23

Prescribing Habitat Layouts: Analysis of Optimal Placement for Landscape Planning

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23.1 Introduction

Physical restructuring of landscapes by humans is a prominent stress on ecological systems (Rapport et al. 1985). Landscape restructuring occurs primarily through land-use conversions or alteration of native habitats through natural resource management. A common faunal response to such land-use intensification is an increased dominance of opportunistic species leading to an overall erosion of biological diversity (Urban et al. 1987). Slowing the loss of biodiversity in managed systems will require interdisciplinary planning efforts that meld analysis approaches from several fields, including landscape ecology, conservation biology, and management science.

The objective of this chapter is to review emerging methods from this set of disciplines that enable analysts to make explicit recommendations (prescriptions) concerning the placement of wildlife habitat in managed landscapes. We first define what we mean by habitat prescriptions and compare two general habitat-placement planning strategies. We follow this with a discussion of critical thresholds and their influence on landscape planning analyses. This conceptual summary is followed by a review of two theoretical and two management application examples of these planning strategies. Our examples focus on conservation problems involving the response of a single species to varying amounts and arrangements of habitat. The last three sections of the chapter use the findings from these case examples to derive general principles related to spatially explicit habitat prescriptions; to define theoretical and empirical knowledge gaps that appear to be impeding the implementation of habitat prescriptions in landscape planning; and to propose specific research approaches that may help close those knowledge gaps and extend our capability to incorporate spatial complexity into resource planning.

23.2 Concepts, Principles, and Emerging Ideas

Wildlife are rarely distributed uniformly in space. Species exhibit a spatial structure in their occurrence and abundance that is caused by habitat heterogeneity, natural disturbance patterns, land use, and resource management activities. Ac-

counting for the interplay among vegetation, animal abundance, and human activity poses increasingly complex problems for landscape planners. Questions concerning the likely persistence of populations within a network of habitat patches, or questions about the most appropriate layout and schedule for land management actions are now commonplace.

Despite a shared landscape perspective, these questions have typically been addressed using different analysis protocols. Population persistence questions are most often addressed by *spatially explicit simulations* that combine species population models with geographic depictions of habitat resources (Dunning et al. 1995). Such simulation approaches permit a detailed mechanistic representation of population dynamics and are used to address planning questions *predictively* (i.e., what "will" the animal response be to a given habitat arrangement). Conversely, questions pertaining to the placement and scheduling of resource management actions are being addressed by *spatial optimization methods* that enable analysts to select the "best" habitat arrangement from an essentially infinite number of spatial landscape choices (Hof and Bevers 1998). Because the outcome of spatial optimization analysis is a habitat design, management recommendations are *prescriptive* (i.e., what "should" the habitat arrangement be to meet specified population objectives most efficiently). Our focus in this chapter is on *prescriptive planning,* by which we mean planning that results in spatially explicit habitat placement recommendations. Although we have linked optimization with prescription, we do not mean to imply that simulation cannot be used to prescribe habitat layouts. However, the use of simulation in prescriptive planning has limitations because a great many potential habitat arrangements must be analyzed before planners can infer a specific habitat design.

Regardless of which strategy is chosen, it is important to realize that these planning approaches are decision tools that carry with them a set of strengths and weaknesses. Neither approach is inherently better than the other, and both involve simplifying assumptions about complex ecological systems. Whether these approaches capture sufficient ecological detail or not will have to be evaluated on a case-by-case basis, which serves to remind us that no one planning tool can be regarded as a panacea to resolve all conservation problems.

23.2.1 Habitat Prescription From Simulation

Resource managers concerned with maintaining target-species populations are typically presented with the task of predicting population response to management activities that alter the amount and geometry of habitat. A number of modeling approaches are available to address this type of planning problem, including *empirical models* derived from statistical estimation (e.g., Morrison et al. 1987), *analytical models* that have exact solutions derived from a few fundamental mathematical relationships (e.g., Lande 1987), and *simulation models* derived from mechanistic mathematical relationships whose number and complexity requires that solutions be explored numerically with digital computers (e.g., Fahrig 1997). Because empirical models tend to be correlative in nature and have not

performed well predictively (Block et al. 1994), and because analytical models tend to become intractable in all but the simplest cases of spatial heterogeneity (Fahrig 1991), simulation modeling has become the method of choice for managers (Simberloff 1988).

Simulation modeling is often used to evaluate population response to alternative landscapes *a posteriori.* Management choices are thus made by ranking the various landscape alternatives by some criterion (e.g., organism abundance, persistence) and selecting the strategy that ranks highest. This use of simulated predictions in conservation planning has been termed *relative ranking* by Turner et al. (1995:13) and is a form of prescriptive planning because the result specifies a habitat arrangement that will "best" address some set of management objectives. The primary shortcoming of this approach is that the outcome is only "the best" alternative from among the limited number of landscape layouts investigated (Conroy 1993).

23.2.2 Habitat Prescription From Optimization

When managers must choose from a large set of possible habitat layouts, spatial optimization methods become useful as an alternative to running numerous simulations. With simulation, we can estimate effects in great detail one habitat layout at a time, whereas optimization models forego some ecological detail to search the entire set of available layouts by simultaneously solving a large system of equations. This equation set formalizes the relationship between various ecosystem goods and services that often involve tradeoffs. A *tradeoff* occurs when one ecosystem output cannot be increased without reducing another. Although simulation can generate different scenarios with different output mixes, only optimization can reduce the search to those tradeoffs that are efficient (e.g., provide the greatest abundance of a particular species for a given amount of land devoted to timber harvesting). From this reduced set of efficient output mixes, optimization can then select a solution that best meets the planner's objectives.

23.2.3 Critical Thresholds and Species Movement

Within the landscape-ecology literature, there is accumulating evidence that landscapes exhibit critical thresholds (Turner and Gardner 1991). *Critical thresholds* refer to changes in some attribute of landscape structure (usually habitat amount) that result in an abrupt shift in some property of landscapes or some ecological phenomenon of interest (Green 1994). One case receiving increased attention is the relation between habitat amount and species extinction (Lande 1987; With and King 1999). Although a relatively recent topic in landscape ecology, the notion of critical thresholds associated with species extinction was actually introduced in the early 1950s when Skellam (1951) mathematically demonstrated a threshold relationship between the size of a single habitat patch and species persistence using a reaction-diffusion model. *Reaction-diffusion* models represent a general class of spatial models that account for reproduction as well as move-

ment. They are closely allied to biochemical reaction-diffusion models (Turing 1952), with reproduction and dispersal as the reaction and diffusion components, respectively (Kareiva 1990). The simplicity of reaction-diffusion models has made them particularly useful in situations in which information on the exact movement paths of individuals is lacking (Turchin 1998).

One implication of critical thresholds that we want to emphasize is the existence of regions in the parameter space (as defined by landscape attributes or population vital rates) where model behavior exhibits fundamental shifts. These regions not only define thresholds, but they also can be used to delimit *domains of applicability* for particular habitat arrangement recommendations, serving as a framework for defining habitat prescriptions for different ecological circumstances.

