SUSTAINING WILDLIFE POPULATIONS IN PRODUCTIVELY MANAGED FORESTS

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Abstract: Wildlife population status is becoming a key consideration in determining whether wood fiber production from managed forests can be sustained. Concerns for wildlife have become a very important part of public land management in many areas of the world and are being given increased weight on privately owned lands. Jointly maintaining wood fiber production and wildlife populations requires an ability to spatially and temporally design management activities so as to mitigate negative impacts on wildlife habitat. Consequently, research efforts that blend wildlife population persistence modeling with traditional forest management modeling can potentially play a crucial role in maintaining future forest productivity. In this chapter, we synthesize recent and ongoing research combining population reaction-diffusion models with spatial forest management optimization methods for planning the location, timing, and intensity of harvests to simultaneously sustain wildlife and wood fiber production.

1. INTRODUCTION

Policies aimed at protecting wildlife as a cornerstone of sustainable forest management appear to be expanding on public and private lands internationally. In 1994, the United States joined nine other temperate zone countries in endorsing a non-binding set of seven criteria to be measured by 67 indicators of sustainable management for temperate and boreal forests in what has become known as the "Santiago Declaration" (Coulombe 1995).

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The first of seven criteria is "Conservation of Biodiversity," to be measured by nine indicators that reflect concern for the abundance, distribution, and status of forest-dependent wildlife populations and their habitats.

On public lands in the United States, the Endangered Species Act of 1973 has provided strong protection for species determined to be at risk of extinction, while regulations implementing the National Forest Management Act of 1976 (NFMA) have called for providing habitat to support a viable number of well distributed reproductive individuals of existing native and desirable non-native vertebrate species. The U.S. Forest Service has been working with a Committee of Scientists to update NFMA regulations with a proposal (now implemented) that goes further, endorsing a notion of primacy for ecological sustainability over social and economic considerations on the national forests (Johnson et al. 1999, USDA Forest Service 2000).

On private lands, forest products companies are also working to sustain wildlife populations in their managed forests. In the United States, members of the American Forest & Paper Association are seeking ways to protect and enhance the diversity of flora and fauna impacted by industrial forestry practices through their "Sustainable Forestry Practices" and "Implementation Guidelines." In Canada, MacMillan Bloedel (formerly that nation's largest forest products company) announced plans to emphasize wildlife habitat on about 25 percent of its 1.1 million ha land base, while largely protecting an additional 10 percent comprising old-growth stands. Even on the 65 percent considered their "timber zone," partial retention management that will keep sizable portions of forest intact has been planned (Anonymous 1998). Weyerhauser, who recently acquired MacMillan Bloedel, has announced their intent to continue this policy. Internationally, forest owners that meet the Forest Stewardship Council's wood certification standards (currently accounting for more than 20 million hectares) must strive to maintain biodiversity as well as providing protections for rare, threatened and endangered species and their habitats.

Increasingly, the objectives of sustainable forest management are intertwined with objectives for sustaining forest-dependent wildlife populations. An important research question, then, is how do we sustainably manage productive forests (e.g., drawing a perpetual supply of wood products over time from those lands) in ways that protect the abundance and distribution of resident wildlife species?

2. METHODS

Just as mathematical programming models have helped us manage for long-term timber supplies over the past few decades, we anticipate that similar optimization models might provide a useful framework for developing management programs that can sustain both wood fiber production and wildlife. Because the distribution of individuals is important to population persistence, these models must be spatially explicit. Furthermore, because wildlife reproduce and disperse across landscapes, these models must account for the interactive effects of arrangement, timing, and intensity of forest treatments in order to help design efficient management strategies that provide suitable habitat complexes. Population reaction-diffusion models offer one promising approach to this problem.

