Temporal Dimensions of Landscape Ecology

Wildlife Responses to Variable Resources

John A. Bissonette • Ilse Storch

Editors

Springer

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Introduction

Landscape ecology is about spatial heterogeneity; and when applied to animal population responses, it has often focused on the effects of large-scale habitat fragmentation. However, Haila (2002) has pointed out that fragmentation has been treated as a unitary phenomenon, whereas in reality, empirical work has shown a wide variety of direct and indirect effects. Haila (2002) refers to the unitary approach as the "schematic view" and credits its origins to the theory of island biogeography (McArthur and Wilson, 1967), where habitat fragments were compared to oceanic islands: homogeneous patches of habitat surrounded by an inhospitable matrix. He then suggested that the schematic view is limited in its ability to describe accurately the range of possible landscape configurations created by a variety of disturbances. The reality is that more than a simple binary classification of habitat and non-habitat exists. Earlier, McIntyre and Barrett (1992) recognized from their work in the northern tablelands of New South Wales that patchiness existed without a hostile matrix that presented barriers to movement by animal species. Indeed by 1999, McIntyre and Hobbs proposed a framework for conceptualizing the effects of human activities on landscapes. They visualized a synthesizing scheme that recognized a continuum of habitats (intact, variegated, fragmented, relictual) that depended on the degree of habitat modification and the amount of original habitat that remained. Manning et al. (2004) added reality to the concept of landscape heterogeneity and the idea of fragmentation with the suggestion that if two key concepts were brought together, namely: the presence of continua in nature; and the existence of species-specific perception and response (Umwelt), the resulting model would have major implications for understanding landscapes. They described two types of continua; spatial and environmental, and argued that recognition of individual species perception and response to the continua leads to the conclusion that different organisms perceive and respond differently to the environment in different ways. The essence of their argument is an organism-centered approach to landscape-animal relationships which coincides more closely with the physical reality of the landscape. A major point of the development of the idea of how we conceptualize habitat heterogeneity is that the continua-Umwelt model recognizes that landscapes change over time, while the fragmentation model (schematic view) reflects a "human-based perception of the landscape," and the present time (Manning et al., 2004, p. 626).

Ecologists have not been blind to time and temporal dynamics. For example, there is a large literature including studies of chronosequences (e.g., Bonet and Pausas, 2004), long-term climate change (e.g., Oliveira and Pillar, 2004); land-use history (Latty et al., 2004; Spooner and Lunt, 2004); fire histories (MacKenzie et al., 2004, Sanchez-Flores and Yool, 2004); long-term watershed studies (e.g., the work of Bormann and Likens (1979) and their students on the Hubbard Brook Watershed); and ecosystem effects of predator–prey dynamics (Ripple et al., 2001; Ripple and Beschta, 2004) that incorporate time as an important variable. Further, many species-specific books have reported on long-term studies of vertebrates and have been available for some time; e.g., Geist (1975), McCullough (1979), Clutton-Brock et al. (1982) and Berger (1986) to name a selected few. Fewer have addressed the idea of temporal discontinuities in resource availability, especially as it might influence animal population response (but see, e.g., Jaksic and Lima, 2003; Schmidt, 2003; Schmidt and Ostfeld, 2003; Stapp and Polis, 2003).

Time as a Discontinuity

Wildlife species live in heterogeneous landscapes. If heterogeneity is conceived as a discontinuity (Lord and Norton, 1990a,b), one can easily think about "patchiness" not only in space, but also in time and in process. For example, a fire regime, by definition, is a patchy distribution of fire events (processes) over time and over space. Likewise, resource availability and abundance change over time and space. Resource pulses occur as *episodic* events with long inter-pulse intervals. Ostfeld and Keesing (2000) placed the idea of pulsed resources into a community ecology perspective. Their argument was as follows: (1) In recent years, community ecology has begun to integrate the ideas of "top-down" and "bottom-up" control of animal populations; (2) This insight logically includes the idea of interaction strength, which may be direct or indirect; (3) *temporal fluctuations* (italics ours) in the strength of interactions among species have not been integrated into the "top-down/bottom-up" paradigm; (4) episodic resource pulses will change the balance between "top-down" and "bottom-up" interactions; and (5) integrating the impacts of the pulsed nature of resource availability into the argument begins to address the "top-down/bottom-up" paradigm more effectively, but requires the incorporation of the ideas of time delays and animal mobility to understand community dynamics more fully.

As landscape ecologists working primarily with wildlife species, we identified a logical extension of this most heuristic idea. Could all resources be considered, in some sense, to be pulsed or discontinuous? What would be the population consequences if this were so? How might ecologists identify and measure these effects?

We looked at two journals, Landscape Ecology and the Journal of Wildlife Management (JWM). In some sense, these journals represent two complimentary but very different outlets. Landscape Ecology publishes papers that address issues of space and time explicitly, while the Journal of Wildlife Management primarily publishes species focused papers aimed at managers and conservationists. We found that in the first 2006 issue of the Journal of Wildlife Management (Vol. 70, No.1) for example, 6 of 34 papers mentioned spatial aspects overtly, 4 mentioned temporal effects, and 2 papers considered both; 23 papers (67.7%) did not address either spatial or temporal issues directly. However, one paper did mentioned temporal change in relation to species ecology. We then looked at the January 2006 issue of Landscape Ecology (Vol. 21, No.1). Of 10 articles published, 6 (60.0%) addressed spatial issues primarily, and 4 (40.0%) addressed both space and time. But the key was *how* time was addressed; temporal analyses were treated either as a single time step, i.e., the time duration between two calendar dates, or as a repetitive time step variable, typically from year to year. Only one paper in JWM addressed the timing of resource availability and its acquisition overtly.

We realize that the idea of pulsed resources has been addressed for over 30 years by botanists and plant ecologists who have studied nutrient availability. Indeed, in the October 2004 issue of Oecologia, many papers were published under the general heading “Pulse Events and Arid Ecosystems.” Many addressed directly or indirectly the “two-layer” or “pulse-reserve” hypotheses (Ogle and Reynolds, 2004) that examined the relationship between rainfall and plant productivity. Additionally, the idea of patch dynamics dates to at least the late 1970s, and in the mid-1980s, Pickett and White (1984) addressed temporal issues when they linked the ideas of disturbance regimes and patch dynamics. Patch dynamics imply ecological systems with relatively discrete spatial patterns, characterized by a relationship between patches and matrix generated by disturbance (Turner et al., 2001). Of course, resources can be found in patches, or not, or may be synonymous with a patch, or not, but the key element of interest for this book is a focus on the temporal, pulsed nature of the resources themselves, not disturbance-generated patches. There is also a vast literature on population cycles and the temporal factors that might cause them.

For the wildlife manager or land use planner, basic animal needs are simple. Animals need food, water, cover for shelter and from predation, and access to mates. Were the world homogeneous, satisfying these needs would be relatively simple for organisms. Complications arise when spatial heterogeneity is introduced across the landscape. Anthropogenic impacts that change spatial heterogeneity rapidly over time present a real complication and one many ecologists have been trying to understand. We argue that an approach that addresses only spatial complications may be addressing only part of the relevant dynamics. Resource availability and quality are not distributed homogeneously over *time*. For primary consumers in temperate environments, plants ‘green up’ in the spring, and over the growing period the quality of nutrient content changes. At the same time, where plant resources are found is influenced by the disturbance regimes imposed on the system and by the patterned landscape. The same argument can be made for secondary consumers. Prey availability is pulsed and discontinuous. Prey are often most vulnerable during the egg and fledgling stages, and for a few days right after birth.

Additionally, prey energy value changes with growth. We argue that understanding this idea and incorporating the temporal discontinuities of resource availability into our studies is critical if we are to make progress in both theory and practice. The ideas embodied in this book are an attempt to bring together papers that address the idea of temporal explicitness of resource availability and quality. We hope to bring a focus to the neglected temporal issues so important to understanding species and community responses.

The Structure of This Book

This book is divided into three sections: (a) Relevant Temporal Theory (Chapters 1–5), (b) Statistics of Time (Chapters 6 and 7), and (c) Temporally Focused Case Studies (Chapters 8–14). In the first chapter of section 1, Relevant Temporal Theory, Bissonette makes the argument that an enhanced understanding of animal response to resource availability may be possible if two elements are added to the standard, single currency quantity approach. The first element relates to measuring resource *quality* and requires adding an additional currency to our ecological ledger book. The second element incorporates the idea of temporal discontinuity in resource quantity and quality. Bissonette suggests that a broader incorporation of these two elements into wildlife ecology will enhance our understanding of animal response to resource availability at both small and larger spatial extents. In the second chapter, Ostfeld and Keesing argue that pulses of resources are major bottom-up drivers in ecological systems, leading to a suite of responses by consumers that interact with those resources either directly or indirectly. Given that the ability to predict system-wide consequences is still somewhat limited, they describe several axes of variation for resources and consumers that will influence the responses of ecological systems to pulsed resources. In Chapter 3, With argues that most landscapes bear the imprint of past human land use (legacy effects) that in some cases date back centuries or even millennia, even after the landscape seemingly has been restored to its natural pre-settlement state. She explains that as a result, current species distributions may thus better reflect historical than contemporary landscape configurations, owing to the lagged response of species to landscape change. With illustrates these "ghosts of landscapes past" with several case studies. In Chapter 4, Grimm and his colleagues use individual-based models that incorporate adaptive behavior to understand animal response. They explain that the adaptive responses of individuals to short-term environmental conditions give rise to population- and community-level phenomena. They provide a rationale for the framework and provide case examples to illustrate the concepts. In Chapter 5, the last of section 1, Gunderson and his colleagues concentrate on the scaling axis of time, and describe cycles in temporal patterns in the Everglades ecosystem. They relate the temporal frequencies of ecosystem structuring processes to the interaction of animals with their environment, and describe how spatial and temporal turnover and variability in animal communities relate to variation in the availability of resources in time and space. They posit that discontinuous distributions of key structuring variables in time should be manifest as a few resonant frequencies in temporal processes and test their ideas with time series data of rainfall, evaporation, water-flow, air temperature, sea level, and fire history. In section 2, *Statistics of Time,* Gutzwiller and Riffell address in Chapter 6 the issue of measuring temporal variation in animal responses to landscape conditions. They suggest that several statistical modeling approaches are appropriate for explicitly incorporating time into analyses of animal–landscape relations, but landscape ecologists have not commonly used them. They explain that the analytical assessment of temporal variation may involve independent or dependent data. If independent data are used, interaction effects involving time and landscape metrics can be estimated using cross-product terms. With dependent or repeated measures data, Gutzwiller and Riffell explain that the analytical assessment of temporal variation may involve up to three dimensions. They provide a clearly explained approach for the analysis of larger scale temporal data. In Chapter 7, Cushman and McGarigal develop and demonstrate for the reader a flexible multivariate approach to analyze landscape pattern trajectories over time. They combine a habitat suitability model for marten, metrics from FRAGSTATS, and a multi-temporal principle components analysis to define a parsimonious suite of independent landscape gradients and to project changes in marten habitat as a series of trajectories in space. Section 3, Temporally Focused Case Studies, contains 7 chapters. In Chapter 8, Storch illustrates limitations of conventional habitat assessments caused by smaller-scale temporal variation in rainfall patterns that may lead to inappropriate management action, using case examples of Capercaillie *Tetrao urogallus* in the German Alps. The examples show that standard "snapshot" habitat assessments ignore temporal variation and may have major consequences for species-habitat relationships and population dynamics, and thus, for management and conservation planning. In Chapter 9, Mooij, Martin, Kitchens, and DeAngelis explore the viability of the Florida snail kite *Rostrhamus sociabilis plumbeus* population under different spatially and temporally explicit seasonal drought regimes in its wetland habitat. The Florida snail kite is an endangered raptor that occurs as an isolated population of about 2000 birds in the wetlands of southern and central Florida. To explore the interplay between the timing and spatial synchronization of water resource availability, Mooij and his colleagues used an individual-based snail kite simulation approach that modeled kite behavioral responses. Because of its weekly time resolution, the model discriminated relatively subtle temporal variations in hydrological patterns. Their results revealed the complexity of the effects of temporal variation in water levels on snail kite population dynamics. Specifically, they found that management decisions should not be based on annual mean water levels alone, but must consider intra-annual variability. In Chapter 10, Reynolds and Mitchell argue strongly that the spatiotemporal resolution of observations should match the level of the ecological process under study if reliable insights are to be gained. They present a concept of designing ecological studies that integrates three axes: temporal resolution of the study, spatial resolution of the study, and the resolution of the ecological process addressed. To buttress their arguments, Reynolds and Mitchell provide two examples from their long-term research on black bears

Ursus americanus. They show that the temporal scales at which different vital rates are manifested in a bear population may differ, and affects the way disturbances (e.g., clearcuts, roads) affect habitat quality. In Chapter 11, Felix, Linden, and Campa argue that land-cover databases can be used to understand wildlife-habitat relationships but do not identify vegetation structure, temporally explicit vegetation trends, successional dynamics, or vegetation types on distinctive soils that may have different wildlife values. They suggest that the use of ecological classification systems, where ecosystems are classified and mapped according to specific biotic and abiotic properties, can facilitate assessment of distributions and movements of wildlife populations based on spatial and temporal identification of resources necessary for survival. They use a habitat-type classification system, which is a specific type of ecological classification system, as a basis to predict vegetation development and successional change. They discuss three case studies from Michigan to demonstrate how to build and apply models to assess temporal changes in forest wildlife habitat. One case study determined the potential of habitat types to provide white-tailed deer *Odocoileus virginianus* habitat, a second characterized how structure and composition of aspen *Populus* spp. changes throughout succession in different habitat types, and a third case used GIS to analyze differences in land use and land cover over the last century and model changes in the location and suitability of habitat for the threatened Canada lynx *Lynx canadensis* in the Upper Peninsula of Michigan. In Chapter 12, Lewis explains how the historically common but now endangered Gouldian finch *Erythrura gouldiae* of Australia has suffered dramatic reductions in population numbers during the last 40 years. Possible causative scenarios, including (a) increased commercial livestock grazing, (b) commercial trapping, and (c) parasite infections, have had limited success in explaining the continued decline in the number and size of Gouldian finch populations. Unlike other Australian finches, the Gouldian finch is solely granivorous and relies upon native grass species for survival. In this chapter, Lewis presents experimental evidence to show that different patterns of seed production are dependent upon fire periodicity and the intensity of burning, and that in breeding seasons following periods of reduced fire intensity and therefore higher seed production, there is about a 30% increase in reproductive success and increased survival of adult Gouldian finches. Lewis argues that understanding the temporal patterning and spatial distribution of resources across the landscape provides valuable perspectives on how to manage landscapes for declining species such as the Gouldian finch. In Chapter 13, Drever and Martin argue that in the mixed forests of interior British Columbia, Canada, temporal trends may have more dramatic effects than spatial patterns on species responses. Time and space interact and the drivers of temporal change differ spatially for short and long distant migrant species that respond to ecological conditions at a continental scale extent compared to resident species where temporal trends are driven by climate change and forest management conditions at a landscape or regional scale extent. The authors conducted a study that involved multi-annual responses of cavity nesters to an ongoing major outbreak of mountain pine beetle (*Dendroctonus ponderosae*) and other bark beetles and forest insects in British Columbia that resulted in large-scale increases in the availability of dead and dying trees. In addition to the annual variation in phenology, breeding density, and reproductive success, unexpected and dramatic directional temporal changes occurred. Drever and Martin were able to fit a linear trend model to 100 species observed during point counts, of which 21 showed a significant decline in abundance over the study period, 21 showed an increase in abundance, and 58 showed no trend. These concurrent declines and increases in abundance mean that community-level measures such as species richness and abundance within cavity-nesting guild did not change following the outbreak, indicating that community structure, per se, has remained stable during the large increase in resource availability. These results suggest that species' responses to the availability of resources may thus also depend on the current status of competitors, predators, and facilitators. In Chapter 14, MacLeod, Parish, and Robinson used an introduced bird species, the yellowhammer *Emberiza citrinella* L. in New Zealand as a model to test predictions based on the niche opportunities hypothesis. They tested the prediction that the success of yellowhammers in New Zealand can be explained by differences in temporal variation in availability of better quality food resources in its introduced range compared to its native range; specifically that (a) winter seed resources were more abundant; and (b) there was less temporal variation in resource availability during the breeding season in New Zealand. They found that Yellowhammer breeding territory densities were over three times higher in New Zealand (0.40 territories per ha) than in comparable British farmland (0.12 territories per ha), however, they also found that niche availability and quality, as indexed and measured by habitat availability and invertebrate densities, could not explain the higher density of yellowhammers in New Zealand.

Objectives

In this volume, we have compiled 14 papers that cover a wide range of topics and approaches, but all address the issue of time in landscape ecology research. If successful, these chapters may provide a prolegomenon of a conceptual framework for a spatially *and* temporally explicit landscape ecology. Our overall objective was to illustrate that time and temporal variation have in large part been a neglected dimension in landscape ecology. Animal response to *spatial* heterogeneity is complicated enough to understand; to include temporal heterogeneity explicitly in our thinking and research will certainly not make the work of landscape ecologists any easier. It should however make the science more realistic and result in better and more reliable management recommendations. If the book succeeds in stimulating thought and discussion, we will be satisfied.

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I

Relevant Temporal Theory

1

Resource Acquisition and Animal Response in Dynamic Landscapes

Keeping the Books

JOHN A. BISSONETTE

Abstract. Quantification in ecology has been the *sine qua non* that has differentiated rigorous science from something less. It is how we have "kept the books." Quantifying the quantifiable to account for population response to resource availability usually has meant that the *quantity* of some resource (e.g., for herbivores, plant biomass, or areal coverage of the plant community or habitat) has been assumed to have some causal effect on some quantitative measure of animal response (e.g., the number or organisms surviving and recruited into the population). As scale effects have been recognized as important, landscape ecologists have followed a similar methodology and have assumed that the habitat area coverage (*quantity*) bears some relation to population and species performance and health. The explanatory power of the spatial amount of habitat elements seems inconsistent, and available metrics to assess the effects of spatial arrangement are problematic. Further, organisms respond to the quality of their food resource. In this chapter, I make the argument that an enhanced understanding of animal response to resource availability may be possible if two elements are added to the standard, single currency quantity approach. The first relates to measuring resource *quality* and requires adding an additional currency to our ecological ledger book. The second element incorporates the idea of temporal discontinuity in resource quantity and quality. I suggest that consideration and a broader incorporation of these two elements into wildlife ecology will enhance our understanding of animal response to resource availability at both small and larger spatial extents.

1.1. Introduction

If habitats can possess a spatial structure relevant to ecology, is it possible that the temporal structure of habitats is also potentially important? Johnson (2000a)

Animal populations, in particular, have often been considered limited by resource *quantity*, but not by the chemical composition of the resource.... Resource *quantity* limitation is a single currency approach.... (italics added) Moe et al. (2005)

ac·count·ing: Pronunciation: ($^{\text{ə}}$ˈka$^{\text{ʊ}}$nt$^{\text{ɪŋ}}$) &-kaun-ti[ng], Function: *noun,* 1 : the system of recording and summarizing business and financial transactions and analyzing, verifying, and reporting the results; *also* : the principles and procedures of accounting, 2 a : work done in accounting or by accountants b : an instance of applied accounting or of the settling or presenting of accounts.

cur·ren·cy: Pronunciation: (ˈk$^{\text{ʌ}}$r$^{\text{ə}}$ns$^{\text{ɪ}}$) ˈk&r-&n(t)-sE, ˈk&-r&n(t)-, Function: *noun*, Inflected Form(s): *plural* –cies; 1 a : circulation as a medium of exchange b : general use, acceptance, or prevalence c : the quality or state of being current: currentness. 2 a : something (as coins, treasury notes, and banknotes) that is in circulation as a medium of exchange b : paper money in circulation c : a common article for bartering d : a medium of verbal or intellectual expression (Merriam-Webster Online Dictionary, www.m-w.com).

Accounting in ecology is accomplished by recording and summarizing data (explanatory and response variable interactions) and by analyzing, verifying, and reporting results. Perhaps insufficiently appreciated is the idea that ecologists use different currencies and accounting to understand ecology, and the differences matter. The term "observation set" (O'Neill et al., 1986) has been used to define and delimit different approaches to science and includes the phenomena of intellectual interest, the nature of the measurements taken (i.e., the currencies), and the statistical and analytical techniques (the accounting) used to derive conclusions (Bissonette, 1997). For example, geneticists, population ecologists, and ecosystem scientists all use different measurements (e.g., gene frequencies, number of animals, or nutrient cycling and energy flow, respectively) to account for the interactions they observe. Quantities of some variable most often represent the currency measured. Given the different observation sets used, accounting in ecology involves ledger books that have fundamentally different currencies that measure "quantity" and often are difficult to reconcile. Quantifying the essentially qualitative nature of nature is arguably more difficult and done less often. However, for behavioral, population, community, and landscape ecologists with an interest in animal response to resource availability, new theoretical developments suggest that single currency approaches, i.e., consumer response to the *quantity* of resources can be informed by addressing temporal differences in resource *quality* as well as quantity. Indeed, net trophic transfer of energy and biomass (both often represented by carbon, C), is often limited by the availability of other key elements such as nitrogen (N), phosphorous (P), and trace elements (Moe et al., 2005). The primary objective of this chapter is to address the idea of basic organisms needs and how spatial and temporal heterogeneity complicate our ecological accounting. To do that, I: (a) examine the idea of temporal explicitness in resource availability (quantity) and quality; (b) discuss the different ways that we keep the books; (c) briefly describe two simple but sometimes neglected distinctions relevant to our understanding of the effects of special complexity, viz., the components of pattern and the differences between fragmentation and habitat loss; (d) suggest that the fragmentation model of conceptualizing landscapes is but one possible way of thinking about heterogeneity and may hinder our accounting and hence our understanding of the effects of varying temporal and spatial variation in resource availability on animal response; and (e) attempt to address the problems inherent in single currency approaches by reference to ecological stoichiometry. Throughout, I place these ideas in the context of temporal explicitness.

1.2. Basic Organism Needs Get Complicated

Basic vertebrate organism needs are surprisingly simple to list. Minimal resource needs include access to food, free or metabolic water, cover from predators and perhaps inclement weather, and to mates, all at variable rates that influence fitness. However, resource acquisition is complicated when resources are distributed heterogeneously. One might get the impression from the current voluminous literature in landscape and population ecology that the complexity stemmed primarily from spatial complications. Indeed, much is promised by an understanding of the effects of spatial scale on animal population response. At one time, panmictic mixing and homogeneous landscapes were common assumptions used in population dynamics (Fisher, 1930) before the broad acceptance that habitat heterogeneity had causal effects and that appropriate scaling of our accounting metrics was essential for a more complete understanding of animal and population response (Wiens, 1989). For ecologists, scale effects or scale complications mean, among other things, that discrete populations exist with different vital rates, i.e., averaging statistics for populations cannot be used as they were traditionally when panmixis was assumed (Ritchie, 1997). The reason is that animal movement in naturally heterogeneous landscapes is often hindered (Merriam, 1998) and panmixis is not commonly possible. Panmixis is probably always a simplifying assumption given mate competition, social hierarchies, as well as individual variation in vagility. Regardless, how organisms fulfil their resource acquisition needs is complicated and often difficult for them to do because individuals need to move across potentially dangerous heterogeneous landscapes in response to temporally discontinuous resource availability. It is not surprising that our ecological accounting is similarly difficult. Both pattern, as well as the dynamics of heterogeneity, need to be accounted for to better understand organism and species responses in space and time.

1.3. Temporal Discontinuities

Temporal resource discontinuities can be regular or pulsed (Ostfeld and Keesing, 2000) or occur stochastically at irregular intervals. They may occur at temporal scales spanning from time of day (e.g., activity patterns, and thus availability of prey), to seasons (primary production) and years (mass seeding events), to decades and even centuries (succession of some desert and forest ecosystems). Temporal resource discontinuities are caused by factors such as seasonality (Norrdahl et al., 2002), phenological events (Kelly, 1994), trophic relationships (Khan and Ghaleb, 2003), or disturbances (White and Pickett, 1985). They can include ephemeral habitats such as ponds (Loman and Claesson, 2003) and “rotting logs, dung, carrion, gravel bars in rivers, and forest openings” (Johnson, 2000b). One of the most obvious discontinuities in resource availability in time is the fruiting of plants. The availability of acorns is a good example of a resource that exhibits strong temporal discontinuities (Abrahamson and Layne, 2003). Wolff (1996) found that rodent densities were positively correlated with oak mast production over a period of 14 years. However, much temporal heterogeneity of resources is gradual; i.e., it concerns variation in resource quality. In this ecological sense, all resources may be considered pulsed or discontinuous to some degree (see Ostfeld and Keesing, Chapter 2, this volume). Most resources appear seasonally in temperate and tropical environments. Additionally, resource quality changes over time as well as over spatial gradients. There is a voluminous literature on the response of species to environment resource gradients. These were largely a result of two papers by Tilman (1980, 1982) who proposed what has come to be known as the resource-ratio theory. The theory essentially describes interactions of competing species through their use and effect on shared resources, and had its antecedents in work by MacArthur (1972), Maguire (1973), and others. Miller et al. (2005) summarized the use of the theory by ecologists, and I will not address that issue here, except to suggest that the idea of "use and effect" would appear to be a multiple currency or bivalent approach at the producer-herbivore trophic interface.

1.4. Temporal Explicitness

The term *spatial explicitness* is common and we have become accustomed to thinking about spatial complications. For population ecologists, the term implies among other things, spatially discontinuous populations, inhibited movement of individuals across heterogeneous landscapes, and processes whose effects are understood only if viewed at the appropriate spatial resolution and extent (Addicott et al., 1987). As a result, vital statistics—viz., birth, death, survivorship, recruitment, and genetic composition may vary in space, and thus, cannot simply be averaged across populations (Ritchie, 1997). Temporal explicitness has been treated far less extensively in those studies that relate animal response to resource availability.

A common temporally explicit approach in ecology is to develop simulation models to explain observed spatial pattern differences caused by ecological processes such as disturbance and succession. For example, Wiegand et al. (1998) explored the impact of disturbances on spatio-temporal shrub land pattern evolution, Franklin and Tolonen (2000) modelled the temporal relationship between fire and vegetation using pollen and charcoal data, and Tian et al. (2002) simulated the spatial and temporal effects of microbial contaminants on grazed farmlands. Because most studies are of relatively short duration, often on the scale of a few years, a space for time substitution is most often used (Hargrove and Pickering, 1992) where landscapes are replicated in space rather than time. The powerful effects of unique historical events on subsequent dynamics, e.g., violent disturbances, are often muted or ignored and lost. System history disappears. Almost... (see With, Chapter 3, this volume). Johnson (2000a, p. 1697) suggested that temporal structure generally "exists when habitat dynamics are defined independently of population density." Thus, temporal variation of processes in landscapes has important implications for metapopulation studies (Holyoak and Ray, 1999). Johnson (2000b, p. 67) considered that "species in successional landscapes may represent the most appropriate examples of classical metapopulations" and explored the idea that species coexistence and metapopulation dynamics can be influenced profoundly by the temporal dynamic of habitat succession (Johnson, 2000a,b). Clearly a major problem lies with the observation that landscapes are changing more rapidly than slower changing animal populations can accommodate (With, Chapter 3, this volume).

The implication of the term "temporal explicitness" is that differences in individual performance (different rates of resource acquisition, and hence presumably fitness) and in vital rates of populations can be caused generally by temporal discontinuities, and specifically, in the present context, by temporal differences in both resource availability and quality. The apparent novelty and general lack of appreciation of this idea points to the problem. There are at least two reasons why temporal dynamics have not been widely addressed explicitly in fragmentation studies of animal response. First, we appear to have lacked a generally accepted conceptual and methodological framework with which to address its effects. Second, the single-currency approach may have limited our ability to measure the important effects of resource quality that vary through time.

One reason that time has not often been addressed explicitly may be because the concept of fragmentation has most often been conceived in a very limited spatial sense. If we think of habitat fragmentation as a *discontinuity* in space and time, and thus in function and process (Lord and Norton, 1990), we then can find a way to address the complexities of time as a variable influencing organism response to habitat fragmentation, and hence to resource availability. For example, a fire regime is a discontinuous process in time. Disturbance regimes are by definition discontinuous. Hurricanes, tornados, and severe weather events occur in some sense predictably, but are discontinuous in time. An important consequence of thinking of resources as not only spatially, but also temporally discontinuous is that quantitative descriptors can be measured using metrics borrowed from disturbance theory. In other words, the currency we have available for ecological accounting is expanded. For example, temporal (as well as spatial) distribution of resources, predictability in the timing that resources are available, differences in amount and quality, and possible concurrent interactions of the availability, quality, and timing of other resources i.e., synergisms, can be measured (See Ostfeld and Keesing, Chapter 2, this volume). Disturbance metrics (White and Pickett, 1985) are well known and lend themselves to measuring resource discontinuities because disturbances themselves are discontinuous. When we are able to consider temporal discontinuities in resource availability (quantity) and resource quality, our understanding of ecological reality is enhanced, because these are the attributes to which animals respond.

1.5. Two Important Distinctions

Words have specific meanings and when we blur definitions, the result is more often than not confusion. I make two important distinctions here. First, landscape pattern has at least two distinct characteristics of importance to those who study fragmentation effects and species response: composition (sometimes given as total amount of habitat (Schiemegelow and Mönkkönen, 2002) and spatial arrangement (Turner, 1989). Both influence and constrain animal response. The colloquial expression might be stated as, "what habitats are present (composition) and where are they (arrangement)?" Given that most organisms need to move to access resources (Merriam, 1998), one should expect different responses from different species to these two characteristics. It is of little consolation that many (but not all) metrics used to quantify landscape heterogeneity confound the effects of composition and arrangement (Gustafson, 1998; Li and Wu, 2004; Neel et al., 2004), i.e., they measure multiple components of spatial pattern and often are correlated, making causal interpretation difficult. Li and Reynolds (1995), Riiters et al. (1995), McGarigal and McComb (1995), and Jaeger (2000), using different methodological approaches, have provided assessments of which landscape metrics appear to be most useful. A priori and clear thinking about species natural history requirements as well as about the processes suspected to be operating, coupled with reasonable hypotheses about pattern composition and arrangement effects would seem to be necessary initial steps in any ecological accounting of species response to fragmentation and resource-related effects.

Second, it is possible that when we think about fragmentation as a process, we make assumptions that seem reasonable but may not hold. Fahrig (2003) provided insight into one of the reasons that fragmentation studies often produce mixed or counter-intuitive results. She suggested that many studies have not differentiated between "fragmentation per se," i.e., the breaking apart of habitat, and habitat loss. The two are not the same, although both are part of the *processes* that occur when landscapes change over time. See Cushman and McGarigal (this volume) for examples of an analysis that distinguishes between the two. When fragmentation is viewed as a process, four effects are implied: (1) a reduction in habitat amount; (2) an increase in the number of habitat patches; (3) a decrease in mean patch size; and (4) an increase in patch isolation. These effects appear logical because we make the tacit assumption that the starting point is an unfragmented landscape. If we relax that assumption, then it is easier to understand that different scenarios may result. Fahrig (2003) provided five possible scenarios where one or more of the expectations were not met, suggesting strongly that we should keep these differences in mind in both the studies we design and the analyses we use. To do otherwise is unhelpful, as Debinski and Holt's (2000) review of 21 experimental fragmentation studies clearly suggests. An additional component relates to the idea that the concept of "habitat" is species-centered and not an arbitrary decision on the part of the observer. This leads to an overt consideration of when "habitat" is really habitat. Additionally, how we conceive "landscape" as a working construct is germane here.

The concept of landscape fragmentation has often been used as if it were a "unitary phenomenon" (Haila, 2002, page 322); the schematic view has its origins in Island Biogeographic theory (MacArthur and Wilson, 1967). However, when translated to terrestrial systems, some of the early assumptions remained: (1) habitat islands were the result of disturbance and breaking apart of once contiguous habitat;

(2) were isolated from one another by an essentially inhospitable matrix that was hostile to a majority of organisms (Haila, 2002); and (3) movement of biota often depended on corridors or long-distance dispersal movement to move between patches (Saunders et al., 1991; McIntyre and Barrett, 1992). This schematic view led to the description of landscapes in terms of patches (usually homogeneous), corridors (usually linear), and matrix (the most connected part of the landscape (Forman, 1995; McIntyre and Hobbs, 1999). Of course, depending upon the degree of disturbance, the matrix can be original habitat or the disturbed area. Observations in Australia in the early 1990s led McIntyre and Barrett (1992) to suggest that the schematic view of landscape did not apply to systems heavily modified by agriculture. They observed that the "intervening areas" were modified versions of the original habitat and were not totally inhospitable to movement; animals moved through these areas. This was a significant finding and implied that habitat modification may result in more than just a binary option of "habitat" vs. "non-habitat" (McIntyre and Hobbs, 1999). A significant conceptual advancement, and one that modifies a significant assumption of the schematic view, is that disturbed habitat is not always inhospitable. McIntyre and Hobbs (1999) presented a modified version of the schematic view where various levels of habitat modification were represented on a continuum of habitat destruction while at the same time considering spatial arrangement, resulting in landscapes ranging from intact ($<10\%$ modified, connectivity high), to relictual ($<10\%$ intact habitat, no connectivity). The schematic view of landscape fragmentation had its "assumption descendants" in the "community-unit theory" (Manning et al., 2006), which holds that plant communities were "homogeneous, discrete, and recognizable units" (Austin, 1985, p. 39). Viewing landscape patches as "habitat" for animals homogenizes them into discrete and recognizable units. The relevant question is: do animals recognize habitat patches in the same manner that we do, i.e., according to the schematic view? Manning et al. (2004) suggested viewing landscapes as evidencing both environmental and spatial continua, i.e., gradients. Indeed, Lindenmayer et al. (2002) found strong gradients in bird assemblages in eucalypt and pine forests in Australia that were governed by a combination of landscape context, and remnant patch size and shape. Manning et al. (2004) suggested that environmental continua occur in abstract ecological space while spatial continua or gradients occur in geographical space. Their concept of "Umwelt" incorporates species response and perception into both environmental and geographical gradients, hence is a significant departure from the schematic or fragmentation model. Finally, Fischer and Lindenmayer (2006) proposed a process based conceptual "continuum" model that provides for individual species response to gradual changes in spatially distributed ecological variables such as food and shelter. It seems to me that the schematic fragmentation model allows assessment of the effects of pattern, while the continuum model (Fischer and Lindenmayer, 2006) may allow linking animal response to ecological processes. The continuum model will be especially valuable if temporal discontinuities in resources can be taken into consideration.

Attention to spatial distinctions is necessary but not sufficient. Note that we essentially are measuring some *quantity* rather than *quality* effect as the explanatory variable. This has been referred to in a general sense as a single currency approach (Moe et al., 2005), where the clear implication is that "currency" refers to either quantitative or qualitative effects, but not both. Regardless, if the objective is to learn how species respond to changing landscapes and hence changing resource availability (quantity) and quality, attention to spatial details gets us only part way there. Attention to temporal effects as well as consideration of the qualitative differences in resources is necessary.

1.6. Resource Quality: Keeping the Books

So then, how might we improve our keeping of the books in ecology? Keeping the books, i.e., accounting in ecology, implies that we are capturing the essence of the interactions so that understanding is enhanced. Specifically, it implies that our observations are buttressed by a conceptual understanding that makes sense. Put another way, the assumption is that the variables we measure, i.e. the currencies, are appropriate and up to the task. Studies of habitat fragmentation that have addressed animal responses to resources availability have used almost exclusively the currency of *quantity* of resource as the explanatory variable. Indeed, many habitat use/preference studies appear to be based on the hypothesis that the *amount* of habitat is more or less directly causally related to response variables such as animal density, growth, reproduction, survivorship, and birth and death rates. Additionally, even though habitat types themselves are often assumed to represent areas of different resource quality, the connection is not at all direct, and begs again the question of when "habitat," arbitrarily defined, is really habitat. In habitat selection studies, habitat quality is inferred by assessing individual performance or by some measure of population performance (Morrison, 2001), rather than by a more direct measure of quality as the explanatory variable.

At larger spatial scales, studies using GIS have used time step analyses of landscape changes that elucidate differences in habitat *composition* and *spatial arrangement* over time to explain, for example, changes in biodiversity. Indeed, a large proportion of habitat fragmentation studies have used landscape composition variables (i.e., how much) to imply or show changes in population abundance or biodiversity (number of species). The literature suggests that ecologists most often simply use quantity over some specific time period as the explanatory variable to explain animal response. However, most ecologists would agree that trophic transfer of energy and biomass can be limited by key elements (Liebig's law of the minimum; but see Muller et al., 2001, for a discussion on multiple and simultaneous limiting factors). For herbivores, nitrogen (N) and phosphorous (P) have been the elements usually measured, although other trace elements have been implicated (White, 1993). Moe et al. (2005) used the convention of referring to carbon (C) as representing energy and biomass, and phosphorous (P) and nitrogen (N) and other elements as nutrients. The idea of limiting resources over a longer time constant can be extended to animal populations. For example, population growth may be limited by the minimum amount of resources available to that population at the time of year of greatest scarcity and not by the total amount of resources available throughout the year. The clear implication is that the single currency of *quantity* of resource that ecologists have used to understand animal response may not be adequate to reflect what ecologists inherently suspect: i.e., dynamic changes in resource quality across heterogeneous landscapes are important determinants of population performance. This begs a need for an appropriate currency with which to measure quality effects.

1.6.1. Ecological Stoichiometry: Another Currency

Ecological stoichiometry, an emerging branch of ecology (Sterner and Elser, 2002; Anderson et al., 2004) has been variously described as "the study of the balance of energy and multiple chemical elements in ecological interactions" (Hessen and Elser, 2005, p. 3), "the study of the balance of elements in ecological processes" (Moe et al., 2005, p. 29), "the study of the balance of energy and materials in living systems" (Kay et al., 2005, p. 6), and "dealing with the balance of energy and chemical elements in ecological interactions and especially in trophic relationships" (Anderson et al., 2004, p. 884). The field developed primarily from pelagic, freshwater studies (Hessen and Elser, 2005). One field of concentration has explored how an imbalance of elements and energy can place strong constraints on individual organism growth and reproduction (Bruning, 1991; Sterner and Schultz, 1998; Aerts and Chapin, 2000). Another approach (Kay et al., 2005) has examined stoichiometry in an evolutionary context across multiple scales, exploring the reciprocal interactions between evolutionary processes and the elemental composition of organisms and their resources, and relating elemental ratios in organisms to phenotypic and genetic variation upon which selection can act. Yet another approach has expanded the ideas of a stoichiometric approach to biogeochemical cycles to address the sustainable acquisition of ecosystem services (Ptacnik et al., 2005). Schade et al. (2005) have provided a conceptual framework for thinking about ecosystem stoichiometry. Importantly for this book, ecological stoichiometry has implications for understanding temporal explicitness in resource quality and its influence on terrestrial populations in fragmented landscapes.

Ecological stoichiometry is well established in aquatic ecology but not yet in terrestrial ecology. Two recent papers on stoichiometry (Anderson et al., 2004, Moe et al., 2005) argue persuasively that ecologists interested in animal population response to resource availability need to consider the currency with which they examine plant-animal interactions. They argue that ecological stoichiometry provides a multiple currency approach to understand the effects of resource *quality*. By multiple currency, they mean that rather than "abstracting populations as aggregations of individuals or biomass," organisms are represented by carbon (C), phosphorous (P), and other trace elements that allow "key feedbacks, such as consumer-driven nutrient recycling" processes (Anderson et al., 2004 p. 884). The argument is that both food quantity and quality can be incorporated into a single framework. The concept of "currency" here has two related parts: one meaning refers to the difference between the effects, or explanatory variables, being measured, viz., quality versus quantity; the other meaning refers to the metrics used. The term "multiple currency," therefore, can be interpreted to refer to measuring not only *quantitative* but also *qualitative* aspects of the resource using *quantitative* metrics. The message is that measuring only quantity is insufficient; quantification of the qualitative aspects of the resource base is needed. Owen-Smith (2005, p. 613) reinforced this idea when he stated, "the numerical approach to population dynamics is seductive, but potentially misleading through overlooking the material basis for changes in N." These papers suggest a conceptual basis for some of the observations that ecologists have made concerning plant quality and its importance to herbivore response. An understanding of ecological stoichiometry can be gleaned from these papers as well as from other papers from a workshop called "Woodstoich 2004" sponsored by the Center for Advanced Study at the Norwegian Academy of Sciences and Letters and published in 2005 in volume 109 of Oikos. An additional group of papers appeared in volume 85(5) of Ecology 2004 as a Special Feature edited by D.O. Hessen and called Stoichimetric Ecology.

Box 1.1. What is stoichiometry?

Stoichiometry is the accounting, or math, behind chemistry. Traditional textbooks in chemistry explain that stoichiometry is used to calculate masses, moles, and percents within a chemical equation. While it is beyond the purpose of this chapter to delve into this in detail (readers are encouraged to look at a basic chemistry textbook for a full explanation) the following is given to provide background to understand the developing field of ecological stoichiometry. The balanced chemical equation $8\mathrm{Al} + 3\mathrm{Fe_3O_4} \rightarrow 4\mathrm{Al_2O_3} + 9\ \mathrm{Fe}$ contains aluminium (Al), iron (Fe), and oxygen (O). The numbers 8, 3, 4, and 9 are coefficients that show the relative amounts (molecules or moles) of each substance present, and can represent either the relative number of molecules, or the relative number of moles. A mole is equal to Avogadro's number (6.023×10^{23}) of molecules. A mole is simply a term to denote an amount. For example, if have a half dozen apples, you have six of them. If you have a mole of apples, you have 6.023×10^{23} apples. If no coefficient is shown, a one (1) is assumed. Given the equation above, we can tell the number of moles of reactants and products. Hence we have an accounting system to work with chemical formulas. Ecological stoichiometry is extending this basic accounting system to ecological systems. Essentially, the accounting considers both the quantitative as well as the qualitative relationships involved; here the quantity and quality of the resource base are considered important and incorporated into analysis of their influence on heterotroph population response (UNC Chapel Hill Chemistry Fundamental Program 2006).

1.6.2. Resource Quality and Population Response

Anderson et al. (2004, p. 884) have argued that "population dynamics theory forms the quantitative core from which most ecologists have developed their intuition about how species interactions, heterogeneity, and biodiversity play out in time." They show that by using stoichiometric models to examine trophic interface dynamics, one derives qualitatively different predictions (sec. 1.6.3) about the resulting dynamics. A fundamental principle of ecological stoichiometry is that "the requirements of multiple elements vary within and among species, and can cause mismatches between demand and supply at ecological interfaces" (Moe et al., 2005). What this means for herbivores is that plant quality varies over time and space and the conversion of plant biomass into herbivore biomass is often constrained by plant quality and not necessarily plant quantity. The other side of the coin (Anderson et al., 2004) suggests that nutrient cycling back across the trophic interface, e.g., by excretion and elimination, will also be constrained by herbivore nutrient needs relative to what is needed, with the surplus being recycled back. Examining stoichiometric imbalance between carnivores and their prey may be less fruitful because the stoichiometric imbalance in nutrients between food (prey) and consumer (predator) is less for carnivores; the prey themselves are heterotrophs. Hence, the physiological variation between D:N:P ratios is "typically an order of magnitude less" between predator and prey (heterotrophs) than what is encountered between autotrophs (food) and consumer (heterotroph) (Anderson et al., 2004, p. 885). This suggests that predator heterotrophs may be seldomly limited by food quality. More work is evidently needed in this area.

Stoichiometric theory has formalized these constraints (Anderson et al., 2004) by what is known as the threshold elemental ratio (TER). This is the carbon: element threshold where the resource limitation shifts from carbon (C) to nutrient (P, N), that is, where the quality of the plant resource makes a difference. With plant C:element ratios <1, plant quality is always adequate for the herbivore and a single currency approach based on quantity of food will not deviate significantly from a stoichiometrical approach (Urabe and Watanabe, 1992; Urabe and Sterner, 1996). In these cases, ecologists have correctly used quantity to reflect herbivore response. It is when TER ratios >1 that a stoichiometric model approach can be illuminating.

1.6.3. Different Predictions

Perhaps the fundamental key for population ecologists is that because stoichiometric models incorporate *both* food quantity (which ecologists usually measure) and quality, which is inferred but much less frequently incorporated into the measurements, there may appear empirical phenomena that cannot be predicted by single currency models. Examples from laboratory experiments include the observations of a (1) positive density dependence and a shift in the nature of the interaction from competition to facilitation (Sommer, 1992), similar to the Allee effect; (2) coexistence of more than one predator on a single prey item in contrast to predictions based on the single (quantity)-currency theory (Grover, 2003; Hall, 2004; Hall et al., 2005); and (3) the diversity enhancing effects on herbivores of poor food quality (Anderson et al., 2004). Although these results come primarily from aquatic system experiments, terrestrial ecologists may find that similar shifts in predictions may occur if one could take plant quality changes over time into consideration. McNaughton (1985) and Grasman and Hellgren (1993) have shown for African ungulates and for white-tailed deer *(Odocoileus virginianus)* in the United States, respectively, the preference for foods with high nutrient quality. Wildlife ecologists have studied energy and food quality for a long time. Seldom, however, have the results been put into a larger landscape context. Future field studies will demonstrate if different predictions and results obtain.

Food quality may provide a better explanation for vole cycles than the other hypotheses that have been proposed (Ergon et al., 2001). Recent work in Europe (Nolet et al., 2005) on beaver has shown that stoichiometric changes in leaf quality have impacted beaver populations in the Czech Republic and the Netherlands. Nolet et al. (2005) suggest that these qualitative changes may be of greater importance than a shift in food quantity. Likewise, Owen-Smith (2005) has argued that a shift from a numerical currency allows closer modelling of the true dynamics. However, he has argued that placing emphasis on intake responses that determine the capture of resources provides little insight, because population growth is largely fixed by evolutionarily adapted responses; i.e., there is a finite rate of recruitment for any population. He argued (2005, p. 613) that actual realized population growth is an "outcome of environmental restrictions, expressed largely through mortality losses" and that our efforts are better placed there because environmental restrictions include failures to conceive as well as mortality at all life stages. I suggest that focusing on both the intake response, i.e., the influence of forage quality on population response, and on the final outcome, i.e., realized population growth as measured by multiple currencies would appear to provide a nice integration of approaches to inform ecology.

1.6.4. Global Warming: An Added Complication

Temporal differences in resource abundance and quality have been influenced globally by climate change, and have had significant effects on wildlife species. The Normalized Difference Vegetation Index (NDVI) provides a standardized method of comparing vegetation greenness between satellite images. When two or more images are compared over several to many years, it is possible to distinguish changes in vegetation reflectance values that can be represented as a percent change from a long-term average. In this way, trends in the timing of spring bud break and leaf growth, i.e., phenophase, can be detected. In Washington, DC (USA), Abu-Asab et al. (2001) found that 76 of 89 plants whose flowering date was significantly earlier, flowered on average 5.6 days earlier than a 30-year mean Julian date. Flowering dates ranged from 3.2 to 46 days earlier. Numerous other studies have shown similar trends. Changed phenophases mean changed patterns of resource abundance and length of availability. Visser (1998), Visser and Holleman (2001), and Grossman (2004) provided clear examples where global warming and its effects on phenophase have had effects of Great Tit (*Parus major*) demographics. They reported that in the Netherlands, changes in weather patterns have caused oak buds to leaf sooner. Winter moth caterpillars (*Operophtera brumata*), an important food source for great tit chicks, peaked in total biomass 13 days earlier in 2004 than in 1980. However, the date of egg laying has remained the same. For most if not all wildlife species, a primary selection factor on the timing of reproduction is synchrony between offspring energy requirements and food availability (Grossman, 2004). The earlier bud break in oaks and the subsequent earlier increase in winter moth caterpillars have resulted in a mismatch between the availability of food and the needs of the young chicks. Visser (1998) Visser and Holleman (2001) report serious demographic consequences for the Great Tit population near Arnhem, the Netherlands. Clearly, as these studies demonstrate, over larger spatial extents, the timing of resource availability is critical.

1.7. Conclusions: The Truth Is Always Beyond the Perception of Truth

Throughout this chapter, the theme has been to try to find a way to get closer to understanding the true state of nature as it applies to resource availability and animal population response. However, in science generally, and in ecology specifically, the idea of "truth" is an elusive concept. What we know or what we think we know is always based on (often unstated) assumptions; is filtered through our methodological approaches, and is always constrained by the observation set we employ. Put in different terms, "truth" as a science concept is nuanced, and it is so because science is the one enterprise where we continually attempt to falsify our hypotheses and predictions, and examine our premises in order to test what we know. When one thinks about individual animal or population response to the spatial and temporal distribution of required and necessary resources, it seems reasonable that future advances in our understanding of animals that live in dynamical landscapes may be facilitated by diversifying our accounting currency to include measures that do more than just relate the number of individuals (response) with the quantity (area, biomass) of their habitat (explanation). To the extent that we can quantify the qualitative constraints that influence populations, we can at least come a little closer to an ecological "perception of truth."

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2
Pulsed Resources and Community Responses
An Exploration of Factors Influencing Outcomes

RICHARD S. OSTFELD AND FELICIA KEESING

Abstract. Pulses of resources are major bottom-up drivers in ecological systems, leading to a suite of responses by consumers that interact with those resources either directly or indirectly. Although some progress has been made in characterizing the nature of responses to resource pulses, our ability to predict system wide consequences is still somewhat limited. Here we describe several axes of variation for resources and consumers that will influence the responses of ecological systems to pulses. For the resource itself, these axes include the magnitude, timing, and spatial extent of the pulse. For the principal consumer of the resource, axes include its degree of specialization on the resource, its trophic position, its interconnectedness with other members of the community, its mobility, and its generation time. Together, these characteristics of resource and consumer will influence the spatial extent of the community response to resource pulses, the degree to which the pulse ramifies through the community, and the duration of these effects. While a number of excellent case studies of the effects of resource pulses on community dynamics now exist, we suspect that a general conceptual framework that incorporates variation along the axes we describe will be necessary before a truly predictive understanding of the consequences of resource pulses will be possible.

2.1. Introduction

The notion that all life is interconnected is pervasive in public perceptions of ecological systems. This assertion appears to be based more on faith than on science, and indeed until recently, little evidence existed with which to assess it. Determining the nature, strength, and extent of interconnections among species in natural systems is a major challenge that only recently has been undertaken by ecologists. One approach to understanding these interconnections is to create categories of interactions among relatively small numbers of species and then explore their dynamics (Holt and Polis, 1997). For example, two species that compete with one another can also be in a predator–prey relationship, a phenomenon that has been termed "intraguild predation" (Holt and Polis, 1997). Theoretical models of intraguild predation demonstrate that this type of interaction can lead to unexpected outcomes. For example, the removal of a predator could lead to a decrease in its primary prey if the removal also allowed an increase in its intraguild prey (Holt and Polis, 1997).

An alternative approach to studying community interactions is to describe general properties of large and complex networks of species in terms of, for example, the average number of connections among species (Dunne et al., 2002). For example, Thompson et al. (2005) characterized trophic connections in an intertidal food web when the parasites in the web were either included or not. The inclusion of parasites resulted in an increase in the average food chain length, but did not increase the average number of links between species.

The study of resource pulses provides a third approach for assessing the consequences of interconnectedness in ecological systems. With this approach, ecologists describe a general pattern of system behavior that is observed in a suite of diverse systems and then use this general pattern to predict outcomes in systems with similar properties.

Systems characterized by pulses of resources have in common a major bottom-up driver impacting the abundance of resource consumers. The consumers in turn may then constitute a pulsed resource for their predators or parasites (Ostfeld and Keesing, 2000). As resources are depleted, so too are primary, secondary, and tertiary consumers. When consumers are generalists capable of switching to alternative resources when the pulse is declining, species with no direct link to the resource can be affected strongly. The indirect effects of resource pulsing can extend over several trophic levels and many species.

Pulsed resources can be defined as the episodic or periodic production of superabundant resources (usually food) followed by periods of scarcity. Examples include masting by various forest trees in the tropics (Curran and Leighton, 2000), temperate zone (Ostfeld et al., 1996), and boreal zone (Koenig and Knops, 2000), outbreaking insects such as periodical cicadas (Yang, 2004) and locusts (Despland et al., 2004), and heavy seed production in shrubs and annual plants in arid ecosystems, often caused by rains driven by El Niño Southern Oscillation (ENSO) events (Stapp and Polis, 2003). Resource pulses can also include predictable, seasonal increases in resource availability. A resource, by definition, implies that at least one consumer species exists, so any characterization of a resource pulse requires the identification of consumers. Understanding the consequences of pulsed resources for entire communities of interacting species is an important goal. But despite the characterization of a number of systems that illustrate resource pulses (Ostfeld and Keesing, 2000), much remains to be learned to allow us to be able to predict the consequences of these pulses. To provide a conceptual framework for advancing this purpose, here we characterize both the resource and the primary consumer along several axes of variation. We expect that the placement of resources and primary consumers along these axes will provide for a better predictive understanding of the strength and nature of interconnections in these communities.

2.2. The Resource

Resource pulses can be arrayed along at least three axes of variation; magnitude, timing, and spatial extent (Fig. 2.1A). The magnitude of the pulse can be determined quantitatively relative to either other (nonpulsed) resources or the same resource during inter-pulse intervals. For example, acorn (mast) production by oak trees might be 10 or 20 times greater during mast years than in other years, or seed production by desert shrubs might be several orders of magnitude higher during an ENSO event than otherwise. In the case of resources such as bamboo seeds or cicada adults, which might be completely unavailable between pulse events, the pulse can either be characterized qualitatively (on or off) or quantitatively relative to other resources eaten by the same consumers.

The second axis is the timing of the pulse. Important parameters here include whether the pulse is seasonal, multiannual, regular, or predictable. For example, 17-year cicadas emerge on a regular, multiannual basis, but unpredictably with respect to their consumers. In contrast, elemental resources such as nitrogen and phosphorus might become superabundant in aquatic systems with spring rains; i.e., a seasonal, regular pulse. In many cases, resources pulses are multiannual, irregular, and unpredictable. This temporal component also includes the length of time that the resource is available, which can be defined either in absolute terms or relative to consumer longevity or generation time. Some pulsed resources are extremely ephemeral, such as white oak acorns, which germinate within a few

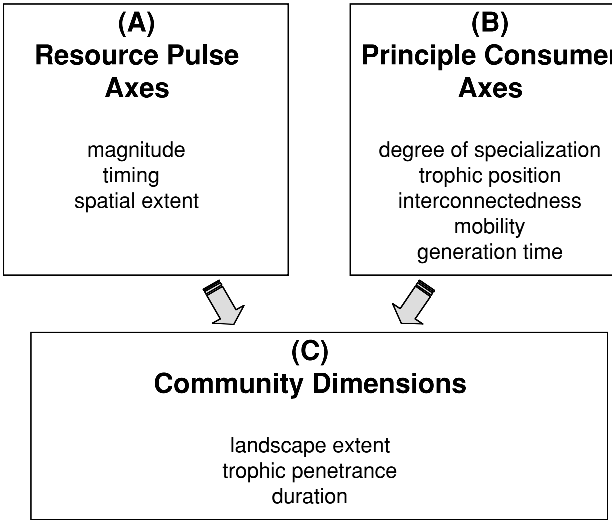

FIGURE 2.1. Conceptual model of the major features of the pulsed resource and the principal consumer that synergistically influence the consequences of the resource pulse for the community in which it is embedded.

weeks of falling to the ground, whereas others, such as seeds of desert shrubs, might remain a viable resource for many months or years.

The third axis is the spatial extent of the pulse. This again can be described either qualitatively, e.g., patchy versus widespread, or quantitatively. Quantification can be either absolute, e.g., number of hectares affected, or relative to movement distances or home range size of consumers. Some resources can be synchronized over tens to hundreds of thousands of square kilometers (Liebhold et al., 2004), whereas others might be limited to much smaller areas. In many cases, habitat destruction and fragmentation by human activities might limit formerly quite widespread resource pulses to small spatial extents. Some resource pulses, e.g., locusts in arid portions of Africa, are themselves mobile, making the characterization of spatial extent a challenge. However, for any given region, even these resources can be characterized by the magnitude, timing, and spatial extent of the pulse.

Characterization of the magnitude, timing, and spatial extent of any pulse may ultimately allow researchers to predict the strength, temporal dynamics, and area of community responses to such resource variability. However, despite a growing number of case studies of resource pulses, the development of a synthesis of the effects of variation in these parameters on community dynamics remains a major challenge for the future.

2.3. The Principal Consumer

A resource implies the existence of a consumer. Although many, perhaps most, resources are consumed by multiple species of consumers, the consequences of resource pulses may be most predictable when a principal consumer can be identified. However, the identification of a principal consumer in no way implies that this is the only important pathway through which community-wide effects of resource pulses can act. The principal consumer can be selected based on its conspicuousness, biomass, or numbers.

The principal consumer can be arrayed on at least five axes of variation; specialization, trophic position, interconnectedness, mobility, and generation time (Fig. 2.1B). The degree to which the consumer specializes on the pulsed resource is an important consideration. Many species that respond to pulsed resources do so highly opportunistically, consuming alternative resources during inter-pulse intervals. Examples include white-footed mice (*Peromyscus leucopus*) that consume acorns during mast years but eat insects and other seeds and fruits outside of mast years, and various insectivorous birds that opportunistically consume periodical cicadas during emergence events but eat other arthropods or fruits otherwise. With white-footed mice, dramatic population growth and high density are stimulated by the resource pulse, but population growth occurs even in the absence of a mast crop (Ostfeld et al., 1996; Wolff, 1996). More than a dozen species of insectivorous passerines respond numerically to the availability of periodical cicadas, and the impact of this pulsed resource on long-term population dynamics of some birds seems strong (Koenig and Liebhold, 2005). Other consumers, such as weevils that attack acorns, are extreme specialists. These species are likely to undergo population fluctuations closely tied to fluctuating abundance of the resource, becoming scarce in the interpulse interval (Maeto and Ozaki, 2003).

Perhaps the key distinction between generalist and specialist consumers of the resource is the potential for the impact of the resource to propagate downward in the food web. Specialists by definition will not switch from the pulsed resource to alternative resources when the former is rare; consequently, the potential for fluctuating abundance of specialist consumers to propagate downward in the foodweb is weak. Population responses by specialist consumers can, of course propagate upwards, influencing their predators. Generalist consumers are expected to switch from the pulsed resource to alternatives when the former resources become scarce; consequently, their potential to cause downward-propagating effects is strong. Similar to specialists, population responses by generalists can propagate upwards, but in general, their effects are expected to be less variable.

A related axis of variation is the trophic position of the principal consumer. If the consumer is an herbivore or granivore, i.e., a primary consumer, its response to the pulsed resource is likely to propagate upwards in the food web, affecting predators at least one trophic level above. This is the situation expected when the resource undergoing pulses in availability is a plant species or a primary consumer in a food web containing multiple trophic levels of consumers. However, if the consumer is a top predator, no potential exists for upward propagation of its response to the resource pulse.

A third axis, related to the first two, is the degree to which the principal consumer is interconnected with other species in the community. By this we mean the number of other species that respond to resource-driven fluctuations in abundance or behavior of the principal consumer. We distinguish this axis from the first two (specialization and trophic position) because interconnections need not be trophic in the strict sense. For example, if the primary consumer modifies the physical or chemical environment for many other species, or if it spreads parasites or pathogens, pulse-driven fluctuations in the community could be pervasive.

A fourth axis of variation is the mobility of the principal consumer. For consumers of very limited mobility, the response to the pulsed resource is expected to be driven by local increases in survival and reproduction that accompany superabundant food. Consequently, population responses are expected to be relatively slow, requiring at least one generation. For those with greater mobility, the movement response will include dispersal into pulse-affected areas as well as survival and reproduction. Immigration to resource pulsed areas affected can be nearly instantaneous, and if this is accompanied by enhanced survival and reproduction, the response by the consumer can be both prolonged and rapid.

The fifth axis of variation is related to the fourth: the generation time of the principal consumer. If generation time is short, then the numerical response to the resource pulse can be quite rapid. Mobile consumers with short generation times (flying insects, some rodents) are expected to mount both a rapid and pronounced numerical response to the resource, whereas more sedentary consumers with long generation times (territorial birds and larger mammals) are expected to respond more slowly and modestly.

2.4. Synergies Between Resource and Consumer

These characteristics of resource and consumer together will determine the consequences of the resource pulse along three dimensions; landscape extent, trophic penetrance, and duration (Fig. 2.1C). Resource pulses that are synchronized among different habitat patches, such as might accompany ENSO-driven rains, are likely to have spatially extensive effects, as are pulses that feed highly mobile consumers. Resources that are highly patch-specific and that feed sedentary species should influence one or a few habitat types.

The second dimension synergistically affected by characteristics of resource and consumer is the trophic level penetrance, or how many trophic levels and taxa will be affected by the pulse. For example, effects on multiple trophic levels are promoted by high-magnitude pulses driving high magnitude fluctuations in consumer response, as well as by principal consumers that are generalists, at low trophic levels, and well connected to other taxa. Effects of resource pulses that are more modest in either magnitude or spatial extent and that are consumed by specialists predators are more likely to have low trophic penetrance and to dampen quickly.

The last dimension is the temporal extent (duration) of the pulse-driven impacts on the community, i.e., how long after initiation will pulse effects still be experienced by members of the community. Brief pulses that are consumed by specialists with short generation times are likely to have only short-term effects on communities, whereas more sustained pulses consumed by generalists or those with long generation times can have protracted impacts.

2.5. A Case Study System

We have been assessing multiple impacts of acorn masting on forested landscapes of the northeastern United States since 1991. Our field studies are largely confined to a series of approximately 2.5-ha plots within oak-dominated forest on the grounds of the 1,000-ha Institute of Ecosystem Studies (IES) in southeastern New York State. Acorn production has varied >1 order of magnitude among years, as measured by seed traps placed under tree canopies (Ostfeld et al., 2001). The interannual variability in acorn production tends to be considerably higher than that of other co-dominant tree species in these temperate deciduous forests (Schnurr et al., 2002). Moreover, the dominant species of oaks in most of our plots, *Quercus rubra* and *Q. velutina*, produce acorns that do not germinate until the spring following maturation and dispersal, and therefore provide a high quality over-winter food resource for consumers. Other oak species in our forests (*Q. prinus* and *Q. alba*), whose acorns germinate in the autumn of their maturation, can be stored if the radicle is clipped by consumers (Steele et al., 2001). However, the combined effects of consumption by a suite of consumers, germination, and decomposition result in complete depletion of the resource within about 4–6 months of the onset of the pulse. Acorn production appears not to be truly cyclic, although quantitative assessment of cyclicity must await a longer time series than is currently available. Heavy acorn years tend to occur at intervals of two to five years. Although we have not documented the spatial extent over which acorn masting is synchronized, casual field observations suggest that it is on the order of tens to hundreds of thousands of square kilometers. Other species of temperate and boreal trees characterized by mast fruiting are synchronized over similarly large spatial scales (Koenig and Knops, 2000).

Box 2.1. Mice as reservoirs of zoonotic pathogens.

Rodents in the family Muridae, which include many of the mice and rats worldwide, harbor dozens of pathogens and parasites that are capable of infecting humans and causing disease. Entries in the list of rodent-borne zoonotic pathogens include numerous viruses such as several arenaviruses that cause hemorrhagic fevers (Lassa fever, Argentine and Bolivian hemorrhagic fevers), several hantaviruses that cause a variety of mild to severe human illnessess (hantavirus pulmonary syndrome, hemorrhagic fever with renal syndrome), monkeypox virus, and lymphocytic choriomeningitis virus. Rickettsial diseases that can be transmitted from rodents to humans include Rocky Mountain spotted fever, human granulocytic anaplasmosis (formerly ehrlichiosis), murine typhus, and Rickettsial pox. Other bacterial diseases in which the pathogen proliferates in rodents include Lyme disease, bartonellosis, plague, and tularemia. Finally, rats and mice can act as zoonotic hosts for protozoal parasites, including *Babesia* and *Cryptosporidium*, which cause babesiosis and cryptosporidiosis, respectively. In some, but not all of these diseases, risk of human exposure has been linked to flucutating density and changing behavior of rodent hosts (Ostfeld and Mills, in press).

Possible reasons why rodents are so important as hosts for zoonotic pathogens include: (1) high maximal population density and growth rates, which can facilitate transmission of pathogens within rodents and from rodents to "spillover" hosts, such as humans; (2) the occurrence of social organizations, including colonial group living, and associated amicable and agonistic social encounters that offer opportunities for pathogen transmission; and (3) the ability of many species to adapt to, and even proliferate from, environmental degradation that accompanies human activities and settlements. This latter feature reaches an extreme in the case of some rodents, such as Norway rats (*Rattus norvegicus*), black rats (*R. rattus*), and house mice (*Mus musculus*), that have evolved commensal habits. Given the granivorous diet of many of these species, a high potential exists for pulsed seed production to influence zoonotic disease risk and incidence via its effect on rodent reservoirs. Given this reasoning, one might also expect some colonial and commensal passerines, such as some sparrows, finches, and thrushes (e.g., American robins) to be masting-driven contributors to zoonotic risk, a scenario that seems to apply to West Nile virus.

Although several conspicuous consumers of acorns, e.g., turkeys (*Meleagris gallopavo*), blue jays (*Cyanocitta cristata*), various sciurid rodents, raccoons (*Procyon* *lotor*), white-tailed deer (*Odocoileus virgnianus*), and others, occur in our plots, we focus on white-footed mice (*Peromyscus leucopus*; hereafter "mice"). Mice are extreme trophic generalists that eat seeds, fruits, arthropods, fungi, bark, and bird eggs (Wolff et al., 1985; Derting and Hornung, 2003). In addition, mice are important components of the diets of mammalian, avian, and reptilian predators, including foxes, weasels, bobcats, hawks, owls, and snakes. Mice are also key hosts for ectoparasites such as ticks as well as for zoonotic pathogens such as the agents of Lyme disease, Anaplasmosis, Babesiosis, and Bartonellosis (Ostfeld. and Mills, in press; Box 1). Because they are widespread geographically, locally abundant, and ubiquitous in their habitat occupancy, and owing to the large numbers of taxa that either eat or are eaten by mice, they can be considered a "hub species" (P. Turchin, pers. comm.) that interacts strongly with many other species in these communities.

Individual mice are capable of dispersing >1,000 meters, and populations are typically highly mobile, occupying multiple patches within heterogeneous landscapes (e.g., Maier, 2002; Burns, 2005). Both the direction and magnitude of movements by mice appear to be influenced strongly by spatial variation in food availability. Within their home ranges, mice tend to use space in a fine-grained manner, and activity density is influenced by both predation risk and prey availability (Schmidt et al., 2001). In addition, because the generation time for mice is approximately 2 months, and litters of 4 to 6 young are common, mouse populations have a great potential to respond numerically to pulsed resource availability, and to do so quickly. Inter-annual variation in mouse abundance, which is highly correlated with mast production, spans two orders of magnitude (Ostfeld et al., 1996, 2001).

These combined features of the acorn resource and the mouse consumer result in mast-driven fluctuations in mouse abundance that influence a large number of other forest species and processes. High mouse density is correlated with the suppression of gypsy moth (*Lymantria dispar*) outbreaks, because mice are efficient consumers of gypsy moth pupae, and their attack rates increase with increasing mouse density (Jones et al., 1998). In fact, mice appear capable of driving low-density gypsy moth populations extinct, but moth extinction appears to be avoided in part by spatial heterogeneity in foraging intensity by mice, which allows moths to persist and reproduce in areas of reduced predation risk (Goodwin et al., 2005). Crashes in abundance of mice, driven by acorn failures, appear responsible for releasing gypsy moth populations from regulation and allowing the moths to increase to peak densities at which they can defoliate vast expanses of forest trees (Jones et al., 1998).

