Biotic Interactions and Global Change. 1993.
Edited by Peter M. Kareiva
Joel G. Kingsolver
Raymond B. Huey
Sinauer Assoc. Inc., Sunderland, Massachusetts

CONSERVATION PLANNING FOR SPECIES OCCUPYING FRAGMENTED LANDSCAPES:

The Case of the Northern Spotted Owl

Kevin McKelvey, Barry R. Noon, and
Roland H. Lamberson

Landscape fragmentation can be a major threat to the persistence of species with very specific habitat and area requirements (e.g., Wilcove et al., 1986). Such a species is the northern spotted owl (*Strix occidentalis caurina),* whose populations are experiencing fragmentation at a number of spatial scales. The analyses we discuss here focus on the geographic scale (Lord and Norton. 1990) and are concerned with the fragmented pattern of old-growth forests that results from timber harvest. In the case of the northern spotted owl, concerns over the fragmentation of habitat have been translated into a specific plan for the owl's conservation (Thomas et al., 1990). In this chapter we report some of the models that were used to guide decisions and thinking about the size and geometry of the habitat reserves that form the core of this conservation plan. We would like to emphasize that we are reporting only a small fraction of the studies and analyses that have been pursued to help maintain spotted owl populations. and that our results represent the synthesis of a massive team effort. Before discussing the specific details of the models. we briefly discuss the general issues surrounding the relationship between spotted owls and old-growth forests, as well as some basic biology and demography of spotted owls.

THE NORTHERN SPOTTED OWL

More than any threatened or endangered species before it, the northern spotted owl epitomizes the struggle between groups representing disparate value systems in a land of dwindling resources. The dilemma is often portrayed as a choice between resource utilization, employment, and economic vitality versus diverse, healthy ecosystems that provide habitat for a large array of species and populations. The confrontation has been particularly intense and prolonged because northern spotted owls are largely restricted to coniferous forests in mature and old-growth age classes, which have high economic value (see review in Thomas et al., 1990). During the last 3-4 decades, these forests have been greatly reduced and fragmented by timber harvest and there is concern that continued habitat reduction will severely threaten the species' viability. For more than a decade, debate has focused on the degree of threat to the species and on the amount and distribution of mature and old-growth forests required for the species' conservation.

Throughout its range, the northern spotted owl is closely associated with old, dense, large-diameter forest stands (i.e. old growth) that provide forage, cover, and suitable nest sites. Nearly all observations of successful nesting, breeding, and fledging of young are from old-growth forests, or from those younger forests that include the structural characteristics of old-growth forest (Thomas et al., 1990, Appendix F).

Timber harvest, fire, and clearing for agricultural and urban development have reduced spotted owl habitats to less than 10 percent of their original area. Most of this habitat loss has occurred since 1950, a precipitous trend that is projected to continue into the future unless strong conservation policy is instituted (Murphy and Noon, 1992). This broad regional decline in old-growth forests and the associated decline in northern spotted owl numbers prompted a petition for federal intervention under the Endangered Species Act, and the species was given threatened status in 1990 (Federal Register 55(123): 26114-26194, 26 June 1990).

Reproductive success in northern spotted owls can vary greatly from year to year. In some years, most pairs nest and produce offspring, whereas in other years most pairs do not even attempt to nest. This variation may be related to fluctuations in the owl's primary prey, mostly small mammals. A key aspect of the species life history is that almost all juvenile birds are forced to disperse from their natal areas, sometimes over long distances, in search of both a suitable site and a mate (Allen and Brewer, 1985; Forsman et al., 1984, Meslow, 1985; Gutierrez et al., 1985; Miller, 1989).

This chapter presents the results of our efforts to characterize the life history structure of the spotted owl, to determine the demographic parameters that most influence rates of population change, and to integrate, in the form of computer simulation models, the species' demography with variation in habitat amount, distribution, and quality. The computer simulation models were developed specifically to aid the development of a conservation plan. The models therefore parallel the evolution of our thoughts, starting with simple models designed to answer the most basic questions (e.g., are owl populations declining?) to complex models designed to test the efficacy of particular reserve designs on the landscape.

METHODS

First we employed standard Lotka-Leslie methods to make inferences about the effects of variation in certain life history parameters on population growth rate (Keyfitz, 1968; Mertz, 1971; Nichols et al., 1980; Caswell, 1989). We examined the effect of changes in one demographic character at a time with all others held constant. We assumed (1) reproduction was characteristic of a birth-pulse population (Caughley, 1977, p. 6), (2) no density dependence, (3) a 1:1 sex ratio, and (4) formulated our models exclusively in terms of females.

Parameter estimates and model structure were based on information from the study of marked populations. Owls were captured during the breeding season, aged, sexed, and individually marked with both colored and U. S. Fish and Wildlife Service leg bands. Reproductive status was determined for all individuals using methods outlined by Forsman (1983). Young were counted after fledging had occurred. Individuals were initially placed into four age classes (juvenile, first-year subadult, second-year subadult, adult) according to criteria developed by Moen et al. (in press). Because of similarity in survival rates and breeding status, second-year subadults were considered in the adult stage. Annual survival rates for banded juveniles were estimated empirically (number observed in year t + 1/number banded in year t). Estimates for banded subadults and adults were calculated using Jolly-Seber capture--recapture models for open populations (Jolly, 1965; Seber, 1965) using program JOLLY (Brownie et al., 1986). The method assumed that an owl was dead when it was replaced on its territory by another owl and subsequently went undetected for two or more years (Franklin 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 or older that breed. (Age at first breeding is variable, but for most birds it occurs at age two years.) Fecundity was estimated each year as the mean number of young fledged per pair, and assumed a 1:1 sex ratio at birth. We believe our estimates for most demographic parameters (e.g.

Franklin et al., 1990) are quite accurate because the data represent a large number of marked birds studied for 5 to 8 years.

LIFE HISTORY STRUCTURE

The basic demographic life history of the spotted owl is presented in Table 1. The parameter b_x denotes the expected number of female fledglings produced by a female of age x. Annual survival probabilities were assumed distinct for the three age classes: juvenile (s_0), subadult (s_1), and adult (s). The parameter l_x represents the probability of survival to age x (by definition $l_0 = 1.0$). For $x \leq 2$, probability of survival to age x is given by $l_x = s_0 s_1 s^{x-2}$ (Table 1). Adult refers to ages subsequent to the second year of life. Within the adult age class, survival rate was assumed to be constant. We used parameter estimates from Franklin et al. (1990) (Table 2), except where otherwise noted. For our projection 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.