2.1 Reaction-diffusion

Equation (1) shows the Levin-Allen reaction-diffusion model for reproduction and dispersal of a population occupying a fragmented complex of N habitat patches (Levin 1974, Allen 1987):

Reaction + Diffusion

$$\frac{dV_i}{dt} = V_i f(V_i) + \sum_{j=0}^{N} D_{ij}(V_j - V_i) \quad ; \; i = 1,\ldots,N \tag{1}$$

$$D_{ij} = D_{ji} \geq 0 \;\; \forall \; i, j$$

$$V_0 = 0$$

where V_i is the adult population in patch i as a function of time t, and $f_i(V_i)$ is the per capita rate of reproduction (net of mortality unassociated with dispersal, as discussed below). D_{ij} is a patch-to-patch passive diffusivity constant (or function) that determines the net patch i population gain from (or loss to) patch j based on the difference between the patch populations. Nonhabitat is indexed by j=0. In this model, dispersing organisms can successfully traverse regions of nonhabitat, but some of them perish and are treated as dispersers into nonhabitat (other assumptions can also be

modeled). The nonhabitat population V_0 is fixed at zero so that D_{i0} times $-V_i$ defines a population loss due to unsuccessful dispersal from any patch i. The habitat complex comprises those patches (indexed by i) which are "connected" by positive diffusivity ($D_{ij} > 0$) with at least one other patch (some $j \neq i > 0$) in the complex. By letting i and j index cells that represent breeding sites or other forest subdivisions instead of patches, Bevers and Flather (1999a) show that Eq. (1) becomes suitable for modeling population distribution and abundance across complex landscapes. The model can also be refined to include greater detail on population structure and behavior (see for example, Hof et al. 1999).

Management and conditions in forests change over time in a manner that is often modeled in mathematical programs using discrete time periods (e.g., Johnson and Scheurman 1977). For compatibility with those models, Eq. (1) can also be adapted to discrete time. For example, Eq. (2) is a difference equation form of Eq. (1) expressed as a constraint set in which we have assumed constant rates of reproduction (r), with offspring maturing in a single breeding period and dispersing like adults (i.e., $D_{ji} = [1 + r]\ g_{ji}$, where g_{ji} is the proportion of organisms from cell j expected to disperse to cell i per unit of time):

$$V_{it} \leq \sum_{j=1}^{N} (1 + r)\, g_{ji} V_{j,(t-1)} \quad \forall\ i; t = 1, \ldots, T \tag{2}$$

where V_{j0} is set to the initial population in cell j. Again, other assumptions could also be modeled.

2.2 Spatial Optimization

The reproduction and dispersal processes reflected in Eqs. (1) and (2) represent only one set of many possible factors that might limit a wildlife population. In particular, forest management activities can affect wildlife habitat quality as well as arrangement, which in turn can limit the size and distribution of a population. We model this locally at the cell level. For species that require only a single habitat type to meet all of their subsistence needs, we include Eq. (3) as a constraint set:

$$V_{it} \leq \sum_{h=1}^{H_i} \sum_{k=1}^{K_{hi}} c_{hkit}\, X_{hki} \quad \forall\ i;\ t = 1, \ldots, T \tag{3}$$

$$\sum_{k=1}^{K_{hi}} X_{hki} = A_{hi} \quad \forall\ h, i$$

where X_{hki} is the area from initial condition class h allocated to management schedule k in cell i, c_{hkit} is the breeding adult (or female) capacity in cell i at time t per ha of forest initially in condition class h that is managed under schedule k, and A_{hi} is the number of ha of cell i initially in condition class h. Combined with an objective function that maximizes the population in each cell and time period (subject to constraints), Eqs. (2) and (3) form a simple spatial optimization model based on population reaction-diffusion. Alternatively, timber management objective functions can also be used in concert with a constraint specifying lower limits on the population total. Other minor variations in this model include using integer management variables (Hof et al. 1994), and incorporating direct population management actions such as reintroductions (Bevers et al. 1997) and removals (Hof 1998). An important characteristic of these models, and those that follow, is that when the g_{ji} parameters reflect a decline in dispersal probabilities as a function of the distance between the two cells (j and i), the probability of dispersers surviving is proportional to the amount of available habitat surrounding the natal cell, with distance decay.

Looking across a number of the models of this type that we have investigated, we are able to observe several solution properties that appear to capture well-recognized ecological characteristics. It is encouraging that we obtain these effects even from models with such simple assumptions as constant periodic reproduction and dispersal. These effects will be described in the following section.

3. RESULTS

The single habitat requirement expressed in Eq. (3) seems most suitable for modelling interior specialists rather than edge dwellers. We will begin by reviewing results from this simpler model before considering edge-dependent species.