Interactions between fluctuating mouse populations and ground-nesting songbirds show some similarities to the mouse-moth interaction. Mice and eastern chipmunks (*Tamias striatus*) (the latter also responds numerically to acorn production) are avid consumers of eggs and nestlings of ground-nesting and shrub-nesting forest songbirds. Six years of monitoring nesting success of Veeries (*Catharus fuscescens)*, Wood Thrush (*Hylocichla mustelina)*, American Robins (*Turdus migratorius)*, and other nesting songbirds at our study sites have revealed that the daily nest mortality rate is a strong linear function of rodent (mouse plus chipmunk) abundance (Schmidt and Ostfeld, 2003). Analysis of data from the Breeding Bird Survey revealed that breeding density of the three thrush species declined strongly in the years following high rodent density (Schmidt and Ostfeld, 2003). However, breeding density was also strongly reduced in years following very low rodent density. This relationship appears to be due to a three-way interaction between songbirds, their rodent nest predators, and generalist raptors that prey on both birds and rodents. In years of extreme rodent scarcity (which follow mast failures), some evidence suggests that hawks and owls switch from preying on sparse rodents to preying on fledglings and nestlings of forest songbirds. Thus even though reduced nest predation during the mouse crash results in current-year high breeding success, low breeding density occurs in the subsequent year due to raptor attacks on adults (Schmidt and Ostfeld, 2003).

Fluctuating mouse numbers also influence risk of human exposure to Lyme disease. Mice are an important host for immature stages of the tick *(Ixodes scapularis*) vector of Lyme disease bacteria (*Borrelia burgdorferi*) in the eastern and central United States. The abundance of the nymphal stage, which transmits the vast majority of Lyme disease cases to humans (Barbour and Fish, 1993), is highly correlated with prior year mouse density (Ostfeld et al., 2001, 2006). In addition, mice are the principal source of infection for immature ticks (i.e., the "natural reservoir" for Lyme disease bacteria; LoGiudice et al., 2003), and consequently the abundance of infected nymphal ticks is highly correlated with prior year mouse density (Ostfeld et al., 2001). Through its impacts on the abundance of infected nymphal ticks, the abundance of mice can also affect the probability of exposure of other vertebrates to pathogen-bearing ticks, as well as their ability to transmit pathogens back to ticks (Schauber and Ostfeld, 2002). Finally, abundance of mice in the prior year, or of acorns two years previously, significantly influenced the (de-trended) number of human cases of Lyme disease in the New York county in which our monitoring of acorns and mice is conducted (Schauber et al., 2005; Box 2).

As a result of the number, nature, and strength of the interactions between mice and other taxa in oak forests, the impacts of masting permeate through at least three trophic levels and dozens of species in at least five major taxonomic groups (Insecta, Arachnida, Mammalia, Aves, and Eubacteria). Similarly extensive effects of masting have been observed in several other forest ecosystem types in Europe, Asia, and New Zealand (reviewed by Ostfeld and Keesing, 2000). The ramifying impacts of acorn masting are experienced >2 years after the depletion of the resource, as exemplified in indirect effects of acorns on songbirds, gypsy moth dynamics, and Lyme disease risk years later. This protracted effect is due largely to the number of species affected combined with their generation times.

The landscape extent of masting effects is perhaps least well studied in our system, but some evidence suggests that impacts can be spatially widespread. Acorn-induced outbreaks of infected ticks in oak-dominated patches appear to trickle into adjacent non-oak-dominated forest patches, where Lyme disease risk can be elevated despite the absence of oaks (Van Buskirk and Ostfeld, 1998). The

Box 2.2. Acorn production and human cases of Lyme disease in the northeastern United States.

Lyme disease is a bacterial illness in which the etiological agent, *Borrelia burgdorferi*, is acquired by ticks from mammalian and avian hosts and transmitted by ticks to humans. In eastern and central North America, the white-footed mouse (*Peromyscus leucopus*) is the tick host most likely to cause infection (LoGiudice et al., 2003). Dense populations of white-footed mice offer tick populations ample opportunity to acquire infection, and peaks in mouse populations have been linked to the abundance of infected ticks in the environment (Ostfeld et al., 2001). Population dynamics of mice are influenced strongly by acorn production (Ostfeld et al., 1996; Wolff, 1996), leading to the expectation that acorn abundance might predict subsequent abundance of infected ticks, and therefore risk of human exposure to Lyme disease. A correlation between acorn availability and Lyme disease risk has now been established from both observational (Ostfeld et al., 2006) and experimental (Jones et al., 1998) studies. Whether acorn-driven variation in Lyme disease risk translates into variation in Lyme disease incidence (cases per capita in human populations) was tested recently for a county in the epicenter of the United States Lyme disease epidemic—Dutchess County, New York (Schauber et al., 2005).

Data on acorn and white-footed mouse abundances were collected from representative forest sites on the grounds of the Institute of Ecosystem Studies (IES) in central Dutchess County. Data on human cases from Dutchess County were collected from the county Department of Health, and those on human cases in surrounding states were obtained from state health departments. Because Lyme disease incidence has been increasing in the northeastern United States over the past 10–15 years, the incidence data had to be de-trended in order to evaluate effects of acorns and mice on incidence. Schauber et al. (2005) used an information theoretic approach to select the models that best fit the data on changes in incidence over time at each location, fit these models to data, and calculated residuals from these trend lines. Residuals became the response variables in an exploration of the importance of acorns and mice versus more widely accepted weather variables. Models with either acorns or mice at IES as the independent variable were considerably better than models that included weather variables at explaining de-trended Lyme disease incidence in Dutchess County. Models with acorns or mice at IES as the sole independent variables were similarly superior at explaining detrended Lyme disease incidence in Connecticut, which borders Dutchess County to the east. Models for more distant states sometimes included IES acorns or mice and sometimes included state-specific weather variables, suggesting that the power of IES acorn/mouse abundance to predict Lyme disease incidence declines with distance. Given that acorn and mouse abundance were not measured in these states, and that populations might be out of synchrony with IES populations, this result is not surprising. It appears that pulsed resources can be epidemiologically valuable leading indicators of disease incidence.

underlying mechanism appears to be dispersal by tick-infested mice from oak to non-oak habitat during and after peaks in mouse abundance, although the evidence for this is circumstantial. The impact of acorn abundance measured on our forest plots at IES on detrended Lyme disease incidence in humans was significant not only for the local county, but also for the adjacent state of Connecticut (Schauber et al., 2005), suggesting that the spatial extent of masting, or the dispersal distances of hosts, or both, are considerable.

2.6. Conclusions

We have described a series of axes that may prove useful in characterizing the consequences of resource pulses for community dynamics of ecological systems. For the resource pulse itself, these include its magnitude, timing, and spatial extent. For the principal consumer species, these axes include the degree of specialization of the consumer, its trophic position, the degree of its interconnectedness to other species, its mobility, and its generation time. Within any ecological system, the interaction of these factors will determine the spatial extent of the effects of the resource pulse, the degree to which its effects ramify through the community, and the duration of these effects. While a number of excellent case studies of the effects of resource pulses on community dynamics now exist, we suspect that a general conceptual framework that incorporates variation along the axes we describe will be necessary before a truly predictive understanding of the consequences of resource pulses will be possible.

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3

Invoking the Ghosts of Landscapes Past to Understand the Landscape Ecology of the Present . . . and the Future

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Abstract. Most landscapes bear the imprint of past human land use that in some cases dates back centuries or even millennia. Land use has the potential to create strong legacy effects on biotic communities that may persist for decades or centuries, even after the landscape has been abandoned and seemingly restored to its natural pre-settlement state. Current species distributions may thus better reflect historical than contemporary landscape configurations, owing to the lagged response of species to landscape change. These "ghosts of landscapes past" have been found to haunt the biota of both terrestrial and aquatic systems. This chapter examines several case studies that illustrate the magnitude of human land-use legacies, and considers the types of species and landscape scenarios for which lagged responses to landscape change are especially likely, in the hopes that we can better detect delayed responses to land use, should we ever wish to attempt to exorcise the ghosts of landscapes past. Ignoring the ghosts of landscapes past is potentially risky from a conservation or land-management perspective. Past land use may incur an extinction debt, especially in landscapes that have undergone rapid transformation and if the remaining habitat lies below the extinction threshold for many species. Because time lags to landscape change are expected to be especially long at the extinction threshold, we may be seriously underestimating extinction risk and the impact of past land use on biological communities. Thus, knowledge of current landscape structure may not be the best basis for assessing extinction risk, or for predicting the response of species to future landscape change, in the absence of information on landscape history. The ultimate value of adopting a historical perspective, however, is a better understanding of the temporal dynamics of landscapes, which not only provide a frame of reference for evaluating the impact of past human land-use activities within an ecological context, but may also contribute to the development of land-management systems that are more in tune with the dynamic landscape systems they are designed to manage.

3.1. Introduction

In many parts of the world, humans have emerged as the primary drivers of landscape change, ushering in an era of widespread habitat transformation, rapid climate change, and diminished biological diversity. Never before has there been a greater need—or urgency—for understanding the impact of human land-use activities on landscape structure and hence on the ecology of human-modified landscapes. Given that 50–80% of the Earth's land surface has been transformed, altered, or influenced by human activities (Vitousek et al., 1997; Sanderson et al., 2002), nearly all landscapes can be considered human-modified, at least at some point in human history. Habitat transformation driven by human land use represents the single greatest threat to biodiversity, followed by the threat posed by invasive species (Wilcove et al., 1998; Hilton-Taylor, 2000). Land transformation contributes to the outright loss, fragmentation, and degradation of habitat and may also facilitate invasion by non-native species, creating a positive feedback that further enhances land transformation (Hobbs, 2000; With, 2002).

Little wonder, then, that conservationists and landscape ecologists tend to focus on the spatial dimensions of landscape change, particularly in terms of identifying how much habitat is enough to avert extinction or to mitigate fragmentation effects on biodiversity and invasive spread (Fahrig, 2001, 2003; With, 2004). Even studies that purport to examine the effect of "habitat loss" on biodiversity, which implies an analysis of landscape change, generally have assayed only the effect of "habitat difference" among contemporary landscapes that vary in the amount of habitat (Schrott et al., 2005a). Such studies make a space-for-time substitution (Hargrove and Pickering, 1992) by analyzing landscapes that are replicated in space rather than time. For this approach to be valid, one must assume either that all landscapes lie on the same trajectory of change (Fig. 3.1a), or that landscape history—the rate and process by which landscapes have achieved their current state—is not important.

Ignoring the temporal dimensions of landscape change is potentially risky from a conservation or management standpoint. Clearly there is an urgent need to recognize landscapes that are currently undergoing broad-scale transformation at unprecedented rates (e.g., humid tropical forests in Southeast Asia; Achard et al., 2002), but landscape history increasingly is seen as integral to sound environmental science and for providing the proper context and guidance for ecosystem management (Swetnam et al., 1999; Foster et al., 2003). Partly this stems from: (1) the growing recognition among natural resource and land managers that landscapes are inherently dynamic systems, with important ecosystem processes and disturbance regimes operating over many different scales in space and time, spanning decades, centuries, or even millennia; (2) that human land-use activities may lie outside the range of natural variability for the system; and (3) that adopting a historical perspective may enable managers to set goals with a better chance of maintaining and protecting ecosystems while continuing to meet societal demands for the goods and services provided by those systems (Landres et al., 1999; Parsons et al., 1999). The reconstruction of historical landscapes thus provides a frame of reference for assessing how past environmental changes have driven changes in biodiversity through time (Delcourt and Delcourt, 1998; Swetnam et al., 1999), as a means of documenting how these changes may have been altered by human

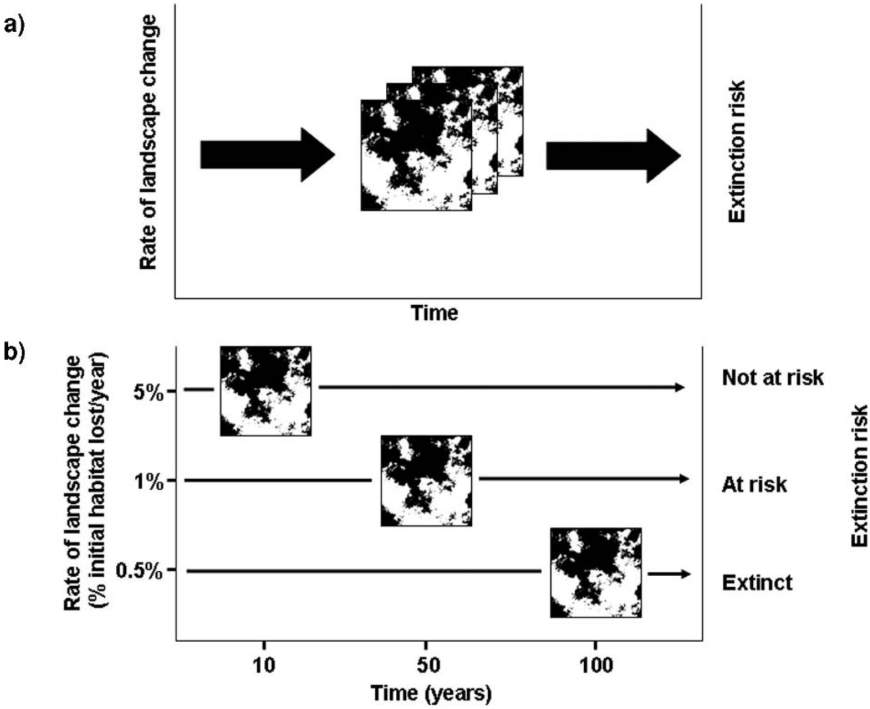

FIGURE 3.1. The importance of landscape history for assessing a species' risk of extinction from habitat loss and fragmentation. Most studies ignore landscape history and assume that all landscapes lie on the same trajectory of change: (a) Extinction risk is thus assessed probabilistically for populations on landscapes for a given amount and distribution of habitat (e.g., 50%). If these landscapes achieved their current state at very different rates, however, then assessment of extinction risk will be dependent on this aspect of landscape history; (b) Populations may be variously assessed as "not at risk," "at risk," or "extinct," depending upon how long the landscape has been subjected to human land use. In particular, extinction risk may be underestimated in landscapes undergoing rapid rates of change because of demographic lags. (based on results of Schrott et al. 2005a).

activities that have transformed more natural landscapes into more cultural ones (Delcourt and Delcourt, 1988, 2005).

The cultural footprint left on landscapes is typically large, deep, and long-lasting. Some landscapes have a long history of human land-use spanning many centuries or millennia, and the modern landscape may still bear the imprint of ancient land-use activities produced by clearing, plowing, draining, or terracing (Dupouey et al. 2002; Foster et al., 2003; Davidson and Simpson, 2005). Land use creates a strong legacy effect on biotic communities that may persist for decades or centuries, even after the landscape has been abandoned and seemingly restored to its "natural" pre-settlement state (Swetnam et al., 1999; Foster et al., 2003). Such appearances may be deceiving, however, because the recovered post-settlement landscape may only superficially resemble its pre-settled state or a comparable landscape that had never been disturbed by such land use. Thus, present-day communities may better reflect past landscape states than current ones, especially if species exhibit lagged responses to landscape change.

In this chapter, I present several case studies that illustrate the enduring legacy of land use on populations and communities. In particular, I review the potential for lagged responses to landscape change to occur, in which the decline or extirpation of species may not happen for many decades and may continue long after the initial period of human-induced disturbance has ceased and the landscape appears to have recovered. Because past land use may incur an *extinction debt* (*sensu* Tilman et al., 1994), knowledge of current landscape structure may not be the best basis for understanding species–habitat relationships or for predicting the response of species to future landscape change in the absence of information on landscape history.

3.2. Legacy Effects of Landscape Change

The "ghosts of landscapes past" have been found to haunt the biota of both terrestrial and aquatic systems. Land-use legacies on vegetation communities are especially prevalent and well documented. In central Massachusetts (USA), for example, the legacy of past agricultural land-use from the 18th century is still reflected in the vegetation of today's forests. This landscape has undergone a complete transformation during the past three centuries: from a primarily forested region that was largely cleared for timber and agriculture by the mid-1800s following European settlement, to a now mostly forested region once again as industrialization during the latter half of the 19th century led to farm abandonment and migration to urban centers, thus allowing for natural reforestation over the past 100–150 years in spite of a steadily increasing human population (Foster et al., 1998). Despite the return to forest, the structure and composition of these forests have been dramatically—and perhaps permanently—altered by this relatively brief but intense period of deforestation and agricultural land use, such that current landscapes are much more homogeneous across the region than during Colonial times. Forests are now dominated by trees such as paper birch (*Betula papyrifera*), red maple (*Acer rubrum*) and white pine (*Pinus strobum*) that were relatively uncommon in Colonial forests, but which are essentially "pioneer species" that were capable of broad-scale dispersal and rapid establishment following severe disturbance wrought by clearing, cutting, and cultivation of the region (Foster et al., 1998). In contrast, species such as eastern hemlock (*Tsuga canadensis*) and beech (*Fagus grandifolia*), which are long-lived and poor dispersers, have yet to recover their former abundance or extent.

Looking past the trees, the forest contains other land-use legacies from America's Colonial period. The current impoverishment of forest herbs is also thought to be a legacy of 18th-century forest clearing. The understory flora of woodlands that had been cleared and plowed, but which were allowed to reforest naturally following agricultural abandonment, still bear the signature of past cultivation: they contain more weedy species and fewer ericaceous shrubs (e.g., wintergreen, *Gaultheria procumbens*; huckleberry, *Gaylussacia baccata*; wild raisin, *Viburnum cassinoides*) than woodlands that escaped the plow (Foster et al., 2003). Many forest herbs have low seed production, lack persistent seed banks, and are dispersal-limited (i.e., their seeds are ant-dispersed or lack morphological structures for long-distance dispersal) because they are adapted to relatively stable forest ecosystems that are characterized by fine-scale patch disturbances (Bellemare et al., 2002). These species have not exhibited rapid recovery and recolonization following their extirpation from areas that had been cleared and cultivated. In a modeling study of land-use change over a 300-year period, Matlack (2005) showed that seed dispersal ability was critical to the regional survival of forest herb species. Further, the model predicted that the legacy effects of agricultural land-use would likely persist for at least another century. Given the spatial and temporal scale of human land-use, slow-migrating species and those lacking gap-crossing abilities are most at risk of regional extinction, raising the possibility of an extinction debt for herbaceous species in these forests. Additionally, past land-use may affect nitrogen cycling and the spatial heterogeneity of soil resources (Fraterrigo et al., 2005), which could produce effects that persist for many decades, resulting in a fundamental shift in the composition and diversity of these forested ecosystems. If true, it may not be possible to recover historical vegetation even if dispersal limitation is eventually overcome in time (see also Dupouey et al., 2002).

Past land use also influences the biological diversity of aquatic systems. Aquatic systems have a strong dependence on the surrounding landscape, and land-use practices throughout the watershed may affect a wide range of conditions, such as hydrology, organic inputs, temperature, and water chemistry, and are thus capable of contributing to strong legacy effects (Allan et al., 1997). For example, patterns of fish and invertebrate diversity within streams draining two watersheds in the southern Appalachians were best explained not by current land use, but by the intensity of agricultural land use some 40 years earlier (Harding et al., 1998). Although some streams currently flow through watersheds that are mostly forested, their complement of fish and invertebrate species more closely resembled those found in agricultural streams. Significantly, these "anomalous" forested streams were in watersheds that had formerly experienced a high degree ($\sim$40%) of deforestation and agriculture in the 1950s. Reforestation over the past half-century has thus resulted in little effective recovery of these stream communities. As in terrestrial systems, the recovery of aquatic biota from high-impact disturbances such as deforestation or agriculture—even though seemingly removed from the stream or lake in question—can still take decades to achieve.

It comes as no surprise that landscape transformation has such profound effects on biological communities; rather, the surprise is that these effects are so persistent even after human activities have ceased and vegetation has been allowed to recover (however illusory that recovery may be). Even if transformation was not complete or particularly extensive, human land use can still have other more subtle effects on landscape structure, which may have no less a dramatic effect on patterns of diversity. For example, a seemingly trivial loss of habitat at a critical point can effectively disrupt the habitat connectivity of the entire landscape, which may have consequences for biodiversity that far exceed the actual amount of habitat lost (e.g., nonlinear or critical threshold responses; With and Crist, 1995). A disruption of landscape connectivity can reduce dispersal or colonization success and enhance species extinction risk (With and King, 1999a,b), even when local conditions are not directly affected by land-use activities. As with landscape transformation, a disruption of connectivity has the potential to produce strong legacy effects in diversity patterns. For example, high plant species diversity within the small remaining patches of semi-natural grassland in Sweden is a relic of a formerly connected open farming landscape that existed nearly a century ago (Lindborg and Eriksson, 2004). These grasslands have declined more than 90% during the past 80 years, such that historical grasslands had much higher connectivity than present-day remnants. Subsequently, these grasslands have maintained a higher diversity of plants than might otherwise be expected based on the current amount and distribution of habitat. Similarly, historical habitat connectivity still exerts an influence on the distribution of carabid beetles within hedgerow networks of France (Burel, 1992; Petit and Burel, 1998). Hedgerows have been declining since the 1950s as a result of a shift from traditional to modern farming practices, resulting in increased isolation of beetle populations. It may take many decades, however, before beetle populations disappear from isolated hedgerows. Beetle distributions thus exhibit a 'memory' of past landscape structure, with the result that current carabid beetle assemblages better reflect the historical landscape structure of a half-century ago than the present-day hedgerow network. It is worth noting, then, that land-use legacies are not always negative (e.g., depauperate herb or fish communities in reforested landscapes following agricultural abandonment), but may actually appear to be positive (a retention of native species, such as carabids or grassland plants, in spite of past land clearing), at least in the short term.

3.3. Of Time Lags and Extinction Debts

As these examples illustrate, legacy effects of past land-use are ultimately produced by lags in species' responses to landscape change, which leads to a decoupling of landscape pattern and species distributions. Despite the severity of the impact, the response by the biological community to human land use is usually not immediate. Instead, communities may undergo a slow hemorrhaging, with some species eventually going extinct many decades or centuries even after the initial disturbance has ceased. *Extinction debt* is an extreme manifestation of a lagged response to past landscape change (Tilman et al., 1994). Time lags are expected to be especially long near the extinction threshold—the critical amount of habitat required for species persistence (Hanski and Ovaskainen, 2002). As habitat loss and fragmentation push the metapopulation closer to its extinction threshold, theory predicts increasingly longer delays in the time required for the metapopulation to achieve a new equilibrium in the changed landscape (extinction, in this case). In other words, extinction debts are likely in landscapes that exceed the extinction threshold for many species. If so, then we may be seriously underestimating the threat posed by past land-use to current biodiversity. For example, the rich diversity of freshwater mussels in the Midwestern United States has undergone a precipitous decline following a century of landscape conversion to agriculture that entailed draining almost all (>90%) of the wetland habitat (Poole and Downing, 2004). In Iowa, nearly half of the stream mussel species that had ever been recorded in the state were extinct by 1985. Freshwater mussels have the dubious distinction of suffering the highest extinction rates of any taxonomic group, terrestrial or aquatic, but then such a dire statistic is hardly surprising given the scale of habitat loss and degradation. Over the ensuing decade (1985–1998), however, mussel species continued to go extinct and had totally vanished from half the streams surveyed, an alarming discovery given that land use has changed little over the past several decades (Poole and Downing, 2004). The extinction debt incurred by near total habitat transformation more than a century ago continues to pay out, and is greatest where historically habitat destruction had been the most complete (i.e., watersheds that had the most habitat converted to farmland suffered the greatest loss of species). As grave as the present situation appears to be for freshwater mussels, the future may be far bleaker than previously imagined as these lagged extinctions play out. Nor are these land-use effects on mussels a relatively recent phenomenon. An analysis of prehistoric shell middens revealed declines in freshwater mussels that are coincident with the advent of broad-scale maize agriculture by Native Americans throughout the eastern half of the Mississippi River basin some 1,000 years ago (Peacock et al., 2005). Prehistoric land use was thus capable of exacting a toll on biological communities that was similar—if less acute—than that exerted by modern societies.

An extinction debt also has been inferred for primates inhabiting the forests of Africa (Cowlishaw, 1999). Nearly half of all primate species are threatened with extinction, yet none has gone extinct since 1600, suggesting there may be a long extinction lag. Cowlishaw (1999) developed species-area relationships based on past deforestation levels to quantify the magnitude of the extinction debt. Forest loss over the past 50 years should have resulted in the extinction of several forest primates, yet none has yet occurred. In most countries, the debt is estimated to comprise over 30% of the forest primates (a debt of 4–8 species), with Cameroon and Nigeria having the largest extinction debts. Extinction debts for forest primates may thus take thousands of years to pay out. Historical deforestation poses a grave threat to forest primates, but this extinction debt is only exacerbated by the rapid rate at which forests are currently being lost in Africa (e.g., Achard et al., 2002).

The problem, then, lies with rapidly changing landscapes and slow-changing populations, a situation which may describe the plight of Neotropical migratory songbirds, which have demonstrated widespread declines in North America over the past 30 years or so. Using a spatially structured avian demographic model, Schrott et al. (2005a) showed how extinction risk in songbirds could be underestimated in populations on landscapes undergoing rapid habitat loss, relative to landscapes where populations were subjected to low-level chronic disturbance over a long time period. In the former scenario, the rate of landscape change exceeded the response time of the population (Fig. 3.2a). That is, there was not sufficient time for the demographic consequences of habitat loss and fragmentation, such as

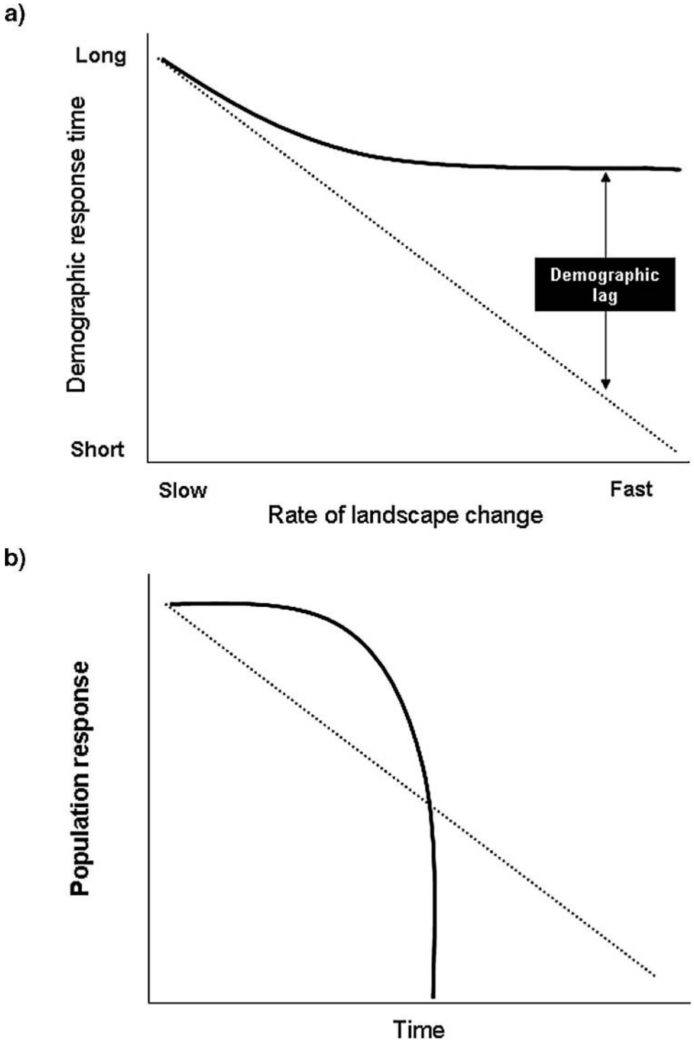

FIGURE 3.2. Demographic lags may produce discordant responses to landscape change. Species incapable of rapid response to landscape change tend to be found in more stable landscapes subjected to infrequent or low levels of disturbance (diagonal line, a). In landscapes undergoing rapid rates of change owing to human conversion, however, such species will exhibit delayed population responses to landscape change as a consequence of demographic lags, such as initially high survivorship or longevity (a). Even if habitat loss and fragmentation have a negative effect on fecundity or survivorship, it may take awhile before these demographic consequences are translated into obvious population responses such as negative exponential growth (b). At that point, populations may suddenly undergo rapid declines (i.e., a nonlinear or threshold response). Such threshold responses may come as a surprise if landscape history is not taken into consideration.

reduced nesting success and fledgling production, to be reflected in population-wide measures of viability such as intrinsic growth rate (λ) that are used to assess extinction risk. As a consequence, the population may not be assessed as "at risk" in these landscapes undergoing rapid habitat loss, and yet the population ultimately goes extinct, often abruptly with little apparent warning (Fig. 3.2b). There thus appears to be a scaling mismatch between the temporal scale of landscape change relative to the temporal scaling of the species' demographic response (Fig. 3.2). The past history of landscape change—such as the rate of habitat loss—is thus important for evaluating extinction risk in current landscapes.

In assessing a species' risk of extinction from habitat loss and fragmentation, the time it has taken a landscape to achieve its present state may be just as important as the amount of habitat lost or how fragmented the current landscape has become. For example, three landscapes may have similar amounts of habitat (e.g., 50%) and levels of fragmentation, but depending upon the rate at which habitat was destroyed and thus how quickly these landscapes achieved their current state, populations on these landscapes may be variously assessed as either (l) locally extinct (habitat lost at a rate of 0.5%/year over 100 years), (2) at risk for extinction (habitat lost at a rate of 1.0%/year over 50 years), or (3) not at risk of extinction (habitat lost at a rate of 5%/year over 10 years; Fig. 1b). In the latter case, extinction risk is underestimated because the landscape has changed more rapidly than the demographic potential of the population, resulting in a lagged response of the population to habitat loss and fragmentation as discussed previously. Such lagged responses to landscape change may also have implications for recovery of songbird populations through habitat restoration (Schrott et al., 2005b). Although it is generally assumed that populations will recover once habitat has been restored (either naturally or through human intervention), demographic lags to landscape change—even positive changes—can also affect the potential for recovery. Although populations may have declined in response to habitat loss and fragmentation (they are habitat-sensitive), recovery of these populations may no longer be limited by the amount of the habitat on the landscape. For example, populations subjected to chronic low-level disturbance over a long time period may suffer demographic erosion (e.g., reproductive success and fecundity decline as habitat continues to be lost and fragmented), such that complete habitat restoration will not be sufficient to offset mortality and recover the population (Schrott et al., 2005b). Recovery for these species is considered to be more demographically limited than habitat-limited. In such cases, conservation efforts would need to focus on measures capable of boosting fecundity and/or survivorship (e.g., improve quality of nesting habitat, control nest predators) to rescue such species, in addition to restoring habitat (see Bissonette, Chapter 1, this volume).

3.4. Management and Conservation Implications of Landscape Ghosts

If most landscapes bear the legacy of past land use, which in some cases dates back centuries, then many extant species may be relics of a bygone landscape that no longer exists, or at least, has been significantly altered. This raises some important practical—as well as ethical—considerations regarding the management and conservation of such species. If the species are associated with the native habitat and have persisted in spite of human land-use activities, then the concern might be whether these are the collateral of an extinction debt that has yet to be fully paid. If population declines lag well behind the loss and fragmentation of habitat, then extinction risk could be greatly underestimated, especially if habitat transformation occurred rapidly relative to the species' generation time (Schrott et al., 2005a). Most assessments of extinction risk ignore landscape history and are based only on the current landscape configuration, or use this as a baseline for evaluating the effect of future land-use change. This approach may not be valid if the manner by which the landscape achieved its current state affects the population trajectory (Fig. 1b).

Alternatively, if a species' presence is a legacy of the past land use (e.g., "weedy" or early successional species associated with cultivated or grazed habitats), then is their decline following the abandonment and subsequent recovery of the landscape a concern for conservation? Or, are these non-native and potentially invasive species that should be actively expunged from the landscape? What if these early-successional species are now globally rare because they were maintained historically by land-use activities such as grazing that no longer occur? Do biological assemblages that have developed as a consequence of past human activity have value, and if so, should we actively manage to preserve these cultural landscapes (Landres et al., 1999)?

Such a case has been made for the flora associated with the grasslands, heathlands, and shrublands of coastal New England, which support the highest concentration of rare and uncommon species in the Northeast. Despite the common belief that these habitats were native and had been widespread in the pre-European landscape, these open-land habitats are apparently anthropogenic, having been created and maintained by farming practices such as plowing, prescribed burning, and grazing by sheep following European settlement and clearing of the region in the 17th century (Motzkin and Foster, 2002). These open habitats are in fact a cultural artifact, which have been dwindling in the face of widespread reforestation of the region, such that the early-successional species associated with these habitats now are rare and considered a high priority for conservation. Many of these species have continued to decline in spite of active management involving prescribed burning and mowing, which has not been entirely successful in halting the encroachment of woody vegetation and the return to forest. Motzkin and Foster (2002) recommend a return to traditional grazing practices to recover these plants, despite the fact these species are relics of a bygone—and cultural—landscape. They still represent a unique and important component of regional biodiversity.

Clearly, then, not all ghosts of landscapes past are necessarily unwelcome or even undesirable. Humans inevitably bring a cultural bias to the problem of which species or habitats to conserve. Throughout Europe, for example, where landscapes have had a more pronounced history of human occupation and alteration, environmental legislation puts high conservation value on numerous habitat types and species communities that resulted from traditional land-use practices, and are now at risk from abandonment of these practices (e.g., semi-natural grasslands; European Union Habitats Directive 92/43/EEC; Redecker et al., 2002).

3.5. Ghost-Busting and the Exorcism of Landscapes

In cases where land-use legacies have an undesirable effect on biodiversity, however, we are faced with the dual problem of detecting (or anticipating) lagged effects, as well as potentially exorcising these ghosts of landscapes past. By definition, a lagged response to landscape change means that the effects of land use will not be immediately apparent. Short of a séance, then, how can we detect such lagged effects? What types of species are most likely to exhibit lagged responses to landscape change? When are time lags to landscape change to be expected? Can we ever hope to exorcise the ghosts of landscapes past?

3.5.1. How Can We Detect Lagged Responses to Land Use?

As illustrated by the case studies in this chapter, time lags may be revealed through "ghost hunting" (Nagelkerke et al., 2002), which reveals whether current species distributions match a historical landscape configuration better than the current landscape (e.g., Petit and Burel, 1998; Lindborg and Eriksson, 2004), or through statistical analyses that demonstrate a significant relationship between the species present (or lost) and the type or intensity of past land use (e.g., Harding et al., 1998; Poole and Downing, 2004). Alternatively, it may be possible to quantify the magnitude of the extinction debt by developing species–area relationships based on past habitat amounts or relative to some type of "reference landscape" (e.g., Cowlishaw, 1999). Modeling approaches may also be used to predict extinction debt, to assess extinction risk, or to forecast population trends based on simulations of past landscape change (e.g., Tilman et al., 1994; Hanski and Ovaskainen, 2002; Nagelkerke et al., 2002; Schrott et al., 2005a).

3.5.2. What Types of Species Are Most Likely to Exhibit Lagged Responses to Landscape Change?

The types of species most likely to exhibit lagged responses to landscape change are species with poor colonization abilities; species with large or stable local population sizes; species with long individual lifespans or seed banks; species with low turnover or population growth rates; and species with low sensitivity to environmental fluctuations (Nagelkerke et al., 2002; Lindborg and Eriksson, 2004). For example, Lindborg and Eriksson (2004) have suggested that short-lived or highly mobile organisms (such as insects or birds, respectively) may not be as sensitive to landscape history as, say, long-lived plants. As the case studies in this chapter have illustrated, however, even carabid beetles (Burel, 1992; Petit and

Burel, 1998) and songbirds (Schrott et al., 2005a,b) may show legacy effects or lagged population responses to landscape change. Time lags are thus determined by the interaction between species' life-history attributes and landscape dynamics (e.g., rate of habitat change).

3.5.3. When are Time Lags to Landscape Change to be Expected?

The ghosts of landscape past are most likely to haunt habitats that historically have been relatively stable (e.g., old growth forests), where species tend to react slower and exhibit greater lags (Nagelkerke et al., 2002; Fig. 3.2). For example, the high diversity of crustose lichens within recently isolated remnants of old-growth boreal forest in northern Sweden—relative to naturally fragmented forest patches that have been isolated for millennia—suggests an extinction debt incurred by logging (Berglund and Jonsson, 2005). Such old-growth species are also expected to recover slowly, producing a large difference between the timing of decline and recovery. Time lags may be particularly long in landscapes where the amount of remaining habitat is near a species' extinction threshold (Hanski and Ovaskainen, 2002).

No habitat type is immune to the effects of land-use legacies, especially if the disturbance is novel within the context of the system (as human land-use activities often are), and exceeds the extent, intensity, or frequency of natural disturbances that have shaped the landscape historically. Lagged responses are likely following a relatively fast landscape change that exceeds the demographic potential (or response time) of the population, leading to delayed local extinction that may contribute to an extinction debt (Nagelkerke et al., 2002; Schrott et al., 2005a). Conversely, there is also the potential for a lag in recovery following landscape restoration due to a "colonization credit", which is the slow reappearance of species owing to low colonization rates (Nagelkerke et al., 2002; Matlack, 2005). Slow recovery is not limited to just poor colonizers, however. Populations may also be demographically limited in their ability to respond to habitat restoration, such as when habitat fragmentation decreases fecundity or survivorship of individuals in habitat remnants (Schrott et al., 2005b).

3.5.4. Can we Ever Hope to Exorcise the Ghosts of Landscapes Past?

Because biological communities bear the legacy of past environmental change, the real issue here concerns the extent to which we will be able to reverse or prevent the negative impacts of human-driven landscape change on biodiversity. This is obviously the mission of conservation biology, but adopting a historical perspective provides the necessary vista from which to gauge what direction we should be heading given where we have been.

Clearly, the protection of the current landscape is unlikely to be sufficient to guarantee the long-term survival of species impacted by past land use (Nagelkerke et al., 2002), but is restoration of the historical landscape absolutely necessary in order to rescue these species? Given that dispersal limitation characterizes many species that exhibit lagged responses, increasing connectivity of the remaining habitat should at least increase colonization rates and help to mitigate extinction risk. For example, Cowlishaw (1999) recommended constructing habitat corridors between remaining forests as a means of averting extinction in some forest primates, thus canceling part of the debt. Turning a negative into a positive, it might even be possible to exploit time lags because such lags in species' responses to landscape change also give time for action before it is too late (Nagelkerke et al., 2002).

Nevertheless, we should anticipate that recovery from past land use may be slow, owing to demographic lags (Schrott et al., 2005b) and colonization credits (Nagelkerke et al., 2002), which predict that species may also lag in response to habitat restoration. In addition, the amount of habitat required for population recovery (the restoration threshold) may be far greater than that leading to the species' extirpation from the initial landscape (extinction threshold). That is, restoring just the minimum amount of habitat that was initially required to avert extinction (i.e., slightly above the species' extinction threshold) may no longer be sufficient to recover populations on landscapes that have fallen below the species' extinction threshold. It is sobering to realize that the impact of some past land-use activities may well be irreversible, having set the landscape on a different trajectory such that it may no longer be possible to recover the historical conditions that once favored certain species. For example, past cultivation may greatly alter soil carbon and nitrogen levels, causing long-lasting and sometimes permanent changes in productivity and plant species composition (e.g., Foster et al., 2003; Davidson and Simpson, 2005). In such cases, it is important to recognize the limitations of habitat restoration as a management tool for species recovery (e.g., Schrott et al., 2005b) to avoid wasting valuable time and resources that could be better applied elsewhere.

To conclude, the ghosts of landscapes past are omnipresent and will continue to haunt the ecology of landscapes future. The ultimate value of adopting a historical perspective is a better understanding of the temporal as well as spatial dynamics of landscapes. This provides not only a frame of reference for evaluating the impact of past human land-use activities within an ecological context, but may also contribute to the development of management systems that are more in tune with the management of these dynamic landscape systems (Landres et al., 1999; Swetnam et al., 1999).

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4

Modeling Adaptive Behavior in Event-Driven Environments

Temporally Explicit Individual-Based Ecology

VOLKER GRIMM, RICHARD STILLMAN, KURT JAX, AND JOHN GOSS-CUSTARD

Abstract. The dynamics of ecological systems are driven by continuous processes and discrete events. Events typically are of short duration but with long-lasting and usually significant ecological effects. This implies that to understand the ecological significance of events, for example, rainfall events, disturbance events, or resource pulses, we need to understand how individual organisms respond to short-term changes in their environment. Individual-based models that incorporate the adaptive behavior of individuals are an ideal tool to explore the consequences of events. The growing awareness that resources are discretely distributed in space and time leads us to address individual behavior more directly, because it is the adaptive response of individuals to short-term environmental conditions that gives rise to population- and community-level phenomena. A recently formulated general framework for developing and using individual-based models for ecological research is referred to as "individual-based ecology." We describe the rationale of this framework and present examples: winter mortality of coastal birds, habitat selection by stream fish, and bioenergetics of lake fish. The examples show that carefully designed mechanistic individual-based models can be used to understand and to predict the consequences of individual behavioral responses to discrete events for population level phenomena. We discuss the costs and benefits of the individual-based approach and conclude that a general framework for a temporally explicit ecology already exists: individual-based ecology.

4.1. Introduction

The earliest ecologists understood that ecological systems are driven by either more or less continuous processes or by discrete events. Researchers dealing with successional dynamics not only observed continuous processes, such as competition or interaction with the abiotic environment, but also recorded abrupt disturbances, such as fires, windfalls, landslides, or volcanic activities, which opened up space for succession (e.g., Warming, 1896; Cooper, 1913; Clements, 1916; Gleason, 1917; Elton, 1927). Others described short-term "catastrophic" outbreaks of insects in forests (e.g., Friederichs, 1928). Likewise, pulsed propagule production and the recruitment of animals and plants (e.g., mast seeding) have also long been observed.

However, the efforts to conceptually deal with the two kinds of processes—continuous versus discrete—have been distributed quite unevenly across ecological science. While there exist a large number of theoretical approaches that address continuous processes (e.g., competition theory, food web theory, optimal foraging theory), dealing with discrete events to develop theoretical frameworks has proved to be much more difficult. A more systematic treatment of discrete events only started in the late 1970s with growing interest in the study of natural disturbances in communities (see White, 1979; Pickett and White, 1985; Jax, 1999; White and Jentsch, 2001 for overviews), "pulsed" ecosystems (Odum et al., 1995), or birth and death events in populations (Goel and Richter-Dyn, 1974). Indeed, it was only recently (Ostfeld and Keesing, 2000) that ecologists became fully aware that virtually all resources required by organisms occur as discrete, or episodic, events. It could thus turn out that ecological systems are "event-driven" in general (Walker, 1993).

Why, then, did discrete events receive so much less empirical and theoretical attention than continuous processes? There seem to be three main reasons. First, events have a short duration but long-lasting consequences. To detect events and their consequences adequately, we would need empirical studies that have both a high temporal resolution and a long duration, which is not usually feasible. Second, until recently, there seemed to be no explicit definition of the concept "event" that would allow a clear delineation of a single event from the background of continuous processes. Third, traditional theoretical ecology has long been dominated by calculus, an approach that is not able to deal with discrete events: in differential equations, time is sliced into infinitesimally small pieces so that change of state variables is continuous.

It seems time to fully acknowledge the central role of discrete events in ecology. Empirical evidence of the significance of pulsed resources is accumulating (Ostfeld and Keesing, 2000), explicit definitions of discrete events are being developed, and theoretical ecology is increasingly using simulation models that, in principle, can include discrete events. A definition of ecological events is given by Jax (1999, translated from German):

> An *ecological event* is an abruptly occurring process which significantly affects variables of an ecological unit for a period longer than its own duration. It must have a clear beginning and end, and must be of relatively short duration in relation to the time scale of the organisms considered.

Ecological events are thus not only characterized by the episodic character of some cause (e.g., rainfall event, mast seeding, occurrence of carrion), but also by their long-lasting ecological effects. For example, rainfall in temperate zones may be episodic, but does not constitute an ecological event because water usually is not a limiting factor. In arid zones, however, rainfall is almost always an ecological event, where, for example, it prompts dormant seeds to germinate.

This definition and the accumulating empirical evidence of their importance can now be used as the basis for dealing explicitly with discrete events in ecological models. The definition of ecological events indicates that to adequately account for them, we need time steps that are much shorter than the life span of the organism of interest. Years, weeks, even days may be too coarse. What we need is a temporal resolution that allows the adaptive behavior of individual organisms to be tracked because it is the individual organism, not the population, or the community, that responds to resources that are distributed discretely in both space *and* time. All population and community level effects of discrete events emerge from the adaptive behavior of individual organisms, and there seems to be no way to predict these effects *a priori*, i.e., without explicitly considering behavior. And this, exactly, is the research program of individual-based ecology (IBE; Grimm and Railsback, 2005): to explore the mutual relationship between emergent properties of ecological systems and the adaptive behavior of individual organisms.

Individual-based models have been used in ecology for about 20 years, but the focus was more on the discreteness of individuals, local interactions, and a full representation of life cycles (Uchmański and Grimm, 1996; Grimm, 1999) and less on adaptive behavior. Behavior played, however, a central role in two new approaches to individual-based modeling that were developed independentlyin: a) “behavior-based models” (Goss-Custard, 1985; Goss-Custard and Durell, 1990; Goss-Custard et al.,1995a; Sutherland, 1996; Goss-Custard and Sutherland, 1997), which were based on concepts from behavioral ecology, and b) “agent-based models” that were based on design concepts from research on Complex Adaptive Systems (Railsback, 2001a,b; Railsback and Harvey, 2002). Individual-based ecology, as proposed by Grimm and Railsback (2005) is the attempt to integrate these two new approaches with individual-based modeling in general.

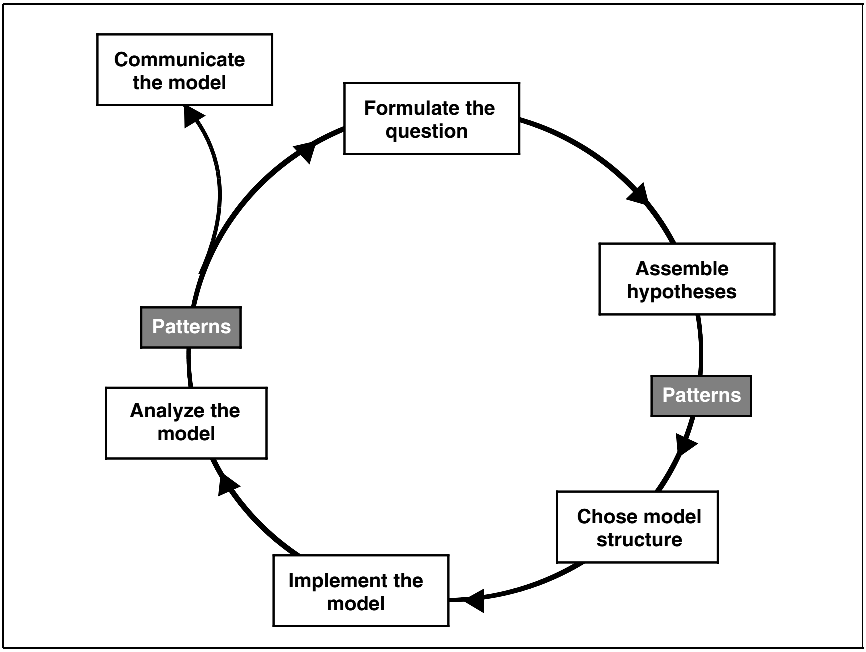
In the following sections, we describe the key ideas of individual-based ecology and how it deals with events, adaptive behavior, and temporal explicitness in general. Then, we describe a long-term modeling project on coastal birds which, to our knowledge, provides the most comprehensive example of an individual-based model able to cope with discrete events. We will also briefly describe two further modeling projects on trout and lake fish that explicitly deal with abrupt changes in the environment. Finally, we discuss the costs and benefits of the individual-based approach as a predictive tool to deal with temporal explicitness in ecology.

4.2. Individual-Based Ecology

In individual-based ecology (IBE; Grimm and Railsback, 2005), higher organizational levels (populations, communities, ecosystems) are viewed as complex systems with properties that arise from the traits and interactions of their lower-level components, i.e., individuals. IBE employs a specific notion of so-called “theories,” which are models of *individual* behavior that are useful for understanding system dynamics. Theories are developed using a hypothesis-testing approach. The standard for accepting theories is how well they reproduce observed patterns. These may be system-level patterns, such as demographic rates or population dynamics, or patterns of individual behavior that arise from the individual interactions with the environment and other individuals ("pattern-oriented modeling"; Grimm et al., 2005). A pattern in this context is defined as any indicator of a non-random process. Marked patterns in time and space are trends, cycles, outbreaks, waves, gradients, mosaics, etc., but also weaker patterns can contain a lot of indirect information about the internal organization of the system in question: state variables may be confined to certain ranges; the response of the system to a certain disturbance may be known, i.e., magnitude of the response and time needed for recovery; population structure may contain certain patterns; and results of experimental treatments may be available.

Models in IBE ideally are not designed *ad hoc* but follow certain design criteria (Railsback, 2001a,b). The two most important criteria are emergence and fitness. Emergence means that an organism's behavior is not imposed by, for example, empirical rules, but emerges from the individual's behavioral decisions. It is assumed that individuals try to adapt their behavior to their current state and environment in order to optimize their fitness. The fitness measure employed by the individual may be direct; i.e., the expected survival or number of offspring, or it may be an indirect proxy of fitness such as food intake. The entire rationale of IBE is thus based on including not only individual behavior but also the decisions individuals make in order to cope with their changing state and environment. Individuals adapt to heterogeneities in space and time: they select habitat according to habitat quality, which may change abruptly due to episodic events. As a consequence, discontinuities in space and time have to be taken into account.

Box 4.1. Individual-based modeling.



Box 4.1. (continued)

Individual-based models are not developed in one step, but by iterating the steps of a modeling cycle (Grimm and Railsback, 2005):

1. Formulate the question to be addressed with the model, or the problem to be solved. Formulating a clear question is an essential and productive part of the overall problem, and while repeating the cycle, the questions are often revised or refined.
2. Assemble working hypotheses about how the system works. For example: what are the decisive processes at the individual and environmental level? What are decisive constraints in system dynamics? Modeling provides a means by which we can explore the consequences of our assumptions, so all these hypotheses are provisional and experimental and will be discarded or revised as the cycle is repeated.
3. Identify a set of patterns that are considered to be characteristic of the real system. Some of these patterns might require us to include state variables that were not included in the original working hypotheses; for example, spatial patterns or patterns in population structure or individual behavior. The patterns are also used to parameterize, verify, and validate the models.
4. Chose a model structure that (i) characterizes individuals and their environment, and (ii) includes processes that cause the state variables to change over the course of time. In more empirical individual-based models, only a few variables might be sufficient, such as sex, age, position, and weight. More mechanistic models might include variables describing such characteristics as energy reserves, somatic and gonadic biomass, social rank, memory, behavioral strategies, and genes.
5. Implement the model. With individual-based models, this means writing a computer program. The models described in the Examples section are implemented with different software platforms: A modern version of *Pascal* (coastal birds); *Swarm* (Minar et al., 1996), a software library for agent-based models (trout); *Simula*, a programming language for object-oriented simulation models (lake fish).
6. Analyze the model. This means designing and conducting controlled simulation experiments with the model. The model is a kind of "virtual laboratory," and alternative submodels and sets of parameters are tested in terms of their potential to reproduce observed patterns and to provide answers to the original research question.
7. The modeling cycle usually ends when a certain "stopping rule" is fulfilled. This might be the reproduction of certain patterns with sufficient precision, a sufficiently clear explanation of a certain phenomenon, or—most frequently—the end of funding of the research project. This modeling cycle, its extension to "pattern-oriented modeling," and the "theory development cycle" of individual-based ecology are described in more detail in Grimm and Railsback (2005). Figure: Modified after Grimm and Railsback (2005).

Individual-based models that are designed according to the design criteria of IBE are thus temporally explicit at a resolution required to cope with behavior that to a large degree is event-driven in both space and time. Obviously, this high resolution implies several methodological challenges: the models easily could become too complex to be understood, uncertainty in model structure and parameters could be too large, and they simply could run too slowly to allow for comprehensive analyses. The following examples will show how these challenges can be met. A general framework for designing, testing, and analyzing individual-based models is provided by Grimm and Railsback (2005) and very briefly summarized in Box 1.

4.3. Individual-Based Models for Event-Driven Environments: Examples

4.3.1. Coastal Bird IBMS

Estuaries and coastal flats often provide vital inter-tidal feeding areas for migratory shorebirds and waterfowl, particularly outside the breeding season. Most of the birds can only feed on their macro-invertebrate and plant food supplies when these are exposed on the inter-tidal flats at low tide. Bird populations may suffer as a result of human activities on the coast, such as land reclamation and resource harvesting and recreation. Policy decisions are frequently required on how best to maintain biodiversity and to reconcile its protection with economic development. IBMs of coastal birds were developed to provide a scientific basis for policy decisions.

There are three reasons for using individual-based models rather than some other kind of model. First, many responses by birds to environmental change are behavioral; e.g., changes in feeding location or prey selection (Goss-Custard and Durell, 1990). IBMs can easily encapsulate these behavioral responses to events, for example interference with competing individuals, the tides, or disturbance by humans. Second, coastal birds occupy habitats with a high degree of spatial (e.g., variation in exposure time and prey quality with height on the shore) and temporal (e.g., successive covering and exposure of feeding areas) heterogeneity, details that can easily be incorporated into IBMs. Third, predictions often are required on how bird populations may be affected by as yet untried management scenarios and policy options. There is often no way of knowing whether the empirical relationships upon which traditional regression and demographic models are based will hold under the new conditions, meaning that predictions are of uncertain accuracy. To have confidence in predictions, models need to operate on basic principles, underpinned by theory that will still apply in the new scenarios, rather than on present-day empirical relationships which may no longer hold in the scenarios for which predictions are required.

The overall purpose of coastal bird IBMs is to predict how environmental change during the non-breeding season (e.g., habitat loss, changes in human disturbance, climate change, mitigation measures in compensation for developments, and changes in population size itself) affects the non-breeding survival rate and body condition of bird populations. Key variables in these models are the successive ebb and flow of the tide, which determine the availability of inter-tidal feeding areas, and temperature, which has a large impact on the daily energy requirements of coastal birds, and hence the amount of food they need to consume to survive. The habitat is divided into a number of discrete patches, which vary in their exposure through the tidal cycle and the quantity, quality, and type of food. Time is divided into discrete time steps (typically 1 to 6 hours in duration), during each of which birds choose where and on what to feed, or whether to roost. A single simulation covers the winter season, i.e., 6–7 months. Individual birds are characterized by a suite of state variables, including foraging efficiency, dominance, location, diet, assimilation rate, metabolic rate, and amount of body reserves. Social interactions are incorporated through interference competition (e.g., food stealing), which reduces the feeding rate of lower dominance individuals at higher densities, and hence means that these individuals tend to avoid patches with higher competitor densities. The models predict how individual birds respond to environmental change by altering their feeding location, consuming different food, or adjusting the amount of time spent feeding. Optimal foraging theory and game theory provide a conceptual basis for predicting the decisions made by model birds (Goss-Custard et al., 1995a; Sutherland, 1996; Goss-Custard and Sutherland, 1997). Model individuals are assumed to always behave in order to maximize their own chances of survival, no matter how much the environment changes, thereby mimicking their live counterparts (Goss-Custard et al., 1995a; Sutherland, 1996; Goss-Custard and Sutherland, 1997).

4.3.2. History of Coastal Bird IBMs

A series of IBMs have been developed to predict the consequences of environmental change for shorebird and waterfowl populations. The development of these models followed the modeling cycle shown in Box 1. At each stage of model development, predictions were compared with as many observed patterns as were available (e.g., changes in the distribution of birds through the tidal cycle or season, the type of food consumed by birds and the rate at which food is consumed, the total amount of food consumed by birds during the season, the amount of time birds spend feeding per day, changes in the body mass of birds during the season, and the stage of the season at which most birds die as well as the total number of birds dying). The success or failure of these tests guided the way in which models were structured and the numbers and types of parameters included. The aim at each stage was to develop the simplest model capable of accurately predicting a range of observed patterns.

The first two shorebird models (Goss-Custard et al.,1995a; Clarke and Goss-Custard, 1996) described in increasing realism the oystercatcher–shellfish system in the Exe estuary, United Kingdom, where the model was developed and its predictions first tested. The third shorebird model was also developed for oystercatchers *Haematopus ostralegus* on the Exe estuary, and accurately predicted the observed density-dependent mortality of oystercatchers (Fig. 4.1), as well as

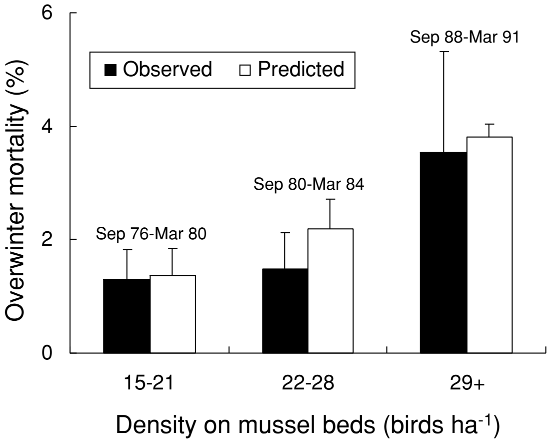


FIGURE 4.1. Predicted and observed density-dependent over-winter mortality rates of adult oystercatchers on the Exe estuary, United Kingdom during 1976 to 1991. The bars show mean mortality rate and associated standard deviation. Predictions were based on the observed numbers of oystercatchers present in September each year. Modified after Stillman et al. (2000).

several behavioral patterns from which the mortality predictions were derived (Stillman et al., 2000; 2001). This model was subsequently parameterized for oystercatchers and other shorebirds in Strangford Lough, Menai Strait, Dee estuary, Humber estuary, The Wash, and Burry Inlet in the United Kingdom, and Baie de Somme and Baie de Seine in France. Using the shorebird model as the starting point, Pettifor et al. (2000) developed IBMs for migratory barnacle *Branta leucopsis* and brent geese *B. bernicla* populations on a much larger spatial scale than had the previous shorebird models. Although these early models were developed for shorebirds and waterfowl, the principles on which they were based—that animals attempt to maximize their chances of survival and reproduction—apply to any system. The types of environmental issues that the models are designed to address are not restricted to the coast. This was the incentive to develop a much more flexible model (Stillman et al., 2005a), capable of being applied to a much wider range of species and environmental issues. To date, this model has been applied to shorebirds in the Exe estuary, Poole Harbour, and Southampton Water in the United Kingdom, Baie de Somme, France and Bahia de Cadiz, Spain (Stillman et al., 2005a, Stillman et al., 2005b), brent geese in western Europe (Stillman et al., 2005a), and common scoter *Melanitta nigra* in the Irish Sea (Kaiser et al., 2005).

If individual-based models are to be of value in advising coastal management, they must produce accurate predictions and be developed within a relatively short time-scale. Each coastal bird IBM has been tested as thoroughly as possible using all data available for each study system. Although the tests varied between sites, data were available to test the predicted distribution of birds throughout a site as well as the major prey species consumed by birds. Typically, patch selection and prey choice were accurately predicted for the majority of species for which data were available (e.g., Durell et al., 2005; Stillman et al., 2005c). The proportion of time spent feeding, an important indicator of the difficulty birds are having in surviving winter, also was accurately predicted on several sites for a variety of species (Fig. 4.2a). Testing predicted mortality rates is difficult because intensive,

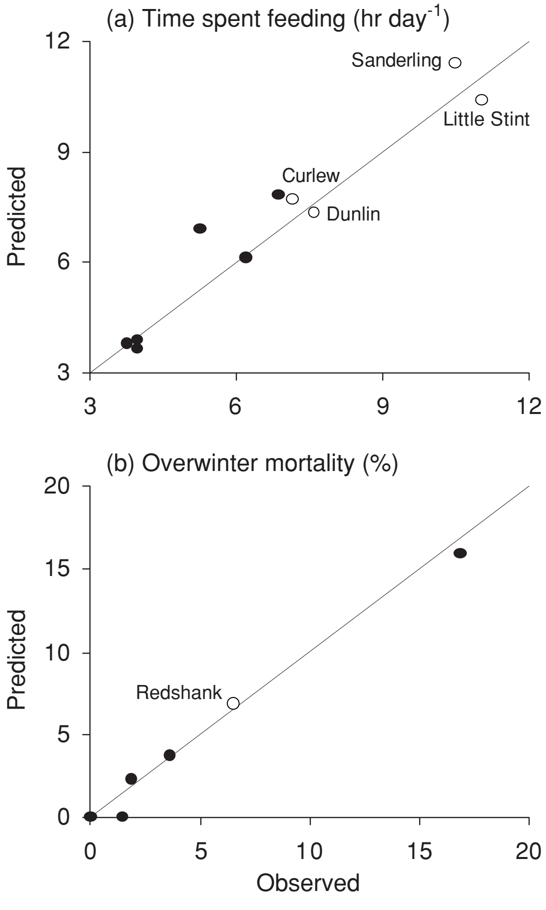


FIGURE 4.2. Tests of individual-based shorebird models. Comparisons between model predictions and (a) the observed amount of time spent feeding by an average bird over a single daylight tidal cycle (closed symbols: oystercatcher *Haematopus ostralegus*, open symbols: little stint *Calidris minuta*, sanderling *C. alba*, dunlin *C. alpina* and curlew *Numenius arquata*; data from the Exe estuary, Burry Inlet, and Bangor flats in the United Kingdom, Seine estuary in France, and Bahia de Cadiz in Spain), (b) the observed winter mortality rates of oystercatcher (closed symbols; data from the Burry Inlet, Exe estuary, and the Wash in the United Kingdom) and redshank *Tringa totanus* (open symbol; data from the Rhymney flats of the Severn estuary, United Kingdom). In both cases, linear regression equations of observed against predicted values have intercepts which are not significantly different from zero ($p > 0.05$), and gradients which are not significantly different from one ($p > 0.05$). Modified after Goss-Custard and Stillman (in press).

long-term marking studies are required to estimate over-winter mortality rates in wild bird populations. Such studies have been conducted on just a few sites and so this limits the number of systems in which model predictions can be tested. The need to predict over-winter mortality in systems where it was difficult to measure empirically was, in fact, one of the major reasons for developing shorebird individual-based models in the first place; Goss-Custard (1985). However, mortality rate was accurately predicted in those sites for which suitable data were available (Fig. 4.2b), increasing confidence that predictions will also be accurate on sites for which observed data are not available. Importantly, with the exception of the original model, models have been developed relatively quickly (1–2 years including data collection), especially when compared to the time and effort required to develop demographic models (one estimate of mortality rate per year).

4.3.3. Applications of Coastal Bird IBMs

The following examples of issues that the shorebird model has been used to address illustrate that individual-based models are capable of predicting population-level consequences (e.g., mortality rate) of discrete temporal events, whether these occur just once (e.g., habitat loss) or frequently on a regular (e.g., shell fishing, and unpredictable disturbance) basis.

Coastal habitat can be lost due to industrial developments (e.g., ports, tidal barrages), land claim schemes, or sea-level rise. Habitat loss forces birds to feed in a smaller area, which may intensify competition between birds for food or space, and may change the average habitat quality if habitat of above or below average quality is removed. Two coastal bird IBMs have directly addressed habitat loss through industrial developments and sea-level rise. Durell et al. (2005) predicted that a development causing 20% loss of habitat on the northern shore of the Baie de Seine, France, would increase the mortality rates of dunlin *Calidris alpina* and oystercatcher. They also predicted the size of a proposed new mitigating mudflat required to compensate for this increased mortality. Stillman et al. (2005c) predicted that 8% loss of habitat from the Humber estuary, caused by developments and sea-level rise, could increase the mortality rate of five of eight bird species modeled. These examples show how coastal bird IBMs can be used to predict the effects of a discrete environmental event, such as a loss of habitat, on the subsequent demographic rates of the population.

Most of the coastal bird IBMs developed to date have addressed the interaction between shellfishing and shorebirds. Mussel *Mytilus edulis* and cockle *Cerastoderma edule* fishing removes the large-sized shellfish, which are also eaten by birds like oystercatchers. If shellfishing occurs at low tide when shorebirds are feeding, it can disturb birds and force them to expend energy by moving to poorer quality habitat. In contrast, when artificial shellfish beds are created in the inter-tidal zone by dredging mussels from deep waters, the amount of food available to birds can be increased. IBMs have been used to predict the effect of shellfishing on the Exe estuary (Stillman et al., 2001) and Burry Inlet, United Kingdom (West et al., 2003)

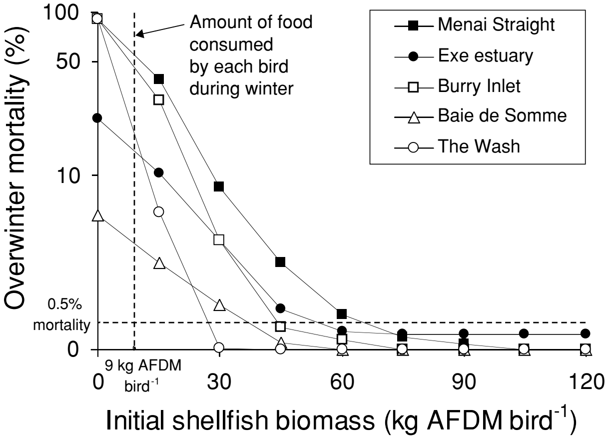


FIGURE 4.3. Predicted over-winter mortality rate of oystercatchers in Menai Straight, Exe estuary, Burry Inlet, and the Wash in the United Kingdom, and Baie de Somme in France in relation to the shellfish stocks per bird present in autumn. The horizontal dotted line represents a mortality rate of 0.5%. The vertical dotted line represents the 9 kg ash-free dry mass (AFDM) consumed by each oystercatcher over the course of winter. Modified after Goss-Custard et al. (2004).

and have shown that shellfishing was highly unlikely to increase the oystercatcher mortality rate at its current intensity. Models of oystercatchers in Menai Straight (Caldow et al., 2004) and the Wash, United Kingdom (Stillman et al., 2003) have shown that by varying exposure of mussel beds to the tidal cycle, the number of mussels consumed by oystercatchers, and hence lost to the fishery, can either be minimized to maximize fishery yield, or regulated to maximize oystercatcher survival in years of low food availability.

Shellfishery managers frequently need to ensure that sufficient shellfish remain after harvesting to meet the demands of co-dependent shorebirds, but it has traditionally proved difficult to assess exactly how many shellfish should be reserved. Goss-Custard et al. (2004) used IBMs to predict how different food reservation strategies would influence oystercatcher mortality on five different sites (Fig. 4.3). One possible policy to prevent shellfishing from harming birds would be to ensure that enough food remains after harvesting to meet most or all of their energy demands (shown by the vertical dotted line in Fig. 4.3). However, in all sites such a policy would cause extremely high mortality rates in the oystercatcher populations. Instead, up to almost eight times this amount was needed to maintain low oystercatcher mortality rates (shown in Fig. 4.3 as the shellfish biomass at which predicted mortality crosses the horizontal line). This happened because some birds were less efficient foragers and so needed more available food to survive and because interference competition, due to food stealing (Goss-Custard, 1980), reduced the access of some birds to the food supply. The results from the five systems suggested a simple policy guideline for managing shellfisheries to sustain oystercatchers: shellfish stocks measured in autumn should not be allowed to fall below 2.5–8 times the biomass that the birds need to consume.

Human disturbance excludes birds from areas which would otherwise be used for feeding or roosting, and increases the energy demands of birds by causing them to take flight, reducing the amount of time they have to feed. The behavioral responses of birds to human presence in coastal areas are often very obvious; large bird flocks may be seen flying from people, and areas where people occur often have few birds. However, these large behavioral responses do not necessarily mean that more birds will die, as they may compensate for disturbance by simply moving to another feeding area after being disturbed. West et al. (2002) predicted that the current level of human disturbance on the Exe estuary had no influence on oystercatcher mortality or body condition, but that greatly increased disturbance would cause more birds to die. Goss-Custard et al. (2006) predicted how the effect of disturbance on oystercatcher mortality interacted with food abundance in the Baie de Somme, France. In this model, the birds were unaffected by up to three disturbances per hour, provided that cockles stocks were high. However, if, as sometimes happens on the Baie de Somme, large amounts of the cockle stock died in mid-winter, the model predicted disturbances should be kept below one per 2 hours to prevent increased oystercatcher mortality. Thus, the consequences of a given level of disturbance depended on the environmental circumstances prevailing at the time.

