Chapter 9

Stability Properties of the Spotted Owl Metapopulation in Southern California

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Spotted owls in the Southern California Province have an insular population structure characterized by large (about 200 pair sites) to small (about 2-4 pair sites) local populations distributed among discrete mountain ranges (fig. 9A, table 9A). The distribution of habitat "islands" is discontinuous across the landscape, reflecting natural discontinuities in vegetation structure and composition, in topographic conditions, and in the effects of extensive human-induced habitat disturbance and fragmentation. Lowland areas surrounding these mountain ranges are primarily desert scrub and chaparral habitats that are unsuitable for spotted owls. Relatively narrow gaps between populations, like the 6-mile separation at Cajon Pass, between the San Gabriel and San Bernardino populations (fig. 9A), are probably not complete barriers to dispersing owls. Longer separations, however, such as that of about 30 miles through the Los Angeles Basin, between populations in the San Bernardino and Santa Ana Mountains (fig. 9A), may present significant survival risks to dispersing owls such that successful colonization is very unlikely. The degree to which these gaps act to severely reduce or eliminate demographic rescue between populations is unknown. To date, however, no banded spotted owl has been located within any population outside that of its origin (LaHaye pers. comm.). The most significant gaps between owl populations are discussed in table 3K and shown on a distribution map in that chapter (fig. 3A).

Even within many of the mountain ranges, the distributions of habitat and owl sites are discontinuous. For example, in the Cleveland and Los Padres National Forests (NFs), most suitable spotted owl habitat is patchily distributed because it is resticted to deeply dissected canyons dominated by oaks and surrounded

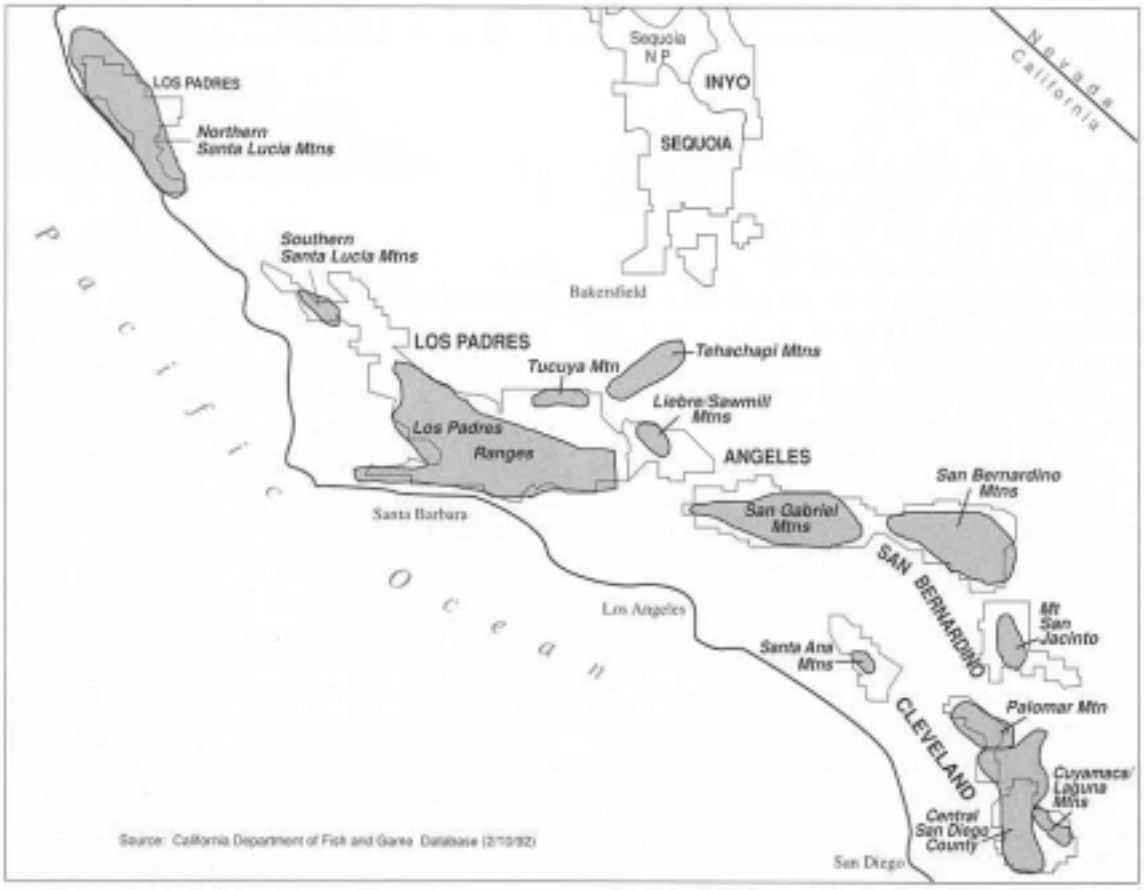


Figure 9A-"Island" populations that comprise the southern California metapopulation of spotted owls. Estimated numbers of owl sites for each "island" are given in table 9A.

Table 9A-*Owl sites,[1] pairs and status of pairs on these sites, and nearest neighbor distances of California spotted owl populations in southern California (from Stephenson 1991 and Chapter 3). Compare values tabled here with the locations of these areas, shown in figure 9A.*

Area	Owl sites (all years)	Pairs since 1987	Breeding since 1987	Potential population[2] (no. sites)	Nearest neighbor distances[3]
San Diego Ranges	37	18	6	76	18 - 33 miles
Palomar Mountain	(18)				
Central San Diego County	(9)				
Cuyamaca/Laguna Mountains	(10)				
Santa Ana Mountains	2	1	-	12	30 - 40 miles
San Jacinto Ranges	20	16	9	29	11 - 18 miles
San Bernardino Mountains	124	114	66	125	6 - 11 miles
San Gabriel Mountains	54	22	5	95	6 - 20 miles
Liebre/Sawmill Mountains	14	10	2	20	12 - 20 miles
Tehachapi Mountains	4	0	-	12	unknown
Tecuya Mountain area	5	3	-	10	9 - 12 miles
Los Padres Ranges	65	32	17	100	8 - 12 miles
So. Santa Lucia Mountains	12	6	2	19	32 - 45 miles
No. Santa Lucia Mountains	39	22	1	80	45 miles
Southern Monterey	(14)				
Northern Monterey	(25)				
Total	**376**	**244**	**108**	**578**	

[1] See glossary in Appendix B for a definition of "owl site."
[2] If each site were assumed capable of supporting a pair, the total population would be the number of sites times 2.
[3] Where two distance values are shown (that is, 12-20 miles), they represent the distances to the two closest neighboring populations.

by unsuitable chaparral habitat. Thus, many of these populations have an insular structure at both landscape and local scales. The present modeling study was prompted by the need for a better understanding of the potential effects on population persistence of isolation between subpopulations, and changes in habitat continuity within otherwise continuous habitat islands.

Although spotted owl records in southern California exist from the early part of this century (Stephens 1902, Clay 1911), careful population studies are recent. LaHaye et al. (1992) have studied the demography of the owl population in the San Bernardino Mountains, and Gutiérrez and Pritchard (1990) reported on surveys done on Mt. San Jacinto and Palomar Mountain. In addition, infrequent surveys in NF lands provide a cumulative record of spotted owl locations outside of these study areas (Gould et al. 1987, Stephenson 1991).

The largest population occupies the San Bernardino Mountains (about 124 owl sites), with considerably smaller populations in the other ranges (table 3H). The cumulative total number of known owl sites within the southern California "archipelago" is estimated at 376 (table 9A), with an approximate population of 300-350 pairs at any point in time. The population trend is known for only one location. During the interval 1987-91, the resident, territorial population in the San Bernardino Mountain study area declined by about 17 percent per year (LaHaye et al. 1992; Chapter 8). If this rate of decline were to continue, the territorial population would decline by 50 percent in about 4 years.

Based on theory and limited empirical data (reviewed in Gilpin and Hanski 1991), we believe the ultimate stability of this metapopulation will depend upon several factors. These include the persistence of one or more populations large enough to escape the negative effects of demographic and environmental stochasticity, and with demographic characteristics resulting in a production of excess individuals to serve as potential colonists for other local populations. Many of the small, isolated populations that occur in southern California are probably maintained by occasional immigration from these more productive source areas (see Pulliam 1988 and Howe et al. 1991 for a discussion of source-sink dynamics). In addition, given a high likelihood of significant environmental variation (for example, wildfires, prolonged periods of drought, or rapid urbanization) at least two source populations will be needed, and they should be sufficiently separated to minimize the likelihood of their simultaneously experiencing negative perturbations.

The human population in southern California continues to expand into the forested mountain habitats of the spotted owl. In the San Bernardino Mountains, for example, the human population has grown from about 19,000 in 1970 to over 40,000 in 1992, with 5 million annual visitors (Dib and Griffone 1991). Accompanying this growth is a reduction in the quality and

amount of forested habitat for spotted owls-a consequence of urbanization, highways and smaller roads, and recreational developments. Although we lack earlier estimates of spotted owl population sizes or densities, we nonetheless consider it likely that spotted owls have declined in both number and distribution from historic levels.

Given the metapopulation structure of the southern California spotted owl population, recent declines within the largest and most contiguous population in the region, and significant threats to loss of suitable habitat due to rapid human population growth, we believe that a specific conservation strategy is warranted for the subspecies in this part of its range.

This chapter has two main purposes: to explore, in a general sense, the stability properties of the southern California metapopulation structure, and to make specific recommendations for conservation of the subspecies in this part of its range. Toward this end, we make frequent reference to pertinent population theory and use results of simulation models to explore conservation alternatives. Our goal was not to estimate extinction likelihoods-we believe it is premature to conduct such analyses at this time. Currently, the only estimate of population change from this region suggests a rapid decline in the territorial population (Chapter 8). Under a strict assumption of constancy in the vital rates, projecting forward at this rate shows a rapid decline to extinction. Until more is known about natural fluctuations in vital rates of populations, however, such projections are unwarranted.

Rather, our goal was to explore the geometry of the metapopulation, including both habitat and owls, to gain insights into what spatial arrangement of habitat would minimize future extinction risks. In this chapter we present the results of our efforts to integrate, in the form of computer simulation models, the species demography with variations in the amount, distribution, and quality of owl habitat. The computer simulation models were developed specifically to aid the development of a conservation plan for spotted owls (Thomas et al. 1990, appendix M; Lamberson et al. in press; McKelvey et al. in press). We used the results of computer simulations to test basic principles of reserve design (Murphy and Noon 1992) and to provide guidance about the necessary spatial design of a reserve system implemented on real landscapes.

Methods

Parameter estimates and model structure were based on information from the study of marked populations (LaHaye et al. 1992; Chapter 8). Owls were captured during the breeding season, aged, sexed, and individually marked. Reproductive status was determined for all individuals using methods outlined by Forsman (1983). Young were counted after fledging had occurred (that is, after they left the nest). Individuals were initially placed into four age classes (juvenile, first-year subadult, second-year subadult, adult) according to criteria developed by Moen et al. (1991). Because of similarity in survival rates, first- and second-year subadults were pooled with adults and collapsed into a single stage. Annual survival rates for banded juveniles, subadults, and adults were calculated using Jolly-Seber capture-recapture models for open populations (Jolly 1965, Seber 1965) using program JOLLY (Pollock et al. 1990).

