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Developing an Analytical Context for Multispecies Conservation Planning

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Summary

This chapter attempts to apply population modeling techniques that have been applied to single species, and use them to plan conservation strategies for multiple species when species are well known and have common life history features divisible into prereproductive and reproductive phases. Using three exemplary endangered species, we were able to ordinate them on a common response surface to analyze their sensitivity to habitat loss and fragmentation. The modeling strategy enables managers to assess which species are least sensitive to habitat loss, and therefore reduce costs in monitoring such species. Although at present, the strategy of protecting biological diversity through protecting areas large enough to allow the persistence of habitat mosaics and dynamic processes of change within them is the most effective, the modeling strategy presented here is a promising addition to the tools available to managers, and merits further development. The method should be of most utility for sympatric species in habitats threatened by reduction and fragmentation.

Introduction

We have been involved in practical conservation planning for more than a decade-which is to say that we have applied the principles and theories of ecology in attempts to solve real-world conservation problems. One recurring constraint that we have encountered when attempting to incorporate ecological principles into conservation solutions is the desperate lack of time and money available to those who take on the challenge of balancing environmental protection with the rest of the human. endeavor; We know that the number of species. at risk of

extinction is extensive and that their individual ecologies are diverse. The spatial and temporal scales at which those species respond to environmental degradation vary over several orders of magnitude, and imperiled species differ extensively in their life history attributes. We contend that the diversity of life history attributes, and the multitude of physical and biotic forces that affect landscapes and the ecosystems that they support, interact in such complex wavs that they currently defy direct application of existing ecological principles in a conservation context. To a large extent, what we hope to accomplish in this chapter is to prompt ecologists to critically examine whether any general ecological principles are emerging that may prove to be applicable to the conservation of communties of species occupying diverse ecosystems.

Here we advance one method that might enable us to move from single-species to multispecies conservation planning. At the outset, we make it clear that we currently cannot offer a definitive algorithm for multispecies analysis. Rather, we are making an initial attempt toward that goal using a life history model applicable to species with the following generalized characteristics: their life histories can reasonably be represented as having two discrete stages (prereproductive and reproductive), a seasonal breeding pulse exists that is short relative to the rest of the annual cycle, the concept of territory or home range is meaninful, and prereproductive individuals search (to varying degrees) for breeding territories and mates. Using this model, we simultaneously explore the relative sensitivities of three species to habitat loss and fragmentation. The three species, all protected under the Endangered Species Act, are the California gnatcatcher (*Polioptila californica californica),* the Bay checkerspot butterfly *(Euphvdryas editha bayensis);* and the northern spotted owl *(Strix occidentalis caurina*). All are found in California. Each, however, resides in very different habitat associations. has widely differing area requirements, and extremely distinctive life histories.

In the process of examining the population dynamics of these species in the face of habitat loss and fragmentation, we address the following questions: First, how do we as conservation scientists move from single-species conservation planning to a multispecies approach? Second, is there any possibility that the umbrella or keystone species concept might reemerge to ease the burden of multispecies conservation planning? Finally, is there a common analytical framework for evaluating multispecies sensitivity to habitat loss and fragmentation? As a starting point, we focus here primarily on the third question We revisit the first two questions relative to how well we have answered the third.

A Common Framework for Population Viability Analysis

Levins (1970) described the dynamics of populations occupying a system of habitat patches of identical size and even spacing. Although this structure may be rare in natural populations (Harrison, 1993), it can be common in human-

dominated systems. In a classic example, the U.S. government gave railroad companies every other section (1 mi^2) of land along railroad right-of-ways. As a result, "checkerboard" patterns of ownership and subsequent habitat disturbance and conversion are common in the western states today. In this context, Levins' metapopulation paradigm therefore can provide a useful starting point for analyzing the impacts of human-induced habitat fragmentation.

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

$$\frac{dp}{dt} = mp(1 - p) - ep, \tag{4.1}$$

where p is the proportion of habitat patches occupied, m is the colonization rate, and e is the extinction rate of patches. The equilibrium proportion of occupied patches is

$$\hat{p} = 1 - \frac{e}{m}, \tag{4.2}$$

hence the population $\rightarrow$ for all $e \geq m$.

The linear density dependence in Levins' model assumes that potential colonizers are only able to search a single habitat patch, and that all patches are suitable for colonization. We can relax these conditions, allowing for multiple searches and unsuitable habitat patches (Noon and McKelvey, 1996):

$$\frac{dp}{dt} = mp\{1 - [(1 - h) + ph]^n\} - ep, \tag{4.3}$$

where h is the proportion of habitat patches that are suitable and n is the number of patches that a colonizer can search. The associated equilibrium occupancy proportion of patches, in discrete form, is

$$\hat{p} = 1 - \left\{ \frac{\left[1 - \left(1 - \frac{e}{m}\right)^{1/n}\right]}{h} \right\}. \tag{4.4}$$

If $h = 1$ and $n = 1$, equation (4.3) collapses to equation (4.1) and the equilibrium collapses to equation (4.2).

Although these changes in Levins' model are relatively minor, they increase the generality of the model and make it algebraically identical to Lande's (1987) individual territory model (Noon and McKelvey, 1996). This crosswalk enables us to exploit the best features of both models: Levins' model has simple equilibrium

criteria., but *e* and *m* are not clearly defined; whereas Lande's model is parameterized on the basis of clear biological understanding and measurable criteria. In Lande's model *e* and *m* are functions of birth, death, and the mobility of individual organisms. Hence we are able to rewrite Levins' equilibrium solution in terms of Lande's (1987) model as

$$\hat{p} = 1 - \left\{ \frac{\left[1 - \left(1 - \frac{1-s}{b} \right)^{1/n} \right]}{h} \right\}, \tag{4.5}$$

where *s* is the adult survival rate, *b* is the average fecundity of adults, and *n* is the number of potential territories (habitat patches) that a dispersing juvenile is capable of searching (Noon and McKelvey, 1996). The parallel between equations (4.4) and (4.5) assumes that $e \propto (1 - s)$ and $m \propto b$.

Given these understandings, if we have estimates of an organism's life history parameters and some knowledge of its dispersal behavior, we can estimate its sensitivity to changes in the amount and fragmentation of habitat (*h*). Because both dispersal (*n*) and habitat fragmentation (h) scale to the territory size of the organism, species of different sizes, from different taxonomic groups, and that exhibit different vagility can be directly compared within the same parameter space. This rescaling enables a comparative assessment of species that respond to environmental variation at distinct spatial scales in a common analytical framework.

This parameter space can be presented as a stability response surface, combining habitat proportion, dispersal ability, and growth potential (Fig. 4.1). The stability condition for population equilibrium (eq. [4.5]), $|f'(p)| < 1$, is

$$\frac{b[1 - (1 - h)^n]}{1-s} > 1. \tag{4.6}$$

The surface represents the threshold between population persistence and extinction. Combinations of points that lie above this surface have an equilibrium occupancy proportion greater than zero. For the sake of generality we refer to the ratio of fecundity to mortality as growth potential (note that this variable is not equivalent to Lande's [1987] definition of demographic potential). A priori, we expect organisms with low fecundity and low vagility to be sensitive to fragmentation.

