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A Common Framework for Conservation Planning: Linking Individual and Metapopulation Models

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Many populations exhibit pronounced spatial structure: dispersed areas of high population density embedded in areas of low density, with population centers connected through dispersal. This recognition has led many conservation biologists to embrace the metapopulation concept (Levins 1970) as the appropriate paradigm for reserve design structures (reviewed in Hanski 1991 and Harrison 1994). This concept seems appropriate for those species that have patchy distributions because the critical resources on which they depend are distributed in this fashion. This paradigm may be less applicable, however, to species that historically have had a more or less uniform distribution of individuals across the landscape. If such species are faced with threats to their persistence, is a metapopulation reserve structure appropriate for their conservation? Or is the tailoring of reserve design to a single paradigm similar to attempting to force a square peg into a round hole?

As a species, spotted owls are widely distributed, show extensive geographic variation in their habitat relationships, and, at a landscape scale, have a territory distribution that is spatially variable. Because of threats to their long-term persistence, conservation strategies for all three subspecies of spotted owl have recently been proposed (Thomas et al. 1990; Verner et al. 1992; USDI 1991). Despite striking similarities in the ecologies of these three subspecies and similar threats to their population viability, their conservation strategies appear quite distinct, suggesting that contrasting sets of ecological principles may have been applied in the planning process. Despite appearances, a common hypothesis-testing framework justified the process of conservation planning and a common set of population dynamics principles underlies each conservation strategy (Noon and Murphy 1994).

Conservation plans for the northern spotted owl (Thomas et al. 1990; USDI 1992), the population of California spotted owls in southern California (Verner et al. 1992; LaHaye et al. 1994), and the Mexican spotted owl (USDI 1991) are similar in that all propose a highly structured spatial distribution for the owl population- a population composed of numerous local subpopulations widely distributed across the landscape in the form of a metapopulation (Levins 1970). The metapopulation reserve structure in southern California, Arizona, New Mexico, and Utah is a logical consequence of a historical metapopulation distribution, the result of variation in topographic relief, and the concomitant patchy distribution of suitable habitat across var. ious mountain ranges.

In contrast, the metapopulation reserve structure in northern California, Oregon, and Washington is not a logical consequence of a historical distribution pattern. Rather, the reserve design was imposed primarily by constraints arising from human-induced changes to the landscape and secondarily by confidence in the legitimacy of the metapopulation concept. Since about 1950, harvest of late seral stage forests has created an insular distribution pattern of owl habitat in the Pacific Northwest. Thus, constraints imposed by the current condition of the landscape, the likely pattern and rate of habitat recovery over the next 100 years, and acceptance of economic pressures have prescribed a metapopulation reserve design (Thomas et al. 1990; Murphy and Noon 1992).

The conservation plan for spotted owls in the Sierra Nevada is distinctly different than in other parts of their range. In the Sierra Nevada, Verner et al. (1992) did not propose a discrete reserve design or impose a metapopulation reserve structure. Rather, they recognized that the current distribution of owl territories was more or less evenly distributed throughout this part of its range, and they proposed a dynamic landscape management plan with the goal of maintaining the current distribution. Instead of viewing the dynamics of spotted owls at the scale of local subpopulations, they proposed a strategy operative at the scale of the individual territory,

It is reasonable to ask how one can reconcile two very different conservation strategies for members of the same species, particularly when one strategy proposes millions of acres to be set aside in forest reserves (Thomas et al. 1990), while the other establishes no discrete reserve boundaries and allows active timber management (Verner et al. 1992). Our goal in this chapter is to demonstrate that a common understanding of population dynamics in structured populations was invoked for both the northern and the California spotted owls. We will demonstrate that the original, single-species metapopulation model of Levins (1969, 1970), when generalized to include the added realism of multiple patch searches and variable habitat quality, is generally equivalent to Lande's (1987) spatial model of local population dynamics. We then offer guidelines for deciding which model is most appropriate as a conceptual framework for a specific conservation problem. The choice among model paradigms, as well as the logic and arguments brought to bear, are illustrated by comparing the conservation strategies for the northern and California spotted owls.

The Metapopulation Model

We have developed a model that incorporates various spatial and temporal scales of biological processes and enables us to compare birth and death rates at the territory scale with colonization and extinction rates at the population scale.

Original Model

Levins' (1970) metapopulation model describes the dynamics of populations occupying a system of identically sized and evenly spaced habitat patches. The multiple populations are discontinuous at some spatial scale **but** connected by migration. At a given point in time, each patch is either occupied or unoccupied by a local population-thus the response variable is the proportion of occupied patches equal to P_t at time t.

Levins' model represents one extreme of a continuum of metapopulation models that can be arrayed along a gradient of variation in the distribution of increasing habitat patch sizes (Hanski and Gyllenberg 1993). At the opposite extreme from Levins' model are models that assume a large and stable source population that provides colonists to distant but smaller habitat patches. These are a single-species variant of MacArthur and Wilson's (1967) multispecies mainland-island model. In a recent review, Harrison (1994) has argued that available data suggest this paradigm as appropriate for most natural populations. Intermediate to these two models are numerous possibilities that allow for spatial variation in habitat patch size (Hanski and Gyllenberg 1993).

The dynamics of the original Levins model are described by the following differential equation:

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp\left(1 - p\right) - e\,p \qquad (1)$$

where p = fraction of habitat occupied, e = rate of local extinction of occupied patches, and m = colonization rate of empty patches.

Levins' model is similar to the logistic model (Hanski 1991), and Equation (1) can be rewritten as

$$\frac{dp}{dt} = (m-e)p\left[1-\frac{p}{1-\left(\frac{e}{m}\right)}\right]$$

where $(m - e)$ is equivalent to the rate of increase, and $(1 - e/m)$ is equivalent to the carrying capacity.

The general solution to Equation (2) is

$$p_t = \frac{p_0\left(1-\frac{e}{m}\right)}{p_0+\left(1-\frac{e}{m}-p_0\right)e^{-(m-e)t}} \qquad (3)$$

Its dynamic behavior (Figure 7.1) is identical to the familiar logistic, showing a stable equilibrium at $\hat{p} = 1 - e/m$.