3.1 Interior Species

For interior species, the effects we wish to review include:

- Sigmoid population growth
- Extinction thresholds
- Negative edge effects

- Traveling propagation waves
- Habitat clustering
- Quasi-random distributions

We will also briefly examine empirical evidence from the North American Breeding Bird Survey.

3.1.1 Sigmoid Growth

Under conditions of constant periodic reproduction and dispersal, a small population in a large habitat complex can initially grow at a fairly constant rate. Gradually, however, those cells with the highest influxes of dispersers become saturated so that the overall growth rate slows. As more and more cells either become saturated or approach a local balance between reproduction, immigration and emigration, populations eventually approach steady-state conditions, producing sigmoid growth curves for the population as a whole. Figure 1 illustrates this with projected growth curves resulting from a constant (density-independent) rate of reproduction ($1 + r = 1.8175$) for six alternative habitat complexes of different sizes modeled for reintroduction of black-footed ferrets (*Mustela nigripes*) into Badlands National Park and the Buffalo Gap National Grassland in southwestern South Dakota (Bevers et al. 1997). For the four alternatives that add incremental portions of National Grassland habitat between the initial situation and total allocation, the habitat complexes were spatially optimized. Thus, in addition to showing the sigmoid nature of the capacity-limited reaction-diffusion growth curves, diminishing marginal returns between the alternatives are also apparent.

3.1.2 Extinction Thresholds

When habitat complexes are too small or are poorly arranged, they can fall below a critical persistence threshold, implying that populations can no longer be supported given a particular set of reproduction and dispersal characteristics. This is illustrated in Figure 2, in which an initial population of 90 organisms of a hypothetical species with locally fixed rates of reproduction and dispersal either grows or declines based solely on the areas of square habitats in sizes ranging from 9 to 121 cells (Bevers and Flather 1999a). We note that the realized rate of overall population growth or decline also depends strongly on the size of the habitat complex. Similar thresholds have been shown for poorly arranged habitats; blocky shapes are generally better than elongated or fragmented complexes (but see Hof and Flather 1996 for alternative configurations when spatially correlated risk factors must be considered).

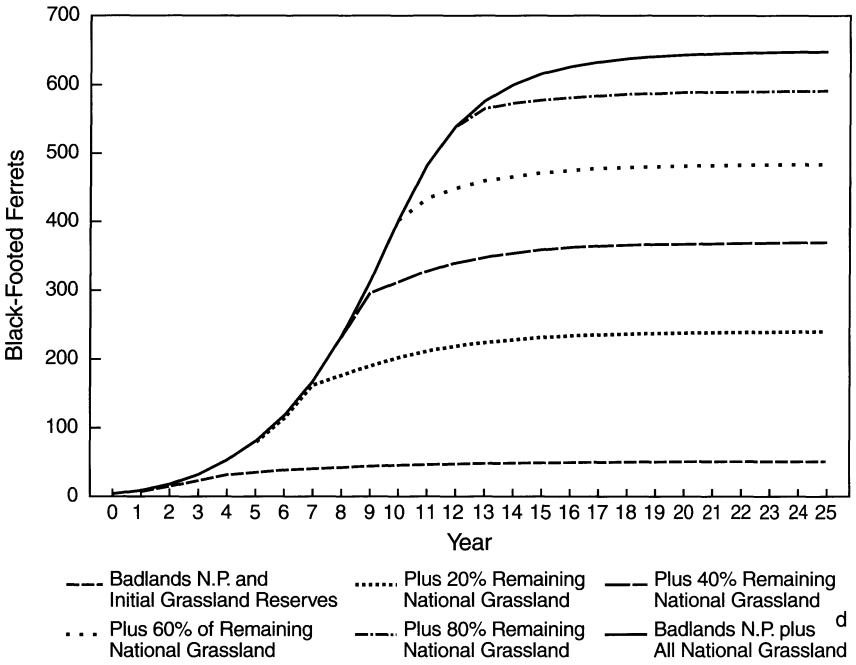


Figure 1. Populations projected over time from black-footed ferret reintroductions for six alternative habitat allocation strategies on the Buffalo Gap National Grassland, South Dakota.