The estimate of fecundity combines two important components-the number of females fledged per nest and the proportion of females ≥2 years of age that breed. Thus, "adult" refers to ages subsequent to the second year of life. Fecundity was estimated each year as the mean number of young fledged per pair, assuming a 1:1 sex ratio at birth. Within the adult age class, survival rate was assumed to be constant, and we assumed no reproductive senescence. For our simulation models, we divided the population into three stages juveniles, subadults, and adults. Time was expressed on an interbirth interval of 1 year, and we assumed an age at first reproduction of 2 years (that is, birds just beginning their third year of life).

Lambda (λ), the estimated annual, finite rate of population change from the San Bernardino study was 0.827 (table 8G), indicating that the territorial population there was in precipitous decline. Because λ represents a simple exponential rate of change, using the vital rates estimated from this study to project future populations would be a trivial exercise. All populations would decline exponentially regardless of the amount and distribution of suitable habitat. To evaluate possible effects of variation in landscape geometry, we initially adjusted the survival rates by multiplying them by $1/\lambda$ to yield a λ=1.0 in suitable habitat. A11 demographic rates were again slightly increased to allow for the possibility of a 2 percent annual rate of population growth (λ = 1.02). This scaling of the survival rates allowed for a growing (source) population in suitable habitat. Differences in model results based on the landscape model (see below) would, therefore, reflect the effect of differences in distribution and amount of suitable habitat, and not an assumption of depressed demographic rates. Based on current field studies (Chapter 8), however, the adjustments we made to the demographic rates for suitable habitat were optimistic.

Dynamic Projection Models

No natural population is exposed to purely deterministic forces. Thus, population dynamics of the spotted owl should be examined relative to both demographic and environmental stochasticity. Further, simple deterministic analyses are also limited in that they provide no insight into the dynamics of mobile populations in real landscapes. That is, they incorporate no information on the movement behavior of animals in heterogeneous environments and the uncertainties of finding suitable habitat and mates. Failure to account for the spatial component

of both animal locations and their habitat distributions ignores the covariance between demographic rates and habitat variation.

A conservation strategy for any species is ultimately described by a map that integrates information on the species' distribution; the distribution of current and potentially suitable habitat; and economic, political, and legal constraints (Thomas et al. 1990; Murphy and Noon 1992). To develop a general set of conservation recommendations for the southern populations of the California spotted owl, we needed insights into how the landscape-scale arrangement of owls and their habitat affected their population dynamics. The data available to us lacked detail and were imprecise (see Chapter 3). As a result, we could explore the effects of landscape geometry and variation in the distribution of habitat types only in a nonspecific way, and make general recommendations about the significance of different components of the landscape.

To provide a framework to guide the conservation evaluation of the California spotted owl, we drew general inferences from several simulation models incorporating various degrees of spatial information. Our approach, which investigated the effects of variable dispersal efficiencies on the population dynamics of territorial animals occupying heterogeneous landscapes, had its foundation in previous work by Lande (1987, 1988). Lande's model was based on a hypothetical species with a monogamous, territorial breeding system and with obligate juvenile dispersal from the natal area. This model was directly applicable to the life history structure of the spotted owl.

Nonexplicit Spatial Models

In the following, we briefly review the structure and assumptions of two models used to assist in the design of a reserve strategy for the northern spotted owl (see Thomas et al. 1990, appendix M). We do not discuss these models exhaustively but simply make reference to results from those models that are most applicable to the conservation of spotted owls in southern California. Additional details can be found in Thomas et al. (1990, appendix M), Lamberson et al. (in press) and McKelvey et al. (in press).

The Individual-Territory Model

Model Description

This model (Lamberson et al. in press) extended that of Lande (1987) by relaxing the assumption of demographic equilibrium and allowing the simulated landscape to be dynamic. Life history was expressed as a three-stage, two-sex projection model. The model assumes that all newly fledged juveniles disperse, and that adult birds who experience loss of their territory (for example, due to logging) also disperse. Lande's model allowed some likelihood of a juvenile's inheriting its natal territory. Based on the settling patterns of owls first banded as juveniles, however, inheritance of the natal site is a very rare event. Our model focuses on a landscape with a fixed spatial extent and with a fixed number of potential territories (or "sites"). Sites were either suitable for survival, mate attraction, and reproduction, or they were unsuitable. Only the suitable sites were capable of being occupied. The key response variable in our model is the occupancy rate of sites by pairs. As in Lande's model, this model lacks realism because of the global nature of juvenile and adult search-all cells had an equal likelihood of being sampled.

The search process was simulated as sampling with replacement. The key equation describing search success in our model (see Lande 1987) was

$$\Pr(\text{success}) = 1 - (1 - \text{unoccupied suitable sites/total sites})^{m}, \quad (1)$$

where m is the number of sites that can be searched prior to mortality (additional equations describing the model dynamics are given in Lamberson et al. [in press]).

A nesting pair will annually produce young (according to a deterministic or stochastic likelihood), and these will disperse at the end of the season, the males seeking an unoccupied site and the females seeking a site occupied by a solitary male. Dispersal success is density-dependent, calculated by assuming random search of accessible sites. Search capabilities, together with the occupancy ratio of searched sites, determines the bird's potential for successful dispersal (consistent with Lande 1987).

Relevant Model Results

The most significant conclusions from Lande (1987) and Lamberson et al. (in press) are (1) that the occupancy of suitable habitat declines with a declining proportion of the landscape that is suitable habitat (fig. 9B), and (2) that if the amount of suitable habitat declines below some threshold value, the population will become extinct (fig. 9C, curve A). That is, because of uncertain-

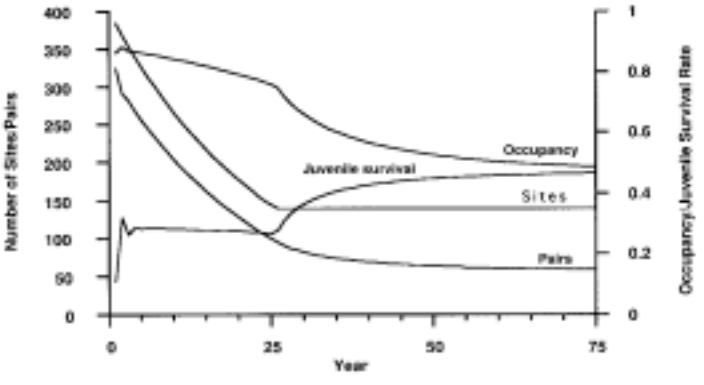


Figure 9B-Trend in the number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. The simulation assumed that 4 percent of the suitable owl habitat was lost per year until 14 percent remained, and that juvenile owls could search 20 sites.

ties associated with search and mate finding, a species can be critically habitat-limited even in the presence of suitable but unoccupied habitat.

New findings, beyond those reported by Lande (1987), resulted from the model of Lamberson et al. (in press), because of its dynamic and nonequilibrium nature. First, survival probability, as a function of the percent of suitable habitat, is affected by environmental variation. Once again the deterministic case shows a stairstep function, with the jump from 0 to 1 occurring at the threshold point (fig. 9C, curve A). Adding environmental variance makes the extinction threshold less abrupt (fig. 9C, curves B and C). Second, in a scenario involving incremental loss of suitable habitat (for example, by logging), the crowding of older owls into remaining suitable habitat is likely to produce temporarily high occupancy rates-much higher than expected under long-term stable conditions (fig. 9B). Thus, predicting long-term population status from short-term occupancy data can be very misleading.

The Territory-Cluster Model

The primary limitation of the individual-territory model was the global nature of search. In reality, organisms search locally and are primarily influenced by the local nature of the landscape rather than its global condition. The basis of the territory-cluster model (Thomas et al. 1990, appendix M; Lamberson and Noon 1992) is a fixed, rectangular array of circular clusters containing a variable number of owl sites (territories). Every site within a cluster, assumed to be of identical size, was either suitable or unsuitable (defined as in the individual-territory model). Clusters could be either totally or partially suitable-the carrying capacity of a cluster equalled the number of suitable sites. For a given simulation, all clusters were the same size (that is, they contained the same number of sites). As in the individual-territory model and Lande (1987), the response variable was the proportion of suitable sites occupied at any point in time.

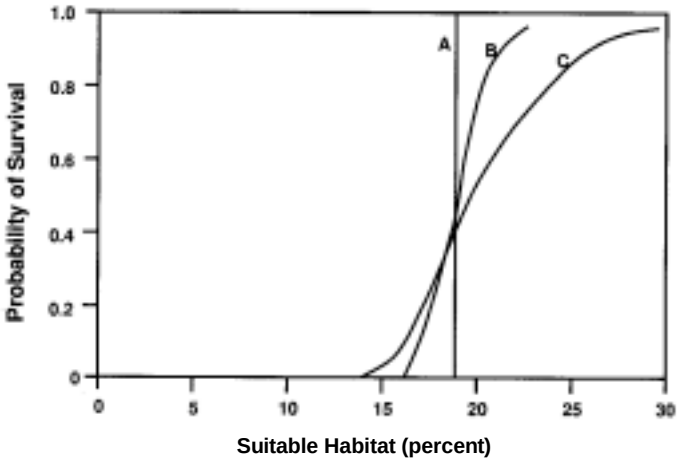


Figure 9C-The 250-year survival probability in relation to the percentage of suitable sites in the landscape. Curves A, B, and C represent the conditions of no, low, and high environmental variability, respectively.

The matrix between clusters was assumed to be entirely unsuitable for owl sites. Assuming a constant percentage of the habitat as potentially suitable Habitat and restricting the habitat to clusters had two important consequences: (1) as cluster size increased, the distance between adjacent clusters increased predictably (fig. 9D); and (2) the dispersal angle between adjacent clusters (see fig. 9E), and the probability of selecting this angle, were independent of cluster size.

The landscape simulated by the model had a "wrap-around" structure to exclude possible anomalous results that might arise from edge effects. The clusters on the right side of the grid were treated within the model just as though they were immediately to the left of those on the left side of the grid. The top and bottom rows of clusters were treated in a similar manner.

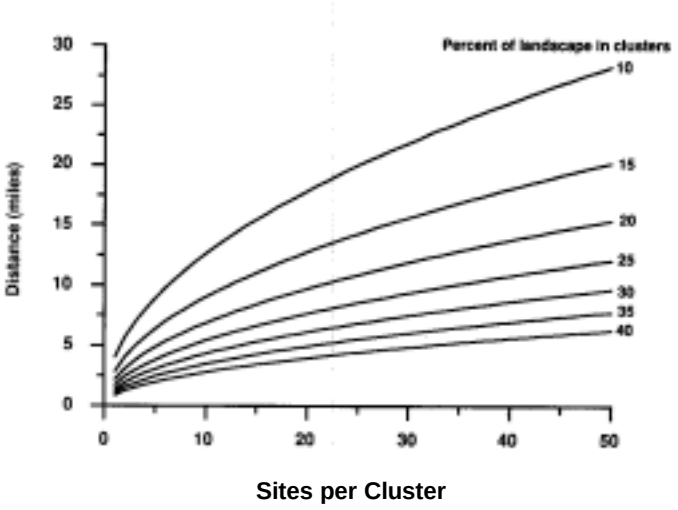
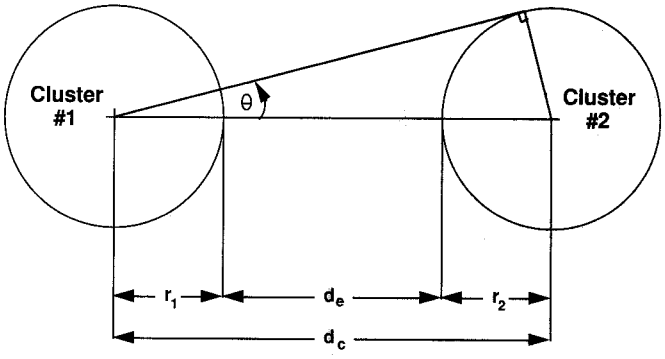


Figure 9D-Nearest-neighbor distance between clusters in relation to cluster size. Each curve represents a different percentage of the landscape assumed to be suitable habitat and located in the clusters.