4.3.4. Lessons from Coastal Bird IBMs and Future Developments

The original coastal bird IBM of oystercatchers in the Exe estuary was developed as part of a long-term intensive field study, and evolved over several years (Goss-Custard and Stillman, in press). Although this model accurately described the real system, it was important to show that IBMs could be developed more quickly and in less intensively studied sites, if they were to be useful tools for advising coastal management. Using procedures summarized in Goss-Custard and Stillman (in press), subsequent models were in fact developed more quickly, typically within one to two years including data collection, and these models have been used to advice coastal management, particularly with regard to shellfishery management. The most time-consuming aspect of each new model has been quantifying the food supply as this typically involves an intensive field survey.

The successful development of coastal bird IBMs raises the question of whether similar IBMs could be developed for many other species. Coastal birds feed in restricted, open habitats in which their behavior can be observed, and feed on a relatively narrow range of relatively non-mobile prey species, the abundance and quality of which can be estimated through simple surveys. Additionally, coastal managers often are interested in relatively short-term predictions, such as how many more birds will die over the course of winter if a specified amount of shellfish are reserved for oystercatchers; these are more straightforward than predictions which span multiple bird generations. These factors have simplified the development of coastal bird IBMs and their use in advising policy, and so the next step is to identify species that share some or all of these characteristics. Marine ducks, such as the common scoter and common eider *Somateria mollissima*, feed on similar, bottom-dwelling prey as do inter-tidally feeding shorebirds, and the extent of their feeding habitat changes through the tidal cycle as water depth changes. An IBM has recently been developed to predict the effect of habitat loss and disturbance from wind farms on common scoter wintering in the Irish Sea (Kaiser et al., 2005). Seed-feeding farmland birds have relatively simple diets and the abundance and food value of seeds can be quantified. These birds have considerably declined in recent decades, thought in several species to be associated with over-winter food shortages caused by change in agricultural practices (Robinson and Sutherland, 2002). IBMs can potentially predict how changes in agricultural practices, driven by new management subsidies, will influence farmland bird populations, and test the costs and benefits of different schemes before they are implemented (Bradbury et al., 2001; Stephens et al., 2003). Marine ducks and farmland birds are the most likely candidates for the application of the coastal bird IBMs.

4.4. Other Examples

The coastal bird IBMs described above probably represent the most comprehensive example of how in individual-based ecology temporal explicitness is achieved by modeling the adaptive behavior of individuals. This work has a history of more than 20 years (Goss-Custard and Stillman, in press). Another set of models, with a shorter history of about 10 years, are the stream fish models (mainly cutthroat trout *Oncorhynchus clarki*) developed by Railsback and coworkers (Railsback, 2001a,b; Railsback and Harvey, 2001, 2002; Railsback et al., 1999, 2002, 2003; see also the precursor model of Van Winkle et al., 1998). Their purpose is to predict the effects of river management on fish populations where dams and water diversions affect the flow regime and thus fish populations. Fish adapt to changes in flow by moving to different habitat, so to predict how fish populations react to new flow regimes we need to know how fish select their habitat. The trout model of Railsback and Harvey (2001) uses daily time steps, with stream habitat represented as rectangular cells. Within a day, individuals carry out four sets of actions: spawn, move to maximize fitness, feed and grow, then survive or die according to survival probabilities that vary with habitat cell and fish characteristics. Model runs cover a time span of years or decades.

A specific feature of the trout model is a new habitat selection model, or theory, that combines earlier, state-based approaches with the concept of prediction: fish base their daily decision on the prediction that habitat quality remains unchanged for the next 90 days (Railsback et al., 1999). This is not to say that real or model fish really predict the future. Rather, they extrapolate current conditions to a larger time horizon in order to explore consequences for survival and growth. Railsback and Harvey (2002) show that their "state-based, predictive" theory of habitat selection is, in contrast to alternative theories, capable of reproducing a set of six patterns observed in reality. The trout model has also been used to demonstrate the limitations of empirical habitat selection models (habitat models) that are based on the assumption that observed animal density indicates habitat quality (Railsback et al., 2003). Further theoretical issues addressed with the trout model include self-thinning relationships, periods of high density-dependent mortality among juveniles, density-dependence in juvenile size, and effects of habitat complexity on population age structure. In a management application, the trout IBM was used to predict the population-level consequences of stream turbidity (Harvey and Railsback, in prep.): over a wide range of parameter values, the negative effects of turbidity on growth (and, consequently, reproduction) outweighed the positive effects on risk.

Further individual-based models that include adaptive behavior are the lake fish (e.g., roach *Rutilus rutilus*) models by Hölker and coworkers that are based on detailed submodels of bioenergetics, energy allocation and reallocation, and physiological and behavioral activities (Hölker and Breckling, 2001, 2002, 2005; Hölker et al., 2002; Hölker and Mehner, 2005). Temporal explicitness is here achieved by an asynchronous updating scheme: fish schedule their actions (feeding, movement, spawning) in response to events in their environment. As with the trout and coastal bird IBM, the base model is quite complex and took several years to be developed, tested, and parameterized. Further applications of the model to new questions, environments, and species were relatively easy to implement.

4.5. Discussion

Traditional ecological modeling focused on the population and community level and ignored individual behavior. The growing awareness that resources are discretely distributed in space and time, however, leads us to address individual behavior more directly, because it is the adaptive response of individuals to short-term environmental conditions that gives rise to population- and community-level phenomena. Individual-based models provide an ideal tool for this important characteristic of ecological systems because they are designed to explore the mutual relationship between the adaptive behavior of individuals and system-level properties. The examples presented above clearly show the benefits, but also costs, of the individual-based approach. The benefits are obvious: the models can be used to explore the reaction of a population to all kinds of changes in their environment. This is because the models are mechanistic, not empirical: they are based on behavioral or bioeneregtic submodels, which mimic the fitness-seeking biology of real organisms.The costs, or limitations, are also obvious: individual-based models that include mechanistic submodels are considerably more complex than, for example, individual-based models that use empirical demographic rates (e.g., Grimm and Storch, 2000). Usually it takes several years to develop, parameterize, calibrate, and test these models. The typical time frame for research grants, which last for 3, or even 5 years, will usually not be sufficient to complete the first full model. However, once this first model exists, a modeling project can be very productive: the model can be used for more than just one problem or environment; it can be adjusted relatively easily to new species or environments; and it helps to deduce quite general submodels ("state-based, predictive" habitat selection) or to develop more general, and more simple full models that more easily can be adjusted to different systems and which are based on the experience with more specific models (Stillman et al., 2005a). Thus, if we are to take temporal explicitness seriously, it may require us to revise the schemes for funding of ecological research: not only monitoring and experiments, but also modeling may require a time frame for funding that exceeds the typical 3 to 5 years.

Another limitation of mechanistic IBMs is that they tend to include so many individual-level processes (behavior, physiology) described at a very high temporal resolution, that they simply run too slowly on the computer to be applied over several decades or more. So far, this limitation has usually been met by focusing on proxies of population performance, such as over-winter mortality or habitat selection, to in some way assess the likely long-term consequences at the population level. Obviously, however, the full population-level consequences of these proxies are not yet fully known or understood, so some caution is required when interpreting the results.

One solution is to combine mechanistic IBMs with more traditional aggregate population models. With this approach, the IBM delivers as output, demographic parameters for a wide range of environmental conditions and population densities. The population model is then used to explore population-level consequences, for example mean abundance or extinction risk. Fahse et al. (1998) showed that such a "separation of time scales" is possible: population structure becomes quasi-stationary on a much shorter time scale than, e.g., population size. As an example, the predictions of the shorebird individual-based model for winter mortality rate following habitat loss have been used as an input parameter for a traditional demographic population model so that the long-term population consequences of a single discrete temporal change in the environment could be predicted (Goss-Custard et al., 1995b).

The above examples demonstrate that the old stereotype about simulation models in general and individual-based models in particular being too complex to be understood, is not necessarily true. If IBMs are carefully designed and tested, e.g., by linking model structure to patterns observed at different scales and hierarchical levels, they will certainly be more complex than demographic models, but certainly understandable. Submodels that describe behavior or bioenergetics can and should be parameterized and tested before they are used in the full model (Grimm and Railsback, 2005). This allows us to minimize the number of parameters that are varied in the analysis of the full model (see also Mullon et al., 2003). We conclude that individual-based modeling can be used as a powerful and predictive tool for an ecology that tries to fully acknowledge not only spatial, but also temporal heterogeneity.

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5

Temporal Scaling in Complex Systems

Resonant Frequencies and Biotic Variability

Lance Gunderson, Craig R. Allen, and Don Wardwell

Abstract. Structure in complex systems, such as ecosystems, is scale specific, with discontinuities bounding domains within which scaling laws apply. Concordantly, changes in spatial pattern across different ranges of scale are described by different scaling relationships. The spatial aspect of scale has continued to receive considerable attention in the field of landscape ecology; however, scale has dimensions of time as well as space, and the consideration of one without the other neglects half the picture. In this chapter, we concentrate on the scaling axis of time, and describe cycles in temporal patterns in the Everglades ecosystem. We relate the temporal frequencies of ecosystem structuring processes to the interaction of animals with their environment, and describe how spatial and temporal turnover and variability in animal communities relates to variation in the availability of resources in time and space. We posit that discontinuous distributions of key structuring variables in time should be manifest as a few resonant frequencies in temporal processes. We test this idea with time series data of rainfall, evaporation, water-flow, air temperature, sea level, and fire history. The dominant temporal frequency for most data sets was the annual cycle, but secondary frequencies of 8 to 11 years were present in these data. Longer frequencies occurred at approximately decadal cycles in the water-flow and fire data, suggesting that key structuring processes are separated by an order of magnitude. Both spatial and temporal variation is observed in animal communities at discontinuities, reflecting the interplay of dimensions of space and time. The complex phenomena of migration, nomadism, invasion, and extinction are all associated with discontinuities in animal body mass patterns. Additionally, we investigate the variation in bird species abundance in relationship to their proximity to discontinuities in the body-mass distribution of this assemblage. Species whose body mass places them closer to discontinuities have population abundances that are more variable over time. These analyses support the theory that ecosystems are structured around a few keystone variables of mixed spatial and temporal dimensions.

5.1. Introduction

Ecosystems are complex adaptive systems comprised of biotic and abiotic components that interact across a wide range of spatial and temporal scales (Holling, 1986; 1992). The interactions of these components generate loosely linked hierarchical structures. For example, in a forest, leaves, stems, and trunks compose a hierarchical level of a tree. In turn, a group of trees make up a patch, and a group of patches make up a forest stand. Within a level, a key set of processes and components interact to generate characteristic behaviors and dynamics. Across levels, patterns and features change, as different keystone processes dominate across different scale domains (Holling and Gunderson, 2002).

Holling (1992) was the first to indicate the correlation between the cross-scale structures in ecosystems and the types of biotic patterns that emerge. The *Textural Discontinuity Hypothesis* proposed that body mass distributions of animal communities reflect landscape structure (Holling, 1992), and are discontinuous. The discontinuities in ecological systems derive from self-organizing interactions between biological and non-biological components at specific scales; that is, it is not appropriate simply to consider landscapes as a template upon which animals interact; rather, landscapes reflect the interactions of animals, existing landscape structures, and processes at key scales.

This discontinuous world is characterized by a small set of scale-invariant regimes, within which scaling rules apply. In the temporal domain, the small set can be measured by a few frequencies of key structuring variables. Many authors (Craighead, 1971; Davis and Gunderson, 1993; Davis and Ogden, 1994) argue that the hydrologic regime and the fire regimes are key ecological processes that determine spatial and temporal patterns, e.g. in the Everglades. The signature, or ecological legacy, of these processes is present in long lasting physical patterns upon landscapes. In the Everglades, these patterns include the distribution, size, and position of tree islands, the distribution of sloughs and features such as alligator holes, and a myriad of other structures at a variety of spatial and temporal scales (Holling et al., 1994).

The importance and prevalence of discontinuities in spatial and temporal patterns of attributes of ecological systems has been well documented (Allen and Holling, 2002). For animals residing within an ecosystem, the discontinuities in process and structure are manifest in discontinuous body mass distributions. For animals, the edges of discontinuities in body mass distributions reflect scale breaks that are analogous to phase transitions between two scales of landscape pattern. This suggests that there is greater environmental variability at the scale breaks. Allen et al. (1999) predicted that biological phenomena that are associated with greater variability would be more likely to occur at the edges of body mass aggregations and tested this model by analyzing the role of body mass pattern as a predictor of invasions and extinctions in the vertebrate fauna of the Everglades. The results supported the hypothesis; successful invaders and extinct or declining species were concentrated at the edges of body mass aggregations. Other independent biological attributes or phenomena were associated with temporal or spatial variability and occurred more often than expected at discontinuities (i.e., invasions, extinctions, migrations, and nomadism; Lambert and Holling, 1998; Allen et al., 1999; Allen and Saunders, 2002, 2006; Allen, 2006; Allan and Holling, 2002; Allen *unpub. data*).

Populations that exhibit higher temporal variability may be more prone to extinction than those with lower variability (Pimm, 1991). Given this and the evidence that populations situated at the edges of body mass aggregations (i.e., discontinuities) are also prone to extinction, Allen et al.'s (1999) model may be expanded upon to suggest that edge populations will exhibit higher temporal variability in abundance than populations that represent the interior of body mass aggregations. May (1973) hypothesized that as environmental variability increases, the effects of competition are enhanced and there is a greater chance that one or more species will become extinct. Furthermore, he suggested that even a small amount of environmental variability may have a dramatic effect. Thus, greater environmental variability at the edges of body mass aggregations should intensify interspecific competition. The combined effect may result in higher temporal variability of population abundances, and potentially increase the likelihood of extinction.

In this chapter, we investigate temporal aspects of the cross-scale structure of the landscape of southern Florida (USA). We first use time series analyses and other techniques to investigate the key processes responsible for structuring the Everglades ecosystem to search for discontinuities and dominant frequencies. We then analyze the avian fauna of the Everglades to determine if temporal variability in population abundance is randomly or non-randomly distributed in terms of discontinuities in the avian body mass distribution.

5.2. Methods

5.2.1. Process Frequencies

The Everglades is a well-studied and monitored ecosystem, with much available data on the biotic and abiotic components. We use multiple decade time series of hydrologic and fire data from the system to look for dominant frequencies in these key variables. Three types of hydrologic data were analyzed for temporal patterns: rainfall, stage (water level), and surface flow. Two data sets were used in the analysis of temporal rainfall patterns. Daily rainfall totals from May 1948 through December 1989 were obtained for Tamiami Ranger Station and Royal Palm Station. Daily water levels were obtained from sites designated P33, P35, P37, and P38 in Everglades National Park. Monthly summaries covering the time period January 1954 through December 1975 were analyzed. Total monthly flow data from October 1939 through 1983 under the Tamiami Trail flow section were analyzed. Area burned by month during the period 1958–1979 was used in determining fire frequencies. The analyses were conducted with the fast Fourier algorithm in the SYSTAT software for the Macintosh (Systat, 1990). For each data set the mean was subtracted from every value and the data de-trended, so that the values varied above and below zero with no overall change or trend in the mean. The Fourier analysis searches the data for multiple sine waves, and identifies the multiple wavelengths (and frequencies) present in the data set (See Box 1 for details of the Fourier technique).

Box 5.1. Fourier analysis

Fourier analyses were developed to decompose complex waveforms into simple waveforms. The Fourier analysis fits a series of sine waves of increasing frequency to a data set. The approach uses a fixed window (extent of data in time) and a variable grain to discern component patterns. The fast Fourier technique is a modification that utilizes data sets with windows that are 2^n units. The essence of the Fourier analysis is in the transform, whereby the discrete data points are transformed from a time domain to a frequency domain. The amplitude is calculated for each frequency ranging from intervals of the entire data set (one sine wave fit to the entire set) to a frequency of one-half the number of data points (wavelength every two data points). Frequencies that correlate to a large number of data points have high magnitude values. The magnitudes represent the amount of variance explained by the corresponding frequency. Statistics of mean and variance can be calculated from the magnitude values and represent the amount of noise or random behavior in the data. Dominant frequencies (that correspond to a sine wave of a given length) in the data set have high magnitude values.

5.2.2. Biotic Variability

We investigated the relationship between discontinuities in time and space and variability in biota by determining the variability in bird abundance over time in relation to discontinuities in the bird body mass distribution of the Florida Everglades sub-ecoregion (Allen et al., 1999). Species distribution and body mass estimates were determined for the avian fauna of the Florida Everglades using data collected by Allen et al. (1999). Only species that had established breeding populations in the Everglades sub-ecoregion were included. Non-indigenous species were not included. Pelagic birds were also excluded because they interact with their environment differently than other avian species (Allen et al., 1999). In all cases, adult male and female body masses were averaged to estimate a body mass for each species. Variance associated with the estimation of mean mass, which can vary in species exhibiting size dimorphism, does not have a discernable effect on determination of gaps and aggregations (Sendzimir, 1998).

All species within the community were ranked in order of log transformed body mass, and the data were examined for discontinuities with the Gap Rarity Index (GRI) (Allen and Holling, 2002). The GRI compares observed body mass distributions with a unimodal null distribution that is produced by a kernel density estimator, which smoothes the observed data into a unimodal continuous null. The observed distribution of body masses is compared with values generated from sampling the null distribution 10,000 times. Unusually large gap values are considered significant and determine the location of discontinuities. Discontinuities bound aggregations of species with similar body masses, which perceive and interact with their environment at the same, or very similar, domains of scale. The results were confirmed with Cluster analysis based on variance reduction (Ward option; SAS Institute, Inc., 1999).

Population abundances were determined for Everglades birds using Breeding Bird Survey (BBS) data (Breeding Bird Survey, 2005). Three BBS routes were selected from the Everglades (Flamingo, Homestead, and Pinecrest) and abundances were recorded over a 5-year period (1999–2003) for each route. We used the same species list for each route; however, the same birds were not always recorded on each route or year. For each species, the coefficient of variation (CV) was determined for each route over the 5-year study period. Distance to edge is a measure, in terms of log body mass units, of how far a species is to the edge of a discontinuity in the overall body mass distribution of Everglades birds. Those species directly on the edge of an aggregation (located at the edge of a discontinuity) have a distance to edge of zero. For "interior" species, the distance was measured to the closest edge.

We used a mixed model, blocking by BBS route, for the regional analysis of temporal variability in population abundance. In our model, CV was the dependent variable and distance to edge, aggregation, and the edge-by-aggregation interaction were fixed effects and BBS route was a random effect.

5.3. Results

5.3.1. Process Frequencies

5.3.1.1. Rainfall

Rainfall data from January 1949 through December 1988 exhibited four resonant periodicities. The complex pattern of rainfall can be decomposed into waveforms with cycles of 1 year, 3 months for the daily and monthly data, and a longer-term 6–11-year cycle for annual rainfall (Table 1). The dominant period is the annual cycle, characterized by a summer wet season and winter dry season (Hela, 1952; Thomas, 1970; MacVicar and Lin, 1984). Summer rainfall is mainly a result of convective thunderstorms associated with the daily sea- and land-breeze cycle (Hela, 1952; Bradley, 1972; MacVicar and Lin, 1984). The generation of convective thunderstorms is related to the annual variation in heat budget associated with the earth's orbit. During the fall, winter, and spring months (November through April), rainfall is associated primarily with the passage of cold fronts (Hela, 1952; Bradley, 1972; MacVicar and Lin, 1984). The multiple-year cycle had significant peaks of approximately 11, 5, and 3 years, like the dominant frequencies reported for

TABLE 5.1. Summary of Fourier analyses of time series data.*

			Frequencies (yr)		
Data set	Length (yr)	Resolution	1°	2°	3°
Rainfall	39	Day	1	0.25	0.3
	39	Month	1	0.25	0.3
	44	Year	6	8	11
Stage	22	Day	1	7	3
		Month	11	1	3
Flow	44	Month	1	8	22
Pan evaporation	22	Month	1	11	5
Temperature	22	Month	1	5	0.5
Fire	22	Month	11	1	5

*The length of time and resolution of data are given for each data set of rainfall, stage, flow, evaporation, sea-level temperature, and fire sizes analyzed. For each data set, the primary (dominant), secondary, and tertiary frequencies of from each Fourier analyses are given.

south Florida by Thomas (1970) and Isaacs (1980). These inter-annual variations have been attributed to the degree of tropical storm activity (MacVicar, 1983), or to influences from the El Niño Southern oscillation (ENSO; Rasmussen, 1985; Ropelewski and Halpert, 1987). The 3–4-month cycle evident in the data is less well understood. This cycle is evident as the bimodal summer peaks of rainfall. Thomas (1970) and MacVicar (1983) attribute the summer depression to a combination of two processes. During the late summer months, convective activity may decrease due to feedback dynamics of changing albedo, lapse rates, and heat budget after the freshwater system is full of water (Gannon, 1978). The latter peak may also be a result of the increased frequency of tropical storms and hurricanes in August and September that add to rain during these months (Gentry, 1984).

5.3.1.2. Surface Water

As with the rainfall data, the dominant frequency in the water level data is the annual cycle, although the presence of multiyear cycles in the surface waters (levels and flows) suggests fluctuation over longer frequencies. For example, the monthly water level data indicates the presence of three cycles; the strongest cycle is about 11 years, with smaller ones at frequencies of 1, 7, and 3 years (Table 1). The monthly water flow data vary on frequencies of 1 and 8 years, with minor frequencies of 22 years. The effects of water management are included in this analysis. The period in the early 1960s of extremely low flow was when the Tamiami Trail was closed while the S-12 structures were completed. The period of regularity in the 1970s through early 1980s was when the minimum flow regime was in effect. Flows greater than 3×10^8 m^3 per month occur on the long-term frequencies (22+ years). The 3.2×10^8 m^3-month break seems to correlate with the 9-year return interval. The 2.3×10^8 m^3-month break is roughly observed on the 5-year cycle;

the 1.5×10^8 m^3-month, the 3-year cycle; and the smallest break seems to correlate with an annual cycle. These correlations are approximate; certainly high flows don't occur every 9–10 years. The data indicate distinct periodicities, with dramatic annual and decadal cycles, that appear to correlate with distinct volumetric groupings.

5.3.1.3. Pan Evaporation and Temperature

Pan evaporation rates (depth of water lost to the atmosphere over a given time period) vary at multiple cycles. The most significant periodicity in both data sets was the annual cycle. Significant multiyear periods of 11 and about 5 years were also observed in both data sets, although the peaks were not as significant as the annual cycle. A cycle of about 6 months was also present.

5.3.1.4. Fires

The periodicity of fires in the Everglades exhibit the same multiyear frequency (11 years) as the stage and flow data (Gunderson and Snyder, 1994). Significant spectral peaks were measured at return intervals of 11 and 1 years with minor peaks at a 5–6-year interval. Although the periodicities of fires are similar to the flow and stage the phases are different. The years of high fire activity and size (early 1960s and early 197s) are years of low water level and low flow. Fire sizes during the 22-year period from 1959 though 1979 ranged from 10^2 to 10^8 m^2. Fire patterns indicate at least two classes of fires occurred in Shark Slough: more frequent smaller fires and less frequent large fires. Fires above this size may be a result of many factors, including inability of humans to control or contain fires over a given size, or perhaps a less frequent combination of climatic conditions that would support the fire to burn over a broad area and longer time frame. The larger fires burn over longer time periods than the smaller ones.

5.3.2. Biotic Variability

The body mass distribution of the birds of the Everglades sub-ecoregion was discontinuous and distinct aggregations of body mass were detected with both statistical methods used (Allen et al., 1999). The Breeding Bird Survey provided abundance data for 84 of 106 birds in the Florida Everglades species list. Of those 84 species, many were only present at one or two of the three study routes.

Significant edge ($p = 0.010$) and aggregation effects ($p = .003$) were present. Species with the greatest variation in population abundance over time tended to have body masses that were relatively closer to discontinuities than species with body masses that placed them in the interior of body mass aggregations (Fig. 1). There was also a significant interaction between edge and aggregation ($p = 0.002$), suggesting that the exact nature of the relationship between distance to discontinuity CV varies with body mass aggregation.

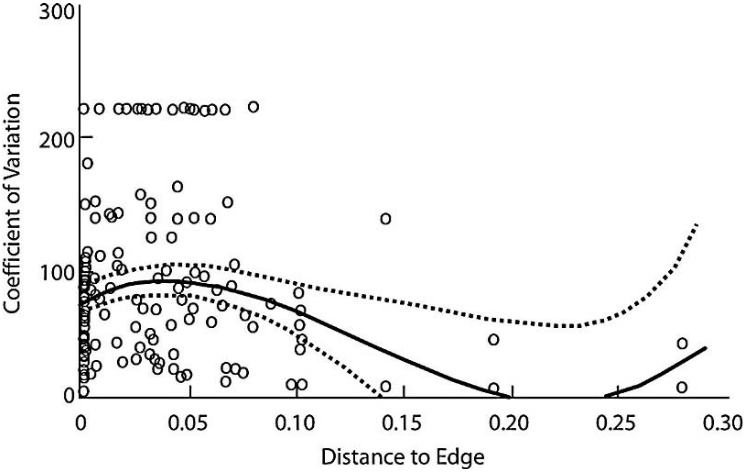

FIGURE 5.1. Coefficient of variation (CV) in relation to distance to edge (DE) of a body mass aggregation in log body mass units for Everglades birds. Solid line represents fitted polynomial ($CV = 72.6 + 835.14 * DE - 12202.63 * DE^2 + 30855.42 * DE^3$), dashed lines represent upper and lower 95% confidence limits, respectively. CV in abundance increases as distance to edge decreases.

5.4. Discussion

Temporal patterns in the hydrologic variables of water level (stage) and flow reflect dominant frequencies resulting from the interplay between the faster dynamics of the atmosphere (such as daily thunderstorms and seasonal storms) and the longer-term dynamics in vegetation, atmosphere (such as ENSO), and sea level (Fig. 2). These analyses support the theory that ecosystems are structured around a few keystone variables of mixed temporal (and spatial) dimensions. The dynamics of these variables are separated by about an order of magnitude; from months to years to decades, which reflect discontinuous patterns that result from the interactions within and among hierarchical levels in time. The discovery of discontinuities in the temporal frequencies of structuring processes are an important step in understanding how discontinuities in spatial and temporal parameters affect landscape structure and dynamics, and ecological and evolutionary processes such as evolution, adaptation, assembly, and competition.

Discontinuities are present in animal body mass patterns as well as the periodicities of processes. We do not attempt to make a mechanistic link between dominant process frequencies and discontinuities in the body mass distributions of vertebrates in the Everglades ecosystem. A strong link such as that would be extremely compelling. Importantly, though, temporal variability in bird population abundance is non-randomly located in terms of body mass distributions, and is highest at discontinuities in the body mass distribution of the birds of the Florida Everglades.

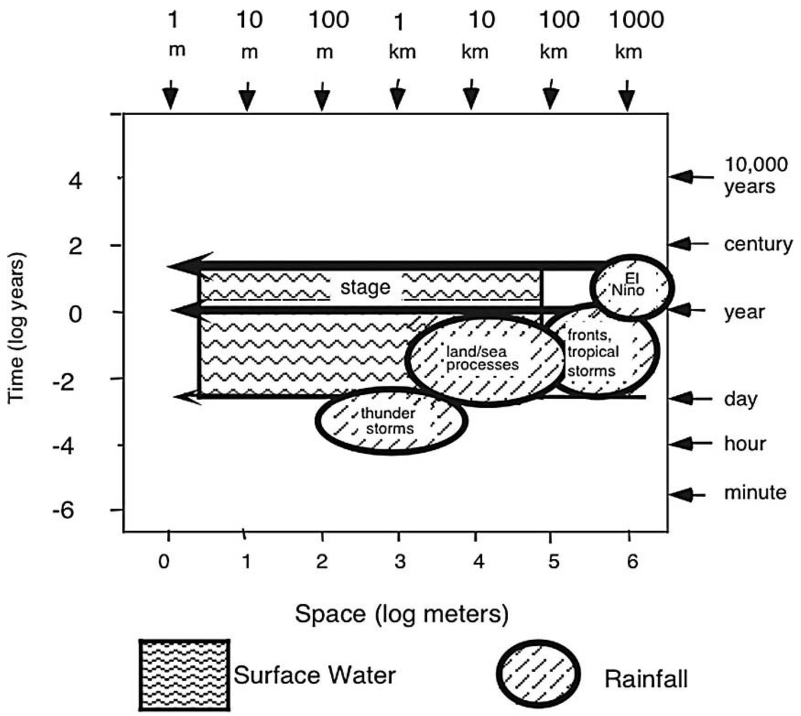

FIGURE 5.2. Temporal frequencies in key ecosystem processes of water stage and flow in the Everglades. Dominant frequencies are depicted by horizontal lines with arrows; with the 1-year cycle (middle line), decadal cycle (top line), and monthly cycle (bottom line). Each of these corresponds to different scales of processes, indicated by the ellipses in the diagram.

Prior research has provided evidence that populations that are more variable are more prone to extinction (Pimm, 1991). Because species near discontinuities in body mass distributions are more prone to decline in the Everglades ecoregion (Allen et al., 1999), this analysis links population variability with that decline. Discontinuities in body mass distributions may be associated with greater resource variability in time and space and higher environmental variability may increase the effects of competition and the possibility that one or more species become extinct (May, 1973).

The most important structuring processes of the Everglades exhibit pronounced temporal periodicities at multiple scales. The body mass distributions of the vertebrates of the Everglades are discontinuously distributed (Allen et al., 1999), with aggregations of species theoretically corresponding to the dominant temporal scales of structure, process and resource distribution upon the landscape. Additionally, abundance in birds whose body mass places them closer to discontinuities is more variable than in birds whose body mass places them farther from those discontinuities, theoretically reflecting higher resource variability to be found at scale breaks, areas of transition from one scale to another. Many investigations in ecology, and landscape ecology in particular, are concerned with process and pattern. However, in almost all cases such analyses default to analyses of spatial patterns upon landscapes. Partially this is due to the relative lack of long-term data sets, but it is also driven by GIS technologies that make spatial analyses so simple. The analyses we report are based on temporal variation; in frequencies of processes and changes in abundance over time. However, landscape ecology in particular and ecology in general will take a giant leap forward when spatial and temporal aspects of process and structure are analyzed simultaneously.

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II
Statistics of Time

6

Using Statistical Models to Study Temporal Dynamics of Animal–Landscape Relations

KEVIN J. GUTZWILLER AND SAMUEL K. RIFFELL

Abstract. Temporal variation in animal responses to landscape conditions may affect animal distributions, population and community structure, and resource use. Measuring such variation and studying its influence is essential for developing a realistic understanding of animal–landscape relations. Several statistical modeling approaches are appropriate for explicitly incorporating time into analyses of animal–landscape relations, but landscape ecologists have not commonly used them. Analytical assessment of temporal variation in animal–landscape relations may involve independent or dependent data. In the case of independent data, interaction effects involving time and landscape metrics can be estimated using cross-product terms. This approach permits direct comparison of animal–landscape regression curves across levels of time, enabling one to infer explicitly how relations vary temporally. With dependent (repeated measures) data, analytical assessment of temporal variation in animal–landscape relations may involve one (time), two (space, time), or three (two space, one time) dimensions. Independent-error methods to test for differences among means or regression curves are not valid in these situations. When data are recorded at equal time intervals, covariance structures that reflect correlations among observations that decrease with time, such as the autoregressive structure, can be used. When data are recorded at unequal time intervals, appropriate covariance structures include the power law, Gaussian, and spherical structures. A mixed-model approach can be used to draw inferences about interactions involving time and landscape metrics when one-, two-, and three-dimensional repeated measures are involved. In summary, several methods accessible to those with moderate training in statistics can be used to incorporate time into studies of animal–landscape relations. Land-use planning and biological conservation will benefit greatly from a better understanding of the temporal aspects of such relations.

6.1. Introduction

The study of animal–landscape relations has mushroomed in recent years as ecologists and conservation biologists have begun to appreciate more fully the potential effects of the surrounding landscape on animals at local sites. This landscape perspective is improving understanding of the broad-scale factors that influence species richness, abundance, population dynamics, and habitat use. Because these advances are leading to better representations of reality, their application may improve conservation effectiveness (Gutzwiller, 2002).

Landscapes and animal populations are dynamic. Disturbances such as plant diseases, storms, fire, floods, commercial and residential development, agricultural development, road construction, and silviculture alter the structure and composition of landscapes at specific extents. The time frame for such changes can range from days to decades. Animal populations can fluctuate seasonally and yearly with changes in food availability and quality, the quality and quantity of habitat, survival and reproduction driven by unpredictable weather, and life-history factors such as nomadic behavior and events occurring on distant wintering ranges.

Together, these sources of variation can lead to temporal variation in animal–landscape relations. For instance, habitats can be population sources in some years, but sinks in others (McCoy et al., 1999). Substantial year-to-year variation occurs in Great Lakes water levels, and coastal wetlands can be inundated one year but not the next, resulting in different animal–landscape relations in successive years (Riffell et al., 2003). Density dependence has been implicated as a source of temporal variation in animal–habitat relations (O'Connor, 1986). Even during periods when broad-scale habitat conditions are stable, considerable interannual variation in bird–landscape relations can occur (Gutzwiller and Barrow, 2001, 2002). Many examples exist for seasonal differences in habitat use, which may reflect niche shifts or niche extensions (Shochat and Tsurim, 2004 and references therein).

If we hope to understand and predict animal–landscape relations, our analytical approaches must incorporate temporal variation in explicit and robust ways. Temporal variation in animal-habitat relations—including relations at broad spatial scales—is poorly understood and in need of immediate study (Morrison, 2002). Compared to studies that do not address temporal factors, studies that explicitly include time are likely to yield information about animal–landscape relations that is more realistic and hence more useful to land-use planners and conservation biologists.

Several statistical approaches are appropriate for explicitly incorporating time into analyses of animal–landscape relations, but landscape ecologists have not commonly used them. The statistical modeling methods we discuss are well-established, and we anticipate their use will increase substantially once landscape ecologists become familiar with their utility and ease of application. The primary goal of this chapter is to increase understanding and application of these techniques so that temporal influences are more frequently incorporated into studies of animal–landscape relations.

6.2. Objectives

To accomplish this goal, we define uncommon statistical terms used in this chapter, explain when techniques for analyzing independent data and dependent data should be applied, and demonstrate statistical-modeling approaches for studying temporal variation in animal–landscape relations. Researchers with modest statistical training—knowledge of basic analysis of variance and regression, for example—can implement the modeling techniques we consider. We use SAS software (SAS Institute, 2002) in our examples because it is widely available, it can be used to model many types of response variables of interest to landscape ecologists, it enables one to model a large array of temporal and spatial covariance structures, and it is the platform with which we are most familiar.

We explain how to use SAS for five statistical modeling approaches that explicitly incorporate time: (1) time-related interaction terms in regression models using independent observations; (2) mixed models for temporally dependent observations that are equally spaced in time; (3) mixed models for temporally dependent observations that are not equally spaced in time; (4) mixed models for temporally and spatially dependent observations; and (5) mixed models for data that exhibit dependence in two spatial dimensions and one temporal dimension. To improve understanding of the techniques discussed in this chapter, we provide simplified definitions of statistical terms (Box 6.1).

Box 6.1. Definitions of statistical terms.

Autocorrelation—correlation between temporally or spatially successive observations of a variable in a data set.

Covariance structures—different patterns of correlation among observations from the same or different sampling units.

Cross-product—the result of multiplying the values of two explanatory variables together for a particular sampling unit. Cross-products for an entire sample can be used as the data for estimating the coefficient for an interaction variable in regression models.

Fixed effect—an effect whose levels in an analysis represent all possible levels, or at least all of the levels about which inference is to be made.

Full model—the most complex mean model under consideration, containing all fixed effects of interest.

Maximum likelihood (ML)—a method of estimating parameter values based on maximizing the likelihood function.

Mixed model—a model containing both fixed and random effects.

Random effect—an effect whose levels in an analysis represent a random subset of the possible levels.

Repeated measures—multiple observations obtained from the same sampling unit (e.g., plot, animal, station) in sequence over time. This term also is used to describe types of analyses designed to accommodate such data (e.g., repeated measures analysis of variance).

Restricted maximum likelihood (REML)—a method of parameter estimation restricted to maximizing the likelihood function over the random effects portion of a model.

6.3. Assessing Temporal Variation in Animal–Landscape Relations Using Independent Observations

6.3.1. Independent Data in Landscape Studies

In a number of research situations, animal metrics (e.g., species richness, abundance, habitat use) may be measured in different landscapes over time. Time frames may include a single season, multiple seasons, or different years. It is not always feasible to gather synchronous observations in many landscapes, or multiple observations through time in each of many landscapes. Remote locations, and constraints on personnel or time available for research, for example, can prevent simultaneous or near-simultaneous surveys of all landscapes. The result can be one measure of the response variable for each of many separate landscapes but across a span of time (e.g., Pearson, 1993; McGarigal and McComb, 1995; Naugle et al., 1999).

For instance, we may need to study mammal–landscape relations during a breeding season based on asynchronous surveys in different landscapes. But mammals might occupy landscapes differently as the season progresses because of the phenology of plants, changes in temperature, or changes in other endogenous or exogenous factors to which mammals respond. Under these circumstances, assessment of the relation between mammals and landscape features would be misleading if time was influential but was left out of the analysis; i.e., if mammal–landscape relations varied with the time of the season, it would be essential to explicitly incorporate time into the modeling process.

As another example, consider a scenario in which snake density was sampled in numerous landscapes during a two-year study. Not enough funding was available to survey any landscape more than once. Instead of obtaining multiple observations over time in the same landscapes, the investigators decided to allocate their resources in a way that would provide information about a larger number of landscapes. This decision was motivated in part by available resources but also by the desire to include a wide range of landscape conditions in the analyses so that any resulting model would have greater potential for robust prediction in the study region. Accordingly, snake density was measured for half of the landscapes during the first year and for the other half during the second year. The landscapes were far enough apart that the estimates of snake density for the different landscapes were independent. Thus, the researchers had a set of independent observations with the potential to exhibit interaction effects between time and landscape features.

6.3.2. Interaction Effects

When data for a response variable are collected at independent locations over time, temporal variation in animal–landscape relations can be studied by analyzing whether there are significant time-related interaction effects involving landscape variables. Returning to our snake research scenario, grassland cover was expected to be a key determinant of snake density, so the researchers used a geographic information system and digital land-cover data to measure percent grassland cover for each landscape. The study objective was to assess the relation between snake density and percent cover of grassland, but the relation between snake density and grassland cover may not have been the same during both years.

Specifically, the change in snake density per unit change in grassland cover (regression slope) may have differed between years. When the effect of an explanatory variable (e.g., grassland cover) on the response variable (e.g., snake density) varies with the level of another explanatory variable (e.g., year), an interaction effect (involving the two explanatory variables) exists on the response variable. Note that a grassland cover × year interaction effect would differ from a significant main effect for grassland cover (in which there would simply be a relation between snake density and grassland cover) and from a significant main effect for year (in which there would simply be a between-year difference in snake density).

With independent data, landscape ecologists can employ interaction terms in standard least-squares and logistic regression models to test whether there is a significant difference in animal–landscape relations over time. A convenient way to test for such dynamics is to calculate the cross-products (Neter et al., 1989) of a landscape and time metric. The cross-products are the data used in the analysis to test for an interaction effect. Any combination of discrete or continuous variables can be used to form the cross-product variable, and the regression coefficient associated with the cross-product variable represents the interaction term in the model. Multiple interaction terms can be examined in the same regression model. Examination of interaction effects enables one to infer how animal–landscape relations vary over time.

6.3.3. Example of SAS Code and Results

Continuing with our snake example, the data for the interaction effect is the product of grassland cover multiplied by an indicator for year; the first year is represented in the data set with a 1 and the second year is represented with a 0. Coding of indicator variables is a common technique in regression (Neter et al., 1989). The data used in this example are available from the authors.

Using `lndscape` to represent landscape, `msnkden` to represent mean snake density, `grasscov` to represent grassland cover in the landscape, `year` to represent the year when mean snake density was measured, and `grssxyr` to represent the cross-products for the grassland cover × year interaction, SAS code for a standard least-squares regression to test for the interaction would look like the following:

```
data snake;
input lndscape msnkden grasscov years;
cards;
1      0.25  10  1
2      0.20  15  1
. . .
. . .
39     0.42  51  0
40     0.35  39  0
run;
grssxyr = grasscov*year;/*calculating the cross-product*/
proc reg;
model msnkden = grasscov year grssxyr;
run;
```

To determine whether there is a significant interaction effect, we examine the table of parameter (regression coefficient) estimates in the output:

Parameter estimates

Variable	DF	Parameter estimate	Standard error	*t*	Pr > |*t*|
intercept	1	0.3272	0.0275	11.92	<0.0001
grasscov	1	0.0014	0.0005	2.70	0.0106
year	1	−0.1451	0.0376	−3.86	0.0004
grssxyr	1	0.0039	0.0007	5.88	<0.0001

The parameter estimate for the interaction term (`grssxyr`) is significantly different from zero, implying that the relation between mean snake density and grassland cover varies with year. We can visualize this result by plotting the relation between mean snake density and grassland cover for each year separately on the same graph (Fig. 6.1). When the regression lines in this type of graph are not parallel (slopes are not equal), there is evidence of an interaction (Neter et al., 1989). In our example, mean snake density increased with grassland cover, but it did so at a higher rate in year 1 compared to year 2. Thus, the animal–landscape relation exhibited temporal flux.

This approach to assessing interaction effects also can be applied in a general linear model context (using SAS's Proc GLM) and in a logistic regression setting (using SAS's Proc Logistic) (SAS Institute, 2002). In Proc GLM and Proc Logistic, an assignment statement to define the interaction is not needed before the model statement; the interaction term is specified in the model statement itself.

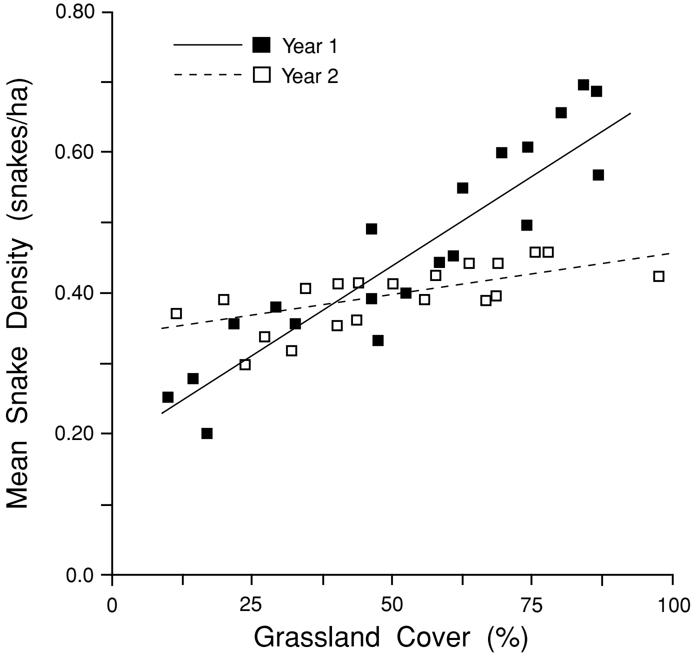

FIGURE 6.1. Relation between mean snake density and percent grassland cover in 40 landscapes based on hypothetical data. The non-parallel regression lines indicate a grassland cover × year interaction effect on mean snake density, which implies that the relation between mean snake density and grassland cover varied with year.

6.4. Assessing Temporal Variation in Animal–Landscape Relations Using Dependent Observations

6.4.1. Repeated-Measures Data in Landscape Studies

Landscape ecologists frequently collect temporally repeated measures data. Typical situations include successive locations of radio-tagged animals, multiple observations of an organism's behavior, abundance or richness data collected at the same sites during successive years, and land-use change within a region. One rationale for collecting data on the same sampling units over time is that animal–landscape relations may vary temporally. By obtaining serial measurements from the same sampling units, one can develop an understanding of the nature and degree of this variation and incorporate it into uncertainty analyses. Another reason repeated measures data are collected is that sequential observations from the same units tend to have less variation than an equal number of observations from different sampling units, because intrinsic and extrinsic sources of variation are reduced. This condition can improve a landscape ecologist's ability to develop better inferences about the issue at hand because there is less noise that may obscure relations.

6.4.2. Statistical Nature of Repeated-Measures Data

Data collected over time from the same sampling unit (organism, plot, landscape element, watershed, physiographic region) tend to be correlated. This violates the independent errors assumption of many statistical procedures for comparing the means of two or more groups (e.g., the t-test, standard analysis of variance) and for assessing relations between response variables and landscape characteristics (e.g., standard correlation and regression). Violations of this assumption can lead to artificially low standard errors, inflated Type I error rates, and hence spurious conclusions.

Common methods for analyzing repeated measures data are to conduct separate analyses for each time period, or to average responses across time periods. But these approaches avoid the temporal component entirely (Littell et al., 1998), do not permit simultaneous inference about both spatial and temporal components, and can result in less power because the sample size for one period of a study will be smaller than the sample size for all periods combined. Another option is to use a procedure that accommodates temporally correlated observations, such as traditional repeated-measures analysis of variance. However, this method requires that all pairs of measurements on a sampling unit are equally correlated regardless of the amount of elapsed time between observations (Littell et al., 1998), and that sets of observations taken at various points in time have equal variances. These conditions are rarely met in studies of animal–landscape relations. Observations on the same sampling unit taken close together in time are often more highly correlated than are observations obtained farther apart in time (Littell et al., 1998), and the variance of animal response variables often differs among time periods.

6.4.3. Advantages of Using Mixed Models to Analyze Repeated-Measures Data

Development of general mixed models (Laird and Ware, 1982) has provided straightforward and flexible methods for assessing temporal dynamics of animal–landscape relations. Mixed models permit tests of fixed effects through either maximum likelihood (ML) or restricted maximum likelihood (REML) estimation. Temporal autocorrelation is accounted for by including temporal variables. The syntax for mixed models is similar to that of classic analysis of variance, and one can easily describe models, include interactions, and write code with basic SAS familiarity.

Mixed models represent a significant improvement over traditional repeated-measures analysis of variance in several ways:

- Mixed models allow for simultaneous inference about both spatial and temporal factors through the use of fixed and random effects.

- Mixed models apply more generally to a variety of covariance (correlation) structures and permit investigators to choose an appropriate covariance structure for the data being analyzed.
- Traditional repeated-measures analysis of variance does not readily allow for missing data. For example, if an observation for one individual is missing for one of the time periods, the data for all time periods for that individual must be excluded from the analysis, unless an estimate for the missing datum can be generated. Sometimes it is reasonable to do this by computing a mean based on the other observations in the same treatment group and time period, but this approach reduces the variance of the group and may thereby alter the outcome of the analysis in ways that are not defensible. Mixed models, on the other hand, accommodate incomplete records without the need for such estimates (Littell et al., 1998).

Landscape ecologists may include temporal effects in a mixed model for at least three reasons. One might be to control for effects of temporal variation. Adjusting parameter estimates, standard errors, and test statistics for temporal effects can prevent spurious conclusions and strengthen inferences. A second reason might be to examine potential interactions between time and spatial components. Although the effects of experimental treatments, landscape structure, or both are usually the primary concerns, understanding how these factors vary across time is often of interest as well. A third reason might be to identify the pattern of temporal correlation that best describes the data. For example, one might be interested in whether within-site correlations remain constant over time (compound symmetry) or whether these correlations decrease with time (autoregressive).

Below we demonstrate the basic approach for modeling temporally repeated-measures data with mixed models. We then demonstrate how to model more complex situations involving temporally and spatially dependent observations that landscape ecologists may encounter in analyses of temporal dynamics of animal–landscape relations. For more detailed instruction about mixed models than we provide here, we refer readers to guides for mixed models using SAS (Littell et al., 1996) or S-plus (Pinheiro and Bates, 2000).

6.4.4. Temporally Dependent Observations, Equally Spaced in Time

When the same sampling units (landscapes, sites, individuals) are sampled over time at regular intervals (year, breeding season, week, day, etc.), the observations are equally spaced in time and are likely to be temporally dependent. Regular long-term monitoring of the same sites is a common source of such data. Sequential locations of radio-tagged individuals also may be temporally dependent; indeed, major radio-tracking texts (e.g., White and Garrott, 1990; Millspaugh and Marzluff, 2001) include discussion about the time interval between locations and independence of observations.

In many situations, mixed models can be used to model correlations between successive animal locations (e.g., Bowne et al., 1999). Mixed models can enable analysts to use more of the location data—because no observations have to be discarded—and to gain insight about the time interval within which successive locations are correlated. The example we describe next involves equally spaced repeated measures data and serves as a vehicle for describing the basic steps in analyzing mixed models.

Example: Pine Siskin (*Carduelis pinus*) in Subalpine Forests

During each year of a 5-year experiment to assess effects of human intrusion on wildlife, birds were counted at 30 randomly placed permanent 1.0-ha sites in Wyoming subalpine forest (Fig. 6.2). Investigators randomly selected 20 of the 30 sites to receive experimental intrusions designed to mimic recreational disturbance by solitary hikers. The remaining 10 sites were unintruded controls. The treatments at these 30 permanent sites were the same during all 5 years, and n for the entire study was $5 \times 30 = 150$. Full details of this experiment are available in Gutzwiller et al. (2002) and references therein.

For this example, we analyze the abundance of a small forest passerine, the pine siskin. This species' abundance at each site for a given year was calculated as the mean number of individuals detected during ten weekly point counts. Percentages of a 7.1-ha area around each site that were occupied by several land-cover types were estimated, but here we only use data for non-forested openings. Thus, for our example analysis, the important variables are pine siskin abundance, site, year, intrusion treatment, and percentage of the surrounding landscape covered by non-forested openings. Readers may obtain these data from the authors.

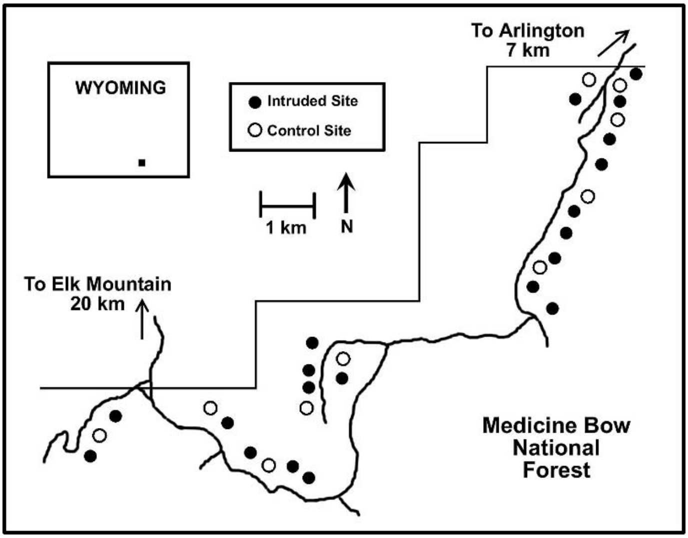

FIGURE 6.2. Map of study area in which pine siskin abundance was sampled during 1989–1993.

For purposes of demonstration, we asked two questions, one relating to a categorical landscape variable and another relating to a continuous landscape variable. Our first question was, “Does experimental intrusion, which mimicked human recreational activity in the landscape, increase or decrease pine siskin abundance?” Intrusion treatment was modeled as a categorical (1 or 0) variable. We consider a categorical variable in our example because evaluating animal–landscape relations often involves relating animal responses to categorical variables. Examples of such evaluations include comparing animal responses (e.g., nest success, movement rate, turning behavior, abundance) between edge sites vs. interior sites, between connected vs. unconnected patches, among different forest-cutting patterns, or among different landscape contexts.

Our second question, which involved a continuous variable, was, “Did pine siskin abundance vary with the percentage of the surrounding landscape covered by non-forested openings?” Landscape ecologists frequently investigate animal–landscape relations involving continuous landscape variables. Examples include species-area relations, relating animal metrics to gradients of urbanization or fragmentation, and using principal components of correlated landscape characteristics as predictor variables (e.g., Saab, 1999; Gutzwiller and Barrow, 2001; Riffell et al., 2003).

Step 1: Specifying Fixed Effects

The first step in modeling repeated-measures data is to specify the fixed effects portion of the model. Temporal components are usually modeled using the `repeated` statement (see below). The initial model should contain all fixed main effects and interactions of interest. That is, the initial model should be a full model, and this full model should be fit using REML (Wolfinger, 1993). Using the pine siskin example, a program in SAS would look like this:

```
data pisi;
input site treat year pisi nfor;
cards;
1      0  1989  0.0  74
2      1  1989  0.0  64
. . .
. . .
29     1  1993  0.4  0
30     0  1993  0.5  0
run;
proc mixed method = reml;
class year treat site;
model pisi = treat nfor year treat*year nfor*year/
             ddfm = kenwardroger;
repeated year/subject = site(treat) type = cs r;
run;
```

This code enabled us to test whether pine siskin abundance (`pisi`) differed between intrusion treatments (`treat`), was related to amount of non-forested habitat in the surrounding landscape (`nfor`), and differed among years (`year`). To test whether the effects of intrusion and non-forested habitat varied from year to year, we used the interaction terms `treat*year` and `nfor*year`, respectively.

In the `proc mixed` statement above, the `method=reml` option requests restricted maximum likelihood estimation. In the `model` statement, the `ddfm=kenwardroger` option provides a small-sample adjustment of degrees of freedom for tests of fixed effects (Kenward and Roger, 1997). The `repeated` statement indicates that `year` is the repeated measure, and the options indicate the following specifications: `subject=site(treat)` specifies the individual sites (nested within treatment) as the subjects (sampling units) that are repeatedly sampled; `type=cs` specifies a compound symmetry covariance structure; and `r` causes printing of the estimated variance-covariance matrix (covariance matrix hereafter).

Step 2: Selecting a Temporal Covariance Structure

Because we collected data on the same sites during each of 5 years, the five data points for a particular site may not have been independent. To address this issue, we can use a mixed model and consider the five yearly observations at each site to be repeated measures. Rather than ignoring or avoiding the implications of temporally correlated observations, the covariance structure of such data can be directly modeled, thereby supplying more detailed information about temporal dynamics of animal–landscape relations.

The ability to compare and select a covariance structure is a key advantage of the mixed model approach for repeated measures. SAS Proc Mixed offers over three dozen covariance structures (SAS Institute, 2002; see Table 6.1 in this chapter for five common examples), and they provide extraordinary flexibility in modeling temporal correlations. With so many possible structures, however, there is the possibility that selecting a covariance structure could become a “fishing expedition.” To prevent this, we provide a general procedure for selecting an appropriate covariance structure (Box 6.2).

Selection should be done with two considerations in mind. First, are there any ecologically plausible temporal covariance structures? In our example below, we considered the possibility that abundances from the same site were equally correlated (perhaps because of habitat or environmental similarities) regardless of the number of years between pairs of observations; this structure is referred to as compound symmetry. We also considered an autoregressive covariance structure, which represented the possibility that repeated measures of pine siskin abundance obtained closer together in time would be more highly correlated than would observations made farther apart in time. Many passerine species are faithful to breeding sites from one year to the next, but these species typically live only a few years. Thus, abundance estimates from two successive years may involve some of the same individual birds, but estimates obtained more than 1 year apart may involve

Box 6.2. General procedure for selecting a covariance structure.

1. Fit the fixed effects portion of the model.
2. Identify a set of candidate covariance structures.
   - Consider ecological and biological characteristics of the dependent variables. For example, consider whether the biology of the organism suggests that the variance of the response variable might fluctuate from year to year.
   - Consider parsimony of the covariance structure relative to available sample size. Many of the available covariance structures require a large number of extra parameters, which may exceed the number of parameters that can be confidently estimated for a given sample size.
3. Fit a *separate* mixed model (with an identical fixed effects portion) using each of the candidate covariance structures.
4. Select the most appropriate covariance structure using one or more model fit statistics such as Akaike's Information Criterion (AIC) or Schwarz's Bayesian Criterion (SBC or BIC).

increasingly higher proportions of new individuals, reducing potential correlation in responses.

Another characteristic of many animal populations is the potential for both the abundance and the variance in abundance to fluctuate from year to year. SAS includes heterogeneous versions (Wolfinger, 1996) of the compound symmetry and autoregressive structures. Heterogeneous structures may be useful for modeling variable populations because they allow the diagonals of the covariance structure (the yearly variances in our pine siskin example) to be different each year (see Table 6.1), unlike the standard compound symmetry, autoregressive, and many other structures. We therefore evaluated heterogeneous versions of these covariance structures in the analysis presented below.

A second consideration for choosing a temporal covariance structure should be the number of additional parameters that a particular structure will require. In our pine siskin example, the unstructured covariance structure would have required the estimation of 15 parameters (Table 6.1) just for the temporal covariance part of the model. Including fixed effects and the intercept, we would have had considerably fewer than 10 observations per parameter (our total n was 150). Having few observations relative to the number of parameters can decrease power and increase the probability of spurious effects (Flack and Chang, 1987; Morrison et al., 1998; Burnham and Anderson, 2002). Accordingly, we did not consider the unstructured covariance structure or other covariance structures with a large number of parameters.

This left us with a set of four candidate covariance structures (number of parameters in parentheses): compound symmetry (2), heterogeneous compound symmetry ($t + 1 = 6$, where t = number of time intervals), autoregressive (2), and heterogeneous autoregressive ($t + 1 = 6$). To evaluate these four covariance structures,

TABLE 6.1 Examples of five covariance structures available in SAS Proc Mixed.

Compound Symmetry (CS)	$\begin{bmatrix} \sigma^2+\sigma_1 & \sigma_1 & \sigma_1 & \sigma_1 & \sigma_1 \\ \sigma_1 & \sigma^2+\sigma_1 & \sigma_1 & \sigma_1 & \sigma_1 \\ \sigma_1 & \sigma_1 & \sigma^2+\sigma_1 & \sigma_1 & \sigma_1 \\ \sigma_1 & \sigma_1 & \sigma_1 & \sigma^2+\sigma_1 & \sigma_1 \\ \sigma_1 & \sigma_1 & \sigma_1 & \sigma_1 & \sigma^2+\sigma_1 \end{bmatrix}$
Heterogeneous Compound Symmetry (CSH)	$\begin{bmatrix} \sigma_1^2 & \sigma_1\sigma_2\rho & \sigma_1\sigma_3\rho & \sigma_1\sigma_4\rho & \sigma_1\sigma_5\rho \\ \sigma_2\sigma_1\rho & \sigma_2^2 & \sigma_2\sigma_3\rho & \sigma_2\sigma_4\rho & \sigma_2\sigma_5\rho \\ \sigma_3\sigma_1\rho & \sigma_3\sigma_2\rho & \sigma_3^2 & \sigma_3\sigma_4\rho & \sigma_3\sigma_5\rho \\ \sigma_4\sigma_1\rho & \sigma_4\sigma_2\rho & \sigma_4\sigma_3\rho & \sigma_4^2 & \sigma_4\sigma_5\rho \\ \sigma_5\sigma_1\rho & \sigma_5\sigma_2\rho & \sigma_5\sigma_3\rho & \sigma_5\sigma_4\rho & \sigma_5^2 \end{bmatrix}$
Autoregressive (AR[1])	$\sigma^2 \begin{bmatrix} 1 & \rho & \rho^2 & \rho^3 & \rho^4 \\ \rho & 1 & \rho & \rho^2 & \rho^3 \\ \rho^2 & \rho & 1 & \rho & \rho^2 \\ \rho^3 & \rho^2 & \rho & 1 & \rho \\ \rho^4 & \rho^3 & \rho^2 & \rho & 1 \end{bmatrix}$
Heterogeneous Autoregressive (ARH[1])	$\begin{bmatrix} \sigma_1^2 & \sigma_1\sigma_2\rho & \sigma_1\sigma_3\rho^2 & \sigma_1\sigma_4\rho^3 & \sigma_1\sigma_5\rho^4 \\ \sigma_2\sigma_1\rho & \sigma_2^2 & \sigma_2\sigma_3\rho & \sigma_2\sigma_4\rho^2 & \sigma_2\sigma_5\rho^3 \\ \sigma_3\sigma_1\rho^2 & \sigma_3\sigma_2\rho & \sigma_3^2 & \sigma_3\sigma_4\rho & \sigma_3\sigma_5\rho^2 \\ \sigma_4\sigma_1\rho^3 & \sigma_4\sigma_2\rho^2 & \sigma_4\sigma_3\rho & \sigma_4^2 & \sigma_4\sigma_5\rho \\ \sigma_5\sigma_1\rho^4 & \sigma_5\sigma_2\rho^3 & \sigma_5\sigma_3\rho^2 & \sigma_5\sigma_4\rho & \sigma_5^2 \end{bmatrix}$
Unstructured (UN)	$\begin{bmatrix} \sigma_1^2 & \sigma_{12} & \sigma_{13} & \sigma_{14} & \sigma_{15} \\ \sigma_{21} & \sigma_2^2 & \sigma_{23} & \sigma_{24} & \sigma_{25} \\ \sigma_{31} & \sigma_{32} & \sigma_3^2 & \sigma_{34} & \sigma_{35} \\ \sigma_{41} & \sigma_{42} & \sigma_{43} & \sigma_4^2 & \sigma_{45} \\ \sigma_{51} & \sigma_{52} & \sigma_{53} & \sigma_{54} & \sigma_5^2 \end{bmatrix}$

we used four separate runs of Proc Mixed. Each time we fit the same fixed effects portion of the model but modified the `repeated` statement to include a different covariance structure. We show the different `repeated` statements below; the rest of the SAS code remained exactly as shown previously.

```
repeated year/subject = site(treat) type = cs r;
repeated year/subject = site(treat) type = csh r;
repeated year/subject = site(treat) type = ar(1) r;
repeated year/subject = site(treat) type = arh(1) r;
```

SAS provides several model fit statistics that can be used to select a covariance structure. Of these, Akaike's Information Criterion (AIC) and Schwarz's Bayesian Criterion (BIC or sometimes SBC) are common choices (Littell et al., 1996; Wolfinger, 1996, 1997). Both are based on the log likelihood and include a penalty proportional to the number of covariance parameters (BIC provides a stiffer penalty than does AIC). Burnham and Anderson (2002) recommend using the small-sample version of Akaike's Information Criterion (AIC_c, also provided by SAS) when $n < 40$ per estimated parameter in a model (including all covariance parameters, fixed effect parameters, intercept, and error terms). We used AIC_c to select the most appropriate covariance structure for our example.

AIC_c (smaller is better) indicated that the heterogeneous compound symmetry covariance structure was the most appropriate choice, but that the heterogeneous autoregressive structure was a very close second (difference in $\mathrm{AIC}_\mathrm{c} < 0.1$).

Covariance structure	AIC_c
Compound symmetry	22.7
Heterogeneous compound symmetry	16.4
Autoregressive	23.3
Heterogeneous autoregressive	16.5

When two or more covariance structures have similar measures of appropriateness, it is not clear which structure is more appropriate. If the primary goal is to improve inference about fixed effects, the choice among appropriate covariance structures does not present a major dilemma. Littell et al. (1996, p. 321) note that, "the major impact on inference results from using a *reasonable* covariance model. The specific model used is not nearly as important, as long as it is 'in the ballpark.'"

In many studies, experimental treatments may affect the variance instead of (or in addition to) the mean. One option in this situation is to used the `group=` option in the `repeated` statement, which permits different values for each parameter in the covariance structure for each level of the `group` effect (SAS Institute, 2002). The repeated statement would look like the following:

```
repeated year/subject = site(treat) type = csh group = treat r;
```

In our current pine siskin example, both intrusion treatments would exhibit heterogeneous compound symmetry structure but the variances (diagonals) could be different for sites in each treatment. The `group=` option should be used with caution, especially with small sample sizes, because it greatly increases the number of parameters in and the complexity of the covariance structure.

Step 3: Inference about Dynamics of Animal–Landscape Relations

The third step involves making the statistical inference using the previously selected covariance structure. Thus, we used the following SAS statements. Note that the `type =` option in the `repeated` statement is set to `csh` for heterogeneous compound symmetry.

```
data pisi;
input site treat year pisi nfor;
cards;
1      0  1989  0.0  74
2      1  1989  0.0  64
. . .
. . .
29     1  1993  0.4  0
30     0  1993  0.5  0
run;
proc mixed method = reml;
class year treat site;
model pisi = treat nfor year treat*year nfor*year/
             ddfm = kenwardroger;
repeated year/subject = site(treat) type = csh r;
run;
```

One useful output from this program is the table of parameters for the covariance matrix:

Covariance parameter estimates

Covariance parameter	Subject	Estimate
Var(1)	site(treat)	0.0173
Var(2)	site(treat)	0.0264
Var(3)	site(treat)	0.0389
Var(4)	site(treat)	0.0682
Var(5)	site(treat)	0.0497
CSH	site(treat)	0.1205

In this output in the Estimate column, the yearly variances in pine siskin abundance (i.e., Var(1) for 1989 = 0.0173, Var(2) for 1990 = 0.0264, etc.) are the diagonals of the CSH covariance matrix (see Table 6.1 and Box 6.3). The variances generally increase with year, confirming the choice of heterogeneous structures. The CSH parameter in the Estimate column is the constant (ρ) in the covariance part of the matrix (see Table 6.1 and Box 6.3). Overall, these results imply that heterogeneous compound symmetry was a reasonable covariance structure for our data.

Next, we look at the tests of fixed effects.

Type 3 tests of fixed effects

Effect	Numerator DF	Denominator DF	*F*	Pr > *F*
treat	1	26.9	0.10	0.7582
year	4	58.2	15.75	<0.0001
nfor	1	26.9	4.24	0.0493
year*treat	4	58.2	0.95	0.4424
nfor*year	4	58.2	3.42	0.0140

Box 6.3. Example calculations for a covariance structure.

Generic heterogeneous compound symmetry (CSH) structure (in the first matrix below) compared to the specific CSH structure parameterized for the pine siskin abundance data. Example calculations for the first column of covariances are presented in the second matrix. The specific structure (third matrix) was generated by the analysis described in 6.4.4. *Temporally Dependent Observations, Equally Spaced in Time* (Step 3: Inference about Dynamics of Animal–Landscape Relations).

Generic CSH Structure

$$\begin{bmatrix} \sigma_1^2 & \sigma_1\sigma_2\rho & \sigma_1\sigma_3\rho & \sigma_1\sigma_4\rho & \sigma_1\sigma_5\rho \\ \sigma_2\sigma_1\rho & \sigma_2^2 & \sigma_2\sigma_3\rho & \sigma_2\sigma_4\rho & \sigma_2\sigma_5\rho \\ \sigma_3\sigma_1\rho & \sigma_3\sigma_2\rho & \sigma_3^2 & \sigma_3\sigma_4\rho & \sigma_3\sigma_5\rho \\ \sigma_4\sigma_1\rho & \sigma_4\sigma_2\rho & \sigma_4\sigma_3\rho & \sigma_4^2 & \sigma_4\sigma_5\rho \\ \sigma_5\sigma_1\rho & \sigma_5\sigma_2\rho & \sigma_5\sigma_3\rho & \sigma_5\sigma_4\rho & \sigma_5^2 \end{bmatrix}$$

Example Calculations for Specific CSH Structure (see text)

$$\begin{bmatrix} 0.0173 & \sigma_1\sigma_2\rho & \sigma_1\sigma_3\rho & \sigma_1\sigma_4\rho & \sigma_1\sigma_5\rho \\ \sqrt{0.0264}\sqrt{0.0173}\ (0.1205) & 0.0264 & \sigma_2\sigma_3\rho & \sigma_2\sigma_4\rho & \sigma_2\sigma_5\rho \\ \sqrt{0.0389}\sqrt{0.0173}\ (0.1205) & \sigma_3\sigma_2\rho & 0.0389 & \sigma_3\sigma_4\rho & \sigma_3\sigma_5\rho \\ \sqrt{0.0682}\sqrt{0.0173}\ (0.1205) & \sigma_4\sigma_2\rho & \sigma_4\sigma_3\rho & 0.0682 & \sigma_4\sigma_5\rho \\ \sqrt{0.0497}\sqrt{0.0173}\ (0.1205) & \sigma_5\sigma_2\rho & \sigma_5\sigma_3\rho & \sigma_5\sigma_4\rho & 0.0497 \end{bmatrix}$$

Specific CSH Structure[†]

$$\begin{bmatrix} 0.0173 & 0.002573 & 0.003127 & 0.004139 & 0.003533 \\ 0.002573 & 0.0264 & 0.003858 & 0.005108 & 0.004360 \\ 0.003127 & 0.003858 & 0.0389 & 0.006207 & 0.005298 \\ 0.004139 & 0.005108 & 0.006207 & 0.0682 & 0.007013 \\ 0.003533 & 0.004360 & 0.005298 & 0.007013 & 0.0497 \end{bmatrix}$$

[†] To produce the specific covariance structure as SAS output, use the `r` option in the `repeated` statement of Proc Mixed.