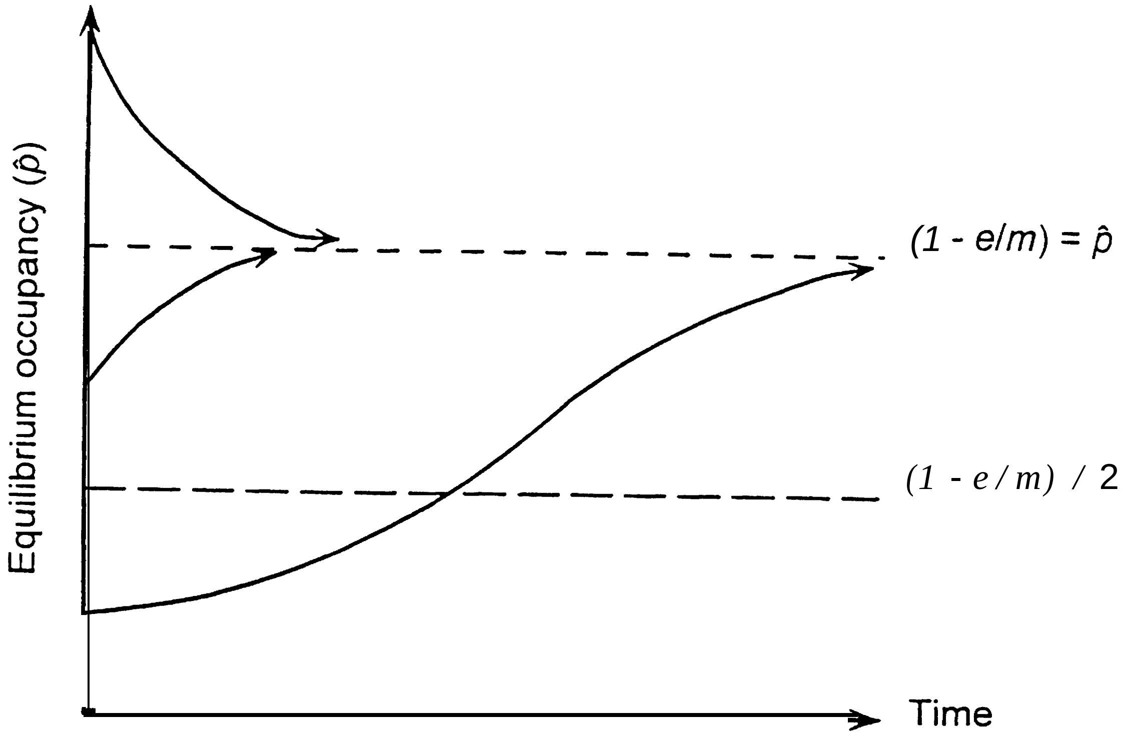

Figure 7.1. General dynamic behavior of the solution equation to Levins' metapopulation model (See Equation 3 in the text.) The graph shows the changes in the occupancy rate (p) of a hypothetical metapopulation starting at three different initial conditions.

Generalized Model

Levins' original model (Equation 1) is limited by two simplifying assumptions: all habitat patches are assumed suitable for occupancy; and dispersal Success is limited to a single transition, or search, and therefore proportional to 1 – p. If we relax assumption 1, we can rewrite Equation (1) as

$$\frac{\mathrm{d}h}{\mathrm{d}t} = mp\left[h\left(1-p\right)\right] - ep \tag{4}$$

where h = proportion of habitat patches suitable for occupancy. The likelihood of successful dispersal is now proportional to h (1 – p). If we also relax assumption 2, allowing n patches to be searched during dispersal, we can rewrite Equation (4) as

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp\left[1-\left[\left(1-h\right)+ph\right]^{n}\right] - ep \tag{5}$$

The likelihood of successful dispersal is now proportional to $1 - [(1 - h) + ph]^n$.

These modifications are quite minor. The first simply redefines the constant m; the second allows for nonlinear density dependence. Equation (5) collapses to Equation (1) when $h = 1$ and $n = 1$.

To facilitate comparison with Lande's (1987) model (discussed below), we rewrite Equation (5) in discrete form as

$$p_{t+1} - p_t = mp_t\left[1-\left[\left(1-h\right)+p_t h\right]^{n}\right] - ep_t \tag{6}$$

Equation (5) is at equilibrium when

$$p_{t+1} = p_t = \hat{p} \text{ or when } 1 - \left[\left(1-h\right)+\hat{p}h\right]^{n} = \frac{e}{m} \tag{7}$$

The equilibrium solution is

$$\hat{p} = 1 - \left[1 - \frac{\left(1-\frac{e}{m}\right)^{\frac{1}{n}}}{h}\right] \tag{8}$$

The Individual Territory Model

Lande (1987) developed an equilibrium-based model to describe changes in occupancy rate (p) as determined by the rates of local extinction and colonization at the scale of individual territories. Thus, in contrast to Levins' model where the unit of suitable habitat is the patch, in Lande's model the unit is the individual territory. Levins' model tracks the colonization and extinction of patches at the scale of local populations; Lande's model tracks birth and death events at the scale of the individual.

Similar to the generalized metapopulation model (Equation 5), Lande's model allows us to determine the proportion of suitable habitat occupied by the population at equilibrium. Assuming a random or uniform distribution of territorial sites, of which a fraction h are suitable, the probability that an obligately dispersing juvenile succeeds in finding a suitable territory in n searches is

$$1 - \left[(1-h) + ph\right]^n \tag{9}$$

Lande (1987) demonstrated that at demographic equilibrium, the proportion of suitable territories is given by equating the lifetime reproduction of female offspring per female, R_0, with unity. Thus R_0, given by the Euler-Lotka equation (Lotka 1956), is

$$R_0 = b\sum_0^{\infty} l_x b_x = 1 \tag{10}$$

where l_x = probability of survival to age x and b_x = fecundity (female offspring/female) at age x.

Lande (1987) assumed a two-stage model with juveniles and adults; thus $l_0 = 1$, $l_1 = s_0$, $l_x = s\,(x \geq 2)$, and $b_0 = 0$, $b_x = b\,(x \geq 1)$. Given these assumptions, we can rewrite Equation (8) as

$$R_0 = b\sum_1^{\infty} s_0\, s^{x-1} \tag{11}$$

with solution

$$R_0 = s_0\left(\frac{b}{1-s}\right) \tag{12}$$

An equilibrium occupancy of suitable territories, conditional on successful female dispersal, occurs when $R_0 = 1$, or when

$$\left[1-\left[(1-h)+\hat{p}h\right]^n\right]R_0' = 1 \tag{13}$$

$R_0' = b/(1 - s)$ incorporates all the life history except s_0, which is now replaced by Equation (9). Thus the first-year survival rate (s_0) is equated with the probability of successful juvenile dispersal (Equation 9). The solution to Equation (13), the equilibrium proportion of occupied territories, is

$$\hat{p} = 1 - \left[\frac{1 - \left(1 - \frac{1 - s}{b}\right)^{\frac{1}{n}}}{h} \right] \tag{14}$$

The similarity between equations (8) and (14) is obvious - and we will demonstrate that their behavior in response to parameter variation is identical. Specifically, there is a biological proportionality among corresponding model parameters, varying primarily in spatial scale: the population extinction rate of an occupied patch is proportional to the mortality rate of an individual territory holder ($e \infty (1 - s)$); the colonization rate of an unoccupied suitable patch is proportional to the number of potential colonists, or the per-individual birthrate ($m \infty b$).

Lande (1987) referred to the quantity $[1 - (1 - s)/b]^{1/n}$ as a measure of the demographic potential of the population. And in a similar fashion we can think of the quantity $(1 - e/m)^{1/n}$ as a measure of the demographic potential of the metapopulation. To distinguish our discussion from Lande (1987) and to address the effects of varying search ability n, we subsequently refer to $b/(1 - s)$ and m/e as measures of a species' colonization potential. The first term reflects colonization at the scale of the territory and is proportional to the ratio of birthrate to deathrate; the second is proportional to the ratio of patch colonization to extinction rates and reflects dynamics at the scale of the local population.

Population Persistence

We are interested in those parameter values for which $\hat{p} > 0$ and in the stability properties for all equilibrium solutions. As the behavior of the individual territory model has been discussed in detail by Lande (1987) and Lamberson et al. (1992), we refer the reader to those publications. We concentrate here on the dynamics of the metapopulation models (Equations 1, 4, and 5).