P_r (disperse from Cluster 1 to Cluster 2) = 2θ/360

$$\theta = \arctan \frac{r_2}{\sqrt{d_c^2 - r_2^2}}$$

Figure 9E-Method of estimating the angle of intersection between two adjacent clusters in the cluster model. The probability of dispersing in the correct direction is a function of the combined angles of intersection of the six neighboring clusters.

The life history was expressed as a three-stage, female-only projection model. Initial values of the vital rates were based on table 8G, and survival rates were scaled by multiplying by 1/0.827 to provide for a stable local population in suitable habitat. Based on observations of recently fledged young near the nest site (Marcot and Holthausen 1987), a predispersal survival component of 0.6 was assumed for the juvenile survival rate. The dispersal component of first year survival arose from properties of search efficiency and landscape pattern, thus allowing the possibility of a growing population. Fecundity was treated stochastically, based on good years and bad years for reproduction, with expected values equal to field data (table 8G). We assumed complete spatial autocorrelation for the reproductive pulses.

Dispersal Dynamics

As in Doak's (1989) model, our model distinguished between dispersal within and among clusters. All clusters were equally accessible in Doak's model, but we introduced the additional reality that search was spatially constrained and was, therefore, affected by the status of neighboring clusters. Within-cluster dispersal in our model was identical to the individual-territory model, with each dispersing owl allowed to sample with replacement a given number, *m*, of sites within the cluster (equation 1). To determine the allocation of search effort within a cluster, we assumed a random walk from a random starting point. By simulation, we estimated the expected number of steps taken by a dispersing bird before it crossed the boundary of a circular cluster. The assumption was that an owl could traverse one site in a single time step. Based on 10,000 simulations of circular clusters of various sizes, and regressing the number of steps taken before crossing the circle, we estimated the following relationship:

$$\text{Expected}(m) = 0.41 * \text{number of sites in the cluster.} \quad (2)$$

For clusters with 20 sites, for example, an average of eight sites were searched within clusters before crossing the boundary into the matrix between clusters. The total number of searches across all clusters (m = 22) was based on the upper bound of the 90th percentile of the maximum dispersal distance of 56 radio-tagged juvenile spotted owls (Thomas et al. 1990, p. 305) and the assumption that each site had a diameter of about 2 miles.

If a dispersing juvenile did not find a suitable site within its natal cluster (based on a fixed number of searches), it was forced to disperse between clusters. Between-cluster dispersal was modeled as a straight-line path moving away from the natal cluster at a random azimuth. Two sources of mortality were encountered. First, the bird must move in a direction that would intersect a neighboring cluster. The probability of intersection for each adjacent cluster was governed by the following equation (see fig. 9E):

$$\text{Probability(disperse from cluster 1 to cluster 2)} = 2\theta/360 \quad (3)$$

$$\text{where } \theta = \text{arctangent}\left(r_2 / \sqrt{d_c^2 - r_2^2}\right)$$

Second, if a correct direction was chosen, the likelihood of successful travel to the neighboring cluster lying a distance d miles away (measured edge-to-edge) was modeled by a declining exponential,

$$\Pr(\text{survive to } d) = \exp(-kd) \quad (4)$$

The value of k was estimated by arranging the maximum straight-line distances attained by the 56 radio-tagged juvenile owls in rank order, then regressing the natural log of the cumulative proportion represented by that distance (dependent variable) on the associated distance and forcing the regression through 0 (r^2 = 0.97) (see fig. 4F). Because search begins in the natal cluster and moves through adjacent clusters, the search success in this model, as in nature, is a function of the condition of the landscape near to the bird's natal site.

Model Parallels to the Southern California Metapopulation

The structure of the cluster model crudely approximates aspects of the southern California spotted owl habitat distribution (fig. 9A). Clusters can be considered analagous to local habitat islands, and gaps between local populations are analagous to the matrix-areas that allow dispersal (with inevitable survival risks) but no reproduction. Model results allowed us to make general inferences to (1) the relation between cluster size and local population stability, (2) the effects of variable spacing among clusters on mean pair occupancy, and (3) the most efficient ways to allocate lands to a reserve design.

Relevant Model Results

Because the number of combinations of model parameters is immense, many sensitivity analyses were done (table 9B). The most significant result, however, was based on the relation between mean pair occupancy and cluster size. For a simulation with 60 percent of the sites suitable within a cluster, occupancy did not stabilize until clusters held at least 15 sites (fig. 9F).

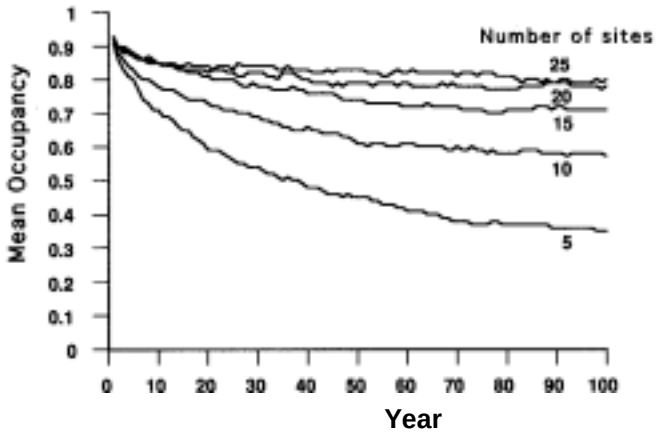


Figure 9F-Mean proportion of cluster occupied in relation to time, based on a 100-year simulation. The number of sites per cluster varied from 5 to 25, and 60 percent were assumed suitable; 35 percent of the landscape was in clusters.

Clusters of 15 sites stabilized at about 70 percent occupancy, while clusters of >20 sites stabilized at about 80 percent, a figure representing nearly full occupancy given adult survival rates. Further increases in cluster size had little effect on occupancy. As the number of suitable sites within a cluster increased, the marginal difference in occupancy among clusters of different sizes became less pronounced.

Based on the relation between the landscape fraction within clusters (habitat islands) and cluster spacing (fig. 9D), different levels of allocation to a reserve system can be viewed in terms of the distance between clusters. We found mean occupancy rate to be strongly affected by increased spacing between clusters for cluster sizes <20 sites (fig. 9G). In contrast, clusters with >25 sites showed minimal distance effects beyond separations of about 20 miles (fig. 9G). Adding low levels of environmental variation in survival rates lowered occupancy rates about 7 percent and suggested slightly larger cluster sizes for the same level of occupancy (fig. 9H).

An alternative approach to choosing an optimal cluster size is to estimate the expected number of owls occupying a fixed amount of suitable habitat. Based on mean occupancies at 100 years from fig. 9F, the efficiency of land use is clearly higher for larger clusters (fig. 9I).

Inferences to Reserve Design from the Nonexplicit Spatial Models

Results from these models suggest that providing for clusters of territories should increase the persistence likelihood of spotted owls, primarily by facilitating juvenile dispersal (compare Doak 1989). If habitat becomes too diffuse at a local scale, populations there will experience extinction events and require recruitment from larger source areas for recolonization (the "rescue effect"). Given assumptions of the cluster model (≥60 percent of sites suitable, moderate connectivity among adjacent clusters), clusters with >20 sites should provide for locally stable populations in the absence of catastophic disturbance. Adding moderate levels of environmental variation in the survival rates, however, raises the desired minimum cluster size to about 25 sites.

Once clusters reach about 35-45 sites, they attain high levels of local stability and become relatively independent of the distance to their nearest neighbor. Within the structure of our model, this occurred because almost all dispersing juveniles found suitable sites within their natal cluster. Given a fixed number of total searches (m = 22), and the allocation of within cluster search following equation 2, all search is expended within

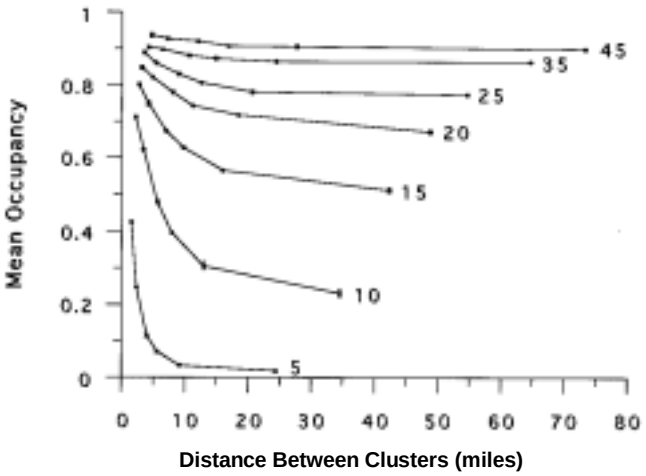


Figure 9G-Mean proportion of clusters occupied as a function of the distance between clusters. The number of sites per cluster varied from 5 to 45, and 60 percent were assumed to be suitable.

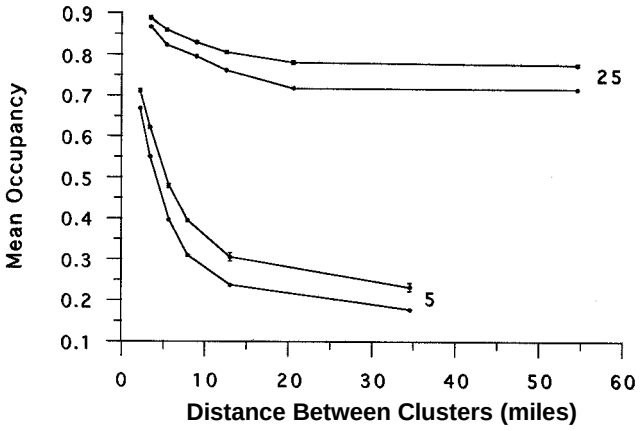


Figure 9H-Mean proportion of clusters occupied as a function of distance between clusters. The number of sites per cluster was either 5 or 25, and 60 percent were assumed to be suitable. The lower curve of each pair represents simulations including environmental variation in survival rates.

