such an apex predator could be critical for the ecological and evolutionary functions of the whole web of interactions to which it is connected. After inbreeding depression was identified as a major threat to the panther population, a conservation scheme was implemented to manage genetic diversity. The aim was to reduce the short-term effects of inbreeding depression, but at the same time preserve those genetic combinations that render the Florida panther adapted to its local environment. Reinforcement with individuals that originated from a different subspecies, the Texas panther F. concolor stanleyana, was recognized as the only way to alleviate the deleterious effects of inbreeding in the remnant population of Florida panthers. The two taxa, however, are neither genetically nor ecologically "exchangeable", in the sense of Crandall et al. (2000), which implies that they are genetically isolated and adapted to different ecological conditions. A particular challenge for this evolutionary conservation plan was, therefore, to avoid loss of the genetic identity and local adaptation attained by the Florida panther. To address this problem, a mathematical model was constructed to evaluate the proportion of introduced individuals that would eliminate the genes responsible for inbreeding depression and maintain both the genes responsible for local adaptations and the neutral genes expressed by typical characters that distinguish the two subspecies morphologically (Hedrick 1995). Action was then undertaken according to these predictions.

Another characteristic example of a conservation program devised from an evolutionary perspective targets the Cape Floristic Region (CFR), a biodiversity hotspot of global significance located in southwestern Africa. To conserve ecological processes that maintain evolutionary potential, and thus may generate biological diversity, is of central concern to managers of the CFR. Over the past few decades, considerable insights have been gained regarding evolutionary processes in the CFR, especially for those that involve plants. Now the goal has been set to design a conservation system for the CFR that will preserve large numbers of species and their ecological interactions, as well as their evolutionary potential for fast adaptation and lineage turnover (Box 1.6). The currently proposed plan recognizes that extant CFR nature reserves are not located in a manner that will sustain eco-evolutionary processes. The plan also highlights difficult trade-offs between the conservation of either pattern or process, as well as between the requirements for biodiversity conservation and other socioeconomic factors.

The ultimate goal of conservation planning should be to foster systems that enable biodiversity to persist in the face of anthropogenic changes. The two examples mentioned above illustrate the grand challenges that evolutionary conservation biology ought to tackle by identifying ways to preserve or restore genetic and ecological conditions that will ensure the continued operation of favorable **Box 1.6** Evolutionary conservation biology in practice: the Cape Floristic Region There are very few ecosystems in the world for which an attempt has been made to develop conservation schemes aimed to preserve biodiversity patterns and ecoevolutionary processes in the context of a rapidly changing environment. One such is a conservation scheme suggested for the Cape Floristic Region (CFR) of South Africa, a species-rich region that is recognized as a global priority target for conservation action (Cowling and Pressey 2001). A distinctive evolutionary feature of the CFR is the recent (post-Pliocene) and massive diversification of many plant lineages. Over an area of 90 000 km², the CFR includes some 9000 plant species, 69% of which are endemic – one of the highest concentrations of endemic plant species in the world. This diversity is concentrated in relatively few lineages that have radiated spectacularly. There is evidence for a strong ecological component of the diversification processes, which involves meso- and macroscale environmental gradients and coevolutionary dynamics in plant–pollinator systems.



Conservation planning for the CFR aims to identify and conserve key evolutionary processes. For example, gradients from uplands to coastal lowlands and interior basins are assumed to form the ecological substrate for the radiation of plant and animal lineages. Suggested conservation targets amount to preserving at least one instance of a gradient within each of the major climate zones that are represented in the region. In addition, recognized predator-prey coevolutionary processes are motivating recommendations for the strict protection of three "mega wilderness areas". Altogether, seven types of evolutionary processes have been listed for conservation management, and by selecting from areas in which one or more of these seven processes are operating, a system of conservation areas has been designed, based on a map of "irreplaceability" (shown above). Units at the highest irreplaceability level (dark gray) include areas of habitat that are all essential to meet conservation goals, whereas units with lowest irreplaceability (white) comprise patches of habitat in a largely pristine state for which conservation goals can be achieved through the implementation of alternative measures. Black indicates units in which existing reserves cover more than 50% of the area. Each planning unit is sufficiently large to ensure the continual operation of critical ecological and environmental processes (in particular through plant-insect pollinator interactions) and a regular regime of natural fire disturbances.

eco-evolutionary processes in a rapidly changing world. In fact, while protecting species may be hard, there is widespread agreement that the conservation of ecological interactions and evolutionary processes will be more efficient and costeffective than a species-by-species approach (Noss 1996; Thompson 1998, 1999b; Myers and Knoll 2001). This does not rule out management measures directed at particular species (based on traditional tools such as population viability analysis), but suggests that we reconsider the motivation for doing so. Species-oriented conservation efforts are expected to be more rewarding when they target endangered species that have passed through the extinction sieve of a long history of natural and anthropogenic disturbances, and therefore should possess a higher potential for evolutionary rescue. Management must also prioritize species that are likely to play a crucial role in mediating the effect of global change on the integrity of entire networks of ecological interactions.