Three Exemplary Threatened Species

If this common modeling framework has merit, species that are believed to be threatened by habitat loss or fragmentation should exhibit combinations of life

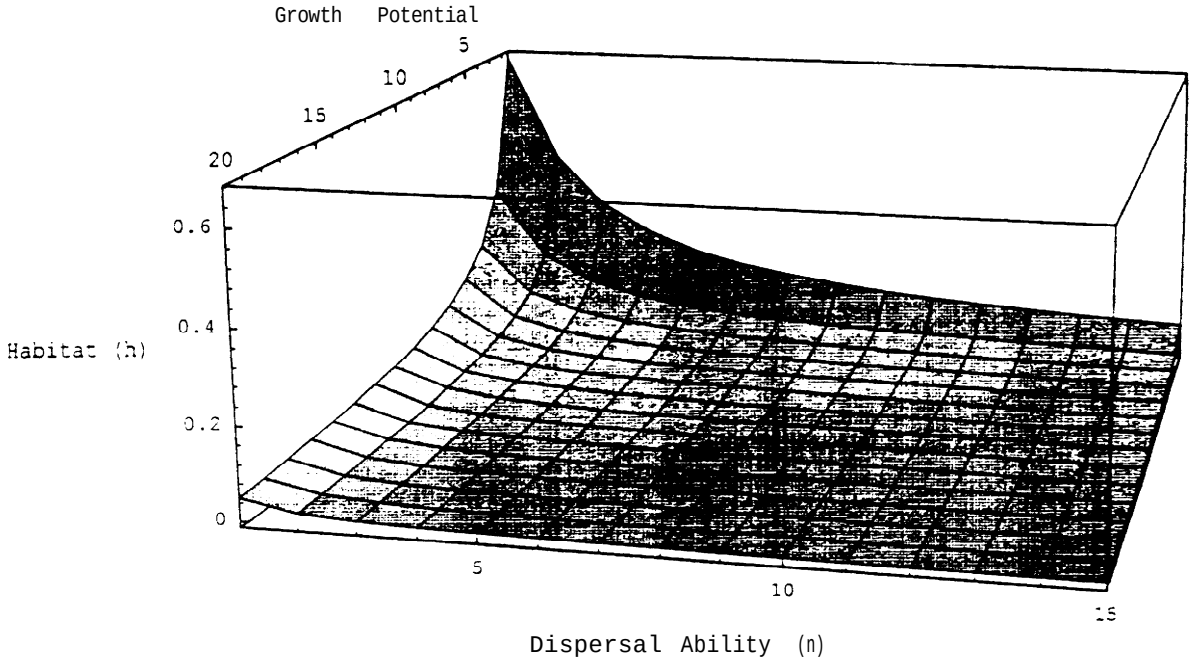

Figure 4.1. Stability response surface for the equilibrium solution to the general metapopulation model. Axes are habitat proportion (h), growth potential [b /(l - *s*)] , and dispersal ability (n). The surface is the equilibrium extinction threshold. Note that $\hat{p} > 0$ for all values above the surface and $\hat{p} < 0$ below it.

history traits (fecundity, adult survival, and vagility) that in the model, are associated with a sensitivity to declines in *h.* To test this premise, we have chosen three well-studied species currently listed as threatened under the Endangered Species Act: the California gnatcatcher, the Bay checkerspot butterfly, and the northern spotted owl.

The California gnatcatcher is a small bird, weighing about 6 grams, that is narrowly restricted to coastal sage scrub habitat in coastal southern California. The coastal sage scrub habitat is naturally patchy in distribution, occurring in a mosaic with other plant communities. Habitat quality for the bird apparently is best where sage scrub is interdigitated with grasslands at low elevations close to the coast (Mock, 1992; Mock and Bolger, 1992). The distribution of the California gnatcatcher ranges from Los Angeies south into Baja California The coastal sage scrub habitat is highly disrupted near to the coast, and the bird now is found largely inland and at higher elevations (Mock, 1992; Mock and Bolger, 1992; Davis et al., 1994; Fig. 4.2). For example, in the southwestern part of San Diego County, urban sprawl restricts the remaining coastal. sage scrub habitat for the California gnatcatcher to the eastern part of its historical distribution (Fig. 4.2). Presumably the highest quality or source habitat occurred within sage scrub at lower elevations and on moderate. slopes, Whether residual higher elevation patches of coastal sage, scrub act as- "sink" habitat for the gnatcatcher is really not known (Mock, 1992; Mock and Bolger; 1992), but a proposed regional conservation plan for the California- gnatcatcher delimits reserves- that are cur-