23.3 Recent Applications

It has been noted that the number of successful collaborations between research scientists and managers in a landscape planning situation is limited (Hobbs et al. 1993; Schemske et al. 1994). We found this to be true in our search for on-the-ground field applications of habitat-prescription concepts. We conducted a review of the literature, sent requests to colleagues, and sent a survey to the Wildlife, Fish, and Rare Plants staff of the U.S. Forest Service requesting information on case examples in which habitat layouts had been prescribed in a resource planning context. This survey was sent to Wildlife Program Managers, Threatened and Endangered Species Program Managers, and Landscape Ecologists within each of the nine National Forest System Regions of the U.S. Forest Service. This review produced examples that were classified into one of two groups. One group was research-driven and focused on examining the response of modeled populations to various habitat layouts on hypothetical landscapes (e.g., Frank and Wissel 1998; Etienne and Heesterbeek 2000).

The second group consisted of conservation planning examples where habitat layouts in actual managed landscapes were proposed for a target species, or set of target species (e.g., Suring et al. 1993; Mellen et al. 1995). Although landscape design concepts were used in these conservation planning examples, conflicts among alternative resource uses, the public review process, and negotiated plan modifications often superseded the proposed habitat prescription. This made it difficult to evaluate the success of these various applications. Furthermore, insufficient monitoring data to date prevented any quantitative evaluation of a particular habitat layout in terms of target species response.

In this section, we review a sample of case examples while acknowledging that none of them represents the situation in which the habitat layout is prescribed, the plan is implemented, and the success of the plan is evaluated through monitoring. We describe four applications of habitat-prescription concepts that have occurred in either a research context (two theoretical examples) or a resource-planning context (two management-oriented applications).

23.3.1 Diffusion and Critical Thresholds—A Theoretical Investigation Using Simulation

When a landscape undergoes fragmentation, habitat is lost, patch sizes decrease, and the distance separating habitat fragments increases (Andrén 1994). The erosive influence of habitat loss on species is widely recognized (Simberloff 1988), but the effects of habitat arrangement on populations is disputed (Fahrig 1997). The contention stems from the multivariate nature of fragmentation and the difficulty in distinguishing the relative influences of habitat amount and habitat arrangement. In this example, we use a spatially explicit reaction-diffusion model (Bevers and Flather 1999a) to simulate long-term equilibrium populations of a hypothetical species with particular attention given to the possible existence of critical thresholds. By varying habitat amount and arrangement systematically, we illustrate the value of simulation experiments in developing general management rules related to prescribing habitat layouts across a landscape.

Many model formulations are available to represent animal movement (Turchin 1998). For species that establish and defend distinct breeding territories, territory size defines a convenient scale for modeling populations across a landscape (Bevers and Flather 1999a). In this example, population abundance over a landscape is estimated using the following reaction-diffusion model:

$$v_{it} = \min(b_{it}, \sum_{j=1}^{N} [1 + f_j(v_{j,t-1})] v_{j,t-1} g_{ji}) \qquad \text{for all } i,\ t,$$

where i and j each index all cells (i.e., potential breeding territories) in the landscape; v_{it} is the population in cell i at time t; b_{it} represents adult carrying capacity in each cell for each time period; $f_j(v_{j,t-1})$ is the net per capita rate of reproduction within a cell (not accounting for mortality associated with dispersal); and g_{ji} reflects the probability of an individual emigrating from breeding territory j to territory i a full breeding season later by any number of possible routes. In this example, we have assumed that the per capita net rate of reproduction is constant across all habitat cells, as is carrying capacity (i.e., we do not let habitat quality vary). We also assume that individuals disperse identically from the center of each habitat cell in uniform random directions with the probability of successful dispersal between habitat cells decaying with distance. Mortality occurs when individuals disperse into nonhabitat, into saturated territories, or outside of the boundaries of the landscape.

We systematically examined the influence of habitat amount and arrangement (Flather and Bevers 2002) by simulating landscape structure using RULE, a computer program that permits the generation of random landscape replicates with user-specified characteristics (Gardner 1999). We generated a total of 2,430 binary (habitat, nonhabitat) landscapes, each composed of 1,024 cells (32 rows × 32 columns). Habitat amount was varied from 10% to 90% of the total area in 10% increments. A fragmentation parameter also was systematically varied over nine levels to cover a range from highly fragmented to highly aggregated spatial

configurations. This resulted in a 9 × 9 factorial simulation experiment with each treatment replicated 30 times (Flather and Bevers 2002). We parameterized the reaction-diffusion model to represent a generic bird species that breeds in forest-interior habitats and defends a 1-ha territory (the area of a landscape cell). The adult carrying capacity within any habitat cell was one breeding pair.

If total bird abundance within each landscape was determined solely by the amount of habitat, we would expect the population response to be proportional to habitat amount. A plot of mean population against habitat amount and fragmentation level appears consistent with a habitat amount effect (Figure 23.1a). Analysis of variance (ANOVA) confirmed this visual inspection—habitat amount accounted for nearly 97% of the variation in abundance (Table 23.1). Fragmentation and its interaction with habitat amount accounted for an additional 1.3% of the variation.

These results suggest that habitat arrangement effects, at least for the hypothetical species being modeled, are inconsequential. However, some distortion of the population response surface away from a pure habitat effect can be observed as habitat was reduced below 40% of our total landscape (Figure 23.1a). That distortion appears to coincide with a persistence threshold as indicated by a rapid decline in the probability of landscapes supporting viable populations (Figure 23.1b). If fragmentation effects become important as landscape structure approaches a persistence threshold, then we would expect to see evidence for a strong difference in the fragmentation effect as our landscapes cross that persistence threshold.