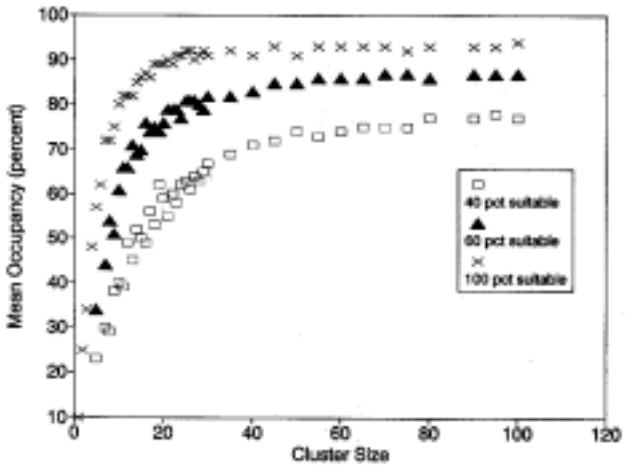


Figure 9I-Steady-state mean occupancy rate in relation to cluster size. The curves represent 40, 60, and 100 percent of the sites within each cluster as suitable habitat.

Table 9B--*Qualitative results of sensitivity analyses for the territory cluster model.*

Factor varied	Sensitivity[1]
Within-cluster search efficiency	Low for large clusters; high for small clusters
Resistance to between-cluster dispersal	Low for large clusters; high for small clusters
Search time outside of natal cluster	Low to moderate for large clusters; high for small clusters
Initial population size	Low if population was in large clusters; high if population was in small clus ters

[1] Measured in terms of reduction in mean pair occupancy.

the natal cluster when cluster size equals 54 sites. At this point in our model, all clusters are acting as independent subpopulations.

Comparing these general model inferences to estimates of the number of sites in various habitat islands in the Southern California Province (table 9A) provides some significant insights. Based on current estimates of owl sites, many of these habitat islands have <25 sites, are isolated by >10 miles, and are therefore expected to be very unstable. That is, they will be subject to extinction events because of both demographic and environmental variation, or act as sink areas (Pulliam 1988). As such, their occupancy status will depend largely upon immigration from neighboring habitat islands. The possible dependence of these populations on immigration from larger source populations parallels results for insular populations of acorn woodpeckers in the southwestern United States (Stacey and Taper 1992), and red-cockaded woodpeckers in the southern Appalachian mountains (Conner pers. comm.).

The cluster model had several optimistic assumptions. Most important were that (1) no uncertainty was associated with mate finding, (2) only low levels of environmental variation in vital rates were simulated, and (3) clusters were assumed to be circular, thus minimizing the perimeter:area ratio. A circular shape (1) maximizes the density of suitable habitat and, given our within-cluster search algorithm, suggests very high search efficiencies; and (2) it affects the estimate of the probability of leaving the natal cluster in an appropriate direction. For both stability of mean occupancy and to achieve a specified occupancy rate, relaxing these assumptions would generally require larger cluster sizes.

A Spatially Explicit Landscape Model

The landscape model links an organism's survival and reproduction explicitly to its current habitat location. In reality, habitats range in quality from those that support demographic rates resulting in a net gain of births over deaths (source areas) to those that yield a net loss (sink areas). The latter habitats would be unoccupied in the absence of immigration from source areas. As Pulliam (1988) has argued, it may be that habitat-specific demographic rates are more important than age-specific rates to a species' long-term population dynamics. In this model, a population's rates of survival and fecundity will vary based on landscape configuration and the distribution of habitat types. The model, a two-sex, single-organism simulator, assumes that each organism must search the landscape to find new territories and mates. Each organism is born, moves, attempts to find a mate and breed, and dies. This format allows the behavior of each individual to be simulated by following a series of probabilistic rules.

Male and female behavior in this model is similar to that in the territory-cluster model. Males search for territories to occupy. If they find a suitable nest site, they stop moving and become territorial. The likelihood of settling in a given site is a function of the habitat quality of that site. Males remain on their selected site until they die or the site becomes unsuitable for nesting. If the site becomes unsuitable, the males become nonterritorial and reinitiate search. Females are born and disperse from the natal site to seek unpaired, territorial males. When they find a territorial male, they obligately pair. Once paired, females remain on site until they die or the site becomes unsuitable for nesting.

Paired individuals split up when one member of the pair dies, or the site becomes unsuitable for nesting. If the female dies, the male remains territorial and stays on site. If the male dies, the female has no site fidelity and will initiate search for a new mate. If the site becomes unsuitable for nesting, both members search independently for a new site. The movement of females after loss of their mate is supported by field data. In general, females move more often then males, occasionally leaving sites to search for new mates even when their previous mates are still alive.

In the landscape model, by contrast with the previous two models, if a juvenile fails to locate an unoccupied, suitable site it does not die-rather, it becomes a floater. As a consequence, search efficiency has less of a direct effect on juvenile survival rate, but a strong effect on the dynamic movement between the reproductive and nonreproductive stages. To the extent that search inefficiency prevents pair formation, fecundity declines and λ decreases accordingly.

Demographics

All demographic parameters are linked to site quality. Individual mortality and fecundity are determined by the quality of the site occupied at the beginning of each time-step. In keeping with the stage-structured approach, risks are assumed to be constant within a stage over the course of a year. The year is divided into *i* time-steps, and the risk per step for an owl in stage-class *j* occupying habitat type *k* is defined as the *i*th root of the yearly risk for class *j* and habitat type *k*.

In the model analyses described below, we allow a maximum of three habitat types: (1) suitable habitat with associated vital rates from table 8G, initially scaled by $1/\lambda$ to provide for a stable or growing population; (2) sink habitat with reproduction and survival below that needed for a stable population; and (3) unsuitable habitat that allows survival at reduced rates, but no reproduction. The model structure will support additional categories of habitat quality, but available data do not support this degree of resolution.

Movement

The map is divided into a fixed array of grid cells, each representing one territory-sized unit. The grid is hexagonal to allow more realistic movement. The rate of movement depends on the size of the grid cell and the number of time-steps per year. Individual moves are restricted to adjacent cells. The mobile classes of the owl (nonterritorial males and females) have an opportunity to move at each time-step. To ensure that certain birds or areas of the map are not given preferential access to open territories or mates, the order of movement is fully randomized at each time-step.

In its simplest implementation, movement is a random walk. The model, however, allows owls to search with "intelligence"; that is, they may favor movement through good habitat and avoid poor habitat. Similarly, females may move obligately to known territorial males, and nonterritorial males may be averse to crossing into defended territories. This intelligent behavior is modeled by giving the owls absolute knowledge of the quality of the cell they occupy and partial knowledge of adjacent cells. They have no knowledge of more distant parts of the landscape. This knowledge takes the form of a series of switches and weighting factors that condition the probability of movement (table 9C).

Three boundary conditions can be specified at the map edges: absorbing, reflecting, and wrap-around. In addition, internal reflecting zones can be created by specifying a land type for which the owls show complete aversion.

Fledglings

Fledglings are defined for model purposes as young that survive to disperse. We assume both good and bad years for fledging and complete correlation in reproductive pulses among populations. If it is a good year, then the pair produces fledglings according to a beta random variable ranging from zero to the maximum clutch size. Two levels occur at which variability can affect the number of fledglings. If the area under the beta distribution is concentrated around the mean clutch size, the population will pulse based on the frequency of good years. When a good year occurs, all pairs at all sites will produce at about the mean number of fledglings. If the probability of a good year is 1.0, variability in the number of fledglings will occur on an individual-territory basis and will depend on the parameters of the beta distribution. Both parameters are linked explicitly to habitat quality and the stage-class of the pair. Because this is a two-sex model, the sex ratio of fledglings is also adjustable.

Relevant Inferences to the Southern California Metapopulation

Effects of Cluster Shape

The cluster model assumed circular clusters, but the landscape models allowed us to closely specify the shapes of clusters

Table 9C -*A summary* of *factors that can affect an individual's movement in the landscape model.*

Factor	Based on	Sex	Form
Becomes territorial	Habitat quality/occupancy	M	Probabilistic switch
Aversion	Habitat quality	M/F	Weighted probability
Site fidelity	Habitat quality	M/F	Weighted probability
Linear propensity	Behavior	M/F	Weighted probability
Territorial aversion	Occupancy	M	Weighted probability
Female finds male (current cell)	Occupancy	F	Absolute switch
Female finds male (adjacent cell)	Occupancy	F	Probabilistic switch
Global boundary	-	M/F	

(habitat islands). To compare general model results between the two models, the landscape model was used to project population trends from a number of hypothetical landscapes with an identical number of suitable sites (McKelvey et al. in press). Other than suitable habitat configuration, there were no differences in the initial values of any model parameters. The map boundaries were wrap-around so that the exact location of the habitat within the map frame was unimportant. In these simulations, only two habitat qualities were simulated: habitat suitable ($\lambda = 1.0$) and unsuitable for nesting. The movement parameters deviated only slightly from a random walk-birds were twice as likely to choose suitable habitat, males treated occupied habitats identical to unsuitable habitat, and birds were twice as likely to move in the same direction as to choose a different direction.

Model results parallel the territory-cluster model, showing that a clustering of suitable habitat is both more efficient in terms of mean population level and more stable in terms of lowered extinction probabilities than is a random structure. We found, however, that the shape of the cluster had an important effect on its stability properties and mean occupancy rates. A cluster with a low ratio of edge to area supported a larger population and was more stable than continuous clusters of identical area but with greater irregularity (compare figs. 9J and 9K). A high edge-to-area ratio had a negative impact on demographic stability: the rate of decline in a large, highly irregular cluster was similar to the decline rate of the dispersed cluster system, but it had a lower extinction likelihood.

Source-Sink Dynamics

Previous results demonstrated the impact of reserve shape when each landscape cell was either suitable or unsuitable for breeding. In that case, the breeding population was limited entirely to the suitable habitat. In a landscape containing a gradient of habitat qualities, source locations would produce an excess of individuals, and sink locations would absorb some of the dispersing juveniles from the sources. Consequently, when a possibility exists of nesting in sink locations, populations will occur exterior to the source habitat areas even though vital rates in the sinks do not allow for a self-supporting population (see similar conclusion in Buechner 1987, p. 71). The presence of sink areas adjacent to habitat clusters may adversely affect the stability properties of the clusters. In our simulations, the mean population size of the entire landscape was higher in the source-sink system, but the mean occupancy of the reserve clusters was lower and the variability among the population size trajectories increased with time.

In summary, the landscape model demonstrated that the shape of clusters is nearly as important as their size. As a result, the size of irregularly shaped clusters must be larger to maintain the same mean occupancy rate compared to clusters more circular in shape. Further, model results indicate a possibility that in landscapes exhibiting a gradient of habitat qualities, the presence of sink habitats adjacent to reserves may have opposing effects. Overall population size is increased but projected population sizes are more variable. In terms of persistence likelihoods, however, we believe that increases in population size associated with increases in the amount of sink habitat should more than compensate for any negative effects associated with increased variability in the sizes of populations within clusters.

Application of the Landscape Model to the Southern California Metapopulation

Constructing the Map

The map, which characterized in a spatially explicit fashion the distribution of owl populations and their habitat islands in southern California, was based on the 1986-91 cumulative spotted owl survey data done primarily on public land (Chapter 3; Stephenson 1991). Each township (6-x-6 miles) in the Southern California Province was characterized according to the estimated number of owl sites it contained (fig. 4C). The collection of sections with owl sites defined the habitat islands and corresponded closely to locations listed in table 9A and shown in figure 9A. Thus, owl locations at a scale of 36 square-mile sections defined the location of suitable owl habitat. Each section, representing about 23,000 acres, was represented by nine hexagonal grid cells. This produced grid cells of about 2,500 acres, roughly corresponding to the size of individual spotted owl home ranges during the breeding season in mixed-conifer forests of the Sierra Nevada (table 6B). If a section had >9 sites, the extra sites were added to an adjacent section. The initial map, as it appears at the beginning of a simulation, is shown in figure 9L.