In any multifactor model with interactions, one should first check for significant interactions (Wolfinger, 1997) because when an interaction effect is present, the influence of one main effect depends on the level of the other main effect involved in the interaction (Underwood, 1997). The `nfor*year` interaction was significant (see above), so we focused our interpretation on the `nfor*year` interaction instead of on the associated main effects. Our conclusions, based on the table above, were: pine siskin abundance was not lower on intruded sites; pine siskin abundance differed significantly among years, but this effect varied with the percent of the surrounding landscape in non-forested area; and pine siskin abundance was related to the percent of non-forested area in the surrounding landscape, but this relation varied among years. These latter two interpretations are alternate ways of viewing the `nfor*year` interaction effect.

To explore the temporal dynamics of the relation between `pisi` and `nfor` further, we can modify our mixed-model code so it produces intercepts and slopes for the relation between pine siskin abundance and non-forested openings for each year separately. This is accomplished by dropping the `nfor` main effect and other non-significant terms, and by specifying two options in the `model` statement: `noint` tells Proc Mixed not to fit a common intercept, but five separate intercepts (one for each year); `solution` requests the estimates for all of the fixed-effect parameters.

```
data pisi;
input site treat year pisi nfor;
cards;
1     0  1989  0.0  74
2     1  1989  0.0  64
. . .
. . .
29    1  1993  0.4  0
30    0  1993  0.5  0
run;
proc mixed method=reml;
class year treat site;
model pisi-year nfor*year/ddfm=kenwardroger noint
             solution;
repeated year/subject=site(treat) type=csh r;
run;
```

This program generated the following output:

Solutions for fixed effects

Effect	Date	Estimate	Standard error	DF	*t*	Pr > |*t*|
year	1989	0.0731	0.0287	28.2	2.55	0.0166
year	1990	0.0901	0.0342	29.2	2.63	0.0134
year	1991	0.1593	0.0415	28.9	3.84	0.0006
year	1992	0.4157	0.0560	27.3	7.43	<0.0001
year	1993	0.4326	0.0479	27.0	9.03	<0.0001
nfor*year	1989	−0.0009	0.0013	28.2	−0.65	0.5222
nfor*year	1990	0.0052	0.0016	29.2	3.35	0.0022
nfor*year	1991	0.0050	0.0019	28.9	2.65	0.0130
nfor*year	1992	0.0007	0.0026	27.3	0.26	0.7964
nfor*year	1993	0.0009	0.0022	27.0	0.43	0.6725

In the Estimate column above, the coefficients for `year` are intercepts, and the coefficients for `nfor*year` are slopes. The intercept estimates indicate that pine siskin abundance and its standard error generally increased over time. The slope estimates indicate the relation between pine siskin abundance and nfor was strongly positive in 1990 and 1991, as indicated by the significant *t* statistics, but not during the other 3 years. Using these results, one can explore, through theoretical arguments or further experiments, why this relation was significant in these 2 years but not the others.

6.4.5. Temporally Dependent Observations, Unequally Spaced in Time

Temporally repeated observations often occur at irregular intervals. Consider the following hypothetical example of an unequally spaced design: an investigative team planted vegetative corridors in different matrix types and then monitored animal use of those corridors 1 year, 2 years, 4 years, 7 years, and 10 years later. A situation like this could arise simply because of funding or other logistical constraints that prohibit sampling at equal intervals. Unequally spaced observations also may occur when weather conditions restrict sampling to specific but unpredictable times, or when a marked animal is relocated after a period of being undetectable.

With unequally spaced temporal observations, landscape ecologists can still use mixed models, but temporal correlations must be modeled as a function of "distance" rather than as a function of a regular time interval. In this situation, "distance" is the single dimension of time, not two- or three-dimensional space, and structures commonly used to model spatial covariance (power law, Gaussian, spherical, etc.) are used to model temporal covariance (Littell et al., 1996). Landscape ecologists have fully recognized the utility of spatial covariance structures for modeling spatial variation in animal–landscape relations (e.g., Selmi and Boulinier, 2001; Keitt et al., 2002; Evans and Gaston, 2005), but the same covariance structures, and very similar SAS code, also can be used to model covariance among unequally spaced, temporally correlated observations. Recent versions of SAS include over a dozen spatial covariance parameters that can be included in the `type=` option of the `repeated` command in Proc Mixed.

Although our pine siskin data contain equally spaced repeated measures, we used it as an example of how to code for unequally spaced repeated measures below. We used a power law spatial covariance, which provides a generalization of the autoregressive (AR[1]) structure for equally spaced data.

```
data pisi;
input site treat year pisi nfor;
cards;
1      0   1989  0.0  74
2      1   1989  0.0  64
. . .
. . .
29     1   1993  0.4  0
30     0   1993  0.5  0
run;
data pisi2; set pisi;
year1=year;
run;
proc mixed method=reml data=pisi2 order=data;
class year treat site;
```

```
model pisi = treat nfor year treat*year nfor*year/
             ddfm=kenwardroger;
repeated year/subject=site(treat)
  type=sp(pow)(year1) r;
run;
```

An important caveat is that the spatial covariance analysis requires that year be a *continuous* variable in the `type=` option of the `repeated` statement. Using a `data` step, we created a second time variable, `year1`, that was identical to the categorical `year` variable, except that it was considered continuous (notice that `year1` is not in the `class` statement).

6.4.6. Temporally and Spatially Dependent Observations, Two Dimensions

Research efforts on animal–landscape relations often result in data that are correlated through both space and time. For example, if invertebrates were sampled in multiple stream reaches in each of several watersheds over time, there might be correlations among reaches located in the same watersheds (spatial dependence) and correlations among temporal observations in the same reaches (temporal dependence). Another example would involve serial sampling of the same patches over time in distinct physiographic regions. A third example would be repeated location data on individual animals that form groups in different areas.

Pine Siskin Example: Doubly Repeated Measures

Returning to the pine siskin example, Fig. 6.2 indicates that the 30 sites occurred in two basic groups, one in the southwestern part of the study area and one in the northeastern part of the study area. These two groups corresponded to two areas that were relatively snow-free and hence accessible during the early part of the breeding season. The sites were positioned randomly, treatments were randomly assigned to sites, and there were no major vegetation differences between treatment groups. For demonstration purposes, we assume that in addition to the temporally repeated measures associated with year, the two groups (or clusters) of sites involve spatially repeated measures within each cluster. Thus, our challenge now is to simultaneously model the correlation among temporally repeated measures and the correlation among sites within a cluster.

Doubly repeated measures can be dealt with in mixed models by using the `repeated` statement, the `random` statement, or both. In addition to the temporal effect `year`, which is specified by the `repeated` statement, we can assign group membership to a categorical variable (coded 1 or 2), named `cluster` here, and model the spatial dependence as a random effect:

```
data pisi;
input site treat year pisi nfor cluster;
```

```
cards;
1      0  1989  0.0  74  1
2      1  1989  0.0  64  1
. . .
. . .
29     1  1993  0.4  0   2
30     0  1993  0.5  0   2
run;
class year treat site cluster;
model pisi=treat nfor year treat*year nfor*year/
model pisi = treat nfor year treat*year nfor*year/
              ddfm=kenwardroger;
random cluster;
repeated year/subject=site(treat) type=csh r;
run;
```

This program generated the following output.

Covariance parameter estimates

Covariance parameter	Subject	Estimate
Cluster	—	0.0072
Var(1)	site(treat)	0.0200
Var(2)	site(treat)	0.0184
Var(3)	site(treat)	0.0284
Var(4)	site(treat)	0.0652
Var(5)	site(treat)	0.0599
CSH	site(treat)	0.0799

In this output, as before, Var(1) through Var(5) in the Estimate column are the yearly variances in pine siskin abundance (diagonals of the covariance matrix), and the CSH parameter is the constant in the covariance part of the matrix (Table 6.1). Notice in the Estimate column for Cluster that the covariance associated with the groups of sites was an order of magnitude smaller than were the other covariance parameters. Furthermore, the fixed-effect results (not shown) did not change appreciably, so in this example the spatial grouping of the sites was not important.

6.4.7. Temporally and Spatially Dependent Observations, Three Dimensions

Three-dimensional repeated-measures data—a temporal correlation (repeated measures over time) and correlation in two spatial dimensions (typically x and y geographic coordinates)—often arise when studying animal–landscape relations. This situation occurs when there is a set of permanent sampling stations located throughout a landscape or region, and these stations are sampled repeatedly over time. Animal metrics measured at nearby stations may be more correlated than are those for distant stations, and animal metrics measured close together in time may be more correlated than are those measured farther apart in time. Furthermore, spatial correlations may change over time, and temporal correlations may change through space. Examples of three-dimensional repeated-measures data include the 30 stations at which investigators repeatedly sampled pine siskins, and the thousands of Breeding Bird Survey routes sampled annually across North America (Robbins et al., 1986; Sauer et al., 2005).

Although Proc Mixed would allow a temporal variable to be treated as a third spatial dimension (e.g., `type=sp(pow)(easting northing year1)`), this is not appropriate because time and space do not have comparable units (Schabenberger and Gotway, 2005). Other possible approaches for three-dimensional situations would be to either conduct separate spatial analyses for each level of the time dimension, or conduct separate temporal analyses for each location. However, these approaches do not account for possible interactions between spatial and temporal processes. The ideal approach would be to model the spatial and temporal correlations and space–time interactions simultaneously, but techniques for doing this are not well-developed or readily accessible in common statistical packages.

If certain assumptions are met, one can analyze 3-dimensional repeated-measures data using either separable covariance structures, or non-separable covariance structures. Separable covariance structures permit joint analysis of spatio-temporal data, but do not permit space-time interactions to be investigated (Mitchell and Gumpertz, 2003; Schabenberger and Gotway, 2005), whereas techniques based on non-separable covariance structures allow for both joint and interaction analyses (Schabenberger and Gotway, 2005). Unfortunately, use of these two types of structures is complex, and writing code for the analyses is not simple in popular statistical packages (but see Mitchell and Gumpertz, 2003 for a spatio-temporal analysis using several SAS procedures). The references cited above are an excellent starting point for researchers interested in pursuing these techniques.

6.4.8. Summary of Mixed Models for Repeated Measures

Mixed models provide an opportunity to explicitly incorporate simultaneous inference about time and space in studies of animal–landscape relations. These models are flexible, allowing temporal and spatial effects to be addressed in different ways and with different levels of dimensionality.

For our inferences about pine siskin, the mixed-model approach was beneficial in three major ways. First, it enabled us to estimate effects of human intrusion treatments and percent of the surrounding landscape composed of non-forested openings after accounting for different covariance structures in the data, which reduced the possibility of spurious conclusions. Second, it provided the ability to use all of the observations in a single analysis and thereby avoid the loss of statistical power that might have been incurred by splitting the dataset and conducting analyses for each year separately. Finally, the mixed-model approach enabled us to make simultaneous inferences about spatial and temporal factors.

The basic protocol for conducting mixed-model analyses in the context of temporally repeated measures can be summarized as follows:

Step 1: Fit the fixed effects portion of the model using REML. Generally, this part of the model should contain all main effects and interactions of interest.

Step 2: With thought to ecological processes and sample size restrictions, choose a set of candidate covariance structures and select the best-fitting structure using a model fit statistic such as AIC.

Step 3: Apply the selected covariance structure for inference in the final model using REML.

Note that after selecting the appropriate covariance structure, investigators may wish to evaluate several different competing fixed-effect models. Often, AIC (or another model selection criterion) is used to select the "best" model(s) for inference (Burnham and Anderson, 2002). There are two important considerations when doing this. First, investigators should use maximum likelihood (use the `method=ml` option in the `proc mixed` statement) when comparing models with different fixed-effect specifications, because REML restricts the optimization of the likelihood function to the random-effects portion of the model (Wolfinger, 1993). Second, one should verify that SAS Proc Mixed uses the number of parameters (including intercepts and error terms) specified in Burnham and Anderson (2002) for AIC calculations (see Stafford and Strickland, 2003).

6.4.9. Additional Information About Mixed Models

Mixed-Model Diagnostics

For classical linear modeling approaches like regression and analysis of variance, various tools are available to assess the overall fit of the model to the data and to examine the influence of individual observations on the model. These tools include residual analysis, collinearity analysis, and influence analysis. Such analyses can be useful for assessing the degree to which model assumptions are met and identifying individual data points that have a strong influence on structuring the model. In mixed models for repeated measures, these assessments are more difficult because it is not the influence of individual observations (e.g., a particular pine siskin survey) that is of interest, but rather the influence of a particular site that was observed multiple times (e.g., over several years). Recent versions of SAS include options to produce influence diagnostics that allow assessment of the fit of both random- and fixed-effect components (Schabenberger, 2004).

Mixed Models for Non-Traditional Data

We have focused on linear models involving continuous response variables that are normally distributed, but the mixed-modeling concepts and techniques we have described can be extended to other types of response variables. Mixed models can be applied to binomial or Poisson distributions via Proc Glimmix (Littell et al., 1996; Schabenberger, 2005) using syntax and theory that are similar to those described above. Mixed-model approaches can be extended to non-linear models via Proc Nlinmixed in SAS (Littell et al., 1996), or with S-Plus (Pinheiro and Bates, 2000). Detailed discussion of these options is beyond the scope of this chapter, but we mention them for readers with interests in applications to binary and count data and to non-linear processes. The references cited above are good portals into the pertinent literature.

6.5. Conclusions

Several established modeling methods accessible to those with moderate training in statistics can be used to incorporate time into studies of animal–landscape relations. Typical advantages of explicitly modeling time in such relations include: results that are more defensible on technical grounds; better understanding of the ecology involved; knowledge of the magnitude of temporal variation in the relations, which can be used to characterize temporal flux in, and level of uncertainty about, the relations; and robust predictions about animal use of landscapes over time. Knowledge about temporal variation in animal–landscape relations also can be used to parameterize and structure simulation models (Gutzwiller and Barrow, 2001).

These advantages hold promise for advancing the disciplines of landscape ecology, land-use planning, and biological conservation for the following reasons. Defensible results are crucial for establishing policy and management guidelines. The value of a model lies largely in the ecological understanding it provides, and models that address temporal flux are more likely to provide better ecological understanding than are models that that do not account for such dynamics. The utility of an animal–landscape model can be constrained by uncertainty about whether it holds over time, and explicitly modeling temporal dynamics can help one identify levels of uncertainty. Predictions from models that consider temporal dimensions also are likely to be more robust because they probably represent reality more accurately. Simulation models are frequently used to predict consequences of environmental disturbances and management decisions. By incorporating temporally explicit statistical models as key components (sub-models), simulation models may represent temporal dynamics more realistically.

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7

Multivariate Landscape Trajectory Analysis

An Example Using Simulation Modeling of American Marten Habitat Change under Four Timber Harvest Scenarios

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Abstract. Integrating temporal variability into spatial analyses is one of the abiding challenges in landscape ecology. In this chapter we use landscape trajectory analysis to assess changes in landscape patterns over time. Landscape trajectory analysis is an approach to quantify changes in landscape structure over time. There are three key concepts which underlie the approach—landscape structure, structure space, and location—and there are four useful measurements for analyzing landscape trajectories—displacement, velocity, acceleration, and divergence. We illustrate the approach with an analysis of American marten habitat under four timber harvest scenarios. We used the RMLands simulation model to project changes in forest composition and successional stage across a landscape in the Colorado Rockies under scenarios that varied cutting pattern (clumped or aggregated) and rotation length (200 or 300 years). Next, we used a multi-scale habitat capability model to predict American marten habitat at each time step. We then used FRAGSTATS to quantify 31 metrics describing the extent and pattern of marten habitat. We employed multi-temporal principal components analysis to describe the independent suite of major landscape structure components (i.e., the extent and pattern of marten habitat) as well as their trajectories of change under each disturbance scenario. We demonstrate that trajectory analysis in landscape structure space provides a rigorous, intuitive, and highly interpretable description of the interaction between disturbance, ecological process, spatial pattern, and temporal variation. For example, one can quantitatively understand the nature of the impact of each scenario on marten habitat by inspecting the route that each trajectory takes through landscape structure space. Threshold behavior is readily apparent as rapid changes in direction and rate of change in the landscape structure space. In addition, relative to initial conditions, the impact of each modeled disturbance scenario is readily calculated based on the degree of displacement of each scenario from the original extent and pattern of habitat. Furthermore, the relative similarity between scenarios in their impact on marten habitat is obtained by plotting and analyzing the divergence between the trajectories of the various scenarios through time.

7.1. Introduction

7.1.1. *Patterns and Processes Through Space and Time*

Temporal variability is a central attribute of ecological systems. Accurate description and conceptualization of ecological systems requires both quantification of spatial patterns and explicit consideration of their temporal dynamics. In a dynamic system, descriptions of current conditions are necessary precursors for understanding ecological relationships. However they are not sufficient. Understanding relationships between mechanisms and responses in ecological systems and predicting future changes likely to result from natural and anthropogenic disturbances requires that scientists integrate analysis of patterns and processes through both space and time.

7.1.2. *Ecosystem and Landscape Dynamics: A Conceptual Framework*

Ecological systems can be described as collections of state variables (measurable attributes that describe the "state" or condition of the system) depicting ecosystem structure and function at each location in a landscape at each moment in time. The description of the system is constrained by the resolution (i.e., lowest limit in space and in time at which each variable is resolved) and the extent (i.e., spatial and temporal domains over which the variables are measured) of the observations. The structure of the ecological system is described by patterns in each of the state variables across space and time. A key challenge facing landscape ecologists is simultaneously integrating ecological variability across locations in space with measurements of dynamics through time. It is relatively easy to describe the temporal trajectory of a single location through time, as it is to describe the static spatial structure of a landscape consisting of millions of pixels. It is more difficult conceptually and analytically to integrate the analysis of spatial structure across large extents and at fine grains with analysis of temporal variability.

Integrating analysis of spatial structure with that of temporal dynamics is fundamental to linking process to pattern. A landscape is a dynamic system. In quantitative landscape ecology, a landscape is represented by a model, typically defining the landscape as a mosaic of discrete patches. As a dynamic system, a landscape should be defined by its state and dynamics, where the state is given by a vector describing the condition of the landscape at a given moment, and dynamics result from changes in the state over time. The elements of the vector are state variables, elemental qualities describing attributes of the landscape (Horning and Randell, 1973). In landscape pattern analysis, these state variables are landscape metrics, which quantify different spatial properties of the landscape mosaic. These landscape metrics define the phase space, or all possible states of the system given the state variable set. In landscape pattern analysis, phase space is usually called landscape structure space; it is a space defined by all possible combinations of values that can be taken by the collection of landscape metrics describing the structure of the landscape.

The value of landscape variables will change over time as processes impact patterns in the landscape. Over continuous time, this results in a curve in landscape structure space. When measured over discrete time, this curve will appear as an ordered set of points in landscape structure space. The pathway described by these points we call a trajectory and its characteristics reflect the temporal dynamics of that landscape under the influence of disturbances and biotic interactions within that spatial and temporal domain.

In this chapter, we present an approach for integrating spatial and temporal analysis of landscape patterns using American marten habitat as an example. We focus on ways to (a) quantify the multivariate character of landscape structure; (b) measure its change over time; and (c) quantitatively compare the rates and patterns of landscape change among multiple landscapes over time.

7.1.3. Trajectory Analysis Approach

Landscape trajectory analysis is a quantitative approach for measuring differences among landscapes over time. There are three key concepts which underlie the approach: landscape structure, structure space, and location; and there are four useful measurements for analyzing landscape trajectories: displacement, velocity, acceleration, and divergence.

Landscape Structure

The first step in any spatial analysis is to define the landscape. In this chapter we limit our attention to landscapes represented by categorical raster maps, where the cell size specifies the spatial resolution of the data and the classification scheme depicts the cover classes. There are a number of limitations to categorical representations of continuously varying ecological attributes (McGarigal and Cushman, 2005); however, the vast majority of landscape ecological research today is based on categorical maps of landscape structure, hence our use here. Within this framework, a landscape is a map consisting of a mosaic of patches representing different cover types. There are three important attributes of this landscape: classification, resolution, and extent. Classification describes the number and kinds of cover types resolved in the map. Resolution specifies the minimum resolvable spatial unit, and is defined as minimum patch size or pixel size. Extent is the spatial domain of the landscape. Classification, resolution, and extent fundamentally influence patterns that are perceived and measured, and therefore must be defined appropriately with respect to the system and questions being addressed (McGarigal and Cushman, 2005).

The composition and configuration of the patch mosaic represented in categorical landscape maps can be described with landscape metrics (McGarigal and Marks, 1995). These metrics quantify a variety of attributes of patch size, shape, and distribution (McGarigal et al., 2002). There are many different metrics available to quantify the composition and configuration of landscape mosaics. It often becomes cumbersome and confusing to analyze dozens of metrics simultaneously. Many metrics measure similar attributes of landscape structure (McGarigal and

Marks, 1995; Gustafson, 1998; Jaeger, 2000; Li and Wu, 2004; Neel et al., 2004) and several efforts have been made to describe the multivariate relationships among large numbers of metrics (Riitters et al., 1995; McGarigal and McComb, 1995).

Landscape Structure Space

Landscape structure space is derived from a p-dimensional space, where each dimension represents a different landscape metric. It is usually necessary to standardize the landscape metrics to zero mean and unit variance, as landscape metrics often have different ranges and scales of measurement (McGarigal et al., 2002). We refer to this p-dimensional space as landscape metric space, denoting that the dimensions are defined by the individual landscape metrics (but in standardized form). Because many landscape metrics are partly redundant (Riitters et al., 1995) it is often preferable to obtain orthogonal combinations from an unconstrained ordination technique (McGarigal et al., 2000), such as principal components analysis (PCA) (e.g., McGarigal and McComb, 1995; Cushman and Wallin, 2000) or non-metric multidimensional scaling (NMDS) (Kruskal, 1964; Clarke, 1993). In this manner, the p-dimensional space is reduced to an m-dimensional space, where hopefully $m \ll p$. We refer to this reduced m-dimensional space as landscape structure space, noting that the dimensions now represent composite structure gradients whose exact definitions will vary among data sets depending on the suite of landscape metrics measured and idiosyncrasies of the specific landscapes.

For our purposes, the choice of ordination technique used to derive the landscape structure space is not particularly relevant, as it will depend on the exact variance structure and other characteristics of the particular data set. For example, the appropriate technique will depend on whether is it reasonable to assume a linear relationship among variables—at least within the data space being represented. What is important here is recognizing that ordination techniques (albeit in different ways) seek to summarize redundancy among many variables, in this case landscape metrics, by combining them into a few new composite variables (e.g., principal components) that capture or explain the dominant gradients of variation in the full data set (McGarigal et al., 2000). Moreover, the derived composite variables are generally orthogonal; that is, they are completely independent of each other. Orthogonal axes insure that all dimensions of landscape structure space are independent, and facilitates quantitative interpretation of landscape trajectories.

Representing multivariate measurement of landscape structure as an m-dimensional landscape structure space greatly facilitates analysis when multiple metrics are measured simultaneously. The challenge of describing each landscape across all measured metrics is replaced by describing the relative locations and rates and directions of change in a much reduced landscape structure space. This makes for much more concise and meaningful analyses. Note, however, that the trajectory analysis described below can just as easily be conducted on the original p-dimensional landscape metric space, although the solution is not as concise. Ultimately, the choice of approach depends on how successfully the variance structure of the measured landscape metrics can be summarized by ordination. In the description that follows, we will presume the use of an ordination approach.

Location

Location is defined by the coordinates of the landscape on each axis of the landscape structure space. These coordinates are simply the values of the orthogonal axis scores (e.g., from PCA or NMDS). Location is defined by the position vector specifying the direction and distance of the landscape from the origin of the structure space. Vectors are represented as lowercase, non- italicized, non-bold letters. In simplest terms, the position vector describes the location of the landscape in the m-dimensional structure space. The position vector is most easily handled in component form, which decomposes its components along each axis of the structure space:

$$r_i = \mathrm{x}_{i1} + \mathrm{x}_{i2} + \cdots + \mathrm{x}_{im}$$

The coefficients x_{im} are the components of the position vector, defining the magnitude of displacement of the i^{th} landscape (r_i) from the origin along each of the m dimensions of the structure space. For example, consider a landscape r_i drawn from a large set of landscapes. This landscape has a unique landscape structure based on the computed values of many different landscape metrics. Suppose that PCA is used to summarize these landscape metrics into three orthogonal principal components representing the dominant independent landscape structure gradients across the entire set of landscapes: e.g., landscape contagion, diversity of patch types, and patch shape complexity. These principal components represent the axes of a three-dimensional landscape structure space. The focal landscape has a unique position or location along each of these principal component axes based on the computed values of the original metrics. The exact location along each axis is given by the corresponding principal component score. If, for example, the landscape happens to be more contagious than the average condition, it will have a positive score on the first axis. Furthermore, if the landscape happens to exhibit less diversity of patch types than the average condition, it will have a negative score on the second axis.

When one calculates the same standardized metrics for multiple landscapes, each landscape has a singular location in the landscape structure space. The matrix of landscape scores describes the relative locations of all sampled landscapes within the landscape structure space. We refer to this matrix as the location matrix; it contains a row for each landscape and a column for each landscape structure axis (e.g., principal component). Consequently, each row represents a position vector that gives the singular location of the corresponding landscape in the landscape structure space. Comparison of these locations is the basis for quantifying differences in structure among landscapes.

Multivariate analysis of landscape structure at single moments in time is ideal for quantifying relationships among landscapes at a given time, but is not capable of addressing multi-temporal phenomena. A key adaptation of the location matrix allows the direct inclusion of temporal patterns in the landscape structure space. In the basic location matrix, each landscape is a single row. The adaptation for multi-temporal analysis is to assign a separate row for each landscape at each date. For example, suppose that we measure landscape r_i at five equally spaced dates. This results in a matrix now with five rows, one landscape at each of the five dates, and

TABLE 7.1. Example of a multi-temporal matrix, where columns represent landscape metrics measured, and rows represent each landscape at each time.*

Landscape ∗ Date	Metric 1	Metric 2	Metric *m*
L1D1	5	7	...
L1D2	6	6	...
L1D3	8	7	...
L1D4	12	9	...
L1D5	16	12	...

*Thus, row 1 contains the landscape metrics measured for landscape 1 in time 1, and row 5 contains the metrics measured on this landscape in time 5.

columns for each derived landscape structure axis (Table 7.1). Plotting the location of landscape ri in this space at each time produces a trajectory (Fig. 7.1). It is the characteristics of this kind of trajectory, and its relationships with trajectories of other landscapes that are the focus of landscape trajectory analysis. This kind of multi-temporal analysis of landscapes appears to be quite rare in landscape ecology, although there are a few examples (e.g., Cushman and Wallin, 2000; Nonaka and Spies, 2005).

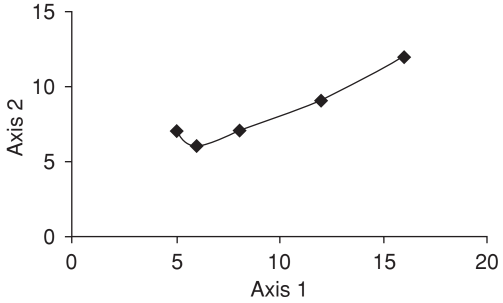

FIGURE 7.1. Example of a landscape trajectory; the path of one landscape in a two-dimensional landscape structure space across five sampling times. The dimensions of the space represent orthogonal landscape structure gradients derived by applying ordination to the full suite of measured landscape metrics.

Displacement

One of the simplest measurements of a landscape trajectory is the displacement of the landscape at any time period from initial conditions. Displacement is defined as the Euclidean distance between the location of the landscape at any time $j = t$ and its initial or starting location at $j = 0$:

$$\overline{\mathrm{d}_i} = \sqrt{\sum_{k=1}^{m} (x_{ijk} - x_0)^2}$$

where x_{ijk} is the score for landscape i (1...n) at time j (0, t) on axis k (1...m). Thus, displacement is simply the Euclidean distance between two points in m-dimensional landscape structure space.

Alternatively, displacement can also be expressed in component form:

$$\overline{\mathrm{d}_i} = \Delta \mathrm{x}_{i1} + \Delta \mathrm{x}_{i2} + \cdots + \Delta \mathrm{x}_{im}$$

where $\Delta \mathrm{x}_{ik}$ is the difference in scores between time $j = t$ and 0 for landscape i (1... n) on axis k (1... m). In this form, displacement is defined as the change in the landscape structure space along each dimension. This form facilitates interpretation because displacement can be described directly in relation to the particular aspects of landscape structure represented by each dimension.

Velocity

Velocity is a vector quantity consisting of both rate and direction of change in the landscape trajectory:

$$\overline{\mathrm{v}_i} = \Delta \mathrm{r}_i / \Delta t$$

where $\Delta \mathrm{r}_i$ is the change in position vector for the i^{th} landscape and Δt is the interval under consideration.

Velocity can also be expressed in component form:

$$\overline{\mathrm{v}_i} = (\Delta \mathrm{x}_{i1} + \Delta \mathrm{x}_{i2} + \cdots + \Delta \mathrm{x}_{im}) / \Delta t$$

where $\Delta \mathrm{x}_{ik}$ is the difference in scores for landscape i (1... n) on axis k (1... m) for that interval. In this form, velocity is defined as the rate of change along each dimension of the landscape structure space. As with displacement, this form facilitates interpretation because velocity can be described in relation to the particular aspects of landscape structure represented by each dimension.

Acceleration

In trajectory analysis, acceleration measures the rate and direction in the landscape structure space in which the velocity of a landscape is changing. Acceleration is also a vector quantity, with both magnitude and direction:

$$\overline{\mathrm{a}_i} = \Delta \mathrm{v}_i / \Delta t$$

where $\Delta \mathrm{v}_i$ is the change in velocity vector for the i^{th} landscape and Δt is the interval under consideration.

Acceleration can also be expressed in component form:

$$\overline{\mathrm{a}_i} = (\Delta \mathrm{x}_{i1} + \Delta \mathrm{x}_{i2} + \cdots + \Delta \mathrm{x}_{im}) / \Delta \mathrm{t}^2$$

In this form, acceleration is defined as the rate of change in velocity along each dimension of the landscape structure space. As with the other trajectory measures, this form facilitates interpretation because acceleration can be described in relation to the particular aspects of landscape structure represented by each dimension.

Divergence

Comparing the trajectories of multiple landscapes, or of the same landscape under different scenarios, provides a means to quantify differences between trajectories. Divergence is defined as the Euclidean distance between the location of different landscapes at the same point in time:

$$\overline{g_j} = \sqrt{\sum_{k=1}^{m} (x_{ajk} - x_{bjk})^2}$$

where x_{ijk} is the score for landscape i (a,b) at time j (0. . . t) on axis k (1. . . m). Like displacement, this is simply the Pythagorean theorem applied to m dimensions, the difference being that here the distance is between two different trajectories at the same point in time, instead of the distance a single trajectory has moved away from the starting point after any time period.

Alternatively, divergence can also be expressed in component form:

$$\overline{g_j} = \Delta x_{j1} + \Delta x_{j2} + \cdots + \Delta x_{jm}$$

where Δx_{jk} is the difference in scores between any two landscapes at time j (0. . . t) on axis k (1. . . m). In this form, divergence is defined as the difference in the landscape structure space along each dimension.

7.2. Demonstration and Application

In this section, we provide an example of landscape trajectory analysis. The example is based on simulating landscape change and resulting changes in American marten (*Martes americana*) habitat in a 40,000 ha landscape in the San Juan Mountains of Colorado under four different timber harvest scenarios. The study area is described in greater detail elsewhere (Blair, 1996; McGarigal et al., 2001; Romme et al., 2002).

7.2.1. Methods

Landscape Simulation

For our purpose, we classified the landscape at a spatial resolution of 25 m into a variety of well-established cover types and seral stages, which provided a useful model of landscape structure sufficient for assessing marten habitat. We used the RMLands simulation model (Fig. 7.2) (http://www.umass.edu/landeco/research/rmlands/rmlands.html) to simulate four different timber harvest scenarios representing the combinations of a two-way factorial of cutting pattern (dispersed or aggregated clearcutting) and rotation length (200- or 300-year rotation). In all scenarios, harvesting was restricted to certain cover types and seral stages. Under dispersed cutting, 4–18-ha harvest units were maximally dispersed in a staggered-setting fashion; whereas, under aggregated cutting, harvest units were

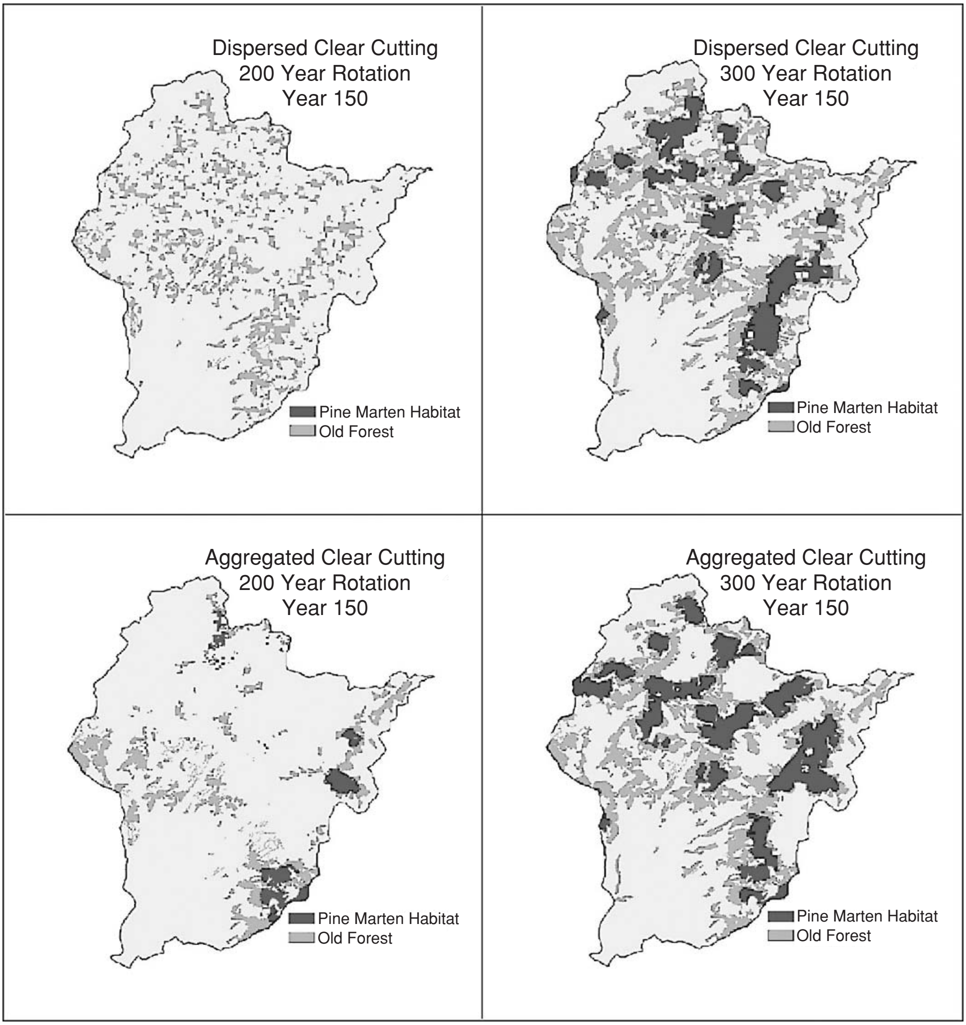

FIGURE 7.2. The four simulated timber harvest scenarios compose a combination of two levels of cutting pattern (aggregated and dispersed), and two-levels of rotation length (200 and 300 years). Shown here are the configurations of American marten habitat (and "old forest") after 150 years of a single simulation.

clumped into larger, contiguous blocks. Under short- and long-rotation scenarios, the intensity of timber harvest (i.e., total area harvested per time step) was adjusted accordingly. The model operates with a 10-year time step and produces an output of landscape condition (i.e., distribution of cover types and seral stages) at each step. Each simulation consisted of a 200–300-year period of disturbance and succession, depending on the rotation period of the scenario, and was replicated ten times. Additional details of the model parameterization are beyond the scope of this chapter and are not essential to our purpose. Under each scenario, disturbances and succession were implemented as stochastic processes in an attempt to mimic real-world patterns of disturbance and succession. Nevertheless, we made a number of simplifying assumptions (e.g., clearcutting as the only disturbance) to better illustrate habitat fragmentation differences among scenarios.

American Marten Habitat

We assessed marten habitat capability at each time step from each replicate run under each scenario based on the output from the landscape simulation. Habitat capability was defined as the ability of a location and its surrounding neighborhood to provide conditions important to survival and reproduction (sensu McComb et al., 2002) We applied a spatially-explicit, multi-scale marten habitat capability model (HCM) to assign a habitat capability index (HCI) value to each grid cell. The HCM was based on semi-quantitative information on marten habitat-associations, spatial attributes of marten habitat derived from local and regional syntheses of habitat-use studies, and expert opinion. In addition, the HCM was reviewed by several wildlife biologists with expertise on marten (Crist, 2002).

Although the details of the HCI model are not presented here, each cell was assigned a value between 0 (low value) and 1 (high value) based on the local composition (e.g., cover type, seral stage) and context (e.g., distance from edge) of each grid cell and the amount and spatial configuration (i.e., fragmentation) of suitable local habitat within a window scaled to the average home range size of the species (250 ha). Thus, each cell was given a habitat capability score that indicated its likelihood of supporting a pine marten. For our purpose, we classified HCI scores into two classes representing habitat (HCI $\geq .7$) and non-habitat (HCI $< .7$). Here, we are interested in analyzing trajectories of change in the extent and fragmentation of capable habitat under the different timber harvest scenarios.

Landscape Trajectory Analysis

We used FRAGSTATS (McGarigal et al., 2002) to compute 31 landscape metrics (Table 7.2) describing the area and configuration of marten habitat at each time step for each replicate run under each scenario. Because of partial redundancies among landscape metrics, we used PCA to transform the 31-dimension landscape metric space into a set of four uncorrelated gradients of landscape structure. There is some debate as to the most appropriate way of combining multiple landscape gradients into orthogonal axes, as there are frequently non-linear relationships among the constituent metrics (Neel et al., 2004). Some researchers have advocated using NMDS because it replaces the linearity assumption with the apparently less severe assumption of monotonicity. However, many metrics have known non-monotonic relationships (such as Edge Density to Class Area). In our own work, we have found that PCA analysis produced more interpretable gradients than NMDS, and that these gradients were qualitatively identical to those produced when the data were corrected for non-linear relationships. This may have been the result of sampling over relatively short landscape structure gradients where the problems of non-linearity are less severe. In the case considered here, we found PCA to produce meaningful axes consistent with our intuitive expectations. PCA was conducted

TABLE 7.2. Landscape metrics included in the analysis.*,[a]

	Acronym	Metric name
1	AI	Aggregation Index
2	AREA_AM	Area-Weighted Mean Patch Size
3	AREA_CV	Patch Size Coefficient of Variation
4	CAI_AM	Area-Weighted Mean Core Area Index
5	CAI_CV	Core Area Index Coefficient of Variation
6	CLUMPY	Clumpiness Index
7	COHESION	Patch Cohesion Index
8	CONNECT	Connectance Index
9	CONTIG_AM	Area-Weighted Mean Contiguity Index
10	CONTIG_CV	Contiguity Index Coefficient of Variation
11	CORE_AM	Area-Weighted Mean Core Area
12	CORE_CV	Core Area Coefficient of Variation
13	CPLAND	Core Area Percent of Landscape
14	DCAD	Disjunct Core Area Density
15	DIVISION	Landscape Division Index
16	ED	Edge Density
17	ENN_AM	Area-Weighted Mean Euclidean Nearest Neighbor Distance
18	ENN_CV	Euclidean Nearest Neighbor Coefficient of Variation
19	FRAC_AM	Area-Weighted Mean Fractal Dimension
20	FRAC_CV	Fractal Dimension Coefficient of Variation
21	GYRATE_AM	Area-Weighted Mean Radius of Gyration (Correlation Length)
22	GYRATE_CV	Radius of Gyration Coefficient of Variatoin
23	LPI	Largest Patch Index
24	NLSI	Normalized Landscape Shape Index
25	PD	Patch Density
26	PLAND	Class Percentage of Landscape
27	PROX_AM	Area-Weighted Mean Proximity Index
28	PROX_CV	Proximity Index Coefficient of Variation
29	SHAPE_ AM	Area-Weighted Mean Shape Index
30	SHAPE_ CV	Shape Index Coefficient of Variation
31	SPLIT	Splitting Index

*All metrics are class-level metrics describing the spatial properties of the mosaic of American marten habitat patches.

[a] Please refer to the FRAGSTATS website (www.umass.edu/landeco/research/fragstats/fragstats.html) for information on the definition and calculation of these metrics.

on the correlation matrix and included all time steps for all replicate runs under all scenarios. Thus, the landscape structure space encompassed the complete range of realized landscape structures. To facilitate trajectory analysis, we averaged over all runs (replicates) for each PCA factor score at each time step for each scenario. This provided a single value or score on each landscape structure axis (principal component) at each time step for each scenario.

Based on the multi-temporal location matrix, we computed the displacement, divergence, velocity, and acceleration of each scenario across the 200- or 300-year simulation period. For the purposes here, we limited the trajectory analysis to the component form of each measurement (i.e., where the trajectory is evaluated separately for each dimension). In addition, to facilitate illustration we restricted the trajectory analysis to the first 180 years of each simulation and the first two dimensions of the landscape structure space. Analysis was limited to the first 180 years because under one of the scenarios predicted marten habitat was entirely eliminated after year 180 making PCA results undefined. Plotting the trajectory of landscape change in the first two dimensions helps visualize the rates and patterns of change among the four scenarios with regard to the measured landscape metrics.

7.2.2. Results

Multi-Temporal Prinicipal Components Analysis

Nearly 80% of the variance among the 31 landscape metrics was explained by the first four axes (Table 7.3). We interpreted the axes based on the factor pattern (McGarigal et al., 2000; Table 7.3) as follows:

- Axis 1 is a gradient in marten *habitat extent*; landscapes characterized by large, extensive (i.e., far-reaching) and geometrically complex patches of habitat, in which a single patch may dominate the distribution, lie on one end of the gradient, while landscapes with little or no habitat lie on the opposite end.

TABLE 7.3. Multi-temporal principal components analysis of American marten habitat area and configuration under four simulated timber harvest scenarios in a 40,000-ha landscape in Colorado*

Axis	Eigenvalue (cumulative % variance)	Landscape metric	Factor loading
Axis 1	15.5 (49.7%)	AREA_AM	0.96
		LPI	0.96
		CORE_AM	0.95
		GYRATE_AM	0.95
		SHAPE_AM	0.95
		CPLAND	0.91
		SHAPE_CV	0.90
		PLAND	0.90
		FRAC_AM	0.88
		ED	0.80
		GYRATE_CV	0.78
Axis 2	3.93 (62.3%)	PD	0.93
		DCAD	0.90
Axis 3	3.36 (73.2%)	CLUMPY	0.95
		AI	0.93
		CONTIG_AM	0.92
		COHESION	0.87
		CAI_AM	0.83
Axis 4	1.89 (79.3%)	CAI_CV	0.88
		CONTIG_CV	0.76

*Eigenvalues represent the variance associated with each axis (i.e., variance in principal component scores on that axis). Cumulative % variance is the cumulative percentage of the total variance in the data set explained by the first 1–4 axes. Factor loadings are the correlation coefficients between the landscape metrics and the principal axes, after varimax rotation. Only loadings greater than 0.7 are shown.

- Axis 2 is a gradient in marten *habitat subdivision*; landscapes characterized by many disjunct patches of habitat lie on one end of the gradient, while landscapes with comparatively few patches lie on the opposite end. Given that this axis is orthogonal to axis 1, we can interpret this axis as a gradient in habitat configuration independent of habitat extent. In other words, landscapes on the positive end of the gradient possess more habitat patches compared to other landscapes with the same habitat extent, and conversely, landscapes on the negative end of the gradient possess fewer habitat patches compared to other landscapes with the same habitat extent.
- Axis 3 is a gradient in marten *habitat aggregation*; landscapes characterized by clumpy distributions of habitat lie on one end of the gradient, while landscapes with disaggregated distributions lie on the opposite end. Again, given orthogonality among axes, we can interpret this axis as a gradient of clumpiness independent of habitat extent.
- Axis 4 is a gradient in *variability of patch size and compaction*; landscapes characterized by high variability in habitat patch size and shape lie on one end of the gradient, while landscapes with relatively homogenous patches sizes and shapes lie on the opposite end. Again, we can interpret this axis as one of patch variability independent of overall habitat extent.

There were clear differences among the four scenarios in their trajectories of landscape structure (Fig. 7.3). While the overall patterns of change in marten

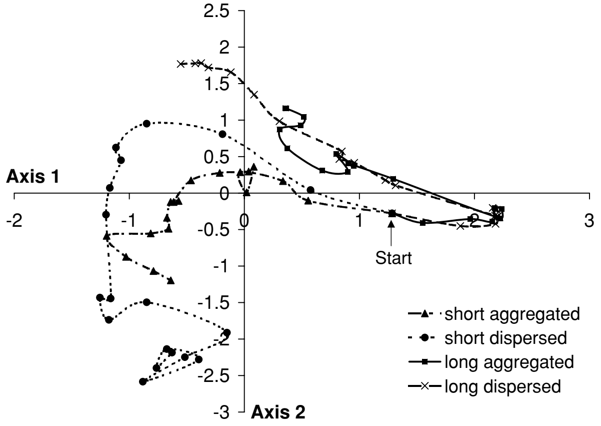

FIGURE 7.3. Landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here are trajectories in a two-dimensional landscape structure space defined by the first two axes of multi-temporal principal components analysis. Axis 1 is a multivariate gradient dominated by area of the landscape occupied by predicted marten habitat. As you move from right to left the predicted area of marten habitat decreases. Axis 2 is a multivariate gradient dominated by the density of patches of predicted marten habitat. As you move from top to bottom the density of patches of marten habitat decreases. Thus, the lower left quadrant, where both of the short cutting rotation scenarios end, is an area of landscape structure space represented by low area and low density of habitat patches.

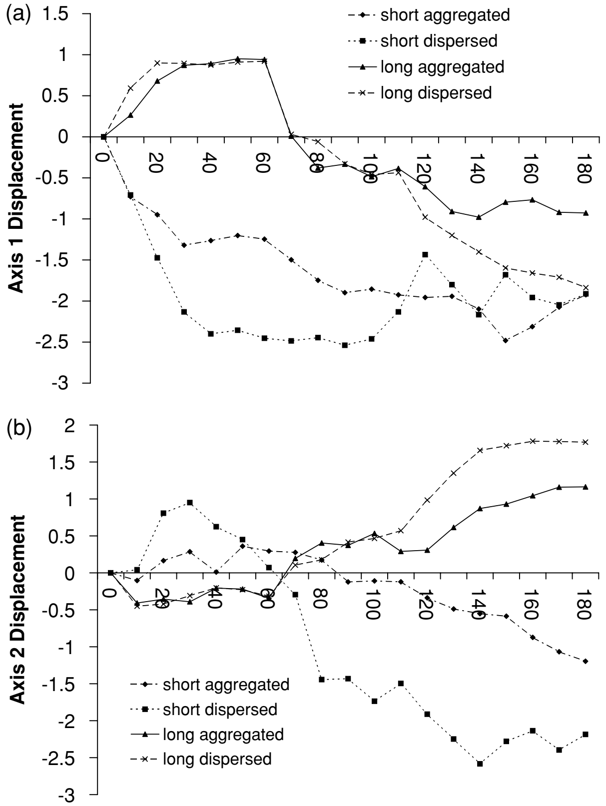

FIGURE 7.4. Displacement of landscape trajectories from initial conditions in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here is displacement along axis 1 (a), representing the magnitude of change in habitat extent, and displacement along axis 2 (b), representing the magnitude of change in habitat patch density. Positive displacement indicates a net increase along the axis, while a negative displacement indicates a net decrease. In this example, the two short-rotation scenarios drop farther and faster on the first axis than the two long-rotation scenarios, indicating that the short-rotation scenarios result in greater habitat loss; although, note that the long rotation dispersed scenario ultimately achieves the same total negative displacement. Overall, the long rotation aggregated cutting scenario results in the smallest reduction in the area of the landscape occupied by marten habitat.

habitat are evident in Figure 7.3, the differences are more thoroughly examined by considering their displacement, divergence, velocity, and acceleration, as follows:

Displacement

Displacement (the Euclidean distance between the location of the landscape and its origin at any moment in time) of the trajectories illustrates the magnitude and nature of marten habitat change under each scenario (Fig. 7.4). Both 200-year rotation scenarios move rapidly toward the negative on axis 1, indicating a rapid decrease in the extent of marten habitat as forest is harvested (Fig. 7.4a). Both of these scenarios initially increase on axis 2, then decrease (Fig. 7.4b). Axis 2 is a patch density gradient and the initial increase is a result of fragmentation of marten habitat into disjuct patches. The decrease that follows reflects the elimination of habitat fragments as harvesting continues. The two 300-year rotation scenarios, in contrast, initially move toward the positive end of axis 1, indicating short-term increase in marten habitat. This initial increase is due to a rather large proportion of the landscape existing in mid-seral stages at the start of the simulation and the rate of in-growth to late-seral forest temporarily exceeding the harvest rate (Fig. 7.4a). However, after approximately 60 years these two scenarios both move strongly negatively on axis 1, indicating reduction in the extent of marten habitat. On axis 2 these two scenarios show a directional increase in patch density throughout the simulation period (Fig. 7.4b). This indicates that while habitat area is being reduced and fragmented in the 300-year rotation scenarios, the remaining fragments are not being eliminated and are accumulating at increasing densities.

Divergence

Divergence of the trajectories (the Euclidean distance between the location of different landscapes at the same point in time) illustrates differences among scenarios at any time in terms of the magnitude and nature of their impacts on marten habitat (Fig. 7.5). The 200- and 300-year rotation scenarios, regardless of cutting pattern, diverge rapidly on axis 1 over the first 40 years, reaching a peak in divergence at 60 years (Fig. 7.5a). This indicates large differences in how the short and long rotations impact the amount of marten habitat over the first half-century of harvest. The two 200-year rotation scenarios differ substantially from each other in the rate and extent to which they result in reductions of marten habitat. The divergence between these two scenarios rises to a peak at 40 years and begins to decrease after 60 years. This indicates that under a 200-year rotation, cutting pattern substantially interacts with rotation length such that habitat area is reduced substantially faster in the dispersed cutting scenario, but that eventually both cutting patterns result in similar levels of habitat loss. The initial divergence results from the nature of the habitat model, which predicts that old forest near edges, which is substantially greater under the dispersed cutting pattern, will have reduced habitat capacity. Conversely, the two 300-year rotation scenarios diverge very little from each other over the first 110 years. However, after 110 years we see some divergence, indicating that cutting pattern does influence habitat amount in the longer rotation, but that its influence appears relatively late in the simulation period and to a lesser degree than in the shorter rotations. As the simulation period approaches 200 years, the divergence among most scenarios on axis 1 decreases, indicating a convergence in landscape structure among scenarios to a condition with low levels of marten habitat area. The exception is the 300-year aggregated cutting scenario. The combination of relatively low rate of habitat loss and low level of habitat fragmentation in this scenario result in substantially less total habitat loss than occurs in the other

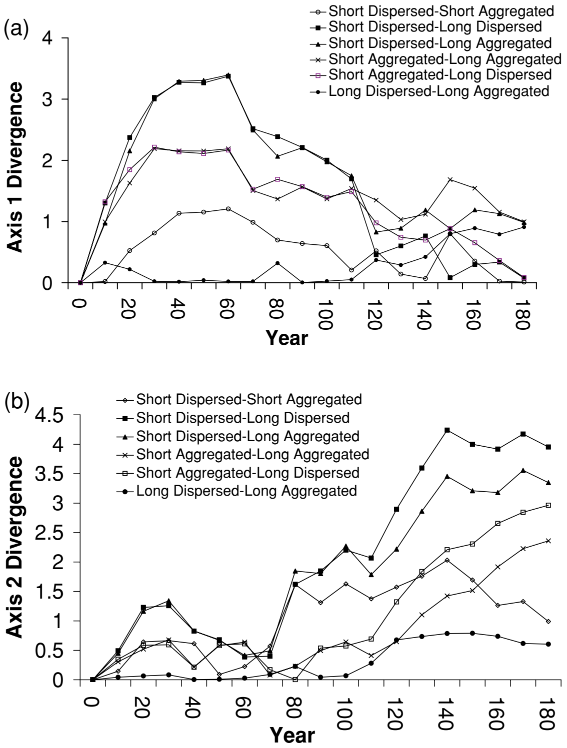

FIGURE 7.5. Divergence of landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here is divergence along axis 1 (a), representing the magnitude of change in habitat extent, and divergence along axis 2 (b), representing the magnitude of change in habitat patch density. Divergence measures the Euclidean distance between each pair of scenarios at each time step. Scenarios that have a large divergence differ greatly in the attribute of landscape structured measured on that axis. For example, the short dispersed and long aggregated scenarios diverge rapidly and relatively greatly along axis 1, and then slowly converge toward the end of the simulation period.

three scenarios, as illustrated by its final location on axis 1 relative to the other scenarios in Figure 7.3.

The trajectories of divergence along axis 2 are substantially different from those on axis 1 (Fig. 7.5b). In contrast to axis 1, divergence among scenarios on axis 2 shows a bimodal pattern of both short-term and long-term divergence. Initially, the 300-year rotation scenarios increase slowly on axis 2, while the 200 year scenarios remain relatively constant (Fig. 7.3), leading to the short-term pattern of divergence. From year 40 to 70 divergence among scenarios on axis 2 decreases as the 200-year rotation scenarios result in increasing patch density. After year 70 there is a rapid divergence among scenarios, as the two 200-year rotation scenarios experience rapidly decreasing patch density as the remaining fragments of marten habitat are eliminated.

Velocity

Velocity is a measure of the rate and direction of change in marten habitat under each scenario (Fig. 7.6). For illustration, we focus only on the 200-year rotation, dispersed-cutting scenario. Under this scenario, there is an initial rapid decrease in the area of marten habitat, as indicated by the large negative velocity on axis 1 over years 10–40 (Fig. 7.6a). Simultaneously, there is a substantial increase in rate and direction of change of marten habitat along axis 2, which reflects the increase in patch density as well-connected, large patches of habitat are broken into smaller and more isolated fragments (Fig. 7.6b). The combination of these two velocities provides a strong quantitative picture of the simultaneous habitat loss and fragmentation that is occurring in the landscape over the first 50 years of the simulation. From year 50 to100 there is a substantially different pattern of

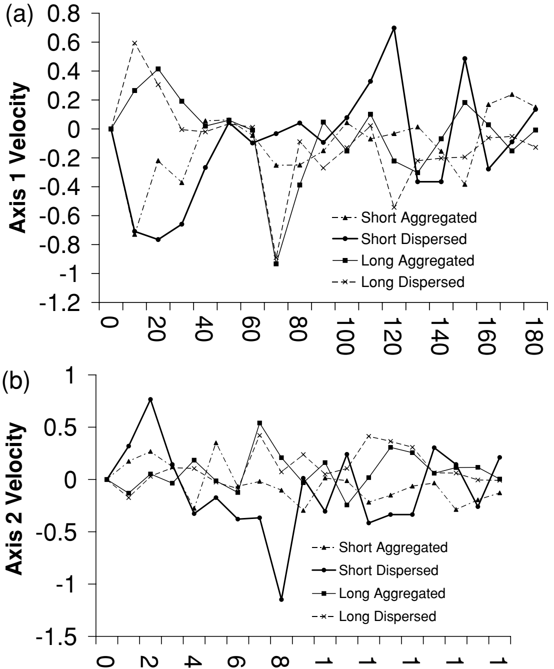

FIGURE 7.6. Velocity of landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here is velocity along axis 1(a), representing the magnitude of change in habitat extent, and velocity along axis 2 (b), representing the magnitude of change in habitat patch density. As an example, the 200-year rotation, dispersed-cutting scenario shows a large negative velocity along axis 1 over the first 50 years of the simulation period, indicating a rapid decrease in the extent of marten habitat during this period. Along axis 2, this scenario shows an initial positive velocity corresponding to increasing patch density as marten habitat is being fragmented, followed by a period of negative velocity corresponding to the rapid reduction in patch density as remaining patches of habitat are lost to clear-cutting.

velocity along the two axes, with virtually zero velocity on axis 1 and negative velocity on axis 2 reaching a peak at year 80. This pattern of velocity indicates a phase in which the amount of habitat has equilibrated at a low percent cover while patch density is rapidly decreasing as small habitat fragments are eliminated. From year 100 to year 180 there are large shifts in velocity from positive to negative on both axes, gradually attenuating toward equilibrium. This third period reflects an approach to a dynamic equilibrium of habitat area and configuration, in which there is very low habitat area and very few habitat fragments.

Acceleration

Acceleration is a measure of the rate and direction of the change in velocity across the length of the simulation (Fig. 7.7). The acceleration at each time period in

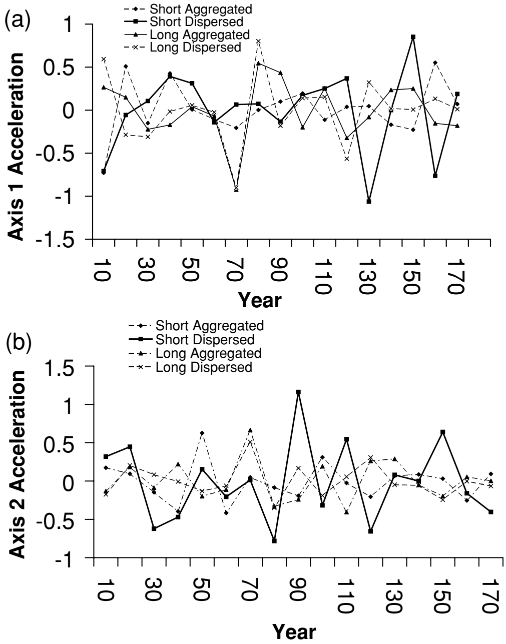

FIGURE 7.7. Acceleration of landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40, 000-ha landscape in Colorado. Shown here is acceleration along axis 1 (a), representing the magnitude of change in habitat extent, and acceleration along axis 2 (b), representing the magnitude of change in habitat patch density. As an example, the 200-year rotation, dispersed-cutting scenario shows an initial negative acceleration along axis 1, indicating increasing rate of habitat loss, followed by a period of positive acceleration, corresponding to a slowing of habitat loss as marten habitat is reduced to very low area. Along axis 2, the initial positive acceleration reflects initial increase in the rate of fragmentation of marten habitat, and the following period of negative acceleration corresponds to a reduction in patch density as remaining habitat is eliminated.

Figure 7.7 is the slope of the line segment between the previous and current time period in Figure 7.6. For illustration purposes, we will again focus only on the 200-year rotation, dispersed-cutting scenario. Under this scenario, there is initial rapid negative acceleration on axis 1, and positive acceleration on axis 2 in the first phase of landscape change in which habitat is being rapidly reduced in area and broken into fragments. The direction of acceleration reverses on both axes from year 30 to 50, indicating the transition into the second phase of the trajectory in which habitat area changes little and the patch density decreases rapidly. This reversal of acceleration is diagnostic and quantifies both the magnitude and direction of the change in landscape velocity.

7.3. Discussion

Trajectories of change in landscape structure space provide a direct means to integrate temporal variability into spatial analyses. In our example, trajectory analysis enabled us to quantitatively compare the predicted impacts of several alternative disturbance regimes on the extent and configuration of American marten habitat continuously through time, with respect to multiple dimensions of landscape structure. Our results showed substantial differences both in the rates and the patterns of habitat loss and fragmentation resulting from these different timber harvest scenarios. More specifically, trajectory analysis allowed us to assess the displacement, divergence, velocity, and acceleration of landscape change in marten habitat under these scenarios.

Comparing the *displacement* of each scenario from inital conditions over time provided a means to evaluate the nature and extent of change from the original state. Computing the *divergence* among scenarios over time provided an objective measure of the relative differences among scenarios in their impacts on marten habitat area and fragmentation. In our example, we compared displacement and divergence with respect to habitat amount and habitat patch density, as reflected by the first two axes of a multi-temporal principal components analysis. The temporal patterns of displacement and divergence among scenarios revealed some interesting findings. First, cutting pattern may have little consequence on marten habitat area over the long term if the cutting intensity is high enough. Both short-rotation scenarios result in substantial and comparable habitat loss after 180 years, regardless of cutting pattern, as evidenced by similar displacement (Fig. 7.4a) and minimal divergence (Fig. 7.5a) on axis 1. Second, cutting pattern and harvest intensity may interact to affect marten habitat patterns. For example, in contrast to the short-rotation scenarios (as just noted), the magnitude of habitat loss under the long-rotation scenarios after 180 years depended strongly on the cutting pattern, as evidenced by their differences in displacement (Fig. 7.4a) and large divergence (Fig. 7.5a) on axis 1. Lastly, there may be substantial time lags in marten habitat response to changes in disturbance regimes, suggesting that short-term changes in habitat patterns could lead to erroneous conclusions about the long-term consequences of alternative disturbance regimes. For example, major displacement in habitat patch density (Fig. 7.4b) and divergence among scenarios (Fig. 7.5b) was not realized until at least 60–80 years of harvesting had elapsed. The most dramatic and potentially misleading time lags were evidenced as complete reversals in displacement direction after the initial several decades of harvesting (Fig. 7.4). Time lags of this nature demonstrate that landscapes may contain tremendous momentum that may take decades of active management to overcome.

With the measures of *displacement* and *divergence* in landscape structure space we have the means to quantify the impact of scenarios both with respect to initial conditions and relative to each other. These are the two comparisons most needed by landscape managers to provide information on the effects of land management alternatives. Also, quantifying *velocity* and *acceleration* through landscape structure space provides rigorous description of the rates and directions of changes in landscape structure. These measures facilitate quantitative comparison among scenarios and are critical to linking patterns of change to mechanistic drivers and in particular to revealing thresholds.

The topic of thresholds has received much interest in recent landscape ecology literature (Kareiva and Wennergren, 1995; With and Crist, 1995; Hill and Caswell, 1999; Jansson and Angelstam, 1999; Radford et al., 2005). A threshold is often defined in landscape ecology as a point where a measured phenomenon changes abruptly (Turner et al., 2001). There are three key parts of the definition: phenomena, change, and abruptness. The *phenomenon* may be a process or a pattern. The *change* can be in any measured variable that describes an attribute of the phenomenon. In practice one hopes to measure attributes that apply most directly to a causal relationship between pattern and process. Rigorous definition of a threshold will require careful consideration of the phenomenon, the attributes measured, and the criteria used to determine if a change in location or in velocity is sufficiently *abrupt* to be called a threshold. These are decisions which must be made by researchers on a case-by-case basis.

While there are no established methods for determining thresholds in landscape structure space, we suggest that thresholds could be defined using several different criteria. First, one could define thresholds based on a certain degree of observed change in landscape structure. The diagnostic characteristic in this definition is amount, or magnitude of *displacement* in landscape structure space. Second, one could define thresholds based on the rate and direction of landscape structure change. The diagnostic attribute in this definition is *velocity*. Peaks in velocity along any dimension of landscape structure space could define the location of a threshold because large velocities indicate rapid changes in landscape structure. In our example, significant peaks (or troughs) in velocity exist on the first two landscape structure axes for most scenarios at 70–80 years (Fig. 7.6), which coincides with the major changes in displacement and divergence among scenarios noted above. Third, one could define thresholds based on the *acceleration* of change in landscape structure space. As noted above, a key attribute of thresholds is abruptness. Abruptness in landscape trajectory analysis could be defined as a rapid change in the rate and direction of landscape change through structure space, which could be measured directly by acceleration. In our example, each scenario typically exhibited one or two disproportionately large peaks (or troughs) in acceleration which coincided with substantial changes in rate and direction of the trajectory (Fig. 7.7).

In conclusion, the trajectory analysis approach described here provides a powerful framework for integrating temporal variability into spatial analyses. Trajectory analysis is a flexible approach to quantify changes in location (displacement and divergence), velocity, and acceleration of landscapes in a multivariate landscape structure space. As such, trajectory analysis provides a rigorous, intuitive, and highly interpretable description of the interaction between disturbance, ecological process, spatial pattern and temporal variation.

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III

Temporally Focused Case Studies

8

Assessing Grouse Habitats in the Alps

The Complication of Small-Scale Spatiotemporal Variation in Rainfall Patterns

ILSE STORCH

Abstract. While spatial variation in the habitat has been widely addressed, temporal changes within these spatial patterns have received less attention. Yet, even subtle spatiotemporal variations in factors such as rain and snowfall amounts may have pronounced effects on habitat availability and quality and thus, species–habitat relationships. This complicates habitat evaluation studies for management and conservation planning that are rarely allowed more time than one or two field seasons. In this chapter, I illustrate limitations of "snapshot," i.e., single-year, habitat evaluation approaches caused by smaller-scale fluctuations in weather conditions that may lead to inappropriate management decisions, using the case example of grouse in the Alps. Capercaillie (*Tetrao urogallus*) are closely associated with old coniferous forest. Still, population abundances vary between sites and years without noticeable differences in the habitat. In a 2000 ha study area of the Bavarian Alps, changes in an annual (1992–2004) index of capercaillie abundance were best explained by rainfall during chick rearing. Early summer rainfall sums from 1961 to 1990 for 16 weather stations showed that a wet summer in one mountain range did not necessarily coincide with a wet summer elsewhere in the Bavarian Alps, independently of the geographical distance. Asynchrony of rainfall pattern in the Alps may result in a dynamic "temporal" source-sink metapopulation system, with vital rates, and thus, habitat quality, varying not only due to differences in local habitat structure, but changing over time. Weather-related population fluctuations operate at the scale of years, and may thus mask longer-term population trends related to habitat change caused by natural succession and human land use, that are more likely to operate at the scale of decades. The case example illustrates that standard "snapshot" habitat assessments, as they are typical in environmental impact studies, are insufficient to reliably assess habitat-population relationships because they ignore temporal variation that may have major consequences for population dynamics, and thus, for management and conservation planning.

8.1. Introduction

In conservation biology, habitat availability and quality are generally considered as the key to population persistence. Consequently, species–habitat relationships are commonly studied to provide a basis for land-use management and conservation planning (e.g., Morrison et al., 1992). Landscape ecology has taught wildlife managers that population rates such as reproduction, mortality, and survival may be discontinuous in space, i.e., vary across a landscape in response to spatial heterogeneity. Limited movement of individuals between sites and across landscapes will result in differences among local populations, and may lead to spatially explicit dynamics such as source-sink and metapopulation phenomena. It is now widely acknowledged that habitat concepts should include multiple spatial scales (Johnson, 1980; Bissonette, 1997; Storch, 2002b) because landscapes by definition are spatially heterogeneous and include various habitat types that each contain various resources.

While spatial variation in the habitat has been widely addressed, temporal variations within these spatial patterns have received less attention (Bissonette and Storch, 2002). Yet, changes in habitat availability and quality over time may have pronounced effects on population-habitat relationships. Ephemeral habitats such as ponds, mast seeding events, and rainfall in arid regions are among the more obvious examples for temporal resource changes. However, also more subtle spatiotemporal variations in abiotic factors such as rain and snowfall amounts may have pronounced effects on habitat availability and quality and thus, species–habitat relationships. This complicates habitat evaluation studies for management and conservation planning that are rarely allowed more time than a single field season: the "snapshot picture" drawn will not necessarily be representative for longer temporal extents.