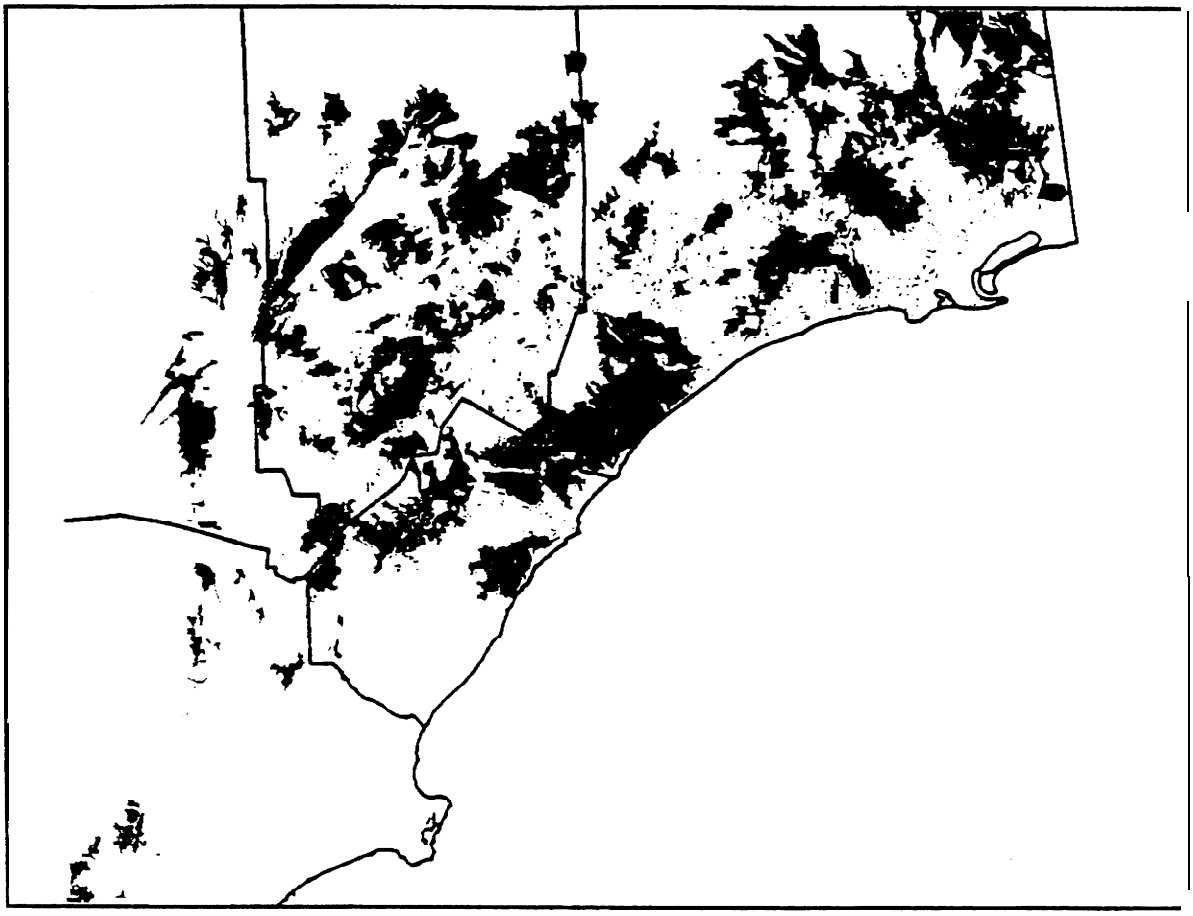

Figure 4.2. Distribution of California gnatcatcher habitat (coastal sage scrub) north of Mexico. The figure includes the entire Natural Community Conservation Planning Region. Lower-elevation habitat has been disproportionally destroyed or disturbed due to agriculture and urbanization.

rently suitable habitat or have the potential to be restored to suitable habitat, and designates specific areas to develop as corridors. Corridors would be restored to enhance connectivity between the reserves (Reid and Murphy, 1995).

The Bay checkerspot butterfly occurs in residual patches of native annual grasses and forbs that are restricted to serpentine-based soils (Harrison, 1989; Murphy et al., 1990; Lamer and Murphy, 1994). In most other grasslands that fall within the historic range of the species, the required larval hostplants and adult nectar sources have been replaced by exotic species, but serpentine soils with their unique physical and chemical characteristics have allowed remnant natural habitat to persist.

The remaining amount of serpentine soil habitat in California is quite small, the patches disjunct (Fig. 4.3), and local populations of checkerspot butterflies are therefore prone to local extinction-at this time the butterfly populations are restricted to two large population centers. A reserve has been set aside for the Bay checkerspot butterfly within habitat- that supports the more southern of the two population centers. The reserve consists of a portion of one large "mainland"

Figure 4.3. Distribution of serpentine-soil-based habitat in south San Francisco Bay area in central California. Habitat designated MH (Morgan Hill) supports a source population of butterflies that sustains apparent sink populations on habitat patches designated with other initials. Habitat patches not designated with letters have been unoccupied during the past decade..

or source area, whereas a number of smaller "satellite" patches exist nearby but are unprotected.

Spatial scale plays an important rule in the dynamics of the Bay checkerspot butterfly population. Habitat quality varies on a microscale, and reproductive success is tightly linked to fine-scale microclimatic and topographic variation (Singer, 1972; Dobkin et al., 1987; Murphy et al., 1990). A map of the thermal environment for the butterfiy (Fig. 4.4) indicates the extent of microclimate variation, and suggests that habitat quality varies as a function of the environmental conditions unique to each given year, combined with habitat area, slope, and aspect (Weiss et al., 1993). In simplified terms, the butterflies tend to experience greater reproductive success on warmer, drier slopes during cooler, wetter years, and the converse during warmer, drier years.

The northern spotted owl occupies primarily closed-canopy, late seral stage coniferous forests with nest sites characterized by particularly large diameter trees (Thomas et al., 1990). During the past 50 years, the number and distribution of spotted owls may have been reduced by as much as 50 percent from pre-

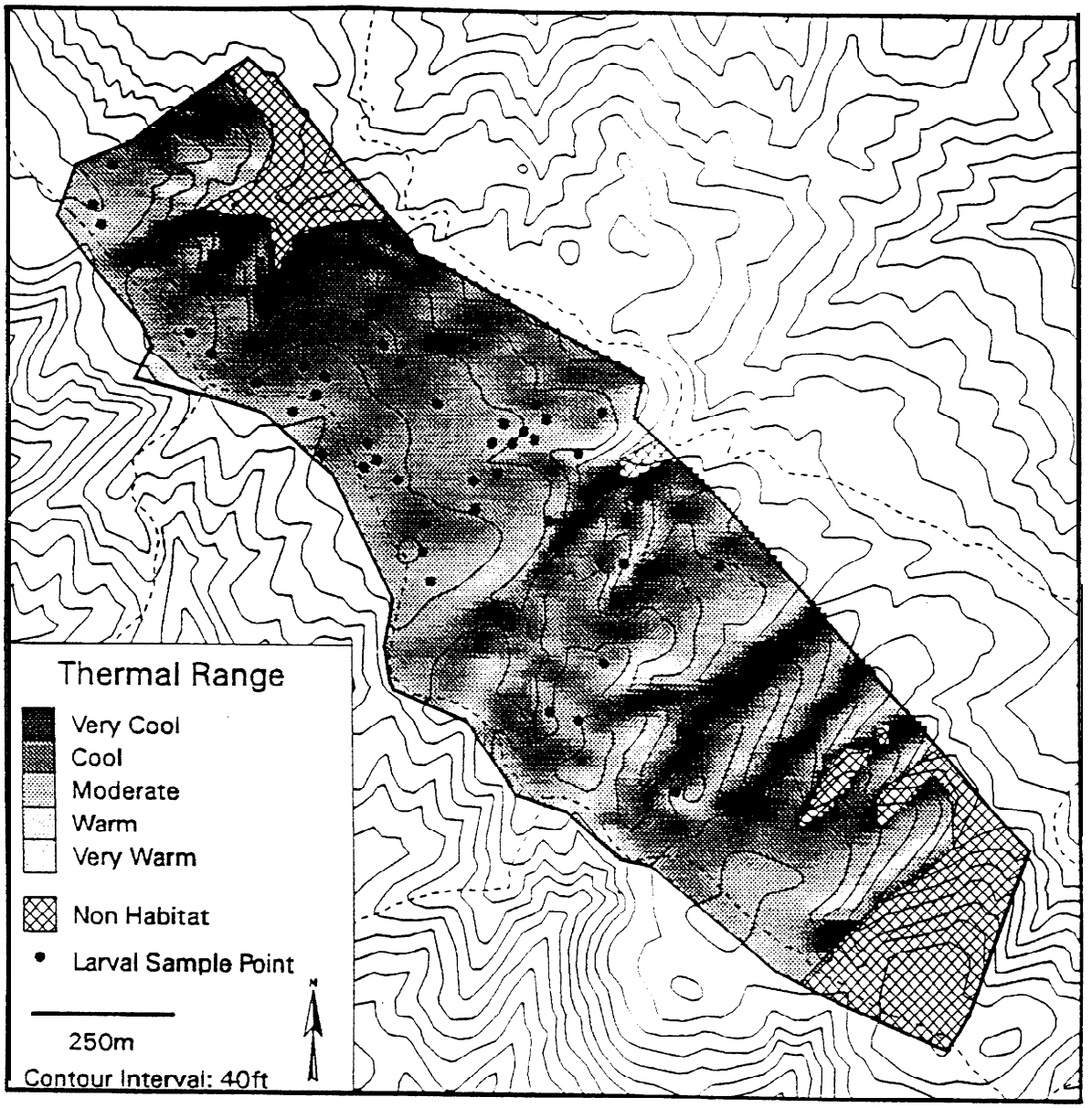

Figure 4.4. The thermal environment within 100 ha of the Morgan Hill habitat patch butterfly reserve in central California. Vital rates for the Bay checkerspot butterfly vary across the topographic gradient from year to year, with substantially higher survival of larvae on cooler slopes in warmer, drought years and slightly higher survival on warmer slopes in cooler, wetter years.