From Equation (1) we observe an equilibrium at $1 - e/m$ (Figure 7.1), which is stable only if $m > e$. Equation (4) reaches a steady state at $\hat{p} = 1 - e/mh$, which is stable only if $mh > e$. Thus decreasing the proportion of suitable patches, h, lowers the equilibrium patch occupancy rate, The generalized metapopulation model (Equation 5) has an equilibrium given by

Equation (8). Changes in equilibrium patch occupancy $\hat{p}$ (Equation 8) show steep thresholds for persistence as habitat proportion declines (Figure 7.2). As found by Lande (1987) and Lamberson et al. (1992) for the individual territory model, the key inference from Figure 7.2 is that $\hat{p}$ can equal zero when $h > 0$. These steep persistence thresholds are strongly ameliorated by increases in allowable number of searches, but less so by increases in colonization potential (m/e; Figure 7.2).

A three-dimensional plot shows the response of $\hat{p}$ to simultaneous variation in habitat proportion (h) and search ability (n) (Figure 7.3). At extreme levels of habitat limitation ($h < 0.1$), slight increases in h greatly increase $\hat{p}$, but the point at which this occurs is strongly dependent on search ability being in the range of $n = 1 - 5$ (Figure 7.3).

Somewhat surprisingly, the effects of increases in colonization potential m/e affect $\hat{p}$ primarily at low levels of search ability and are most pronounced when h is also low (Figure 7.4). Once search ability n reaches about 10, $\hat{p}$ is only sensitive to extremely low levels of h (≤ 0.1; Figure 7.4). If we look just at the effects of variation in n or p, for a fixed value of m/e, we observe both the critical threshold values and the extreme sensitivity to declines in the density of suitable habitat, h (Figure 7.5). This figure is analogous to Figure 1 in Lande (1987). Examining the $\hat{p}$ response surface with respect to simultaneous variation in habitat proportion (h) and demographic potential m/e clearly shows the interaction between these variables (Figure 7.6). Species with

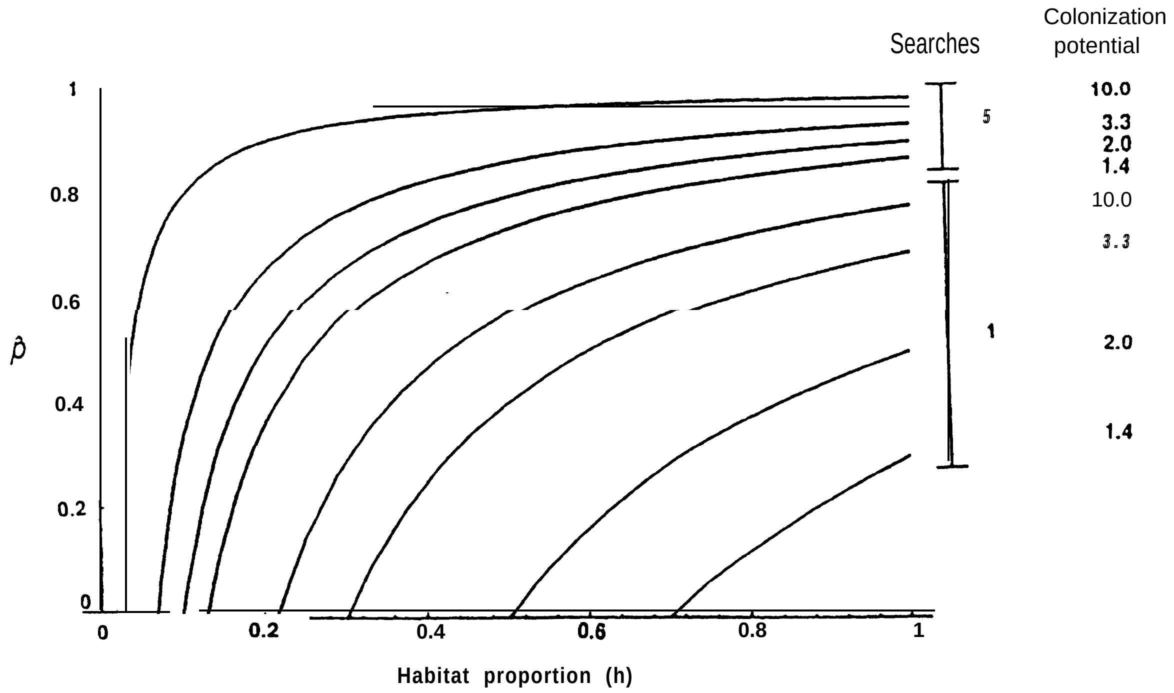

Figure 7.2. Changes in equilibrium occupancy rate $\hat{p}$ of a metapopulation against habitat proportion (h) for various levels of search ability (n) and colonization potential (m/e).

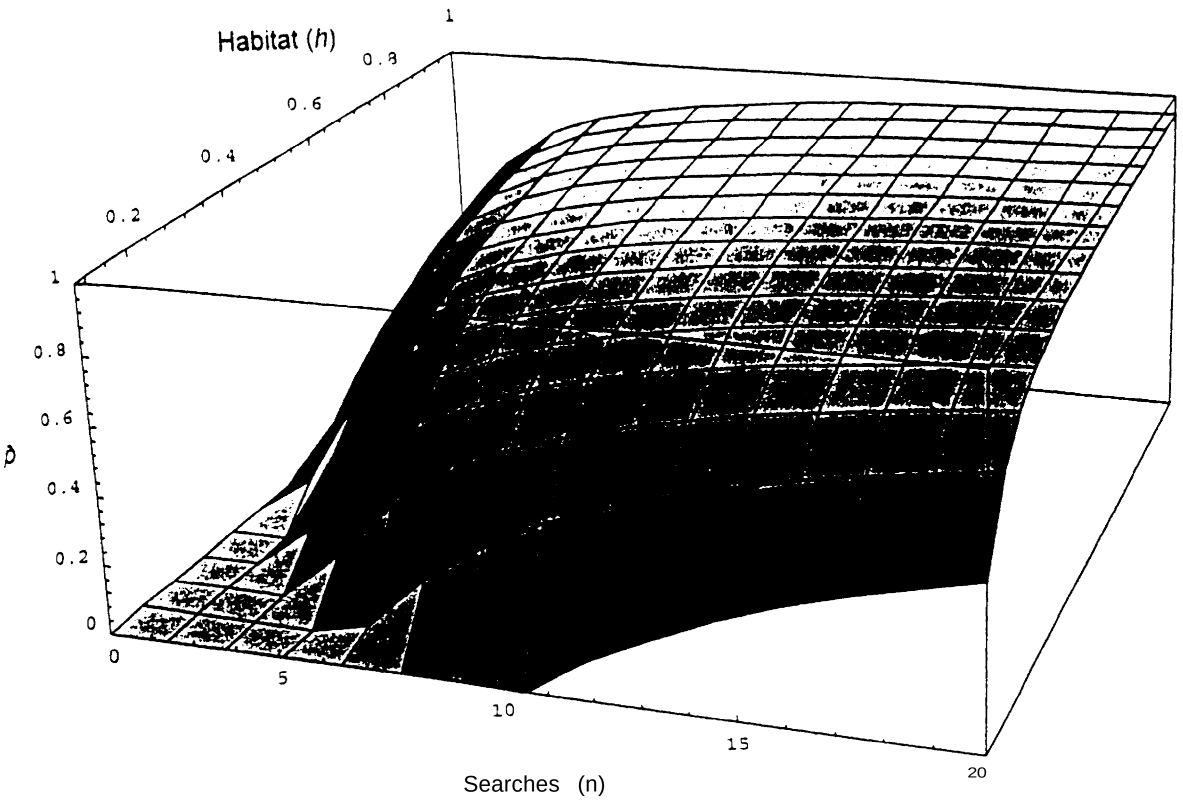

Figure 7.3. Changes in equilibrium occupancy $\hat{p}$ of a metapopulation, portrayed as a response surface, against habitat proportion (h) and search ability (n).