1.5 Structure of this Book

This volume is divided into five parts. In Part A, the basic determinants of population extinction risks are reviewed, after which Part B surveys the empirical evidence for rapid adaptive responses to environmental change. Unfolding the research program of evolutionary conservation biology, Part C shows how to integrate demographic, genetic, and ecological factors in models of population viability. Part D explains how these treatments can be extended to describe spatially heterogeneous populations, and Part E discusses embedment into the overarching context of community dynamics.

This structure leads to a development of ideas as follows:

- Part A explains how to devise population models that integrate interactions between individuals (sharing resources, finding mates) with sources of random fluctuations (demographic and environmental stochasticity). Such models are the basis for extinction-risk assessment. Different forms of dependence – which lie at the heart of population regulation and the environmental feedback loop – are shown to differ dramatically in their impact on population viability. In particular, the life cycles and spatial structure of populations must be considered if extinction risks are to be evaluated accurately.
- One motivation behind denial of a role for adaptive evolution in the dynamics of threatened populations might come from a belief that evolutionary change always occurs so slowly (e.g., at the geological time scale of paleontology) that it does not interact significantly with ecological processes and rapid environmental changes. To help overcome this widespread conception, Part B reviews recent observational and experimental studies that provide striking demonstrations of fast adaptive responses of morphological and life-history traits to environmental change. Convincing evidence is available for the existence of substantial genetic variation in life-history traits, and a current exciting line of research investigates whether genetic variability can sometimes even be enhanced by stressful environmental conditions.

- The challenge to assess the quantitative impact of life-history adaptation on extinction risk has nourished new developments in evolutionary theory. Three different stances are presented in Part C. A first option is to capitalize on a well-established modeling tradition in population genetics to investigate how mutations affect the extinction risks of small or declining populations in constant environments. Quantitative genetics offers an elegant alternative approach and allows the study of the conditions under which selection enables a population to track a changing environmental optimum. Integration of all the components of the environmental feedback loop requires the effects of density- and frequency-dependent ecological interactions to be respected, and the framework of adaptive dynamics has been devised to enable this.
- Issues that arise from the spatial dimensions of population dynamics and environmental change are tackled in Part D. Spatial heterogeneity be it intrinsic to a habitat's structure (given, for instance, by an uneven distribution of resources) or resulting from a population's dynamics (leading to self-organized patterns of abundance) modifies existing selection pressures and creates new ones. In particular, the option of individual dispersal as an evolutionary alternative to local adaptation exists only in spatially structured settings. In this context, the ecological and evolutionary role of peripheral populations must be analyzed carefully. Empirical studies suggest that processes of evolutionary rescue and evolutionary suicide may have occurred through adaptive responses of dispersal strategies to environmental degradation.
- Today, a scarcity of biological information still tends to confine the scope of viability analyses to single populations. Nevertheless, it is clear that the network of biotic interactions in which endangered species are embedded can strongly affect their viability. Environmental change may impact the focal species directly, or indirectly through its effects on other interacting species. Specific environmental changes that directly act on a single population only may be echoed by feedback responses from interacting species. To elevate our exploration of the adaptive responses to environmental change to the community level provides the motivation for the final Part E.

In addition to pursuing the main agenda of ideas outlined above, this volume also offers coverage of a broad scope of transversal themes. Chapters written in the style of an advanced textbook can be used to access up-to-date and self-contained reviews of key topics in population and conservation biology and evolutionary ecology. Crosscutting topics include:

- Extinction dynamics of unstructured and physiologically structured populations (Chapters 2 and 3);
- Dynamics of metapopulations and evolution of dispersal (Chapters 4, 14, and 15);
- Adaptive responses of natural systems to climate change, pollution, and habitat fragmentation (Chapters 5, 12, and 15);

- Empirical studies of life-history evolution in response to environmental threats (Chapters 6, 7, and 8);
- Population genetics and quantitative genetics of small or declining populations and of metapopulations (Chapters 9, 10, 12, 13, and 15);
- Adaptive dynamics theory and its applications (Chapters 11, 14, 16, and 17);
- Explorations of the demographic and genetic causes and consequences of rarity (Chapters 5, 9, 14, 15, and 18); and
- Community dynamics through evolutionary change in interspecific relations (Chapters 16, 17, and 18).