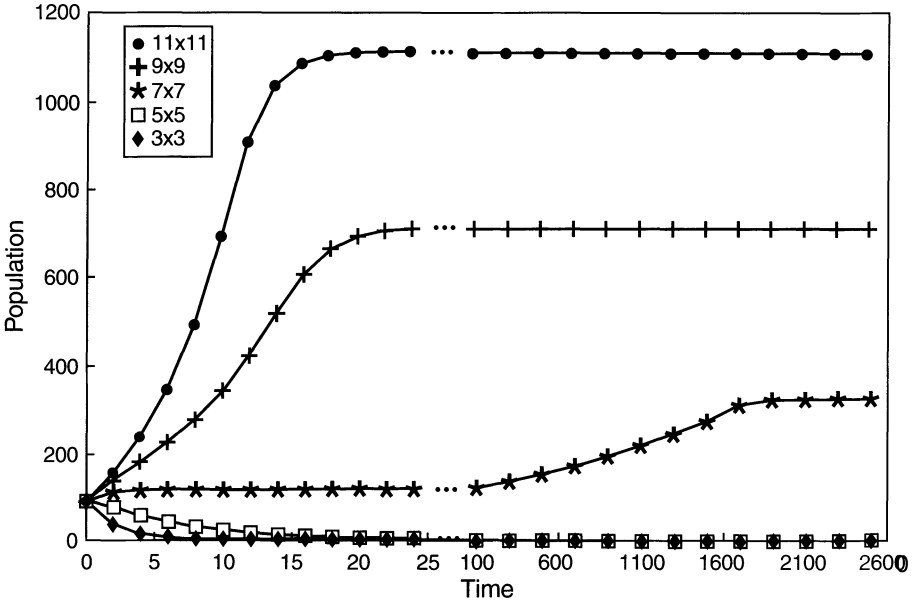


Figure 2. Populations projected over time from 90 organisms of a hypothetical species for square habitat complexes of five different sizes.

3.1.3 Negative Edge Effects

The model produces negative effects at the habitat edges for interior species, as shown in Figure 3 (Bevers and Flather 1999a). Shaded areas indicate saturated cells, while unshaded cells indicate those whose populations are below capacity. The surface in Figure 3a indicates the spatial distribution of organisms in a complex that just exceeds threshold conditions, resulting in a Gaussian-like distribution that reflects negative edge effects almost to the core of the complex. As the complex size is increased (Figure 3b), negative edge effects become less predominant. While many species may actually select interior habitats, these results demonstrate that observations of lower abundance near habitat edges could also arise simply from random dispersal processes.

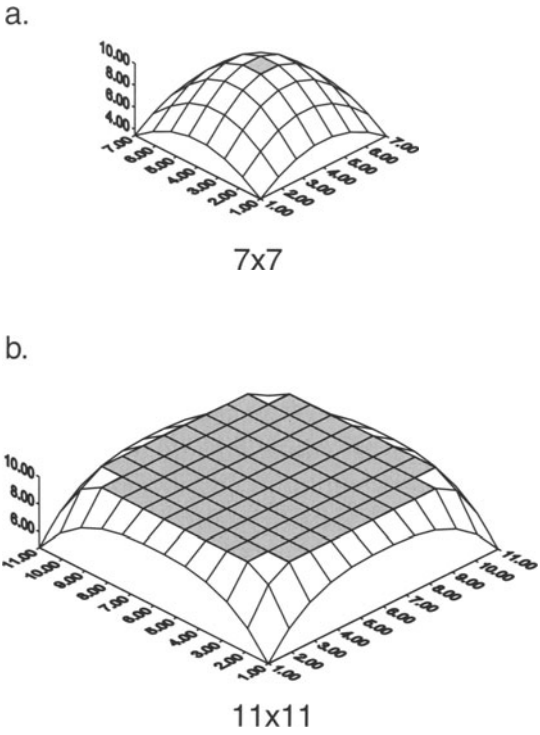


Figure 3. Equilibrium population distributions for a hypothetical species a) in a habitat complex close to extinction threshold conditions, and b) in a larger habitat complex of the same configuration.