With long-lived species, estimates of age-specific parameters are impossible to attain or have large sampling variances because of small sample sizes. A useful approximation to an age-structured model is a stage-structured model (Lefkovitch, 1965; Caswell, 1989). Estimating the population dynamics of spotted owls with a stage model would yield misleading conclusions only if the species experienced reproductive senescence prior to

TABLE 1. Spotted owl life history.

x[a]	l_x[b]	b_x[c]	$l_x b_x$[d]
0	1.0	0	0
1	s_0	0	0
2[e]	$s_0 s_1$	b	$s_0 s_1 b$
3	$s_0 s_1 s$	b	$s_0 s_1 s b$
4	$s_0 s_1 s^2$	b	$s_0 s_1 s^2 b$
⋮	⋮	⋮	⋮
x	$s_0 s_1 s^{x-2}$	b	$s_0 s_1 s^{x-2} b$

[a] Age expressed in years.

[b] Probability that an individual aged 0 (a newly hatched bird) will survive to enter age class x

[c] Expected number of female fledglings produced by a surviving female of age x

[d] Net maternity function.

[e] Age at first reproduction is 2 years.

TABLE 2. Demographic parameters for the northern spotted owl.

Parameter [a]	Estimate	Sample size	Standard error
Juvenile survival (s_0)	0.159	63	0.046
Subadult survival (s_1)	0.868	34	0.008
Adult survival (s)	0.868	80	0.008
Fecundity (b)	0.382	197	0.190
Rate of population change (λ)	0.925	-	0.032

(Data from Franklin et al., 1990; Franklin, in press.)

[a] $H_0 = \lambda \geq 1.0$; $H_A = \lambda < 1.0$
$Z = (0.925 - 1)/0.032 = 2.343$
$P < 0.01$; Decision: reject H_0

about 15 years (Noon and Biles, 1990). Given the current high estimates for s (Table 2), early senescence seems unlikely.

RESULTS: DETERMINISTIC ANALYSES

Finite rate of increase

In general for the spotted owl, λ can be defined as the single, positive, real root of the equation (see Table 2)

$$1 = \sum_{x=1}^{\infty} \lambda^{-x} l_x b_x = b s_0 s_1 / (\lambda^2 - \lambda s), \; 0 < s < 1, \lambda > s \qquad (1)$$

which can be rewritten as

$$\lambda^2 - s\lambda - b s_0 s_1 = 0 \qquad (2)$$

and solved for λ as

$$\lambda = [s + (s^2 + 4 s_0 s_1 b)^{1/2}] / 2 \qquad (3)$$

Alternatively, λ can be computed as the dominant eigenvalue of the stage projection matrix.

The solution to Equation 3, based on the parameter estimates we used (Table 2), yields the estimate $\lambda = 0.925$. This is equivalent to a 7.5 percent annual decline in population size with a population half-life of 9 years. However, λ merely estimates population change over the period of study, and the projection of future population size is based on the unrealistic assumption of constant parameter values.

Sensitivity analyses

If simplifying assumptions are made about adult survival and fecundity, implicit differentiation of the characteristic Equation 2 can be used to evaluate the effects of changes in the vital rates. Survival and fecundity rates are measured on different scales, however, which makes direct comparison of their sensitivities difficult. Elasticities, a measure of the sensitivity of λ to proportional change in the vital rates, solve this problem (Caswell et al., 1984). For the spotted owl, population change is most sensitive to variation, in adult survival rate and relatively insensitive to variation in prereproductive survival or fecundity. In addition, Noon and Biles (1990) found λ to be relatively insensitive to age at first breeding.

Interval estimates of λ

A simple deterministic calculation of λ neglects the fact that birth and survival rates are estimated with some sampling error. For this reason, a formal statistical test of the $H_0:\lambda \geq 1.0$ is relevant to any species whose populations are believed to be declining. Methods to estimate the sampling variance of λ are provided by Lande (1988, p. 206) and Caswell (1989, p. 185). When we applied these methods we found that spotted owls are apparently declining in northern California (Table 2; Franklin et al., 1990; Franklin, in press). Similar findings of significant population decline have been reported for the Oregon Coast Range (E. D. Forsman, pers. comm.; Thomas et al., 1990, Appendix L).

Senescence

The effects of a senescent decline in fecundity are explored by incorporating a maximum age, w - 1, beyond which no reproduction occurs (i.e., $b_x = 0, x > w$) (Mertz, 1971; Nichols et al., 1980). The life span of spotted owls, and whether or not fecundity remains constant, are unknown. However, it is unlikely that one could obtain survival estimates for all adult owls as high as 87 percent if spotted owls lived less than 15 years. Thus we feel confident that adults do readily live to age 15 without significant senescence. This is an important point because mathematical analysis reveals that any senescence occurring after age 15 has little effect on λ, sensitivities, or elasticities.

Given evidence of declining populations in two geographically separated portions of their range, coupled with the precipitous loss of their preferred habitat, the logical conclusion was to attribute the owl's decline to habitat loss. We were then led to investigate how the amount, distribution, and quality of habitat might affect the demography of owl populations.

DYNAMIC PROJECTION MODELS

No natural population is exposed to purely deterministic forces. Thus the population dynamics of the spotted owl should be examined in light of both demographic and environmental stochasticity. Further, estimating the sensitivity of population growth to variation in individual demographic parameters can be misleading. Demographic parameters do not vary independently and thus should be considered simultaneously. Unfortunately, the effects of stochastic factors and the covariance of life history attributes are usually not amenable to analytic models. These factors, and their effects on rates of population change, however, can be explored in simulation models.

A conservation strategy for any species must ultimately be 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. To develop a conservation strategy for the northern spotted owl we needed insights into how the arrangement of owls and their habitat across the landscape affected their population dynamics. Our task was to test and refine various iterations of the conservation map until the arrangement of conservation areas described a reserve system with a high likelihood of ensuring the owl's persistence for 100 years (Thomas et al., 1990; Murphy and Noon, 1992).