Merging these approaches will make it possible to acquire new insights into the responses of ecological and evolutionary processes to environmental change, as well as into the implications of these responses for population persistence and ecosystem diversity. The chapters herein are intended to pave the way for such integration.

The aim of this volume is to convince readers of the urgent need for systematic research into eco-evolutionary responses to anthropogenic threats. This research needs to account for, as accurately as is practically feasible, the type of environmental change, the species' life cycle, its habitat structure, and the network of ecological interactions in which it is embedded. This is a call for innovative experimental work on laboratory organisms, for a more integrative assessment of the living conditions of threatened populations in the wild, and for an extension of our theoretical grasp of processes involved in extinction and rescue. We hope that the book will entice students and researchers in ecology, genetics, and evolutionary theory to step into this open arena.

Part A Theory of Extinction



Introduction to Part A

Local changes in biodiversity happen through migration or speciation and through extinctions. The latter have been at the focus of conservation biology since the field's inception, and the purpose of this opening part is to review the rich theoretical foundations for our understanding of population extinction.

Specifically, we aim to understand how mechanisms that operate at the level of individuals scale up to the dynamics of populations and thus determine extinction risks. In the context of evolutionary conservation biology, this step is necessary to identify potential targets that impact on population viability. Such targets include classic life-history traits (e.g., demographic parameters such as survival probabilities, fecundity, or age at maturity) and behavioral traits that determine the effective interactions between individuals (e.g., propensities to move or migrate, competitive ability, or mate choice).

Connecting individual characteristics to population properties is also necessary to understand the origin of the selective pressures by which populations exert a feedback to individuals. Adaptive evolution usually proceeds by small steps: new phenotypes arise from mutation or recombination, and the individuals thus affected must compete with their conspecifics. Questions of viability and extinction are therefore important to address in assessing whether evolutionary innovations are retained through the persistence of their carriers or, instead, are eliminated through their extinction.

The theoretical material in this part should also be relevant to investigators with a primary interest in population viability analysis (PVA). For more than two decades, PVA has provided a fruitful approach to the quantitative assessment of endangered species; it is used to facilitate the design of management programs and to compare the relative merits of alternative conservation measures prior to their implementation. The species-oriented and short-term perspective of PVAs is not necessarily at odds with the ecosystem-oriented and long-term perspective suggested in this book: there are at least two important reasons for emphasizing the role of PVAs in the context of evolutionary conservation biology.

First, PVAs often target large vertebrates that are the ecological and evolutionary cornerstones of their ecosystems. Major ecological and evolutionary knock-on and ripple effects are expected for smaller species (and, indeed, for biotas as a whole) from the decline or extinction of such keystone species. An example is the current decline of elephants in African savannas. This species and many other large mammals have little hope of innovation in their evolutionary future, but their role in the ecosystem is so central that their extinction could alter the ecological interactions and evolutionary paths of many other species in a disastrous manner. Thus, PVAs are very useful to help maintain keystone species, especially if these are perched on the brink of extinction. This may sometimes win sufficient time to design and implement management measures at the broader level of communities and ecosystems. In a similar vein, the implementation of reserve systems to conserve ecological and evolutionary processes, like the ambitious conservation plan for the Cape Floristic Region, can only be gradual. It is therefore critical that actions be undertaken to minimize the extent to which conservation targets are compromised before measures of evolutionary conservation can take effect.

Second, the endangerment of species targeted by PVAs may often have an evolutionary basis. We now understand that small population size and a resultant high vulnerability to environmental stress can arise as a by-product of behavioral and life-history evolution toward large body size and competitive superiority, both of which have to be traded against low reproductive output. Species that have evolved such attributes are likely to have low abundance; such species must have passed through highly selective extinction sieves during their evolutionary history, and only those endowed with particular demographic and genetic features that enabled them to buffer environmental disturbances have been retained. Thus, rare species still extant today presumably are properly "equipped" by the evolutionary and coevolutionary processes to cope with perturbations. Conservation managers should therefore be aware of how and to what extent current and forthcoming challenges posed by human activities (often unprecedented in their scope and interaction) differ from the evolutionary history and context of a threatened species.

The three chapters in this part introduce the theoretical tools needed to evaluate the risk of extinction for a given population. This issue is addressed, in turn, for unstructured populations (Chapter 2), populations with structured life cycles (Chapter 3), and spatially structured populations (Chapter 4).