3.1.4 Traveling Expansion Waves

Species introduced into new areas with abundant habitat often spread in a traveling wave fashion (Okubo 1980) once established. The deterministic model portrayed in Eqs. (2) and (3) exhibits these expansion waves, as shown in Figure 4. Figure 4a shows the release locations for a limited number of captive-bred black-footed ferrets from the study mentioned previously (Bevers et al. 1997). In the model, most of the ferrets were released near the center of the National Grassland habitat complex. Figure 4b shows the projected population distribution seven years later, just prior to a global constraint on available carrying capacity becoming binding (at the

first 20 percent increment of new habitat in this case). The nearly circular wave-like expansion of abundance is shown clearly.

3.1.5 Habitat Clustering

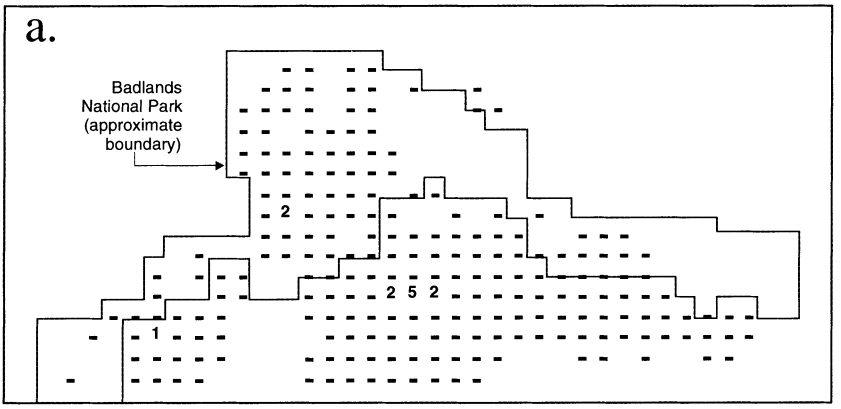
In our black-footed ferret example from Figure 4b, the optimal strategy for year 7 was to spread the arrangement of available carrying capacity across the entire area, with some concentration in the center of the National Grassland. Once the global carrying capacity constraint began limiting the population, though, the model began clustering habitat against the boundary of the National Park (where habitat arrangements were inflexible) forming the three fairly distinct and blocky concentrations shown in Figure 5 (Bevers et al. 1997). This tendency to form clusters around established habitats appears to be characteristic of these models (Bevers and Flather 1999b), and the ability to efficiently change spatial strategies over time is noteworthy.

3.1.6 Quasi-random Distributions

So far, we have only considered the effects associated with the simple carrying capacity constraint from Eq. (3). Populations are also potentially limited by a number of additional factors operating at a variety of scales. For example, random predation may tend to hold a population in dynamic equilibrium well below the habitat carrying capacity. If we know the overall population level, we can model this by imposing Eq. (4) as a constraint:

$$\sum_{i=1}^{N} V_{it} \leq P \quad \forall\, t \tag{4}$$

where P is the upper limit on total population as imposed by predation effects. When the habitat complex is well above threshold conditions, this constraint can result in many random equilibrium population arrangements, such as the two shown in Figure 6 (Bevers and Flather 1999b). In our experiments, the ability to observe fragmented equilibrium populations was reduced, however, as habitat complexes approached persistence threshold conditions. At threshold conditions only Gaussian-like equilibrium populations like the one shown in Figure 3a were observed.



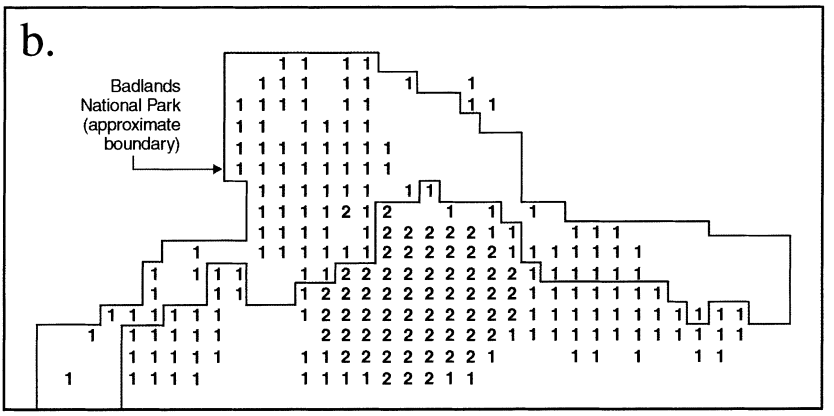


Figure 4. a) Captive-bred black-footed ferret release locations selected by a spatial optimisation model, and b) the projected distribution of adult ferrets seven years later for the alternative that allocates an additional 20 percent of available Buffalo Gap National Grassland habitat for ferret recovery.