Grouse in the Alps make good case examples to illustrate this problem. In black grouse (*Tetrao tetrix*) in the Bavarian Alps, winter habitat capacity largely depends on the availability of dwarf pine (*Pinus mug*o) and green alder (*Alnus viridis*) for winter food. Accessibility of these shrubs varies with snow conditions: a layer of several meters accumulates through the winter, and few feeding patches remain during maximum snow depth in March. In particularly snow-rich years, the area of accessible feeding habitat may be reduced to 10% of the availability in early winter (Zeitler, 2003). Thus, black grouse winter habitat capacity is highly variable both between and within years, and impossible to assess in a single field season. Also summer habitat capacity for grouse in the Alps varies with weather conditions. Particularly in the capercaillie (*Tetrao urogallus*), high chick mortality may occur in wet and cold conditions during the first 3 to 4 weeks after hatching (Marcström, 1960; Slagsvold and Grasaas, 1979; Wegge, 1980; Lindén, 1981; Moss, 1985; 2001). Annual variation in early summer weather conditions may cause marked short-term fluctuations in capercaillie population density, while climate change may lead to longer-term population trends (e.g., Schröder et al., 1982; Moss, 2001).

The capercaillie is well known as a habitat specialist closely associated with habitat structures typical of old boreal forests. A small set of variables has proved sufficient to describe its habitat preferences. Several capercaillie habitat models have been published that all infer habitat suitability from observed differences in population incidence and abundance (Picozzi et al., 1992; Schroth, 1992; Storch, 2002a; Graf et al., 2005). Because of the species' close habitat association, capercaillie habitat models typically show high predictive power: a habitat suitability index model for capercaillie in the Bavarian Alps explained $>90\%$ of the variation in capercaillie use of forest stands (Storch, 2002a) and $>50\%$ of the variation in capercaillie abundance at the scale of individual mountain ranges (Storch, 2002b). The question remains, how chick-rearing weather that operates at the scale of months, coupled with the close association of this habitat specialist to particular forest structures that depend on forestry operations and natural succession, processes that operate at scales spanning from years to decades, affect the dynamics of capercaillie populations in space and time.

In this chapter, I illustrate limitations of "snapshot," i.e., single-year, habitat evaluation approaches caused by smaller-scale fluctuations in weather conditions that may lead to inappropriate management action, using the case example of capercaillie in the Alps. First, I explore changes in capercaillie population abundance on a 50-km^2 study area in the Bavarian Alps, southernmost Germany, between 1992 and 2004 in relation to habitat suitability and early summer rainfall patterns. Second, I assess spatiotemporal variation in rainfall patterns across the Bavarian Alps to discuss implications for capercaillie metapopulation dynamics, and thus for monitoring and management planning.

8.2. Material and Methods

8.2.1. Study Area

The Alps have the widest distribution of capercaillie in central Europe. The species occurs throughout montane and subalpine forests, but population density varies locally. In the Bavarian Alps in southernmost Germany, the landscape is characterized by mountain ranges reaching elevations of 1,000–3,000 m and covering areas of typically 50–100 km^2, separated by farmland valleys at 600–900 m elevation and up to a few kilometers wide, and with treelines at 1,300–1,800 m. In this landscape, the distribution of capercaillie is spatially structured, with distinct local populations on separate mountain ranges (Storch, 2002a). Intensive forestry has influenced capercaillie habitats for more than 200 years (Klaus et al., 1989) and is considered a major driver influencing capercaillie abundance (Storch, 2001). The climate in the Bavarian Alps is moist and temperate, with mean annual temperatures of about 5°C, mean annual precipitation of 1,500–2,200 mm, wet summers, and snow-rich winters.

The Teisenberg study area is a 50-km^2 mountain range of the foothills of the Bavarian Alps, Germany (47°48'N, 12°47'O). Elevations vary between 700 m and 1,300 m. Forests of Norway spruce (*Picea abies*) (70%) mixed with fir (*Abies alba*) (10%) and beech (*Fagus sylvatica*) (15%) cover more than 90% of the area.

Stands of varying ages form a mosaic with patches of 1–100 ha. On Teisenberg, capercaillie habitat-relationships have been studied since the late 1980s. Broods hatch between early June and mid-July (Storch, 1994), similar to other parts of the Bavarian Alps (personal observation; A. Zeitler, personal communication). Thus, chick survival during the critical first three weeks may be most severely affected by weather in June and in July. As an index to weather conditions during the early chick stage of capercaillie in the Bavarian Alps, I obtained monthly rainfall sums for the years 1961–2005 for a weather station (elevation 830 m) on Teisenberg and for 1961–1990 for 15 other weather stations located across the Bavarian Alps.

8.2.2. Capercaillie Population Abundance

In the central 2000 ha of Teisenberg, indirect signs of capercaillie such as feathers, feces, tracks, or dust baths were recorded in the summers of 1992, 1997, and 1999–2004 to obtain an index of population abundance. Field work was done during 3 to 4 weeks in July and August because in summer, capercaillie males do not aggregate at leks as they do from late autumn through spring, and thus, the bird's range use is not affected by social attraction (Storch, 1995). During that time of summer, broods are still together and the presence of chick and hen signs is recorded together; therefore, the population index reflects the spring population density, i.e., before breeding.

In 1992, a total of 735 random plots were distributed over the 2,000-ha study area; in 1997, a regular grid of sample plots spaced 200 m apart was established, and a total of 467 plots was sampled each year (1997 and 1999–2004). Sample plots in all years were 5 m in radius, and presence or absence of capercaillie signs was recorded during a standardized 15-min search in each plot. The percentage of sample plots with signs was used as an annual index of capercaillie abundance on Teisenberg. I assumed a linear relationship between the frequency of signs and capercaillie abundance.

8.2.3. Capercaillie Habitat Evaluation

In 1992, 1997, and 2002, the same sample points used for recording capercaillie sign were also used for habitat evaluation. Around these points, a set of habitat variables (successional stage, canopy closure, tree species composition, composition and height of the ground vegetation, steepness of slope; see Storch, 2002a, for details) was recorded within a 20-m-radius sample plot to calculate habitat suitability index (HSI) scores according to the habitat model described in Storch (2002a). HSI scores for all sample plots within the study area were aggregated into mean HSI scores as a basis to assess changes in overall habitat suitability between 1992 and 2002.

8.2.4. Analyses

Data were analyzed using SPSS 13.0. I used stepwise linear regression analyses to assess the relation between the capercaillie population index (dependent variable) and early summer rainfall data, using June and July rainfall, respectively, of the same year (year t), and of 1, 2, and 3 years back (years t-1 to t-3) as explanatory variables. To account for autocorrelation in the capercaillie data, I also included the population indices of the previous two years (t-1 and t-2) as explanatory variables. To assess spatiotemporal correlation of rainfall patterns across the Bavarian Alps, I used 30 years (1961–1990) of June and July monthly rainfall sums from 16 weather stations. I calculated bivariate correlation coefficients between all weather stations, and plotted the resulting 120 correlation coefficients against the Euclidian distances between these 16 stations.

8.3. Results

For the study period 1992–2004, the annual frequencies of capercaillie signs on Teisenberg suggested fluctuations in population abundance in an order of 50% (Fig. 8.1). The population apparently had declined between the early and mid 1990s and then increased after 1999. During the same time, changes in overall habitat suitability scores were not significant (Fig. 8.2) and did not parallel the observed changes in capercaillie abundance. Thus, habitat change offered no explanation for the short-term fluctuations in capercaillie abundance.

Early summer rainfall patterns on Teisenberg had remained unchanged since the 1960s (Fig. 8.3), and there was no significant trend in the rainfall sums for either June ($r = -0.09$, $p = 0.54$) or July ($r = 0.07$, $p = 0.63$). Total early summer rainfall (June plus July) varied greatly between years (range 250–560 mm;

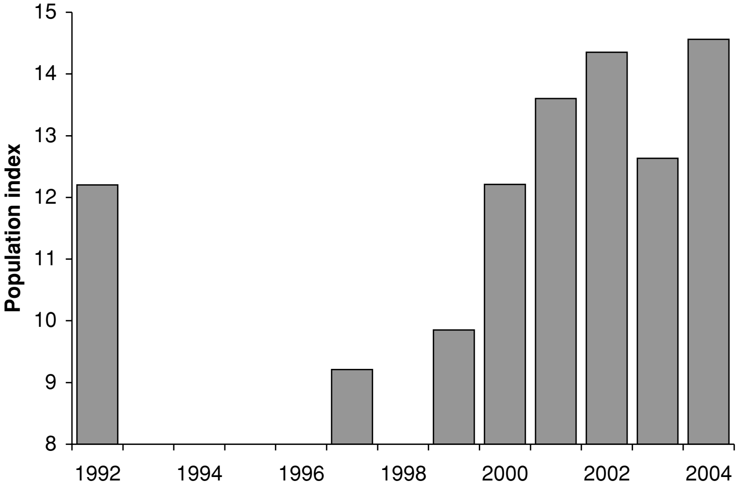

FIGURE 8.1. Abundance of capercaillie on Teisenberg between 1992 and 2004, as indicated by the proportion of sample plots with capercaillie signs (population index) distributed over a 2000 ha study area. For years 1993–96 and 1998, no data were available.

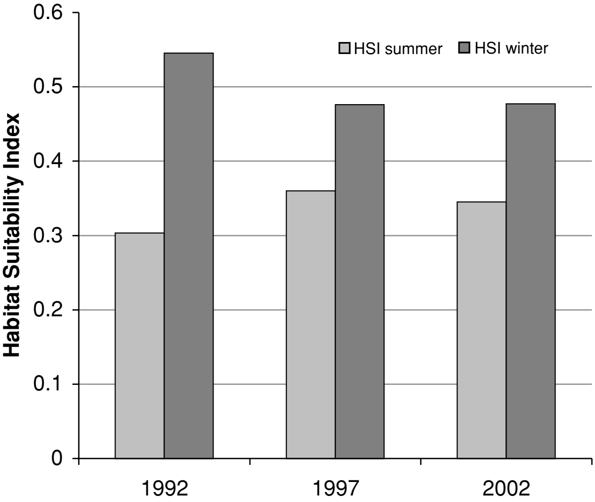

FIGURE 8.2. Mean capercaillie Habitat Suitability Index scores (HSI) for the 2000 ha study area on Teisenberg, Bavarian Alps, as recorded in the years 1992, 1997, and 2002.

mean = 401, SD = 96 mm) and within years, June and July rainfall sums were not significantly correlated (r = −0.208, $p = 0.17$).

Regression analysis suggested that early summer rainfall played a major role in capercaillie population dynamics. July rainfall in the previous year (t-1) significantly affected the population index ($R^2 = 0.77$, $p = 0.009$; Fig. 8.4), whereas all other variables tested (June rainfall years t to t-3; July rainfall years t, t-2, and t-3;

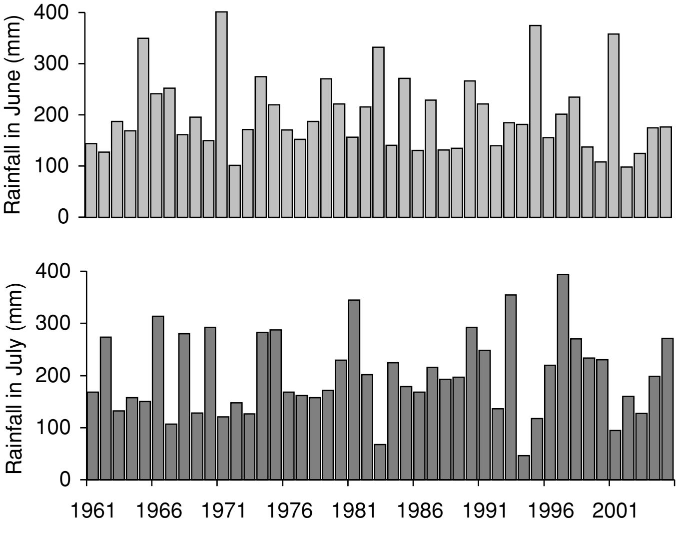

FIGURE 8.3. Monthly rainfall sums for the months June and July 1961–2005, as recorded at the Anger-Stoissberg weather station on Teisenberg, Bavarian Alps, at 830 m elevation.

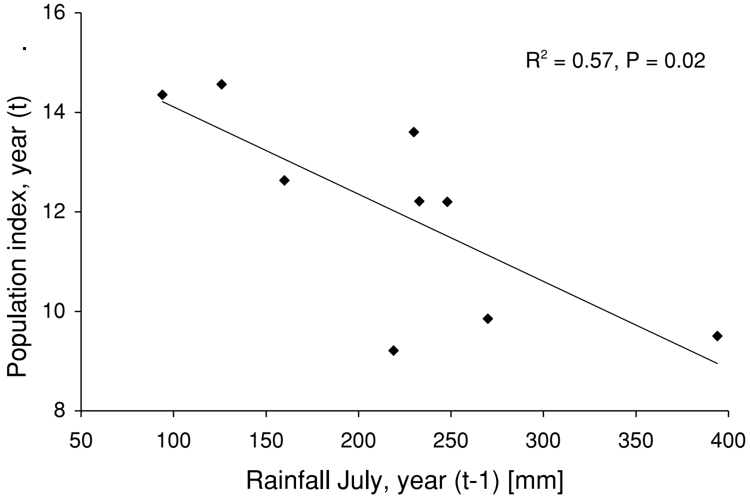

FIGURE 8.4. Relationship between an index of capercaillie abundance (population index) and the amount of rainfall in July of the previous year (year t-1) on Teisenberg, Bavarian Alps, years 1992, 1997, 1999–2004.

capercaillie population index years t-1 and t-2) showed no significant effects. Because capercaillie live for several years, longer time lags may be involved; I was unable to assess those effects because my study was conducted over a relatively short time period.

If rainfall affects capercaillie abundance, spatial correlation of rainfall patterns may lead to spatially correlated population dynamics. Therefore, I explored July rainfall amounts for all 16 weather stations within the Bavarian Alps for which long-term data (1961–1990) were available. Rainfall sums at individual stations were highly variable and a wet summer at one station did not necessarily coincide with a wet summer elsewhere in the Bavarian Alps: July rainfall sums were only weakly correlated among the 16 weather stations (mean r = 0.45; SD = 0.27; N = 120). Distances among these stations varied between 5 and 211 km (mean = 89 km; SD = 56 km), and one might expect closer correlations of rainfall amounts between neighboring than between distant sites. However, bivariate correlation coefficients for July rainfall, 1961–1990, for all 120 combinations of the 16 weather stations showed no significant relationship with the geographic distances between stations (Fig. 8.5). Thus, extreme years for capercaillie chick survival were not closely correlated in time and space across the Bavarian Alps.

8.4. Discussion

The study clearly indicates that capercaillie abundance on Teisenberg fluctuated on an order of 50% between the early 1990s and the mid-2000s. Frequencies of indirect signs certainly are not the same as more exact direct counts, and may

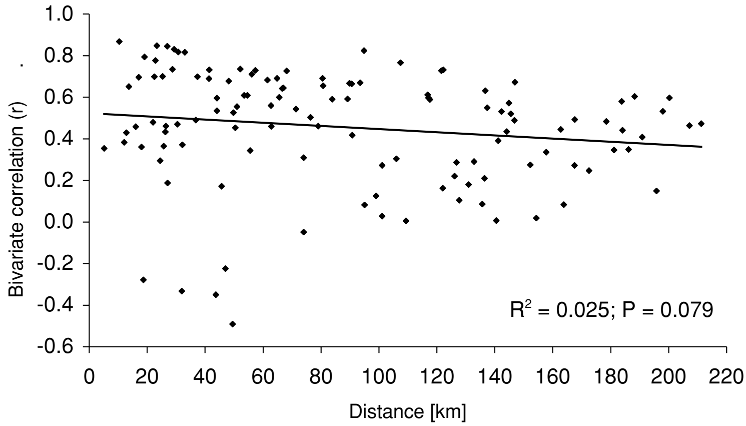

FIGURE 8.5. Spatial pattern of July rainfall sums across the Bavarian Alps, as based on bivariate correlation coefficients for all 120 combinations of 16 weather stations and 30 years 1961–1991, plotted against the geographical distance (km) between stations. Coefficients were not significantly correlated ($R^2 = 0.0254$, $p = 0.079$) with the distances between stations.

contain sampling biases. Yet, this is the only recent time-series available for any capercaillie population in the Bavarian Alps, and the data were collected under a standardized methodology.

Based on current knowledge of capercaillie ecology, four factors may significantly affect capercaillie populations in central Europe: habitat change, changes in predation pressure, human disturbance related to leisure activities, and weather fluctuations and climate change (Storch, 2000, 2001). For the Teisenberg population, no data were available on predation and human disturbance; however, there was no indication that major changes had taken place during the period of study. Therefore, I concentrated on habitat and weather.

Capercaillie on Teisenberg have been found to prefer habitats with the best quality, as indicated by habitat-type specific survival (Storch, 1993a,b, 1994, 1995), and the habitat suitability index model used in this study explains >90% of the variation in capercaillie use of Teisenberg forest stands (Storch, 2002a). Because of this close habitat association, one might assume habitat change to be the major cause of the population change observed. Yet the changes in habitat suitability scores observed between 1992 and 2002 were minor (Fig. 8.2) and did not parallel the population index (Fig. 8.1). In 1997, when the HSI for summer, that is limiting for capercaillie in the Bavarian Alps (Storch, 2002a), reached its highest score, the capercaillie population was at its lowest. Clearly, habitat changes largely resulting from forestry practices occur at a slower rate than the year-to-year fluctuations in capercaillie.

Climate change is believed to possibly play a role in capercaillie populations in Atlantic climates (Moss, 2001). For the Bavarian Alps, (1961–2005 data from Teisenberg) there is no indication of a trend in early summer rainfall sums (see

Fig. 8.3). In both June and July, when Teisenberg capercaillie raised young chicks, rainfall was highly variable. Regression analysis for the period 1992-2004 showed that July rainfall significantly affected the population index on Teisenberg. Reduced chick survival in wet conditions is the most likely explanation. Although well known from Scandinavia (Marcström, 1960; Slagsvold and Grasaas, 1979; Wegge, 1980; Lindén, 1981) and Britain (Moss, 1985; Moss, 2001), weather-related fluctuations in grouse populations had not been documented for the Alps before.

The study suggests that fluctuations in early summer rainfall cause significant year-to-year variations in capercaillie populations that are superimposed on longer-term population trends that are related to habitat structure. A study across the Alps showed that differences in habitat suitability index scores explained >50% of the variation in capercaillie abundance at the scale of individual mountain ranges (Storch, 2002b). Unfortunately, weather data are unavailable for most of these sites. Within the 5,000 km^2 of the Bavarian Alps, the German weather service (Deutscher Wetter Dienst) maintains only 16 recording stations, for which longer-term data are available. This analysis, based on July rainfall sums for 1961–1990, showed that rainfall patterns in the Bavarian Alps varied significantly both in time, i.e., between years, and in space, i.e., among sites. A year with a wet summer on Teisenberg that causes poor survival of capercaillie chicks may coincide with exceptionally little rain and favorable brood rearing conditions in other parts of the Bavarian Alps.

Spatial asynchrony of rainfall patterns in the Bavarian Alps has two important implications. First, local population fluctuations are probably not closely correlated in space. Capercaillie populations in the Alps are spatially structured, and there is evidence of a metapopulation system (Segelbacher and Storch, 2002; Segelbacher et al., 2003). In terms of metapopulation persistence, the vital question is if and to what extent local dynamics might be correlated. With asynchrony of local population fluctuations, a dynamic source-sink metapopulation system can be hypothesized (Storch, 2002b). Secondly, locally distinct weather patterns limit the possibility of using data from near-by weather stations in studies of population dynamics of species such as grouse. The spatial resolution and extent of weather records available for the Bavarian Alps is insufficient to account for variation at the scale of mountain ranges.

8.4.1. Implications for Land Use Planning and Conservation

The case study of capercaillie populations affected by rainfall presented in this chapter as well as the example of black grouse winter habitat accessibility in relation to snow depth (Zeitler, 2003) sketched above illustrate that abiotic stochasticity may cause significant spatiotemporal discontinuities in habitat availability and quality for wildlife species such as grouse. The resulting population fluctuations operate at the scale of months to years, and may thus mask longer-term population trends related to habitat change caused by natural succession and human land use, that are more likely to operate at the scale of decades.

The message for research into wildlife–habitat relationships is that the temporal study extent or horizon should match the scale of environmental variability that is relevant for the question of interest. When the question is how rainfall patterns affect capercaillie reproductive success, a few years of study in different sites might be sufficient. When the task is, however, to assess population trends in habitats changing due to changing forestry policies, a decade of study may not be sufficient. As a basis for land use decisions and conservation planning, study extents of several, if not many, years are not realistic. For red-listed species such as grouse in the Alps, nature conservation legislation commonly requires environmental impact assessments prior to any development or construction project that might negatively affect a population or its habitat (e.g., Gassner and Winkelbrandt, 1997). For grouse, the construction of a wind park and the extension of a ski resort are typical examples. Environmental impact studies typically have to come to a conclusion regarding the value of a particular site for the species of interest within a single field season. Habitat quality is assessed based on indices of population density under the assumptions that first, highest abundance indicates best habitat (but see van Horne, 1983), and second, abundance in the year of study is representative of the site in the longer term. This study demonstrates clearly that this is not likely to be the case in species that are exposed to spatiotemporal discontinuities in habitat availability and quality.

Conservationists at the state agencies and the authors of environmental impact studies, who are often not specialists of the species of interests, should be aware of the serious limitations short-term studies may bear. Here are two hypothetical case examples that are typical of current environmental impact assessment practices in the Alps.

Example 1

Capercaillie abundance is assessed to be higher in site A as compared to site B; the conclusion that site B is of minor importance as a capercaillie habitat might not be justified because different rainfall pattern in the previous years may have caused the difference.

Example 2

A local black grouse population has increased in abundance since a conservation measure was implemented. The conclusion is that the measure was successful. This conclusion is not justified if the increase is a result of favorable conditions the previous winter. Similarly, a population may appear stable or even increasing despite a deterioration in the habitat, simply because favorable weather had a short-term compensating effect and masked a longer-term downward trend.

For conservation planning, there is no simple solution for the problem of temporal discontinuities in habitat availability and quality for wildlife species. Longer temporal horizons for studies are rarely realistic, and data on the more subtle, site-specific environmental fluctuations are often not available. In this situation, our advice to the conservation agencies is to involve specialists with species-specific experience in the design and interpretation of conservation planning and monitoring studies.

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9
Exploring the Temporal Effects of Seasonal Water Availability on the Snail Kite of Florida

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Abstract. The Florida snail kite (*Rostrhamus sociabilis*) is an endangered raptor that occurs as an isolated population, currently of about 2,000 birds, in the wetlands of southern and central Florida, USA. Its exclusive prey species, the apple snail (*Pomacea paludosa*) is strongly influenced by seasonal changes in water abundance. Droughts during the snail kite breeding season have a direct negative effect on snail kite survival and reproduction, but droughts are also needed to maintain aquatic vegetation types favorable to snail kite foraging for snails. We used a spatially explicit matrix model to explore the effects of temporal variation in water levels on the viability of the snail kite population under different temporal drought regimes in its wetland breeding habitat. We focused on three aspects of variations in water levels that were likely to affect kites: (1) drought frequency; (2) drought duration; and (3) drought timing within the year. We modeled a 31-year historical scenario using four different scenarios in which the average water level was maintained constant, but the amplitude of water level fluctuations was modified. Our results reveal the complexity of the effects of temporal variation in water levels on snail kite population dynamics. Management implications of these results are discussed. In particular, management decisions should not be based on annual mean water levels alone, but must consider the intra-annual variability.

9.1. Introduction

Many wetlands undergo seasonal cycles in precipitation and water depth that are reflected in patterns of reproduction of fish and invertebrate biomass, which in turn influence the phenology of other components of the food web. Longer term cycles due to the El Niño–southern oscillation phenomenon create hydrologic variations on decadal time scales. In addition, human activities, such as drainage or other alterations of the hydrology, can either exacerbate or moderate these natural cycles and result in changes to both lower trophic level production and the higher trophic levels dependent on this production.

Seasonal water level changes are especially important in landscapes of central and southern Florida. Because of the flat landscape, relatively small differences in mean water level amplify into large differences in the amount of wetted area and flooding duration, which affect many plant and animal communities. The vast areas of wetland vary in habitat suitability seasonally, but also between years (e.g., Curnutt et al., 2000). Because the natural areas of southern and central Florida are so extensive in size, temporal variations generally are not highly correlated over the landscape and hence over the ranges of many species populations. It is essential to consider spatial and temporal variation together. These combined effects in the Everglades have been studied in recent modeling papers (e.g., Gaff et al., 2000; Mooij et al., 2002; DeAngelis et al., 2005).

Increasing the focus of modeling on coupled spatial and temporal variation is becoming more relevant than ever, as ecologists learn more about the mechanisms that maintain populations and communities. Human impacts are changing both the spatial extent of habitat and the frequency of disturbances, leading to conservation concerns.

A case in point is the snail kite (*Rostrhamus sociabilis*), an endangered raptor whose distribution in the United States is restricted to the wetlands of central and southern Florida, including watersheds of the Everglades, Lake Okeechobee, Kissimmee River, and Upper St. Johns River. Dreitz et al. (2002) estimated the population size of snail kites in Florida between 1997 and 2000 to be approximately 3,000 birds. The snail kite is an obligate wetland-dependent species that feeds almost exclusively on one species of aquatic snail, the apple snail (*Pomacea paludosa*). Because frequent droughts can severely impact local apple snail populations, the viability of the kite in the United States is dependent on both long and short-term hydrologic conditions appropriate for maintaining a mosaic of both its forage and nesting habitats across the region. High mobility of the snail kite and the spatial extent of its range across central and southern Florida are essential in maintaining the population (Bennetts and Kitchens, 2000; Kitchens et al., 2002). Droughts are seldom spatially correlated across the whole range of the population, and snail kites have sufficient mobility to escape from local droughts by long-distance (tens to hundreds of kilometers) movements.

The influence of spatial extent and mobility on the dynamics of snail kite populations in relation to the hydrological conditions of central and southern Florida has been studied using an individual-based, spatially explicit model called *Everkite* (Mooij et al., 2002). The model shows clearly that weak spatial autocorrelation of droughts, plus the ability of snail kites to move from unfavorable to favorable sites quickly, have a major effect on population survival and growth. Therefore, it is important to maintain the spatial extent and heterogeneity of the snail kite's range. However, the nature of the temporal variability of the hydrologic conditions in the snail kite's range is also important. Temporal variability is expressed particularly in the occurrence of periodic droughts. When these droughts lead to a drying out (drydown) of a kite-breeding site during the breeding season, they have a negative effect on kite survival and reproduction (Bennetts and Kitchens, 2000; Kitchens et al., 2002). Although a few studies have investigated the effect of drought frequency on kites (Beissinger, 1995; DeAngelis et al., 2001; Mooij et al., 2002), little attention has been given to the temporal extent of droughts. Nevertheless, survival of the apple snails is known to decrease dramatically with drought duration (Darby, 1998). Drought duration is likely to affect apple snail availability to kites both in the short term (months) and long term (years). Indeed, during drought conditions, kites spend considerably more time and energy in capturing snails than under non-drought conditions (Bennetts and Kitchens, 1997). Thus, increased drought durations are likely to reduce the chance of kites breeding successfully and, more importantly, to increase kite mortality. However, occasional droughts are needed to maintain the vegetation type, primarily *Eleocharis* marsh, most favorable to snail kite foraging. Therefore, we hypothesized that an intermediate frequency of drought disturbances would be optimal for long-term viability of the snail kite population.

The natural frequency of disturbances is threatened by human impacts. The system of levees and canals built in southern Florida to divert water for urban and agricultural water use and flood control has caused changes in hydrological cycles over large portions of the Everglades (Fennema et al., 1994). After a period of apparent population increases or stabilization, snail kite breeding success and numbers have declined precipitously starting about 2001 (Martin et al., unpublished data). The recent declines seem to be due in part to drought conditions and in part to the way that some of the breeding sites are being managed. It is important therefore to explore the role that changes in temporal variability may have played. For this reason, we have focused this chapter on modeling the uncertainty associated with the causes of the recent decline in an attempt to find management solutions. We use *Everkite* to examine the general properties of temporal variation in water depths and drought frequency and try to extract relevant management recommendations. Management decisions that rely on single annual average values of water levels can be problematic and very misleading, given large seasonal variation in water levels. *Everkite* simulations are useful in investigating the temporal variance in water levels. We simulated different water regulation schedules that had the same annual water level average values, but differed in their variance. We also examined the effects of varying drought duration and drought timing on snail kite simulated population growth.

9.2. Methodology

9.2.1. Description of the Snail Kite Model

Everkite has been developed as an individual-based, spatially explicit model to project population changes under diverse hydrologic scenarios. As basic information for any predictive model, good empirical studies are required. A large number of empirical studies have been completed on the Florida snail kite and provide the correlative relationships between specific aspects of its life-history and behavior with the hydrology of the system. These relationships form the building blocks of the hydrologically driven population-dynamics model.

For clarification we outline how *Everkite* works here. The model is designed to predict temporal and spatial patterns of snail kite numbers under various hydrological scenarios. It does so by following the lives of all individual kites in the model population on a weekly time step. The spatial structure of the model consists of a network of wetlands, each representing one of the major wetlands inhabited by snail kites in southern and central Florida. Some of the important characteristics of the *Everkite* model are as follows:

1. Each snail kite is individually modelled. Attached to each individual are state variables, representing sex, age, spatial location, and reproductive status.
2. In the model, snail kites nest across an array of 14 disjunct wetlands of southern and central Florida that are linked to GIS map layers of the hydrological model. The habitat quality within each of these areas is assumed to be relatively uniform. There is also one aggregated "peripheral" habitat (making fifteen total wetlands in the model), representing areas of inferior quality that snail kites may use for foraging, though not for nesting.
3. Each individual wetland is allowed to undergo changes in spatially averaged water level, which affect apple snail density. Foraging activities are not modeled explicitly, but instead water levels are directly translated into a habitat quality parameter, representing the foraging conditions. Decreasing conditions in a given wetland result in a tendency for the kites to move away and, for those that stay, a reduced reproductive rate and an increased mortality rate. Carrying capacities were not assigned to the wetlands, so the model does not attempt to examine the population dynamics close to an upper bound in the population size.
4. Although *Everkite* was built as an individual-based stochastic (Monte Carlo) model, a deterministic matrix model version is used here. Transition values for activities, such as the starting of breeding or the movements of the kites from any given site to another, are described by matrix elements representing the fractions of the population that start breeding or make the move to particular sites. There is a general tendency for kites to move to nearby wetlands rather than to very distant ones. *Everkite* produces the number of kites in each wetland in each week for the duration of the hydrological scenario. A good way to characterize a given scenario in a single number is to calculate the long-term yearly population growth rate (λ) for the whole period covered by the scenario. The whole period used in the simulation was determined by the record of hydrological data, which was 31 years.

Two versions of *Everkite* have been developed, which differ in the level of detail in which the kites were described. A simple spatially-explicit individual-based model was developed to perform a sensitivity analysis of a system with the properties of the kite population in southern and central Florida. This model is described in details in Mooij et al. (2002). A more detailed version of the model was developed to incorporate most known details about kite population dynamics and behavior, based on extensive field studies. Both versions of the model handle space by distinguishing the fifteen major wetlands that constitute the fourteen main nesting habitats of the snail kite, plus a peripheral non-nesting habitat component, and both models were run with a time step of one week. They also both cover four biological processes: ageing, reproduction, movement, and mortality. They differ, however, in the way these processes are described. The detailed model can be run in a stochastic, individual-by-individual mode (*Everkite* version 3.01) and in a deterministic, fine scale matrix model mode (*Everkite* version 4.01). We used the deterministic version of the complex, parameter-rich model for this chapter (*Everkite* 4.01). It is totally data-driven. The hydrological scenarios were entered as forcing functions, based on detailed hydrological models for the various parts of southern and central Florida. Descriptions of the weekly dynamics of kites were also entered in tabular format.

The approach followed is best explained by making a comparison with the ANOVA approach in statistics. For each of the six major events (nest initiation, nest failure, nest desertion, nest success, movement and death) that a kite could perform in a given week we determined, using empirical data, which factors significantly modified the probability of a specific event happening. Here probability is interpreted as the percent of the population to which the event happens. For example, there are several modifiers that influence the probability of nest initiation, including a seasonal effect, a nesting attempt effect, a wetland effect, a habitat quality effect and a crowding effect. For each of these independent variables, an appropriate number of discrete states were defined (i.e., 12 months, five life stages, five environmental states). Then, for each state, a multiplicative parameter was entered in the model that represented the specific modifying effect of that state to the overall probability. The overall probability of a nest initiation was then calculated by multiplying the basic probability with all the relevant state specific multipliers. This approach produced a very versatile model. An inhibitory effect of a specific state on a specific process (e.g., drought on nest initiation) could easily be achieved by entering a value of zero for the modifier, which then automatically resulted in an overall probability of zero of that event happening.

The empirical information needed for this parameter-rich model comes from a detailed study of the demography and movements of kites (Bennetts and Kitchens, 1997). Fecundity and fledgling survival were estimated through nest studies. Radio telemetry of 282 birds and mark-resighting of banded snail kites were used to estimate survival, to evaluate the influences of environmental conditions (e.g., hydrology) on survival, to evaluate the movement patterns of snail kites in Florida, and to relate these movement patterns to environmental conditions.

Model input for the four scenarios included historical weekly water levels per wetland for the period January 1, 1965, to December 31, 1995. Water levels determine the environmental state of each of the 15 wetlands (Beissinger, 1995). The primary water level states are classified as *high*, *low*, *drought,* and *lag* (where *lag* refers to a year following a drought). After prolonged inundation the habitat status of vegetation cover, which affects foraging success will change from suitable habitat to one of two degraded states: *moderately degraded* or *severely degraded.* Degraded habitats provide less useful foraging habitat and are less suitable for reproduction. The time lags of degradation are much longer than those of the primary states because they represent a much slower process.

The within-year variation in water levels and environmental states interacts with the breeding cycle of the kite. The breeding cycle is implemented in *Everkite* by varying the nest initiation rate between months. Highest initiation rates are in the period February through May whereas nest initiation rate is assumed to be zero in September and October.

9.2.2. Description of Simulation Scenarios

The simulations were intended to test the effects of the amplitude, timing, and duration of temporal variations in water depth on the long-term growth rate of the model snail kite population. The effects of differences in temporal variation could be tested by using historical hydrology data from the important breeding sites. These data exist for long time periods for nearly all (13 of the 14) of the major breeding sites. We used historical data from 1965 to 1996 (31 years).

Using the known historical hydrologic data as the control, we could apply various treatments in the model by making artificial modifications in the way the water levels varied, while keeping the average long-term water levels the same between simulations. This allowed us to examine the effects of each aspect of temporal variation in hydrology by itself. We simulated four scenarios with the model. Note that for all scenarios the long-term average stage in each wetland is the same and equal to the historically observed long-term average. In each scenario the hydrological data were manipulated in order to demonstrate the population effects of different temporal patterns of the forcing function. The biological input data to the model were unchanged. The first two scenarios related to changes in the amplitude of water level fluctuations. The other two scenarios related to within-season changes in the timing of water levels and the duration of droughts.

The main output variable we focused on was the change in λ for a given scenario relative to the λ of the run based on the historical data. There is disagreement among studies on both the current numbers of kites and the realized population increase in kite numbers during the period 1965–1995 (e.g., Bennetts et al., 1999; Dreitz et al., 2002). Focusing on the relative change in λ avoids an impact of these uncertainties on the comparison between scenarios. This limits the possibility of a wrong interpretation of the results of this study. *Everkite* 4.01 does not take density dependence into account. The four scenarios are described in detail below.

9.2.2.1. Scenario 1

In this scenario the hydrological data were manipulated to study the effect of a decrease or increase in the *amplitude* of water levels relative to the Long-Term Average Stage or water level (*LTAS*). The hydrological data were manipulated in the following way. The basic data consist of stages ($S_{w,t}$) in each of the 15 wetlands (w) at weekly time steps (t). For each wetland the *LTAS* in the period 1965–1995 was calculated, resulting in 15 $LTAS_w$'s, where w is the index for the wetland. The variation was manipulated by defining an amplitude, a, which was varied in the range 0.0 to 2.0, with steps of 0.25. For a given level of this amplitude parameter a, the new stage in wetland w at weekly time step t ($S'_{a,w,t}$) was calculated as:

$$S'_{a,w,t} = a*(S_{w,t} - LTAS_w) + LTAS_w \tag{9.1}$$

This formula implies that a value of $a = 1.0$ results in no change from historical values. A value of $a = 0.0$ resulted in constant water levels during the whole period of 31 years (see Fig. 1a for examples).

9.2.2.2. Scenario 2

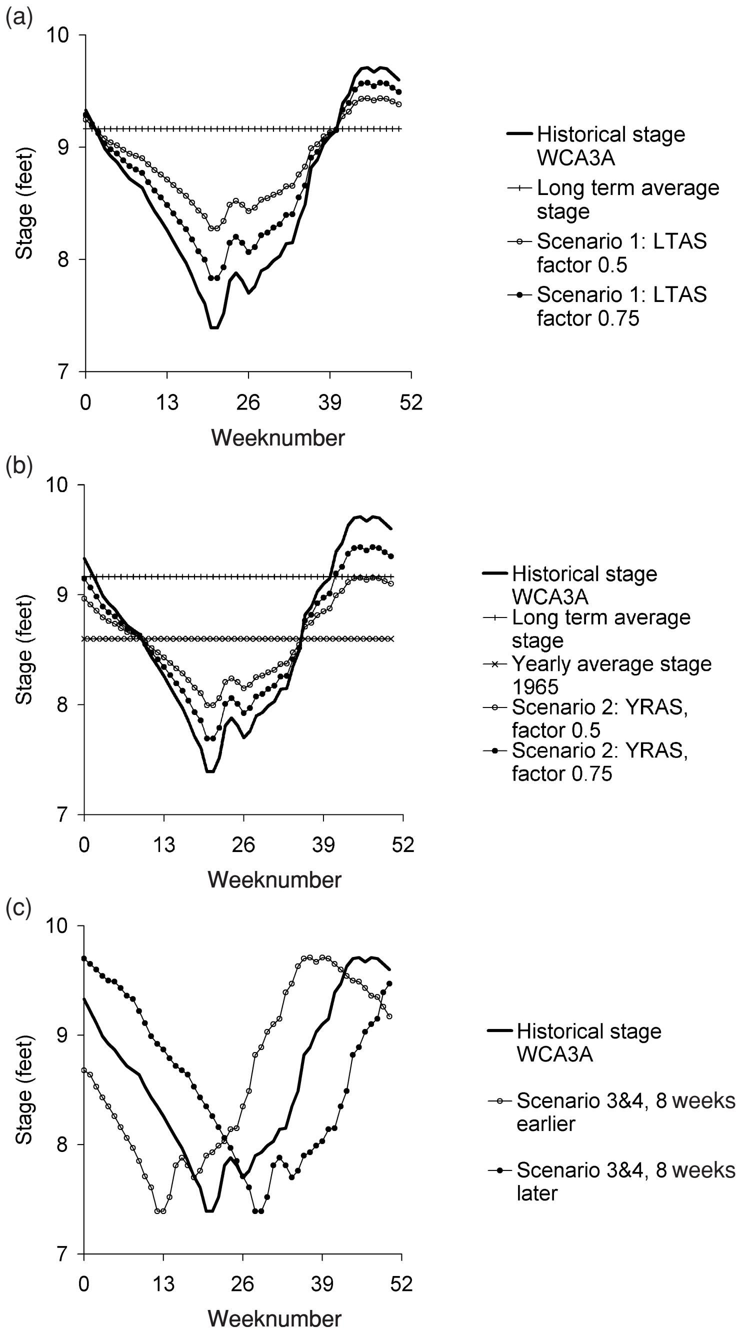
In this scenario the hydrological data were manipulated to study the effect of a decrease or increase in amplitude of water levels relative to the Yearly Average Stage (*YRAS*). To implement this scenario, for each wetland (w) for each year (y) in the 1965–1995 the average stage was calculated, resulting in 15∗31 $YRAS_{w,y}$'s. We used the same range of amplitude multipliers as in scenario 1. For a given level of the amplitude parameter a the new stage in wetland w in a given year y at weekly time step t ($S'_{a,w,y,t}$) was calculated as

$$S'_{a,w,y,t} = a*(S_{w,t} - YRAS_{w,y}) + YRAS_{w,y} \tag{9.2}$$

Again, a value of $a = 1.0$ represents no manipulation. A value of $a = 0.0$ represents in constant water levels within years, but not between years. Note that the formulation used in scenario 2 produced in most years an abrupt change in water levels between the last week of a year and the first week of the next year. The advantage of the method used in scenario 2, however, is that the average water level in a given year remains the same. This means the long-term trends in water levels are better represented by this scenario. The method employed in scenario 1 modifies water levels relative to the long-term average (*LTAS*). When we increase amplitude ($a > 1.0$) water levels above *LTAS* become higher and water levels below *LTAS* become lower. This implies that wet years—during which stage is often above *LTAS*—become even wetter, and dry years—in which stage is often below *LTAS*—become even dryer (see Fig. 9.1b for examples).

9.2.2.3. Scenario 3

In this scenario the historical variation in water level was maintained, but the observed stages were shifted in time by a given number of weeks (Δt). The new


(a)
10
9
8
7
Stage (feet)
0
13
26
39
52
Weeknumber
Historical stage WCA3A
Long term average stage
Scenario 1: LTAS factor 0.5
Scenario 1: LTAS factor 0.75
(b)
10
9
8
7
Stage (feet)
0
13
26
39
52
Weeknumber
Historical stage WCA3A
Long term average stage
Yearly average stage 1965
Scenario 2: YRAS, factor 0.5
Scenario 2: YRAS, factor 0.75
(c)
10
9
8
7
Stage (feet)
0
13
26
39
52
Weeknumber
Historical stage WCA3A
Scenario 3&4, 8 weeks earlier
Scenario 3&4, 8 weeks later

stage in wetland w at weekly time step t ($S'_{w,t}$) was simply calculated as

$$S'_{w,t} = S_{w,}(t - \Delta t) \tag{9.3}$$

For instance, a value of $\Delta t = 4$ means that the observed water levels in the first week of January are used in the scenario as if they were observed 4 weeks later, at the end of January. We studied values of Δt in the range of -16 to $+16$ with 4-week time steps. This shifted the period of the drought in relation to the breeding period, which could change the consequences of the drought period (see Fig. 9.1c for examples of this and scenario 4).

9.2.2.4. Scenario 4

In this final scenario the same hydrological data were used as in scenario 3 but we had the shift in time accompanied by a shift in the duration of a drought. This was implemented by manipulating the time lag (*TLD*) of the environmental state *DROUGHT* in the model. In the standard parameterization this time lag was set to 52 weeks, meaning that a wetland goes from *DROUGHT* to *LAG* one year after the water has risen above the drought trigger level. We implemented the new time lag of the drought $TLD'_{\Delta t}$ as a function of the shift in water levels Δt:

$$TLD'_{\Delta t} = TLD - 2\,\Delta t \tag{9.4}$$

This manipulation of the time lag after a drought had the following consequences. In simulation runs in which droughts occurred later (positive values of Δt) they lasted for a shorter time period, whereas in runs where droughts occurred earlier they lasted longer. Changing *TLD* by twice Δt made the shift symmetrical. For example, drought that occurred 4 weeks earlier, compared to the historical scenario, lasted until 4 weeks after the end of the drought in the historical scenario, so in total it lasted 8 weeks longer.

←

FIGURE 9.1. Illustration of the manipulations with the water levels in the scenarios. All panels show the historical stages in Water Conservation Area (WCA) 3A in 1965 (thick line). (a) In scenario 1, water levels are manipulated relative to the long-term average stage (*LTAS*) for WCA3A (line with + symbols). Shown are the water levels for a multiplier of 0.5 (open circles) and 0.75 (closed circles). (b) In scenario 2, water levels are manipulated relative to the yearly average stage for WCA3A in 1965 (line with x symbols) which is about half a foot lower than *LTAS* (line with + symbols). Shown are the water levels for a multiplier of 0.5 (open circles) and 0.75 (closed circles) (c) In scenarios 3 and 4 water levels are shifted in time. Shown are the inputs for the simulations for the 8 weeks earlier (open circles) and 8 weeks later scenario (closed circles). In scenario 4, when the water levels are shifted to an earlier time, “drought” conditions are assumed not just to shift in time, but to last longer as well. The opposite is true for a shift to a later time.

9.3. Results

The results are expressed as the change in the mean population growth rate (λ) of the population, averaged over the studied period, relative to the mean population growth rate of the model using the historically observed stages.

9.3.1. Scenario 1

The simulations with *Everkite* 4.01 predicted that a change in the amplitude of water level fluctuations while keeping the long-term mean constant would have a strong and mostly negative effect on the population growth rate of the kite. The effects were strongest when we decreased variation (i.e., $a = 0.0$ or $a = 0.25$). Both a values resulted in an enormous change in λ of -0.3 (Fig. 9.2, open bars). These negative effects can be attributed to the habitat degradation that follows a prolonged inundation and the absence of droughts. Increased drought frequency, obtained by increasing the fluctuation amplitude a to 1.75 or 2.0, resulted in a decrease of λ by about 0.15 (Fig. 9.2, open bars). The latter negative impacts can be attributed to the direct negative effects of droughts on kite breeding and kite survival. At intermediate levels of a, the effects were smaller, but still resulted in a rather strong decrease in λ except for $a = 0.75$. The results of *Everkite* for that scenario suggest that a slight decrease in water level amplitude would be beneficial for the kite, given the pattern of droughts that occurred in the past 31 years. A more

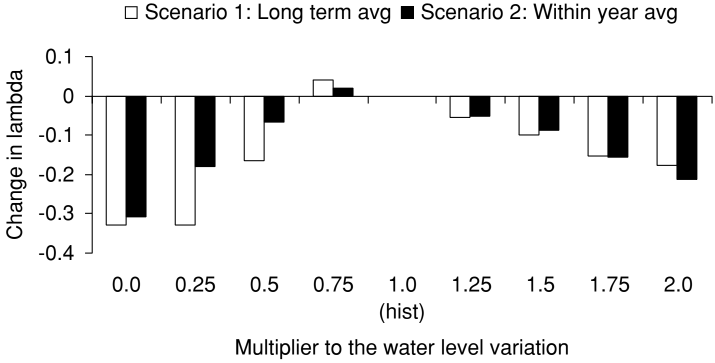


FIGURE 9.2. Changes in λ of scenario 1–long-term mean water level (open bars) and scenario 2–yearly mean water level (black bars) compared to the λ obtained for the historical scenario. In scenario 1, the amplitude of water level variation was changed relative to the long-term average water level (*LTAS*) of each wetland. In scenario 2 the amplitude of water level variation was changed relative to the yearly average water level (*YRAS*) of each wetland. The multiplier, a, to the amplitude in both scenarios is given on the x-axis. The term "hist" indicates the historical hydrological scenario, i.e., the reference mean population growth rate (λ) averaged over 31 years and 15 wetlands.

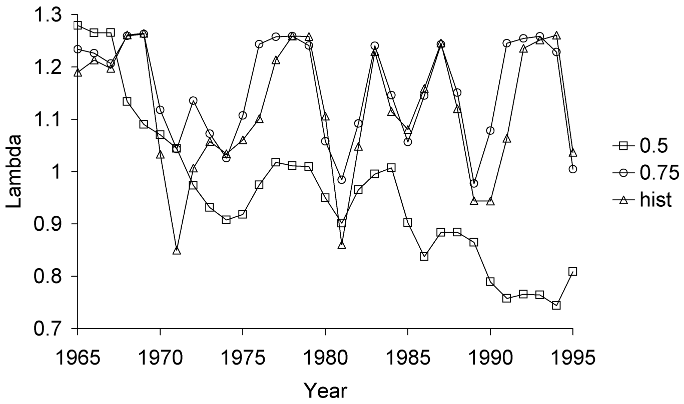


FIGURE 9.3. Yearly values of λ for the 0.5, 0.75, and historical amplitude runs using *LTAS* (scenario 1–long-term mean water level). The patterns of the yearly values of λ provide an explanation for the long-term patterns in λ for these scenarios (given as open bars in Fig. 9.1). For the 31-year period (actual historical data) there were three system-wide droughts (1971, 1981, and 1989–90). These drought would have been less severe had the amplitude been characterized by $a = 0.75$, a situation in which water level amplitudes are slightly dampened. Given the $a = 0.5$ scenario, however, droughts would have become so rare that severe habitat degradation associated with decreased λ values would have occurred.

detailed analysis of the output data shows why a reduction in water level amplitude to 0.75 times the current amplitude of fluctuations is beneficial. When the yearly values for the 0.5, 0.75, and historical amplitude runs are plotted (Fig. 9.3), they show that $a = 0.75$ results in higher values of λ than the historical amplitude in 1971 and 1981. This positive effect can be attributed to the fact that with $a = 0.75$ some of the major droughts that occurred (in particular 1971 and 1981) would have had a smaller spatial extent and, therefore, would have allowed for a better survival of the kite. Had the actual major droughts that occurred been instead droughts that followed model predictions with water fluctuations based on $a = 0.75$, they would not have been as severe because water levels would have been higher. Also, when $a = 0.75$, enough dry-downs still occur to prevent wide-scale habitat degradation due to prolonged inundation.

9.3.2. Scenario 2

The results for scenario 2, which uses yearly average stage (*YRAS*) to manipulate the data rather than long-term average stage (*LTAS*), are strikingly similar (Fig. 9.2, black bars; see numerical values in Box 9.1). This implies that the long-term patterns in average water levels, which are quite prominent for some of the wetlands, have relatively little impact on the predictions for changes in the amplitude of water level fluctuation.

Box 9.1. Comparison of scenarios 1 and 2.

In order to compare different amplitudes of variation within a year of a particular driving variable, water level in our case, we must choose a baseline from which to measure the deviations. This baseline can be supplied by a time-average value. But because there may be long-term trends in a variable such as water level, there is a question of whether one should measure the variation relative to the mean value over just that year or the mean value over many years. We have done both, comparing within-year variation in water level to both the long-term mean over the 31 year historical record (scenario 1) and separately with each particular year in the record (scenario 2); see equations (9.1) and (9.2). There is little difference in the results from these two assumptions, as shown in Figure 9.2, which compares the changes in λ that result when the amplitude, a, of the within-year variation in water level is increased or decreased relative to the historical variation. Let $\Delta\lambda_1$ and $\Delta\lambda_2$ represent the changes in the historical λ for multipliers of the deviation in scenario 1 and 2, respectively: $a = 0.0$, $\Delta\lambda_1 = -0.33$, $\Delta\lambda_2 = -0.31$; $a = 0.25$, $\Delta\lambda_1 = -0.33$, $\Delta\lambda_2 = -0.18$; $a = 0.5$, $\Delta\lambda_1 = -0.16$, $\Delta\lambda_2 = -0.07$; $a = 0.75$, $\Delta\lambda_1 = 0.04$, $\Delta\lambda_2 = 0.02$; $a = 1.0$ (historical), $\Delta\lambda_1 = 0.00$, $\Delta\lambda_2 = 0.00$; $a = 1.25$, $\Delta\lambda_1 = -0.05$; $\Delta\lambda_2 = -0.05$, $a = 1.5$, $\Delta\lambda_1 = -0.10$, $\Delta\lambda_2 = -0.09$; $a = 1.75$, $\Delta\lambda_1 = -0.15$, $\Delta\lambda_2 = -0.16$; $a = 2.0$, $\Delta\lambda_1 = -0.18$, $\Delta\lambda_2 = -0.21$.

9.3.3. Scenario 3

In general, the results of simulations with *Everkite* for the scenarios 3 and 4, in which the historical amplitudes were not changed but the hydrological patterns were shifted in time, show a much smaller response than scenarios 1 and 2, in which changes in amplitude occurred. When the hydrological data were only shifted in time, the resulting shift in λ was always smaller than 0.01, even for shifts up to 16 weeks (Fig. 9.4, open bars). This is evident if we examine model output on the percentage of model snail kites that are breeding at any given week under the historical scenario and +8-week and −8-week shifts in the occurrence of drought (Fig. 9.5). The pattern of reproduction varies little between scenarios. Without empirical data on the relation between the week in which a drought occurs in a given year and reproductive output of that year, it is hard to judge how realistic this model result is. Also, apple snail dynamics are not explicitly dealt with by the model and therefore the effect of temporal shifts in hydrology on apple snail dynamics is not accounted for by the model. But from field observations, kites appear to have little variation in the timing of breeding.

9.3.4. Scenario 4

The model predicts a stronger response in population growth rate if droughts are not only shifted in time, but also varied in their duration (Fig. 9.4, black bars). Earlier, longer lasting droughts have a clear negative effect on the population growth rate

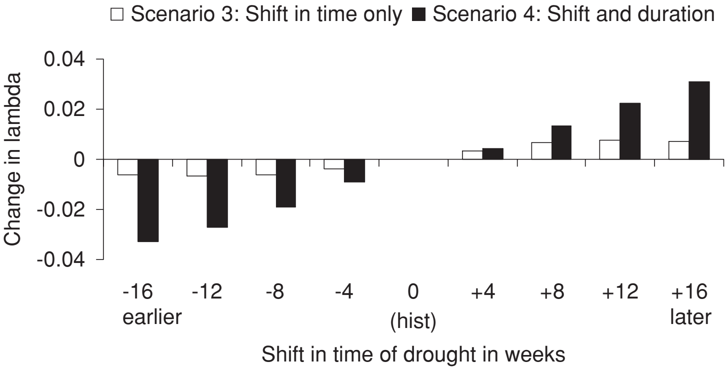


FIGURE 9.4. Changes in λ of long-term scenario 3–water levels shifted in time (open bars) and scenario 4–both time and duration of drought shifted (black bars) compared to the λ for the historical scenario. In scenario 3 the historical data are shifted in time (negative = earlier, positive = later) by the number of weeks given on the x-axis. In scenario 4, they are also prolonged (in case of negative shifts in time) or shortened (in case of positive shifts in time) by double the amount of time given on the x-axis. The term “hist” indicates historical hydrological scenario, which is associated with the reference population growth rate (λ).

compared to the historical situation. Droughts that occur later and have shorter duration have a definite positive effect on kite population growth rate. Note that scenarios 3 and 4 both employ the same hydrological data (see Box 9.2). The effect on drought duration in scenario 4 is implemented by simply prolonging the

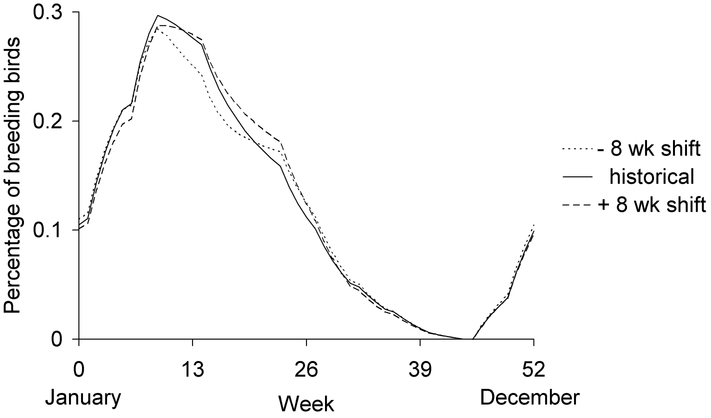


FIGURE 9.5. The proportion of birds breeding, as modeled by *Everkite* 4.01 during the year. Breeding peaks around March 1; by November 1 no breeding birds are left. Also shown are the seasonal breeding patterns for the runs in which the hydrological data were shifted backward and forward in time by 8 weeks (scenario 3). According to the model, these shifts have a limited effect on the percent of birds breeding and result in only minor changes in long-term values of λ for this scenario (open bars, Fig. 9.2).

time it takes the ecosystem to recover from a drought, once the water has come back (see section 9.2.2.4). Comparison of scenarios 3 and 4 shows that the strong effect observed in scenario 4, relative to the control, is mostly due to changes in drought duration (varied in scenario 4) and to a lesser extent to shifts in the timing of droughts (varied both in scenario 3 and 4).

Box 9.2. Scenarios 3 and 4.

In these two scenarios, the temporal patterns of variation in water depth were not changed in amplitude, but were shifted (scenario 3) and both shifted and stretched to either prolong or shorten droughts (scenario 4). In scenario 3, the total number of weeks the system is in any of the environmental states stays constant and any response in kite numbers is therefore solely due to a potential mismatch between the timing of the breeding cycle of the kite and the timing of droughts. According to the model the kites respond in a flexible way to such shifts, without strong effects on the long-term population growth rate. In scenario 4, the total number of weeks that wetlands are in any of the environmental states is variable. Droughts that occur earlier last longer and droughts that occur later last shorter. In this case we observe a strong response of the kites. The comparison with the results obtained for scenario 3 show that this is not due to purely timing of the drought, but due to the manipulation of drought duration. Let $\Delta\lambda_2$ and $\Delta\lambda_3$ represent the changes in the historical λ for multipliers of the deviation in scenario 3 and 4, respectively: $\Delta t = -16$, $\Delta\lambda_3 = -0.006$, $\Delta\lambda_4 = -0.033$; $\Delta t = -12$, $\Delta\lambda_3 = -0.007$, $\Delta\lambda_4 = -0.027$; $\Delta t = -8$, $\Delta\lambda_3 = -0.006$, $\Delta\lambda_4 = -0.019$; $\Delta t = -4$, $\Delta\lambda_3 = 0.004$, $\Delta\lambda_4 = 0.009$; $\Delta t = 0$ (historical), $\Delta\lambda_3 = 0.000$, $\Delta\lambda_4 = 0.000$; $\Delta t = +4$, $\Delta\lambda_3 = 0.004$, $\Delta\lambda_4 = 0.005$; $\Delta t = +8$, $\Delta\lambda_3 = 0.006$, $\Delta\lambda_4 = 0.014$, $\Delta t = +12$, $\Delta\lambda_3 = 0.008$, $\Delta\lambda_4 = 0.022$; $\Delta t = +16$, $\Delta\lambda_3 = 0.008$, $\Delta\lambda_4 = 0.031$.

9.4. Discussion

9.4.1. Drought Frequencies

Our results emphasize that several components of temporal variations in environmental conditions are critical to the persistence and abundance of snail kites. We found that simple modification of the amplitude of water level changes (while mean annual water levels were kept constant) could have dramatic effects on population growth. Surprisingly, it was not the scenarios with the largest amplitudes (largest differences between minima and maxima in water levels) that reduced the population growth rate by the greatest magnitude. The smallest amplitude fluctuations had the greatest effect, because they led to a decrease in the frequency at which wetland sites had drydowns, which had a long-term negative impact on wetland vegetation type and thus habitat suitability. Increases in amplitude also had a negative effect on population growth. This was mostly due to the resultant increased frequency of droughts, which are known to be directly detrimental to kites when they occur at a sufficiently high frequency (Beissinger, 1995; Mooij et al., 2002).

Thus, simple hydrological indicators based on a single factor, such as annual mean water levels (see, for example, the drought indicator developed by Bennetts and Kitchens, 1997) should be interpreted with caution. Indeed, such indicators may fail to identify drought events within a year when the amplitude of water level variation within a year is high relative to the yearly mean water level. Although scenarios with large amplitudes resulted in rapid decreases in intrinsic population growth rates, scenarios with substantially reduced variation (or amplitude) in water levels also led to even greater negative population growth rates over the long term, due to longer-term degradation of the habitat caused by prolonged hydroperiod and the near absence of dry downs (Kitchens et al., 2002; Mooij et al., 2002). Kitchens et al. (2002) hypothesized that occasional drying is critically important for maintaining the vegetation communities that provide the requisite habitat conditions for supporting both foraging and nesting activities of kites. Darby et al. (2005) also suggest that maximum egg clusters of apple snails occur when water depth falls below a certain threshold (e.g., <40 cm at a study site in WCA3A that is heavily used by nesting kites). Hence, there is some moderate level of within-year variation in water level that is more favorable to the persistence of kites than is either extreme.

9.4.2. Drought Duration

Another important hydrological variable related to temporal variability in water levels is drought or drydown duration (length of time an area is dry). We were able to vary drought duration in the model, and found significant effects on population growth rate. This response reflects the direct effect of drought duration on survival and reproduction. During droughts, snail availability is dramatically reduced (implicitly taken into account in the model), thus increasing the probability of kites dying from starvation. The longer the drought conditions persist, the greater the reduction in kites. The same reasoning applies to kite reproduction. During drought, reproduction is dramatically reduced, and the longer the drought the less opportunity to reproduce.

9.4.3. Limits of the Everkite Model and Perspective for Future Developments

The current version of *Everkite* ignores the effects of several potentially important hydrological components. One component is the frequency of flooding (very high water), which, if too high, could be highly detrimental to kite habitats, even if followed by dry conditions. Flooding can affect kites by reducing recruitment of apple snails (Darby et al., 2005) or by degrading the vegetation communities characterizing both nesting and foraging kite habitats (Kitchens et al., unpublished).

Including the effect of flooding into *Everkite* would cause scenarios with large amplitude (i.e., large multiplier *a* to the water level variation as in Fig 9.1) to reduce population growth rate of kites even further. Adding this effect will require additional empirical data of the effect of flooding on apple snails.

Another limitation of the model is that the effect of prolonged drought on apple snails is not taken into consideration. Darby (1998) found that mortality increased substantially while recruitment decreased dramatically during longer drying events. We predict that incorporating the effect of drought duration on apple snail dynamics would increase the negative effects of drought duration on snail kite population growth. The last limitation that we wish to discuss is related to the drought criterion used in *Everkite*. The current version uses a criterion for occurrence of a 'drought' based on the number of standard deviations below the long-term average water level, which is very convenient, because it allows for the comparison of drought effects among various wetlands. However, this criterion may misidentify the occurrence of droughts because in the last 15 years kites have shifted from habitat located at lower elevation toward habitats located at higher elevation (Bennetts et al., 1998). Therefore, habitats currently used by kites appear to be much more susceptible to drying than formerly (than, for instance, in the 1980s). This was verified by the drying event of 2001, during which most birds left WCA3A (or died), even though water levels in this area would not have reached the drought threshold used in *Everkite* (Martin et al. unpublished data). In the 1980s drying events whose minimal water levels would reach the lowest values recorded in 2001 did not appear to cause kites to exhibit the typical kite response to drought described by Bennetts and Kitchens (2000), during which birds move or die. Water elevations located in most kite habitat obtained from hydrological models, as well as distributional map of kites over time, should allow us to rectify these limits in future versions of *Everkite*.

9.5. Conclusions and Conservation Implications

Our simulation work shows the preponderance of temporal variation of water level fluctuation in determining the dynamics of the snail kite. Any management actions aiming at helping kites recovery should, therefore, carefully examine the frequency, duration, and timing of dry downs. Interestingly, the hydrograph presented in Figure 9.6, indicates that drought duration and drought frequency have been considerably reduced during the last 13 years (1993–2005), which may have initially promoted higher snail kite population growth. On the other hand, prolonged hydroperiods and increases in flooding frequency observed during the 13 year period (Fig. 9.6) may also have led to degradation of the habitat and to lower apple snail abundances.

In order to understand the causes for the more recent population decline and lack of recruitment, especially in WCA3A during the last eight years (Martin et al., unpublished data), we may need to focus more attention on the effect of flooding events and extended hydroperiods on kite demography and habitat dynamics.

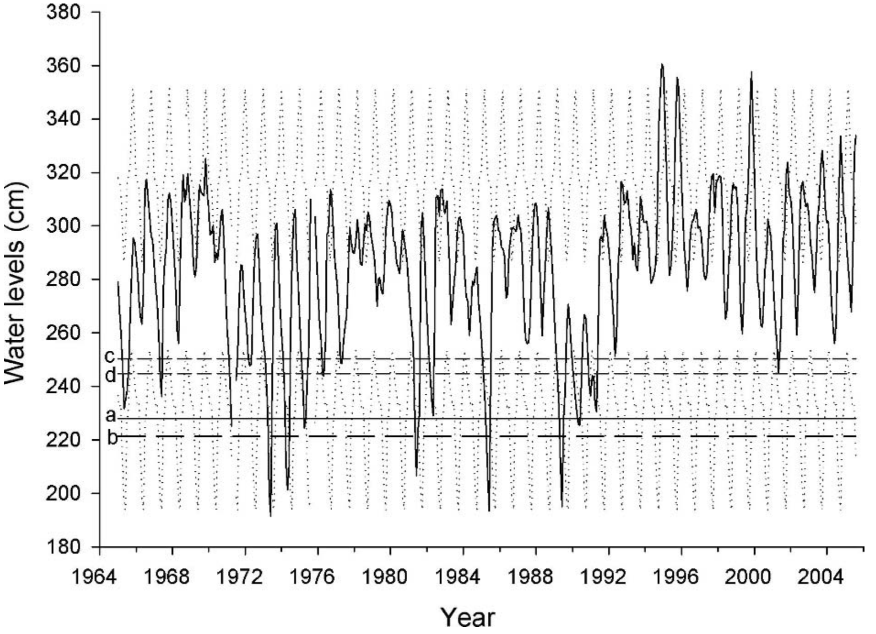


FIGURE 9.6. Average monthly water levels in Water Conservation Area 3A (WCA3A, station 3A-28 and 3-65 combined; location for 3A-28 was N 25° 48′ 44″ W 80° 43′ 19″; location for 3A-65 was N 25° 48′ 53″ W 80° 43′ 11″). Solid fluctuating curve indicates monthly water levels; the gray dotted fluctuating curves correspond to the 95% upper and lower percentiles. The dark horizontal line (a) indicates ground elevations at the recording stations. The black long-dashed horizontal line (b) corresponds to the water level threshold used in *Everkite* that would determine drought conditions in WCA3A (drought conditions result in substantial kite movement and mortality). The black short-dashed horizontal line (c) corresponds to the water level threshold used in *Everkite* that would determine low water conditions in WCA3A (low water conditions result in moderate movement and mortality of kites). The horizontal, gray short-dashed line (d) corresponds to the minimum water levels in WCA3A in 2001 that triggered a typical kite response to drought conditions (movement and mortality).

The principal constraint for not including this factor in the model is the lack of adequate empirical evidence relating flooding effects on vegetation and snails and mechanistic information regarding the impacts of changes in vegetation and snail abundances to kite population dynamics. Given the stakes involved in the enormous Everglades ecosystem restoration project and the Federally Endangered status of the kite, it is apparent that this challenge will need to be addressed. Our study, therefore, emphasized the deep practical implications of carefully considering temporal explicitness in key environmental variables, an aspect which is too often neglected in studies trying to uncover the ecological dynamics of natural populations inhabiting heterogeneous landscapes (Jonze et al., 2004). In many cases this important component of environmental variation is ignored because of the level of complexity it may add to the study of already complex systems. The integration of detailed demographic studies into flexible mechanistic models (e.g., individual-based models) may therefore provide a powerful framework to unravel these critical issues.

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10

Three Axes of Ecological Studies

Matching Process and Time in Landscape Ecology

MELISSA J. REYNOLDS-HOGLAND AND MICHAEL S. MITCHELL

Abstract. The spatiotemporal resolution of observations should match the level of the ecological process under study to yield reliable insights. We present a concept of designing ecological studies that integrates three axes: temporal resolution of the study, spatial resolution of the study, and the resolution of the ecological process addressed. Focusing on the integration of the temporal axis in landscape ecology, we provide two examples from our long-term research on black bears (*Ursus americanus*) where erroneous selection of temporal resolution yields inaccurate results. In both examples, we incorporate temporal dynamics into spatial phenomena to understand complex systems. We synthesize demographic and behavioral results from our bear research and invoke hierarchy theory to understand the effects of timber harvesting on habitat quality for bears. We propose that the temporal scales at which different vital rates are manifested in a bear population may differ, which may affect the way perturbations (e.g., clear-cuts, roads, etc.) affect habitat quality for bears.

10.1. Introduction

10.1.1. Three Axes of Ecological Studies

Ecological processes operate over various spatial and temporal scales (Turner, 1989; Allen and Hoekstra, 1992; Levin, 1992; Wiens, 1996). We often overlook the fact that data collected to understand these processes are also proscribed by specific spatial and temporal scales that define the observation window through which ecological processes can be evaluated reliably (O'Neill et al., 1986; Allen, 1998). The spatiotemporal scaling that defines the observation window of a particular study should depend on the resolution of the ecological process being addressed. Thus, it is easy to visualize that for ecological studies, three axes should be considered explicitly; the resolution of the ecological process of interest, as well as the temporal and spatial resolutions of the study (Fig. 10.1A). All three axes should match closely to yield reliable insights.