An initial map showing the distribution of owls and their habitats indicated that the strategy for persistence of the northern spotted owl would need to be evaluated in the context of a metapopulation (Levins, 1970; Shaffer, 1985). The distribution of habitat polygons was discontinuous across the landscape, reflecting natural discontinuities in vegetation structure and composition, in topographic conditions, and the effects of extensive human-induced habitat disturbance and fragmentation.

To provide a framework to guide reserve design for the northern spotted owl, we developed a number of 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, was based on previous work by Lande (1987). Lande's model, based on monogamous territorial breeders with. obligate juvenile dispersal, was directly applicable to the life history structure of the spotted owl.

NONEXPLICIT SPATIAL MODELS

The individual territory model

The individual territory model, assumes that all newly fledged juveniles disperse, and that adult birds who experience loss of their territory (e.g., due to timber harvest) also disperse (Lamberson et al., in press). The model assumes a landscape which is of fixed spatial extent and contains a fixed number of potential home range territories (or "sites"). However, only a fraction of these sites are capable of being occupied, namely, those that contain suitable habitat for spotted owls.

The state variables in the model, updated annually, are (1) the number T of currently suitable sites (which may be decreasing over time due to timber harvest); (2) the number P of suitable sites that are occupied by nesting pairs; and (3) the number S of suitable sites that are occupied by single males. The key equation which describes search success in this model (see Lande, 1987) is

$$P\,(\text{success}) = 1 - [1 - (\text{unoccupied suitable sites/total sites})]^{m} \qquad (4)$$

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, determine the bird's potential for successful dispersal (consistent with Lande, 1987).

Due to the dynamic and nonequilibrium nature of this model, there were several new findings including:

1. The probability p of population survival for 250 years as a function of initial population size (expressed as a percentage of suitable sites occupied) is affected by assumptions about environmental stochasticity. When there is no stochasticity, p is a stair-step function, rising abruptly from 0 to 1 at the unstable equilibrium threshold point. Adding environmental stochasticity smooths out the stair-step; that is, the extinction threshold becomes "blurred."
2. In a similar fashion, survival probability p, as a function of the percentage of suitable habitat, is affected by environmental variation. Once again the deterministic case shows a stair-step function, with the jump from 0 to 1 occurring at the threshold point (Figure 1). As before, adding environmental variance makes the extinction threshold less abrupt.
3. The crowding of older owls into the remaining suitable habitat as timber harvest continues temporarily produces very high occupancy rates--much higher than would be expected under long-term stable conditions (Figure 2). Thus, predicting long-term population status from short-term occupancy data can be very misleading.

The territory cluster model

In the individual territory model, search is based on simple sampling with replacement: all cells are equally likely to be searched. In reality, dispersing

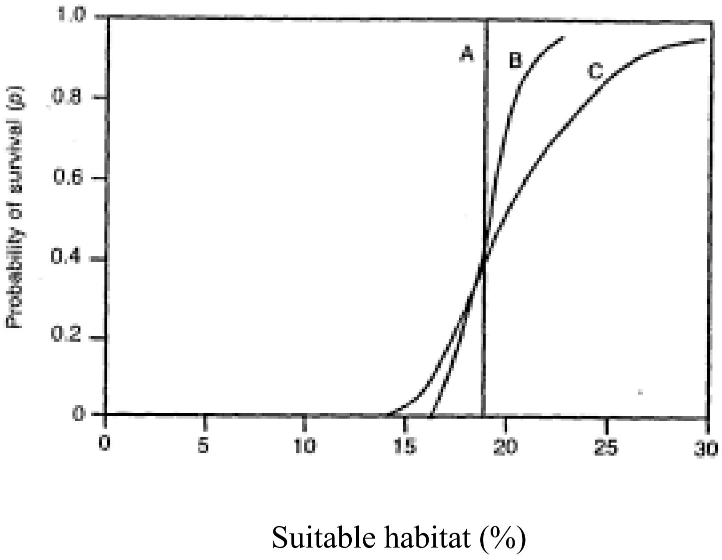

FIGURE 1. The 250-year survival probability as a function of the percentage of sites that are suitable owl habitat in the landscape. Curves A, B, and C represent the conditions of low, medium, and high environmental variability.

juveniles have a high probability of searching the areas close to their nest sites and a low probability of searching distant areas. Their success will therefore be based on the local habitat availability. If suitable habitat is unevenly distributed, then the search efficiency in areas where the habitat is clustered may be significantly higher than the global proportions would suggest.

The basis of the territory cluster model (Thomas et al., 1990, Appendix M; R. H. Lamberson and B. R. Noon, unpublished) was a rectangular array of circular clusters containing a variable number of owl sites (territories) All sites within a cluster were assumed to be of identical size, and a site was either suitable or unsuitable. A suitable site was capable of supporting survival, mate attraction, and reproduction. Clusters could be either totally or partially suitable-the carrying capacity of a cluster equaled the number of suitable 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.

The matrix between clusters was assumed to be entirely unsuitable as owl habitat. Assuming a constant percentage of the habitat as potentially suitable and restricting the suitable habitat to clusters had two important consequences: (1) as cluster size increased, the distance between adjacent clusters increased predictably; and (2) the probability of choosing a dispersal azimuth that intersected an adjacent cluster was constant.