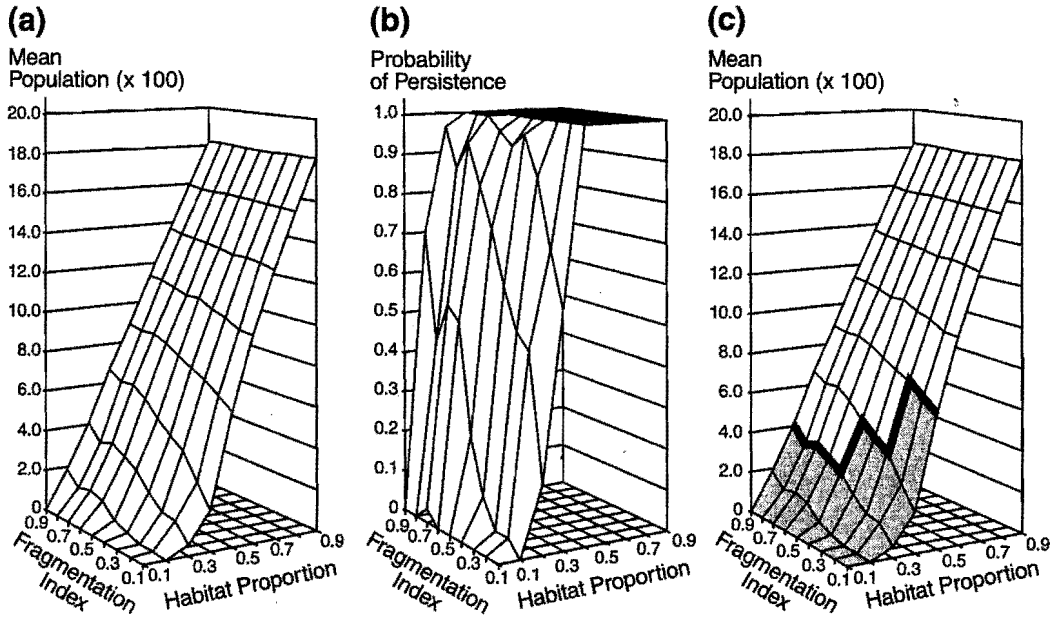

FIGURE 23.1. Population response of a hypothetical species to simulated landscapes with specified amounts of habitat and levels of fragmentation: (a) mean abundance across 30 replicates per treatment pair, (b) probability of replicates supporting viable populations, and (c) identification of the persistence threshold (bold line). Adapted from Flather and Bevers (2002).

TABLE 23.1. Summary ANOVA findings for simulated landscapes for the full 9 × 9 factorial experiment, above a persistence threshold, and below a persistence threshold (*DF* = degrees of freedom, *SS* = partial [Type III] sums of squares). Persistence threshold is as defined in Figure 23.1c.

Source of variation	*DF*	% of Total *SS*	*F*	*P*
Full experiment				
Habitat amount	8	96.8	15871.5	0.0001
Fragmentation	8	0.7	124.4	0.0001
Habitat amount × Fragmentation	64	0.6	13.3	0.0001
Error	2349	1.8	—	—
Above threshold				
Habitat amount	6	96.3	10497.2	0.0001
Fragmentation	8	0.7	55.8	0.0001
Habitat amount × Fragmentation	42	0.5	8.3	0.0001
Error	1653	2.5	—	—
Below threshold				
Habitat amount	3	30.3	122.3	0.0001
Fragmentation	8	6.2	9.4	0.0001
Habitat amount × Fragmentation	12	6.1	6.2	0.0001
Error	696	57.4	—	—

We used Classification and Regression Trees (CART; Breiman et al. 1984) to define a persistence threshold across our set of landscapes. CART defined a simple set of rules based on habitat amount and fragmentation level that maximizes the accuracy of a classification into species-persistent and species-nonpersistent landscapes. The set of rules estimated by CART can then be mapped directly onto the population response surface (Figure 23.1c). Defining the persistence threshold in this manner enabled us to partition landscapes objectively into sets above and below the threshold. Rerunning the ANOVA on these two sets of landscapes supports the hypothesis that fragmentation effects become more important as one approaches a population persistence threshold (Table 23.1). Above the persistence threshold, habitat amount accounts for 96% of the variance in population abundance across treatments. Below the persistence threshold, habitat amount only accounts for 30% of the abundance variation. Note, however, that the error term in the below-threshold ANOVA indicates that 57% of the variation in abundance is still unexplained. This observation is consistent with Green's (1994) finding that variation is greatest close to the critical threshold.

To reduce the uncertainty associated with explaining variation in abundance below the persistence threshold, we characterized the structure of each landscape according to the following simple measures: fragmentation level (as specified during landscape generation), number of habitat patches, mean size of habitat patches, mean distance to nearest patch, total length of edge, size of largest habitat patch, shape (perimeter-to-area ratio) of largest patch, and edge length of

TABLE 23.2. Summary stepwise regression results using landscape structure variables within simulated landscapes to predict species abundance. This analysis was run on those landscape scenes that fell below the persistence threshold defined in Figure 23.1c.

Variable	R^2	F	P
Size of largest patch	0.572	956.06	0.0001
Edge length of largest patch	0.692	279.78	0.0001
Fragmentation	0.727	91.64	0.0001
Average patch size	0.728	2.43	0.1193
Shape of largest patch	0.729	2.74	0.0985

largest patch. Stepwise regression resulted in a five-variable model that accounted for 73% of the variability in population abundance (Table 23.2). Two variables, the size and edge length associated with the largest patch, accounted for nearly 70% of the variation in abundance. This suggests that population persistence in these landscapes was critically dependent on having a single patch that was large and "blocky" enough (i.e., had relatively little edge) to sustain the population within the landscape.

This example has demonstrated, at least theoretically, that manipulation of habitat arrangement can be an important management consideration in maintaining persistent populations in patchy landscapes. However, simulation approaches often cannot feasibly examine all possible habitat layout choices. As a result, habitat arrangement designs prescribed from simulations may be suboptimal (Van Deusen 1996).

23.3.2 Optimal Placement—A Theoretical Investigation Using Spatial Optimization

Given that resources devoted to conservation are limited, managers should seek a habitat layout that is in some sense optimal. In this section, we review an analysis (Hof and Flather 1996) that demonstrates the utility of spatial optimization in making general habitat layout recommendations. We assume, for this particular management problem, that resource extraction and conservation of some target species are simultaneous objectives for a given landscape. Furthermore, resource extraction is assumed to destroy the species' habitat. The problem presented to the resource manager is to determine how to arrange the habitat remaining after resource extraction in a way that will most benefit the target species.

When habitat is going to be lost, it is common to see planning recommendations to maintain well-connected habitats. These recommendations stem from observations that populations found in fragmented habitats may be more prone to local extinction events (Pimm and Gilpin 1989). But wildlife populations also are affected by environmental disturbances (e.g., extreme weather events, fire, epizootics) that have different degrees of spatial covariation (Gilpin 1987). Consideration of these environmental disturbances raises the possibility that population persistence times may actually be longer in fragmented landscapes because the

risk of local extinction is spread among independent populations (Palmqvist and Lundberg 1998). These various population pressures define an ecological tradeoff: minimizing demographic extinction pressures would lead managers to recommend clumping remaining habitat, whereas spatially correlated catastrophic events suggest that some degree of habitat spreading would be advantageous (Hof and Flather 1996).

We can define a statistically based formulation that enables us to capture the tradeoff between habitat connectivity and spatial covariation by treating this as a problem of estimating the total population (T) with a certain level of confidence:

$$T = E(P) + \delta\, V(P)^{1/2}, \tag{1}$$

where $E(P)$ is the expected value of population size across all habitat patches, $V(P)$ is the variance of population size in space and time, and δ is the standard normal deviate for some given confidence level (e.g., $\delta = 1.96$ for 95% confidence).