twentieth century levels (Thomas et al., 199020). Threats to the subspecies are primarily a consequence of loss and fragmentation of habitat as a consequence of timber harvest (Fig. 4.5; Murphy and Noon. 1992). The primary silvicultural method in the Pacific Northwest, west of the Cascade crest, was clear-cutting. Because these cutting methods have dominated in the Pacific Northwest, particularly over the last 50 years, habitat within the range of the owl is either undisturbed and suitable, or cut within the last 50 years and unsuitable. The result has changed the forested landscape to an island-like distribution of late seral stage forests imbedded in a matrix of young forest (Ripple et al., 1991).

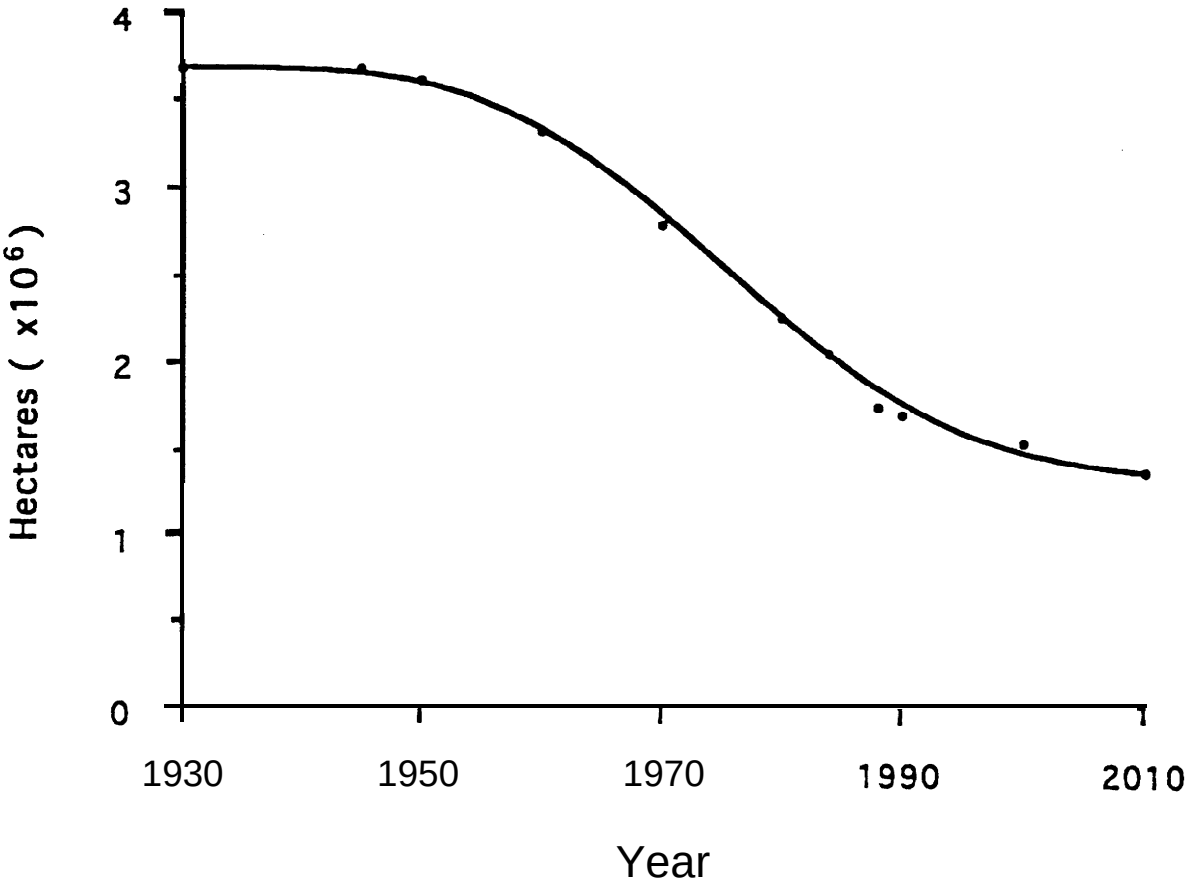

Figure 4.5. Estimated trend in the areal extent of suitable northern spotted owl habitat on National Forest lands in Oregon and Washington for 1930-2010. Estimates for 1990-2010 are projections based on Forest Plans approved prior to 1989.

Developing a Common Modeling Framework

Parameterizing the model requires estimates of vital rates, dispersal ability, and area requirements for breeding. Such data are available for only a handful of species-extensive field work is required to obtain the necessary parameter estimates for any wild population. For these three species, published estimates of fecundity based primarily on field studies and direct enumeration of progeny, estimates of adult survival rates based on mark-recapture studies, and estimates of home range size and mobility derived from following the movement of marked individuals, were available (Table 4.1).

Primary sources for parameter estimates for the Bay checkerspot were Harrison et al. (1988), Cushman et al. (1994), and Carol L. Boggs (personal communication); for the California gnatcatcher, Mock (1992) and Mock and Bolger (1992); and for the northern spotted owl, Burnham et al. (1996). The essential parameters were (1) fecundity, expressed as the number of female offspring per adult female; (2) survival rate during the period of spatial fidelity (the territory period for gnatcatchers and owls, and the period from diapause until metamorphosis for butterflies); and (3) dispersal ability, computed as the average distance moved

Table 4.1. Estimates of the mean annual vital rates (birth and death) and dispersal ability of three species listed under the Endangered Species Act. Dispersal ability is scaled by mean breeding season home range size: Maximum parameter values provide insights into biological potential. These parameter estimates were used as input for model analyses.

	Species		
Parameter	Northern Spotted Owl	California Gnatcatcher	Bay Checkerspot Butterfly
Fecundity[1] (b)	0.35	1.05	85
Maximum	0.70	1.50	120
Adult survival[2] (s)	0.87	0.55	~ 0.01
Maximum	0.92	0.61	—
Growth potential[3]	2.69	2.33	86
Maximum	8.75	3.85	121
Dispersal ability[4]	10	4	6
Maximum	>20	>20	>>l00
Home range	100 ha	14 ha	4 m^2

[1] Fecundity for the bay checkerspot was based on the average number of eggs reaching diapause.

[2] Adult survival for the bay checkerspot was computed as the mean probability of survival from postdiapause to egg laying.

[3] Computed as $b/(1 - s)$.