The life history was a three-stage, female projection model. Fecundity

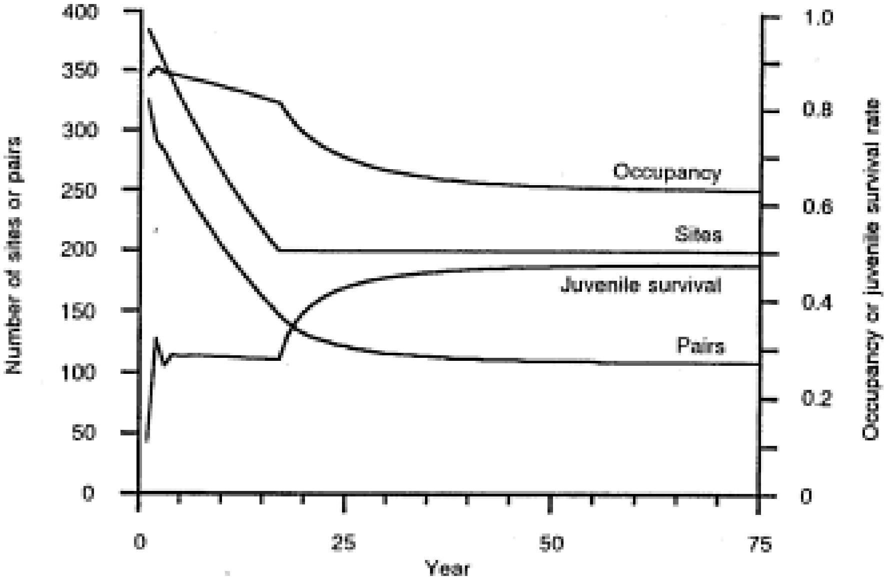

FIGURE 2. Trends in the number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. The simulation assumed that 4 percent of the suitable habitat was lost per year until 20 percent of the landscape remained suitable, and that juveniles could search 20 sites in the landscape. Note that juvenile survival increases as adult occupancy decreases.

was treated stochastically, with expected value equal to field data (see Table 2). Parameter estimates were identical to Franklin et al. (1989, 1990), except that the value of adult survival (*s*) was increased to provide the possibility of a stable population. (Thus, the model assumes that habitat conditions within the clusters would be better than those in regions where previous demographic studies of owls have been conducted.)

Dispersal dynamics The model distinguished between dispersal within and among clusters (cf. Doak, 1989). Within-cluster dispersal 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 4). If a dispersing juvenile did not succeed in finding 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 existed: first, if the direction chosen did not intersect a neighboring cluster, the bird died; second, if a correct direction was chosen, the risk per unit of distance traveled was assumed to be constant. This assumption means that as distance between the clusters increases, the probability of reaching an adjacent cluster declines exponentially.

The number of possible combinations of model parameters is immense and a large number of sensitivity analyses were performed (Table 3). The most significant results, however, were based on the relationship between mean occupancy and cluster size. The number of sites per cluster was varied across a range of values and the 100-year occupancy trend plotted. For a simulation in which 60 percent of the sites within a cluster were suitable, occupancy did not stabilize until clusters held at least 10 sites. Clusters of 10 sites stabilized at about 70 percent occupancy of the suitable sites, while clusters of 15 stabilized at about 85 percent, a figure representing nearly full occupancy given the adult survival rates. Further increases in cluster size had little effect on occupancy (Figure 3). In general, mean occupancy increased as the percentage of sites that were suitable in each cluster increased. The marginal difference in occupancy among clusters of different sizes, however, was less pronounced beyond cluster sizes of 30 (Figure 4). Another approach to choosing an optimal cluster size is to estimate the number of owls occupying a fixed amount of suitable habitat. Based on the mean occupancies at 100 years from Figure 3, the efficiency of land use (owl pairs per unit of area) is clearly higher for larger cluster sizes.

In summary, the results suggest that providing for clusters of territories should increase the persistence likelihood of spotted owls, primarily by facilitating juvenile dispersal (cf. Doak, 1989). Given the assumptions of this model, clusters containing 15-20 sites with at least 60 percent being suitable at any point in time, and with moderate connectivity among clusters, should provide for a stable reserve system.

TABLE 3. Qualitative results of sensitivity analyses for the territory cluster model.

Factor varied	**Sensitivity**[a]
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-moderate for large clusters; high for small clusters
Initial population size	If population was in large clusters, low; small clusters, high

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

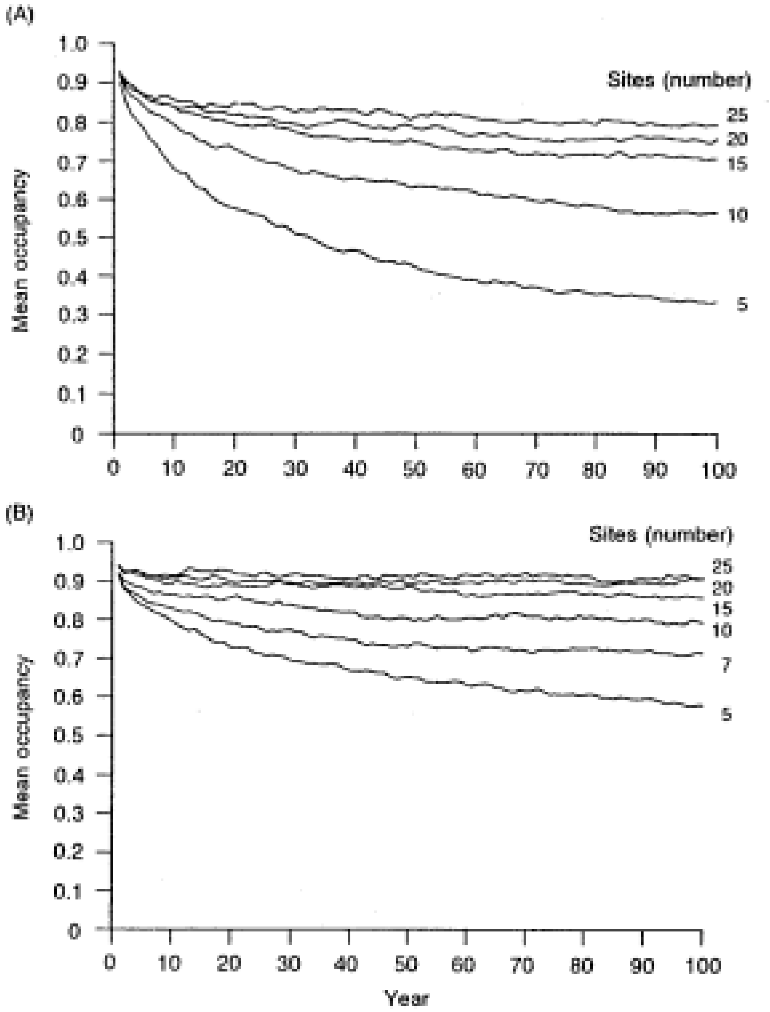

FIGURE 3. The mean proportion of sites occupied in clusters over a 100-year simulation. The number of sites per cluster varied from 5 to 25, with 35 percent of the landscape in clusters. Dispersal exponential coefficient was 0.0354. (A) 60 percent of the sites in the clusters were assumed suitable. (B) 100 percent of the sites in the clusters were assumed suitable.