Ecological processes can be conceptually organized according to hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986; King, 1997), a framework of

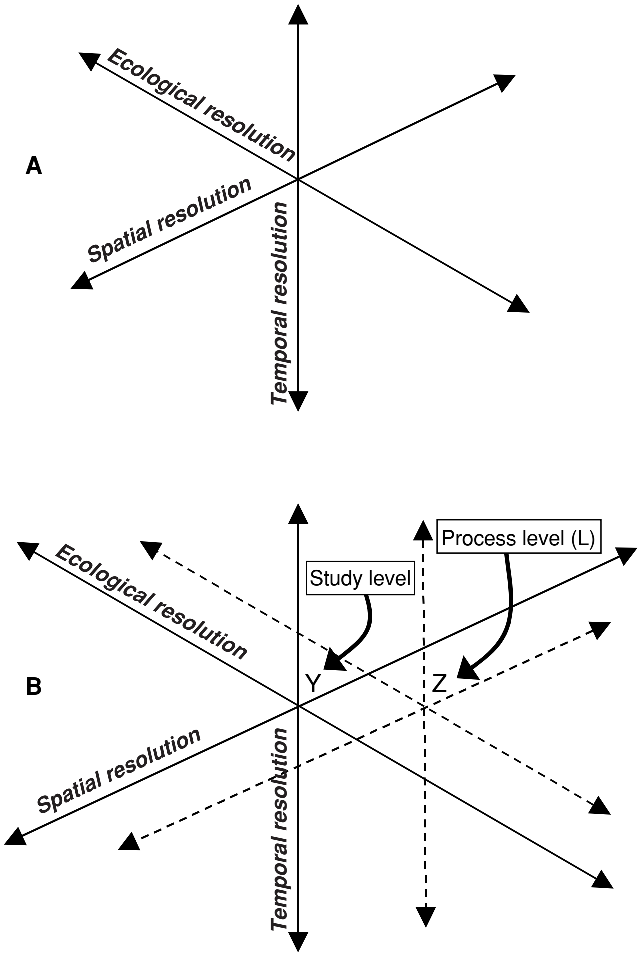

FIGURE 10.1. (A) The 3 axes implicit in every study design for ecological research: temporal resolution of the study, spatial resolution of the study and the resolution of the ecological process under study. (B) Three axes are inextricably linked. When the focal level changes along the ecological resolution axis, complementary movements in spatial and temporal resolution axes also occur. If the focal level moves from Y to Z along the ecological resolution axis, the temporal and spatial resolutions must also move from Y (solid lines) to Z (dotted lines). Study designs are flawed when the focal level of the process (L) occurs at a spatiotemporal resolution that differs from the spatial and temporal resolutions of the study.

system organization whereby ecological processes are understood in terms of both lower-level mechanisms and higher-level constraints. The framework comprises a triadic structure such that the focal level (L) includes the ecological process of interest; the L − 1 level includes lower-level mechanisms, defined by faster process rates and stronger interactions than those seen at L; and the L + 1 level includes the

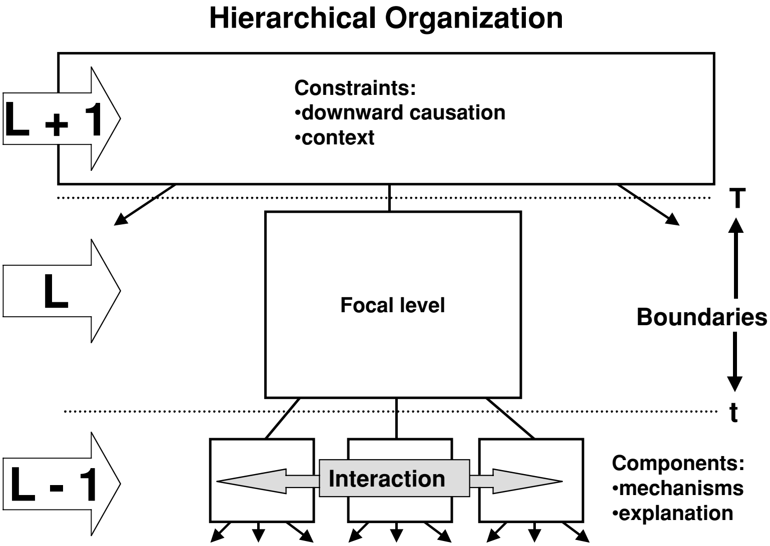

FIGURE 10.2. Hierarchical organization of ecological systems, where the focal level of the ecological process is explained by processes occurring at L − 1 levels and constrained by processes occurring at L + 1 levels.

higher-level constraints, defined by slower process rates and interactions that constrain those seen at L (Fig. 10.2). We define T to represent the spatial and temporal extent (i.e., the dimensions in space and the length in time over which observations are made), whereas t represents the spatial and temporal grain (i.e., the smallest spatial or temporal intervals in an observation set). Each level, and each holon (i.e., strongly interacting processes: Allen and Starr, 1982) within levels, is demarcated by differences in rate structure. If an ecological process is hierarchically organized, the focal level (L) of the process dictates the resolution of its temporal and spatial axes (O'Neill and King, 1998).

The range of focal levels of an ecological process is represented along the ecological resolution axis (Fig. 10.1A). The spatial and temporal resolution axes represent the spatial and temporal grain and extent of the study. All three axes are inextricably linked. As the focal level (L) of an ecological process changes along the axis, complementary movements along the spatial and temporal resolution axes are required. For example, if the focal level of an ecological process moves from Y to Z in Figure 10.1B, then corresponding movements along the spatial and temporal resolution axes must occur. Conceptually, this concerted movement is similar to movements required to fly a helicopter, with respect to three axes of orientation, up/down, left/right, and fore/aft. Movement of a control to change orientation of a helicopter along one axis automatically requires complementary movements of controls for the other two axes. Applying this analogy to the three axes of ecological studies, shifting the ecological resolution automatically implies a shift in the spatial and temporal resolution axes, too.

Similarly, shifts in the spatial and temporal resolution axes automatically imply a shift in the ecological resolution axis. If funding or logistics constrain the spatial and temporal resolutions such that a chosen focal level of an ecological process cannot be appropriately addressed, then the focal level of the ecological process must be shifted to match that of the spatiotemporal resolutions of the study.

10.1.2. Implications for Study Design

Failure to design studies without considering all 3 axes may underlie much of the contradictory or confusing insights often generated by ecological studies. Studies whose focal level is characterized by a certain ecological resolution, but that use spatial resolutions that are too small, can erroneously generalize highly localized phenomena to broader spatial scales. Consequences of failure to acknowledge choice of resolutions explicitly can be compounded if the study design includes the erroneous selection of resolution for >1 axis. For example, Figure 10.1B represents what may be the most common error in designing ecological studies, choosing the duration and spatial scope of a study that is inappropriate to the ecological resolution of the problem (e.g., attempting to model population growth of a large mammal in a year-long study conducted in a 1-ha study area). Clearly, incorrect alignment of the three axes within a given study can result in misleading inferences. Because so few studies address each axis explicitly in their design, the confidence which we can have in the bulk of empirical research to date becomes less certain (even, and perhaps most dangerously, for those studies with results that appear to make good sense).

Whereas defining spatial resolution has been widely discussed in landscape ecology, similarly defining the temporal axis in ways appropriate for landscape-scale research is commonly neglected. We devote the remainder of this chapter to an evaluation of how extent and grain of the temporal axis is best understood in the context of landscape ecology. We demonstrate the importance of matching the resolutions of ecological processes with appropriate temporal resolutions of data by providing two examples from our long-term research on black bears (*Ursus americanus*) where erroneous selection of temporal resolution yields inaccurate results. After providing background information on our research necessary to understand our two examples, we evaluate the effect of resource availability on demography of bears over three temporal extents. In our second example, we evaluate resource selection by female bears over two temporal grains. In both examples, we incorporate temporal dynamics into spatial phenomena to understand complex systems. We conclude by synthesizing our results within the framework of hierarchy theory and offering suggestions for the design of research that fully integrates all three axes.

10.2. Temporal Scale in Landscape Ecology

The role of time and the importance of temporal scale have received considerably less attention in landscape ecology than issues of spatial scale, even though relationships between landscape patterns and ecological processes, if they exist,

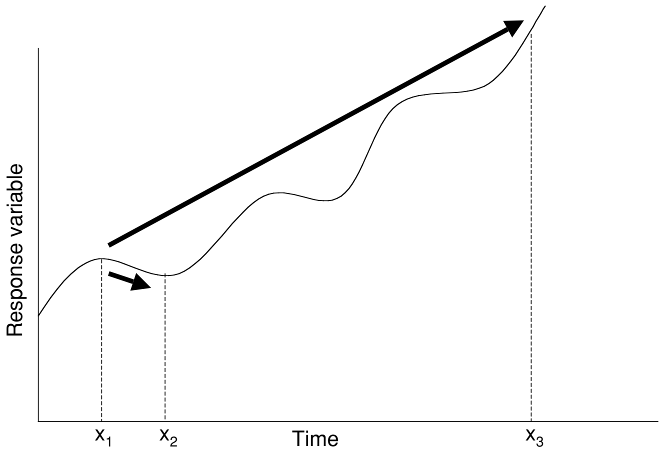

FIGURE 10.3. Contrast between inferences about an ecological process drawn at different temporal extents. Observations collected from time points X_1 to X_3 would correctly capture process variation, those collected from X_1 to X_2would not.

typically change through time due to disturbance, succession, and other temporal dynamics (Reice, 1994). Understanding complex systems requires linking space with time, over the appropriate spatial and temporal scales (O'Neill et al., 1986; King et al., 1990). Mismatches in temporal scale can yield biased results similar to those stemming from mismatches in spatial scale. For example, when the temporal extent over which data were collected is smaller than the temporal extent of the ecological process under study, the results may reflect only a brief glimpse of a long-term process and can be problematic, depending upon whether temporal patterns are consistent across scales.

10.2.1. Incorrect Selection of Temporal Extent

Consider the hypothetical scenario in Fig. 10.3 where the temporal extent over which the ecological process operates is the time between x_1 and x_3. If the response variable were measured between x_1 and x_3, the overall trend would be positive. If, however, the response variable were measured during the time period between x_1 and x_2 (i.e., a mismatch in temporal extent), results would indicate a declining trend. By definition, many studies within the field of landscape ecology examine processes occurring over relatively large spatial extents, which often correlate with large temporal extents (Urban et al., 1987; Bissonette, 1997; George and Zack, 2001). Yet most ecological studies last only 2 to 3 years.

10.2.2. Incorrect Selection of Temporal Grain

Similarly, mismatches in temporal grain may yield unreliable insights. For example, consider a scenario where fall and summer foods are evaluated to determine whether their landscape pattern affects resource selection by a population of wild animals. For the landscape pattern to be effective (Ritchie, 1997; Bissonette, 2003), the arrangement of the foods (not just the amount) must influence resource selection by the animals. To test if spatial arrangement of foods is effective, clustering of food-bearing patches within home ranges might be estimated. If the temporal grain of 1 year is used (i.e., annual home ranges), which is common among studies of resource selection, information critical for testing whether pattern is effective may be masked. For example, seasonal foods may be distributed in numerous ways within the annual home range, 2 of which are demonstrated in Fig. 10.4 (A1 and B1; Reynolds, unpublished data). In A1, summer foods are clustered with summer

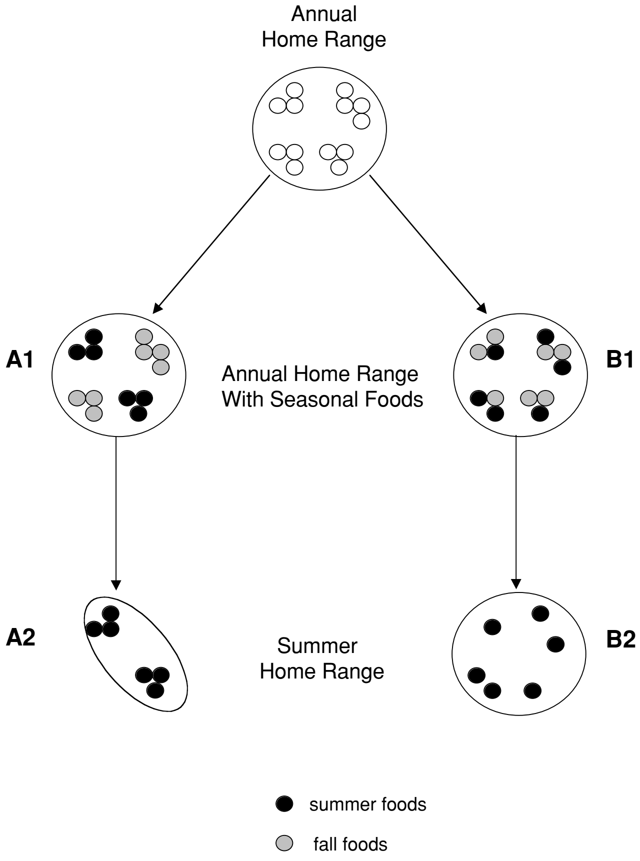

FIGURE 10.4. Hypothetical spatial arrangement of seasonal foods within annual and seasonal home ranges for 1 animal. A1 represents an annual home range where summer foods are clustered with summer foods and fall foods are clustered with fall foods, B1 represents an annual home range where summer foods are spatially intermixed with fall foods. A2 represents the summer home range that would be estimated from A1, B2 represents the summer home range that would be estimated from B1.

foods and fall foods are clustered with fall foods. Alternatively, summer foods are spatially intermixed with fall foods in B1. Although amount of each seasonal food is equal between A1 and B1, seasonal foods in A1 are more clustered than those in B1; therefore, the seasonal home range A2 differs considerably from the annual home range A1, whereas B1 and B2 are essentially the same. Differences between A1 and A2 could be masked if the larger temporal resolution is used; the temporal resolution of 1 year is not appropriate for evaluating effects of resource clustering on resource selection when animals select foods seasonally.

More generally, using the appropriate temporal grain for studies of resource selection increases the accuracy of preference indices. Most studies of resource selection calculate preference indices using a ratio of resource use and resource availability. Availability of resource i, for 3rd order selection (i.e. resource selection within a home range; Johnson, 1980), is typically estimated as the proportion of the home range containing resource i (Manly et al., 1993). The spatial extent of the home range, therefore, affects estimates of resource availability, which in turn affects estimates of preference. Availability of resource i will be smaller in a large home range (Fig. 10.4; A1) compared to that in a small home range (Fig. 10.4; A2), all else equal. This is the critical point because spatial extents of home ranges often depend upon temporal grains. If the temporal grain is inappropriate, the spatial extent may be biased, which will subsequently bias estimates of preference.

10.3. Habitat Quality and Black Bears

We have studied habitat quality and how forest management affects habitat quality for black bears in Pisgah Bear Sanctuary (PBS) in western North Carolina (35°17′ N, 82°47′ W) since 1981. Habitat quality is the capacity of an area to provide resources necessary for survival and reproduction, relative to the capacity of other areas (Van Horne, 1983). Forest management includes timber harvesting and roads building, which can influence bear fitness by affecting food availability and exposure to people and vehicles, respectively. Because we defined habitat quality in terms of fitness (e.g., survival, reproduction, etc.), our goal was to determine how forest management affected bear survival, reproduction, and population growth rate (λ).

10.3.1. Understanding How Timber Harvesting Affects Habitat Quality

The relationship between timber harvesting and habitat quality for bears is complex. Distilling this complexity requires understanding how timber harvesting affects the availability of resources that are important to bears and also understanding how bears respond, demographically and behaviorally, to changes in resources through time. Resources important to bears include foods, escape cover, and den sites. Early research on PBS bears focused on habitat quality by considering all three life requirements (Zimmerman, 1992; Powell et al., 1997; Mitchell et al., 2002), but we focus on only foods in this chapter to make our point because foods are probably the most important resources for most bear populations (Rogers, 1987; Powell et al., 1997). In the southern Appalachian Mountains, foods important to black bears include herbaceous vegetation, squaw root (*Conopholis americana*), soft mast (fleshy fruit), hard mast (acorns and nuts), insects, and carrion (Beeman and Pelton, 1977; Eagle and Pelton, 1983). Of these foods, hard and soft mast have been shown to affect reproduction or survival of different bear populations (Jonkel and Cowan, 1971; Rogers, 1976; Eiler et al., 1989; Elowe and Dodge, 1989; Pelton, 1989; Clark and Smith, 1994; Costello et al., 2003). To understand how timber harvesting affected habitat quality for PBS bears, we focused on the relationships between timber harvesting, hard mast, soft mast, and bears.

10.3.2. Temporal Availability of Soft Mast and Hard Mast Within Clear-Cuts

Timber harvesting affects the availability of soft mast differently than hard mast. Clear-cutting (removal of all trees within a stand) was the primary harvesting technique in PBS so we measured percent plant cover and estimated berry production of soft mast genera within 100 clear-cuts (ranging from 0 to 121 years old) across PBS and used these data to develop statistical models for predicting the availability of soft mast in clear-cuts as it changed through time. The availability of soft mast was highest in 2–9-year-old clear-cuts, lowest in ~10–49-year-old clear-cuts, and moderate in 50+ year old clear-cuts (Fig. 10.5; Reynolds et al., unpublished data).

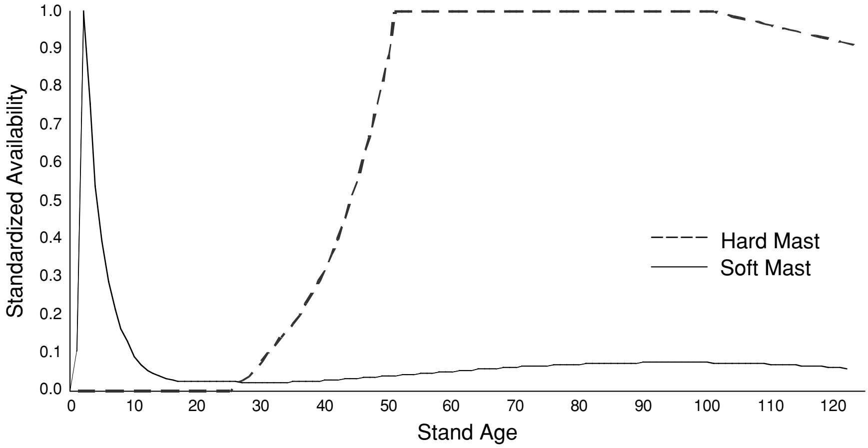

FIGURE 10.5. Temporal availability (standardized) of soft mast (*Gaylussacia* spp., *Vaccinium* spp., and *Rubus* spp. combined) and hard mast in clear-cuts in western North Carolina. The statistical model for soft mast availability was developed from field data collected in 100 clear-cuts throughout PBS in western North Carolina 2001–2002 (Reynolds et al., unpublished data), whereas the statistical model for hard mast was taken from Burns and Honkala (1990).

Alternatively, clear-cuts produce little to no hard mast for 25–50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns and Honkala, 1990).

10.3.3. Demographic Response of Bears

Because clear-cutting affects availability of soft mast and hard mast differently, the overall effect of clear-cutting on habitat quality for a bear population will depend, in part, on whether hard mast, soft mast, or both limit the population. A resource is limiting if changes in its availability affect the population equilibrium level (Williams et al., 2002), which is a function of individual survival and reproduction. Therefore, linking estimates of bear demography with estimates of resource availability as they change over time should provide insights into resource limitation.

We evaluated competing hypotheses about the degree to which hard mast and soft mast limited PBS bears by estimating annual demographic parameters and linking them with annual estimates of mast availability (Reynolds et al., unpublished data). Using capture-recapture data from 101 females captured during 1981–2002 and the temporal symmetry method (Pradel, 1996) in Program MARK (White and Burnham, 1999), we estimated apparent survival, fertility, and λ. We also modeled annual distributions of hard mast and soft mast across the landscape each year from 1981 to 2001, as they changed due to timber harvesting and succession. We separated productivity of soft mast in 2–9 year old clear-cuts from that of the remaining landscape to evaluate their effects on demography of bears separately. The spatial grain of our resource data was 30 meters and the spatial extent was PBS. For each demographic parameter (survival, fertility, and λ), we incorporated annual estimates of hard and soft mast availability (across the landscape and in 2–9-year clear-cuts), as well as their interactions, as covariates using methods described by Franklin et al. (2000). To evaluate competing hypotheses, we ranked models using Akaike's Information Criterion (AIC) with an adjustment for small sample sizes (Akaike, 1973). Based on the life history of bears, we incorporated a time lag in the effect of resource availability on demography. Female bears mate in the summer, but delay implantation until fall. If a female has not acquired sufficient stores of energy by fall, she will abort her pregnancy. Therefore, if availability of a food resource affects fertility during year t, the effect will be measurable during year $t + 1$ when cubs are born. Similarly, any effect of a resource on survival at time t will be measurable at time $t + 1$. Therefore, covariate estimates for year t were calculated using covariate data from year $t - 1$.

We found the additive effect of hard and soft mast across the landscape was most important to both fertility and λ. In addition, the availability of 2–9-year-old clear-cuts was important to fertility. Results for survival were inconclusive because the null model ranked relatively high for survival, indicating the null model could have explained survival as well as availability of soft or hard mast (Reynolds et al., unpublished data).

10.3.3.1. Example 1: Mismatch in Temporal Extent

Did the temporal resolution (grain and extent) of our demographic and resource data match the resolution of the ecological processes (i.e., the effect of resource availability on survival, fertility, and λ)? The temporal grain (t in Fig. 10.2) was 1 year, which was appropriate because we wanted to test whether annual availability of resources affected annual demographic rates. Determining if the temporal extent (T in Fig. 10.2), 22 years, was appropriate was more challenging because we did not know *a priori* the temporal extent of the ecological processes.

We could not extend our data set to test if our temporal extent may have been too short, nor could we compare our results with previous studies on demography of black bears because none exist with temporal extents as long as ours. Instead, we truncated our data set and evaluated how relationships between resources and demography changed as the temporal extent of the data changed. We re-ran the demographic analyses using both the first 5 years of data and the first 10 years of data and then compared results with those from the 22-year data set.

For all three demographic parameters, results from the 5-year and 10-year data sets differed qualitatively from results based on the 22-year data set. We present model results for fertility in Table 10.1, which includes only the top 3 of 15 models we evaluated for each temporal extent. All models ranked third or higher had Δ AIC_c values >4.0, indicating these models had relatively little support (Burnham and Anderson, 2002). For the two truncated data sets, the null model ranked highest

TABLE 10.1. Three models associating covariates representing productivity and availability of hard and soft mast with fertility of a black bear population, Pisgah Bear Sanctuary, North Carolina, 1981–2002*.

Data set	Model	AICc	ΔAICc	AICc weights	Model likelihood	Parameters	Deviance
5-year	Null	157.38	0.00	0.80	1.00	10	12.99
	Soft mast in young clear-cuts	160.60	3.22	0.16	0.20	11	12.20
	Hard mast + soft mast across landscape	163.27	5.89	0.04	0.05	12	10.55
10-year	Null	331.22	0.00	0.86	1.00	20	120.02
	Soft mast in young clear-cuts	335.19	3.97	0.12	0.14	21	119.66
	Hard mast + soft mast across landscape	338.79	7.56	0.02	0.02	22	118.71
22-year	Hard mast + soft mast across landscape	1012.21	0.00	0.77	1.00	46	342.05
	Soft mast in young clear-cuts	1015.67	3.46	0.14	0.18	45	349.31
	Null	1016.70	4.49	0.09	0.11	44	344.18

*Each model represents a different use of the 22-year data set; the first used only the first 5 years, the second used the first 10 years, and the third used all 22 years of the data.

and had relatively high model weight. Conversely, the model that included the additive effect of hard mast and soft mast across the landscape ranked relatively low with a Δ AIC$_c$ value >4.0. Results for both truncated data sets suggest bear fertility was not explained well by availability of soft mast or hard mast.

In strong contrast, results from the 22-year data set showed the top ranked model was that which incorporated the additive effect of hard mast and soft mast across the landscape, whereas the null model ranked low (Δ AIC$_c$ value >4.0) and had little model weight. Overall, the 22-year data set indicated the availability of hard mast and soft mast across the landscape affected fertility, whereas the two truncated data sets indicated neither resource was affective.

Although our results do not demonstrate conclusively the temporal extent of 22 years was appropriate to the ecological process we wanted to understand, they do strongly suggest the two shorter extents were inappropriate for estimating accurately our ecological process of interest. The temporal extents of the 2 truncated data sets were likely too short, perhaps capturing short-term dynamics that, though accurate, do not parallel longer-term dynamics (e.g., Fig. 10.3). Alternatively, differences in results could have occurred because precision in response and explanatory variables for the two truncated data sets was insufficient to detect relationships because sample sizes were too small. In the latter case, and assuming annual sample sizes could not be increased, an argument could be made that estimating vital rates would be a problem that could not be resolved, given the temporal extent of 5- or 10-year-long studies. The focal level must shift to some level below population demography, which is analogous to going from Z to Y in Fig. 10.1B. Specifically, a coarser, less data-intensive approach (e.g., patch occupancy) would need to be selected.

It is clear that relationships cannot be detected unless sufficient changes in related components have occurred (Allen and Hoekstra, 1992). In our case, understanding how resource availability affects population demography requires a temporal extent long enough to capture sufficient variability in both resource availability and demographic rates. Variability in hard mast and soft mast was relatively minimal (except availability of soft mast in 2–9-year-old clear-cuts; Reynolds et al., unpublished data) in both the 5- and 10-year data sets; this helps explain why the null model ranked highest for both truncated data sets.

Our exercise in temporal extents has important implications for ecological research. In a field where study durations typically last 2 to 3 years, a temporal extent of 10 years is considered relatively long. Yet, a decade was still too short to completely understand how resources across a landscape affected the demography of bears. As landscape ecologists, we should be very concerned about mismatches in temporal extent. On the bright side, knowing that inferences can differ across temporal extents is useful for resolving conflicting results from multiple studies that evaluated the same ecological process. Inconsistent results among studies may be explained, at least in part, by their differing temporal extents.

10.3.3.2. Example 2: Mismatch in Temporal Grain

Results from our demographic analyses showed hard mast and soft mast across the landscape limited female bears in Pisgah. The additive effect of hard mast and soft mast across the landscape ranked highest for both fertility (Table 10.1) and λ (Reynolds et al., unpublished data). In addition, availability of 2–9-year-old clear-cuts helped explain bear fertility (Table 10.1). During years when availability of young clear-cuts was high, annual fertility increased. Our results indicated the relationship between clear-cuts and habitat quality was complex and involved tradeoffs. On one hand, clear-cuts had a negative effect because they removed hard mast (a limiting resource) for 25–50 years. On the other hand, clear-cuts had a positive effect because they increased availability of soft mast (a limiting resource), at least for $\sim$7 years (Fig. 10.5).

Importantly, our demographic analyses assumed bears used hard mast and soft mast when these resources were available. Similarly, we assumed bears used 2–9-year-old clear-cuts, and the resources within them, when they were available. If this assumption was invalid, our demographic results may have been spurious. Because we were interested in understanding the effects of clear-cuts on habitat quality, we needed to understand behavioral response of bears to clear-cuts.

A previous study on resource selection by PBS bears found females avoided young clear-cuts (Mitchell and Powell, 2003). The spatial grain of the resource data was 250 meters, which matched the spatial grain of the telemetry data. The Pisgah Bear Sanctuary defined the spatial extent (for 2nd order selection; Johnson, 1980). The temporal grain was 1 year and the temporal extent was 16 years.

For the study by Mitchell and Powell (2003) on resource selection by PBS bears, did the temporal scale (grain and extent) of the data match that of the ecological process? The study used a temporal extent of 16 years, which should have been long enough to incorporate both short-term and longer-term variability in resource selection. For example, if bears usually prefer hard mast stands in fall (long-term dynamic), but avoid them during years of hard mast failure (short-term dynamic), 16 years should have been sufficient to capture more than short term fluctuations. The temporal grain of the data was 1 year (annual home ranges). Though appropriate for understanding how clear-cuts affected habitat quality on an annual basis, a temporal grain of 1 year may not be the best choice for testing seasonal use of young clear-cuts by bears. During summer and early fall in the Southern Appalachians, bears forage extensively on soft mast (Beeman and Pelton, 1977; Eagle and Pelton, 1983). Assuming that soft mast is the only valuable resource available to bears in clear-cuts, the high availability of soft mast in 2–9-year-old clear-cuts in summer suggests summer home ranges should be used to understand the behavioral response of bears to young clear-cuts. By using the temporal grain of 1 year, the potential high use of clear-cuts during the summer could be obscured by low use during the rest of the year (Fig. 10.4). We re-ran analyses of resource selection by female bears in PBS using summer home ranges. If 2–9-year-old clear-cuts affected habitat quality positively by increasing availability of soft mast, we predicted females would prefer 2–9-year-old clear-cuts during summer.

We also expanded the analyses to evaluate behavioral response of bears to older clear-cuts. Although our demographic results indicated 2–9-year-old clear-cuts affected fertility positively (when the proportion of the landscape comprised $<5\%$ young clear-cuts), this analysis was insufficient for gauging the full effect of clear-cuts on habitat quality because it incorporated only the earliest portion of the successional life of a clear-cut. Availability of resources inside clear-cuts changes through time due to succession (Fig. 10.5). Therefore, the effect of clear-cuts on habitat quality will also change through time. Assuming that a primary effect of clear-cuts on habitat quality for bears is increased availability of soft mast, the positive effect of clear-cuts should be relatively short. After clear-cuts age beyond 9 years, availability of soft mast plummets and remains low for a relatively long time (40+ years; Fig. 10.5). We predicted, therefore, that PBS females would prefer 2–9-year-old clear-cuts and avoid 10–49-year-old clear-cuts during summer.

Using a temporal extent of 22 years and 103 summer home ranges, we found our observations matched our predictions. Females preferred 2–9-year-old clear-cuts, avoided 10–49-year-old clear-cuts, and used >50-year-old clear-cuts randomly during summer (Reynolds and Mitchell, unpublished data). Clearly, using annual home ranges to evaluate the importance of 2–9-year-old clear-cuts represented a confounding of seasonal patterns; relative lack of use during the portion of the year when berries were not produced obscured the seasonal importance of clear-cuts to black bears revealed in the demographic analyses. Whereas clear-cuts provide few if any resources important to bears throughout most of the year and most of their successional lives, the seasonal productivity in soft mast in the years immediately following clear-cutting appears to be important to successful reproduction of the bear population. The difference between our results and those of Mitchell and Powell (2003) suggests the temporal grain of 1 year used in the earlier study was too large to adequately capture the ecological process. To make certain the differences in results between the two studies were not due to differing temporal extents, we re-ran the analyses using the same temporal extent used by Mitchell and Powell (2003; 16 years) and found results were similar regardless of which temporal extent we used. Using annual data to understand an ecological process that occurs seasonally is analogous to evaluating the focal level Y in Fig. 10.1B using data collected at Z.

The importance of using the appropriate temporal grain to answer ecological questions cannot be overstated. Using temporal grains that are inappropriate to processes adds unnecessary noise to already complex systems, and may be manifested by inaccurate results. In our case, insights differed substantively depending upon which temporal grain we used. Studies in landscape ecology commonly justify the spatial resolution of data. Our results indicate similar attention should be given to temporal resolution of data.

10.4. Synthesizing Results Using Hierarchy Theory

We invoked hierarchy theory, which posits that levels of ecological processes are demarcated by differences in temporal rates, to understand the effects of clear-cuts and roads on habitat quality for bears in our study area. Hierarchy theory provides a framework for objectively defining levels of explanation (O'Neill and King, 1998). It is important to note that traditional notions of biological hierarchy (i.e., community, population, individual, organs, tissues, cells, etc.) may not be relevant to a study and could actually be inappropriate for understanding ecological systems with hierarchical levels defined by rate structures (King, 1997).

10.4.1. Defining Hierarchical Organization for Black Bears

For our study, we defined habitat quality in terms of survival and fertility, each of which are probably hierarchically organized. The temporal resolution at which each vital rate is manifested for bears, however, is likely to differ.

10.4.1.1. Survival Hierarchy

To understand how clear-cuts and roads affect habitat quality for bears in our study area by understanding the effect on bear survival, one can visualize a realistic hierarchy for bear survival as follows:

Phylogeny	$L + 1$
Annual survival rate	L
Daily survival	$L - 1$
Daily energy intake	$L - 2$
Daily avoidance of mortality factors	$L - 2$
Foraging efficiency	$L - 3$

If we take annual survival to be the focal level (L), then it is constrained by phylogeny ($L + 1$), which occurs slowly over evolutionary time. Bear survival is a day by day, minute by minute process, however, so annual survival is explained by daily survival, which is intimately linked with daily energy intake and daily avoidance of mortality factors (e.g., predators, hunters, and automobile collisions). Hence, daily energy intake and daily avoidance of mortality factors might be visualized to occur at the $L - 2$ level, and, foraging efficiency at the $L - 3$ level. If bear survival is hierarchically organized, then effects on L that occur at $L - 2$ and $L - 3$ levels will be relatively difficult to discern because $L - 2$ and $L - 3$ are buffered from the focal level (O'Neill and King, 1998).

10.4.1.2. Fertility Hierarchy

Alternatively, annual fertility for bears in our study area may be hierarchically organized as follows:

Phylogeny	$L + 1$
Annual fertility rate	L
Energy intake	$L - 1$
Foraging efficiency	$L - 2$

Annual fertility rate is constrained by phylogeny ($L + 1$). Unlike bear survival, bear fertility is not a day-by-day occurrence. If females do not acquire sufficient stores of energy during the year, they will abort their fetuses. Therefore, daily energy intake affects annual fertility, but only as a cumulative effect. Therefore, unlike the day-by-day processes that best explain annual survival for bears, annual fertility is most strongly linked with average energy intake over a year. Average energy intake is explained by foraging efficiency.

10.4.1.3. Combining Demographic and Behavioral Results

Results from our demographic analyses on PBS bears showed availability of 2–9-year-old clear-cuts affected annual fertility positively but had relatively little effect on annual survival. In other work (Reynolds and Mitchell, unpublished data), we have also evaluated the effect of roads on annual survival of PBS bears because roads may increase risk of mortality due to hunting, poaching, and automobile collisions (Pelton, 1986; Brody and Pelton, 1989). We found road use affected annual survival of PBS females negatively ($n = 66$; Reynolds and Mitchell, unpublished data). During years when females avoided areas near gravel roads, annual survival increased.

Results from resource selection analyses showed adult females preferred 2–9-year-old clear-cuts during summer. Because availability of soft mast may be a function of both its amount and arrangement on the landscape, the spatial pattern of 2–9-year-old clear-cuts (in which soft mast was highly available) may affect bear fitness. We tested this hypothesis by comparing resource selection between reproductively successful and reproductively unsuccessful female bears. Because foraging effort is minimized and energy accumulation maximized when foods are relatively clustered (Stephens and Krebs, 1986), we predicted soft mast would be relatively more clustered within home ranges of reproductively successful females if landscape pattern affected reproduction. Our results matched our predictions, but our sample size was small ($n = 10$; Reynolds and Mitchell, unpublished data) so conclusions should be viewed with caution.

We also partitioned the female population into survival groups (i.e., bears that survived and bears that did not survive) and compared resource selection for areas near paved, gravel, and gated roads, as well as resource selection for 2–9-year-old clear-cuts, between the two survival groups. We found females that were known to have survived ($n = 26$) avoided areas near gravel roads in fall more than females that were known to have died ($n = 15$), suggesting gravel roads exerted a selective pressure on survival. Conversely, preference for 2–9-year-old clear-cuts did not differ between the two survival groups, which corroborated our demographic results.

10.4.1.4. Survival, Time, and Space

We found gravel roads affected annual survival, but not annual fertility. Gravel roads affected annual survival negatively (demographic results) at the $L - 2$ level by affecting daily avoidance of mortality factors (i.e., hunters, poachers, and automobile collisions). In addition, females that were known to have died used areas near gravel roads more than did females that were known to have survived (behavioral results). We envision the hierarchy for bear survival as follows:

Phylogeny	$L + 1$
Annual survival rate	L
Daily survival	$L - 1$
Daily energy intake	$L - 2$
Daily avoidance of mortality factors	$L - 2$ (gravel roads)
Foraging efficiency	$L - 3$

10.4.1.5. Fertility, Time, and Space

We found 2–9-year-old clear-cuts affected annual fertility, but not annual survival. Availability of 2–9-year-old clear-cuts affected annual fertility positively (demographic results) at the $L - 1$ level by affecting energy intake. In addition, adult females preferred 2–9-year-old clear-cuts during summer (behavioral results). Moreover, the spatial arrangement of clear-cuts may have been effective, so 2–9-year-old clear-cuts may also have affected annual fertility by influencing foraging efficiency at the $L - 2$ level. We envision the hierarchy for bear fertility as follows:

Phylogeny	$L + 1$
Annual fertility rate	L
Energy intake	$L - 1$ (availability of 2–9-year-old clear-cuts)
Foraging efficiency	$L - 2$ (spatial arrangement of 2–9-year-old clear-cuts)

10.4.1.6. Using Hierarchical Organization to Interpret Effects of Forest Management

Overall, 2–9-year-old clear-cuts affected annual fertility positively at $L - 1$ and $L - 2$ levels while gravel roads affected annual survival negatively at the $L - 2$ level. According to hierarchy theory, higher levels have a relatively large effect on the focal level. Therefore, positive effects of clear-cuts on annual fertility at $L - 1$ level appear to be larger than the negative effects of gravel roads on annual survival at $L - 2$ level.

Individual vital rates (i.e., survival and reproduction), however, may not contribute equally to λ so the overall effect of clear-cuts and roads on habitat quality for bear populations may also depend on which vital rate contributes most to changes in λ. Adult survival is the vital rate with the largest potential to contribute to future changes in λ for bear populations (Freedman et al., 2003; Hebblewhite et al., 2003; Brongo, 2004). Therefore, the negative effects of gravel roads on bear survival may outweigh the positive effects of 2–9-year-old clear-cuts on bear fertility.

The hierarchies we envision for bear survival and reproduction may not be appropriate for evaluating other ecological processes. In our case, hierarchy theory provided a framework for synthesizing demographic results with behavioral results to better understand overall effects of timber harvesting on habitat quality for bears.

10.5. Conclusion

We have presented a concept of designing ecological studies that integrates 3 axes of ecological studies: temporal resolution of the study, spatial resolution of the study, and the resolution of the ecological process under study. We have argued that research that ignores the proper alignment of these axes can result in misleading results. Focusing on the integration of the temporal axis in landscape ecology studies, we provided empirical examples of how incorrect selection of temporal extent and grain biased findings in our own work with black bears. Finally, we proposed the temporal scales at which different vital rates are manifested in a bear population may differ, which may affect the way perturbations (e.g., clear-cuts, roads, etc.) affect habitat quality for bears.

The insights we present in this chapter are best fully considered when designing research, prior to the collection of data. It may be too late to realize that the three axes are insufficiently aligned to develop robust insights, once the data are collected. In developing our examples for this chapter, we had key advantages that few researchers enjoy—a large, long-term data set, the benefit of 20/20 hindsight and its inevitable companion, the realization that things could have been done differently. The challenges posed to a researcher at the beginning of the process, where three axes must be selected *a priori*, are more daunting. Generally, precedents in the literature may suggest candidate focal levels, but unless these precedents represent good (or fortunate) integration of the three axes, the possibility always remains that focal levels they suggest could be wrong. In the end, nothing can replace sound biological reasoning and some hard thinking about what is achievable within the temporal and spatial constraints imposed on any study by funding, time limits, and logistics. The latter are generally the least flexible part of any study and biologists need to be prepared to adjust their targeted levels of the ecological processes accordingly. Doing so might mean settling for less exciting but more accurate insights, or perhaps chasing the funding and study locations needed to address the more interesting questions with accuracy. In any case, mismatched axes of ecological studies should never be acceptable; we argue that researchers reporting their work should be every bit as explicit in presenting their choices along the three axes as they are with other aspects of their study design.

We do not suggest the process we recommend is easy or simple—just necessary. Researchers in landscape ecology do it every day, whether they know it or not. Every study design is implicit with respect to the 3 axes we define although interpretation of research results rarely is. We suggest that hierarchy theory provides one conceptual foundation for explicitly integrating spatiotemporal scales of data with resolutions of ecological processes. Further, we argue that doing so as part of research design and development would go a long way toward minimizing the ambiguous, contradictory, or ecologically questionable research in landscape ecology.

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11
Building and Using Habitat Models for Assessing Temporal Changes in Forest Ecosystems

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Abstract. Natural resources professionals face many long-term issues related to the use and management of forest resources including understanding: (1) the dynamic nature of forest ecosystems; (2) how management activities influence forest characteristics spatially and temporally; and (3) how wildlife respond to changes over time. One method used to assess the effects of long-term temporal changes in forest ecosystems involves the use of ecological classification systems, where ecosystems are classified and mapped according to specific biotic and abiotic properties, and facilitate assessment of distributions and movements of wildlife populations based on the identification of the spatial and temporal characteristics of the resources necessary for survival. Habitat type classification systems, provide a basis for predicting vegetation development and successional change. In this chapter, we describe how we constructed a habitat type ecological classification system using three case studies from Michigan to assess temporal changes in forests and wildlife habitat. In the first case study, we determined the potential of landscapes to provide white-tailed deer habitat components. The second case study addressed how managers and planners can understand the spatial and temporal effects of aspen management practices. The third case study integrated land-use, land-cover, and habitat classification to model temporal changes in locations and habitat suitability for the regionally threatened Canada lynx in the Upper Peninsula of Michigan. We argue that natural resource managers and planners can make more realistic predictions of changes in distributions of forest resources important for wildlife based on an understanding of the structural and compositional dynamics of specific vegetation types through time.

11.1. Introduction

Wildlife and forest biologists, planners, and managers face many long-term issues related to the use of forest resources, e.g., timber harvest sustainability, and understanding wildlife-habitat relationships. In the mid-1900s, forestland was managed primarily to yield specific crops (Kessler et al., 1992). Only within the past 35–40 years has a multiple use philosophy of forest management developed (Kessler et al., 1992). Sustaining forest ecosystems to meet diverse forest and wildlife objectives is a non-trivial challenge and involves understanding the ecological factors that influence vegetation change; how specific forest manipulations affect temporal and spatial changes in forest characteristics; and wildlife response.

The spatial and temporal distribution and availability of ecological resources in landscapes has important implications for wildlife and forest management. It is difficult, for example to understand the dynamic relationships between wildlife and their habitats without understanding the underlying regulatory mechanisms within landscapes and the processes by which habitats within landscapes change over time. This type of information is especially critical as agencies develop management plans within an ecosystem management framework to sustain forests for multiple purposes. Current land-cover classifications and maps are used widely by natural resource managers and planners to understand wildlife-habitat relationships and plan management activities (Box 11.1), but they do not identify vegetation structure, potential vegetation trends and successional dynamics, or vegetation types on distinctive soils that may have different wildlife values. Consequently, it is difficult to use only land cover to evaluate wildlife species responses to management or to ecosystem changes because assumptions about potential vegetation and successional dynamics can lead to unrealistic predictions.

Box 11.1. Using land-cover data to understand wildlife-habitat relationships.

Land-cover classifications and maps portray the spatial distribution of ground features (e.g., urban areas, bare soil, pasture) or vegetation types in an area at a specific time. Most land-cover maps are developed from remote sensing, which is the process of deriving information about the earth's surface from aerial photos, satellite imagery, or other images acquired at a distance (Campbell, 1987). Prior to using land cover maps, accuracy, spatial extent, and resolution should be assessed, and researchers should determine what is acceptable to investigate their specific questions. Accuracy, spatial extent, and resolution are all affected by the method used to collect spatial data. For wildlife habitat assessments, most land-cover maps based on satellite imagery have 15–100-m spatial resolution, but images with resolutions <1 m are becoming more accessible (Glenn and Ripple, 2004). Land-cover maps are widely used in wildlife-habitat assessments because they indicate composition, interspersion, and juxtaposition of vegetation types. For instance, researchers use land-cover maps to determine the composition of vegetation within home ranges of animals, or evaluate habitat suitability. Land cover also does not identify potential vegetation or distinguish between vegetation types on different soils that may have different wildlife values. Consequently, it is difficult to use only land cover to evaluate wildlife responses to management or ecosystem change.

Recently developed approaches using ecological classification systems (ECS) allow evaluations of land-use and land-cover based on biotic and abiotic properties of ecosystems. A useful approach is to use an ECS to describe potential and current ecological conditions that influence wildlife habitat quality as well as describe the spatial and temporal changes in habitat availability and distribution. However, because habitat is species specific (Box 11.2) and has a spatial extent determined by the ecology of a particular species during a particular time (Morrison, 2001), using only one ECS may not be appropriate to assess distributions and quality of habitat for all wildlife species. Nevertheless, ECSs are important tools for assessing spatial and temporal patterns in the potential distributions of wildlife.

Box 11.2. Explanations of terms.

Some terms frequently used in the ecological literature are often vague or misunderstood. Below are definitions and explanations of important terms and concepts that we use in this chapter.

Habitat: Habitat contains the abiotic and biotic factors in an area that interact and provide the minimum conditions for occupancy and reproduction of organisms (Daubenmire, 1968; Morrison, 2001). Vegetation types with specific structural and compositional attributes can provide habitat components for individuals within species, but habitat is the sum of all resources necessary for survival and reproduction.

Habitat classification: Habitat classification places vegetation types or other defined areas into categories to reflect habitat quality for a particular species or population.

Habitat type: Habitat types have “equivalent climax potentialities” if they occur in areas with the same ecological, geological, and climatic attributes (Daubenmire 1966:297). A habitat type has a predictable successional pathway.

Habitat-type classification: Classifications based on vegetation composition that “group communities and their environments into categories useful for management interpretation” (Kotar and Burger, 2000). Habitat type classifications allow an understanding of successional trajectories and distribution of ecological communities that reflect inherent site capabilities, and disturbance and management history.

Vegetation type: A vegetation type is an assemblage of plants that typically occur together in an area and have similar composition. Vegetation types are seral stages of habitat types.

Habitat type classifications, a type of ECS, can facilitate assessment of intraspecific distribution and movements based on a spatially and temporally informed identification of resources necessary for survival (Box 11.2). Abiotic ecological characteristics such as climate, landforms, and soil characteristics (e.g., nutrient content, moisture, texture) influence differences in vegetation structure, composition, and successional patterns within different habitat types (Crawford, 1950;

Daubenmire, 1966). Although the boundaries and dynamics of habitat types are not static, they define a relatively narrow range of environmental conditions (Kotar and Burger, 2000) that can provide a basis for predicting vegetation change over time within natural successional pathways or as a result of certain land-use and management practices. Linking these predictions with habitat suitability modeling can aid in evaluating the probability of species persistence during a given time frame and location in a landscape. This approach can be useful for identifying areas where management would benefit wildlife species. Understanding temporal changes in vegetation distribution, composition, and structure is critical for developing forest management models, which can be used for planning and evaluating effective practices to meet ecosystem management objectives.

In this chapter, we describe how we constructed a habitat type classification system (hereafter referred to as HCS). Using three case studies from Michigan, we demonstrate how we used models with a HCS to assess temporal changes in forest wildlife habitat. In the first case study, a HCS and habitat potential models were used to determine the potential of landscapes to provide white-tailed deer habitat components (viz., fall/winter food, winter thermal cover, spring/summer habitat). The second case study characterized how successional changes in structure and composition of aspen (*Populus* spp.) in different habitat types could be modeled and used by managers and planners for understanding cumulative effects of forest management practices on wildlife communities that depend on aspen. The third case integrated land-use, land-cover, and habitat classification data to model temporal changes in the location and suitability of habitat for the regionally threatened Canada lynx (*Lynx canadensis*) in the Upper Peninsula of Michigan over the last century.

11.2. Habitat Types: Ecological Classification Systems to Characterize Spatial and Temporal Variation

Ecological classification systems generally have three characteristics: (1) they provide maps of land units that have similarities in biotic and/or abiotic characteristics at multiple spatial scales (i.e., extent and resolution), (2) they provide data that can be used to help describe the ecological potential of geographic areas, and (3) they integrate biotic and/or abiotic information at multiple spatial scales to help understand the dynamics of ecosystem processes and wildlife-habitat relationships (Box 11.3). For example, classification systems that are based solely on abiotic attributes (e.g., Bailey, 1976, 1980) such as climate, geological characteristics, landforms, or soils are often used by management agencies to investigate ecological patterns over relatively large spatial extents (e.g., >10,000 ha). In contrast, classification systems that are based solely on biotic attributes, such as vegetation cover (e.g., presettlement vegetation for Michigan; Michigan Natural Features Inventory [MNFI] 1999) or land use, typically are based on a wider range of spatial extents (e.g., perhaps up to 250,000 ha or larger) and can be used by natural resource

Box 11.3. Ecological Classification Systems.

Ecological classification systems (ECS) are used to classify and map ecological units according to specific abiotic and biotic properties of ecosystems. ECS developed from a need for land-use planning assessments. One of the earliest uses of ECSs for natural resources planning and management was the National Hierarchical Framework of Ecological Units developed in the early 1990s by the US Forest Service (Bailey et al., 1994; McNab and Avers, 1994). By 1995, the US Forest Service also developed an additional ESC for aquatic ecosystems (viz., Hierarchical Framework of Aquatic Ecological Units; Maxwell et al., 1995) that was based on physical and biological criteria. Today, state and federal agencies, organizations, and industries are using variations of these ECSs to quantify availability and distribution of resources across a given landscape, and to model how temporal changes in ecological conditions throughout landscapes influence the abundance and population structure of species, the spatial structure of popultions, and temporal changes in wildlife habitat suitability (Morrison et al., 1992).

professionals to plan management activities in individual stands and across landscapes. Lastly, ECSs that have been developed by integrating biotic and abiotic characteristics (e.g., Cleland et al., 1985; Haufler et al., 1996; Kotar and Burger, 2000; Felix et al., 2004), can be used to describe the potential and current ecological conditions that may influence wildlife habitat suitability as well as describe the spatial and temporal scales at which wildlife select habitat components. For example, Kotar and Burger (2000, pp. 1–5) developed a HCS in the Great Lakes Region of the USA for "site classification that used floristic composition of plant community as an integrated indicator of environmental factors affecting species reproduction, growth, competition, and therefore, community development." For this HCS, the environmental factors used to distinguish habitat types were primarily combinations of soil properties such as moisture and nutrients. Abiotic properties like these are useful to help explain variations in ecosystems.

11.2.1. Methods of Constructing Habitat-Type Classification Systems

Several approaches have been used in constructing habitat type classification systems that include biotic and abiotic attributes of a specific geographic region. Felix et al. (2004) constructed a HCS for several regions in Michigan that included digital layers obtained from the Michigan Department of Natural Resources. At the broadest layer, Albert's (1995) eco-regions provided the basis for delineating and classifying habitat types because they defined climatic-physiographic boundaries that affected species composition and plant productivity at broad-scale extents (e.g., 1,000–40,000 ha; Albert, 1995). The next two layers included geological information such as land type associations (i.e., geomorphic features defined by parent material and superficial topography), and soil texture and drainage properties. The last layer included information on potential vegetation and boundaries of forest types from presettlement maps (Michigan Natural Features Inventory (MNFI), 1999). Felix et al. (2004) validated habitat types with current land-cover maps by determining if vegetation composition identified from the maps coincided or was congruent with the successional stage of the habitat type with which it intersected. Some areas were validated on the ground by assessing composition of understory vegetation. Essentially, the boundary of a habitat type was defined by the intersection of eco-regions, geological information, and vegetation layers (Fig. 11.1). Habitat types can potentially include several different vegetation types or successional stages (Fig. 11.1). Successional trajectories within habitat types were identified using information from the literature (Coffman et al., 1980; Burger and Kotar, 1999; Kotar and Burger, 2000). Understanding the potential successional trajectory within habitat types is the basis for understanding distributions and ranges of vegetation conditions caused by temporal changes and successional processes that occur within a geographic region.

11.3. Case Studies

11.3.1. Modeling Spatial and Temporal Distributions of White-Tailed Deer Habitat

One challenge that many state wildlife management agencies have been confronted with in recent decades has been the management of white-tailed deer populations and their habitat. For example, McShea et al. (1997, p. 1) commented that, "... deer populations have burgeoned and currently exist at densities exceeding historical levels ... ." In an effort to meet the challenges of white-tailed deer management, researchers from the Michigan Department of Natural Resources and Michigan State University undertook a project with the goal of developing a process to quantify the ecological suitability of landscapes to support potentially different populations of deer throughout the state. The ability to quantify how deer habitat suitability varies spatially and temporally as a result of different abiotic conditions in landscapes is valuable for setting ecologically based harvest quotas and planning habitat management activities. A desirable outcome of this project was the development of a process to quantify the potential of landscapes to support deer using habitat type classifications and other existing data to generate a spatial and temporal representation of deer habitat suitability patterns statewide.

To gain a greater understanding of the potential of Michigan landscapes to provide suitable habitat over time, Felix et al. (2004) developed a landscape-scale deer habitat potential model, identified how vegetation structure and compositional characteristics within habitat types changed throughout succession, and then used habitat suitability index (HSI) models to quantify how suitability of three deer habitat components (viz., fall and winter food, winter thermal cover,

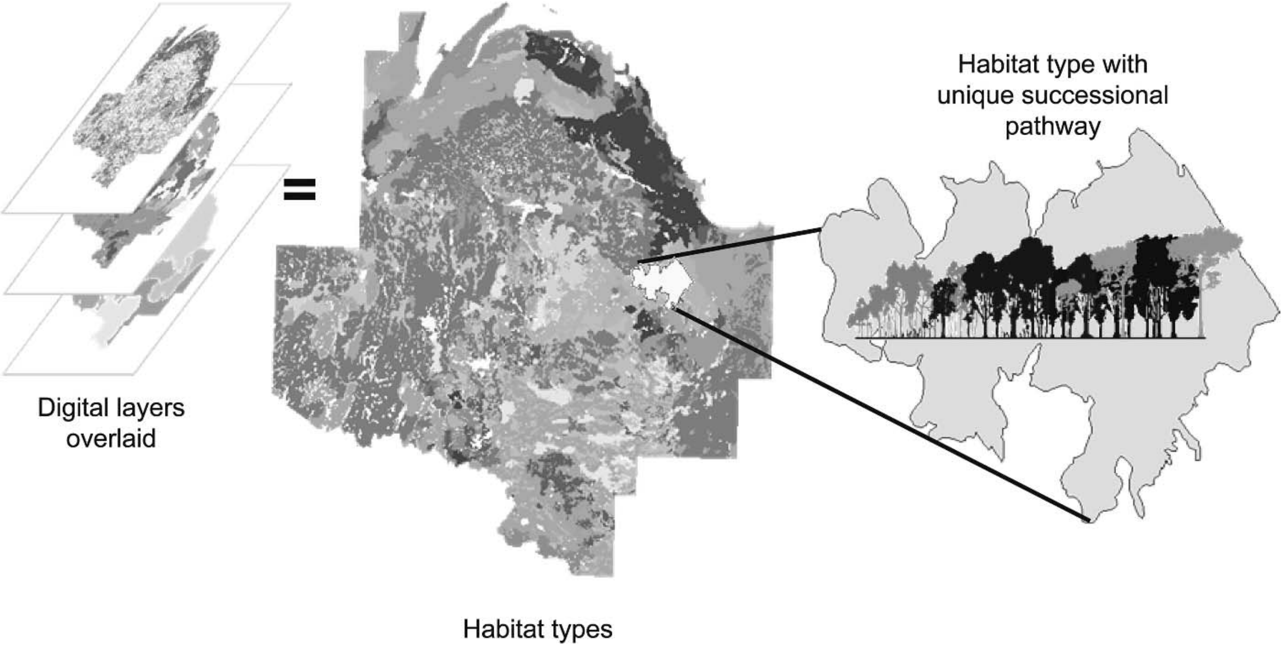

FIGURE 11.1. Building a habitat-type classification system. Boundaries of habitat types can be determined by overlaying digital spatial layers. These layers can include information about climate and broad regional differences, geological characteristics, and potential vegetation, or boundaries of forest types. Each habitat type contains a unique successional pathway that is determined from biotic and abiotic properties. Understanding the successional pathway of vegetation and the biotic and abiotic factors that affect succession can help managers plan forest management activities.

spring and summer habitat) would change throughout succession, given changing vegetation physiognomy within different habitat types. The results allowed managers to identify which successional stages of specific habitat types could provide deer life requisites. For instance, a common habitat type in the western Upper Peninsula of Michigan supports aspen in early successional stages (<30 yr old); sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), and ironwood (*Ostrya virginiana*) in intermediate stages (30–100 yr); and is dominated by sugar maple and hemlock (*Tsuga canadensis*) in late stages (>100 yr). Intermediate successional stages provide high suitability for fall and winter food, whereas spring and summer habitat potential is highest in early stages (Fig. 11.2A,C). Because well-drained loamy soils are not conducive for growing lowland swamp conifers, this habitat type will likely not provide winter thermal cover for deer regardless of successional stage (Fig. 11.2B).

11.3.2. Understanding Temporal Variation in Aspen Forests To Assess Management: Effects on Timber Production and Wildlife Habitat

A major challenge facing natural resource professionals is to sustain natural systems and human commodities in the context of a growing human population and its associated demands on natural resources (Kessler et al., 1992). Aspen, for example, is a commercially valuable timber resource that is used to produce pallets, plywood, and pulpwood for paper, cardboard, and boxes. In the Lake States (Michigan, Minnesota, Wisconsin), aspen constitutes more than half of the industrial timber harvested annually, produces approximately four million cords of pulpwood (Piva, 2003), and with a value of more than \$2 billion annually (\$60 per cord delivered to the mill; Miller, 1998). In addition to economic demands on aspen, several wildlife species including ruffed grouse (*Bonasa umbellus*), white-tailed deer, many small mammals, and cavity-nesters also depend on it to meet their life requisites (Stelfox, 1995). As such, Michigan's aspen management goal includes maintaining a diversity of aspen age classes within the landscape to sustain wildlife habitat, ecosystem integrity, and social and economic values associated with aspen forests (B. Doepker, MDNR, unpublished data). The challenge associated with meeting this goal lies with multiple-use and ecological demands on the aspen resource. For example, aspen in Michigan may live past 100 years old, but begin to show signs of decline in commercial value after 60 years old (Graham et al., 1963). For maximum timber value, most aspen are harvested on a 45–50-year-old rotation depending on site quality (Brinkman and Roe, 1975). As a result, certain aspen age classes are not well represented in the landscape. Approximately 10% of all aspen in the western Upper Peninsula of Michigan, for instance, is 40–60 years old, whereas 42% is 10–30 years old (B. Doepker, MDNR, unpublished data). When certain vegetation types are not represented in landscapes (e.g., 40–60-year-old aspen), wildlife habitat components provided by those vegetation types are also not present. Thompson and Stewart (1998) argued that attempts to manage wildlife

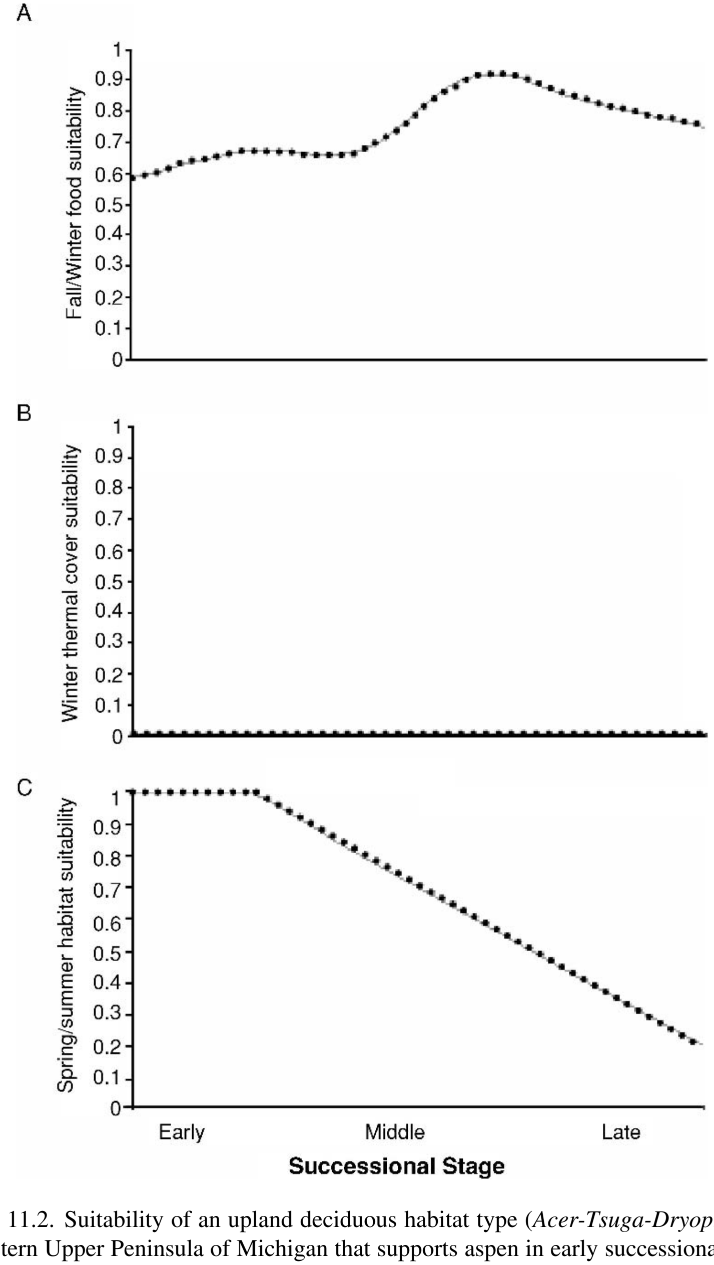

FIGURE 11.2. Suitability of an upland deciduous habitat type (*Acer-Tsuga-Dryopteris*) in the western Upper Peninsula of Michigan that supports aspen in early successional stages (aged <30 yr), sugar maple–red maple–yellow birch–ironwood in middle stages (aged 30–100 yr), and sugar maple–hemlock in late stages (ages >100 years) to provide 3 white-tailed deer habitat requirements throughout succession: fall and winter food (A), winter thermal cover (B), and spring and summer habitat (C). Suitability ranged from 0 to 1; 1 represents optimal conditions. Fall and winter food potential for this habitat type was 0.92 (i.e., 0.92 was the highest suitability to provide deer fall and winter food that this habitat type can attain throughout succession). Thermal cover potential was 0.0, and spring and summer habitat potential was 1.0.

populations without knowing the relationships between the capability of an area to support a population and population productivity is costly and ineffective, wastes time and resources, and may jeopardize wildlife populations. In response to a need to understand how aspen forests are affected by patterns of resource use as well as the cumulative effects of tree harvesting (Kessler et al., 1992; Davis et al., 2001), we recently initiated a study to assess what timber values and wildlife habitat components are provided by different successional stages of aspen, and to assess how harvesting activities influenced the structure and composition of vegetation within aspen stands as well as the spatial arrangement of vegetation types across the landscape. In this case study, a modeling process was developed that allowed managers to understand the critical times when areas are capable of supporting deer during succession (Fig. 11.2) and allowed them to plan management activities that maintained deer habitat components across the landscape and to plan harvest quotas based on the potential of specific areas to support deer populations.

11.3.2.1. Determining Differences in Aspen within Different Age Classes and Habitat Types

The study area was located in the western Upper Peninsula of Michigan and included Baraga, Dickinson, Iron, Marquette, and Menominee counties. Biologists knew the current spatial distribution of aspen in the study area from land-cover data sets (e.g., IFMAP [Integrated Forest Monitoring and Assessment Prescription; Michigan Department of Natural Resources (MDNR), 2003]) and also knew the current distribution of aspen age classes in the landscape from forest records kept by the MDNR.

Using an ECS developed by Coffman et al. (1980), habitat types were identified in the study area (Felix, 2003). By overlaying the current distribution of aspen on the habitat type data layer using a Geographic Information System (GIS), Felix (2003) determined within which habitat type each aspen stand was associated. According to Coffman et al. (1980), aspen occurs as an early successional vegetation type in 14 of 21 habitat types in northeast Wisconsin and in the Upper Peninsula of Michigan. These habitat types have soils ranging from very wet and poorly drained to dry and nutrient rich. Within the habitat types that supported aspen, quaking aspen (*P. tremuloides*) occurred in all 14, whereas bigtooth aspen (*P. grandidentata*) occurred only in half, most of which were characterized by dry-mesic to mesic soil conditions. Because aspen can occur over a wide range of ecological conditions, the successional trajectories of the vegetation type may differ.

To investigate differences in aspen structure and composition throughout succession, three age classes in three distinct upland habitat types were selected to assess forest attributes and their associated wildlife habitat characteristics. The selected habitat types were named for the tree species (genus) that showed the strongest tendency to dominate a community on that site in the absence of disturbance, and the genus of characteristic understory species (Coffman et al., 1980). Aspen stands were selected within the 20–29-, 50–59-, and ≥70-year age classes. Selected habitat types included *Tsuga-Maianthemum* (hemlock-Canadian mayflower), *Acer-Tsuga-Dryopteris* (maple-hemlock-fern), and *Acer-Viola-Osmorhiza* (maple-violet-sweet cicely; Coffman et al., 1980). By determining the habitat type in which each aspen stand was located, managers were able to predict which vegetation types were likely to succeed aspen.

Next, forest attributes of each stand were sampled to determine differences in vegetation structure and composition of stands within different age classes and habitat types. Attributes including stem density, tree diameter, basal area, tree height, canopy cover, species composition, and density and size of down woody debris were measured within each stand. These attributes can be used with habitat models to determine habitat quality for various wildlife species. Wildlife surveys, including breeding and winter bird surveys, were conducted to determine differences in wildlife composition between age classes and habitat types. With this information, a database was compiled that included for each aspen stand sampled, its location, age class, vegetation structural and compositional characteristics, its associated habitat type and successional trajectory, and its wildlife community associations.

11.3.2.2. Modeling Temporal Changes in Aspen Communities

The utility of having a database that included structural attributes of specific forest stands, wildlife associations, and successional trajectories was evident when developing a modeling process to predict the effects of timber harvesting on timber production and wildlife communities over time. Once information is compiled on vegetation structure, composition, and wildlife associations of different aspen age classes within different habitat types, it can be linked to a spatial dataset (Fig. 11.3). Structural and compositional characteristics of stands that were not sampled can be added to the dataset under the assumption that the structure and composition of stands will occur within the range of conditions identified for the sampled stands of the same age, habitat type, and management history. In this manner, forest managers and planners can understand spatial and temporal variation in forest structure and composition.