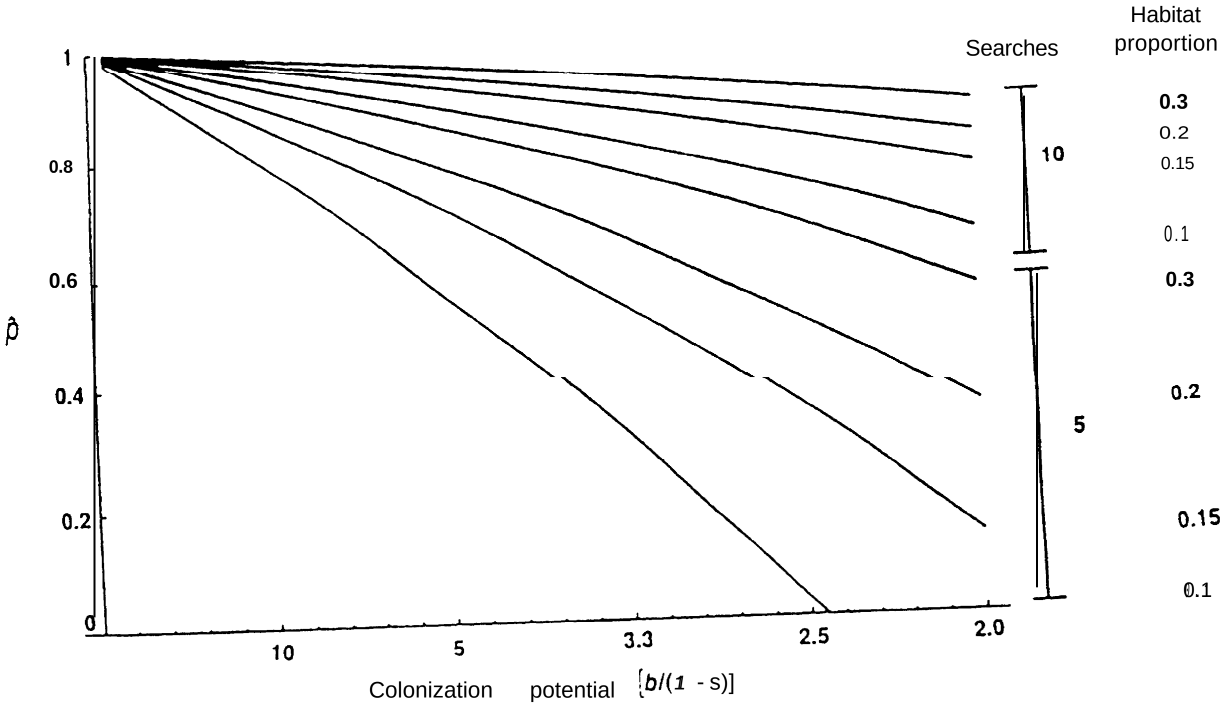

Figure 7.4. Changes in the equilibrium occupancy $\hat{p}$ of a metapopulation against colonization potential m/e for various levels of search ability (n) and habitat proponion (h).

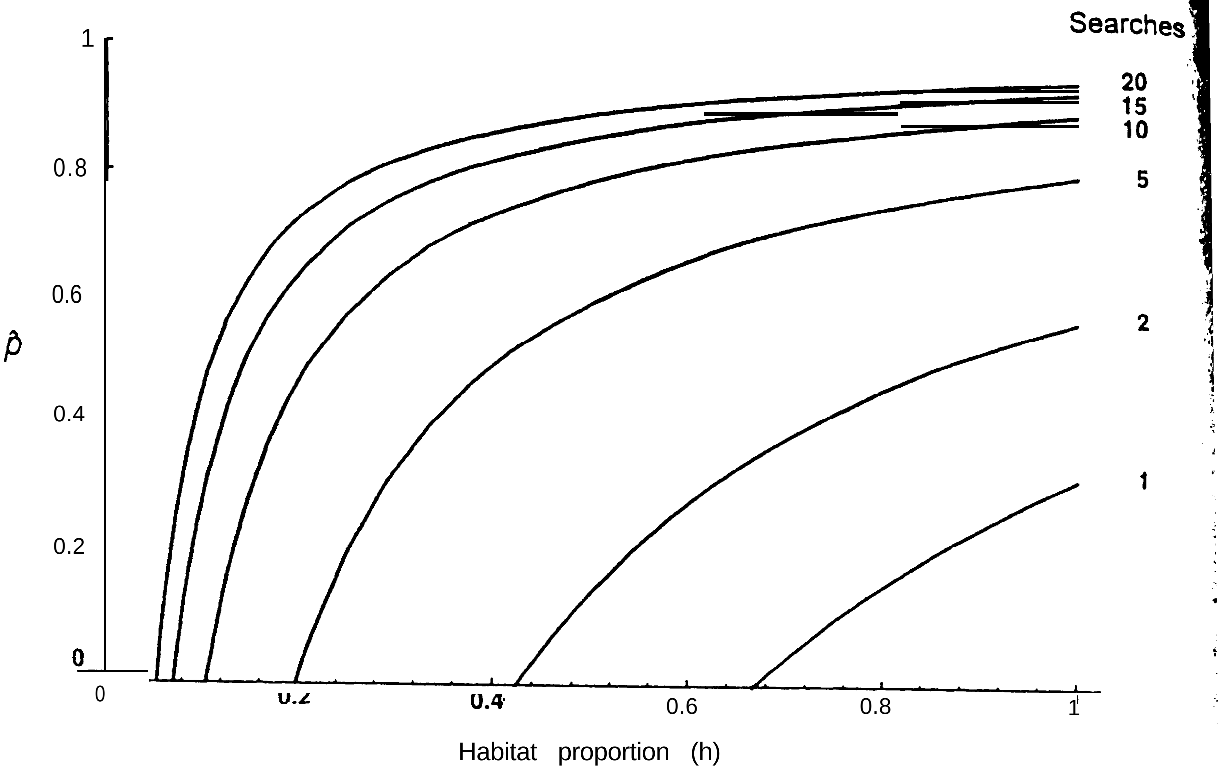

Figure 7.5. Changes in the equilibrium occupancy $\hat{p}$ of a metapopulation against habitat proportion (h) for various search capabilities (n).

naturally low colonization potential will rapidly be driven toward extinction by increasing habitat fragmentation (left-hand region of the response surface in Figure 7.6).