A spatially explicit landscape model

The territory cluster model provides basic rules for achieving reserve design stability, but the landscapes that it can model are limited (evenly distributed

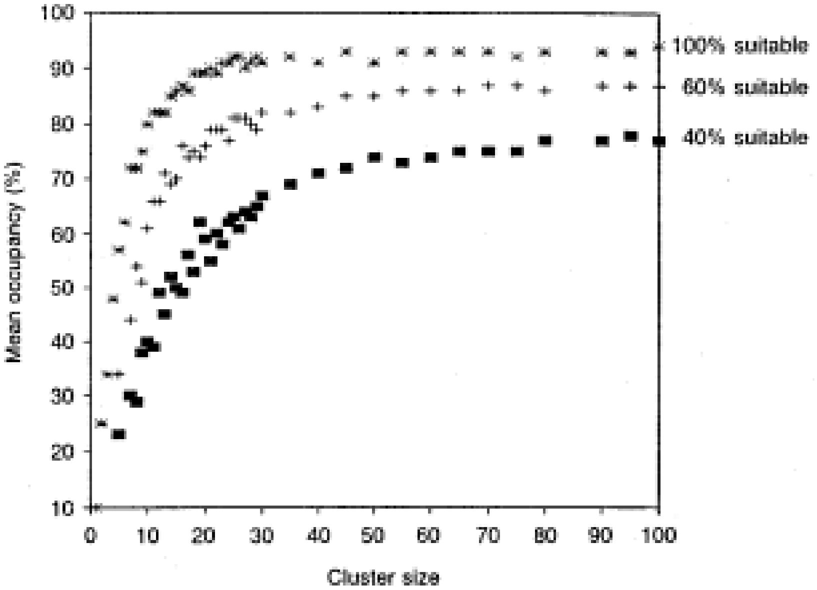

FIGURE 4. Simulated steady state mean occupancy rate as a function of cluster size. The curves represent 40, 60, and 100 percent of the sites within each cluster as suitable habitat.

circular clusters and wraparound boundaries). The landscape model was designed to provide greater spatial flexibility and to allow suitability to be defined along a gradient of qualities, rather than defining a site as simply suitable or unsuitable.

The landscape model links an organism's survival and reproduction explicitly to its current habitat location. As a consequence, a population's rates of survival and fecundity vary based on landscape configuration. In addition, the model allows for habitat areas that vary in their degree of suitability for nesting. Lastly, the model assumes that each organism must search the landscape to find new territories and mates. The model is a two-sex, single-organism simulator. 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 (Figure 5). Females are born and disperse from the

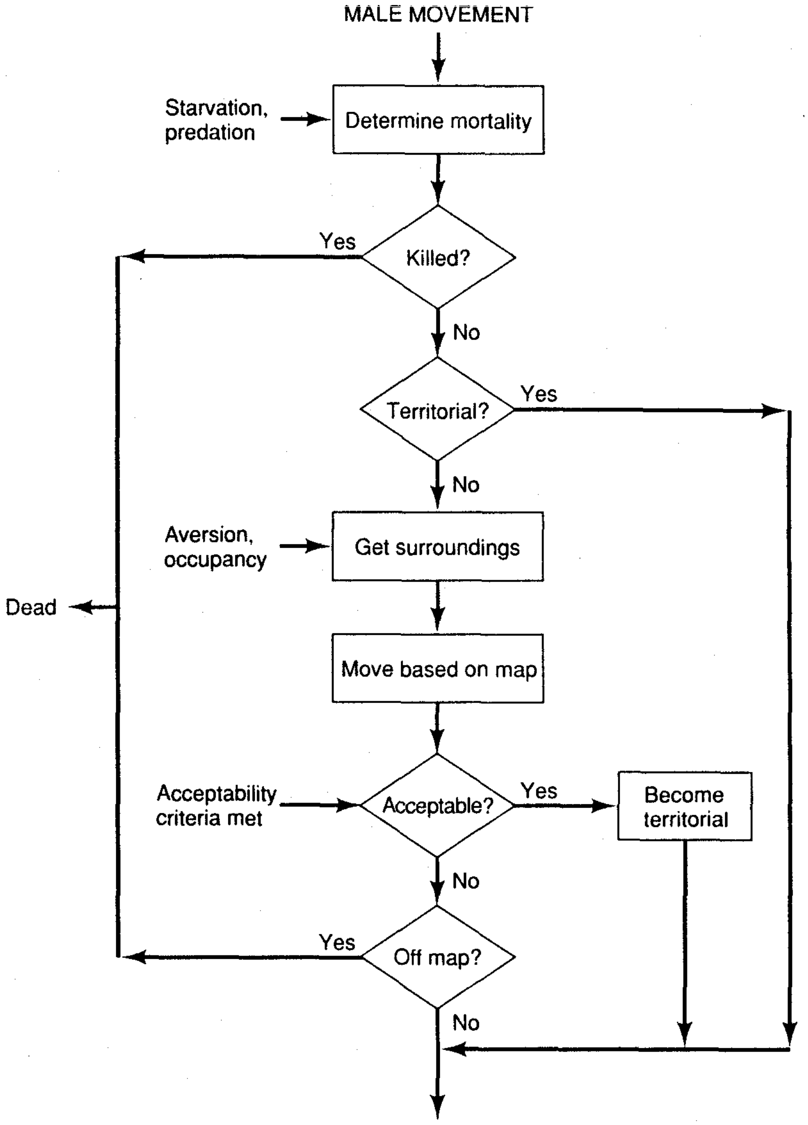

FIGURE 5. Flow diagram representing the process for determining male behavior at each time step in the landscape model.

natal site looking for unpaired, territorial males. When they find a territorial male, they obligately pair (Figure 6). 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 the