How do interactions between individuals influence a population's risk of extinction? In Chapter 2, Gabriel and Ferrière address this question by investigating the properties of unstructured population models in which populations are regulated through density dependence. These models are appropriate for organisms with simple life cycles. Extinction risks, which are inversely proportional to average times to extinction, respond differently to changes in different demographic parameters. Important scaling relationships depend upon the types of stochastic fluctuations to which populations are exposed. Demographic stochasticity originates from the random timing of birth and death events, from individual variation in birth and death rates, and from random fluctuations in the sex ratio. By contrast, external stochastic influences on population dynamics include environmental noise and rare catastrophes. Chapter 2 shows how the type and "color" of stochastic fluctuations interfere with the nonlinear mechanisms of population regulation to shape patterns of population viability and extinction.

As few life-history traits are required to parametrize unstructured population models, these models are particularly amenable to mathematical analysis. Such simplification, however, carries the cost of ignoring those life-history traits that govern transitions in a species' life cycle. This is problematic since developmental transitions, as well as intraspecific interactions that occur in different ways between particular developmental stages, often critically affect population dynamics. Chapter 3 by Legendre introduces, in a didactical manner, the concepts and tools needed to relate population dynamics to the structure and parameters of life cycles that involve discrete stages. The chapter first focuses on age-dependent stages and transitions. After a review of the basic theory, it is explained how to extend classic models to account for the influence of sexual reproduction on population viability. Traits and interactions involved in mating processes can have a dramatic impact on the extinction risks of populations. As a genetic factor of demographic change induced by sexual reproduction, the consequences of inbreeding depression are discussed.

Space introduces an extra dimension of population structure and presents new challenges for the modeling of extinction dynamics. In Chapter 4, Gyllenberg, Hanski, and Metz describe a general framework for modeling spatially fragmented populations. This enables evaluation of the effects on population viability and persistence of traits that determine spatial population structure (such as offspring dispersal). Although the general treatment is mathematically rather sophisticated, the authors demonstrate the utility of their approach for particular examples, which allows the essentials to be grasped easily. The question of metapopulation growth or decline is addressed by deriving the metapopulation's basic reproduction ratio from life-history traits and environmental characteristics. Relating these parameters to metapopulation viability requires the effects of finite population size to be taken into account, which naturally leads to a discussion of stochastic metapopulation models. The resultant analysis disentangles the relative importance of local resource dynamics, regional habitat structure, and life-history traits on the extinction risk of metapopulations.

2

From Individual Interactions to Population Viability

Wilfried Gabriel and Régis Ferrière

2.1 Introduction

Early life in temporary ponds may be tough for many larval anurans. At extremely high densities, all the tadpoles develop slowly enough, in effect because of food limitation, for them to be driven to extinction. At intermediate tadpole densities, predators like salamanders can have a significant impact on small tadpoles and exert strong selective pressures for faster individual growth. At very low tadpole densities yet another aspect comes into play: predatory salamanders have no appreciable impact because tadpole growth rates are high (resources are plentiful) and encounter rates are low because of both contact probabilities and the availability of refuges.

This classic example of density-dependent selection, demonstrated by Wilbur (1984) and Travis (1984), is instructive in several respects. First, it shows that the risk of extinction of these amphibians depends on their density in a nontrivial way. At high density, regulatory mechanisms become so strong that they may result in population extinction. At very low density, the predation risk is relaxed, which facilitates persistence. At intermediate density, the population undergoes strong selective pressures on those traits for which the adaptive changes feed back onto population density, and thereby influence the risk of extinction. This fascinating case makes it plain that regulatory mechanisms that emanate from individual interactions need to be understood to anticipate the impact of environmental change and evolutionary responses on population persistence. In this chapter we examine how different types of density-dependent mechanisms influence the risk of extinction of unstructured populations subject to three types of chance fluctuations in individual traits: demographic stochasticity, interaction stochasticity, and environmental stochasticity (Box 2.1). Chapters 3 and 4 address the cases of physiologically and spatially structured populations, respectively. These chapters provide the theoretical background necessary to investigate how the risk of extinction is affected by evolutionary processes that impact life-history traits and behavioral interactions.