Stability of the Equilibrium Points

It is important not only to compute equilibrium occupancy proportions (for both metapopulation and territory models) but also to ask how sensitive these values are to disturbances that may affect habitat amount (changes in h), demographic rates (changes in m/e or $b/[1-s]$), and dispersal behavior (changes in n) (Equations 8 and 14). The stability condition for metapopulation equilibrium (Equation 8), $|f'(\hat{p})| < 1$, in terms of habitat proportion is

$$h > 1 - \left(1 - \frac{e}{m}\right)^{\frac{}{n}} \tag{15}$$

or, in terms of colonization rate,

$$m > \frac{e}{1-(1-h)^{n}} \tag{16}$$

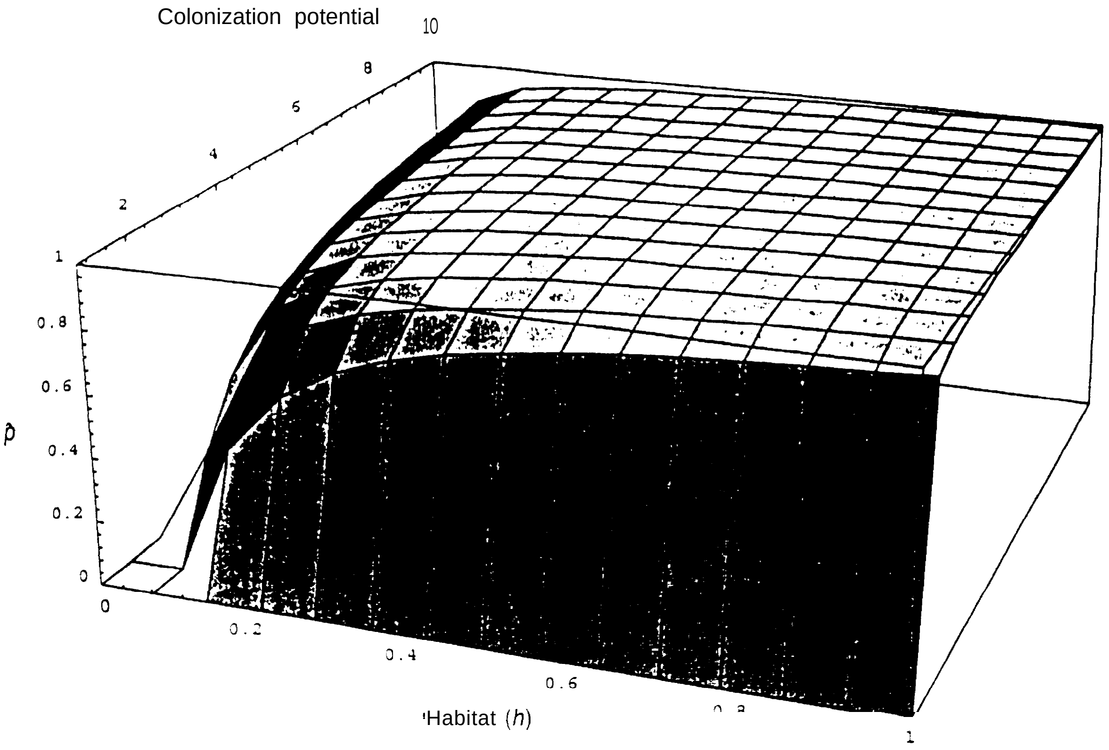

Figure 7.6. Changes in equilibrium occupancy $\hat{p}$ of a metapopulation, portrayed as a response surface, against habitat proportion (h) and colonization potential.

According to Equation (15), for fixed demographic potential, increases in search ability (n) quickly compensate for declines in habitat proportion (h). In the limit of Equation (15) as $n \to \infty$ a stable equilibrium arises so long as $h > 0$. Equation (16) behaves in a similar fashion relative to increases in search ability. In the limit as $n \to \infty$, for a given habitat proportion, a stable equilibrium arises so long as $m > e$.

The stability response surface (Figure 7.7) shows the combinations of habitat amount (h), dispersal ability (n), and colonization potential m/e that just meet the stability requirements for a given equilibrium occupancy rate. Points lying above the response surface represent combinations of h, n, and m/e yielding stable equilibria; points below the surface are unstable. The combination of habitat limitation, limited dispersal ability, and low colonization potential renders a metapopulation particularly extinction-prone (Figure 7.7: upper left).

Model Comparisons

As previously indicated, the equilibrium equations for the generalized metapopulation model (Equation 8) and for the individual territory model (Equation 14) are functionally equivalent if we assume that $m \infty b$ and $e \infty (1 - s)$. Given this, the dynamic behavior portrayed in Figures 7.2 to 7.7 for Equa-

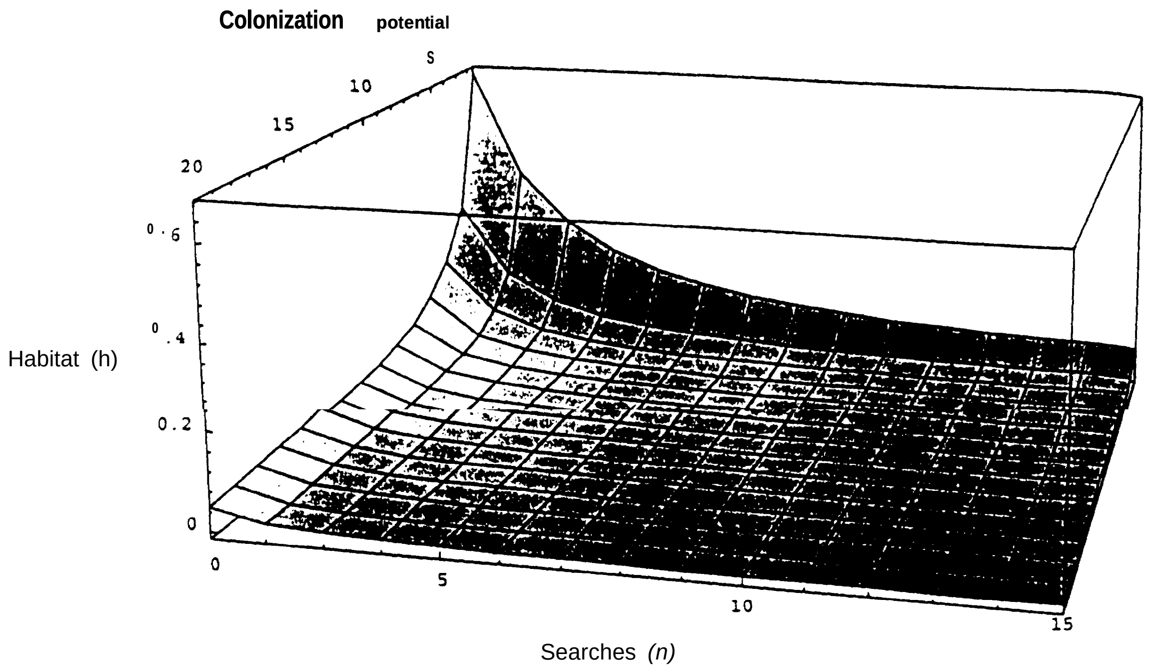

Figure 7.7. Stability response surface for the equilibrium solution to the general metapopulation model. (See Table 7.1.) Axes are habitat proportion (*h*), colonization potential *m/e,* and search ability (*n*). Points in the space lying above the response surface represent combinations of *h, m/e,* yielding stable equilibria.

tion (8) are equally applicable to Equation (14). The metapopulation model and its behavior (Table 7.1) can be directly compared with the individual territory model (Table 7.2). Comparing Tables 7.1 and 7.2 emphasizes the contrast in the appropriate scale for biological interpretation-individual birthrates and deathrates at the territory scale; colonization and extinction rates at the reserve scale.

Model Limitations

There are clear limits to direct extrapolation of our model results to biological populations. The most critical limits arise because we have not considered stochastic fluctuation in the metapopulation rates (*e* and *m*) and in individual vital rates (*b* and *s*). Lande (1987) and Lamberson et al. (1992) have explored the effects of stochastic variation in life-history parameters on inferences from the territory model. Importantly, the threshold valuable of habitat (*h*) necessary for population persistence is increased in the presence of serially uncorrelated environmental fluctuation (Lande 1987). Greater environmental variance, however, means a less abrupt threshold into the high-risk zone (Lamberson et al. 1992). The metapopulation model (Equation 5) would be similarly affected; thus our estimates of equilibrium values are optimistic.