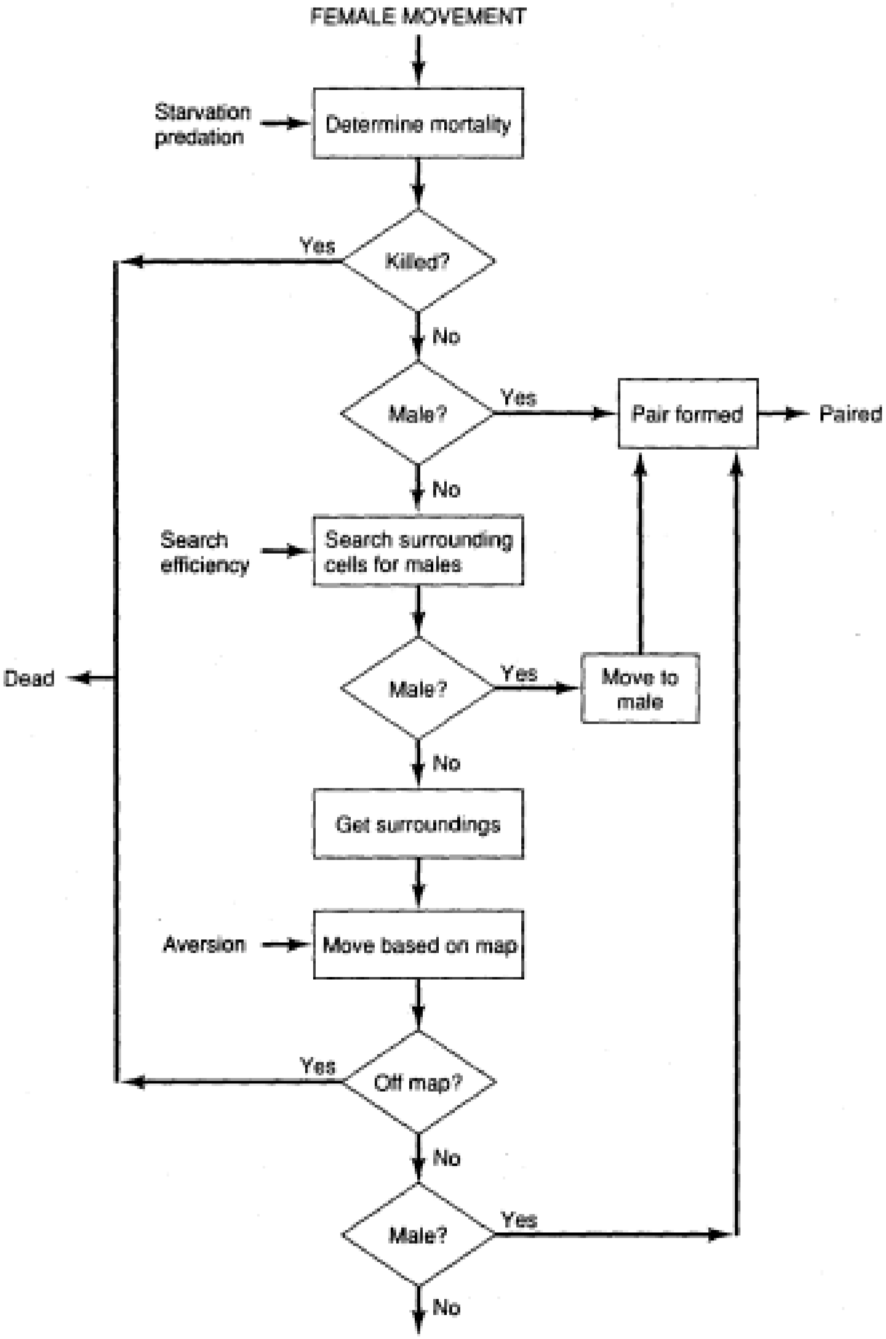

FIGURE 6. Flow diagram representing the process for determining female behavior at each time step in the landscape model.

site. If the male dies, the female has no site fidelity and will initiate search for a new mate (Figure 7). If the site becomes unsuitable for nesting, both members search independently for a new site.

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 broken up into i time steps, and the risk per step for an owl in stage class j occupying habitat type k is defined as one minus the ith root of the yearly survival for class j in habitat type k.

Movement The map is divided into a fixed array of grid cells, with each cell representing one territory-sized unit. The grid is hexagonal to allow more realistic movement. The rate of movement is dependent on the size of the grid cell and the number of time steps per year. Individual moves at each time step are restricted to adjacent cells. All of the mobile classes of owls (nonterritorial males and females) have the opportunity to move at each time step. To ensure that certain birds or areas of the map are not given

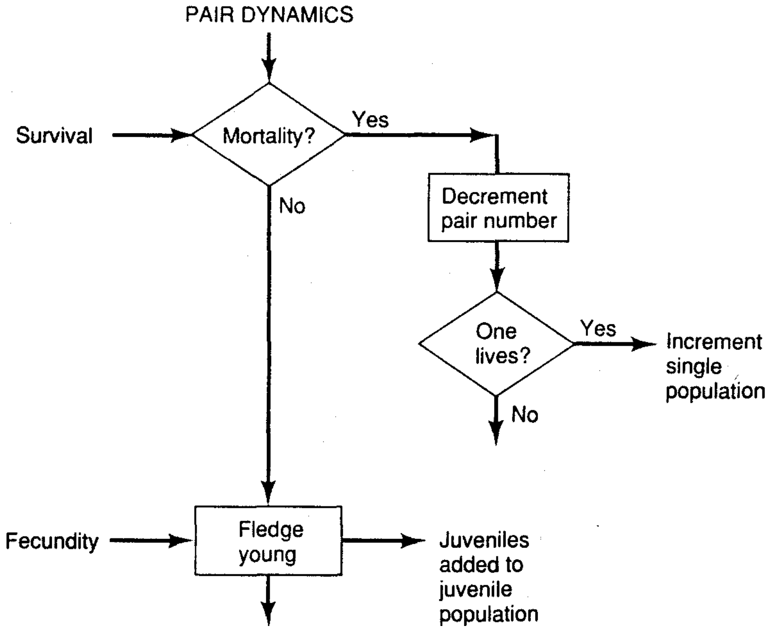

FIGURE 7. Flow diagram representing pair dynamics on a yearly basis in the landscape model. Pairs remain reproductive only if both members survive.

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 move obligately to known territorial males, and nonterritorial males may be averse to crossing 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 weighing factors that condition the probability of movement (Table 4).