Imposing a fixed grid-cell size on a species with geographically variable area requirements is problematic. The number of owl sites will be underestimated in those parts of the species' range where its area requirements are smaller. For those habitats in southern California where home ranges are apparently the smallest (riparian/hardwood areas; table 6G), we examined the distribution and spacing among known owl sites. Most were separated by large areas of chaparral, making it unlikely that a single grid cell would contain two or more home ranges. In some cases where a single cell could contain two or more owl sites, we have probably underestimated the number of sites.

Initializing the Map

The map was initialized, in terms of owl pairs, using the estimated number of suitable sites per township (36 square miles) (see fig. 4C). If a township, for example, was estimated to contain six pair sites, then six sites (grid cells) were randomly selected from among the nine sites representing that township on the map. Each simulation was initialized with about 360 pairs of spotted owls.

For most simulations we used only two habitat types--suitable and unsuitable. Suitable habitats were characterized by a λ, slightly >1.0. Unsuitable habitats (the landscape matrix)

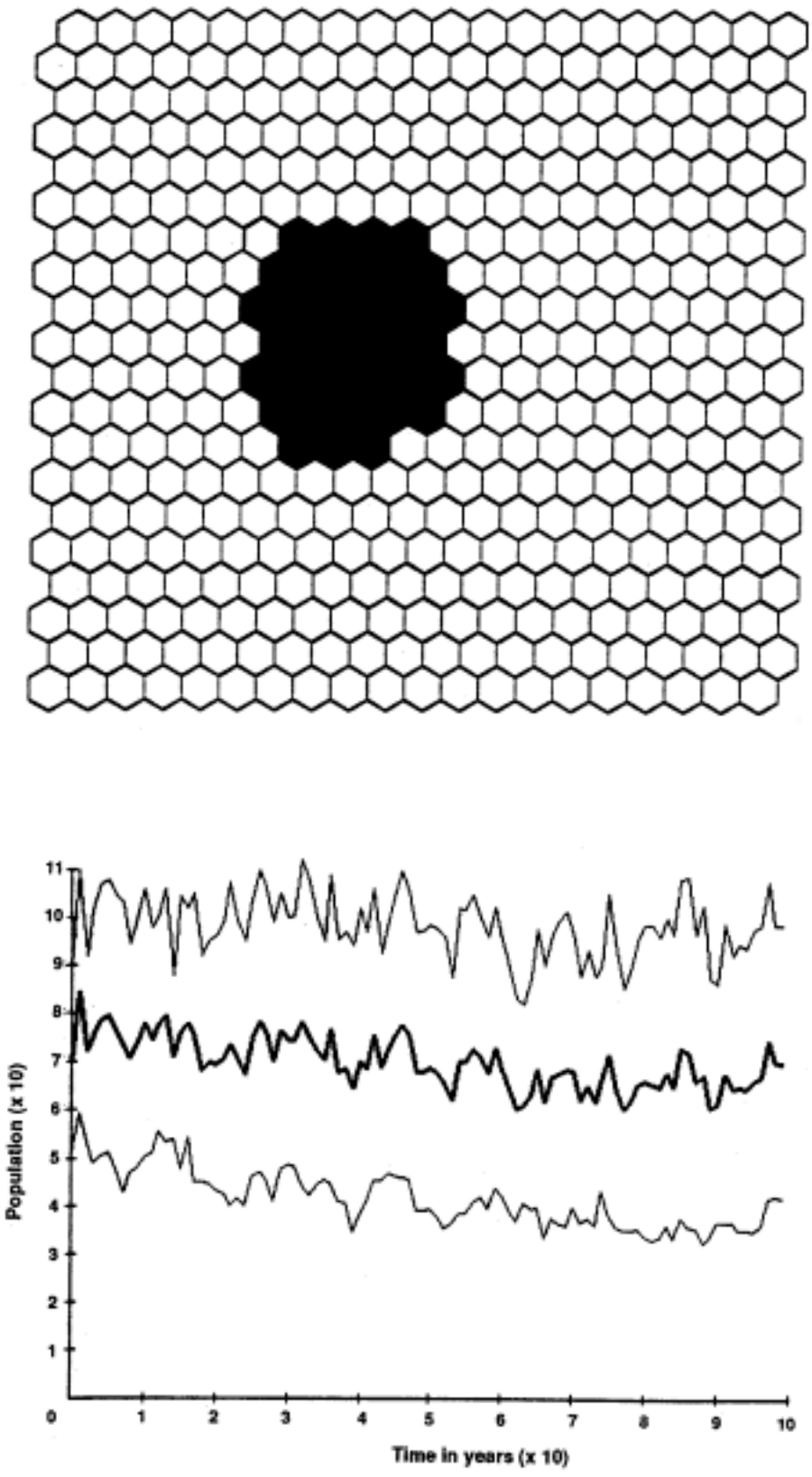


Figure 9J-Landscape model simulation showing simulated landscape with suitable habitat arrayed in one large, regular block. Results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

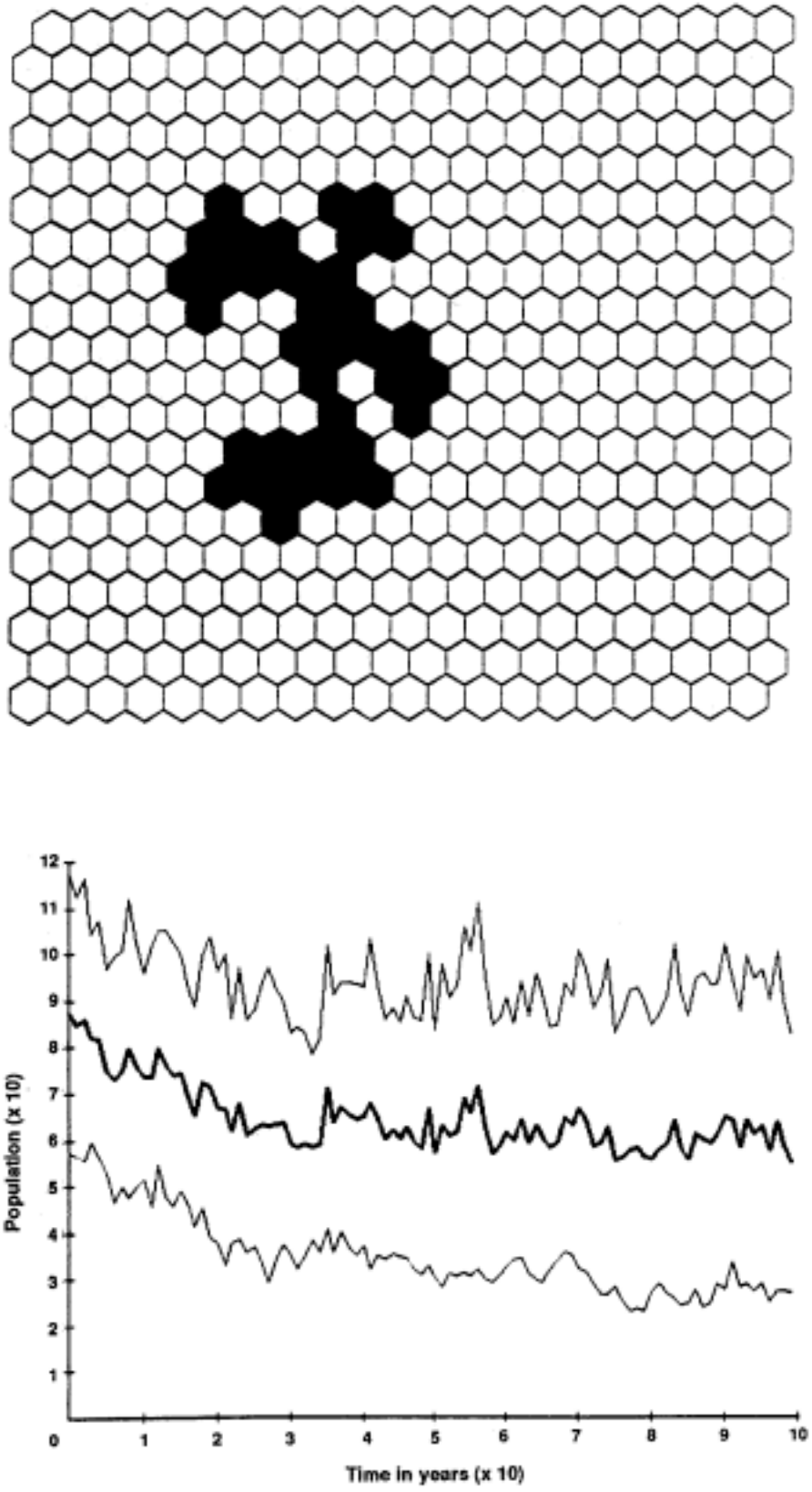


Figure 9K-Landscape model simulation showing simulated landscape with suitable habitat arrayed in one large, irregular block. Results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

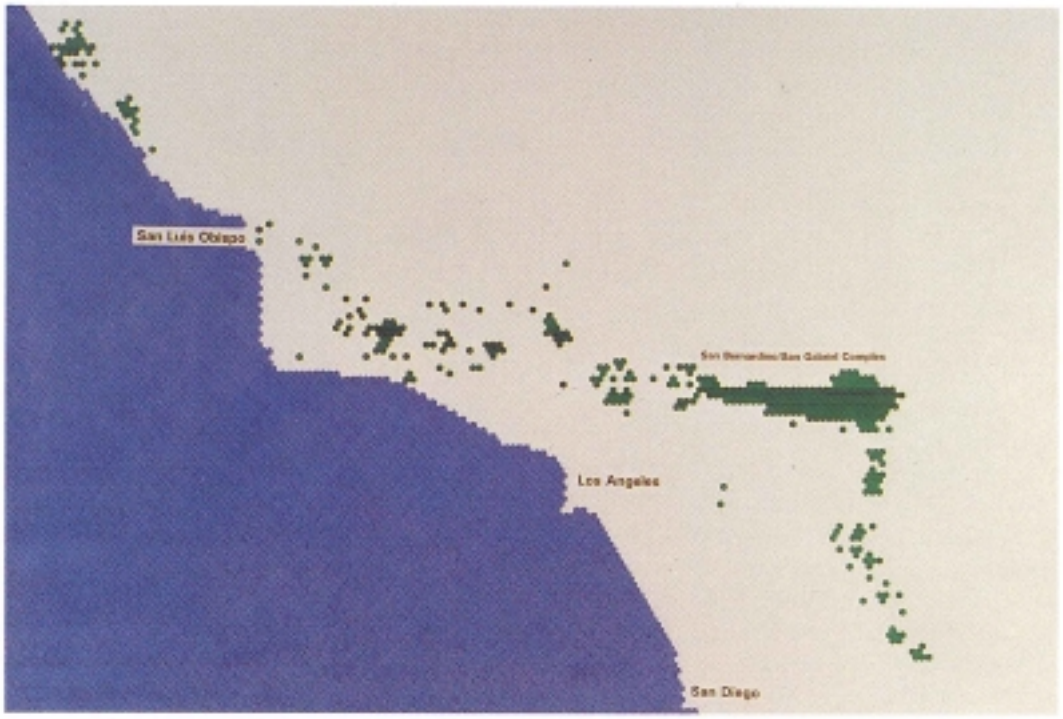


Figure 9L-The southern California metapopulation "map" used as the initial condition for subsequent simulations based on the landscape model. In this map showing the initial condition, hexagonal cells defining the "islands" were assumed to be suitable habitat. Areas outside of the islands (the matrix) were unsuitable.

were characterized in different ways according to expected survival rates (table 9D), but these sites never supported reproduction. Sink habitat was introduced in a third set of simulations; it had an assumed $\lambda_s = 0.80$.