TABLE 7.1.

Metapopulation model

Biological condition	Equilibrium equation	Equilibrium solution ($\hat{p}$)	Stability condition	Model interpretation (persistence requirements)
All patches suitable; one colonization event	$e - m\left(1 - \hat{p}\right) = 0$	$1 - \frac{e}{m}$	$m > e$	Patch colonization rate > patch extinction rate
A proportion *h* of patches suitable; one colonization event	$e - mh\left(1 \quad \hat{p}\right) = 0$	$1 - \frac{e}{hm}$	$hm > e$	Colonization rate of suitable patches > patch extinction rate
A proportion *h* of patches suitable; *n* colonization events (searches) possible	$e - m\left[1 \quad \left[\left(1-h\right)+h\hat{p}\right]^{n}\right] = 0$	$1 - \left[\frac{1-\left(1-\frac{e}{m}\right]^{\frac{1}{n}}}{h}\right]$	$1 - h \quad \left(1 - \frac{e}{m}\right)^{\frac{1}{n}} = 0$ or $m > \frac{e}{1-\left(1-h\right)^{n}}$	For a fixed landscape and colonization potential, inital increases in search ability strongly increase the level and stability of $\hat{p}$; for a fixed landscape and search ability, increases in colonization potential only moderately increase stability at $\hat{p}$

Source: Levins (1970).

Note: $\hat{p}$ = proportion of suitable patches occupied at equilibrium; h = proportion of patches suitable for occupancy; n = total number of patches that can be searched; e = rate of local extinction of occupied patches; m = colonization rate of empty patches

TABLE 7.2.

Individual territory model

Biological condition	Equilibrium equation	Equilibrium solution ($\hat{p}$)	Stability condition	Model interpretation (persistence requirements)
All territories suitable; one search event	$\left(1-\hat{p}\right)R_0'=1$	$1-\frac{\left(1-s\right)}{b}$	$\frac{b}{1-s}>1$	Birthrate > deathrate
A proportion h of territories suitable; one search event	$h\left(1-\hat{p}\right)R_0'=1$	$1-\frac{\left(1-s\right)}{bh}$	$\frac{bh}{1-s}>1$	The proportion of suitable territories h must be greater than the ratio of average deathrates to birthrates (inversely related to colonization potential)
A proportion h of territories suitable; dispersal can involve up to n searches	$\left[1-\left[\left(1-h\right)+\hat{p}h\right]\right]R_0'=1$	$1-\frac{1-\left(1-\frac{1-s}{b}\right)^{\frac{1}{n}}}{h}$	$b\frac{\left(1-\left(1-h\right)^{n}\right)}{1-s}>1$	For a fixed distribution of territories and R_0', initial increases in search ability strongly increase the level and stability of territory occupancy; for a fixed distribution of territories and search ability, increases in R_0' only moderately stabilize local occupancy.

Source: Lande (1987).

Note: $\hat{p}$ = proportion of suitable territories occupied at equilibrium; h = proportion of total "territories" that are suitable; n = total number of territories that can be searched; R_0' = index of colonization potential equal to $b/(1-s)$; b = birthrate; s = survival rate

Levins (1969) has also demonstrated that metapopulation dynamics described by Equation (1) show lower persistence in the presence of environmental fluctuations in extinction rate (*e*). The key point here is that the strong compensation of increased search ability for low *h* and colonization potential *m/e* (as in Figure 7.4) have critical limits set by local demographic and regional environmental stochasticity. Thus increased search ability will compensate for declines in the proportion of suitable patches (*h*) only to limits set by demographic stochasticity (which establishes a minimum size for stable, local populations) and environmental variation, which also affects the minimum size of local populations but in addition affects the proportion of occupied patches (p_t) necessary to reduce the risk that all local populations will simultaneously experience environmental perturbations or catastrophic events (Den Boer 1981). For an example of how these stochastic factors were incorporated into a metapopulation model for butterflies, see Hanski and Thomas (1994). General insights into minimum population sizes for local populations are provided by Lande (1993); a practical example for the spotted owl is found in Lamberson et al. (1994). Significantly, the critical population size necessary to escape the deleterious effects of demographic and environmental stochasticity is significantly reduced as population growth rate (or demographic potential) increases (Lande 1993).

One other important limitation of our models is that they do not incorporate an Allee effect- the reduction in colonization rate (metapopulation model) or fecundity (territory model) that arises from the difficulties of finding mates (Allee 1938). For the territory model, Lande (1987) explored in detail the effects of uncertainty in finding of mates. He found that difficulty in finding a mate decreased the equilibrium occupancy rate $\hat{p}$ and increased the habitat threshold (*h*) necessary for persistence. If the Allee effect were included, the compensatory growth response at low occupancy rates ($m - e$; Equation 2) would not be demonstrated. Rather, “growth” rate would show a depensatory response, which would raise the habitat threshold (*h*) necessary for persistence (that is, the curves in Figure 7.5 would shift to the right).

Finally, the Levins model assumes equal-sized patches within the metapopulation but does not explicitly consider variation in local population sizes across patches. When this additional complexity is included, there is the possibility of multiple stable equilibria where $\hat{p} > 0$ (Hastings 1991).

Comparing the Models

We have demonstrated that the generalized metapopulation model (modified from Levins 1970) and the individual territory model (Lande 1987) are functionally equivalent. Both show steep, nonlinear thresholds to persistence set by habitat proportion; extinction in the presence of suitable, unoccupied habitat; and strong compensation for habitat limitation and low colonization potential with increases in search ability. They differ, however, in spatial scale: the traditional metapopulation model is dynamic at a population level, and the basic unit of analysis is the habitat patch; the territory model is dynamic at the individual level, and the basic unit of analysis is the territory or home range. They also differ in temporal scale: the metapopulation model assumes that within-patch dynamics occur much faster than between-patch dynamics; the territory model has no such distinction. The metapopulation model is more phenomenological; the territory model is more process-oriented.

Both models are sensitive to changes in habitat quality or configuration for species that have both low vagility and low colonization potential (Figure 7.7). Species with these life-history attributes will be "sensitive" species-that is, when faced with habitat loss and fragmentation they will be extinction-prone. While generating reliable estimates of demographic parameters is often a costly and lengthy process, both vagility and fecundity often can be crudely estimated from existing natural history information. Estimation of these parameters for a large number of species may allow rapid ranking of species' extinction likelihood (that is, a coarse filter) without the need to collect exhaustive data.

Which model offers the appropriate conceptual framework for conservation depends on several species-specific considerations. First, for a given species, a patchy distribution of habitat and individuals at a local scale (due, for example, to fine-grained fragmentation) must first be distinguished from patchy distributions of populations (Hanski and Thomas 1994). The former distributions show frequent connectivity within the lifetime of an average individual. The latter demonstrate infrequent connectivity within the average lifetime of local populations; successful between-patch colonization may therefore be a very low probability event on a per-individual basis.

Second, it is important to consider the species' historic pattern of distribution and its suitable habitat. Was the species naturally distributed as a metapopulation prior to habitat loss and fragmentation, or was it more or less continuously distributed across the landscape? If the former, we would expect the evolution of pronounced dispersal ability and decreased sensitivity to regional-scale fragmentation. If the latter, the' species will probably demonstrate more limited dispersal capabilities and greater sensitivity. Valid insights depend on assessment at the correct scale. For a given species, insights into the appropriate scale at which habitat and population distributions should be estimated are provided by consideration of the historical effects of selection for dispersal ability.