2.2 From Individual Interactions to Density Dependence

Density dependence is defined as the phenomenon by which the values of vital rates, such as survivorship and fecundity, depend on the density of the population. The underlying mechanisms involve interactions between individuals, which have either negative (e.g., in the case of competition for resources) or positive effects

Box 2.1 Stochastic factors of extinction

Shaffer (1981, 1987) discussed three stochastic demographic factors of extinction:

- Demographic stochasticity is caused by chance realizations of individual probabilities of death and reproduction in a finite population. Since independent individuals tend to be averaged out in large populations, demographic stochasticity is most important in small populations.
- Environmental stochasticity arises from a nearly continuous series of small or moderate perturbations that similarly affect the birth and death rates of all individuals (within each age or stage class) in a population (May 1974). In contrast to demographic stochasticity, environmental stochasticity is important in both large and small populations.
- Catastrophes are large environmental perturbations that act directly upon population size and cause reductions in abundance. Usually seen as rare events, catastrophes in a broader sense may also involve recurrent external perturbations, such as harvesting.

We introduce the notion of *interaction stochasticity* (mating, social interactions) as a further stochastic factor of extinction in closed populations. Interaction stochasticity does not operate at the level of individuals, but at the level of pairs or groups. It involves the stochasticity of encounters between individuals that may arise in the random formation of mating pairs or of social groups.

In spatially structured populations, *migration stochasticity*, that is the chance realization of dispersal probabilities, also influences the local population dynamics, whereas the *stochasticity of extinction–recolonization* processes operate at the regional scale. Extinction–recolonization stochasticity can be regarded as a form of demographic stochasticity that affects patches instead of individuals (see Chapter 4).

(e.g., as in cooperative behavior). Although each individual's vital rates are influenced by local interactions, primarily with neighbors, the aim of a wide range of density-dependent models is to describe mean demographic parameters (i.e., the average over all the individuals present) as functions of total population size or mean population density (the mean being taken across space). Such models are best used for the mathematical exploration of qualitative phenomena. On the empirical side, the unambiguous identification of density dependence in vital rates is notoriously difficult, and the choice and fit of particular density-dependent models turns out to require massive amounts of data and an in-depth understanding of the demographic processes at work in the population (Box 2.2).

The simplest density-dependent models

The notion of population limitation was first reconciled with density-independent models of exponential growth by defining the population carrying capacity as a ceiling at which exponential growth ceases. The population size N has a constant





Existing statistical tests developed to analyze trends in population densities often yield conflicting results and in general lack the power to detect even moderate density dependence. In fact, the natural heterogeneity of population parameters that influence density serve to mask the effects of density dependence within a population.

Shenk *et al.* (1998) recently reemphasized that to detect density dependence requires investigation of the response of individual life-history traits to changes in population density. This has been achieved in very few studies as yet. By using individual histories of capture–recapture, Lebreton *et al.* (1992) found limited evidence for density dependence of survival probabilities in the roe deer (*Capreolus*). In contrast, Leirs *et al.* (1997) found that the population dynamics of a murid rodent pest (*Mastomys natalensis*) are driven by both density-independent (stochastic) and density-dependent factors, the latter affecting several demographic traits in different ways. Massot *et al.* (1992) applied the same methodology to data obtained from density manipulation of the common lizard (*Lacerta vivipara*); density was shown to have little effect on the survival parameters, whereas reproductive and dispersal traits responded strongly.

A different approach is to calibrate a structured population model that incorporates hypothesized densitydependent factors to a time series of class-specific population censuses. Dennis *et al.* (1995) used this approach to demonstrate the action of nonlinear density dependence in experimental *Tribolium* populations and to obtain a quantitative assessment of the strength of the density-dependent effects on each parameter of the model.



per capita growth rate r, except at the carrying capacity (ceiling) K where growth stops,

$$\frac{dN}{dt} = \begin{cases} rN & \text{for } 1 < N < K \\ 0 & \text{for } N = K \end{cases}$$
(2.1)

For an initial population size N_0 between 1 and K, the population grows exponentially with time t as $N(t) = N_0 e^{rt}$. If r is positive, population growth continues until K is reached. This simple model of exponential growth to a carrying capacity was analyzed by MacArthur and Wilson (1967), Leigh (1981), and Goodman (1987a, 1987b) in their investigations of demographic and environmental stochasticity. If r is negative, the population declines to extinction, which is defined to occur at a population size of N = 1 individual. For a population with an initial population size of $N_0 = K$, the time until extinction $-(\ln K)/r$ then depends on the natural logarithm of the initial size. In the following sections we examine whether a logarithmic dependence of extinction time on the initial population size also holds for stochastic models.

The ceiling-growth model, Equation (2.1), yields important insights into the effect of stochastic factors on extinction risk. Yet it is a very crude representation of population regulation. Instead of piecewise constant growth, that is, at rate r if N < K and at rate 0 if N = K, the celebrated Verhulst–Pearl logistic model assumes that the growth rate of the population decreases linearly with increasing population density,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \,. \tag{2.2}$$

The logistic model makes several assumptions about the population:

- It has a stable age distribution;
- The response to a change in population density is instantaneous;
- The intrinsic rate of increase is reduced by a constant amount for every individual added to those already present;
- Crowding affects all individuals and life stages of a population equally;
- The environment is constant; stochastic and genetic effects are unimportant.