Forest management models such as HARVEST (Gustafson and Rasmussen, 2002) can then be used to evaluate how different harvesting alternatives affect landscape structure parameters such as age distribution, distribution of edge, and interior patches (Gustafson and Rasmussen, 2002). Harvest simulation provides information on interspersion and juxtaposition of vegetation types and age classes following harvest, but does not indicate how vegetation types, stand structure, composition, and wildlife associations may subsequently change throughout time following harvest. Those attributes, however, can be determined with data on habitat type and successional dynamics. If aspen stands are not harvested, we can predict how structure, composition, and wildlife associations will likely change as stands within different habitat types age between 20 and 70+ years (Fig. 11.3). For example, aspen basal area is one descriptive metric of ecological differences among age classes and habitat types. Forest managers and planners can associate aspen basal area measurements with age classes and habitat types and then simulate how basal area may change spatially and temporally following a harvest or over time (Fig. 11.3). Once management alternatives are simulated, each alternative

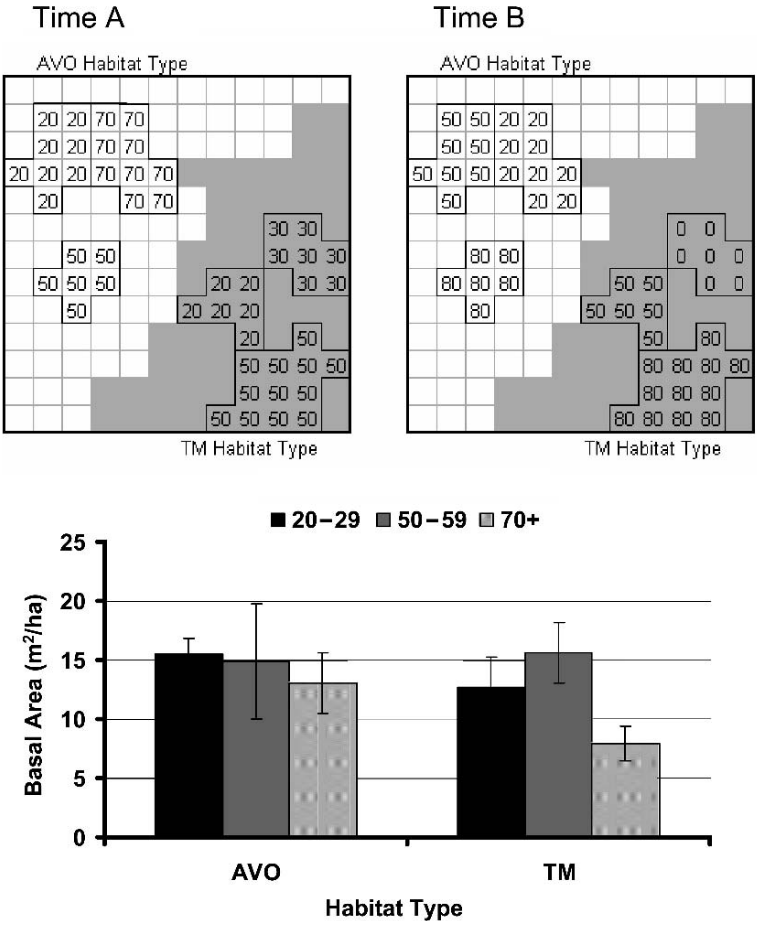

FIGURE 11.3. Spatial and temporal representation of aspen and age distributions within two habitat types (*Acer-Viola-Osmorhiza* [AVO] and *Tsuga-Maianthemum* [TM]) in the western Upper Peninsula of Michigan. Aspen basal area will vary over time and within different habitat types. By understanding variations within habitat types, managers and planners can simulate how age and distribution of aspen will change over time and link structural and compositional characteristics (such as basal area) to those distributions. Spatial and temporal distributions of timber production potential and wildlife habitat suitability can also be simulated following management or throughout natural successional trajectories.

can be analyzed to determine which management decisions would maintain long-term sustained timber yield, enhance wildlife habitat suitability, or evaluate how to meet different wildlife or biodiversity objectives. For example, managers might use habitat types and models of successional changes within forests to understand temporal changes in bird community distribution or timber production potential (Fig.11.4). Changes in habitat suitability for different wildlife species or groups of species can be modeled throughout time from data collected on structural and compositional changes in aspen growing on different habitat types (Fig. 11.3).

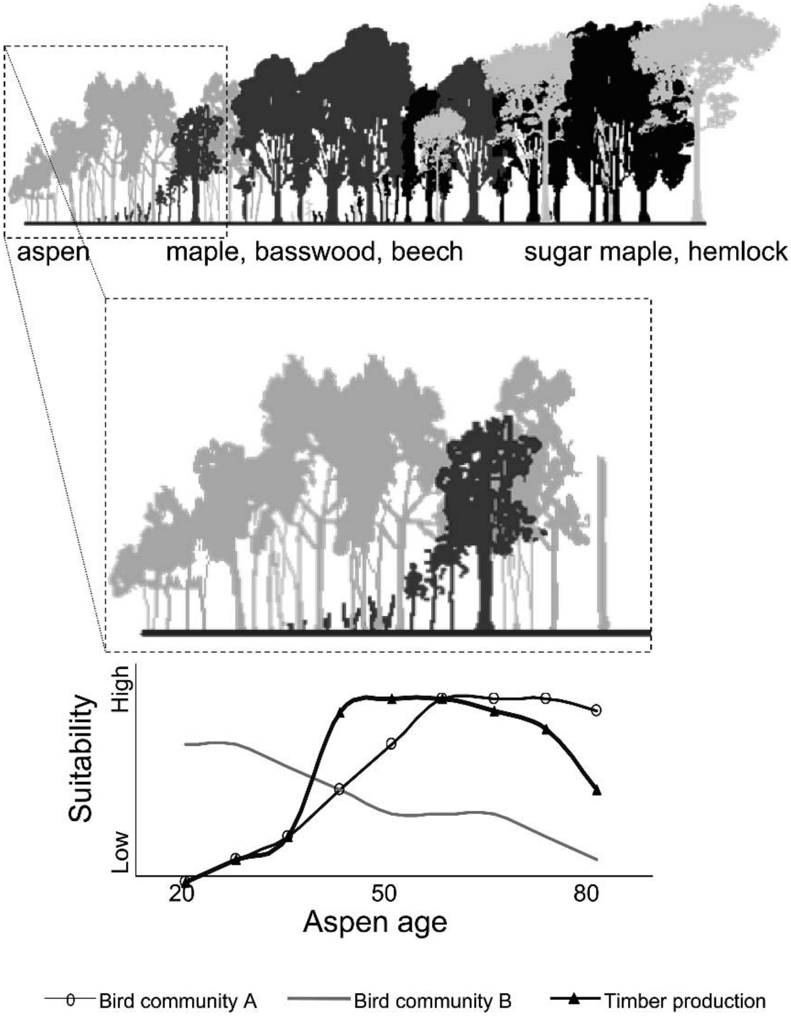

FIGURE 11.4. Hypothetical example of how managers might use habitat types and modeling of habitat and timber production potentials to understand changes in wildlife community distribution and timber harvesting potentials. Output from habitat potential models developed for each wildlife species or community could produce suitability curves that would indicate which seral stages provide habitat for different forest wildlife. For example, throughout aspen succession in certain habitat types, habitat suitability for cavity-nesting birds would likely increase as the availability of large snags increases. Habitat suitability for ground-nesters may follow a different curve. Timber production potential may also have a certain threshold, which may differ among habitat types.

Timber production potential can also be modeled throughout aspen succession (Fig. 11.4). In a dry upland hardwood habitat type, habitat suitability for bird community A (e.g., cavity nesters) increases as aspen ages and the diameter and density of snags increases (Fig. 11.4). Habitat suitability for bird community B (e.g., ground nesters) decreases. Timber production potential is highest when aspen is 40–60 years old, but then decreases with aspen age (Fig. 11.4).

Managing forests for long-term silvicultural and wildlife objectives is challenging. Davis et al. (2001) noted that the key to managing land scientifically lies in the ability to predict the outcomes of current management practices. We argue that combining habitat type classification systems with successional models will help wildlife and forest managers understand the consequences of forest management decisions before they are made and allow them to meet other management objectives; e.g., mature oaks [*Quercus* spp.] for mast production, lowland conifers to provide winter thermal cover for ungulates, or northern hardwoods for timber products. Managers also may wish to know how individual stand treatment might affect wildlife, given the landscape in which the stand is located. For example, when planning aspen management practices, managers may be confronted with the decision to harvest aspen potentially on three sites: a mesic site, a poorly drained site, and a well drained xeric site. The three stands in all probability have vastly different successional trajectories that influence their composition and structure. Within each site, different types of ecological and economic objectives can be met by deciding whether or not to harvest aspen. Aspen stands on the mesic site may be primarily influenced by disturbances such as blow downs or herbivory, since mesic soils likely contain greater nitrogen concentrations that attract herbivores. High water levels may influence aspen on poorly drained soils. Lastly, aspen on xeric sites may be more frequently subjected to wildfires and those stands on south facing slopes may face a greater risk of developing sunscald and/or infusion by pathogenic fungi (e.g., *Cystospora chrysosperma*; Hart et al., 1986). Harvesting each of the three mature stands would likely result in regenerating aspen but with potentially different species and stocking densities. The decision to avoid cutting stands will also create different forest conditions. By considering the diversity of site conditions as well as the temporal dynamics associated with the site conditions, managers can ask "what-if" questions in order to realize a greater range of management options associated with wildlife habitat or timber harvesting planning.

11.3.3. Determining Spatial and Temporal Changes in Lynx Habitat

In 2000, the Canada lynx was listed as a federally threatened species in the contiguous United States in accordance with the Endangered Species Act of 1973, and following an investigation regarding its status (US Fish and Wildlife Service, 2000). The USFWS determined that some current land management practices had the potential to negatively affect lynx and lynx habitat. In light of the final ruling, government agencies have been faced with developing and implementing management strategies that facilitate lynx populations on public lands. The Hiawatha and Ottawa National Forests, located in the Upper Peninsula of Michigan, represent areas where lynx habitat management has become a concern.

Lynx historically inhabited Michigan (Wood and Dice, 1924), but population numbers had dwindled to near extirpation by the first half of the 20th century (Michigan Department of Conservation, 1938). A sharp increase in the number of individuals trapped in the 1960s led to the impression that the species was making a "comeback" (Harger, 1965, p. 152), but McKelvey et al. (2000) attributed the increase to an irruption of lynx populations in Canada, leading to migration of individuals. Biologists have found no recent evidence of a resident population in the state (Beyer et al., 2001). It is possible that individuals dispersing from Canada may enter the state occasionally. A number of factors, including inadequate prey densities, interspecific competition from bobcat (*Lynx rufus*) and coyote (*Canis latrans*), and increased forest fragmentation due to anthropogenic land uses (Koehler and Aubry, 1994) may be inhibiting lynx from persisting in the Upper Peninsula, similar to other areas in the southern part of their range. An examination of the changes in forest conditions and land cover throughout the Upper Peninsula over the last 150+ years may help us understand if these changes have affected lynx habitat suitability. This case study describes how the current amount and distribution of lynx habitat in the Upper Peninsula of Michigan was determined, and how suitability may have changed from presettlement times. The use of a habitat type classification system to assess lynx habitat suitability and temporal changes in suitability facilitated this large-scale analysis.

11.3.3.1. Quantifying Lynx Habitat Suitability

The resource most important to lynx survival is its primary prey, the snowshoe hare (*Lepus americanus*). The patterns of habitat use exhibited by lynx are likely to be strongly correlated with those of hare (e.g., Keith, 1963; Nellis et al., 1972; Brand et al., 1976). The synchronous fluctuation between the two species' populations has been well documented, though there is some debate as to whether southern populations show the same pattern (see review in Hodges, 2000). An adequate amount of early successional vegetation types with dense understory is required to sustain hare populations, and for lynx an interspersion of relatively mature forest is needed (O'Donoghue et al., 1998; Mowat et al., 2000). Lynx use mature forest stands for denning and the amount of down woody debris is the most common characteristic found to be an indicator of good denning conditions (Mowat et al., 2000). Old growth forests with a conifer-dominant climax stage have the potential to provide a mosaic of dense understory beneath the sparse canopy and an adequate array of woody debris, thus containing the structural attributes important to lynx and hare (Buskirk et al., 2000). Some forest types may, therefore, provide a bimodal distribution of suitability for snowshoe hare. Identifying suitable habitat for snowshoe hare and lynx depends upon the ability to locate forest stands throughout the landscape that contain adequate understory cover.

A habitat suitability model for Canada lynx, developed by Roloff and Haufler (1997), integrated the concepts of a habitat suitability index (HSI) with that of population viability at multiple spatial scales through use of a GIS. The model determined the number of viable and marginal lynx home ranges within the landscape based on three components (foraging, denning, and interspersion of non-habitat). The foraging component, considered the most limiting factor, was modeled by a HSI for snowshoe hare, in which horizontal understory cover was the predominant variable. The estimation of lynx home ranges was based on thresholds of habitat quantity and quality that described the minimum requirements of a given area to support a lynx (Roloff and Haufler, 1997). The habitat quantity threshold was determined by calculating the minimum allometric home range for lynx (i.e., 250 ha); the habitat quality threshold was arbitrarily chosen based on relationships between viability indicators (e.g., survival, pregnancy rate) and home range estimates from previous lynx studies. The key to this methodology was the input of an ecological land classification in the form of a GIS grid that stratified the spatial variation in attributes measured by the HSI model (Roloff and Haufler, 1997).

11.3.3.2. Estimation of Current Forest Conditions

Multiple spatial layers (eco-regions, land-type associations, soils, vegetation) were combined to create the HCS which contained compositional attributes and successional trajectories of forest stands. Quantifying the structural attributes to assess current distribution of lynx habitat, however, required the collection of additional information.

Box 11.4. Forest Inventory and Analysis Program.

The USDA Forest Service has been tracking changes in the nation’s forests since Congress mandated a national inventory of all timberland in 1928. The Forest Inventory and Analysis (FIA) program was implemented mainly for the assessment of timber resources. A new emphasis on ecosystem monitoring within the last 20 years has resulted in an expanded set of collected data providing greater information on temporal trends in forested ecosystems (Smith, 2002). Historically, surveys were conducted periodically within a state on 10–12-year rotations. New legislation in 1998 requires that a portion of plots within each state (10–20% depending on the state) be sampled annually on continuous cycles. In Michigan, 20% of all plots are sampled each year, resulting in a completed cycle every 5 years. The temporal and spatial scales of this data collection make it useful for assessing both short-term and long-term ecological issues over large areas. The FIA program is considered “a powerful tool for providing statistically sound and scientifically reliable data and information for monitoring the sustainability of the nation’s natural resources” (Smith, 2002:S235). More information about the program can be found on the FIA website: www.fia.fs.fed.us.

The Forest Inventory and Analysis (FIA) program of the USDA Forest Service collects tree-level plot surveys located systematically throughout forested land in each state, including Michigan (Box 11.4). These stand level data were input to forest modeling software, including the Forest Vegetation Simulator (FVS) and the Stand Visualization System (SVS). Structural variables (e.g., basal area, stem density, canopy cover) necessary for the lynx model were computed. Understory cover was an important variable not directly measured in the plot surveys, so it was estimated by examining simulated diagrams generated by SVS. FIA plot locations were overlaid with a grid of the habitat type classification in a GIS, allowing plot information to be attributed to each spatial class. The sampling protocol for the sixth cycle (2000–2004) of the FIA program (Box 11.4) resulted in data from nearly 4,000 plots in the Upper Peninsula (with 80% of the survey goal complete) being available for the overlay. This sample size of plot data was adequate for describing the current range of forest conditions in the Upper Peninsula, but the grid classes were too coarse to adequately account for the spatial variation in forest structure. Another spatial layer was required to account for structural differences across large tracts of compositionally similar forest types (i.e., within a grid class).

The final spatial layer was created through predictive modeling of forest structure using spectral satellite imagery, which provided a way to map variation at a resolution of 30 m. The methodology used was k-nearest neighbors (KNN) classification, which assigns values to non-sampled pixels based on their feature space distance from sampled pixels (i.e., those associated with FIA plots). Multidimensional feature space is defined by the spectral values measured for each of the band wavelengths at each pixel in the image. A summary of this process and its prior application was described by Franco-Lopez et al. (2001), who utilized FIA plot surveys from Minnesota for KNN classification of stand density, volume, and cover type in multi-temporal satellite imagery. Heterogeneity in forest composition across the landscape can hinder the ability to model relationships between spectral values and forest parameters (Mallinis et al., 2004), so the application of this modeling to large-scale analyses is limited. A balance between the intensity of the ground truth sampling and the extent of the landscape being modeled is needed for accurate predictions. Understory horizontal cover was predicted throughout the Upper Peninsula using a KNN classification of Landsat 7 imagery with limited success (root mean square error equaling 30% of the mean cover). An enhanced capability to predict forest structure using satellite imagery would allow natural resource managers to assess changes across time in an efficient manner, and examine large scale relationships between habitat suitability and species' distributions. Determining the current suitability of the Upper Peninsula to sustain lynx will help guide contemporary management policies; examining the condition of the forests before European influence and the temporal changes in forest conditions will provide additional insight to factors that have contributed to the species' subsequent absence.

11.3.3.3. Estimation of Past Forest Conditions

A major difference between northern forests of the contiguous United States, where lynx populations have existed, and the boreal forests of Canada and Alaska, where populations presently thrive, is the high frequency and intensity of fire disturbance that occurs in the boreal region. This disturbance regime creates widespread areas of early successional vegetation types important to hares, interspersed with a mosaic of mature forest patches (Keith et al., 1993; Agee, 2000). The periodic occurrence of intense fires in the boreal forest has been hypothesized as a driving force behind the lynx-hare cycle (Fox, 1978). The combination of fire suppression practices and naturally longer fire return intervals in the mesic hardwood forests of the Upper Peninsula results in less frequent disturbances of a lower intensity. An examination of the disturbance regimes, and resulting forest conditions during the presettlement era could reveal the inherent capacity of the region to support lynx.

Historical fire regimes in northern Michigan have been examined previously by classifying ecologically similar areas based on abiotic components only, without considering vegetation attributes (Cleland et al., 2004). These components (landform, lake density, soil texture, soil drainage) influence a landscape's susceptibility to fire (Cleland et al., 2004). A similar approach to that in the northern Lower Peninsula of Michigan was applied to the Upper Peninsula (D. Cleland, USDA Forest Service, personal communication), producing a map of estimated fire rotations that occurred prior to European settlement in the 1800s. By combining the spatial layer of presettlement vegetation and that of fire rotations, we simulated different proportions of seral stages that may have existed among the habitat types, based on the frequency of disturbance. For example, mesic northern hardwood habitat types contained mostly mature stands, while xeric upland conifer types had a mosaic of seral stages. The inherent capacities of these two habitat types to support lynx were different, since early successional vegetation necessary for hares was provided more frequently on one than the other, given the disturbance regimes. It is obvious that the temporal dynamics of forest succession were not static in the Upper Peninsula, so an understanding of the cycles that naturally occurred within habitat types allows a better estimation of potential forest conditions during that era. With the pre-settlement spatial layer created, the stand attribute data necessary for the lynx HSI model can be obtained by linking the seral stages and habitat types delineated in the map with those of corresponding FIA plots. Thus, lynx habitat during presettlement times can be projected and compared with current habitat distributions. The inferences that can be made using these data are limited, given the amount of uncertainty in formulating the pre-settlement information. Even so, the ecology of yesterday's landscape can have important implications for the present, and as such, any historical information will be deemed useful in the context of resource management (see Chapter 3, this volume).

11.3.3.4. Importance of Understanding Spatial and Temporal Changes in Lynx Habitat

Habitat is one of many factors influencing the presence of a species, and in the case of Canada lynx in the Upper Peninsula, suitable habitat alone may not result in the persistence of a resident population. Changes in climate which affect snow accumulation in northern temperate regions, coupled with human facilitated range expansions by interspecific predators (e.g., bobcat, coyote) have increased the pressures of possible competition on lynx in their southern range (Koehler and Aubry, 1994). In addition, if dispersing individuals from Canada are to migrate to the Upper Peninsula, they will likely encounter barriers of human development (viz., urban areas, agriculture). We are currently assessing where potential barriers may exist in the Upper Peninsula, to estimate the probability that an individual would be able to move across the landscape. Digital maps describing the location of other factors influencing lynx populations become increasingly important once the resources vital to their survival have been mapped. This methodology can be used to assess the suitability of a landscape for numerous species for which habitat requirements have been quantified. It is important that the resolution at which the habitat is analyzed matches that of the species' resource selection (Roloff and Haufler, 1997). The use of FIA survey data is most applicable to large-scale analyses due to the sampling protocol. Spatial considerations aside, an advantage to this methodology is that the temporal resolutions of data collection for the forest inventory (5 years) and satellite imagery (16 days) allow continuous evaluations at a reasonable time interval (i.e., one that corresponds with forest successional dynamics). Natural resource agencies can use habitat type classifications, which remain static barring a major geologic event, and efficiently keep track of changes in forest structure over time.

11.4. Implications of Understanding Temporal Changes in Forest Ecosystems

Habitat-type classification systems contain structural and compositional characteristics of vegetation within different habitat types that managers can use to predict temporal changes across large spatial extents. This has important implications for meeting multiple-use and ecological objectives. For example, natural resource managers can make more realistic predictions of timber production potential or the availability and distributions of resources important for different wildlife species or communities based on an understanding of the potential availability of specific vegetation types throughout time and an understanding of how structure and composition of those vegetation types change temporally. Knowing those spatial and temporal distributions, managers can then plan forest management activities within landscapes more effectively. State and federal agencies, and some private organizations and corporations are striving toward implementing ecosystem management to conserve, protect, and manage natural resources for current and future generations. The use of ECSs such as habitat type classification systems will help aid managers in accomplishing economically viable and socially acceptable management goals that sustain functional ecological systems. The three case studies described in this chapter describe how those goals might be accomplished, but there is still work to do.

Davis et al. (2001, p. 77) wrote, "The empirical core of our professional claim to manage land scientifically and to ensure that owner objectives are met lies in our ability to predict the conditions and outcomes of current and future stands and stand types when managed under a specified prescription." In essence, if managers cannot predict with acceptable accuracy the conditions and outcomes associated with implementing specific management activities, it will be difficult to determine if ecosystem management goals are being met. Classifying forests into ecological units (e.g., habitat types), compiling vegetation structural and compositional changes within habitat types, and quantifying changes in wildlife habitat suitability or timber production potential throughout time is important for planning forest management activities, accurately predicting management outcomes, and sustaining functional forest ecosystems while meeting human demands for resources.

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12

Foraging Responses of the Endangered Gouldian Finch to Temporal Differences in Seed Availability in Northern Australian Savanna Grasslands

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Abstract. Historically common throughout the grasslands and woodlands of Australia's tropical savannas, the endangered Gouldian finch *Erythrura gouldiae* has suffered dramatic reductions in population numbers during the last 40 years. Possible causes, including (a) increased commercial livestock grazing; (b) commercial trapping for aviculture; and (c) parasite infections have had limited success in explaining the continued decline. Recent research detailing foraging patterns and the temporal distribution of seed patches have given new insights. Unlike other Australian finches, the Gouldian finch is solely granivorous and relies upon native grass species for survival. These grasses produce seed during only a few weeks of the Austral wet season. Survival and reproductive success of finch populations depend upon the abundance of grass seed that persists on the ground as dry seed for about nine months. During the period of Gouldian finch decline, there occurred a concomitant increase in the number and intensity of fires. In this chapter, I present experimental evidence describing the relationships between fire and seed production in the grasses *Alloteropsis semialata*, *Chrysopogon fallax*, and *Triodia bitextura*. I show that different patterns of seed production depend upon periodicity and intensity of fire. Some grass species such as *T. bitextura* respond with dramatic 100% reductions in viable seed after hot, late-dry-season fires. Responses of other grasses vary depending upon resting periods between fires rather than burn intensity. Coupled with the effect of fire, seed production also depends upon localized interactions with topography, soil types, and rainfall patterns. Understanding the temporal patterning and spatial distribution of resources across the landscape provides new perspectives on how to manage landscapes for declining species such as the Gouldian finch.

12.1. Introduction

Research probing the disappearance of the endangered Gouldian finch (Butchart and Pilgrim, 2006) has focused on individual ecological questions that initially appeared unrelated. The species was declining in number of individuals, number of populations, and range. Unfortunately, even with excellent scientific research it appeared that little headway was being made in the attempt to save this iconic Australian species. However, the clues were there, it just required putting the jigsaw puzzle together and collecting a few new pieces. We already knew the species was highly fecund (Tidemann and Lawson, 1999); we also understood that Gouldian finches occupied two quite different habitats on a seasonal basis (Dostine et al., 2001), and consumed a variety of native grass seeds (Dostine and Franklin, 2002). What was needed was a more holistic approach.

The following section deals with basic knowledge that will allow the reader to better understand how the species is related to the distribution of resources, the phenology of grasses, and annual climatic conditions, all variables that influence why this species and a wide range of other granivorous bird species in northern Australia are declining.

12.1.1. Description of Species and Taxonomic Affinities

The Gouldian finch is both sexually dimorphic, sexually dichromatic, and exists as three distinctive head-color morphs (red, black, or yellow) in the wild. Both male and female are brightly colored. In the male the red, black, or yellow facemask is bordered by turquoise blue and the pin-tail feathers of the tail are about twice the length of that in females. Mean male body mass is $\sim$15 g and mean female body mass $\sim$14.2 g. The very distinctive bright colors of this species have lead to a level of popularity in aviculture almost unrivalled by any other species (Marshall et al., 2005) and have resulted in substantial trapping of live birds from the wild for captive collections (Franklin et al., 1999). However, as numbers dwindled and public awareness grew, governments stopped the collection of wild birds. Initially the decline of the Gouldian finch was blamed upon trapping, but after further investigation it was noticed that several other species of granivorous birds not collected for the captive market were also disappearing from much of their northern Australian ranges (Franklin et al., 1999).

12.1.2. History of the Decline

Australia's northern savannah woodlands and grasslands have had a relatively short history of European intrusion but a long history of Aboriginal use. Aboriginal communities have long lived in family groups wandering throughout the landscape on ancestral lands (personal communications with elders of the Jawoyn community). Although described as nomadic, aboriginal people followed predictable, almost migratory, movements revolving around the tropical wet and dry seasons. Fire was used for both clearing access through the long grass and to move and attract game (primarily kangaroos) for hunting. The term "fire-stick culture" has been used to describe land use practices employed by the Aboriginals of the region (Yibarbuk et al., 2001). Patchy seasonal burning during their annual trek across the landscape was an integral factor in determining the floristic structure and favoured a guild of species (including the Gouldian finch) reliant upon seasonal flushes of growth in the patchy landscape. However, during the past 40 years, Aboriginal culture has dramatically changed to small, sedentary communities with little reliance upon resources from the land. During this same period, intensive cattle grazing by non-Aboriginal settlers (Matthias and Smith, 2003), introductions of foreign pasture grasses, different fire patterns (Milchunas and Lauenroth, 1993; Friedel, 1997) that probably are more intense and widespread, the addition of an extensive road network, and the use of aircraft in lighting "controlled" burns have dramatically influenced the landscape.

12.1.3. Research History

Research involving wild Gouldian finches over the past 15 years has largely focused on their rapid decline. At first the presence/absence of Gouldian finches in northern Australia was noted (Tidemann, 1987) followed by research that addressed the role of pastoral practices and land management (Tidemann, 1986, 1990; Franklin, 1999). Banding data described moult patterns and seasonal abundance of birds at waterholes (Woinarski and Tidemann, 1992; Tidemann and Woinarski, 1994). The role of the parasite *Sternostoma tracheacolum* was investigated (Tidemann and McOrist, 1992) and diet analysis showed that Gouldian finches are specialist seasonal foragers of native grass seeds (Dostine et al., 2001; Dostine and Franklin, 2002). Tidemann and Lawson (1999) reported that the Gouldian finch was monogamous but this conclusion was reached without DNA verification. Fox et al. (2002) noted strong mate selection for head color and the possibility of mate infidelity. Importantly, the Gouldian finch shows high fecundity, but is still declining in the wild (Tidemann and Lawson, 1999).

Research on the effects of fire on vegetation focused on pasture management for grazing (Mott and Andrew, 1985; Landsberg et al., 1999), where fire was used for three main purposes: the removal of debris; killing of native plant species; and providing a favourable seed bed for non-native pasture sowing (Johnson and Purdie, 1980). Mott (1992) suggested that low intensity fires in northern Australia would not have a great effect on the fire adapted grassland species apart from the removal of the debris. In some species, e.g., *Heteropogon contortus*, there was evidence that fire stimulated germination (Shaw, 1957). High intensity fires have the potential to reduce regeneration of native species prior to the sowing of native pasture (Johnson, 1964; Johnson and Purdie, 1980); data indicated that hot fires late in the dry season were capable of killing native plants. Unfortunately for seed eating bird species, there has been little research to indicate how fires influence components of crop yield other than general biomass.

12.1.4. Climate

The weather conditions experienced by the Gouldian finch are extreme. Heavy rainfall occurs during the Austral summer, which in the northern Australian tropics is termed the wet season (Fig. 12.1). During this period large storms producing heavy rainfall occur between the months of October and April. The mean rainfall for the Yinberrie Hills between 1995 and 1999 was 1,358.5 mm (SD 230.7 mm).

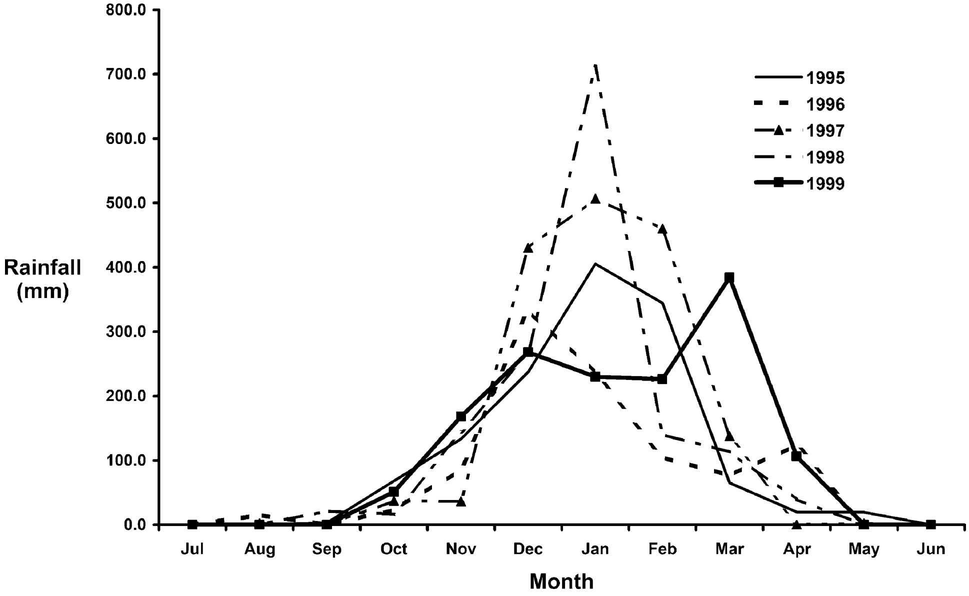

FIGURE 12.1. Annual precipitation patterns for the Yinberrie Hills, Northern Territory as recorded at the Mount Todd Mine between 1995 and 1999. Values per month indicate total monthly rainfall.

All rain falls during the wet season; the northern Austral Winter (dry season) produces little or no rain. This pattern results in a very short growing season in which the majority of grass species produce abundant seed for a period of several months and nothing else for the rest of the year.

12.1.5. *Topography*

The Yinberrie Hills study area where data for this paper were collected can be described by two distinctive landforms: the Hills within the eastern sector of the focal study area for the Gouldian finch (Tidemann and Boydon, 1992; Tidemann and Lawson, 1999); and the Lowlands located to the west of the Hills. The Hills are rugged with poor skeletal soils that contain very little humus or any other nutrients. There is no flowing water within this area during the dry season but there are several permanent small springs (very small pools less than 20-cm diameter) that provide reliable drinking sources for wildlife. To the west of the Hills are the Yinberrie Lowlands. This is an expanse of smaller undulating hills with numerous creeks that remain dry for most of the year; only filled during wet-season deluges, but with several small ephemeral waterholes. The small undulating hills of the Lowlands consist of skeletal soils composed of course granite sands. In the lower creeks the soils are more decayed and formed with humus layers making them slightly richer in nutrients, although all of the soils in the region are generally poor in nutrients.

12.1.6. Flora

Vegetation mapping has been conducted throughout the Yinberrie Hills in a series of transects but is as yet unpublished (C. Michell, pers. communication). In general the area is tropical savannah woodland with a grassy understorey. Tree species composition is dominated by *Erythrophleum chlorostachys*, *Eucalyptus tintinnans*, *E. tectifica*, *Corymbia disjuncta* and *C. foelscheana* to a height of 10–15 m and with a canopy cover of 30–50%. The shrub layer is dominated by *Petalostigma quadriloculare, Galactia muelleri, Xanthostemon paradoxus, Tephrosia polyzyga, Gardenia megasperma*, and *Terminalia ferinandiana* to a height of 0.5 m and highly dispersed with foliage cover of 5–20% when present. The grasses are dominated by *Sorghum intrans* and *H. triticeus* with much less coverage of *Sehima nervosum* and *Mnesithea formosa*. Ground cover in the wet season is 90–100% for grasses prior to dying-off at the commencement of the dry season.

The dominant trees within the Lowlands are *X. paradoxus, Terminalia pterocarya, Acacia platycarpa*, and E. *chlorostachys.* The shrub layer is dominated by *Spermacoce ditricha* and *P. quadriloculare.* Grasses in the Lowlands are more diverse and dominated by a greater number of species than in the Hills. The dominant grasses are *S. intrans, Eriachne obtusa, E. ciliata, Schizachyrium pachyarthron*, and *T. bitextura*. The grasses *Digitaria gibbosa, C. fallax, A. semialata, S. fragile, M. formosa*, and *Urochloa holosericea* are sparse but form substantial patches of vegetation when present.

12.1.7. Fire Behavior

Fires in tropical monsoonal climates generally can be classified by the time of year in which they appear. To a great extent, the wet and the dry seasons determine fire intensity. Natural fires during the wet season in the Yinberrie Hills appear to be most often ignited by lightning and more often occur during the early part of the season when grasses are still dry from the previous months without rain. These fires tend to cover areas of small landscape extent and are extinguished by the rains that closely follow the lightning storms. Fires in the dry season vary depending on when they occur and the weather patterns at the time. At the beginning of the dry season, fires most closely resemble those described for the wet season. At this stage both the grass and the ground are moist, so fires cover small areas and are generally described as “cool.” As the dry season progresses fires increase in intensity as grasses cure, and the humidity decreases as warm winds move across the landscape. Late-dry-season fires burn hotter and cover vast expanses, burning thousands of hectares in each event.

The causes of dry-season fires often are deliberate. At present a large number of fires are started to “burn off” or “clean up” debris in order to prevent larger-scale and less controllable fires from destroying livestock, homes, and other assets. Purposeful fires also are set by weekend hunters and by geologists during mineral exploration to make areas more accessible. Traditional fires started by Aboriginal occupants were used in the past for hunting and improving access to traditional

TABLE 12.1. Precipitation recorded at 10 Lowland sites during December 2001

	Rain gauges									
	1	2	3	4	5	6	7	8	9	10
Total	233.0	161.0	163.0	137.0	199.0	198.0	201.0	268.0	203.0	213.0
Mean	38.8	26.8	27.2	22.8	33.2	33.0	33.5	44.7	33.8	35.5
Std. Dev.	27.8	15.2	23.8	24.8	26.0	26.6	24.2	24.6	21.9	22.5

land but are now limited because of changes in life style (Yibaruk et al., 2001). Graziers also have used fire as a management tool to improve pasture for cattle and in some regions this may still occur (Mott and Andrew, 1985).

12.2. Spatial and Temporal Distribution of Resources

12.2.1. Rainfall

Rainfall in the Yinberrie Hills occurs primarily during the wet season; however, the distribution of rain is patchy, varying extensively on a day-to-day basis as cloud bursts release water at what appear to be random locations. Rain gauges at 10 randomly selected sites within the Yinberrie Lowlands recorded precipitation on a daily basis during field visits to the area in December 2001 (Table 12.1). These sites were relatively close to each other (mean distance between sites = 1,274 m, SD = 367m, distance between furthest sites = 5,539 m, distance between closest sites = 600 m) and only within the lowlands area used for wet season foraging by Gouldian finches. Data from this investigation indicated no pattern to the distribution of rain (Fig. 12.2). Initially, predictions suggested that rainfall pattern may be related to the distance from the hills or other topographic features. There were significant differences in total rainfall between sites over the survey period ($t_{18} = 16.12$, $p = 0.0000$), but the standard deviations varied very little. The weekly totals between rain gauges were significantly different ($F_{1,9} = 107$, $p = 0.0000$), and the weekly means were also significantly different between sites ($t_{18} = 12.47$, $p = 0.04$). In terms of plant growth, this pattern of rainfall would probably cause stochastic differences in seeding periods throughout the Lowlands during the wet season because seed is produced asynchronously in patches over a much longer period of time.

12.2.2. Drinking Water

Water during the wet season is plentiful but during the dry season is restricted to small waterholes along creeks and rivers. Although there are no records of periods when all waterholes we dry, at the conclusion of the dry season there are very few waterholes remaining and these are confined to the Hills. During this period Gouldian finches are confined to areas within the Hills. As waterholes disappear

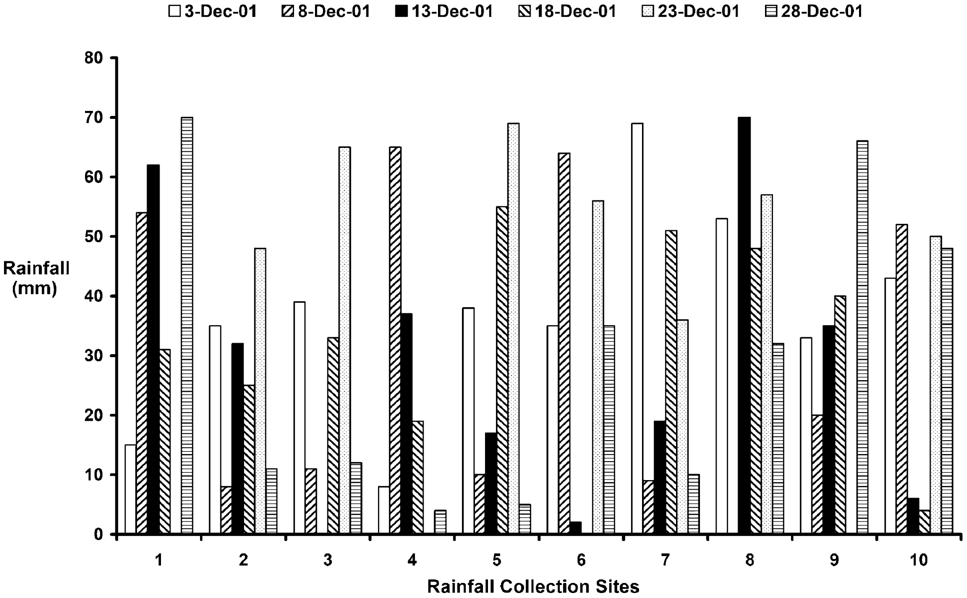

FIGURE 12.2. Weekly rainfall totals recorded at 10 randomly placed sites within the Yinberrie lowlands during December 2001.

birds aggregate at the few remaining sources of water: it was this behaviour that allowed highly successful commercial trapping of the species. Within the Yinberrie Hills there are two main creek systems and a minor creek that provide most of the water. During August when population counts are conducted at waterholes throughout the Yinberrie Hills there are between 27 and 42 waterholes of known location. There are probably more waterholes but human access during this period is difficult. As the dry weather persists many pools disappear until only five or six remain. There is also a small permanent spring within the main gorge that provides a very small pool of fresh water throughout the year.

12.2.3. Grasses and Feeding Resources

Numerous potential seed resources exist within the tropical savanna grasslands of northern Australia, yet it appears that Gouldian finches use only a few of these species (Box 12.1) (Dostine et al., 2001). At the beginning of the wet season, the rains result in a flush of new growth and the first fresh seeds in over eight months. For a few weeks after the first rain and prior to seed production from the wet-season grass, Gouldian finches take on a new and somewhat unusual diet of germinating *S. intrans*. This species provides the major component of the diet during the dry season where large numbers of dry seed lay on the ground. As the rains commence seeds germinate rapidly. Initially, Dostine et al. (2001) and S. Garnett (Charles Darwin University, pers. comm.) suggested that during this period when dry seeds were

Box 12.1. Grass species utilized by Gouldian finches.

Annual: *Sorghum intrans*
Perennial: *Alloteropsis semialata, Chrysopogon fallax, Triodia bitextura, Heteropogon triticeus.*

lacking, finch diets would have been inadequate and responsible for the demise of the species. However, I have documented that Gouldian finches continue to forage on the seed of *S. intrans* even as it germinates.

The first species to produce whole seed in the wet season is *A. semialata*, followed by *C. fallax*, and then *T. bitextura* if the fires have not been too severe during the previous dry season. As the rains stop, seed is provided by *H. triticeus* and finally by *S. intrans*. The seed of *S. intrans* provides food for numerous species of finches throughout the dry winter months as the dry seed lays dormant on the ground. As the first rains commence, *S. intrans* begins to germinate and provides a new source of nutrition for finches prior to the appearance of *A. semialata* seeds. In summary the diet of the Gouldian finch is composed of the seeds of perennial native grass species in the wet season and annual native grass species in the dry season.

12.2.3.1. Alloteropsis semialata

This native perennial grass has a patchy distribution in both the hills and lowlands of the Yinberrie area. In general these patches are formed by dense small clumps in which *A. semialata* is the dominant species. Away from these clumps *A. semialata* is sparsely distributed occupying only 0.64% of total grass cover ($n = 15 \times 25$ m^2 lowland plots). Although *A. semialata* occurs throughout a variety of habitats it is generally more common in the Lowlands in depositional soils rather than in other Lowland soil types ($F_{2,438} = 170.29$, $p = 0.0001$). Gouldian finches are usually observed feeding on *A. semialata* in lowlands during the second or third weeks of December (15 December 1999, 20 December 2000, 17 December 2001, 15 December 2002). These are the first fresh grass seeds to become accessible at the beginning of the wet season and represent an important food source after about eight months of only dry seed availability. These seeds are eaten in a semi-ripe state from the stem, which generally carries two to three terminal seed bearing spikes that potentially carry hundreds of seeds ($n = 67$ plants, 5 stems per plant; mean number of pedicels = 366, SD = 267).

The relationship between *A. semialata* and fire is complex with seed production varying considerably with fire regime. In a 3-year study where a number of grass species were subjected to fires at different times of the year, *A. semialata* performed best where fires were cool and infrequent (Lewis et al., unpublished data). Plants subjected to late-dry-season burns had poor seed and stem production, especially if the fire was in the previous 12 months. A fire regime consisting of three consecutive late-dry-season fires produced the lowest seed production of any of the treatments. Plants that had not been burnt during the three-year study produced the highest percentage of fertile seed, with plants exposed to cool wet-season burns prior to the previous flowering season also producing a reasonably high yield.

12.2.3.2. Chrysopogon fallax

During the last week of December and until the first weeks of January the seeds of *C. fallax* become available as the next food source. Gouldian finches are usually observed feeding on *C. fallax* in the lowlands after the third week of December (24 December 1999, 28 December 2000, 21 December 2001, 22 December 2002). Generally the bulk of the seeds are available for about three weeks but small pockets of later flowering individuals do provide seeds for several weeks longer. The distribution of *C. fallax* is on slightly raised slopes adjacent to creeks but not within creek-beds as is the case with *A. semialata*. *C. fallax* does not appear to grow on metamorphic soils and is not found growing within the Hills adjacent to the Lowlands. *C. fallax* seeds are larger than *A. semialata* (n = 42 plants, 10 seeds per plant; mean length = 3.5 mm, SD = 0.41; mean width = 0.81 mm, SD = 0.12) and appear to be preferred, because Gouldian finches shift to feeding on this seed while *A. semialata* is still available. On average, *C. fallax* produces fewer seeds (n = 42 plants, 5 stems per plant; mean number of pedicels = 214, SD = 125) from long umbrella-like spikes on as many as ten tall stems per plant (n = 42, mean = 4.9, SD = 2.3) and reacted more positively than other wet-season seeding species of grasses to periods of more intensive burning. In years following early-wet-season fires and early-dry-season fires (cool burns) *C. fallax* produced higher percentages of fertile seeds than either *A. semialata* or *T. bitextura*. *C. fallax* produced very little seed in plots that were not burnt for three successive seasons but appeared to produce the most seed if provided with one season every three years without fire.

12.2.3.3. Triodia bitextura

The third perennial grass species forming a major component of the Gouldian finch diet is *T. bitextura.* Data indicate that the time of availability for Gouldian finches are highly variable. Feeding periods have been observed during both December and January (28 December 1999, 18 December 2000, 5 January 2002, 12 January 2003). Generally *T. bitextura* is distributed along ridgelines in the Lowlands and in some of the stony weathered rock outcrops in the Hills. Occasionally, some specimens are found in shallow troughs between ridgelines that have a shallow surface layer (less than 0.5 cm) of depositional material eroded from the surrounding hills but with a granitic subsurface layer. *T. bitextura* seeds are very small (n = 10 plants, 10 seeds per plant; mean length = 2.1 mm, SD = 0.3; mean width = 1.6 mm, SD = 1.2), but plants have the potential to produce high yields (n = 21 plants, 5 stems per plant; mean number of pedicels per stem = 350, SD = 219; mean number of seeds per stem = 118.7, SD = 100). The number of stems per plant was highly variable in those individuals studied during this project (mean = 5.5, SD = 4.1) but several plants produced as many as 19 flowering stems, indicating that there may be further potential for greater seed yields.

Seed was not produced in abundance by *T. bitextura* in any year, apparently as a result of the intensity of dry-season fires. This species does not set seed or produce flowering stems during at least the first two years after hot fires. Limited data from wet-season fires indicated high seed set the following flowering season, suggesting that cooler fires, as experienced during the wet season may be of some benefit in promoting seed production the following season, whereas hot dry-season fires have the opposite effect. Although observations of Gouldian finches using this seed are limited (Garnett and Crowley, 1994), this may only be a result of limited availability due to a regime of numerous late-dry-season fires. In years when *T. bitextura* was available, large numbers of Gouldian finches were observed foraging on this species to the exclusion of all other species of seed. This was perhaps one of the major clues overlooked during initial research.

12.2.3.4. Heteropogon triticeus

This is a poorly studied species in regard to phenology and value as a food source for the Gouldian finch. There have been several observations of Gouldian finches foraging on the seeds of this species while seed is still on the stem, prior to complete ripening and seed drop (Dostine et al., 2001). The species appears to be generally distributed along the edges of creeks within the Hills and a few creeks of the Lowlands where rocky outcrops occur. *H. triticeus* grows as a large tussock with flowering stems up to 2 m in height. Stems produce a mean of 14.11 seeds per stem ($n = 16$ plants, 3 stems per plant) and seeds are relatively large (mean $= 6.5$ mm length, $n = 20$). Seeds are available throughout February and March while still on the stems but it is unknown if they are also used once they have fallen to the ground. The influence of fire on cropping rates has not been studied. *H. triticeus* was detected in general floristic pattern studies of the Yinberrie area (C. Michell, Northern Territory Parks and Wildlife Commission, unpublished data). These data indicated no effect of soil type on the basal diameter of plants within the Lowlands and Hills ($F_{1,333} = 2.4792$, $p = 0.085$).

12.2.3.5. Sorghum intrans

The use of *S. intrans* as the staple food for the Gouldian finch has been well documented by several authors (Tidemann and Lawson, 1999; Dostine et al., 2001). This species is distributed throughout the Yinberrie Hills and slopes of foothills leading to the Lowlands. Unpublished data (C. Michell, Northern Territory Parks and Wildlife Commission) indicated that *S. intrans* is the dominant species throughout the Hills but is much less abundant in the Lowlands. Research describing the value of *S. intrans* for pastoral purposes indicates a close positive association with fire (Andrew and Mott, 1983). This annual species exists as dormant seeds throughout the dry season until germination is triggered by increased soil temperatures and moisture levels with the onset of the first heavy showers. Prior to germination *S. intrans* seeds exist as dry loose surface seed and provide an abundant resource for many species of granivorous birds (Dostine and Franklin, 2002). The seeds are able to survive burning even when exposed to relatively hot fires (Watkinson et al., 1989). It has been suggested that the high lipid content around the germ cells may act as a buffer against extreme temperatures (Watkinson et al., 1989). *S. intrans* forms the staple diet of Gouldian finches during the dry season and is used to raise nestlings when breeding peaks (Tidemann and Lawson, 1999) suggesting that the high lipid content of these seeds may be a valuable resource. When seeds germinate early in the wet season they are also eaten and may provide essential nutrients for completion of the moult; germinating seeds produce high levels of carotenoids at a time when birds are moulting. Captive breeding research suggests that Gouldian finches gain essential amino acids (lysine and methionine) from germinating seeds (Marshall et al., 2005). These amino acids are so important that aviculturalists have termed them "breeding amino acids."

12.2.3.6. Summary

The foraging patterns of Gouldian finches appears to follow an annual cycle driven by the availability of seeds from a select few species of native grasses (Fig. 12.3). This cycle of seed production is relatively predictable from year to year but abundance of seed appears to be linked to a variety of variables including both fire and rainfall. Grasses that dominate the Hills landscape appear to be fire tolerant, whereas grass species found in the Lowlands are varied in their responses to fire. These differences have led to an annual predictable movement by finches to and from the Yinberrie Hills to the Lowlands in the search of food.

12.3. Gouldian Finch Habitat Usage

12.3.1. Wet Season

Rough terrain and unfavorable weather conditions have in the past hindered the collection of basic life-history data of Gouldian finches during the wet season, and this has led to much speculation. At one time it was thought that the species was migratory (Immelmann, 1977; Strahan, 1996). Banding studies yielded very poor data regarding localised movement between feeding locations or watering sites (Woinarski and Tidemann, 1992; Dostine et al., 2001). Recapture rates were very low making it difficult to draw any conclusions regarding longevity or population structure. For example, of 5,376 birds banded over a 4-year period, only 457 were recaptured at least once for a return rate of 8.5 %. The mean period between recaptures was 1.2 months (range: 1 week to 4 years 2 months). Recaptures usually occurred within a very short period after first capture; 52% of captures were within a month of first capture and 31.5% were recaptured within the first 6 months. More useful data regarding daily and seasonal movements were obtained using radio-telemetry (M. Lewis, Northern Territory Parks and Wildlife Commission, unpublished data). Wet-season data clearly showed that birds were moving on a daily basis from the Hills to the Lowlands. During the period in which *A. semialata* became available, both male and female Gouldian finches moved from roosting

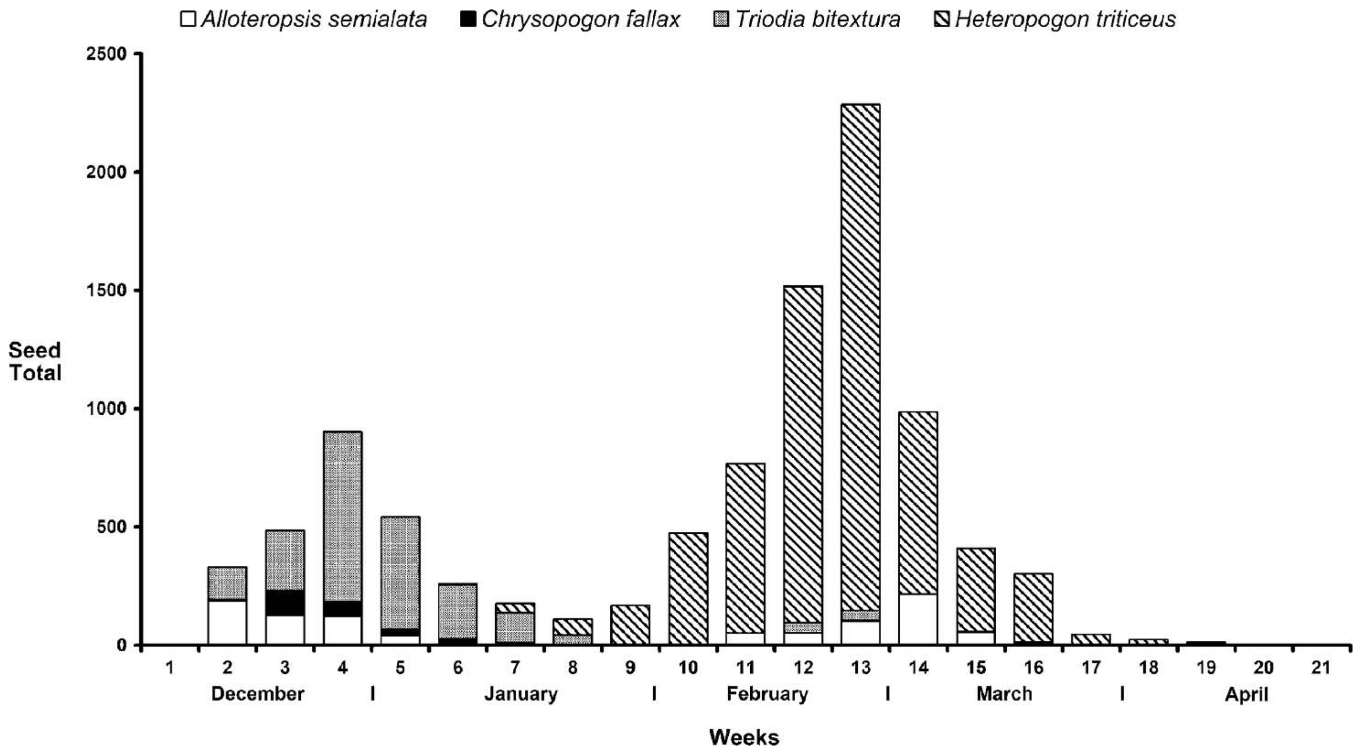

FIGURE 12.3. Totals for weekly seed counts for native grasses favoured as food resources by Gouldian finches in the Yinberrie Lowlands in the 1999–2000 wet season.

sites to feeding grounds where they spent the majority of the day feeding within the Lowlands before moving back to the Hills to spend the night. The mean distance of individual flights during this period was 825 m (n = 9 birds, minimum 10 flights per bird, SD = 269 m) and the mean area covered during daily foraging was 2,054 ha (SD = 1,275 ha, n = 9 birds).

12.3.2. Dry Season

During the dry season, daily bird movements were restricted to feeding sites within the Hills. There was no movement by any of the tracked birds to sites within the Lowlands. There was a general trend for birds to remain within areas relatively close to the waterhole at which they were captured and there were few flights of great distance across the study area. This pattern of remaining near waterholes was probably a reflection of breeding status with birds preferring not to wander too far from the nest site. Unlike most other finches, Gouldian nests are within tree hollows formed by termites, although there are reports of nests in termite mounds (Tidemann and Boydon, 1992). Within the Yinberrie Hills, the Salmon Gum *Eucalyptus tintinnans* is the main tree species supplying nest hollows. These trees grow throughout the Hills on rocky slopes without a dense understorey (Tidemann and Boydon, 1992). The mean distance of individual flights during this period was 924 m (n = 6 birds, minimum 10 flights per bird, SD = 320 m) and the mean area covered during daily foraging was 885 ha (SD = 886 ha, n = 6 birds).

12.4. Discussion

Summarizing the ecological points essential to understanding the survival of the Gouldian finch requires a holistic approach in which consideration is given to the habitat (Lowland and Hills) occupied, the distribution of resources (perennial grasses in the Lowlands during the wet-season and annual grasses in the Hills in dry season), and the abundance of resources in response to annual biotic and abiotic factors such as precipitation and fire.

The Hills and Lowlands of the Yinberrie area are rugged and parched in the dry season, and very hot, wet, and humid in the wet season. The extremes of weather are felt most intensively during a period known as the “break” when the dry season is coming to an end and the wet season is just starting. At this time, when temperatures rise above 40 C and the humidity hovers above 80%, Gouldian finches are under the additional physiological stress of the moult (Tidemann and Woinarski, 1994) at a period of lowest seed availability. Uniquely, no other finch species in the Yinberrie area moults during this period, having completed the task over a month before the increase in temperatures.

To understand the pattern of movement of Gouldian finches on a daily and seasonal basis, it is important to have a sound understanding of what resources are required throughout the year and the temporal distribution of those resources. The annual home range of Gouldian finches in this population typically contains an area of elevated hills and an area of lower hills within flooded lowlands. The finches occupy the Hills during the dry season because of the abundance of three key resources; seed from *S. intrans*, water, and breeding sites in the hollows of *E. tintinnans*. During the wet season the birds fly on a daily basis from the Hills to the Lowlands where a series of perennial grass species provide fresh seed that is not available during the same period in the Hills.

Soil types determine the initial distribution of grasses. In the Lowlands *A. semialata* is found in close association with creeks, *C. fallax* grows on the slopes of hills, and *T. bitextura* occupies the hill crests. Seed acquisition is not a serious consideration for Gouldian finches within the dry season because dry seeds from *S. intrans* are readily available throughout the Hills in close proximity to nesting sites and remain until the beginning of the wet season. Seed resources during the wet season, however, follow a relatively predictable temporal sequence in which the seeds of *A. semialata* first become available in a semi-ripe state followed by *C. fallax*, *T. bitextura,* and finally *H. triticeus* with the approach of the dry season.

Another level of complexity involves the micro-timing in the flowering of each of these perennial species. The local patterning of rainfall is highly patchy in distribution, and leads to small clumps of grass tussocks of the same species producing seed at slightly different times. These times may vary as little as a few days or as much as a week but the variation extends the availability of seed for each grass species. *A. semialata* has completely different flowering periods for populations within the Hills when compared to the Lowlands.

The final twist to understanding the distribution of feeding resources is added by the seeding response of grasses to a variety of burning regimes. Perennial grasses of the lowlands appear better adapted to an environment in which wet season and early-dry-season fires predominate (Fig. 12.4). Annual grasses of the Hills appear to respond best to dry-season fires in general but most importantly suffer less from late-dry-season fires. *T. bitextura* produces the poorest seeding response to fire by failing to produce flowering stems for at least 2 years after a fire. Some seeds are produced following fire in *A. semialata*, while *C. fallax* appears to perform reasonably well in response to fire. In the past it appeared that the predominante fire regime in the Lowlands was probably a mix of early-dry-season fires with the occasional early-wet-season fires and a late-dry-season fire every 3 or 4 years. This periodicity of fire coupled with the rugged terrain of the Lowlands dissected by numerous creeks and other natural fire breaks would have led to a mosaic of grass patches differing in the timing and duration of exposure to fire.

Undoubtedly there are still more levels of complexity yet to be discovered, especially in the responses of grasses to fire, but what has been discovered to date certainly has begun to aid land managers in the recovery of the species. It is clear that the temporal distribution of resources is an important key to understanding Gouldian finch response. Unfortunately, disturbance by humans through the imposition of grazing and new fire regimes has altered this pattern and been at least partially the cause of the species' demise.

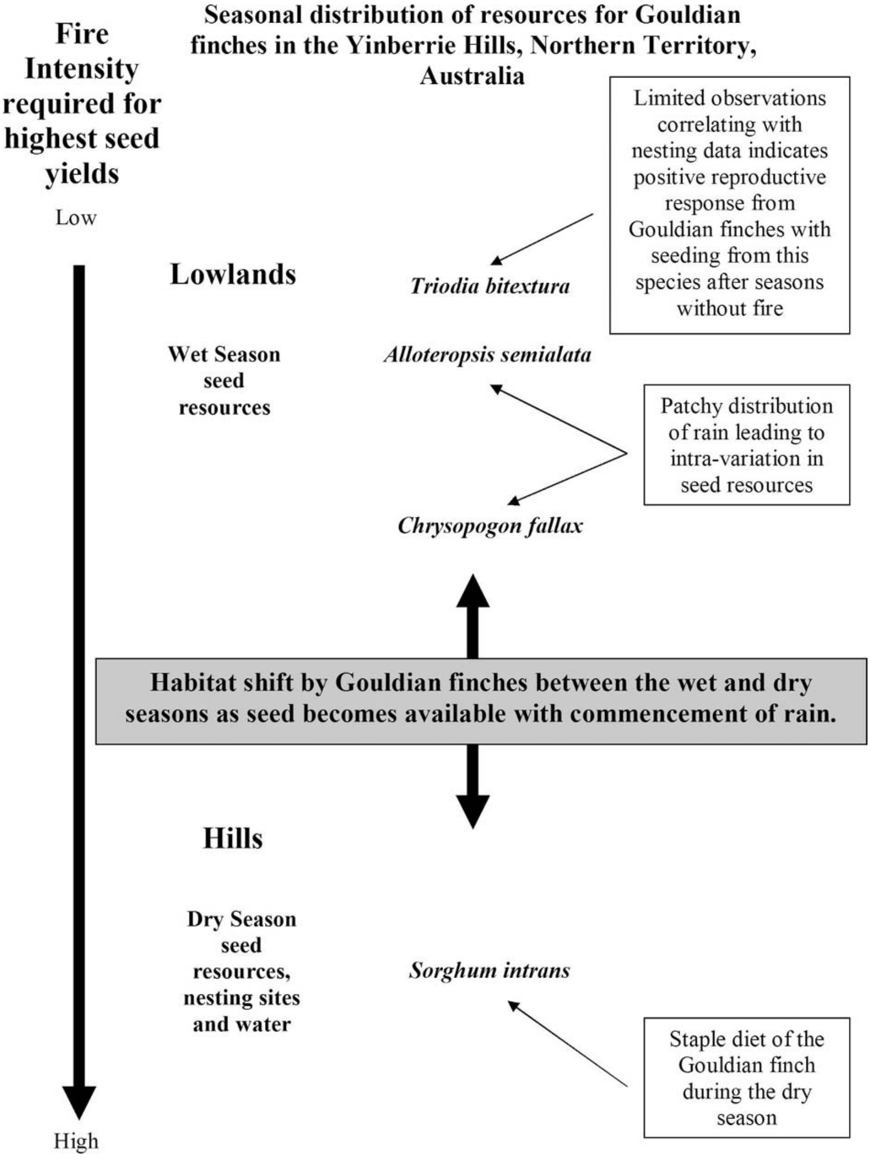

FIGURE 12.4. Seasonal distribution of resources for Gouldian finches in the Yinberrie Hills, Northern Territory, Australia.

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13

Spending Time in the Forest

Responses of Cavity-Nesters to Temporal Changes in Forest Health in Interior British Columbia

MARK C. DREVER AND KATHY MARTIN

Abstract. An ongoing major outbreak of mountain pine beetle (*Dendroctonus ponderosae*) and other bark beetles and forest insects in British Columbia has resulted in large-scale increases in the availability of dead and dying trees. Using point count data from a long-term study on cavity-nesting birds and mammals, we describe how individual populations of cavity-nesting species, and the cavity-nesting community as a whole, have responded to the outbreak. We fit a linear trend model to 100 species observed during point counts, 21 of which showed a significant decline in abundance over the study period, 21 showed an increase in abundance, and 58 showed no trend. These concurrent declines and increases in abundance mean that community-level measures (species richness and abundance within cavity-nesting guild) have not changed following the outbreak, indicating the community structure has remained stable during the large increase in resource availability. These results suggest that species' responses to the availability of resources may thus also depend on the current status of competitors, predators and facilitators.

13.1. Introduction

The questions of how and whether wildlife populations respond and adjust their patterns of resource use to temporal discontinuities in the availability and quality of resources, and how temporal discontinuities might be integrated with spatial heterogeneity in landscapes, are of strong fascination to community ecologists and urgently needed by wildlife managers (Bissonette and Storch, Introduction, this volume). It can be relatively straightforward to measure pulses in resource availability; these pulses can be frequent or irregular, and with long or short intervals (Ostfeld and Keesing, 2000). The question, however, of how animals in complex communities respond to temporal pulses in resource availability has received little attention in landscape ecology. Most studies assume that temporal patterns of resource availability and resource use are strongly correlated, but this may not be the case for several reasons. Animals may have several options in resource use across time and space (Martin et al., 2004), and tradeoffs in resource use may vary temporally with predation pressure (Mahon and Martin, 2006). Thus, when resources vary temporally, wildlife responses may not be symmetrical in terms of positive responses when resource availability increases and negative responses during resource declines.

Mature forests are typically characterized as stable environments where changes in structure are driven by creation and closure of gaps, small openings in the canopy created by the death of individual trees (Whitmore, 1989). These standing dead or dying trees are a critical resource for many wildlife species, as dead and dying trees provide sites for nesting, roosting, and foraging (Harmon et al., 1986; Martin et al., 2004). In particular, cavities excavated by woodpeckers dead or dying trees become a key element enhancing forest biodiversity. Bunnell et al. (1999) estimate that 25–30% of forest vertebrate species in the Pacific Northwest nest or roost in tree cavities, and a majority of these species do so exclusively. Because many of these species cannot create their own nest cavities, and thus depend on woodpeckers for the production of this resource, the process by which these secondary cavity-nesters acquire their nesting sites is analogous to a food web. Martin and Eadie (1999) coined the term "nest web" to describe the hierarchical structure of cavity-nesting communities wherein species can be classified into guilds according to the manner in which they acquire cavities. Woodpeckers, as primary cavity-nesters, excavate cavities in trees as nesting and roosting sites. Secondary cavity-nesters depend on these cavities produced by woodpeckers and on the limited availability of natural holes. This guild includes a range of passerines, ducks, birds of prey, and small mammals. The third guild, weak cavity-nesters, are to some extent able to excavate their own cavities, use naturally-occurring holes, but also adopt the cavities produced by woodpeckers. Thus, cavities in trees become a nesting and roosting resource for many forest species through a processing chain whereby the final availability of this resource depends on the existing supply of dead and dying trees, as well as on the processes (e.g., competition, predation, facilitation) that determine the numbers of "producers" and "consumers" of this resource.

In addition to nesting and roosting sites, dead and dying trees provide food for many cavity-nesting species that forage on insects, including bark beetles and defoliators (Bull et al., 1986). Bunnell et al. (2002) suggested that selectivity of tree species as foraging sites by woodpeckers differs by decay class, such that conifers are preferred foraging sites when these trees are in advanced stages of decay, whereas hardwoods are preferred in early stages of decay. Thus, the availability of dead and dying trees suitable for feeding will depend on tree species composition and can be expected to change over time.

The Nest Web project provides an opportunity to examine how temporal variability in resource availability can affect wildlife populations. This long-term research project has data on the abundance and distribution of cavity-nesting species and their resources that span 10 years over numerous sites (Martin and Eadie, 1999; Aitken et al., 2002; Martin et al., 2004). Here we describe the temporal changes in resource availability that have resulted from large-scale tree mortality events due to a major outbreak of mountain pine beetle (*Dendroctonus ponderosae*) and other bark beetles and forest insects in British Columbia. This outbreak is the largest recorded for the province since 1910, and is thought to have occurred due to a series of consecutive mild winters, which resulted in low over-winter mortality of beetle larvae (Hughes and Drever, 2001; Wood and Unger, 1996). The outbreak has spread over 8.5 million hectares of forests, resulting in the wide-spread death of conifers, primarily Lodgepole pine (*Pinus contorta* var. *latifolia*) (Eng, 2005). Thus, the outbreak provides a unique opportunity to examine how wildlife species respond to a dramatic increase in the availability of a potentially restricted resource.

We describe how individual populations of cavity-nesting species, and the cavity-nesting community as a whole, have responded to the outbreak. In addition, we compared how temporal trends in abundance varied among cavity-nesting guilds and other landbirds, and between species of different migratory status in order to determine whether and how these ecological factors affected responses of individual populations. We reasoned that the ability of a species to respond to this increased availability of dead and dying trees may depend on its position on the processing chain of the nest web. If secondary cavity-nesters depend on primary cavity-nesters for the creation of cavities, then this dependence should create a lag in the response of secondary cavity-nesters, such that these species should exhibit a weaker temporal trend in abundance relative to primary cavity-nesting species. Conversely, if excavation of new holes by primary cavity-nesters releases secondary cavity-nesters, then an increased number of primary cavity-nesters may have a multiplicative effect, such that secondary cavity-nesters may exhibit changes in abundance of larger magnitude than primary cavity-nesters. In addition, a species' response to the beetle outbreak may depend on its migratory status. If warm winter temperatures also affect survival of bird species that use dead and dying trees, then we expected that resident species should exhibit a stronger response to the outbreak than migratory species, as the population dynamics of these species may be regulated by different factors.