The expected value of the population among all patches in a landscape is given by

$$E(P) = \sum_{i=1}^{N} d_i A_i PR_i,$$

where d_i is the density of individuals in patch i, A_i is the area of patch i, and PR_i is the joint probability that the patch i is "connected" to any of the N patches in the complex. The joint probability (PR_i) of each patch being connected is given by

$$PR_i = 1 - \left[\prod_{i=1}^{N}(1 - pr_{ij})\right] \qquad \text{for all } i \text{ patches},$$

where pr_{ij} is the probability that patch i is connected to patch j. Ecologically, one expects pr_{ij} to decrease with interpatch distance, but conditioned on the dispersal capability of the species and the resistance of the interpatch matrix to species movement. A continuous function decaying with distance that captures these conditions is given by

$$pr_{ij} = 1 - \left(1 - \theta^{D_{ij}}\right)^{\beta}, \tag{2}$$

where D_{ij} is the distance between patch i and patch j, β reflects the dispersal capability of the target species, and θ reflects the resistance of the matrix to species movement.

Populations of species inhabiting separate patches show differing levels of covariation in their population dynamics (Gilpin 1987). The definition of covariation between any two patches is given by

$$\sigma_{ij}^{2} = \rho_{ij}\sigma_i\sigma_j,$$

where σ_{ij}^{2} is the covariance between the population in patch i and the population in patch j, ρ_{ij} is the correlation between population sizes in patch i and patch j, and

σ_i and σ_j are the standard deviations of population sizes in patches i and j, respectively. The variance in population size, $V(P)$ from Eq. 1, is then given by

$$V(P) = \sum_{i=1}^{N} \sum_{j=1}^{N} \rho_{ij} \sigma_i \sigma_j .$$

We assume that ρ_{ij} is negatively related to interpatch distance and that its decay can be represented by a function similar to Eq. 2:

$$\rho_{ij} = 1 - \left(1 - \omega^{D_{ij}}\right)^{\tau},$$

where τ reflects the threshold distance beyond which the degree of correlation among patch population sizes declines rapidly, and ω is the rate at which patch covariation declines with distance and reflects the resistance of the interpatch matrix to the spread of a particular disturbance agent. Both τ and ω are specific to a particular kind of disturbance agent.

For purposes of illustration, consider a 10,000-ha management area of homogeneous habitat inhabited by a hypothetical target species that defends a 1-ha territory (occupied by a single breeding pair). We assume that 20% of the habitat will be retained following resource extraction. We define the retained patches to have a circular shape and arbitrarily set the maximum number of patches to be four. The optimization problem is thus to choose a size and location for each habitat patch in such a way as to maximize T in Eq. 1. For most conservation problems, the manager is interested in guarding against catastrophically low populations. Consequently, our focus is on the lower bound of the confidence interval specified in Eq. 1. For this example, we want to maximize the population T with 80% certainty, and set $\delta = -0.84$ accordingly. We fixed β and τ to 50 and systematically varied θ and ω over the values of 0.75, 0.85, and 0.95 to explore how optimal habitat placement varied among species with low, moderate, and high dispersal rates and disturbance agents causing low, moderate, and high degrees of spatial covariation. Disturbances with low degrees of spatial covariation affect patch populations locally, and correlation among patches decays rapidly with distance. Disturbances with high degrees of spatial covariation have broad spatial effects, and correlation among patches decays slowly with distance.

The resulting optimal habitat layouts vary greatly among ecological circumstances (Figure 23.2). Species with low dispersal rates in environments with high degrees of spatial covariation reach maximum populations in a clumped arrangement (Figure 23.2a)—disturbances that affect landscapes broadly decrease the risk-spreading advantage of more isolated patches. Species with high dispersal rates inhabiting landscapes with low (Figure 23.2b) to moderate (Figure 23.2c) spatial covariation reach higher equilibrium populations if at least some of the habitats are separated. Finally, species with low-to-moderate dispersal rates in environments with moderate-to-low degrees of spatial covariation attain maximum populations in habitat layouts that provide "corridors" (Figure 23.2d) or "stepping stones" (Figure 23.2e) to facilitate exchange of individuals.

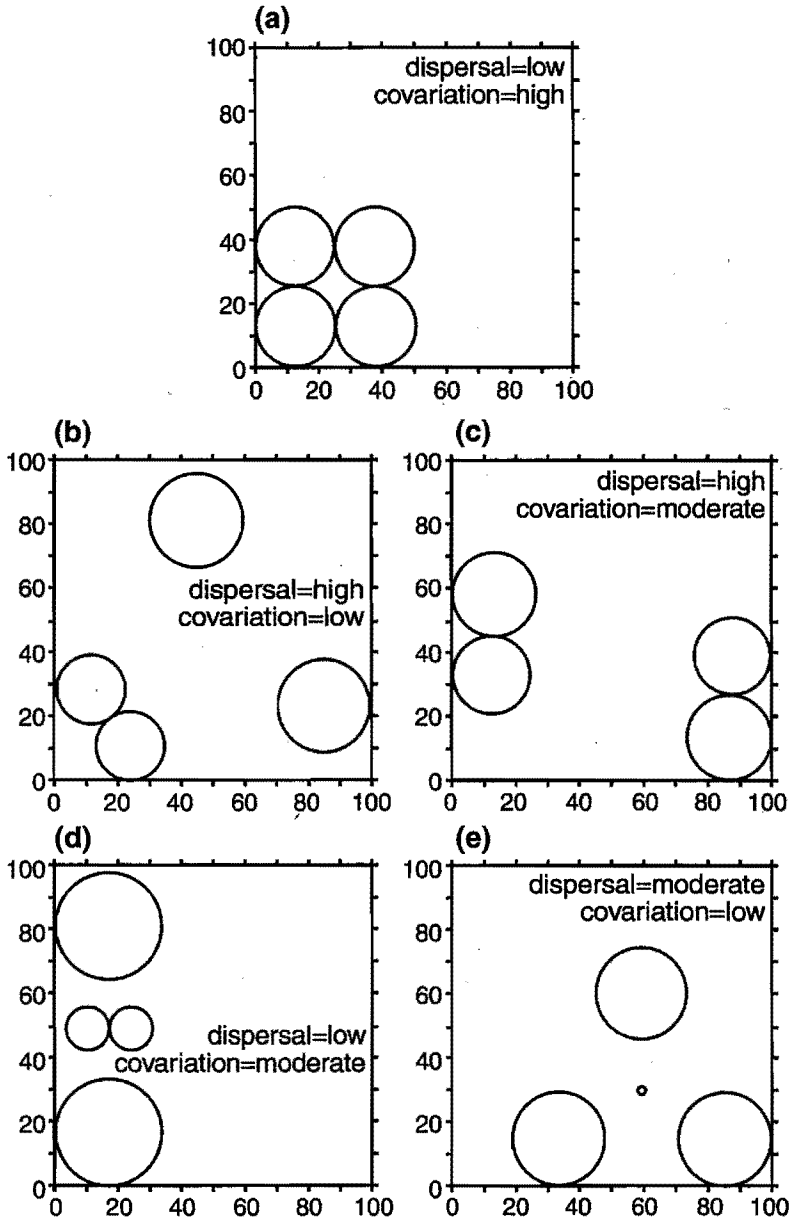

FIGURE 23.2. Spatially optimized habitat layouts for species with different dispersal rates inhabiting landscapes with different degrees of spatial covariation. All layouts are based on the assumption that 20% of the original habitat would be retained in four patches on the landscape after resource extraction. Reprinted from Ecological Modelling, 88, J. Hof and C.H. Flather, Accounting for connectivity and spatial correlation in the optimal placement of wildlife habitat, 143–155, Copyright 1996, with permission from Elsevier Science.