Simulations

All simulations assumed stochastic fecundity rates, expressing both within- and among-year variation (see above). Survival rates only expressed within-year variation based on binomial sampling probabilities. All owls experienced similar pulses in reproduction-that is, we assumed complete spatial autocorrelation within the metapopulation. Simulations represented 150-year projections and were based on 50 replications. Various assumptions were made about the search capabilities of dispersing juveniles and the degree to which the matrix surrounding habitat islands could support owl survival (table 9D). In general, birds were twice as likely to move to a suitable cell than an unsuitable cell. This had the effect of making it less likely to leave an area of clustered, suitable habitat and more likely to be attracted to such an area. The map was static-after setting initial conditions, there were no changes in the amount or distribution of habitat-for all simulations.

Each suitable site was assumed to contain a pair of owls at the initiation of each simulation. Therefore, the population was effectively above its carrying capacity at time zero (figs. 9L-9P). Even under optimum conditions, a suitable site would have an expected pair occupancy rate <1.0 because of random mortality events. As a result, each simulation showed an initial population decline. Comparisons of results based on population trajectories should be made over the last 100 years of each simulation.

Interpreting Simulation Results

Results of simulations should not be interpreted as estimates of extinction likelihoods. We believe it is premature to make reliable estimates of extinction likelihoods at this time, as too many uncertainties exist about the long-term values of the vital rates and the dispersal capabilities of juvenile owls. For example, we do not known whether gaps between adjacent habitat islands are total or only partial barriers to dispersal. The most relevant output from the simulations are the maps, which summarize mean occupancy rates for each cell over the 150-year simulation interval. In general, areas of the landscape with very high occupancy rates represent potential source areas. In contrast, areas of the landscape with low occupancy rates represent sink areas. Interpreting the model results in a visual and spatially explicit way allows insights into areas of the landscape that are particularly vulnerable to local extinction events, as well as areas that represent sources for immigrants to other local populations.

Results

All simulations were initialized according to the spatial pattern of suitable habitat shown in fig. 9L. Suitable habitat supported demographic rates, on average, that yielded a λ slightly >1.0. Differences among the simulations reflect different assumptions about the survival risks experienced by owls moving

Table 9D-*Values of the demographic rates in suitable habitat and in the matrix for different model simulations. Risks to dispersing birds and dispersal capability were varied among the different simulations.*

		Simulation						
	Suitable					Source	Source/sink	
Demographic rates	habitat	A	B	C	D	reduction	Matrix	Sink
Juvenile survival	0.358	0.20	0.20	0.18	0.01	0.18	0.18	0.30
Subadult survival	0.903	0.70	0.70	0.45	0.01	0.45	0.45	0.75
Adult survival	0.903	0.80	0.80	0.45	0.01	0.45	0.45	0.75
Fecundity	0.279	0	0	0	0	0	0	0.175
Dispersal capability		22	44	22	22	22	22	22

through the matrix among the habitat islands. Because dispersal abilities are largely unknown, we bracketed a range of possible responses, ranging from very optimistic to an assumption of almost complete isolation of local populations (see table 9D). None of the simulations assumed any absolute barriers to dispersal in any direction, with the exception of the Pacific Ocean, which acted as a reflecting barrier.

Simulations A and B

In these simulations we made optimistic assumptions about the survival risks experienced by dispersing birds. Survival rates were only slightly depressed from values experienced in suitable habitat (table 9D). Simulation A suggested a relatively stable metapopulation structure with areas of high occupancy concentrated in the San Gabriel-San Bernardino Mountain complex (fig. 9M). Smaller and more isolated subpopulations, such as Tecuya Mountain, the South Santa Lucia Mountains, and Palomar Mountain (fig. 9A), had significantly lower mean occupancy rates, indicating frequent turnover within sites with subsequent recolonization at irregular intervals. In general, the lower the mean occupancy rate of a site, the longer the interval to recolonization after a turnover event.

Parameter values for simulation B were identical to A, except that we doubled the search capabilities of dispersing owls (table 9D) and the equilibrium population was about 15 percent higher than observed in simulation A. Results were similar except that occupancy rates were elevated overall, most significantly in the smaller but isolated clusters (for example, in the Los Padres Ranges of Ventura and Santa Barbara counties, and on Mount San Jacinto) (fig. 9A). Thus, sites were being recolonized at a greater rate.

Simulation C: Increasing Dispersal Costs

Assumptions made in the previous simulations about risks to movement in the matrix were very optimistic. In this simulation we relaxed those assumptions somewhat, and assumed that survival rates in the unsuitable matrix habitat were half those in suitable habitat (table 9D). Results indicated that small, remote subpopulations had occupancy rates in suitable sites of only 20-40 percent (fig. 9N). That is, suitable sites in these habitat islands are unoccupied 60-80 percent of the time. Occupancy rates in the San Gabriel-San Bernardino complex remained high because, having many tightly clustered owl sites, they were effectively immune to costs of dispersal through matrix habitats. Total population size was reduced by about 30 percent, compared to simulation A, but appeared to reach an equilibrium within the last three decades of the simulation (fig. 9N).

Simulation D: Population Isolation

In this simulation, we set movement costs in the matrix very high so that all but the closest clusters were effectively isolated from each other. The effects were dramatic. Overall population size was reduced by about 40 percent, and the population size did not equilibrate until the ninth decade (fig. 9O). High per-site occupancy rates were restricted to relatively large clusters (>40 sites) and with mostly contiguous sites (fig. 9O). In areas with a low density of suitable sites, even habitat islands with about 40 sites, such as the Palomar Mountain/central San Diego County/ Cuyamaca/Laguna Mountains complex (fig. 9A), were unstable and had very low occupancy rates (<15 percent). All local populations between the western part of the San Gabriel Mountains and the San Rafael wilderness (Las Padres NF) experienced frequent local extinction events (fig. 9O). The San Gabriel/ San Bernardino complex remained the most stable locus of high occupancy within the metapopulation.

Simulation E: Source Reduction

The San Gabriel/San Bernardino complex consistently had the highest occupancy rates and was the key source population for immigrants into other areas of the metapopulation. Therefore, we wanted to investigate its resilience to disturbance and the effect that such disturbance would have on the stability of the rest of the metapopulation. To simulate this scenario, we randomly changed 1/3 of the suitable sites within this complex to unsuitable sites and assumed moderate survival costs to movement through the matrix (table 9D).

The effect of the simulated decline in habitat within the largest population was pronounced. The overall size of the metapopulation was markedly reduced, and an equilibrium size had not been attained even after 150 years (fig. 9P). Comparing figures 9P and 9N suggests that loss of habitat within the largest source population would greatly reduce occupancy rates through

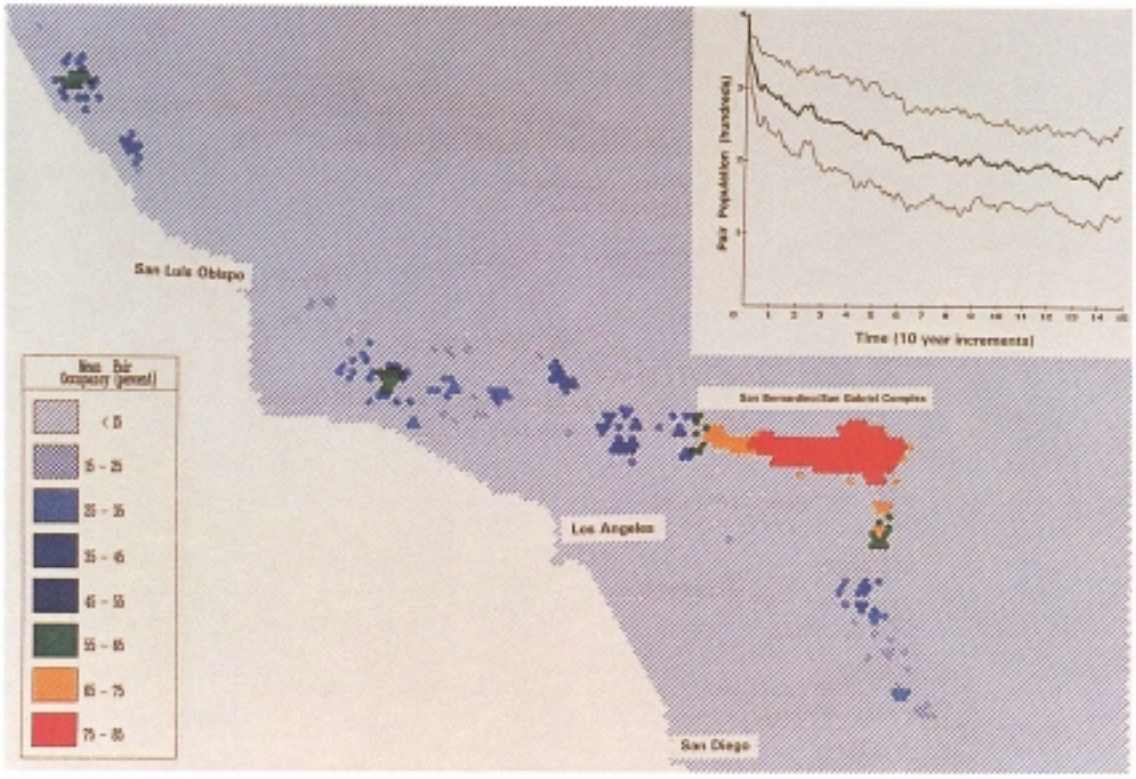


Figure 9M-Landscape model simulation A, showing mean (±1 standard deviation)150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