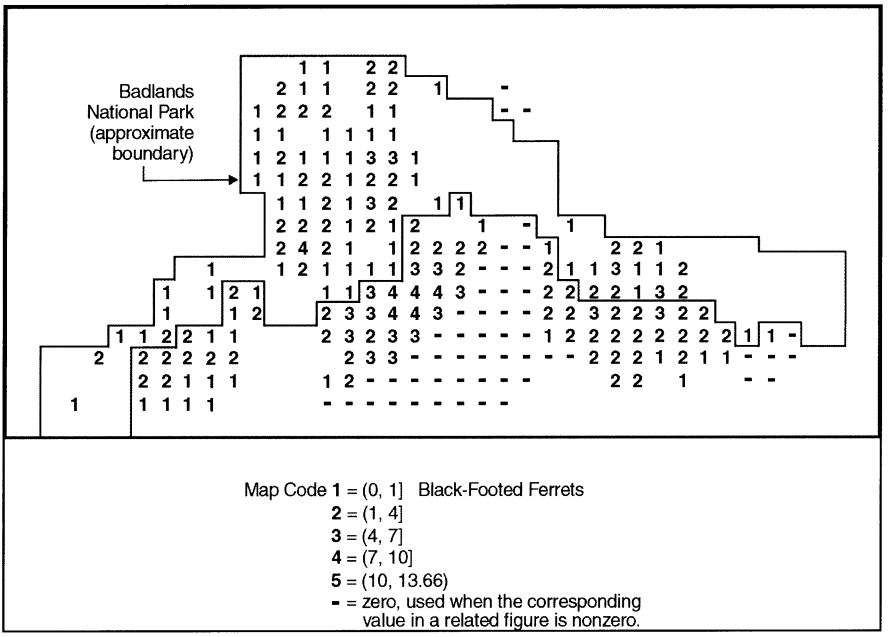


Figure 5. The selected long-term habitat allocation and projected equilibrium black-footed ferret population for the alternative that allocates an additional 20 percent of available Buffalo Gap National Grassland habitat for ferret recovery.

3.1.7 An Empirical Test

Flather et al. (in prep) have observed that across the range of bird species occupying interior habitats of eastern deciduous forests in the U.S., survey routes of the North American Breeding Bird Survey (BBS) exhibit a range of forest habitat area that can be estimated from landscape structure data available from the U.S. Geological Survey (USDI 1987). When the average occupancy rates on BBS routes were compared with forest area for six interior forest bird species, the slopes of those relationships exhibited distinct shifts – declining more rapidly after habitat area passed through an apparent persistence threshold. We hypothesize that the geographic ranges of these species are interspersed with local pockets that may lack sufficient quantities of habitat to independently sustain populations. Where habitat amounts fall below threshold, nonzero occupancy rates are thought to be maintained by immigration from surrounding areas where habitats exceed threshold levels. We looked for this effect in our models by adding a small but constant rate of immigration from an exogenous source to the right-hand side of Eq. (2), and found that the occupancy pattern trends from the BBS and USGS data can be approximated quite well. While this cannot be