[4] Average distance moved from birth to breeding, expressed in home-range-sized units.

from birth to breeding and expressed in home-range-sized units. Survival rate during dispersal was implicit in the model, and arises as a function of search ability (n) and the proportion of the landscape that was suitable habitat (h) (Lande, 1987; Lamberson et al., 1992).

The three threatened species have been subject to extensive habitat loss and fragmentation from human activities since the tum of the century, but particularly during the past several decades, either by urbanization or by deforestation. As a consequence, their populations have discrete spatial structure and the paradigm of the metapopulation, to varying degrees, is an appropriate one for these species (Harrison et al., 1988; Mock, 1992; Lamberson et al., 1992). Hanski (1991b) and Hanski and Thomas (1994) have described the different sorts of metapopulation paradigms that one might bring to bear in the development of a theoretical foundation for conservation planning for-imperiled species. What we have done is to view these species dynamics in a combined, comparative analysis to contrast their sensitivities to habitat loss and fragmentation, As noted earlier, the same model form can be utilized- to look at reserve-level. extinction and colonization (Levins' model) or within reserve dynamics at-the level of the individual territory (Lande's model). In applying these concepts to these three species, we look first at a within-reserve and-then at among -reserve dynamics.

Placing the population dynamics of these three species within a common analytical framework requires some simplification and abstraction. In modeling within-reserve population dynamics, we assumed that the number of suitable sites was static, and that all suitable sites were equally available, There was no within-reserve spatial structure other than the proportion of habitat available. In addition, environmental stochasticity was not modeled, a simplification that is of particular concern in the context of the population dynamics of the Bay checkerspot butterfly (Weiss et al., 1988, 1993).

Population Dynamics Within a Local Population

Both the gnatcatcher and the spotted owl are sensitive to decreases in suitable habitat, with equilibrium populations becoming extinct in the presence of suitable habitat (Fig. 4.6). That is, there is a steep threshold to their population persistence (cf. Lande, 1987; Lamberson et al., 1992). Of the three species. the gnatcatcher is the most sensitive to habitat fragmentation, and the Bay checkerspot, primarily because of its comparatively high reproductive potential, the least sensitive.

Based on available parameter estimates (Table 4.1), we plotted the position of the spotted owl, gnatcatcher, and Bay checkerspot butterfly on the stability

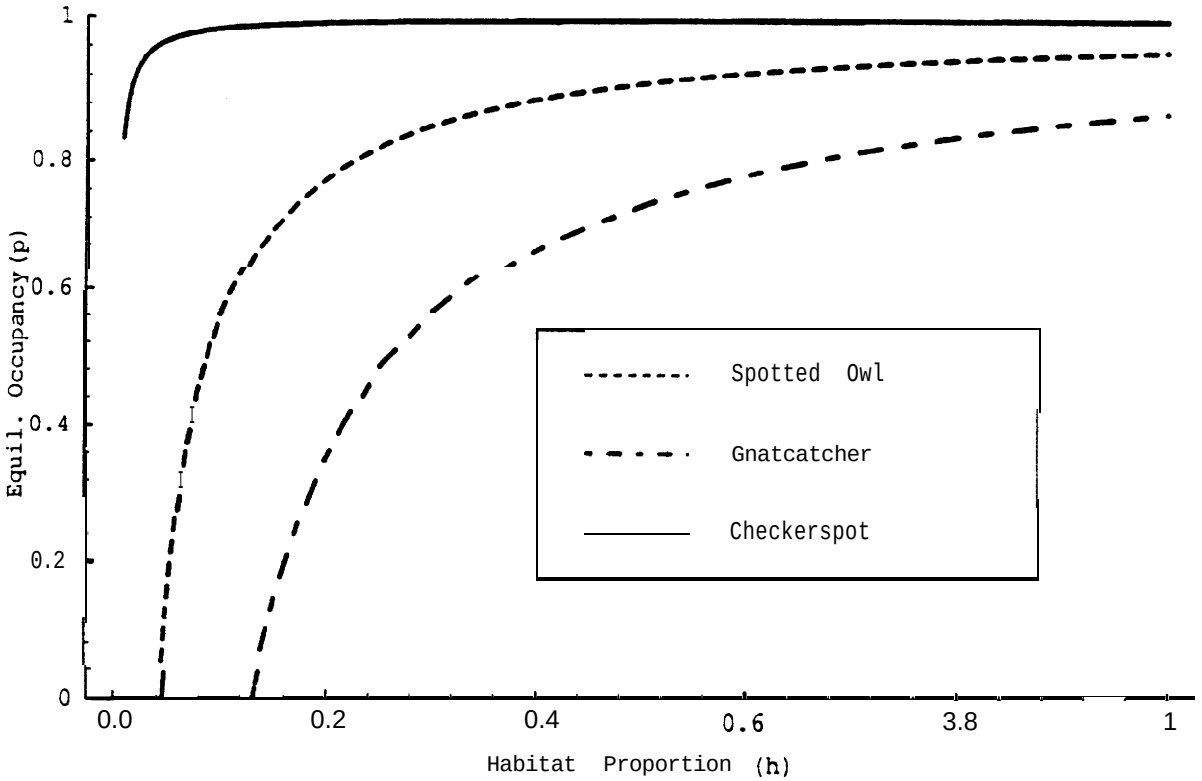

Figure 4.6. Percentage occupancy of breeding- sites (home ranges or territories) for the Bay checkerspot butterfly, the northern spotted owl;-and the California gnatcatcher against the proportion of the landscape, within a local population, that is suitable habitat.

response surface (Fig. 4.7). Note that the spotted owl and gnatcatcher are located in the portion of the surface that is sensitive to changes in habitat proportion, whereas the Bay checkerspot lies in an insensitive region (Fig. 4.7).

One influence on population persistence that this figure fails to capture, and that is of pronounced significance particularly for the Bay checkerspot (Weiss et al., 1988, 1993), is the annual variation around these points. For example, plotting the range in population growth potential observed in field studies of the Bay checkerspot, even for populations of the size of several hundred individuals, extends beyond the range of that axis (Table 4.1). Thus, in this deterministic analysis, which assumes a global availability of a fixed amount of suitable habitat, the butterfly falsely appears extinction-proof.

To further understand the comparative sensitivities of these three species, the next logical analysis is to take "slices" through each of the points representing the three species on this surface (Fig. 4.7). By keeping either dispersal or growth potential constant, we can determine the proportion of "critical habitat" required for population persistence. These functions can enable us to evaluate the allocation of management efforts. For example, to estimate the changes in population stability associated with facilitating dispersal (e.g., establishing corridors or practicing translocation) versus increasing growth potential (e.g., adding nest sites or supplemental feeding sites).