Given the first two considerations, the third concern is the importance of population-level or patch-level dynamics relative to individual or site (territory) dynamics. For a species with both a current and a historical metapopulation distribution, we would expect patch dynamics to be at least as important as site dynamics. In this case, the metapopulation simplification may be justified unless local populations are below the critical minimum set by demographic uncertainty. If $h = 1$ and patch populations are large enough to be insensitive to demographic variation (say, >20 females; Richter-Dyn and Goel 1972; Lande 1993; Lamberson et al. 1994), then for individuals dispersing within the patch we expect an equilibrium $\hat{p} > 0$ even if search is limited to a single site (Doak 1989; Lamberson et al. 1994; McKelvey et al. in review).

For patches that are only partially suitable because they are heavily fragmented or have a great deal of edge, h will be less than 1 Bnd the patch dynamics will be a mixture of the two scales of interaction: individual and local population. The overall population dynamics of the patch may still be stable, but local carrying capacity will be reduced, largely as a consequence of within-patch search inefficiencies (Noon and McKelvey 1992; McKelvey et al. 1993).

For populations whose dynamics depend on the interaction of the metapopulatiun and on processes operative at the scale both of the patch and of the individual territory, the dynamics will operate in the following manner:

1. Territory-level dvnamics will probably dominate the carrying capacity of large pitches. This is because m and e rates defined at this scale represent infrequent events-perhaps an order of magnitude less frequent than those operating at the patch level. Because of these numerical relationships, exterior immigration will seldom provide sufficient support to affect the local equilibrium significantly.
2. As habitat declines within a patch ($h \longrightarrow 0$), the equilibrium population will decline. This will have two effects at the patch level. Patch level e will increase because of an increased probability of stochastic extinction, and patch level m will decrease because there will be fewer dispersers. Parameters m and e are therefore functions of the carrying capacities of the patches and are static only if the conditions within the patches (and hence their carrying capacities) are constant.

For these reasons, once a patch-oriented reserve structure has been chosen, the maintenance of well-distributed, high-quality habitat within each patch is of the utmost importance.

If the habitat is extremely fragmented at both the local and the regional scales, then local territorial dynamics will dominate and determine population processes. The stability of the system will become extremely sensitive to changes in both the birthrates and the deathrates at a local scale and also among-territory dispersal ability. (See Noon and McKelvey 1992 for an example.) In this case, the metapopulation paradigm may lack the resolution and realism necessary for us to understand and manage the dynamics of such a system.

How useful, then, is the metapopulation paradigm for single-species management and the conservation of biodiversity? The answer depends on the species-specific considerations cited above. In many cases, focusing research and management directly on demographic processes may be most relevant, and Lande's (1987) individual territory model may be a more useful paradigm. The models clearly exist along a continuum, however, and to some degree it is possible to scale up directly from the individual to the population. For example, when at least one local population attains the size at which demographic and environmental uncertainties have negligible impacts on persistence, then overall population viability mav be more dependent on among-population dynamics (patch extinction and colonization rates) than within-population dynamics (birthrates and deathrates).

Integrating the Individual and Metapopulation Models

The decision to focus on either within-population or among-population dynamics becomes uncertain in heterogeneous landscapes. In largely continuous landscapes where suitable habitat occurs in large blocks, for example, the management emphasis should be on maintaining habitat quality within blocks. Between-habitat dynamics are less important since the individual subpopulations are locally stable. In heavily fragmented landscapes, by contrast, with only residual small blocks of suitable habitat remaining, the primary emphasis is on maintaining connectivity among local populations. The emphasis shifts because local populations are too small to be demographically stable. Most real landscapes, however, are a mix of these conditions, and the trade-offs between a within-reserve or among-reserve management emphasis are unclear (Harrison 1994).

To clarify the trade-offs among reserve size, spacing, and habitat quality for spotted owl management, we used the simulation model of Lamberson et al. (1994), which includes the dynamics of both Lande’s (1987) individual territory model and Levins’ (1969) metapopulation model. In this model, a given landscape consists of a regular array of equal-sized, equal-spaced, circular reserves (following Levins 1969). Each reserve, in turn, is composed of a number of pair sites, of which a proportion h are suitable (Lande 1987). By varying the number of reserves of a given size, reserve spacing is affected; by varying the proportion of sites within a reserve that are suitable habitat, habitat quality is affected. The likelihood of successful travel between reserves assumed a constant risk per unit of distance and was modeled as a declining exponential function (Lamberson et al. 1994). The number of searches (n) per reserve was limited to that expected from a random walk (0.41 × reserve size; Lamberson et al. 1994). We set the maximum number of sites searched (n_{max}) to 20, an estimate based on the study of dispersing spotted owls (Thomas et al. 1990; Murphy and Noon 1992). This number allowed owls to search two or more reserves.

This simulation allowed us to increase the reality of the dynamics by including demographic uncertainty and an Allee effect (uncertainty in mate finding). Average extinction (e) and colonization (m) rates were estimated directly for a large metapopulation (≥ 250 reserves), each year for 1000 years, for many combinations of reserve spacing and habitat quality. Thus, the extinction/colonization dynamics of the metapopulation arose from the dynamics of individual territories and were a function of local colonization potential $b/(1 - s)$, habitat quality within a reserve (h), and dispersal ability (n). Given these changes, the expected equilibrium occupancy rate within reserves was proportional to Equation (14); the expected equilibrium for the total metapopulation was proportional to Equation (8) with $n \infty n_{max}$.

From the simulation results, we estimated the stability curves ($m/e = 1.0$) for four reserve sizes (Figure 7.8). For a given reserve size, combinations of within-reserve habitat quality and reserve spacing falling below the function ($m/e > 1.0$) have $\hat{p} > 0$; values above the function ($m/e < 1.0$) have $\hat{p} = 0$. The results clearly demonstrate the reserve design trade-offs and provide insight into the appropriate paradigm (local or metapopulation dynamics) for management. The more horizontal the curve, the more the within-reserve population dynamics are independent of reserve spacing. This pattern is most pronounced for reserves with 40 pair-sites that are locally stable so long as $h > 0.5$ (Figure 7.8). Thus, the management focus for a few large reserves is the maintenance of local habitat quality. In contrast, small reserves are seldom locally stable, and colonization among reserves is important even when most of the habitat within a reserve is suitable (Figure 7.8). Thus, the management focus for many small reserves is to maintain metapopulation connectivity by facilitating colonization. Importantly, no reserve structure-regardless of size or spacing- is viable if fewer than 30 percent of the sites within the reserve are suitable habitat (Figure 7.8).