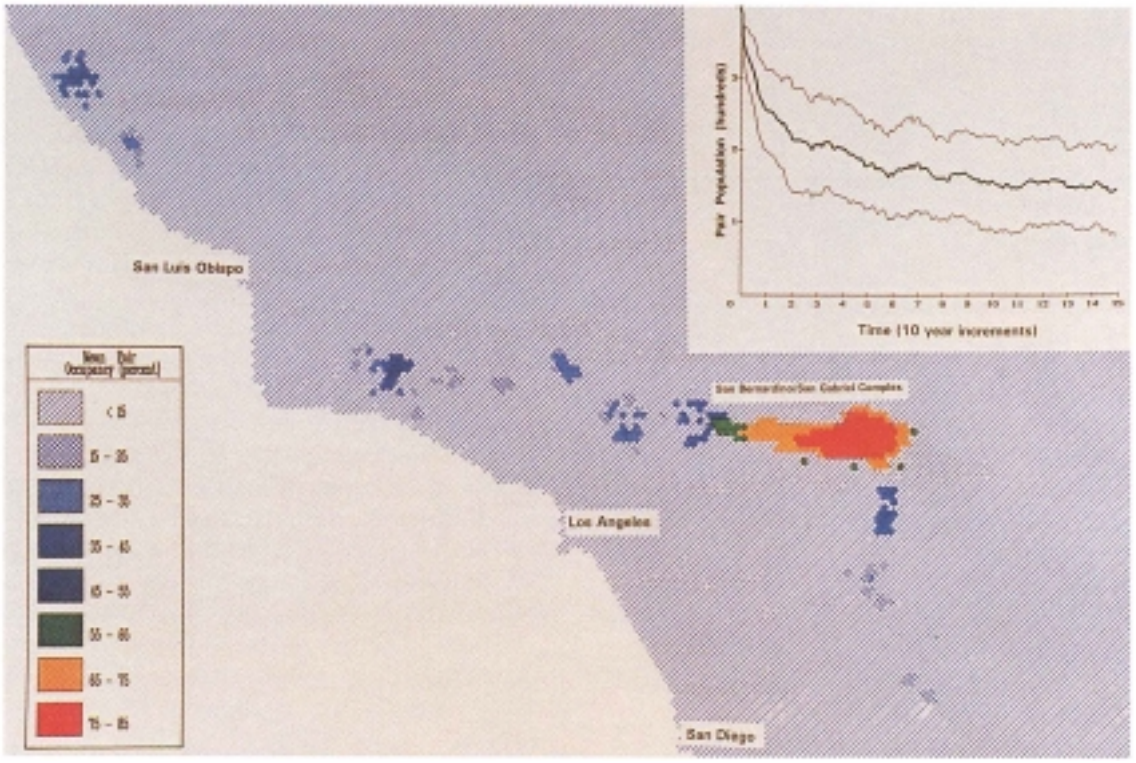


Figure 9N-Landscape model simulation C, showing mean (±1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

out the metapopulation. In addition, the small local populations of owls immediately to the west of the complex had gone extinct or had occupancy rates less than 20 percent. Interestingly, the overall size trajectory for the metapopulation in this simulation showed a steeper decline than that for isolation (simulation D) (fig. 9O). That is, decreasing the net production of potential colonists from the major source population within the metapopulation appeared to have more adverse effects than increasing the degree of isolation among local populations. Collectively, these results suggest that, to a large extent, the persistence of much of the southern California metapopulation relies upon maintaining the habitat integrity of the San Gabriel/San Bernardino habitat complex.

Simulation F: Source-Sink Effects

For this simulation we randomly changed 50 percent of the suitable (that is, source) habitat ($\lambda = 1.02$) within the entire metapopulation (fig. 9L) to sink habitat ($\lambda = 0.80$). This simulation thus represented both a source reduction and the introduction of sink habitat. Sink habitat, unlike matrix habitat, supported both survival and reproduction, but at nonreplacement rates (table 9D). We assumed limited ability by the owls to discriminate between source and sink habitats-searching birds were only 10 percent less likely to settle in sink habitat. Simulation results suggested a dramatic, exponential decline to metapopulation extinction within about 100 years (fig. 9Q). Average occupancy rates over the interval were >15 percent only for the San Gabriel/San Bernardino complex. Even this habitat island was unstable, however, and could not sustain its population over the long-term. Given this level of source reduction (50 percent), even greatly increasing the owl's ability to discriminate source from sink habitats did not stabilize the population.

Discussion

Simulation results suggested that the San Gabriel/San Bernardino owl population plays a pivotal role in maintaining the southern California metapopulation. Unfortunately, the resident, territorial population of spotted owls in the San Bernardino Mountains has declined precipitously since 1987 (LaHaye et al. in press; Chapter 8). If the territorial population is in some sort of dynamic balance with a nonterritorial (floater) population, then these sorts of declines may be accommodated over the short-term and pose no long-term threat (see Franklin 1992). If these trends also characterize the other local populations, however, and were to persist for another 5-10 years, we believe the persistence of the entire metapopulation would be at risk.

Several key factors remain unknown. For example, we do not know if these trends characterize the other local populations. If the decline in the territorial population in the San Bernardino Mountains is a response to region-wide, environmentally induced variation, then other local populations may be responding in a synchronous fashion. The degree of environmental correlation within the metapopulation is also unknown. Regional rainfall patterns, however, suggest that the degree of correlation may be high (figs. 8A and 8B). The effects of environmental correlation on persistence among populations depends upon their life histories, including diet switching and changes in prey availability (for example, Horton and Wright 1944, Vogl 1967). Modeling efforts by Harrison and Quinn (1989) suggest that even strong environmental correlation in extinction risks will not have a major effect on persistence time for large vertebrates, except when local populations become very small-but see a counter argument in Stacey and Taper (1992). Our models all assumed a complete correlation among populations in their response to environmentally induced variation in fecundity.

Persistence in metapopulations also depends critically on dispersal capabilities, distances between local populations, and risks involved in moving between habitat islands. The persistence of small, local populations with high turnover rates depends upon rescue by colonists from other populations in the metapopulation. This, too, is an area involving much uncertainty. The dispersal capabilities of California spotted owls and how they move through heterogeneous landscapes are mostly unknown.

Given the uncertainties regarding synchrony of extinction risks among local populations, whether the declines in the size of the territorial population will continue into the future, and the dispersal capabilities of juvenile owls, we believe it is premature to estimate extinction likelihoods. Simple application of the current estimates of the vital rates for the San Bernardino population (table 8G), for example, would show a rapid collapse to extinction. Our approach has been to gain general insights into the management of owl habitat in terms of its quality, amount, and geometry. We did this by viewing population dynamics as emergent reflections of landscape pattern and the distribution of habitat types. The landscape model was particularly valuable because it allowed us to gain insights into the dynamics of individual populations related to specific locations on the landscape.

Simulation results suggest that, in those parts of the species' range where suitable habitat constitutes only a small fraction of the landscape, populations are unstable and have low occupancy rates. The pattern is improved if the metapopulation contains a large source population. This result parallels the individual-territory model and predictions from Lande's (1987) modeling. That is, when the amount of suitable habitat becomes too small a percentage of the landscape, thresholds are encountered and populations may decline to extinction (fig. 9O). This occurs despite the continued presence of suitable habitat at these locations.

The general predictions from the cluster model were also demonstrated by the landscape model. Specifically, when clusters (habitat islands) became too small, or suitable habitat too diffuse, occupancy rates dropped precipitously. Assuming moderate to strong risks to dispersing birds, only those clusters with more than 40 sites and largely contiguous habitat showed high occupancy rates (figs. 9M and 9N). For example, the isolated sites on the western slope of the San Gabriel Mountains dropped to low occupancy rates when dispersal costs were high (fig. 9O).

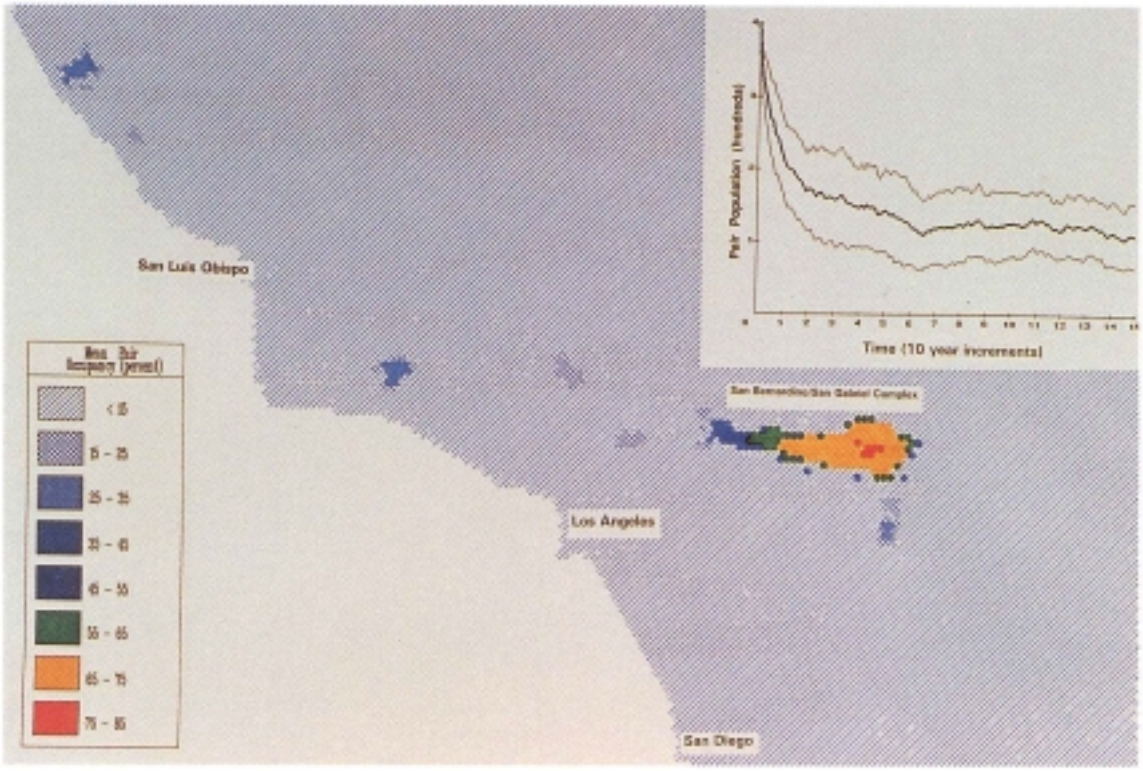


Figure 9O-Landscape model simulation D, showing mean(± 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

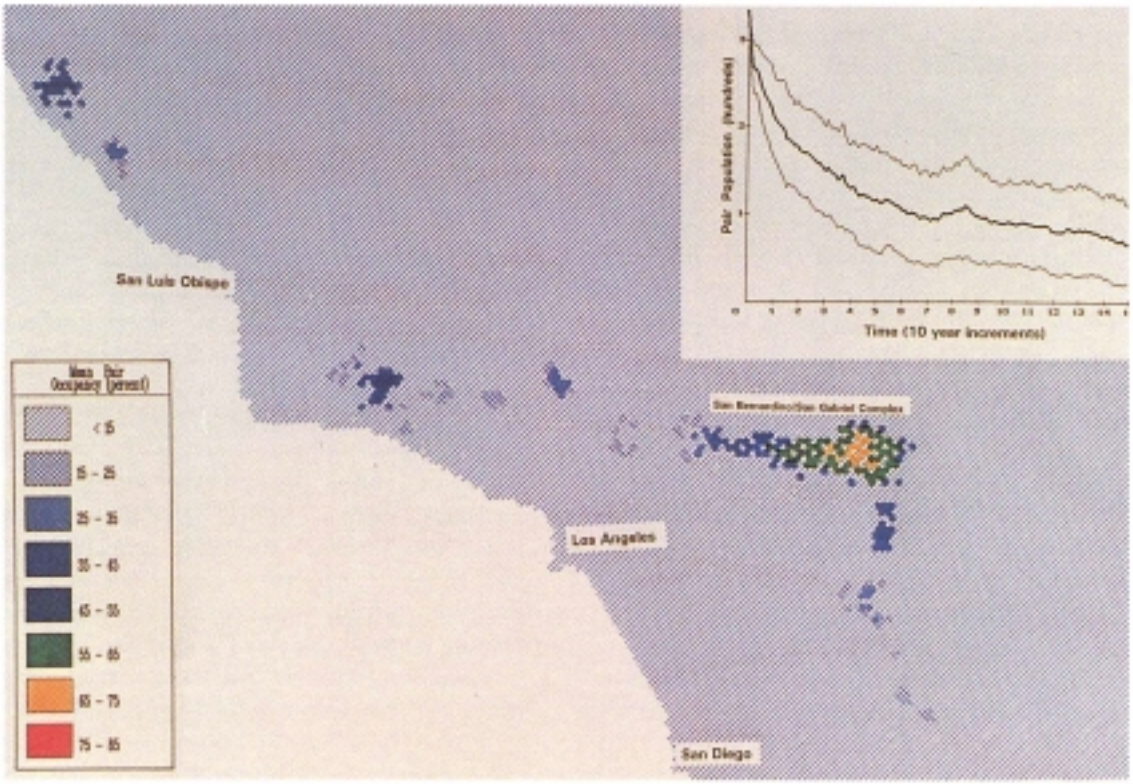


Figure 9P-Landscape model "source reduction" simulation, showing mean (± 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