We first keep dispersal constant and look at the stability requirements, in terms

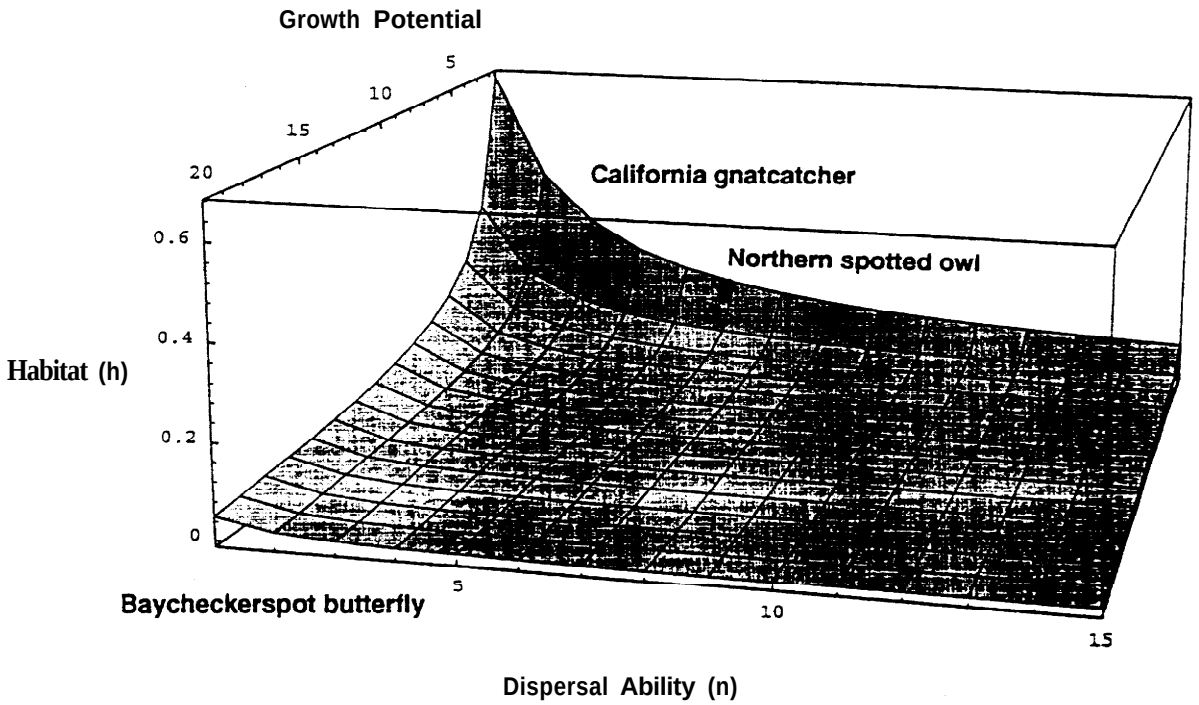

Figure 4.7. Stability response surface for the equilibrium solution to the general metapopulation model. Axes are habitat proportion (h), growth potential [b /(l - s)], and dispersal ability (n). The California gnatcatcher, Bay checkerspot butterfly, and northern spotted owl are plotted on the stability response surface (Fig. 4.1) based on measured demographic parameters.

of h, for the three species (Fig. 4.8). Stable equilibrium points (combinations of *h* and growth potential) lie above a species' curve (Fig. 4.8). The steeper the slope in the region of the biological potential of a species, the larger the marginal gain (greater freedom from risk) associated with an incremental increase in growth potential. Plotting, along the *x* axis, the interval from the mean to the maximum growth potential (Table 4.1) provides additional insights. The maximum value for a parameter represents the upper limit to a management action. By examining the slope of a species' function over this interval, we can estimate the gain in population stability from management actions that increase b or s.

The trade-off between habitat proportion and growth potential required for population stability is similar in all three species (Fig. 4.8). For the California gnatcatcher, growth potential is relatively invariant (Table 4.1). The gnatcatcher therefore cannot compensate for habitat loss by possible increases in growth potential. For the Bay checkerspot, within-population stability is largely independent of increases to its potential fecundity (Table 4.1 and Fig. 4.8). However, reproductive success for this species can range from zero in some years, to well beyond the end of the scale. Successive years of low recruitment therefore could be disastrous. Relative to the other two species, the spotted owl has the greatest potential decline in risk to extinction from habitat loss given its possible increases in growth potential. However, the gain here is also marginal.

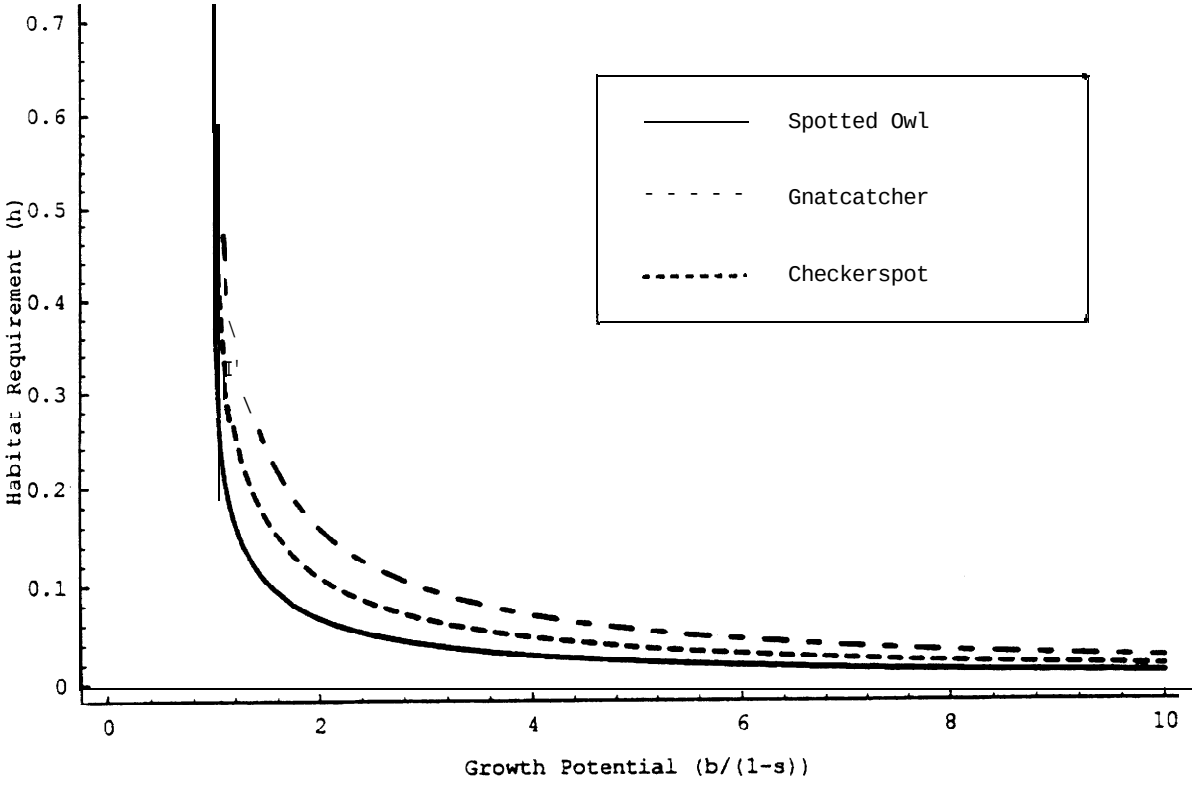

Figure 4.8. Changes in the habitat proportion required for population stability against increases in growth potential, showing the relative sensitivities of the California gnatcatcher, Bay checkerspot butterfly, and northern spotted owl. This figure is based on an orthogonal slice through Figure 4.7; holding dispersal ability constant.