13.2. Methods

13.2.1. Study Sites

Study sites were located in the Chilcotin-Cariboo region of British Columbia, and are located in two basic groupings denoted by their field camps (Fig. 13.1). The "Riske Creek" sites are located approximately 40 km southwest of the city of Williams Lake (52° 08′ 30″ N, 122° 08′ 30″ W), and the "Knife Creek" sites are located east of Williams Lake. The Riske Creek sites have a rich mixture of deciduous and coniferous forest embedded in a matrix of grasslands and shallow ponds and wetlands. The Knife Creek sites have predominantly dry coniferous forest with deciduous riparian zones bounded by small streams. Deciduous species include quaking aspen (*Populus tremuloides*) and occasional balsam poplar and black cottonwood (*Populus balsamifera* spp.). The predominant coniferous species are Douglas-fir (*Pseudotsuga menziesii*), Lodgepole pine, and hybrid white

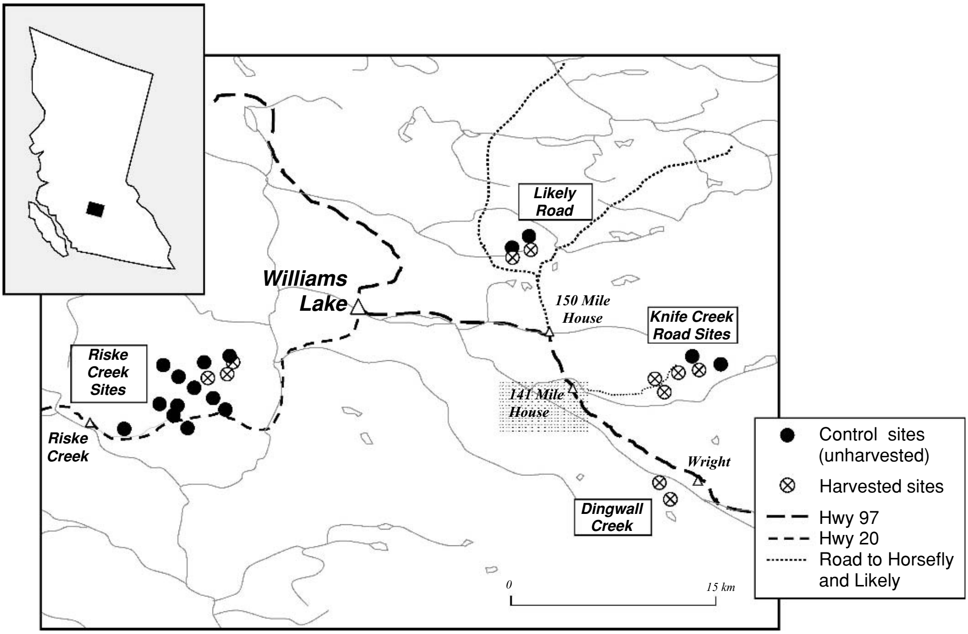

FIGURE 13.1. Study area and locations of point count plots in the Cariboo-Chilcotin region of central interior British Columbia, Canada. Data used to estimate temporal trends in abundance were from unharvested sites only.

spruce (*P. glauca* x *engelmannii*). For this present study, we focused on temporal variability unrelated to timber harvest, and thus included only sites not affected by timber harvesting. These 16 sites were all mature forests that have not been previously harvested for timber, except for 2 sites that had selective cutting of Douglas-fir 20–40 years ago.

13.2.2. Point Counts

Bird populations at study sites were counted during May and June of each year, from 1995 to 2004, using point counts and playbacks (Reynolds et al., 1980). The number of point count stations varied among sites, from 9 to 22, with 100-m spacing between stations. Each point count station was sampled twice every year. From 0500 to 0930 hours, point counts were completed at each station for 6 min. Because woodpeckers are not well surveyed using point counts, we used playbacks of woodpecker calls at every second point count station. After the initial 6-min observation period, the call of each woodpecker was played twice, each call followed by 30 s of listening time. We noted the species and number of birds seen or heard calling, singing, or drumming, or recorded during the woodpecker playback period.

13.2.3. Habitat Measurements

We established 11.2-m radius vegetation plots (standard timber cruise plot size for this forest type and age class) at each point count station. The point count station was situated at the centre of the vegetation plot. For all trees larger than 12.5 cm dbh ("diameter-at-breast height" [1.3 m]), we measured dbh and recorded tree species, decay class, the number and type of nesting cavities present, and any signs of disease or animal use (e.g., feeding). A minimum tree size of 12.5 cm dbh was chosen to conform with tree size categories used in the operational forest inventories, and because this size class was considered to the minimum size for use by cavity-nesters (over 95% of nest trees were >12.5 cm dbh). Decay class of trees ranged from 1 to 8, where 1 was a healthy tree, and 8 was a hollow tree with a broken top that had lost all its bark and branches, according to a classification system described in Backhouse and Lousier (1991). In addition, each tree was examined for evidence of disease, including dwarf mistletoe (*Arceuthobium* sp.), rust broom (*Chrysomyxa arctostaphyli* and *Melampsorella caryophyllacearum*), and boring insects, such as mountain pine beetle, and fungus infections, such as shelf fungus.

13.2.4. Data Analyses: Temporal Trends

To test whether resource availability had changed over time, we calculated three broad habitat measures thought to be important for cavity-nesting birds. These measures were the proportion of all sampled trees each year in healthy condition (Decay Class 1)—as a measure of overall forest health, the proportion of all sampled conifer trees with boring insects (Bull et al., 1986), and the density of aspen trees each year that were dead or dying (Martin et al., 2004). To estimate linear temporal trends, we fit a general linear model with the habitat measure as the response variable, and year and site as independent variables.

To test whether abundance of forest species changed over time, we first totaled the number of individuals in each species observed yearly at each site during point counts conducted in May and June (rounds 1 and 2). We then fit a generalized linear model for each species, modeling the number of individuals of each species counted at each site as a function of year as a continuous variable and site as a categorical variable, using the number of point counts per site as an offset variable, and assuming errors had a Poisson distribution. For woodpeckers, we only used data from point counts where playbacks were used. To determine whether the data support a trend, we used the t-value for the year parameter (t-value = slope parameter divided by its standard error), where a value >1.98 indicated a significant increase, a value of < -1.98 indicated a significant decline, and intermediate values indicated no trend. The value of 1.98 corresponds to the critical value of the t-distribution at 117 residual degrees of freedom in each regression (Zar, 1996). In order to determine whether the temporal trends in abundance differed by cavity-nesting guild or migratory status, we used the slope parameter (β_1) as a measure of the rate of change over time (Thomas et al., 2004). We compared slope parameters among the three cavity-nesting guilds and non-cavity nesting species, and between migratory and resident species, using a general linear model with cavity-nesting guild and migratory status as main effects and with an interaction term.

Using the data from the point-counts, we examined two measures of response at the community-level: overall richness for each year, and the overall abundance of birds and mammals in each nesting guild. To examine temporal changes in species richness, we calculated a rarefied richness for each year. Because richness will vary strongly with sampling effort and with the number of individuals in sample plots, rarefaction is used to standardize species richness to a given number of sampled individuals (Gotelli and Colwell, 2001). We calculated the expected species richness in random sub-samples of 600 individuals from the overall pooled community for each year, following the formulation in Hurlbert (1971), with standard errors following the method described in Heck et al. (1975). We chose a sample of 600 individuals because this represented the largest round number that was less than the minimum total number of individuals observed in any one year (630 individuals seen in 1996). For each year, we calculated the 95% upper and lower confidence limits for rarefied richness by adding or subtracting $1.96 \times \mathrm{SE}$, respectively.

To calculate the overall abundance of birds and mammals in each nesting guild, we totaled the observed number of primary cavity-nesters (PCN), secondary cavity-nesters (SCN), weak cavity-nesters (WPCN), and non-cavity-nesters (NONCAV) for each site/year. This total was divided by the number of point counts each site and year to calculate the density of detections per point count, and we then fit a general linear model such that the density of each cavity-nesting guild was a function of site as a categorical variable and year as a continuous variable.

13.3. Results

13.3.1. Temporal Trends in Resource Availability

The three measured habitat variables showed significant trends over time during the study period (Fig. 13.2). The proportion of live healthy trees at each site decreased over time from a mean of 0.84 in 1995, to a mean of 0.44 in 2004 ($\beta_1 = -0.042$, $\mathrm{SE} = 0.002$, $t = -18.3$, $p < 0.001$). This decline in overall tree health was largely a result in an increase in the proportion of conifers with evidence of boring insects, which increased from a mean of 0.04 in 1995, to 0.46 in 2004 ($\beta_1 = 0.039$, $\mathrm{SE} = 0.003$, $t = 15.6$, $p < 0.001$). The majority of the conifers with evidence of boring insects were a result of attack by mountain pine beetle, with some sites having nearly all conifers showing evidence of beetle attack. In addition, the mean density of dead or dying aspen trees increased from 44.8 to 70.9 trees per ha ($\beta_1 = 2.91$, $\mathrm{SE} = 0.37$, $t = 7.9$, $p < 0.001$).

13.3.2. Temporal Trends in Species Abundance at Point Counts

Between 1995 and 2004, a total of 107 species, including two mammals and 105 birds, were detected at 4,458 point counts. We were able to fit a general linear

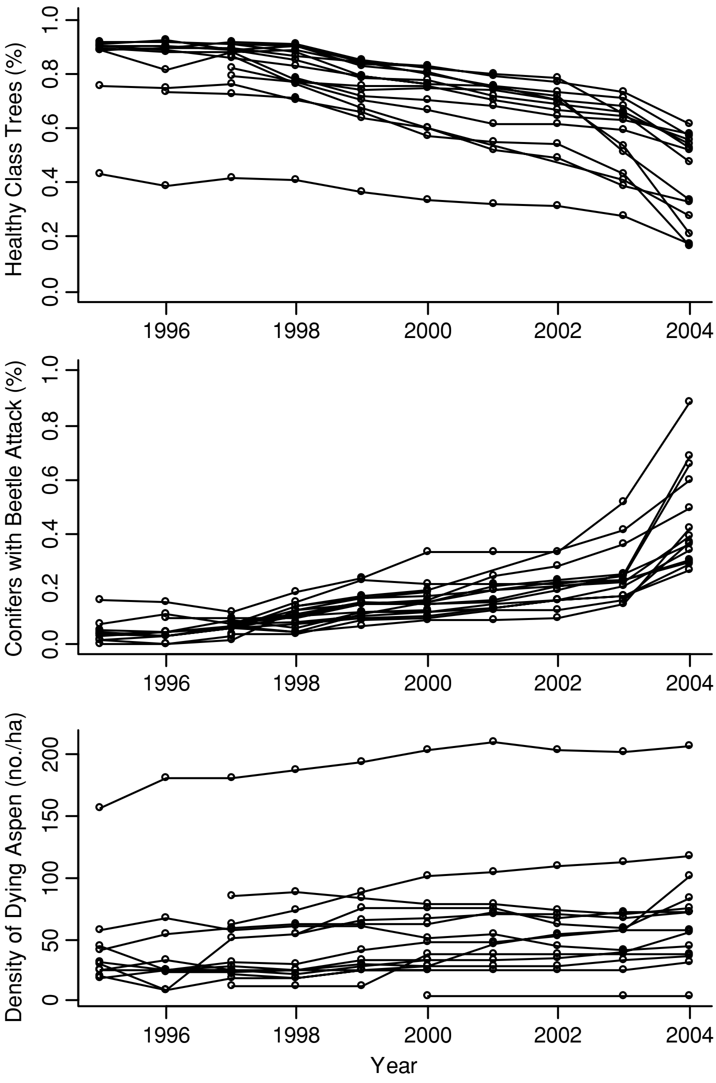

FIGURE 13.2. Temporal trends in habitat attributes at 16 sites in the Cariboo-Chilcotin region of central interior British Columbia, Canada, 1995–2004. Each line represents a different site.

model to counts of 100 species, which included 99 bird species, and one mammal, the red squirrel (*Tamiasciurus hudsonicus*). Of these, 21 showed a significant decline in abundance over the study period, 21 showed an increase in abundance, and 58 showed no trend (Table 13.1).

Trends in abundance of these 100 species, as measured by the slope parameter for the year effect in each regression, did not vary consistently with either

TABLE 13.1. Temporal trends in abundance of vertebrate species detected during point counts at 16 sites in the Cariboo-Chilcotin region of central interior British Columbia, Canada, 1995–2004*

Species	Code	Trend	t	Guild	Migr.
Golden-crowned kinglet (*Regulus satrapa*)	GCKI	−0.08	−5.62	NONCAV	Y
Red-winged blackbird (*Agelaius phoeniceus*)	RWBL	−0.32	−5.27	NONCAV	Y
Common raven (*Corvus corax*)	CORA	−0.16	−4.45	NONCAV	N
Marsh wren (*Cistothorus palustris*)	MAWR	−0.40	−4.43	NONCAV	Y
Brewer's blackbird (*Euphagus cyanocephalus*)	BRBL	−0.55	−4.36	NONCAV	Y
Wilson's warbler (*Wilsonia pusilla*)	WIWA	−0.12	−3.84	NONCAV	Y
Ruffed grouse (*Bonasa umbellus*)	RUGR	−0.15	−3.81	NONCAV	N
Dusky/Hammond's flycatcher (*Empidonax oberholseri/hammondii*)	DUHA	−0.04	−3.78	NONCAV	Y
Western wood-pewee (*Contopus sordidulus*)	WWPE	−0.07	−3.39	NONCAV	Y
Varied thrush (*Ixoreus naevius*)	VATH	−0.26	−3.36	NONCAV	Y
Townsend's solitaire (*Myadestes townsendi*)	TOSO	−0.14	−3.34	NONCAV	Y
Olive-sided flycatcher (*Contopus cooperi*)	OSFL	−0.11	−3.25	NONCAV	Y
MacGillivray's warbler (*Oporornis tolmiei*)	MGWA	−0.40	−2.72	NONCAV	Y
Yellow-rumped warbler (*Dendroica coronata*)	YRWA	−0.02	−2.48	NONCAV	Y
Rusty blackbird (*Euphagus carolinus*)	RUBL	−0.55	−2.38	NONCAV	Y
Savannah sparrow (*Passerculus sandwichensis*)	SAVS	−0.11	−2.29	NONCAV	Y
Red-tailed hawk (*Buteo jamaicensis*)	RTHA	−0.21	−2.22	NONCAV	Y
Lincoln's sparrow (*Melospiza lincolnii*)	LISP	−0.29	−1.91	NONCAV	Y
Vesper sparrow (*Pooecetes gramineus*)	VESP	−0.05	−1.53	NONCAV	Y
American crow (*Corvus brachyrhynchos*)	AMCR	−0.14	−1.51	NONCAV	Y
Canada goose (*Branta canadensis*)	CAGO	−0.13	−1.50	NONCAV	Y
Black tern (*Chlidonias niger*)	BLTE	−0.59	−1.48	NONCAV	Y
Winter wren (*Troglodytes troglodytes*)	WIWR	−0.16	−1.20	NONCAV	Y
Long-billed curlew (*Numenius americanus*)	LBCU	−0.10	−1.15	NONCAV	Y
Song sparrow (*Melospiza melodia*)	SOSP	−0.08	−1.07	NONCAV	Y
Mallard (*Anas platyrhynchos*)	MALL	−0.16	−0.93	NONCAV	Y
Cassin's finch (*Carpodacus cassinii*)	CAFI	−0.32	−0.88	NONCAV	Y
Rufous hummingbird (*Selasphorus rufus*)	RUHU	−0.10	−0.87	NONCAV	Y
Alder flycatcher (*Empidonax alnorum*)	ALFL	−0.11	−0.81	NONCAV	Y
Gadwall (*Anas strepera*)	GADW	−0.37	−0.79	NONCAV	Y
Northern harrier (*Circus cyaneus*)	NOHA	−0.37	−0.79	NONCAV	Y
White-crowned sparrow (*Zonotrichia leucophrys*)	WCSP	−0.09	−0.76	NONCAV	Y
Sora (*Porzana carolina*)	SORA	−0.19	−0.72	NONCAV	Y
Solitary sandpiper (*Tringa solitaria*)	SOSA	−0.35	−0.72	NONCAV	Y
Common nighthawk (*Chordeiles minor*)	CONI	−0.06	−0.50	NONCAV	Y
Greater yellowlegs (*Tringa melanoleuca*)	GRYE	−0.11	−0.41	NONCAV	Y
Sandhill crane (*Grus canadensis*)	SACR	−0.02	−0.36	NONCAV	Y
Killdeer (*Charadrius vociferus*)	KILL	−0.05	−0.32	NONCAV	Y
American green-winged teal (*Anas crecca*)	AGWT	−0.06	−0.30	NONCAV	Y
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)	YHBL	−0.02	−0.25	NONCAV	Y
American robin (*Turdus migratorius*)	AMRO	0.00	−0.24	NONCAV	Y
Gray jay (*Perisoreus canadensis*)	GRAJ	−0.01	−0.16	NONCAV	N
Common yellowthroat (*Geothlypis trichas*)	COYE	−0.01	−0.10	NONCAV	Y
Magnolia warbler (*Dendroica magnolia*)	MAWA	0.00	0.00	NONCAV	Y

(*Continued*)

TABLE 13.1. *(Cont.)*

Species	Code	Trend	t	Guild	Migr.
Northern rough-winged swallow (*Stelgidopteryx serripennis*)	NRWS	0.06	0.17	NONCAV	Y
Red crossbill (*Loxia curvirostra*)	RECR	0.01	0.20	NONCAV	N
Western meadowlark (*Sturnella neglecta*)	WEME	0.02	0.44	NONCAV	Y
Black-billed magpie (*Pica hudsonia*)	BBMA	0.19	0.51	NONCAV	Y
Veery (*Catharus fuscescens*)	VEER	0.19	0.51	NONCAV	N
Cassin's Vireo (*Vireo cassinii*)	CAVI	0.01	0.52	NONCAV	Y
American pipit (*Anthus rubescens*)	AMPI	0.16	0.62	NONCAV	Y
Belted kingfisher (*Ceryle alcyon*)	BEKI	0.32	0.62	NONCAV	Y
Blackpoll warbler (*Dendroica striata*)	BLPW	0.37	0.79	NONCAV	Y
Western tanager (*Piranga ludoviciana*)	WETA	0.02	0.80	NONCAV	Y
Common loon (*Gavia immer*)	COLO	0.66	0.87	NONCAV	Y
Cooper's hawk (*Accipiter cooperii*)	COHA	0.69	0.96	NONCAV	Y
Northern waterthrush (*Seiurus noveboracensis*)	NOWA	0.10	1.00	NONCAV	Y
Sharp-shinned hawk (*Accipiter striatus*)	SSHA	0.24	1.11	NONCAV	Y
Great gray owl (*Strix nebulosa*)	GGOW	0.37	1.12	NONCAV	N
Common snipe (*Gallinago gallinago*)	COSN	0.27	1.37	NONCAV	Y
White-winged crossbill (*Loxia leucoptera*)	WWCR	0.32	1.53	NONCAV	N
Bohemian waxwing (*Bombycilla garrulus*)	BOWA	0.19	1.60	NONCAV	Y
Chipping sparrow (*Spizella passerina*)	CHSP	0.02	1.79	NONCAV	Y
Purple finch (*Carpodacus purpureus*)	PUFI	0.54	2.24	NONCAV	Y
Hermit thrush (*Catharus guttatus*)	HETH	0.07	2.63	NONCAV	Y
Least flycatcher (*Empidonax minimus*)	LEFL	0.08	2.68	NONCAV	Y
Yellow warbler (*Dendroica petechia*)	YWAR	0.18	2.69	NONCAV	Y
Orange-crowned warbler (*Vermivora celata*)	OCWA	0.11	2.86	NONCAV	Y
Swainson's thrush (*Catharus ustulatus*)	SWTH	0.06	3.14	NONCAV	Y
Cedar waxwing (*Bombycilla cedrorum*)	CEDW	0.20	3.32	NONCAV	Y
Ruby-crowned kinglet (*Regulus calendula*)	RCKI	0.04	3.45	NONCAV	Y
Brown-headed cowbird (*Molothrus ater*)	BHCO	0.10	6.59	NONCAV	Y
Willow flycatcher (*Empidonax traillii*)	WIFL	0.27	6.59	NONCAV	Y
Dark-eyed junco (*Junco hyemalis*)	DEJU	0.07	6.70	NONCAV	Y
Warbling vireo (*Vireo gilvus*)	WAVI	0.14	6.78	NONCAV	Y
Townsend's warbler (*Dendroica townsendi*)	TOWA	0.28	7.05	NONCAV	Y
Pine siskin (*Carduelis pinus*)	PISI	0.17	10.66	NONCAV	N
Evening grosbeak (*Coccothraustes vespertinus*)	EVGR	0.39	12.20	NONCAV	Y
Red-naped sapsucker (*Sphyrapicus nuchalis*)	RNSA	−0.19	−5.98	PCN	Y
Northern flicker (*Colaptes auratus*)	NOFL	−0.09	−3.39	PCN	Y
Pileated woodpecker (*Dryocopus pileatus*)	PIWO	−0.03	−0.29	PCN	N
Hairy woodpecker (*Picoides villosus*)	HAWO	0.06	1.21	PCN	N
Black-backed woodpecker (*Picoides arcticus*)	BBWO	0.27	2.50	PCN	N
Downy woodpecker (*Picoides pubescens*)	DOWO	0.29	2.58	PCN	N
American Three-toed woodpecker (*Picoides dorsalis*)	TTWO	0.19	2.66	PCN	N
European starling (*Sturnus vulgaris*)	EUST	−0.10	−4.91	SCN	Y
Red squirrel (*Tamiasciurus hudsonicus*)	TAHU	−0.03	−2.82	SCN	N
American kestrel (*Falco sparverius*)	AMKE	−0.08	−0.57	SCN	Y
Northern saw-whet owl (*Aegolius acadicus*)	NSWO	−0.12	−0.49	SCN	N
Bufflehead (*Bucephala albeola*)	BUFF	0.08	0.34	SCN	Y

(*Continued*)

TABLE 13.1. *(Cont.)*

Species	Code	Trend	t	Guild	Migr.
Great-horned owl (*Bubo virginianus*)	GHOW	0.09	0.37	SCN	N
Violet-green swallow (*Tachycineta thalassina*)	VGSW	0.06	0.53	SCN	Y
Pacific-slope flycatcher (*Empidonax difficilis*)	PSFL	0.09	0.67	SCN	Y
Tree swallow (*Tachycineta bicolor*)	TRES	0.03	1.76	SCN	Y
Mountain bluebird (*Sialia currucoides*)	MOBL	0.12	4.39	SCN	Y
Brown creeper (*Certhia americana*)	BRCR	0.24	6.54	SCN	N
Black-capped chickadee (*Poecile atricapillus*)	BCCH	0.00	−0.15	WPCN	N
Red-breasted nuthatch (*Sitta canadensis*)	RBNU	0.02	1.43	WPCN	N
Boreal chickadee (*Poecile hudsonica*)	BOCH	0.94	2.36	WPCN	N
Mountain chickadee (*Poecile gambeli*)	MOCH	0.10	7.58	WPCN	N

*Trend is measured as slope parameter for year from general linear model of counts as a function of site and year. Species are sorted by cavity nesting guild and *t*-value. Strength of evidence of trend indicated by the *t*-value (slope parameter from regression of abundance by year, divided by its standard error), where a value >1.98 indicated an increase, a value of <-1.98 indicated a decline, and intermediate values indicated no trend. Guild refers to cavity-nesting guild, and Migr. refers to migratory status (Y = migratory; N = resident).

cavity-nesting guild, but varied by migratory status. We found that the mean β_1 of secondary cavity-nesters was higher than the three other cavity-nesting guilds (NONCAV: mean $\beta_1 = 0.01$, SD = 0.25, n = 77 species; PCN: mean $\beta_1 = 0.07$, SD = 0.19, n = 7 species; SCN: mean $\beta_1 = -0.005$, SD = 0.17, n = 12 species; WPCN: mean $\beta_1 = 0.26$, SD = 0.45, n = 4 species), but high variability within each guild meant we could not detect a statistical difference among the 4 groups ($F_{93,3} = 0.54$, $p = 0.65$). Resident species had a higher mean slope parameter (mean $\beta_1 = 0.11$, SD = 0.27, n = 22) than migratory species (mean $\beta_1 = -0.02$, SD = 0.24, n = 78), and this difference was statistically significant ($F_{93,1} = 4.57$, $p = 0.03$).

13.3.3. Trends in Community-Level Measures

Total observed richness at point counts with playbacks each year ranged between 49 to 72 species (mean richness = 60.7, SD = 7.1, n = 10 years). When rarified to 600 individuals, richness ranged between 46.6 and 60.5 (mean rarefied richness = 52.8, SD = 4.7, n = 10 years). Rarefied richness did not have a significant trend over time ($\beta_1 = 0.03$, SE = 0.54, t = 0.6, $p = 0.95$), and appeared to be highest between 1997 and 2000 (Fig. 13.3). Density of detections per site of the 3 cavity-nesting guilds and non-cavity-nesters varied widely year to year, but no guild showed a significant trend in abundance over the study period (Fig. 13.4; NONCAV: $\beta_1 = 0.04$, SE = 0.03, t = 1.5, $p = 0.15$; PCN: $\beta_1 = -0.001$, SE = 0.005, t = −0.3, $p = 0.77$; SCN: $\beta_1 = -0.008$, SE = 0.008, t = −0.9, $p = 0.35$; WPCN: $\beta_1 = 0.007$, SE = 0.007, t = 1.0, $p = 0.30$). Thus, none of the community-level measures (richness or total abundance within cavity-nesting guilds) showed significant trends over the

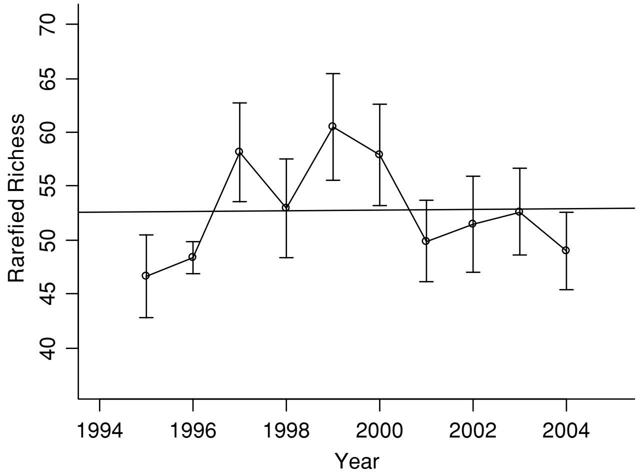

FIGURE 13.3. Temporal trends in rarefied richness of vertebrate species detected during point counts at 16 sites in the Cariboo-Chilcotin region of central interior British Columbia, Canada, 1995–2004.

study period, and temporal changes in abundance occurred primarily at the species level.

13.4. Discussion

The mountain pine beetle outbreak has resulted in a large increase in the availability of dead and dying trees, a key resource for many wildlife species in the interior forests of British Columbia. We found that approximately 40% of the species we could adequately monitor have also exhibited shifts in abundance, approximately equally divided between increases and decreases. This parity and the lack of a trend for the remaining 60% of species, means that the overall abundance of the vertebrate species we monitored has remained stable during the 10 years of study. Thus, the high inter-annual variability in species' abundances we observed at each site exists within a larger context of general stability at the community level (Fig. 13.4). This stability is mirrored by the lack of a trend in species richness (Fig. 13.3), and is consistent with many studies of avian community structure where species diversity changes little over time, although the species *composition* of the community changes considerably (Wiens, 1989, p. 144; Collins, 2000). Community stability is often associated with habitat stability (Bengsston et al., 1997), and may occur because the forests in the study sites are relatively mature and have not experienced major structural changes during the study period (although this condition will likely change as the standing dead trees continue to decay and fall).

Although the densities of dead and dying aspens increased over the study period, we found that trends in abundance varied widely among the three cavity-nesting

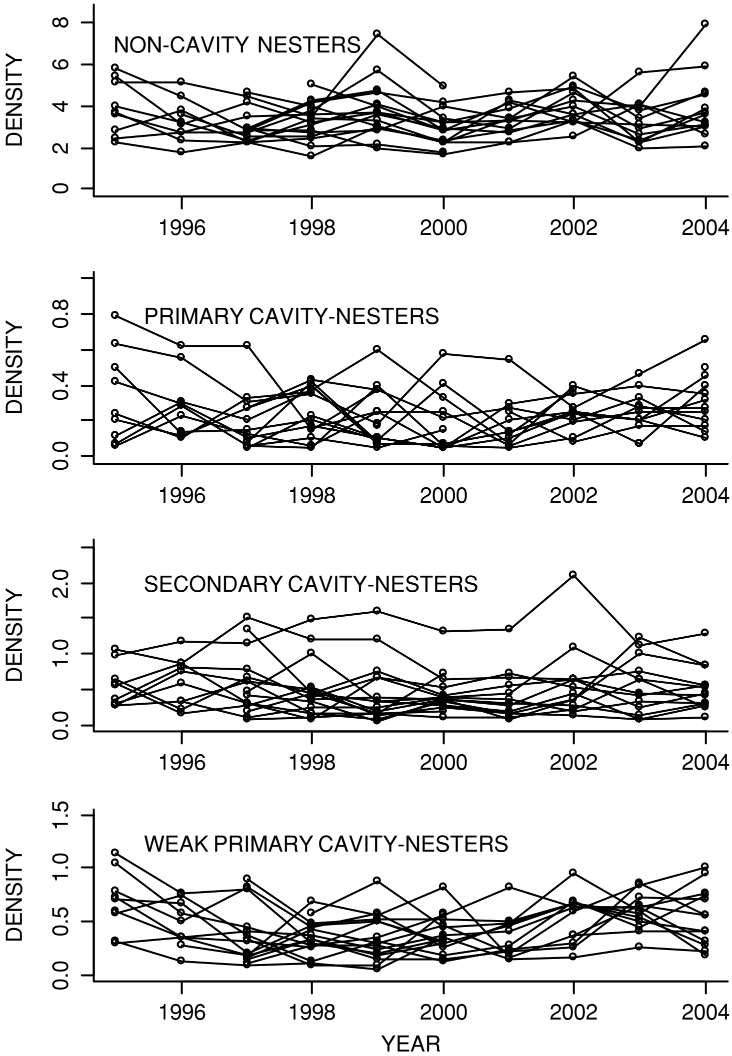

FIGURE 13.4. Temporal trends in density of detections of 3 cavity-nesting guilds and non-cavity-nesting species counted at 16 sites in the Cariboo-Chilcotin region of central interior British Columbia, Canada, 1995–2004. Each line represents a different site. Density of detections was measured as the sum of detections divided by the total number of point counts done yearly at each site. We found no temporal trend in density for the 3 cavity-nesting guilds and non-cavity-nesting species. Species included in this analysis are given in Table 13.1.

guilds and non-cavity-nesters, such that the cavity-nesting guild was not a reliable predictor of trends in abundance of species over the study period. The high inter-annual variability in abundance seen at the site level of all four guilds (Fig. 13.4) is consistent with the previous results of Martin and Eadie (1999). This high variability at the site has consequences for studies of wildlife response to changes in habitat conditions (e.g., due to forestry operations), such that several years of data at pre-treatment or control sites may be necessary to detect differences among treatments (Easton and Martin, 1998, 2002). The lack of a difference in temporal trends among the three cavity-nesting guilds and non-cavity-nesters may result from the high availability of suitable trees for excavation prior to the insect outbreak. Aitken et al. (2004) reported that cavity occupancy rates in the study area ranged between 35% and 44%, which are lower than occupancy rates reported in many other studies, suggesting that nest sites are not strongly limited and other ecological processes, such as foraging and predation, may have stronger effects on cavity-nesting vertebrates than nest-site competition (Aitken et al., 2004; Martin and Norris, 2007). In addition, we found that resident species tended to have greater temporal trends in abundance than migratory species, a pattern that may result from an increase in year-round foraging opportunities, or from some other unmeasured benefit of the relatively warm winters that have enabled the beetle outbreak.

Foraging opportunities may be more limiting than cavity-nest sites, although the use of dead and dying trees as feeding sites has not been as well studied as their use for nesting (Bunnell et al., 2002). Foraging habits may partly explain differences in trends among species within the same cavity-nesting guild. Among woodpeckers, we found that trends in abundance may be related to preferred prey species. Black-backed woodpeckers (*Picoides arcticus*), three-toed woodpeckers (*P. dorsalis*), and downy woodpeckers (*P. pubescens*) are all known to feed extensively on wood-boring beetle larvae (Dixon and Saab, 2000; Leonard, 2001; Jackson and Ouellet, 2002), and these three species had positive trends in abundance (Table 13.1). In contrast, northern flickers (*Colaptes auratus*) and red-naped sapsuckers (*Sphyrapicus nuchalis*), which forage primarily on ants and tree sap (Moore, 1995; Walters et al., 2002), had negative trends in abundance (Table 13.1). Such examples of concurrent increases and decreases in abundances raise the tempting idea that the increase of beetle-killed trees may have shifted competitive relationships among species within the same guild. Such relationships have been inferred for the smaller-bodied cavity-nesters (Martin and Norris, 2007), and this possibility suggests that a detailed study of how abundances of species co-vary over time may be necessary to understand the effect of forest composition and structure on avian communities.

The area affected by the mountain pine beetle outbreak continues to expand, and is predicted to peak in the summer of 2006 when it may kill more than 90 million cubic meters of merchantable timber (Eng et al., 2005). More than 14 million cubic meters of live pine are projected to be harvested in 2006 during efforts to control the outbreak and salvage dead timber, such that by the end of 2006 approximately 40% of the susceptible pine will have been killed or harvested (Eng et al., 2005). The magnitude of the outbreak and the consequent response by industrial forestry remind us that landscape composition is dynamic. As such, attempts to understand how landscape pattern affects wildlife species will greatly benefit from the incorporation of temporal aspects. In summary, we found that the availability of dead and dying trees, a key resource for many wildlife species, has increased dramatically following the mountain pine beetle outbreak in the interior forests of

British Columbia. We found that while many wildlife species have also increased in abundance, perhaps related to increased foraging opportunities, many other species declined in abundance during the same study period. These concurrent declines and increases in abundance mean that community-level measures (species richness and abundance within cavity-nesting guild) have not changed following the outbreak, indicating the community has remained stable during the large increase in resource availability. These results suggest that species' responses to temporal changes in resource availability may thus not only depend on their specific requirements, but also on the current status of competitors, predators and facilitators. These complexities underscore the usefulness of long-term observational and experimental studies which can be rich sources of information for ecologists and wildlife managers.

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14

Niche Opportunities and Introduced Birds

Temporal Variation in Resource Abundance

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Abstract. The niche-opportunity hypothesis predicts that some introduced species establish and spread successfully because their new environment provides expanded niche opportunities (better resources or physical environment) compared with their native environments. We tested the prediction that introduced birds in New Zealand experience increased niche opportunities because (1) winter seed resources were more abundant and (2) there was less temporal variation in resource availability during the breeding season in New Zealand. Our results suggest that in New Zealand an increase in winter resource abundance and a reduction in predation risk may have resulted in more available foraging habitat for introduced birds. However, although the local climatic conditions were less variable during the breeding season in New Zealand, we found no evidence that temporal variation in invertebrate food resources through the breeding season was reduced. This suggests that enhanced niche opportunities, if they exist, are not due to an increased abundance or temporal reliability of invertebrates, but rather enhanced niche opportunities may exist because of a warmer, more stable climate during the breeding season and lower energetic costs associated with foraging activities.

14.1. Introduction

14.1.1. Why Do Some Introduced Species Increase Spectacularly?

As humans have colonized the globe, they have transported and released many thousands of species outside their natural ranges (Long, 1981, 2003). Although many introduced species have established self-sustaining wild populations in their new environments, only a small proportion have increased in abundance spectacularly and become pests (Williamson, 1996). Introduced pest species are a major concern because they can have severe impacts on the ecosystems they have invaded (Vitousek et al., 1997; Wilcove et al., 1998). For example, the common pigeon *Columba livia* is a serious bird pest in the United States and causes problems ranging from nuisance fouling to grain consumption and disease transmission, resulting in damages estimated at $1.1 billion per year (Pimental et al., 2000). Identifying the factors that enable introduced species to succeed spectacularly in their new environments is regarded by Duncan et al. (2003) to be a research priority.

14.1.2. Successful Introduced Bird Species in New Zealand

A number of farmland bird species introduced from Britain to New Zealand in the late 19th century have spread widely throughout lowland farmland (Bull et al., 1985; Heather and Robertson, 1996), and continue to be doing very well in New Zealand (MacLeod and Drew, 2005). In their native ranges, however, they have experienced mixed fortunes (Shrubb, 2003) and populations have declined markedly in Britain and Europe in recent decades (Burfield and van Bommel, 2004; Baillie et al., 2005). Breeding densities of yellowhammers *Emberiza citrinella* and winter densities of skylark *Alauda arvensis,* for example, are approximately three times higher in New Zealand than in Britain (Wakeham-Dawson and Aebischer, 1998; Thomsen et al., 2001; MacLeod et al., 2005a). The yellowhammer and skylark are typical of many farmland passerines, both feed predominantly on seeds in winter and invertebrates in summer (particularly during chick-rearing) and although they do occur in other habitats, greatest numbers are found on farmland. The skylark is a bird of open fields, while the yellowhammer is more closely associated with hedgerows and field margins.

14.1.3. Relevant Hypotheses

Two hypotheses have been advanced to explain the enhanced success of some introduced species. Both are based on the assumption that at least three primary drivers (resources, physical environment, and natural enemies) influence the ability of an introduced species to establish and increase in abundance (Shea and Chesson, 2002). The “enemy release” hypothesis predicts that introduced species leave behind some or all of their natural competitors, predators, and pathogens, and thus are released from natural enemy regulation in their new environment (Keane and Crawley, 2002). Evidence from biological control experiments suggests that release from natural enemy regulation may explain the success of some pest species (Memmott et al., 2000). The “increased niche opportunity” hypothesis predicts that there are increased niche opportunities in the introduced environment as a consequence more abundant and/or more available habitat or resources, a more suitable physical environment, or both (Shea and Chesson, 2002). However, these hypotheses have rarely been tested, perhaps because they require detailed species-specific studies of the species in both their native and introduced ranges.

We have investigated whether the “enemy release” hypothesis could explain the higher breeding densities of the yellowhammer in New Zealand farmland than in comparable British farmland (MacLeod et al., 2005a). We found that yellowhammer nest predation rates were similar in New Zealand and Britain, suggesting the hypothesis could not explain the higher breeding densities in New Zealand.

We also addressed the "increased niche opportunity" hypothesis. It predicts that introduced species experience enhanced success because of greater abundance or better quality resources in the new environment, leading to increased survival and recruitment or both (Shea and Chesson, 2002). Contrary to the predictions, habitat quality (measured as the density and diversity of all invertebrates or the density of preferred invertebrate prey, a key food resource for nestling yellowhammers) was significantly lower in New Zealand than in Britain (MacLeod et al., 2005a,b). We also found no statistical evidence that differences in habitat availability or quality could account for the overall difference in breeding density between the two countries, even though the preferred breeding habitats (hedgerows and ditches) of yellowhammers were twice as abundant on the New Zealand study farms than on those in Britain. Nine of eleven of New Zealand's most common introduced farmland bird species had smaller clutches than in their native range (Evans et al., 2005). In addition, the overall reproductive output per nesting attempt for yellowhammers in New Zealand was significantly lower than in Britain (MacLeod et al., 2005c), suggesting that either higher survival rates or longer breeding seasons are necessary to attain higher lifetime productivity. Little is known about adult survival rates. However, there is some evidence to indicate that 11 introduced farmland bird species in New Zealand, including the yellowhammer, have longer breeding seasons than the same species in their native range (Evans et al., 2005). Introduced birds may experience longer breeding seasons in New Zealand because there is less variation in resource availability due to reduced seasonal variation in climatic conditions (Evans et al., 2005). Similarly, introduced birds may achieve higher rates of winter survival because food resources are more abundant or more readily available during the winter in New Zealand than in Britain (MacLeod et al., 2005a).

Temporal and spatial variation in resource availability may be key factors influencing niche opportunities for introduced species (Shea and Chesson, 2002). In this chapter we consider how temporal variation in resource abundance may apply to the ecology of introduced birds in New Zealand and the yellowhammer and skylark in particular, and what role this may have had in their successful colonization of their new environment. We test the prediction that introduced birds in New Zealand experience increased niche opportunities because of differences in the temporal availability of resources compared to the native range. Specifically, we wanted to know if winter seed resources were more abundant and if there was less temporal variation in resource availability during the breeding season in New Zealand.

14.2. Methods

14.2.1. Breeding Yellowhammers

We recorded daily precipitation and minimum and maximum temperatures and collected invertebrate samples for the duration of each breeding season (May–August 2000 in Britain, November 2001–February 2002 in New Zealand).

Data were collected from the meteorological station nearest to each of our study sites (Data Sources: Meteorological Office in Britain; National Institute of Water and Atmospheric Research in New Zealand). We recorded and calculated mean rainfall amount, as well as mean, minimum, and maximum temperatures for each of six contiguous 3-week periods covering the main period of breeding in each season (where period 1 was 1–21 May in Britain and 1–21 November in New Zealand).

We measured invertebrate abundance throughout the season on two mixed cropping sites in each country to investigate whether there was less temporal variation in invertebrate food resources during the breeding season in New Zealand than in Britain. Invertebrates were sampled at approximately two-week intervals for a single breeding season in each country. We used a stratified randomized sampling technique to ensure that all crop and non-crop habitat types were sampled (see MacLeod et al., 2005a). Five random samples were collected from each habitat type using a sweep net; each sample consisted of 10 sweeps of the net. Samples were frozen until sorted and the number of invertebrates within each taxonomic order recorded. We calculated the mean number of invertebrates in each country for each of the six 3-week periods during the breeding season.

We assessed temporal variation in breeding productivity of yellowhammers by measuring mean daily clutch and brood failure rates as well as the mean number of fledglings per nesting attempt per three-week period. Nests were located by monitoring individual yellowhammer breeding territories, which were identified using the methods of the Common Birds Census (Bibby et al., 1992; MacLeod et al., 2005a,c). Once a nest was located, it was monitored at three to five day intervals to assess the outcome of the breeding attempt. The daily clutch and brood failure rates were calculated using the Mayfield method (Mayfield, 1961, 1975). For nests that failed between two visits, failure was assumed to have occurred halfway between the visits. The mean number of fledglings produced per nesting attempt was calculated using only nests that survived to fledging. Nests were allocated to 3-week periods according to the first egg appearance date for each nest.

T-tests were used to test for significant differences in overall means for weather, invertebrate, and breeding parameters. Coefficients of variation (CV) were used to quantify the extent of temporal variation between 3-week periods in each country. To compare the extent of temporal variation between countries, we calculated the ratio of the coefficients of variation by dividing the British value by the New Zealand value. Thus, a ratio close to one indicated similar levels of temporal variation in each country, whereas a ratio of greater and less than one indicated more temporal variation in the British and New Zealand range, respectively.

14.2.2. Wintering Yellowhammers and Skylarks and their Seed-Food Resources

Seed surveys were undertaken within the main cropping areas in each country to determine whether winter seed food resources were more abundant in New Zealand

(Canterbury) than in Britain (Norfolk) (Robinson and Sutherland, 1999). A total of 18 fields in Britain (317 ha) and 23 fields in New Zealand (88 ha) were surveyed. Crop composition reflected general cropping trends in each area. In Britain, the fields were predominantly arable crops (6 stubbles, 10 winter-sown cereal, 1 non-rotational set-aside, and 1 grass ley; see Box 14.1 for definitions). In New Zealand, the fields were a mixture of arable and grass crops (4 stubbles, 1 cereal, 3 bare ground, 1 brassica, and 14 grass; see Box 14.1). In both countries, surveys were carried out in late winter when food resources would be expected to be lowest. In Britain, 13 and 5 fields were surveyed in March 1995 and March 1996, respectively. In New Zealand, all 23 fields were surveyed in September 2004.

Box 14.1. Description of crop categories.

Crop type	Description
Cereal	A grain crop (usually wheat *Triticum* or barley *Hordeum)*
Brassica	An arable crop from the cabbage family.
Stubble	The cut stalks of crop plants (usually cereal) left in the ground after harvesting.
Bare ground	An area without vegetation that had been either ploughed or recently sown.
Non-rotational set-aside	An area of land British farmers are paid not to grow crops as a production control measure, leaving land fallow for up to five years.
Grass	Grassland (mainly ryegrass *Lolium*) consisted of a mixture of pasture (grazed by cattle and sheep), silage and grass ley (temporary grassland)

In Britain, seeds were sampled from ten randomly selected locations in each field, except in four fields where 24, 40, 138, and 170 samples were collected. In 1994, eight soil cores (5 cm in diameter and 6 mm in depth, equivalent to an area of 0.016 m^2) were collected per sample. In 1995, five soil cores (7 cm in diameter and 6 mm in depth, equivalent to an area of 0.019 m^2) were collected per sample. In New Zealand, seeds were sampled within each field using ten quadrants (50×50 cm) placed at approximately equal distances from corner to corner across the field, starting 1 m from the field boundary. Five random soil core samples (7 cm in diameter and 6 mm deep, equivalent to an area of 0.019 m^2) were collected from each quadrant. In both countries, soil samples collected were washed through two sieves (mesh sizes: 1– 2 mm and 500– 600 μm) to collect seeds, and the number of seeds from each sample was counted. We estimated the abundance of large seeds (>1 mm) and small seeds (i.e., 1 mm <500 μm) because the calorie content of seeds is related to seed size and, therefore, may affect a bird's foraging efficiency (Green, 1978; Robinson, 2004), We also assessed bird abundance during the late winter on the same fields that the seed surveys were undertaken in each country. Our study focused on two seeding-eating bird species, yellowhammer and skylark, that are known to exist at higher densities in New Zealand than in Britain. Observers walked once along parallel transects at 60-m intervals across the length of each field, counting all birds seen in order to produce an accurate estimate of the total number of birds in each field. Care was taken not to record the same individuals more than once, by noting where birds had landed after being flushed by the observer. Observations were not carried out during periods of strong wind or heavy rain, when bird activity may be reduced.

We used generalized linear models (GLM) to test whether large and small seed densities were significant predictors of skylark abundance across all fields in each country separately. (We excluded yellowhammers from our models because in Britain this species was only detected in one field). To control for any potential bias arising from the differences in crop composition between the regions we also tested whether seed densities were significant predictors of skylark densities only within arable crops in each country, Skylark counts were in fields of different sizes, so to convert our response variable (number of birds) to a density measure, we included field area as an offset variable in the model. Initially, we fitted the GLM model specifying a Poisson error distribution and log link function because our response variable was count data (number of birds per field). However, these models were over-dispersed, so instead we specified a quasi-Poisson error distribution to correct for over-dispersion. The significance of each variable was tested using the change in deviance of the fitted model (ΔD), whose distribution approximately follows χ^2.

14.3. Results

14.3.1. Breeding Yellowhammers

There was no significant difference in the overall mean rainfall or in overall mean temperatures during the breeding season between countries. However, temporal variation in mean rainfall was greater in New Zealand than in Britain (Fig. 14.1a, Table 14.1), and temporal variation in mean temperatures was greater in Britain, where temperatures increased more markedly over the course of the breeding season (Fig. 14.1b, Table 14.1). Average minimum and maximum temperatures were lower and more variable in Britain than in New Zealand (Figure 14.1c,d, Table 14.1).

Invertebrate abundance was consistently lower on farms in New Zealand than those in Britain, but temporal variation in invertebrate abundance was similar in each country (Figure 14.2, Table 14.1). In both countries, lowest invertebrate densities were recorded at the start and end of the breeding season.

There was no significant difference in the overall means of breeding parameters between countries. However, temporal variation in daily clutch failure rates was greater in New Zealand than Britain, while the trend was reversed for daily brood

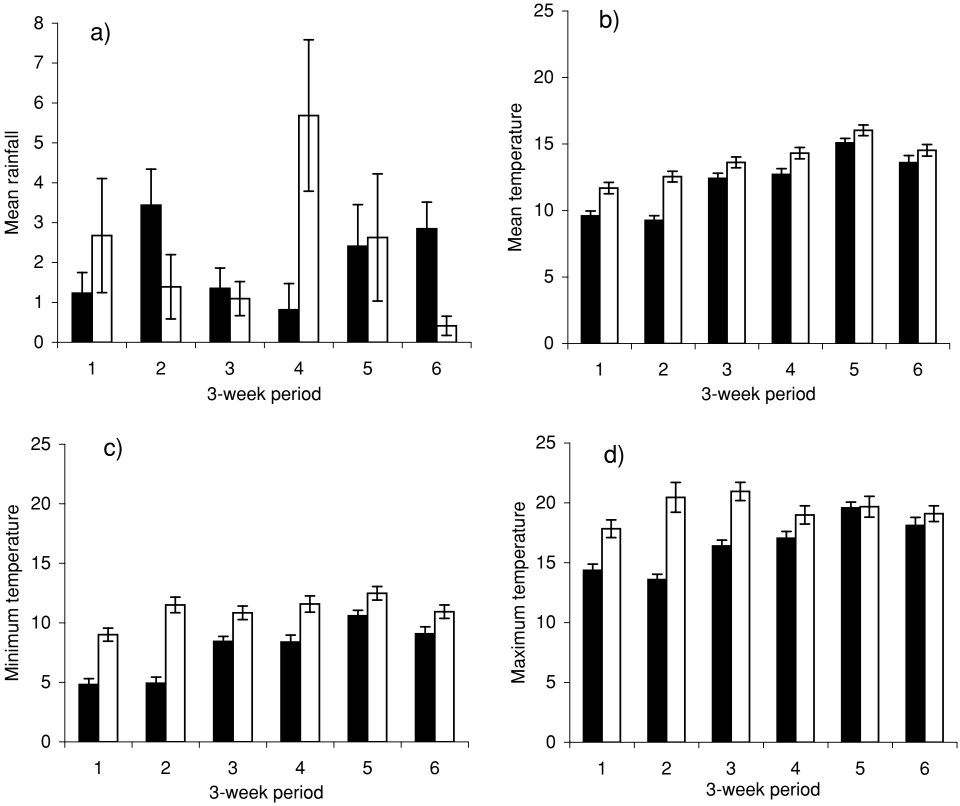

FIGURE 14.1. Mean rainfall and temperature values for six 3-week long periods for study sites in Britain (black bars) and New Zealand (white bars). Period 1 in Britain lasted from 1 May to 21 May and in New Zealand from 1 November to 21 November.

TABLE 14.1. Mean (± standard deviation) and the coefficient of variation ratio (CV ratio) for weather, invertebrate, and breeding parameters over the six 3-week periods during the breeding season in Britain and New Zealand.

	Mean (± SD)					CV ratio
Parameter	Britain	New Zealand	t	df	*p*	Britain: New Zealand
Rainfall (mm)	2.3 ± 1.0	2.0 ± 1.9	0.34	7.80	ns	0.64
Mean temperature (°C)	12.1 ± 2.3	13.8 ± 1.5	1.49	8.77	ns	1.68
Maximum temperature (°C)	16.5 ± 2.3	19.5 ± 1.1	2.91	7.32	0.02	2.40
Minimum temperature (°C)	7.7 ± 2.3	11.1 ± 1.2	3.14	7.34	0.01	2.89
Invertebrate abundance	33.8 ± 14.5	12.1 ± 5.1	−3.45	6.02	0.01	1.02
Daily clutch failure rates	0.04 ± 0.03	0.09 ± 0.07	1.59	5.19	ns	0.92
Daily brood failure rates	0.08 ± 0.09	0.06 ± 0.03	−0.51	4.82	ns	2.26
Number of fledglings	2.52 ± 0.36	2.66 ± 0.37	0.61	8.00	ns	1.04

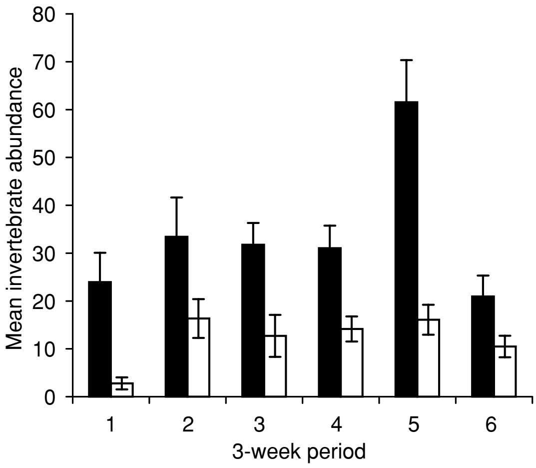

FIGURE 14.2. Average number of invertebrates for each of six three-week periods for study sites in Britain (black bars) and New Zealand (white bars). Period 1 in Britain lasted from 1 May to 21 May and in New Zealand from 1 November to 21 November.

failure rates (Table 14.1). Daily clutch failure rates in Britain increased over the course of the breeding season and peaked during period 4, but in New Zealand were highest at the beginning and end of the breeding season (Fig. 14.3a). Daily brood failure rates, in contrast, decreased over the course of the breeding season in Britain but peaked mid-season in New Zealand (Fig. 14.3b). Temporal variation in the mean number of fledglings produced from successful nests was therefore similar in each region (Fig. 14.3c, Table 14.1).

14.3.2. Wintering Yellowhammers and Skylarks and their Seed-Food Resources

During the winter, yellowhammer and skylark densities were significantly higher on fields in New Zealand than in Britain (Table 14.2). Both species were also

TABLE 14.2. The proportion of fields with skylarks and yellowhammers present ($n_{uk} = 18$, $n_{nz} = 23$) and the median bird densities (per ha) and seed densities (per m^2) during the winter in the native and introduced ranges. (The range of densities is presented in parentheses).

		UK	NZ	Wilcox statistic (W)	*p*-value
% of fields present	Yellowhammer	0.06	0.52		
	Skylark	0.33	0.70		
	Large seed	0.72	0.22		
	Small seed	1.00	1.00		
Density	Yellowhammer	0.00 (0.00–0.50)	0.27 (0.00 –15.52)	106.5	0.001
	Skylark	0.00 (0.00–0.99)	0.58 (0.00–9.89)	115	0.011
	Large seed	2.12 (0–55)	0.00 (0–21)	293	0.013
	Small seed	51.18 (8–1803)	504.10 (5–3685)	91	0.002

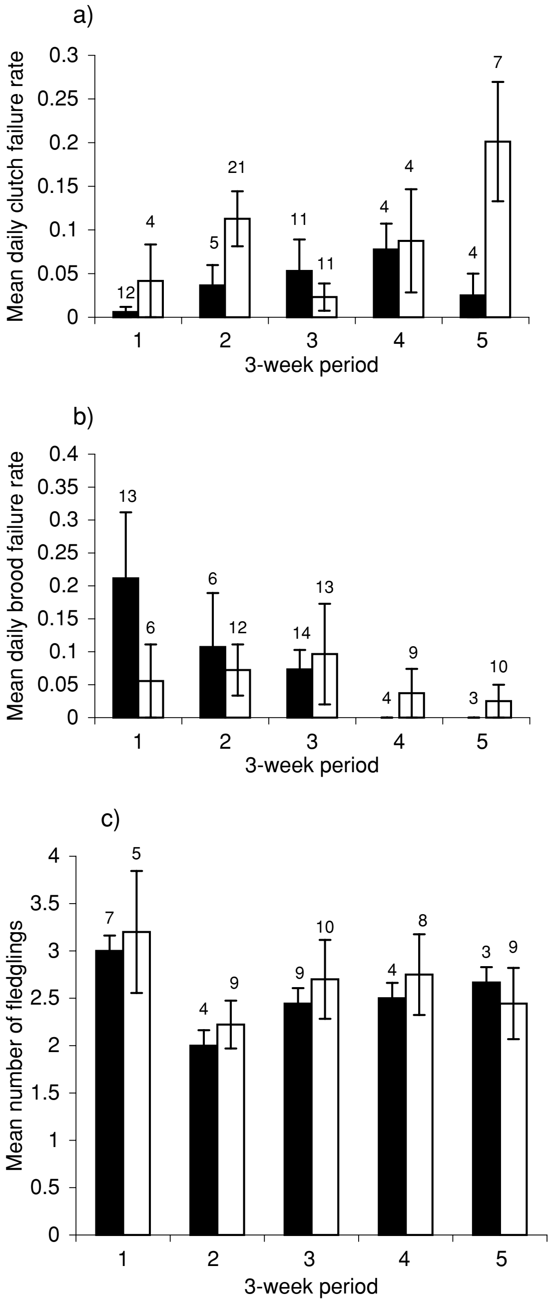

FIGURE 14.3. Variation in the mean daily clutch and brood failure rates and number of fledglings produced per breeding attempt during each three-week period of first egg dates in Britain (black bars) and New Zealand (white bars). Period 1 in Britain lasted from 1 May to 21 May and in New Zealand from 1 November to 21 November. Numbers above each bar are the numbers of nests monitored during that 3-week period.

TABLE 14.3. The median skylark densities per ha and seed densities per m^2 in relation to crop type during the winter in the native and introduced ranges. (Density range in parentheses).

	Stubble		Other arable crops		Grassland	
	UK	NZ	UK	NZ	UK	NZ
Number of fields	6	4	11	5	1	14
Skylark	0.22	1.05	0.00	1.64	0.00	0.31
	(0–0.85)	(0–9.89)	(0–0.99)	(0–2.54)	0.00	(0–3.62)
Large seed	3.74	0.00	2.12	0.00	0.00	0.00
	(2–55)	(0–10)	(0–27)	(0–21)		(0–21)
Small seed	122.98	257.24	46.72	72.76	33.98	984.81
	(48–1803)	(192–603)	(8–480)	(5–483)		(47–3684)

present on a higher proportion of fields in New Zealand. Yellowhammers were detected on over 50% of fields in New Zealand but only found on one field in Britain, while skylarks were present on twice as many fields in New Zealand. Although large seed densities were significantly higher in Britain, small seeds were more abundant in New Zealand (Table 14.2). Large seeds were detected on a higher proportion of fields in Britain. The trend for higher skylark and small seed densities, but lower large seed densities in New Zealand was consistent across different crop types (Table 14.3).

Skylark densities within fields were positively associated with seed densities in Britain (large seed densities: $\Delta D = 64.38$, df $= 16$ $p = 0.01$; small seed densities: $\Delta D = 45.51$, df $= 16$, $p = 0.03$), but not in New Zealand. We also tested whether seed densities were significant predictors of skylark densities only in arable crops in each country, to control for any potential bias arising from the differences in crop composition between the regions. Seed densities were the only significant predictors of skylark density within arable crops in Britain (large seed densities: $\Delta D = 60.15$, df $= 15$, $p = 0.02$; small seed densities: $\Delta D = 42.85$, df $= 15$, $p = 0.04$).

14.4. Discussion

14.4.1. Breeding Yellowhammers

Evans et al. (2005) hypothesized that introduced birds in New Zealand experience longer breeding seasons than the same species in parts of Britain, because there is less variation in resource availability due to reduced climatic seasonality. In our study, we found evidence to support the prediction that yellowhammers in New Zealand may experience reduced climatic seasonality relative to those in Britain, because temperatures were less variable during the breeding season. However, we found no evidence of reduced temporal variation in invertebrate abundance during the breeding season in New Zealand. If introduced yellowhammers experience increased niche opportunities during the breeding season in New Zealand, it is more probably because they are living in a more stable and warmer environment, and not because of a lessened variability in the abundance of resources. Introduced birds may experience reduced energetic costs associated with foraging activities in these climatic conditions compared with those in the more variable, cooler native range and may have to spend less time sheltering the young from inclement weather. Indeed, we found that although invertebrate abundance was lower in New Zealand than in Britain, the introduced yellowhammer achieved similar levels of breeding success. Adult yellowhammers in New Zealand may invest more in foraging effort to compensate for lower invertebrate food supplies without reducing their own survival rates.

Temporal variability may be important at two scales. On a daily basis, temperature range was greater in Britain particularly at the low end of the temperature range. This meant that chicks in Britain experienced colder temperatures and were subject to greater chilling. This is likely to account for the greater variability in chick survival rates in Britain. In many temperate species, mortality, either as chicks or full-grown birds, is likely to be greatest during periods of extreme weather, particularly cold temperatures (e.g., Moss et al., 2001; Robinson, 2001). Hence greater variability can have an impact on demographic rates without any observable change in mean conditions.

On a seasonal basis, temporal variation in daily clutch and brood failure rates in New Zealand reflected, at least in part, temporal trends in invertebrate food abundance and climatic variables: daily clutch failure rates were highest at the start and end of the breeding season when invertebrate food supplies were lowest. The peak in daily brood failure rates coincided with a spell of heavy rainfall. However, in Britain, temporal trends in daily clutch failure rates and daily brood failure rates did not reflect temporal trends in invertebrate abundance. Instead, daily clutch failure rates increased over the course of the breeding season, while daily brood failure rates decreased. The decrease in daily brood failure rate in Britain may reflect a trend toward more favourable climatic conditions or increasing availability of unripe grain or both for chicks later in the season, but it is less clear why clutch failure rates increased during the course of the breeding season.

14.4.2. Wintering Yellowhammers and Skylarks and their Seed-Food Resources

Our study found that both skylark and yellowhammer densities were significantly higher during the winter in New Zealand than in Britain, providing further evidence that these species are examples of introduced species experiencing enhanced success in their new environment (Thomsen et al., 2001; Donald, 2004; MacLeod et al., 2005a). However, it is important to establish that our study sites were representative of national trends in each country. Our study sites in Britain were located in an area which supported some of the highest skylark and yellowhammer densities in the country (Lack, 1991), suggesting that the difference in skylark and yellowhammer densities between countries cannot be explained by selection of sites with low bird densities. Density estimates for yellowhammers and skylarks at the national scale are not available in New Zealand, although similar densities of both species were detected in a larger scale project in the Canterbury region, suggesting that the high densities found in this study are representative of bird densities, at least at the regional scale (MacLeod and Drew, 2004).

To determine whether enhanced winter food resources in New Zealand may explain the success of these introduced bird species in their new environment, we compared seed densities in fields in their introduced and native ranges. We found that small seed densities were significantly higher in fields in New Zealand than in Britain. However, contrary to our prediction, large seed densities were lower and more aggregated in New Zealand. In addition, winter seed densities were only significant predictors of skylark densities in Britain. A key question is, therefore, why is seed density a poor predictor of bird densities in New Zealand during the winter?

In our study, skylark densities in Britain were highest on stubble fields where large seed densities were also highest. Skylarks in Britain are known to select stubbles, which have relatively high densities of spilt grain, because the birds are able to feed more efficiently than in areas with low seed densities (Robinson and Sutherland, 1999; Robinson, 2004). Other studies have shown that skylarks in Britain tend to avoid grassland areas during the winter (Gillings and Fuller, 2001; Donald, 2004). The shift toward more intensive farming practices in grassland systems may have reduced seedbanks associated with this habitat, thereby, reducing their value as winter foraging habitats for granivorous farmland bird species (Vickery et al., 2001; Robinson et al., 2004). Indeed, numbers of seed-eating bird species in grassland-dominated systems in Britain are positively associated with the area of available arable habitat (Robinson et al., 2001). Furthermore, breeding densities for seed-eating birds are higher in areas with stubbles during winter, indicating their importance in maintaining Britain's farmland bird populations (Gillings et al., 2005).

Grassland habitats in New Zealand supported the highest small seed densities. Although skylark densities were also lowest in grassland fields in our New Zealand study site, they were still relatively high compared to stubble fields in Britain. Elsewhere, we found that skylarks at our New Zealand study site avoided grassland fields in the mid-winter and that crop type was a poor predictor of skylark distribution later in the season (MacLeod and Till, in press). However, another New Zealand study found that skylarks congregated on Lucerne *Medicago sativa* and ryegrass pastures and growing cereals during the winter, suggesting that grassland areas may provide important winter foraging habitats in some areas (Thomsen et al., 2001). The differences in habitat selection and relationships between bird and seed densities between the two countries may reflect, therefore, differences in the availability of the different habitats and the food resources associated with them. For example, in New Zealand, stubble fields were found on only 39% of 19 1-km squares surveyed during the winter with an average field size of 7.2 ha

(MacLeod and Drew, 2004), whereas in Britain $\sim$61% of 601 sites 1 km^2 in size had stubbles, with 35% having $<$10 ha of stubble, and 26% with $>$10 ha of stubble (Gillings et al., 2005). Although skylarks have access to more abundant large seed resources in Britain, birds in New Zealand may still have access to better winter seed resources because, at large landscape extents, grassland habitats are more abundant and support high densities of small seeds. The percentage of land classified as grassland or arable land covered by grassland in England in 2000 was 57% of 7.2 million ha (source: Defra); in New Zealand in 2001: 97% of 12.1 million ha was covered by grassland (source: Statistics New Zealand). Seed densities may be poor predictors of bird abundance in New Zealand because seed resources are not a limiting factor.

In Britain, grain is an important component of skylark diet over the winter (Donald, 2004; Robinson, 2004). However, weed seeds are also present but usually compose only a small proportion of the diet (Wilson et al., 1999; Donald, 2004). This pattern may reflect the decline in weed species in farmland habitats. Because small seeds are more abundant in New Zealand, the foraging efficiency of the skylark may be similar or greater than that of skylarks feeding on supplies of large seeds in their native range. To understand the relative importance of small and large seed resources for skylarks in New Zealand, detailed studies of the weed seed composition and distribution are required as well as studies of skylark foraging behaviour and diet composition.

Milder winter conditions may facilitate a longer growing season for grass and weed species in New Zealand, increasing seeding opportunities and hence higher densities of small seeds. Differences in management practices may also explain the differences in seed densities between countries. For example, although there is an increasing trend for use of artificial fertilisers in New Zealand, application rates are generally lower than in Britain (Jarvis and Ledgard, 2002; MacLeod and Moller, in press). In addition, clover Trifolium mixtures are still widely used as a part of the crop rotation for nitrogen fixing in New Zealand (Langer, 1990) and, therefore, may play an important role in maintaining winter seed resources. In addition, livestock husbandry practices differ between countries. In Britain, livestock are usually housed indoors over the winter period, whereas in New Zealand livestock are over-wintered outdoors and provided with supplementary food stuffs that may also provide birds with an additional winter seed supply. Crops in New Zealand may also support higher weed densities because the herbicide application rate is lower.

In Britain, skylark distribution is not only determined by the availability of seed resources. This species is also known to preferentially select large, open fields (avoiding fields that are less than 2 or 3 ha) without boundary features such as hedgerows and trees, which may harbor predators. They take to flight to avoid predators, so they need plenty of time to detect and react to an approaching raptor (Cresswell, 1994). Although predation risk is relatively difficult to quantify, in Britain the density of avian predators is relatively high, with several species (Merlin *Falco columbarius,* Sparrowhawk *Accipiter nisus,* and Peregrine *F. peregrinus*) being significant predators of farmland passerines. However, skylarks in their introduced range were utilising much smaller fields; average field size on our New Zealand study sites was only 3.28 ha. Skylarks may use smaller fields in New Zealand because of a reduced risk of avian predation. Only one avian predator, the Australasian Harrier hawk *Circus approximans* is present at high densities. Reduced predation risk may create increased niche opportunities in New Zealand by increasing the total available food supply, as individuals can (safely) forage in areas that would otherwise have had too high a predation risk. It may also result in higher survival rates too.

14.5. Conclusions

The temporal variation in food abundance on our study areas in New Zealand and Britain was broadly out of phase, with greater breeding season invertebrate densities in Britain and more abundant winter food supplies (seeds) in New Zealand. In New Zealand, an increase in winter resource abundance and a reduction in predation risk appears to have resulted in more available foraging habitat. However, although there was some evidence that local climatic conditions may be less variable during the breeding season in New Zealand, we found no evidence that temporal variation in invertebrate food resources through the breeding season was reduced. This suggests that enhanced niche opportunities, if they exist, are not due to an increased abundance or temporal reliability of invertebrates, but rather enhanced niche opportunities may exist because of a warmer, more stable climate during the breeding season and lower energetic costs associated with foraging activities. Introduced birds in New Zealand are able to maintain high population densities despite relatively poor breeding food resources. Enhanced winter food resources may be a key factor contributing to their success. It appears that winter survival rates of individual yellowhammers and skylarks, mediated via reduced food supplies, are a significant factor in the decline of these and perhaps other species in Britain.

More detailed comparative studies of the diet, foraging patterns, and population dynamics of bird species that inhabit both native and introduced ranges are required to understand better the influence of temporal variation in winter food resources and climate on breeding bird populations. Well-designed studies would aid management programs aimed at either controlling pest bird populations or enhancing declining native bird populations.

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The approach is multidisciplinary involving aspects of both animal and plant ecology (at the population and community level, respectively). Typically the projects are conducted at multiple scales focusing on temporal and spatial dynamics of wetland species and habitats particularly as related to natural and anthropogenic variables that regulate their structure and function (principally, hydrology, water quality, and fire). He has published chapters in several other books on topics as varied as the population demography of the endangered snail kite, landscape analyses of the tree island complexes of the Everglades, to material exchanges between tidal wetlands and contiguous coastal waters. His recreational interests include boating (particular airboats), automobiles, and fishing.

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Richard Stillman is a bird population ecologist and modeler at the Centre for Ecology and Hydrology, United Kingdom. His main interest is to predict how bird populations are influenced by environmental change from an understanding of the foraging behavior of the individual animals within these populations. His main study species to date have been European coastal shorebirds, for which he has developed several individual-based models to predict the effect on survival of habitat loss, shellfishing, and disturbance in a range of estuaries. He is interested in applying this approach to a wider range of systems, including the effect of agricultural change on the survival rates of farmland birds.

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