We acknowledge that these two theoretical analyses (in Sections 23.3.1 and 23.3.2) involve conditions that are simple compared with the ecological complexities encountered in an actual landscape planning problem. To balance the simplicity characterizing analyses on hypothetical landscapes, we now review two case examples of habitat placement prescription in actual landscapes.

23.3.3 Reserve Placement for Northern Spotted Owls—A Simulation Application

The Northern Spotted Owl (*Strix occidentalis caurina*) occurs in the coastal mountain region of the northwestern United States and southwestern Canada (Forsman et al. 1984). Throughout its geographic range, the species is associated with old (>150 years), dense, large-diameter coniferous forest stands (Thomas et al. 1990). Timber harvesting, agricultural development, and urban expansion have reduced the owl's preferred habitat to <10% of its original area (Murphy and Noon 1992). Even with such substantial reductions in habitat, the vulnerability of the owl to extinction was greatly debated. In an attempt to resolve the issue, an Interagency Scientific Committee (ISC), including both researchers and managers, was charged with developing a long-term, scientifically defensible conservation plan for the owl (Thomas et al. 1990). The reserve design task was to determine a configuration of habitat areas that would maintain stable local populations of owls throughout the bird's historic range (Noon and McKelvey 1996).

Addressing the question of how to "best" configure owl habitat reserves relied predominately on simulation modeling (McKelvey et al. 1993; Lamberson et al. 1994). Of particular importance to these simulation experiments was the demonstration of sharp extinction thresholds (Lande 1988; Lamberson et al. 1992). As old-growth habitat was reduced in a series of simulation experiments, a point was reached (~20% habitat) when the ability of juveniles to locate suitable territories became compromised, leading eventually to population extinction (Noon and Murphy 1994). Extensive exploration of model parameter sensitivity resulted in the following habitat reserve design criteria: individual habitat areas should be large enough to support at least 20 breeding pairs; habitat areas should be no farther than 19 km apart; and the matrix between habitat areas should be 50% forested with tree diameters >28 cm and with canopy closure >40% to facilitate juvenile dispersal (Noon and McKelvey 1996). Two findings related to these design criteria warrant remark. First, the amount of habitat prescribed in the reserve design was close to a theoretical persistence threshold, raising some concern about owl viability in the face of parameter uncertainty and catastrophic events (Harrison et al. 1993). Second, the ISC noted that the prescribed habitat layout was not a unique solution to the landscape design question, implying that equally good or better layouts may exist.

In a study following the work of the ISC, Hof and Raphael (1997) formulated a spatial optimization model that located areas for old-growth habitat retention such that owl numbers would be maximized on a small portion of the owl's range, the Olympic Peninsula in northwestern Washington. The value of this study was that habitat layout prescriptions derived from both simulation and optimization approaches could be compared, permitting a verification of the more ecologically simple optimization formulation against the more ecologically detailed simulation model. For the optimization model to be beneficial, the number of owl pairs simulated in the habitat layout generated under optimization should be greater than or equal to the number of owl pairs estimated from the simulation-prescribed habitat layout. Two parameter sets (one with optimistic and one with pessimistic

demographic parameters) from Holthausen et al. (1995) were explored. In both cases, populations simulated on the optimization-derived habitat layout produced a marginally greater number of owl pairs than did the populations simulated on the habitat layout derived from simulation modeling (0.01% for the pessimistic parameter set and 5.2% for the optimistic parameter set). The minimal opportunity for finding better habitat arrangements given a pessimistic parameter set near threshold conditions is consistent with reaction-diffusion theory (Bevers and Flather 1999b). As the parameter set moved away from threshold conditions, the optimization-based layout became more beneficial, even with the simplifications.

A unique contribution of the Hof and Raphael (1997) study is that it demonstrates that simulation and optimization need not be mutually exclusive approaches to conservation planning. The interaction has the potential to offer new planning insights and to suggest which aspects of the respective formulations are key in understanding and predicting species response to landscape structure.

A decision to retain late-successional habitats is a decision that is essentially permanent (Hof and Bevers 1998). The "lifetimes" of these habitats are long relative to those of the target species. Under these circumstances, a static perspective on the habitat layout problem was appropriate. However, if habitats are dynamic over a period that is short relative to the lifetimes of target species, then planning analyses must account for habitat change in the allocation of management activities over time. The applied planning case study described in the next section addresses the problem of prescribing habitat configurations dynamically.

23.3.4 Black-Footed Ferret Reintroduction— A Spatial Optimization Application

Historically, the black-footed ferret (*Mustela nigripes*) ranged sympatrically with prairie dogs (*Cynomys* spp.) across most of the North American grasslands (Anderson et al. 1986). Ferrets live principally in prairie dog burrows and depend primarily on prairie dogs for prey (Clark 1989). The black-footed ferret has become one of the world's most endangered mammals, and in 1987, the last known free-ranging members of the species were taken into captivity (Thorne and Belitsky 1989). Demise of the species in the wild was attributed to loss and fragmentation of habitat due to extensive prairie dog eradication programs, sylvatic plague, and changes in land use (U.S. Fish and Wildlife Service, National Park Service, and USDA Forest Service 1994). A successful captive breeding program was established by the Wyoming Game and Fish Department, setting the stage for a national recovery program of releasing captive-bred ferrets back into the wild (Clark 1989).

In 1994, an area centered around Badlands National Park, South Dakota, was established as a release site for captive-bred ferrets. The Badlands reintroduction site includes a region approximately 1575 km^2 in size, comprising portions of the Park, Buffalo Gap National Grassland, and other ownerships. Federally managed lands with active or readily recoverable prairie dog colonies (i.e., suitable habitat for black-footed ferret) are fragmented, occupying less than one-tenth of the area. Ferrets disperse widely and randomly, particularly as juveniles (Richardson et al.

1987), and the spatial arrangement of prairie dog colonies is expected to affect the number of ferrets that can be supported (Minta and Clark 1989). Because rodenticides are used to control prairie dog populations (Roemer and Forrest 1996), ferret recovery also will be affected by the location and timing of rodenticide treatments in the area.

Bevers et al. (1997) built an optimization model to locate prairie dog colonies in the reintroduction area. For recovery planning purposes, it was assumed that prairie dog control would preclude the establishment of ferret populations on nonfederal ownerships. The expected adult black-footed ferret population on federal lands was maximized over a 25-year planning horizon subject to six different levels of prairie dog population control ranging (in equal 20% increments) from no additional ferret habitat (beyond 1994 conditions) to ceasing rodenticide treatments and allowing maximum ferret habitat. Spatial optimization methods were used to select the timing and locations for rodenticide treatments required to meet each prairie dog population policy constraint. Black-footed ferret populations were estimated using a cell-based reaction-diffusion model similar to that described in Section 23.3.1. Carrying capacity for ferrets was based on expected prairie dog population size, modeled as a function of the location and timing of rodenticide treatments within the recovery area.