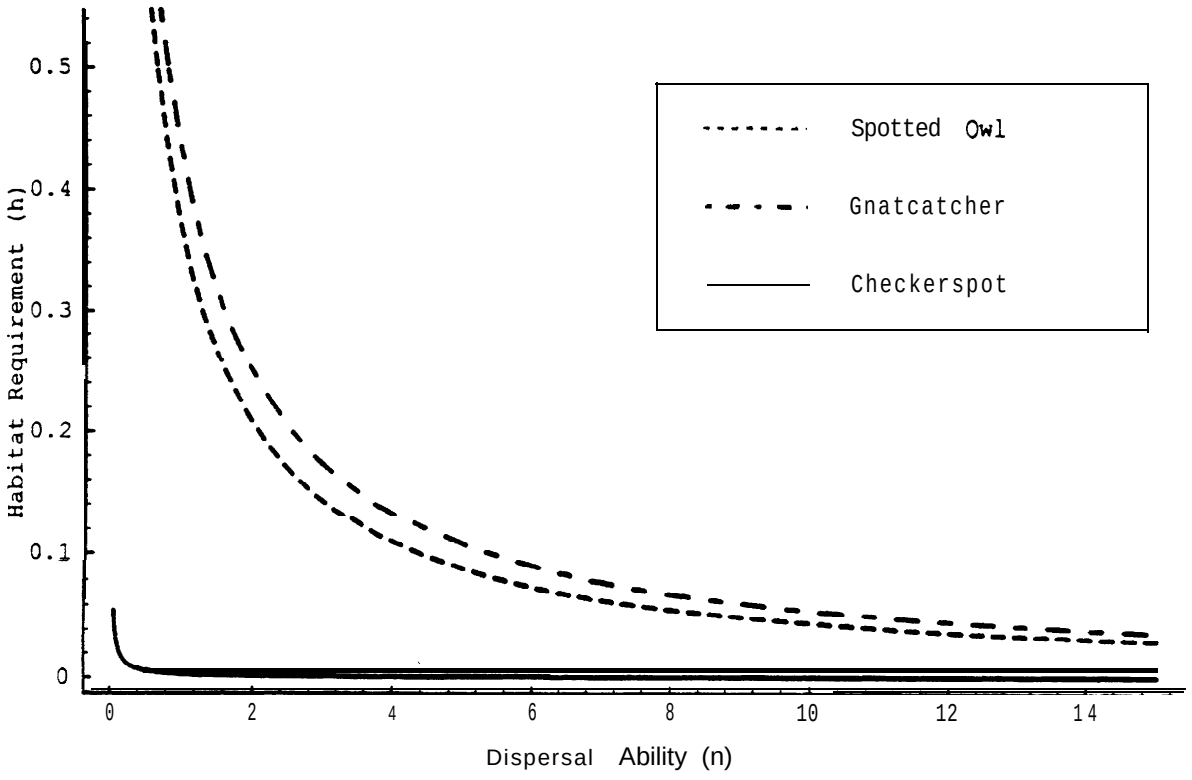

Figure 4.9. Changes in the habitat proportion required for population stability against increases in dispersal ability, showing the relative sensitivities of the California gnatcatcher, Bay checkerspot butterfly, and northern spotted owl. This figure is based on an orthogonal slice through Figure 4.7, holding growth potential constant,

Figure 4.9 shows the trade-off between habitat proportion and dispersal ability required for population stability. At the within-population level, the Bay checkerspot is largely unaffected by changes in dispersal ability. The owl and particularly the gnatcatcher show a greater sensitivity. For these two species, there exists an interval of response in which it is possible to affect population stability by increasing dispersal (Table 4.1). This analysis suggests that specific management actions that increase dispersal success for the two bird species could lead to an important decrease in extinction risk.

Incorporating Between-Population Dynamics

No mathematical differences exist between Lande's (1987) model and our expanded version of Levins' (1970) model, but the biological understanding associated with the model parameters are quite different. The models operate in a strict hierarchical sense both in space and time. Within each local population or reserve, home range (territory) occupancy changes quickly, and vacant sites are recolonized through local recruitment and less frequently by dispersers from other local populations. This is the scale- at which. Lande's (1987) model operates. The likelihood that a given reserve will experience local extinctions is a function of

both the proportion of suitable habitat within the reserve and reserve carrying capacity. The appropriate scales for these dynamics are local and fast.

The proximity and size of other reserves will control recolonization rates and regional population stability. Relative to Lande's model, the appropriate scales for Levins' (1970) are regional and slow. The two temporal and spatial scales- local and fast and regional and slow- and the results of their interactions, collectively determine the overall metapopulation dynamics of the species.

To clarify the trade-offs between within- and among-population dynamics, we used the simulation model of Lamberson et al. (1994). In this model, the metapopulation is composed of a regular array of circular reserves, equal in size and equally spaced, conforming to the original Levins' model. Each reserve, in turn, is composed of a number of breeding sites of which a proportion h are suitable. Individuals first search their local reserve for a suitable breeding site, but if unsuccessful, they leave the reserve and potentially colonize other reserves (Lamberson et al., 1994). To determine $\hat{p}$ for the reserves (eq. [4.2]), we simulated large metapopulations (> 250 reserves) over a long time period (1000 years), counted the reserve transitions: occupied $\rightarrow$ extinct (e) and extinct $\rightarrow$ occupied (m), and computed the ratio (Noon and McKelvey, 1996). We simulated reserves with 10, 20, 30, and 40 sites per reserve and allowed the number of suitable sites per reserve and the distance between the reserves to vary.

On the basis of the Lamberson et al. (1994) model we can examine the trade-offs between the proportion of the landscape that is suitable habitat (landscape level h), the proportion of a given reserve that is suitable habitat (local level h), and local population (reserve) size. In this model, for a fixed reserve size, as the proportion of landscape that is suitable declines, the spacing among reserves increases. The analyses discussed below are for the spotted owl; however, the conceptual insights are applicable to the other species as well.

The curves in Figure 4.10 represent stability boundaries for the spotted owl. For a given reserve size, populations represented by points above the curves are unstable and go to extinction; locations below the curves are stable. None of the metapopulations persists if the proportion of suitable sites within each reserve falls below 30 percent. This is analogous to the steep persistence threshold shown in Fig. 4.6, but with additional uncertainty associated with mate finding (see Lamberson et al., 1994; Lande, 1987). In addition, if all sites are suitable, then reserves containing more than 20 sites are stable regardless of their density on the landscape. Between these two extremes lie diagonal boundaries representing the relative sensitivities of metapopulations to dynamics at the within- and among-population scales.