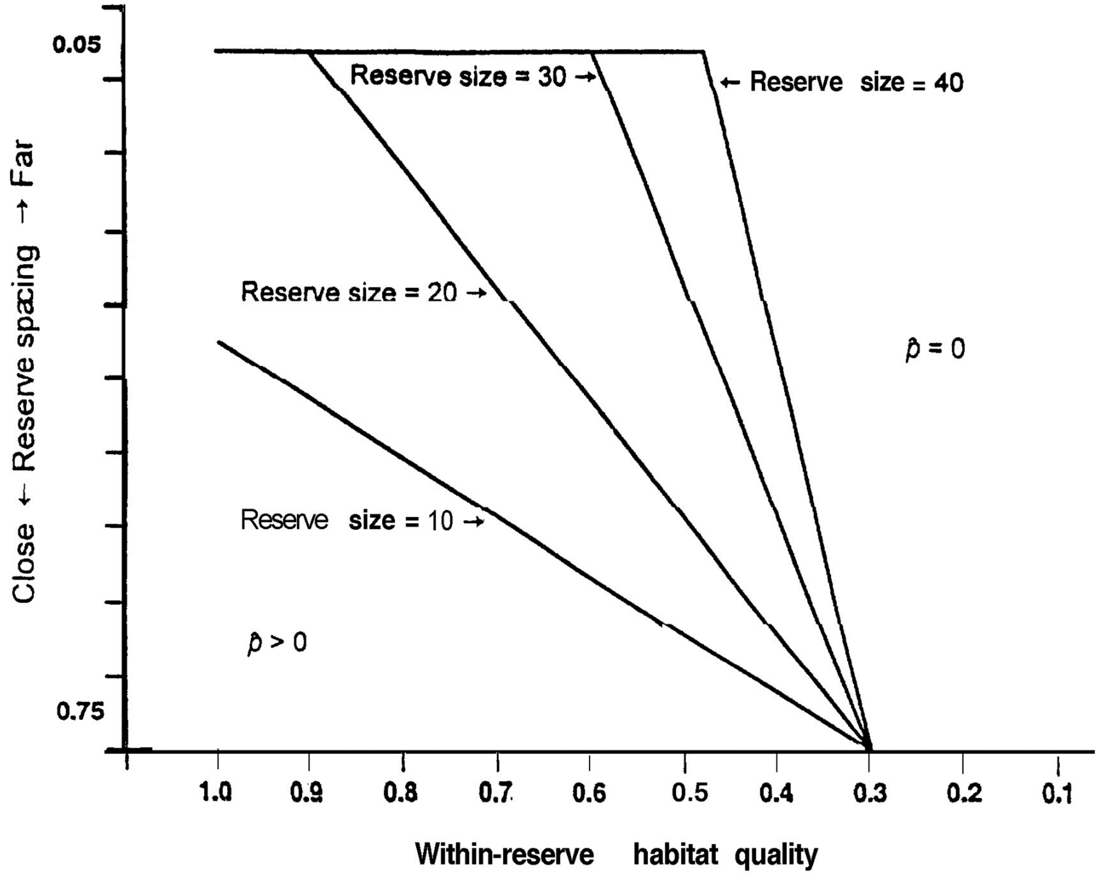

Figure 7.8. Stability response functions for the solutions to the combined individual territory and metapopulation models. Functions illustrate the trade-offs between reserve spacing (proportion of the landscape within reserve boundaries) and within-reserve habitat quality (proportion of sites stocked with suitable habitat) as a function of reserve size.

The Spotted Owl Example

Conservation plans may differ widely in their design and implementation. Essentially there are two extremes: on the one hand are plans that designate fixed reserve boundaries-a spatially explicit distribution of habitat blocks to support locally stable subpopulations given the condition of facilitated dispersal among subpopulations (a metapopulation structure); on the other hand are plans that restrict allowable management activities within certain habitats to retain their suitability or render them suitable at some future time without specifying the boundaries of a fixed reserve system.

The former strategy is most appropriate for species currently in decline because of habitat loss and fragmentation. For these species, the manager's first responsibility is to arrest the population decline by stabilizing both the amount and the distribution of suitable habitat. (See the discussion in Lande 1987, Lamberson et al. 1992, and Lamberson et al. 1994.) In contrast, special management plans may be adequate for species th do not currently demonstrate significant population declines but are exposed to a subtle, landscapewide degradation of their habitat, such as that induced by fine-grained fragmentation. This can occur, for example, if nesting structures become limiting or of low quality because they are being systematically removed under current management plans. Under this scenario a static reserve system is not drawn on maps; rather, a dynamic reserve system that provides for a shifting mosaic distribution of suitable territories through time must be planned. Each type of plan is spatially explicit because at any point in time the manager must be confident that the landscape is providing the amount and distribution of suitable habitat needed for population persistence.

Northern Spotted Owl

Currently the range of the northern spotted owl (Figure 7.9) approximates its historic distribution. The current distribution of both habitat and owls, however, is much reduced from historic levels. The area of suitable owl habitat prior to extensive logging is unknown, but by the early 1980s more than 80 percent of the late seral stage forest had been harvested (Booth 1991). Most of the remaining habitat is on national forest lands. Based on then-current management plans, owl habitat was projected to be completely harvested on national forest lands within 60 years (Mulder et al. 1989).

The primary silvicultural method practiced in the Pacific Northwest has been clear-cut harvest, and most harvest on public lands has occurred since 1950. As a consequence, the landscape is very patchy with sharp contrasts between old and very young forest. The Interagency Scientific Committee (ISC) conservation strategy had two key objectives: first stabilize the owl population by instituting a policy that would eventually lead to no net loss of habitat; then provide sufficient habitat in a spatial configuration that would allow for a balance between local extinction and recolonization events (Thomas et al. 1990). The second objective was achieved by concentrating currently suitable habitat as close as possible to existing reserve lands (national parks and wilderness areas) and designating a large number of habitat conservation areas (HCAs).

HCAs were widely distributed across the landscape. They were selected to have a size and spacing that would provide for locally stable populations, contingent upon some level of migration among local populations (Murphy and Noon 1992). Thus the ISC, in its reserve design, invoked the metapopulation paradigm and imposed this spatial structure on the remaining population of northern spotted owls. Significantly, this structure would become progressively more pronounced as suitable habitat outside the reserve systems was lost to timber harvest.

Figure 7.3. Northern spotted owl, Six Rivers National Forest, California. Photo by R. J. Gutiérrez.

California Spotted Owl

Forests in the Sierra Nevada have been markedly affected by human activity within the last 150 years (McKelvey and Johnston 1992). A combination of logging and natural attrition of the old forest led to a decline in the number of large, old trees (particularly pines); broke up the patchy mosaic of the natural forest; and encouraged the development of dense, understory conifer regeneration. The result was a rather uniform, landscapewide loss of those old forest elements (large, standing live and dead trees and large, downed logs) strongly associated with the habitat use patterns of spotted owls. Verner et al. (1992) viewed this decline in habitat quality as a fine-grained fragmentation effect expressed at the scale of the individual territory.

Based on the current Forest Service land-management plans, loss of old-growth forest elements was projected to continue, resulting in forests susceptible to fire disturbance and nearly devoid of large, old trees. Given these projections, Verner et al. (1992) proposed interim (5-10 year) guidelines that restricted silvicultural activities in habitats selected by spotted owls. These restrictions, invoked at a landscape scale but implemented at a local scale, would retain the large-tree components in harvested stands to greatly accelerate the rate at which these stands would become suitable habitat in the future. They assumed that the locations of suitable territories would shift dynamically across the landscape and that the guidlines retaining large trees would ensure that an adequate amount and distribution of suitable habitat sites would always be available.

Why Two Different Strategies?

Both the northern and California spotted owls select habitats, at both landscape and home-range scales, that retain old-growth forest characteristics. Consequently, timber harvest of old-growth forests, or their components, is responsible for our concern over both subspecies' long-term persistence. Given the wide acceptance by the scientific community of the metapopulation reserve paradigm for the northern subspecies, why was a different strategy adopted for the California spotted owl? There are several reasons why the individual territory paradigm was the preferred conceptual model, leading to a focus on birthrates and deathrates operative at a local scale (Verner et al. 1992).

First, during the past 50 years the number and distribution of northern spotted owls may have been reduced by as much as 50 percent from pre-twentieth-century levels (Thomas et al. 1990). No evidence of similar declines in number or distribution exists for California spotted owls, despite

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