The projected populations for the six alternatives (from lowest to highest habitat allocation) were approximately 51, 240, 369, 483, 590, and 647 adult black-footed ferrets by the end of the planning horizon (Figure 23.3a). The population increases for each 20% increment in habitat amount (adding potential capacity for about 104 adult ferrets per increment) were 189, 129, 114, 107, and 57 adult ferrets, respectively, demonstrating that those habitat locations with the greatest potential to increase total abundance were added to the complex first. By strategically locating new habitats, population increases greater than the potential capacity of each increment (104 adult ferrets) were possible because the initial complex consisted of widely scattered prairie dog colonies that would otherwise be underused.

Preferred habitat arrangements and the resulting ferret populations (Figure 23.3b–d) changed over time. Early in the planning horizon, the model tended to arrange the available habitat thinly across the entire landscape (Figure 23.3c) to support small expanding population "waves" that spread outward from the selected ferret release locations (Figure 23.3b). Once the prairie dog population capacity constraints became binding, however, the model shifted preferred habitat arrangements into dense clusters around the Badlands National Park boundary (Figure 23.3d), consistent with theoretical findings reviewed in Bevers and Flather (1999b). This sort of dynamic habitat layout strategy may be particularly difficult to discern using simulation analyses alone.

23.3.5 Success of Conservation Planning Applications

The two specific planning applications (Sections 23.3.3 and 23.3.4) we have reviewed were based on rigorous, repeatable protocols that resulted in tangible

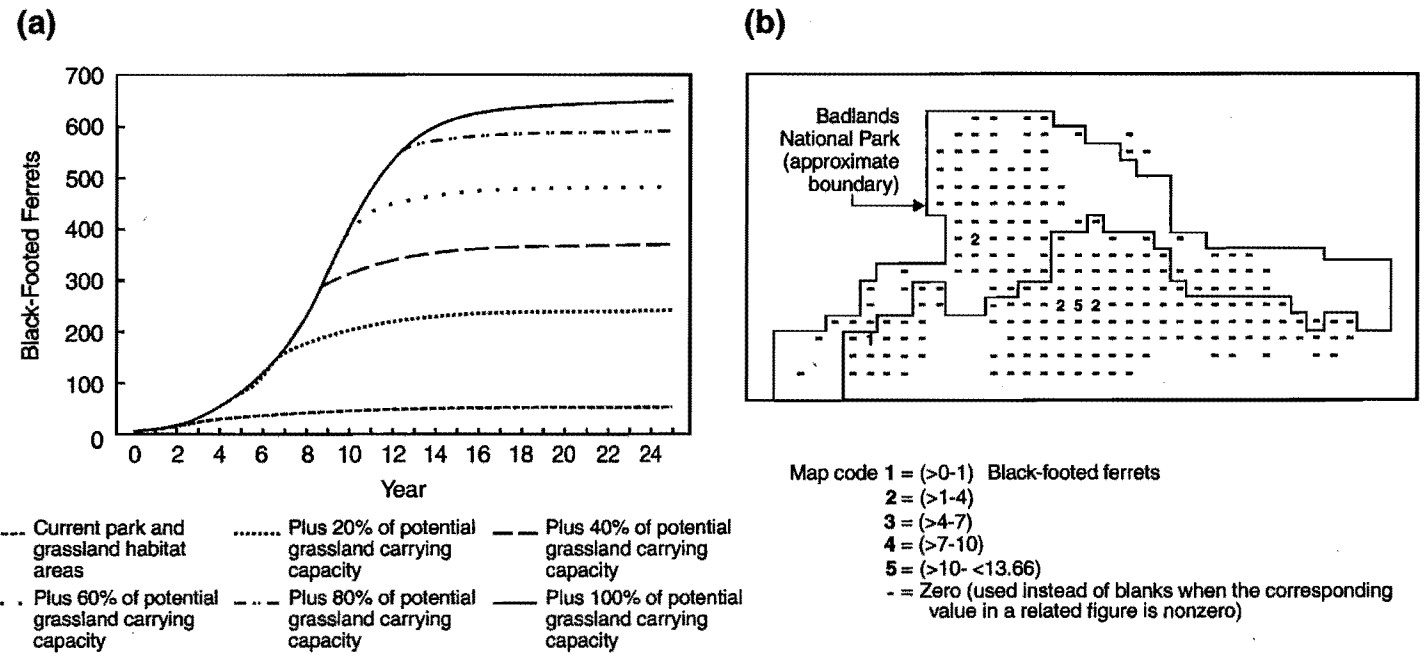

FIGURE 23.3. Black-footed ferret distribution and abundance responses in and around Badlands National Park (South Dakota, USA): (a) population response to 1994 habitat management plans and five alternatives strategies, (b) recommended number of released ferrets and their locations under the +20% alternative, (c) the projected number of black-footed ferrets and their locations under the +20% alternative seven years after release, and (d) the projected number of black-footed ferrets and their locations under the +20% alternative 25 years after release (near equilibrium). Reprinted by permission, M. Bevers et al., Spatial optimization of prairie dog colonies for black-footed ferret recovery, Operations Research, volume 45, number 4, July–August, 1997. Copyright 1997, the Institute for Operations Research and the Management Sciences (INFORMS), 901 Elkridge Landing Road, Suite 400, Linthicum, MD 21090 USA.