As the size of individual reserves declines, metapopulation dynamics become sensitive both to changes in internal habitat quality and in reserve spacing. That is, as the amount of suitable habitat within a local reserve is reduced, individuals spend more time moving among reserves and are impacted by among-reserve survival costs. These dynamics may be particularly relevant to the Bay checker-

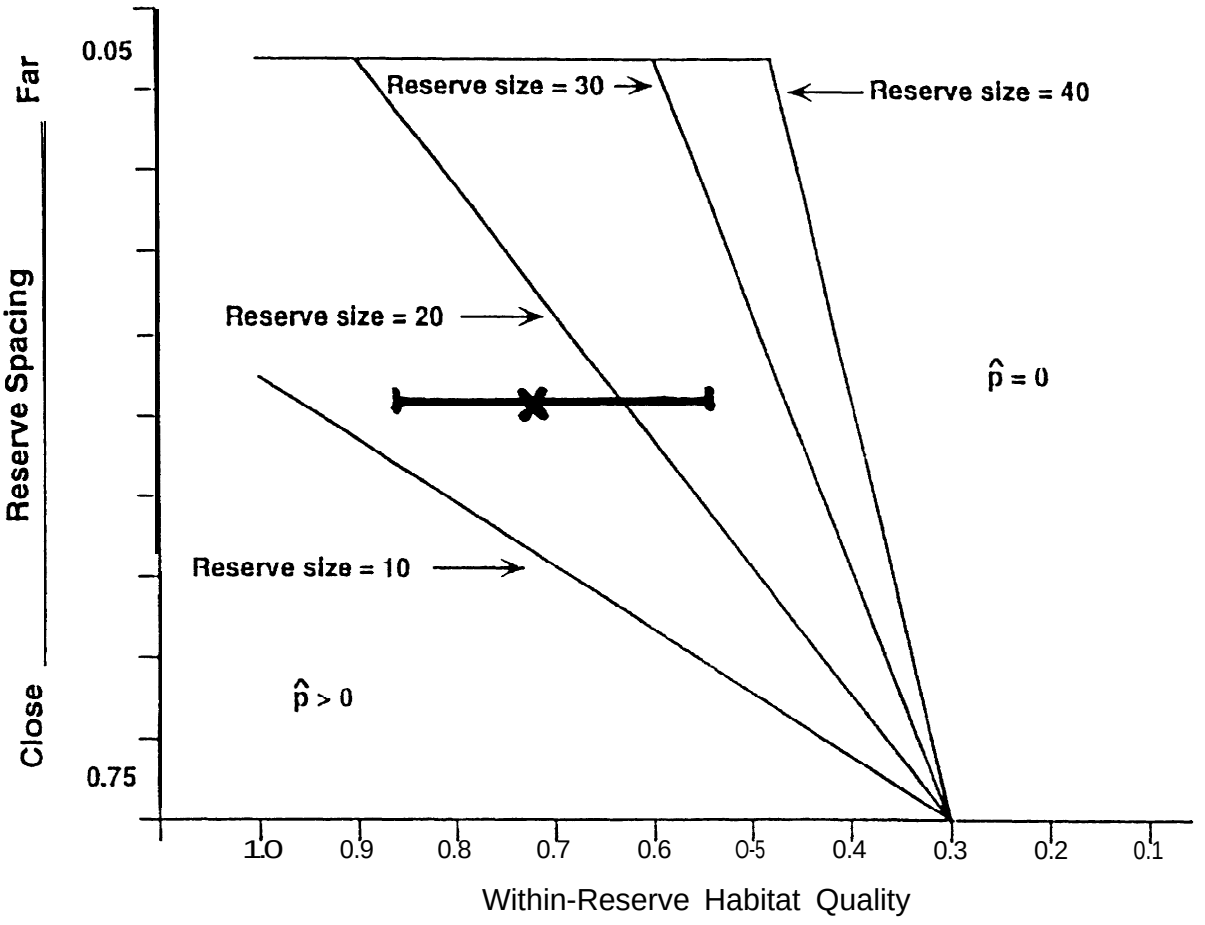

Figure 4.10. Stability response functions based on solutions to the combined individual territory and metapopulation models (Lamberson et al., 1994). Functions illustrate the trade-offs between reserve spacing (proportion of the landscape within reserve boundaries) and within-reserve habitat quality (proportion of sites suitable for colonization) as a function of reserve size. The X in the center of the horizontal bar represents the mean locus of a hypothetical metapopulation. The width of the horizontal bar represents the magnitude of environmental variability in habitat quality. In the deterministic case, if the reserves have 20 or more breeding sites, tie metapopulation is stable, but environmental variation can destabilize it.

spot butterfly. The annual effects of weather on larval hostplants-across microclimatic gradients result in highly variable habitat quality (Weiss et al., 1988, 1993), as is reflected in the demographic values (Table 4.1). The general insight from this result is that even though the boundaries of a reserve are fixed, the habitat quality (h) of the reserve may remain extremely dynamic. Changes in habitat quality and quantity due to environmental stochasticity and catastrophic loss can be portrayed in Fig. 4.10 as a line running parallel to the x axis, For a fixed amount of the landscape in suitable habitat, if the distribution of within-reserve habitat quality is highly variable, a metapopulation which appears to be stable in the deterministic case may follow extinction trajectories a large proportion of the time.

Insights to Multispecies Conservation Planning

The models presented here have been used in the development of single-species conservation plans, most notably for the northern spotted owl. Because of the obvious limitations associated with using single-species plans to protect biological diversity, however, the framework for evaluation needs to be expanded. The first step in multispecies planning is to develop a common analytical framework in which multiple species can be compared. The approach presented here offers a preliminary tool to accomplish this, at least for species with compatible ecologies and life histories. We were able to ordinate different species on a common stability response surface and explore their comparative sensitivities to habitat loss and fragmentation For example, we were able to take slices through that surface and look specifically at marginal gains in reduced extinction risk resulting from incremental increases in fecundity, adult survivorship, or dispersal ability.

Given the impossibility of exploring the threats to persistence for all species, the analyses presented here may help identify those species that are most sensitive to habitat loss and fragmentation, and thus would serve as the best indicators of this type of environmental change. Conversely, it may be possible to determine which species are less likely to be of concern, and thereby potentially reduce the costs incurred by monitoring such species. Furthermore, if a number of species show similar sensitivities to habitat modification, then we could choose to monitor those that are least expensive to study.

The most effective way to protect biological diversity is to protect areas that are large enough to allow the existence of habitat mosaics and the dynamic processes of change within these areas (National Research Council, 1995). For most species, however, details on birth and death rates and dispersal abilities are not and will not be available. So how does one apply the data-intensive methods discussed in this paper to the challenge of multispecies conservation planning? One way is to focus research and monitoring on those species that are both good indicators of habitat change and have large area requirements. Managing habitat in a manner consistent with their persistence may indirectly ensure the persistence of numerous other species with overlapping habitat needs and smaller area requirements.

Our inclusion of the Bay checkerspot butterfly in our multispecies view pointed out a major weakness of our modeling framework. Because of the deterministic structure of the models, the stability of species for which vital rates and habitat quality are both dominated by stochastic environmental factors may be greatly overestimated, Despite this limitation, these models provide a valuable tool to explore the sensitivities to habitat change of multispecies communities and to rankmember species by their sensitivities to change. We believe that the greatest value of the approaches we have outlined will be found in the future in comparative analyses of sympatric species sharing habitats threatened by reduction and fragmentation.

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The Ecological Basis of Conservation

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