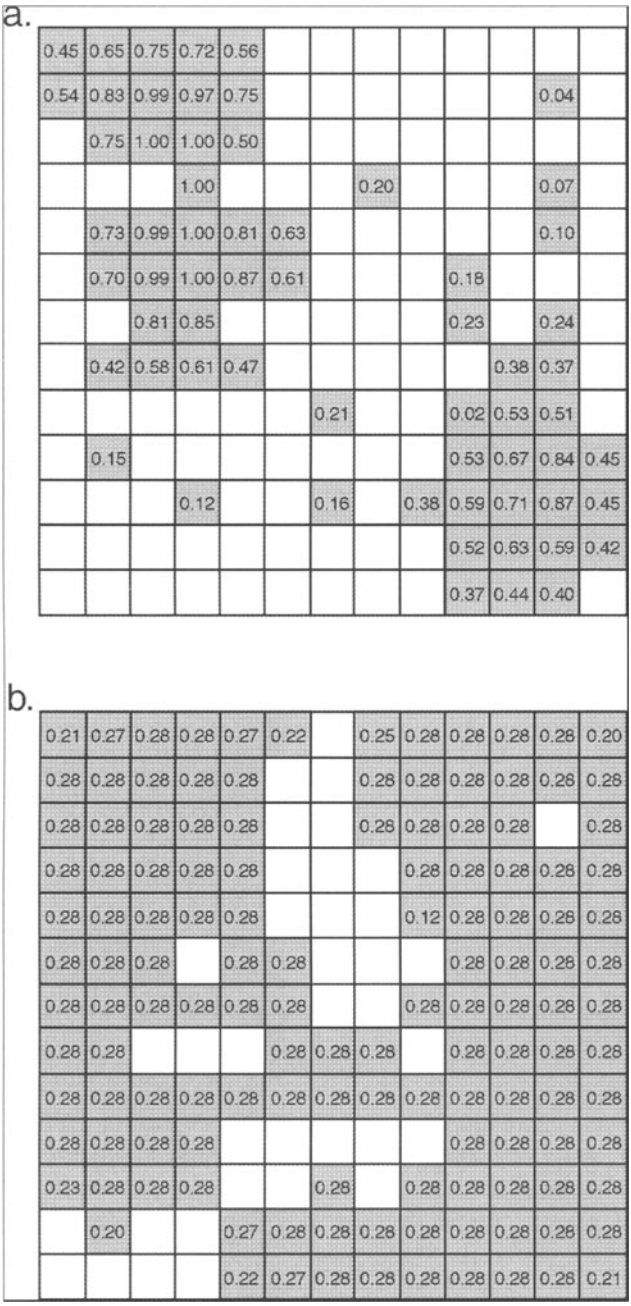


Figure 6. Two of many alternative equilibrium population arrangements on a square landscape of habitat for a hypothetical species when the population is held below capacity by random predation.

viewed as corroborating the reaction-diffusion model, these results and other empirical results from the literature (see Holmes et al. 1994) are encouraging.

3.2 Edge-dependent Species

Many species require a mix of habitats to sustain them. For example, a population could be limited by the amount of, and the distance between, forage from one habitat type and nest sites in another. With these requirements, populations are likely to exhibit some degree of edge-dependency, meaning that they are most likely to be found close to where the two required habitats adjoin. By modeling the separate requirements for forage and nest sites as simultaneously limiting factors, together with our reaction-diffusion constraint (Eq. 2), positive habitat edge effects can be captured. If we redefine the carrying capacity parameter in Eq. (3) to represent only nest site capacity, then we can capture the desired edge effect by adding the following sets of forage constraints (Bevers and Hof 1999):

$$\sum_{i=1}^{N} Z_{jit} \leq \sum_{h=1}^{H_j} \sum_{k=1}^{K_{hj}} f_{hkjt} X_{hkj} \quad \forall\ j;\ t = 1, ..., T \tag{5}$$

$$V_{it} \leq \sum_{j=1}^{N} d_{ji} Z_{jit} \quad \forall\ i;\ t = 1, ..., T \tag{6}$$

where Z_{jit} is a forage allocation variable describing the amount of forage produced in land unit j at time t (based on f_{hkjt} units of forage per ha of initial forest condition class h in cell j managed according to schedule k) that is made available for consumption by organisms nesting in land unit i, and d_{ji} is a parameter describing the utilization efficiency (generally declining with distance) of forage produced in land unit j that is consumed by organisms nesting in land unit i. Because effective forage utilization declines with distance in Eq. (6), nearby forage allocations are favored, and allocations beyond any maximum foraging distance are prevented.

The effects of these forage constraints are shown in Figure 7a for a hypothetical species inhabiting an 81-stand square (9x9) forest (Bevers and Hof 1999). Forest provides nest sites, while forest removals provide forage

a.