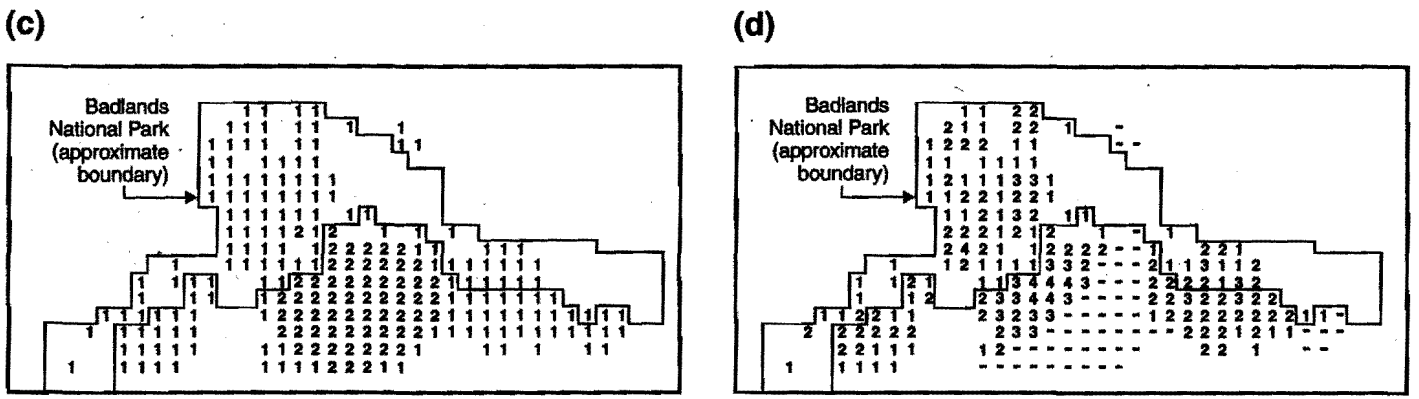

FIGURE 23.3. *Continued.*

management recommendations. Although habitat designs derived from simulation or optimization have yet to be fully implemented, the framework and analyses used make them successful from the perspective of the *process* of conservation planning. From the perspective of *outcome,* the success of these planning efforts must ultimately be judged against the long-term persistence of the species in its natural environment. Unfortunately, evaluating the success of these planning recommendations in terms of population response is premature. The effectiveness of a given habitat prescription may not be detectable for long periods of time because of a species' longevity or for reasons associated with extensive time lags in population responses (Chapter 18). Monitoring in the short term may only document transient behavior not indicative of the prospects for a species' long-term viability (Bevers and Flather 1999a).

23.4 Principles for Applying Landscape Ecology

At present, habitat-placement principles derived from simulation and optimization studies such as those described in this chapter come from theoretical analyses rather than from a distillation of real-world trial-and-error experiences. This situation occurs for two reasons. First, applied spatial habitat prescription, especially spatial optimization, is a relatively new field of study. Second, landscape-level planning is driven as much by political compromise as by analysis. In neither of our planning case studies, involving the Northern Spotted Owl and the black-footed ferret, were the layouts prescribed by the models actually implemented. For these reasons, there are few cases where habitat-placement prescriptions have been tested to the extent that definitive planning guidelines can be formulated (Kareiva and Wennergren 1995). From general theoretical models and planning analyses, however, we can derive several application principles for planners who are involved in using landscape ecology and habitat prescription concepts in biological conservation.

23.4.1 Simulation Versus Optimization

When should planners use simulation or spatial optimization? The answer, to a large degree, depends on the questions being asked and the circumstances surrounding the planning problem. For example, habitat placement choices may be limited because the pattern of land development has reduced the configuration possibilities (Saunders et al. 1991). When habitat-placement options are restricted to a small set, simulation modeling can offer a useful approach for ranking alternative configurations. If, however, placement choices are numerous, then spatial optimization may be useful in determining a layout that is "the best" given the objectives and constraints of the planning problem. Joint use of both strategies, as described in Section 23.3.3, offers planners the opportunity to take advantage of the ecological detail captured by simulation models and the analytical power of spatial optimization to select the best solution.

23.4.2 Placement Rules

An important principle arising from our review is that habitat placement is conditioned on ecological context as defined by species and disturbance. As we have shown theoretically, species movement capability and the degree of spatial covariation caused by different disturbance agents leads to fundamentally different habitat arrangements that will maximize population size within a landscape (see Section 23.3.2). These results suggest that it may be possible to define domains of applicability for different habitat placement recommendations. That is, there may be particular sets of ecological conditions for which different habitat-placement recommendations would offer the best arrangement for a target species (Figure 23.4). However, broadly applicable habitat placement generalizations may be difficult to define because of differences among species' life histories and differences in landscape context. If detailed planning recommendations are necessary, then detailed studies of the target species in a particular setting will be required (Lawton 1999). But incorporation of ecological realism may obscure the detection of general management recommendations that can emerge when studying simplified systems (Doak and Mills 1994). The interplay between ecological realism and generality of recommendations tends to place landscape planning in a dilemma—quick answers based on general rules of thumb will tend to be imprecise, whereas answers specific to a given situation will be expensive and require patience.

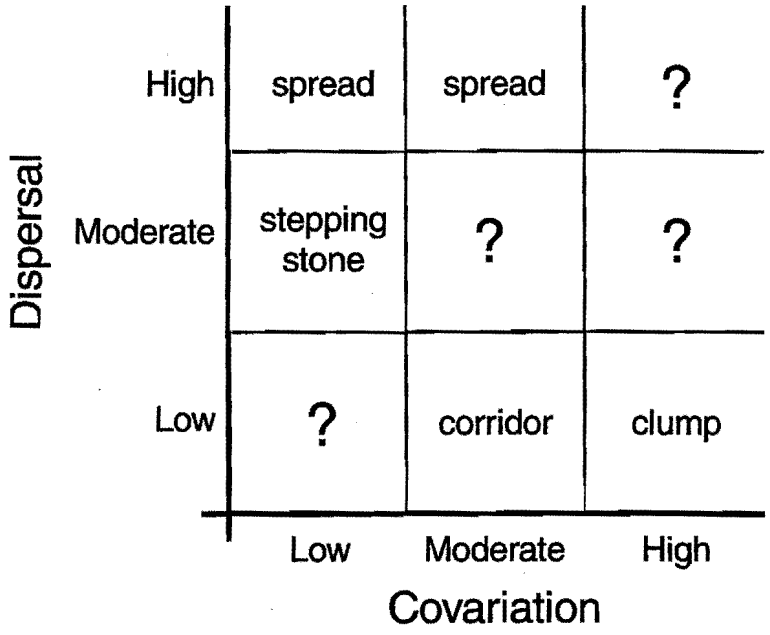

FIGURE 23.4. General habitat placement rules in an ecological parameter space defined by species dispersal rate and degree of spatial covariation based on the results shown in Figure 23.2. The "?" indicates those parameter combinations for which an optimal layout was not estimated.

23.4.3 Critical Thresholds

Do all resource plans need to be spatially explicit? A landscape planning principle that has emerged from our review suggests that spatially explicit habitat prescriptions are not necessarily required under all circumstances. We observed evidence that habitat arrangement effects were unimportant in explaining variation in species abundance as long as the amount of habitat in a landscape remained well above a critical threshold associated with species extinction (see Section 23.3.1). A systematic search for threshold responses would enable planners to tease out conditions for which arrangement effects are important and to identify landscape structure attributes that help assure species persistence in patchy landscapes. An important caveat, however, is that planners should not interpret this principle to mean that habitat arrangement can be ignored prior to reaching a critical threshold. As habitat is lost, future habitat arrangements are constrained by the spatial pattern of habitat destruction—habitat lost randomly offers little opportunity to cluster remnant habitats once the persistence threshold is reached.

23.5 Knowledge Gaps

23.5.1 Theoretical Voids

The recognition that environmental heterogeneity and organism movement interact to affect population dynamics has been key to what Turchin (1998:2) called a "paradigmatic shift from the aspatial equilibrium view . . . to a spatially explicit view." Although theoretical developments in spatial ecology are relatively recent, theoretical research on the concepts reviewed in this chapter has far out paced empirical research. The disparity between theory and empirical research has resulted in a baffling array of models and results that can appear contradictory to conservation planners (de Roos and Sabelis 1995). Consequently, the lack of theoretical synthesis is an important knowledge gap hindering the application of these concepts in conservation planning. There is a need to summarize how different modeling approaches and parameterizations affect habitat prescriptions so that domains of applicability can be recognized by those who develop and implement conservation plans. Our attempt to do this was incomplete (see Figure 23.4). In the absence of a more comprehensive synthesis, landscape planners will continue to be reluctant to implement habitat prescriptions derived from purely theoretical analyses.