An interesting feature of the logistic model is that it enables interpretation of the effects of density dependence of birth and death rates at the individual level. For example, density dependence may affect the death rate *d* linearly while the birth rate *b* remains constant, which leads to logistic growth if b = r and d = rN/K. Notice, however, that the same logistic growth term can be obtained by expressing the birth and death rates in many different ways. This confers a broader scope to the logistic model, but also raises difficulties when defining a stochastic counterpart to Equation (2.2) (Dennis 1989).

The models above approximate birth and death events as processes that are continuous in time. When life-history schedules are markedly seasonal, difference equations formulated in discrete time are more appropriate. The life cycle of many species of plants and animals may often be separated into a few discrete classes with transitions between them over discrete units of time (e.g., a few weeks for beetle cultures, or one year for many birds in temperate regions). By using such units, we give the system time to homogenize, so the critical assumption of a global effect of density on vital rates may be less problematic in this framework.

Density-dependent models in discrete time

Density-dependent models in discrete time take on the generic form $N_{t+1} = \phi(N_t)$, where N_t denotes population size at the time t, and ϕ is a nonlinear function. Beyond the straightforward time-discrete version of the ceiling model, in which

$$\phi(N_t) = \begin{cases} e^r N_t & \text{for } 0 \le e^r N_t < K \\ K & \text{otherwise} \end{cases},$$
(2.3)

there exists a wide variety of unstructured time-discrete, density-dependent models, reviewed in May and Oster (1976), Hassell *et al.* (1976), and Caswell and Cohen (1995). Equation (2.4a) has been used widely ever since it was introduced by Hassell (1975),

$$\phi(N_t) = \frac{e^r N_t}{(1+aN_t)^{\eta}},$$
(2.4a)

where $a = (e^{r/\eta} - 1)/K$ and η is a competition parameter. The neat feature of Equation (2.4a) is that it defines a continuum of simple models that range from the so-called Beverton–Holt model, in which $\eta = 1$ (which is equivalent to logistic growth), to the so-called Ricker model, in which η goes to infinity.

Beverton–Holt model. The Beverton–Holt model is relevant when there is a natural limitation to the recruitment of new individuals. If the survival of young is limited by the number of territories or the number of nesting sites, a fairly constant number of young will be recruited, irrespective of the number of offspring produced. This is illustrative of the notion of contest competition that gives rise to compensatory density-dependence: individuals are either fully successful, or they are not successful.

Ricker model. In contrast, the Ricker model, well-known in the form

$$\phi(N_t) = N_t e^{r(1 - N_t/K)} , \qquad (2.4b)$$

involves an overcompensatory response to population density, which results from scramble competition: all individuals are affected evenly by the competition (Lomnicki 1988). As explained in Box 2.3, the merit of this model is that it relates well-defined properties of individuals that should be accessible to empirical measurement – the size of the home range, the effect of competition per competitor, reproductive success in the absence of competition – to the population behavior. Also, the underlying assumptions (e.g., that of random dispersal) are made explicit in the mathematical derivation of the model.

Other models. Another useful equation was developed by Maynard Smith and Slatkin (1973),

$$\phi(N_t) = \frac{e^r N_t}{1 + (aN_t)^{\eta}} \,. \tag{2.4c}$$

It is only superficially similar to Equation (2.4a). Here, *a* is inversely proportional to the amount of habitat or resource available (approximately 1/K) and η controls the strength of the dependence of population growth on available resources. A further possibility reads

$$\phi(N_t) = \frac{e^r N_t}{\left[1 + (aN_t)^\eta\right]^{1/\eta}},$$
(2.4d)

Box 2.3 Scaling up from individual interactions to population dynamics

Many population dynamic equations in discrete time have been used in the literature. Yet, like the ceiling and logistic continuous-time equations, most of them lack the explicit underpinning of a rigorous derivation that would show them to be mathematically neat derivations from stochastic "first principles" that operate at the level of individuals.

One remarkable exception is provided by the celebrated Ricker model, which assumes discrete generations and a simple life cycle (Royama 1992). Within each time interval (e.g., one year), an offspring may grow to maturity with probability s_0 , and then produce offspring and die. Offspring disperse randomly and establish fixed home ranges; this means that individuals are spread across homogeneous space in a Poisson distribution. Population density is measured at the onset of the reproduction period. Mature individuals compete for resources, and the effect of competition is to reduce fecundity. Competition occurs between "neighbors" only, and the effect of competition is captured by reducing the intrinsic (i.e., maximum, in the absence of competition) fecundity b_0 by a constant factor $\kappa < 1$. Any individual is counted as a neighbor to another if their home ranges overlap.