.28	.38	.43	.45	.46	.45	.43	.38	.28
.38	.50	.54	.46	.46	.46	.54	.50	.38
.43	.53	.40	.40	.40	.40	.40	.53	.43
.45	.46	.40	.40	.40	.40	.40	.46	.45
.46	.46	.40	.40	.40	.40	.40	.46	.46
.45	.46	.40	.40	.40	.40	.40	.46	.45
.43	.54	.40	.40	.40	.40	.40	.54	.43
.38	.50	.53	.46	.46	.46	.53	.50	.38
.28	.38	.43	.45	.46	.45	.43	.38	.28

b.

.06	.09	.10	.11	.11	.11	.10	.09	.06
.09	.11	.13	.13	.13	.13	.13	.11	.09
.10	.13	.13	.13	.08	.13	.13	.13	.10
.10	.12	.12				.12	.12	.10
.10	.12						.12	.10
.10	.12	.12				.12	.12	.10
.09	.12	.13	.12		.12	.13	.12	.09
.08	.11	.12	.12	.12	.12	.12	.11	.08
.06	.08	.09	.10	.10	.10	.09	.08	.06

Figure 7. Optimized cellular populations of a hypothetical species that nests in forest and feeds in nonforest a) without, and b) with a constraint on total area of forest that can be removed.

in addition to that supplied from the surrounding nonforest area. Organisms can forage up to two stands away from the nest site stand, but with declining efficiency. The numbers shown in Figures 7a and b show the fraction of each cell occupied by nesting pairs; thus the larger the number, the greater the adult population in a given cell. In Figure 7a, a positive edge effect is apparent over most of the forest due to the availability of forage from a combination of forest removals and the surrounding nonforest area, although dispersal losses still cause the three cells in each corner to exhibit negative edge effects. When total harvesting (hence, interior forage) is restricted in

the model, the interior of the forest is abandoned in favor of supporting the populations around the edge of the complex (Fig. 7b). In this case, a no-harvesting policy pushes the complex below persistence threshold conditions. Even though organisms in the outer two layers of stands can forage in the surrounding nonforest area, those 56 cells are insufficient to support this hypothetical species.

4. CONCLUSION

These results are encouraging considering the range of realistic ecological effects that can be portrayed with linear programs, but a number of important areas for further research remain on the subject of reaction-diffusion based spatial optimization modeling. In addition to the obvious need for further case studies and empirical tests, four research areas seem particularly critical. Perhaps chief among these is understanding and accounting for stochastic effects. Bevers et al. (in prep) have converted Eqs. (2) and (3) into discrete population - discrete event Monte Carlo simulation models to examine the effects of random demographic and environmental variability on populations ranging from very small to very large numbers in a variety of habitat complexes. The continuous variable assumptions usually associated with reaction-diffusion models produce results that reflect the limit conditions of infinitely large populations. For finite populations, then, the models tend to overestimate abundance and underestimate the amount of habitat required for persistence. These errors decline with population size increases, and decline far more rapidly as the size of the complex increases well above threshold conditions. Thus, conservation strategies where habitat complexes are designed well above threshold conditions seemingly can be depicted with reasonable accuracy. Preliminary results from this research also tend to indicate that habitat arrangements prescribed by these models may indeed be optimal in a long-term sense, but much more research is needed in this area.

A second area for further research is to account for greater ecological detail in these population models. While this can be done fairly easily in simulations, optimization models are another matter. The models described here were all continuous-variable, linear programming models that can be easily solved even for large-scale problems. Incorporating greater ecological detail will often require integer and/or nonlinear programming capabilities that may exceed the current state of computing technology (Hof and Bevers 1998). The third area for further research involves expanding this work to develop community-level models. In order to successfully sustain viable populations in managed forests, we will need to better understand how to

model the interaction effects of our treatment activities. The fourth and final research area that we consider here is monitoring. Once we have better understanding in the other three areas, along with more experience applying the models we already have, we should be in a position to refine our fine-scale monitoring protocols for ecological communities and for populations that are at risk of extinction. Refinements in fine-scale monitoring might, in turn, lead to new insights into adaptive optimization modeling.

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