Another important theoretical gap concerns how one prescribes habitat layouts that are relevant to the broader species assemblage occupying the landscape. We defined the scope of our chapter to be the response of individual populations to varying habitat arrangements, avoiding the issue of conflicting habitat requirements among multiple species. Even if planning models could be developed for some suite of species inhabiting the planning area, the feasibility of deriving habitat prescriptions that are relevant to the group is questionable due to species inter-

actions. The extension to biodiversity conservation as a whole is even less clear (Turner et al. 1995).

23.5.2 Empirical Voids

Quantifying the movement of individuals among habitat patches is seen as critical to understanding the consequences of varying habitat arrangements across the landscape (Law and Dickman 1998). Unfortunately, organism movement is poorly understood and is an extremely difficult area of empirical research (Turchin 1998), particularly at the landscape scale (Harrison and Bruna 1999). It may seem trivial to highlight species movement as a knowledge gap given its oft-cited importance, but we would be remiss not to emphasize the need for more empirical data regarding how (e.g., random or biased diffusion), when (e.g., what ecological conditions promote dispersal), and to what degree (e.g., how often and how far) species move in landscapes.

Even if landscape planners had access to more complete information on species movement, a more fundamental empirical gap is the paucity of tests of spatially explicit conservation plans. The fact that our review of recent applications focused on theoretical examples and conservation planning case studies in which the prescribed habitat design was not implemented is a symptom of this empirical gap. An especially critical need is for well-designed and active monitoring programs that are linked to plan implementation. Monitoring information is needed to assess the success or failure of a given plan, to test basic ecological concepts on which the plan is based, and to identify the mechanisms underlying population response to habitat prescriptions (Hansson and Angelstam 1991). For example, critical thresholds have been demonstrated theoretically, but there have been very few attempts to establish the existence of critical thresholds in field studies of species distribution and abundance (but see With and Crist 1995; Trzcinski et al. 1999).

23.6 Research Approaches

23.6.1 Approaches for Theoretical Research

Although synthesis may lack the intellectual excitement associated with new theoretical developments, it is nonetheless important. We identify two broad approaches to theoretical synthesis. The first is through structured reviews of the literature. This will not be an easy task. Numerous nuances to spatial planning models can quickly overwhelm attempts to distill rules for application (de Roos and Sabelis 1995). It is not uncommon for models of similar ecological phenomena to reach divergent conclusions (e.g., compare the conclusions reached by Hill and Caswell [1999] and Fahrig [1998] regarding the importance of habitat arrangement in facilitating population persistence). Part of the problem is that both model structure and parameterization differ among models, making it difficult to determine what is causing the variability in model results. It is this complexity that may render traditional

narrative reviews for theoretical synthesis flawed, suggesting that the more structured analyses formalized in meta-analysis may be better suited for identifying common patterns among published models (Arnqvist and Wooster 1995).

A second approach to theoretical synthesis involves the systematic manipulation of specific models using sensitivity analysis (Conroy et al. 1995). This would involve the quantification of model response following purposeful and systematic alteration of model parameters (singly and in combination). Comprehensive exploration of model behavior under a wide range of ecologically relevant parameter settings is important for at least two reasons. First, it can help identify those aspects of species life history or habitat arrangement that are critically important for understanding population response to landscape changes. Second, it can determine whether there are fundamental shifts in habitat arrangements in response to relatively small changes in the parameter space (see Figure 23.4).

Moving from single-species to multispecies conservation planning is certainly difficult, and we know of no definitive strategy. One approach that has emerged repeatedly is the use of indicator species (related incarnations include keystone, umbrella, or focal species) to reflect the status of the overall species assemblage. Unfortunately, indicators are often chosen opportunistically (e.g., well-studied and well-surveyed taxa). Tests of this strategy using broad taxonomic groups (e.g., birds, mammals, butterflies) do not support its general applicability (Flather et al. 1997). However, rejection at broad taxonomic levels should not preclude the search for indicators among narrower sets of species. A more refined search to identify life-history attributes that could serve to group species based on critical vital rates (e.g., reproductive potential, dispersal ability) may offer an alternative approach to defining indicators because species that share similar life histories may respond to habitat geometry in a similar fashion (see Noon et al. 1997). In a slight variation of this approach, mathematical taxonomy and ordination techniques (Gauch 1982) could be used to define clusters of species based on measured life-history attributes such that the species pool for a given planning area is partitioned into sets that may be similarly sensitive to habitat arrangement effects.

23.6.2 Approaches for Empirical Research

Techniques for studying animal movement are less-developed than are methods for estimating demographic parameters (Turchin 1998). Choice of methods will depend to a large degree on whether one needs to quantify the movement paths or simply the population-level pattern of redistribution. The kind of movement data required will be dictated by the information needed to address the planning problem. For example, quantifying species-specific search rules used to locate vacant territories would require information on the actual movement paths taken by individual organisms. Alternatively, estimating the distribution of dispersal distances or the resistance of the interpatch environment to movement may only require information on the rate and directionality of population spread. Turchin (1998) provides a comprehensive review of data collection and analysis methods that are appropriate for both types of questions.

Although the use of new approaches to study species movement will extend our abilities to prescribe landscape configurations, the spatial and temporal extent of conservation plans often make detection of population response difficult, replication of conservation treatments infeasible, and identification of mechanisms underlying population change enigmatic. These problems pervade empirical testing of conservation plans, and they have been addressed with several atypical research protocols. Carpenter (1990) reviews pre-treatment and post-treatment time series analyses to infer nonrandom change in system response. Similarly, Hargrove and Pickering (1992) outline the use of "quasi-experiments" to take advantage of natural disturbances that alter habitat configuration. An approach directed specifically at increasing replication is to repeat unreplicated studies in different systems (Carpenter 1990). Such an approach can be approximated by accumulating the efforts of others and analyzing independent research efforts with meta-analysis procedures (Arnqvist and Wooster 1995). Finally, when replication and experimental controls within the planning problem are feasible, active adaptive planning (Walters and Holling 1990) could provide opportunities for stronger inferences from management experiments.

Regardless of the approach used, it is critical that a more concerted effort be directed at designing and implementing monitoring strategies that allow conservation plans to be tested (Havens and Aumen 2000). Because long time periods are required to quantify species response to modified landscapes, researching the relative merits of alternative monitoring designs will be difficult. Wennergren et al. (1995) offer an intriguing and perhaps imperative suggestion for researchers—use spatially explicit population models to test the ability of alternative monitoring designs to detect the effects of habitat layouts prior to implementing those monitoring designs in the field. Failure to devote more effort toward monitoring will perpetuate our current reliance on untested concepts and heighten the contention and uncertainty that surround the use of planning models to derive spatially explicit habitat prescriptions.

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