For mathematical tractability, assume that all home ranges are circular with area σ ; as a consequence of the random (i.e., Poisson) distribution of individuals in space, given that the population density is N, the probability that an individual has i neighbors ($i \ge 0$) is equal to $(4\sigma N)^i e^{-4\sigma N}/i!$. Hence the expected per capita fecundity is $b_0 e^{-4\sigma(1-\kappa)N}$. The recursion for the expected population density given by Equation (2.4b) readily follows, with $r = \ln(s_0 b_0)$ and $K = \ln(s_0 b_0)/[4\sigma(1-\kappa)]$.

which was used, for instance, by Halley and Iwasa (1998) in their analysis of the effect of environmental and demographic stochasticity on the extinction risk (see Section 2.4).

Allee effects

In the study of the preservation of biodiversity, it seems natural to consider the following question posed by Allee (1938, p. 107): "What minimal numbers are necessary if a species is to maintain itself in nature?" The question arises when the per capita growth rate of a species is initially (i.e., at low population density) an increasing function of population density. A potentially important cause for this phenomenon, commonly termed the "Allee effect" [see recent reviews by Stephens and Sutherland (1999) and by Courchamp *et al.* (1999)], is a shortage of mating encounters in sparse populations (Allee 1931; Haldane 1953; Watt 1968; Wells *et al.* 1998). That to find mates might be difficult to achieve at low density has long been hypothesized, such as for sea urchins (Allee 1931), flour beetles (Park 1933), muskrats (Errington 1940), condors (Mertz 1971), and zooplankton (Gerritsen 1980). Three categories of empirical studies have brought relevant insights into mating rates and Allee effects, as reviewed in Dennis (1989), Stephens and Sutherland (1999), and Courchamp *et al.* (1999):

- Experiments that have detected Allee effects possibly due to mating frequency;
- Experiments (with assorted insects in mating chambers) that have shown positive dependence of mating rates on population density;
- Correlative studies for a few species in the field that have demonstrated positive relationships between mating rates and density.

Few data are available on the mating rates and population growth of rare species. Occasionally, rare organisms proved so adept at finding each other that no effects on the mating rates were detected (Teesdale 1940; Surtees and Wright 1960; Burns 1968). In contrast, a more recent study (Madsen *et al.* 1992) on a small, isolated population of adders (*Vipera berus*) suggests that an important determinant of population growth, litter success, correlates positively with mating frequency. Lande (1988) emphasized that such Allee effects in endangered species could have drastic implications for the theory and practice of conservation biology. Yet mathematical models that relate mating rates to population growth remain scarce. To date one of the most comprehensive studies remains that of Dennis (1989), who developed deterministic and stochastic models to describe the growth, critical density, and extinction probability in sparse populations that experience Allee effects. McCarthy (1997) and Poggiale (1998) have developed more recent advances. The construction of these models involves two steps:

- Starting from behavioral rules that apply to individuals, stochastic models are proposed that predict the probability of mating encounters as a function of population density;
- The mating encounter function is then incorporated into a model of population growth.

In the first step, Dennis (1989) recovered a negative exponential function under the following biological assumptions:

- Constant sex ratio;
- The probability that a female encounters a male after searching a small area is proportional to that area and to the density, and it decreases with the number of previous encounters (i.e., there is a saturation effect);
- The probability of encountering two partners in a small area is negligible.

The negative exponential function is parametrized by the effective mating area of a female, that is, the size of the area over which encounters may occur for any given individual times the proportion of males in the population (sex ratio), and by other parameters related to the presumed aggregation structure of the population. Heterogeneity between individuals in effective mating area can be taken into account, as a consequence of individual differences in, for example, mobility, size of home range, signaling, or attractiveness. From the negative exponential function arises a rectangular hyperbola function, which is mathematically similar to the so-called type II functional response heretofore used in ecological modeling to describe the response of predator feeding rate to prey density.