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

Fecundity Fledglings are newborns that survive to disperse. It is assumed that there are good and bad years for fledging. If it is a good year, the pair produces fledglings according to a beta-distributed random variable, scaled to range from zero to the maximum clutch size. The number of fledglings in a clutch is the beta value rounded to the nearest integer. There are therefore two levels 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 will produce about the mean number of

TABLE 4. A summary of factors that can affect an individual's movement in the model.

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

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.

GIS interface An automated link exists between the model and vector-based geographic information systems (GIS). Using this link, a hexagonal grid with a cell size equal to the mean home range size is intersected with a vegetation map, and the habitat quality of the area contained within each grid cell is analyzed. Habitat quality is an index based on the relationship between the attributes of the cell and the demographics of the organism. The number of fledglings, for instance, is correlated with the proportion of old growth in a home-range-sized area around the nest site (J. Bart, pers. comm.).

Maps can also be created by the model and transformed into vector-based GIS maps. The ability to move information freely between the GIS and the model allows a dynamic interaction between land management decisions and the potential impact of those decisions. Vegetation changes can be simulated at the stand level within the GIS, and the impact of those changes can be estimated. Model output, such as mean pair occupancy for each cell (output as a map), can be overlaid on the stand-level map to determine which stand types correlate with areas displaying high or low occupancy rates.

Effects of spatial configuration We have used the model to project population trends for five hypothetical landscapes with an identical number of suitable sites (Figures 8-12). Other than habitat configuration, there were no differences in the initial values of any model parameters. The map boundaries were wraparound, so the exact location of the habitat within the map frame was unimportant. The demographic parameters (Table 5) were set to yield a $\lambda = 1.0$ and were not modified by habitat quality. In these simulations only two habitat qualities, suitable and unsuitable for nesting, were specified. The movement parameters deviated only slightly from a random walk: birds were twice as likely to choose suitable habitats; males treated occupied habitats identically to unsuitable habitat; and birds were twice as likely to continue 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. The shape of reserve areas also has an important effect on their stability properties. A cluster with a low ratio of edge to area (Figure 10) is more stable than continuous clusters of identical area but with varying degrees of irregularity (Figures 8, 9, 11, and 12). A high edge-to-

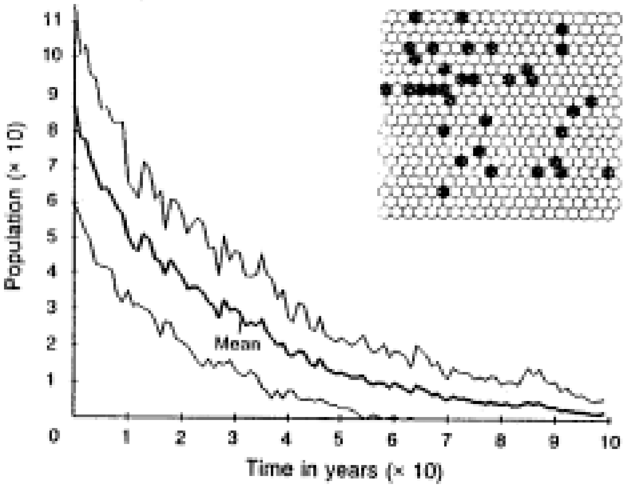

FIGURE 8. Landscape simulation with suitable habitat randomly scattered. The results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

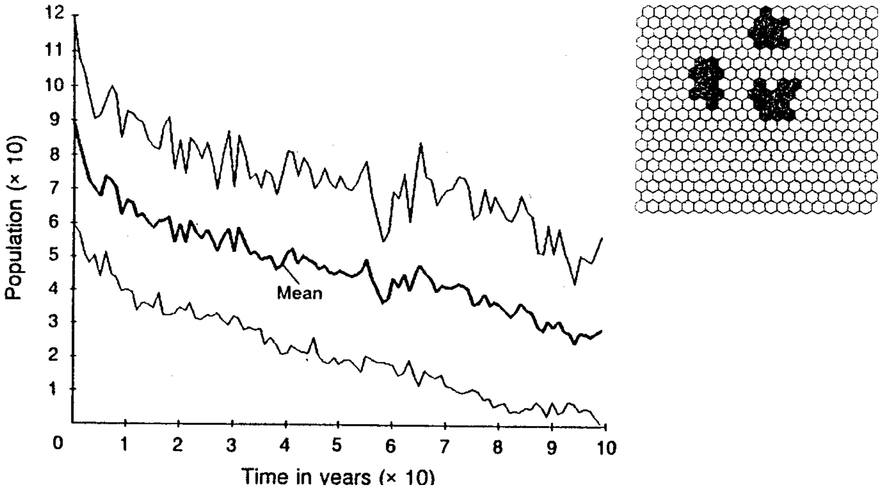

FIGURE 9. Landscape simulation with suitable habitat arrayed in three small blocks. The results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

area ratio has a negative impact on demographic stability: the rate of decline in a large, highly irregular cluster (Figure 12) is similar to the decline rate of the dispersed cluster system (Figure 8).

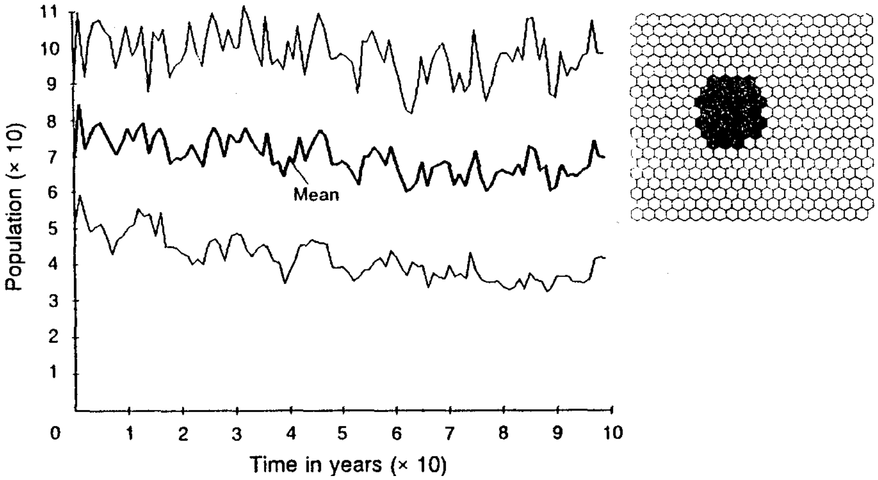

FIGURE 10. Landscape simulation with suitable habitat arrayed in one large regular block. The results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