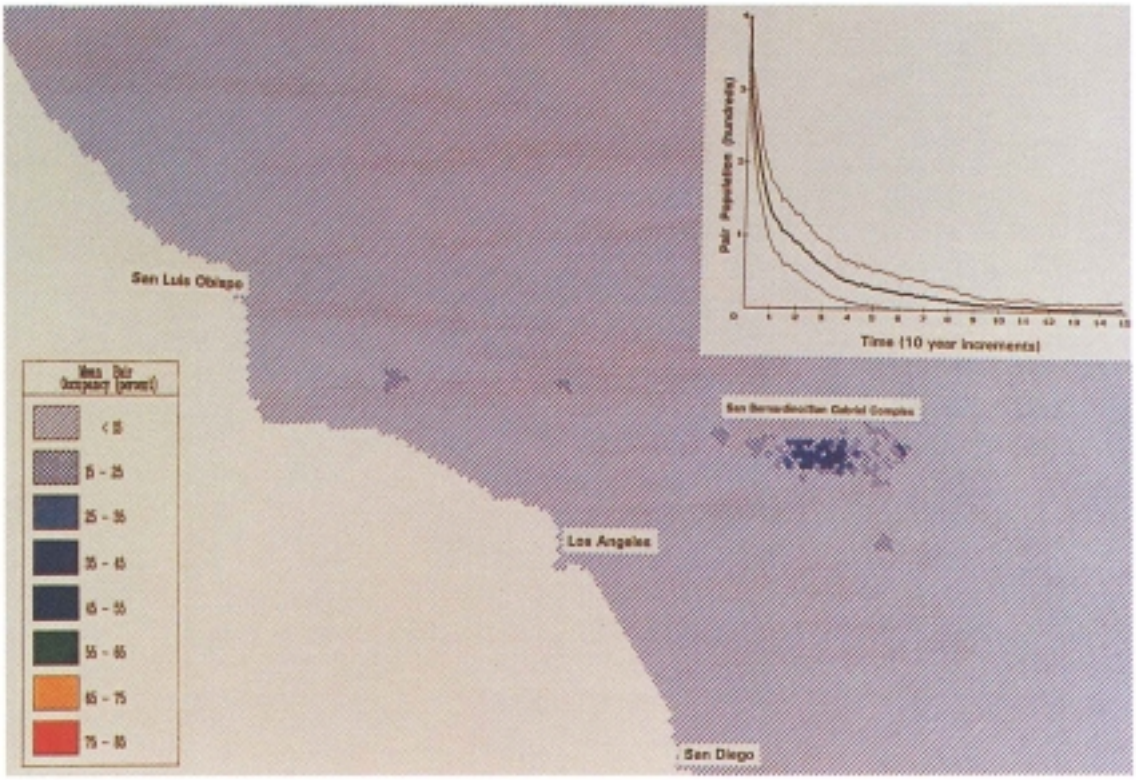


Figure 9Q-Landscape model "source/sink" simulation showing mean (±1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

The simulations also illustrated the interaction between size and spacing (fig. 9G). The islands near the San Gabriel/San Bernardino complex retained moderate occupancy rates even though they were small and dispersal risks were high (for example, the San Jacinto Mountains, 11 miles from the southern San Bernardino Mountains). In contrast, the population occupying the Los Padres Ranges, >30 miles from the western edge of the San Gabriel Mountains, declined to <40 percent mean occupancy even though this habitat island supports at least 65 pair sites. In general, the largest clusters with the shortest nearest-neighbor distances (table 9A) were the most stable and had the highest occupancy rates.

A consistent finding from the simulations, and predictable from our simpler models, was the significance of the San Gabriel/ San Bernardino population to the dynamics of the entire metapopulation. Simulated declines in the amount of suitable habitat in this complex lowered occupancy rates throughout the entire metapopulation (fig. 9P).

Population declines were particularly pronounced when half of the source habitat was changed to sink habitat and the owl's ability to discriminate among these habitats was limited (fig. 9Q). As the ability to discriminate source from sink habitats increased, the rate of decline of the population became less pronounced, but with a 50 percent reduction in source habitat no positive equilibrium was attained. When selection is imperfect, some owls may settle in sink habitat and reduce the occupancy rate in source habitat. The result is a decline in population size, often with no positive equilibrium. This finding is consistent with results reported by Pulliam and Danielson (1991) based on a different model formulation.

In some situations the presence of sink habitat may contrib.- ute to metapopulation size (Pulliam and Danielson 1991, Howe et al. 1991). Whether sink habitat acts to enhance metapopulation persistence depends critically on the owls ability to discriminate between source and sink habitats. If some owls that would otherwise settle in source habitat, are attracted to, and settle in, sink habitat then the effects can be negative. The extent to which spotted owls can discriminate among habitat types in terms of their expected birth and death rates is unknown. It is unlikely, however, that habitat selection is perfect. Because search is finite, population trend ultimately depends upon the amount and distribution of source habitat, even when selection among source and sink habitats is perfect.

In the case of the California spotted owl, the effects of landscape pattern on survival during dispersal may induce high levels of both spatial and temporal variation in juvenile survival rate. If habitat becomes more fragmented, the uncertainty of successful juvenile dispersal will become progressively more relevant to the likelihood of persistence. Even in a diffuse system with many suitable territories, pair occupancy will be low because of low recolonization rates. As a result, in a highly fragmented system, positive density-dependent growth rates usually associated with low population densities are unlikely. The effects of changes in landscape pattern on demographics are particularly significant if losses occur disproportionately in source habitat (fig. 9P).

Habitat-induced population declines also occur at the scale of the individual pair site or territory. Territories, the basic unit for our models, can be thought of as small islands, each having a maximum of one reproducing pair. They are similar to islands in that (1) they have spatial dimension-they occupy a certain area of the landscape; (2) they have some level of habitat quality; and (3) when they experience local extinction (one or both members of the pair either dies or emigrates), they must be recolonized through immigration from outside the territory or by an existing, nonterritorial floater within the territory.

The concept of territories as individual islands, with habitat quality explicitly defined by the expected values for birth and death rates, is key to understanding the dynamics of the spatial models. In all of the spatial models, search for suitable habitat is a sampling process. In the individual-territory model, the landscape is searched randomly and search success depends on the average density of suitable sites on the map. In the territory-cluster model, random search is confined to the clusters, which vary in the number and adjacency of suitable sites. Search success in this model depends primarily on the density of suitable territories within the cluster and secondarily upon the density of clusters in the landscape. In the landscape model, search success is defined at each time-step and for each owl by the density of suitable habitat in the territories immediately adjacent to the cell ("territory") currently occupied. When three or more habitat types occur, each cell on the map is not only a location, but, in terms of search success, a habitat-quality state with specific transition probabilities controlling movement into alternate states.

In a spatial model with search, a system composed of territorial clusters is more stable than a diffuse system because clusters produce regions where search efficiency is maximized. Circular clusters are the most stable because the density of suitable habitat is locally maximized. All other geometric forms will have lower search efficiency when compared with a circular cluster, unless clusters have strongly reflecting boundaries. In a cluster with a sufficient number of suitable territories, a population can recover from low occupancy because search efficiency will remain high. The key to stable populations within clusters is that they contain a sufficient number of high quality (= suitable) sites ($E[\lambda] \geq 1.0$) to support population large enough to avoid local extinction due to stochastic demographic events. Surprisingly, it is possible that the presence of marginal or sink habitat may actually reduce population size even though some individuals may breed in these habitats (Pulliam and Danielson 1991, McKelvey et al. in press).

Management Recommendations

Our recommendations for the persistence of spotted owls in the Southern California Province focus on the dynamics of its habitat at two spatial scales. First is the landscape scale. The arrangement of owls and owl habitat across the landscape shows that most of the population is concentrated in the San Gabriel/ San Bernardino Mountains complex. Every effort should be made to keep this population intact by maintaining the amount and spatial connectivity of suitable habitat there. Current demographic estimates suggest that the resident, territorial population is in significant decline. This population needs to be closely monitored for the foreseeable future, and attempts must be made to better understand the causes of the decline.

Other smaller, local populations do not have the potential to provide a large number of colonists. These populations are important, however, in diminishing the risk that local populations would simultaneously experience adverse impacts (Den Boer 1968, 1981). Advantages are often gained by distributing populations widely across an extensive geographic area (Quinn and Hastings 1987, Gilpin 1990)-the degree of environmental correlation among local populations is reduced, as is the likelihood of simultaneous extinction events (see discussion in Stacey and Taper 1992).

Local populations will continue to function as part of a larger metapopulation only if they remain connected through dispersal. If local populations become increasingly isolated by reduction in the sizes of habitat islands or by the creation of barriers to dispersal, occupancy rates decline because of a decline in the rate of demographic rescue, and the likelihood of extinction increases (table 3K; see discussion of problem areas in Chapter 3). Small, isolated populations will be the first to be lost to extinction, but even the largest, most continuous populations will experience increased risks if the overall size and spatial extent of the metapopulation is decreased.

Options to decrease population isolation through management efforts are severely limited in southern California. Because the current metapopulation structure is largely the natural expression of vegetation patterns resulting from edaphic, topographic, and climatic constraints, little opportunity exists to enhance dispersal habitat between subpopulations. The obvious goal, therefore, is to avoid creating additional barriers to dispersal beyond those not amenable to management.

The second level of concern is at the scale of the individual territory. It may be that the greatest threat to persistence of spotted owl populations is a subtle but continual decline in habitat quality (that is, a gradual conversion of source to sink habitat), on a site-by-site basis. As discussed in Chapter 8, subtle declines in λ will be difficult to detect except in the largest and longest-term demographic studies. Pulliam (1988) and Pulliam and Danielson (1991) concluded that knowledge of habitat-specific

demographic rates is ultimately needed for the effective management of wild populations. We agree. We must be able to target for preservation those habitats needed today for the species' persistence, and learn how to manage for such habitats in the future. Only by understanding the relations between demographic rates and the structure and composition of vegetation at the stand level can we be certain of maintaining habitat that provides for a stable or growing population.

Both scales of research and management-landscape and territory-are equally important, and both must be pursued to address the persistence requirements of spotted owls in southern California.

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