The mating encounter function may be incorporated *ad hoc* into the logistic Equation (2.2): a term proportional to the probability of not mating is subtracted from the per capita growth rate, to represent the reduction of reproduction because of mating shortage. Let *N* denote the population density at any given time. Using the rectangular hyperbola function, the probability of mating can be shown to be $N/(\theta + N)$; parameter θ can be seen as a behavioral trait with a value equal to the population density at which the probability of mating is 0.5. Then $1 - N/(\theta + N) = \theta/(\theta + N)$ is the probability of not mating. Thus, the logistic model adjusted for mating encounters is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{\delta\theta}{\theta + N}N, \qquad (2.5a)$$

where the coefficient δ scales the negative effect of not mating. Kostitzin (1940) was the first to publish this growth model, and Jacobs (1984) examined its behavior. Similar equations arose in the context of populations that experienced harvesting or predation (May 1977; Huberman 1978; Ludwig *et al.* 1978; Brauer 1979).

From the individual perspective, one possible interpretation of this phenomenologic model is to assume that *r* measures the per capita density-independent birth rate, rN/K the per capita density-dependent death rate, and $\delta\theta/(\theta + N)$ the rate at which individuals are removed from the population through not finding a mate. The assumption that not mating leads to permanent removal looks rather artificial. An alternative, and perhaps more natural, way of accounting for the shortage of mating encounters at low density is to condition reproduction upon finding a mate. Assuming negative linear density-dependence of the birth rate and density independence of the death rate yields

$$\frac{dN}{dt} = b\left(1 - \frac{N}{K}\right)\frac{N^2}{\theta + N} - Nd , \qquad (2.5b)$$

where b denotes the intrinsic (i.e., in the absence of negative density-dependent effects) per capita birth rate, and d the density-independent per capita death rate. Swapping the influence of negative density dependence between birth and death processes leads to the following third model

$$\frac{dN}{dt} = b\frac{N^2}{\theta + N} - N^2 d .$$
(2.5c)

A feature common to Equations (2.5a) and (2.5b) is that they predict either extinction or bistability, that is, an outcome – extinction versus persistence at an equilibrium density – contingent upon the initial population density. For persistence, the population can reach its viable equilibrium only if the initial density is larger than a critical threshold identified as an unstable equilibrium of the model. This critical threshold is germane to the notion of a minimum viable population (Soulé 1987). As we show later (Section 2.3), the existence of such a critical density has important consequences when the effect of chance factors of extinction on population viability is assessed. In contrast, Equation (2.5c) describes a kind of degenerate Allee effect: the population growth rate increases with density at low density, but the existence of a viable equilibrium always implies that the extinction equilibrium is unstable.

2.3 Demographic and Interaction Stochasticities

In this section a constant environment is assumed. We concentrate on the most basic extinction risks that result from random fluctuations in the birth and death processes and in the proportion of females in a population (the sex ratio).

Time to extinction under demographic stochasticity

In a finite population, the per capita growth rate r is subject to random variation through the independent chances of individual mortality and reproduction. Thus, for a population of size N, r is a random variable with mean \overline{r} and variance V/N(assuming no autocorrelation). The parameter V is the variance in individual reproduction rate (which comprises birth events and death chance) per unit time (Leigh 1981; Goodman 1987a, 1987b). The growth rate r of a population at a particular time is the mean reproduction rate of individuals in the population, and its variance is equal to the sampling variance of this mean, that is, individual variance divided by population size. The long-run growth rate of a population subject to demographic stochasticity is simply $\overline{r} = r$.

First, we review Lande's (1993) results on the effect of demographic stochasticity on the mean persistence time in the ceiling Equation (2.1). Lande (1993) strongly relies on diffusion theory to approximate the dynamics of stochastic processes; the mathematical basics are introduced in Box 2.4. In Box 2.5, we present the results of Lande's calculations in some detail. These results enable investigation of how the mean extinction time varies with carrying capacity for populations that are initially at the carrying capacity, but that have different mean growth rates. Under the appropriate conditions (made explicit in Box 2.5), there is a nearly exponential scaling of average extinction time with carrying capacity when the mean per capita growth rate \overline{r} is positive (also see Gabriel and Bürger 1992). For $\overline{r} = 0$, a nearly linear dependence is found. For negative \overline{r} , the scaling is dominated by a term proportional to the logarithm of the carrying capacity, as in a population undergoing a deterministic decline.

The simplest approach to incorporating demographic stochasticity in the more sophisticated time-discrete density-dependent models described above is to assume that, given the current population size N_t , the number of individuals actually present at time t+1 is drawn from a Poisson distribution the mean of which is equal to the deterministic projection $\phi(N_t)$ obtained from the corresponding recursion equation, that is,

$$N_{t+1} = \text{Poisson}[\phi(N_t)].$$
(2.6)

Mathematically, this leads to a Markov chain model that is not a branching process (Gabriel and Bürger 1992). (In the following subsection, we describe a modeling alternative based on branching processes.) Monte Carlo simulations can be used