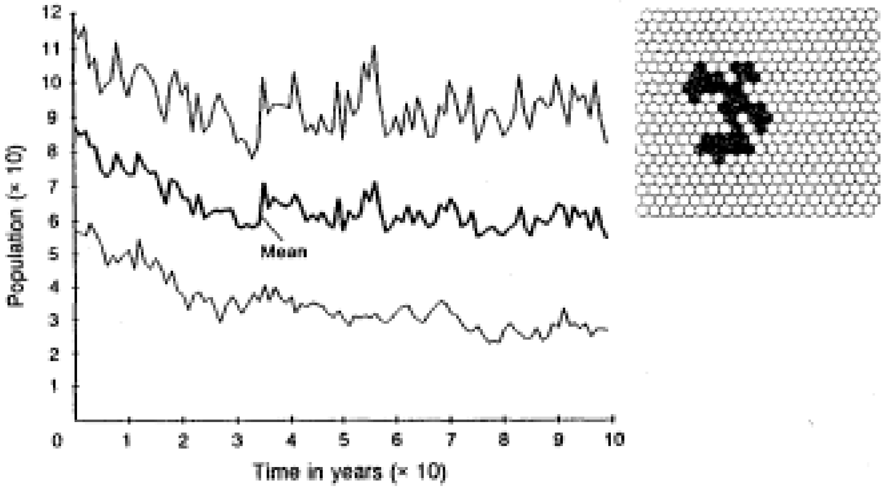

FIGURE 11. Landscape simulation with suitable habitat arrayed in one large, irregular block. The results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

Source-sink relationships The previous results demonstrate the impact of reserve shape when each landscape cell is either suitable or unsuitable for breeding. In that case, the breeding population is limited entirely to the

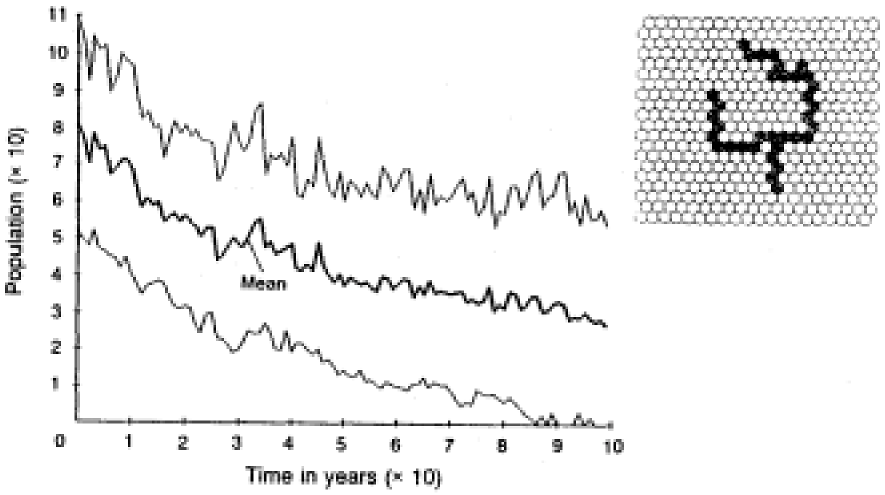

FIGURE 12. Landscape simulation with suitable habitat arrayed in one very irregular block. This is similar to the form of reserves expected in riparian corridors. The results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

TABLE 5. List of the parameter values used for landscape model simulations.

Parameter[a]	Value	Source
Juvenile survival	0.29	Franklin et al., 1990
Subadult survival	0.935	Thomas et al., 1990
Adult survival	0.935	Thomas et al., 1990
Birth rate	0.335	Franklin et al., 1990
Aversion	1.0, 0.5[b]	
Boundary	Wraparound	
Linear propensity	2.0	
Site fidelity	0.5	
Territorial aversion	0.5	
Female finds male	0.5	
Time steps	40.0	
Runs	30.0	

[a] Parameters were chosen to produce as optimistic an estimate of owl survival as could be supported by these data. Parameters varied with site quality only where explicitly stated.

[b] Only two habitat types were placed in the map, one representing the best habitat and the other representing the worst. This split corresponds to suitable/unsuitable designations found in the individual territory and territory cluster models.

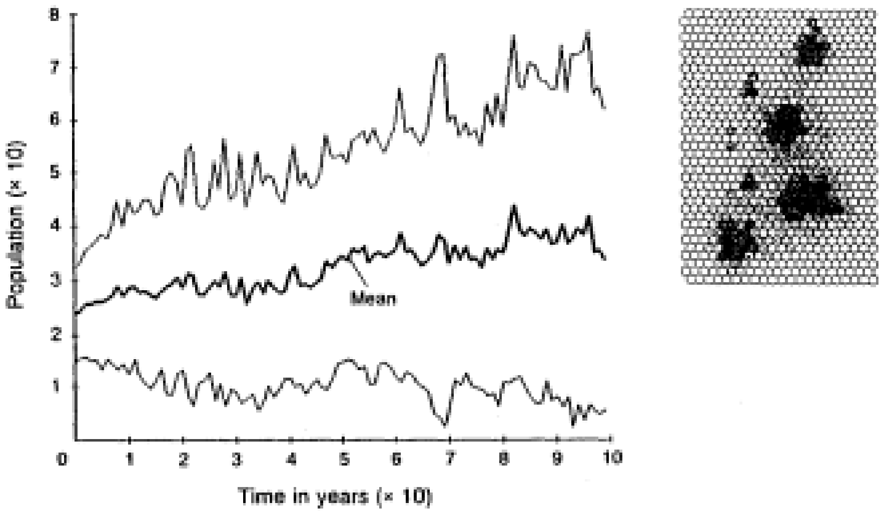

FIGURE 13. Landscape simulation with a reserve system consisting of clusters of suitable habitat surrounded by marginal habitat. The population was initialized with owl pairs occupying all suitable sites. The results are based on 30 simulations. Shading is based on mean pair occupancy.

suitable habitat. In a landscape containing a gradient of habitat qualities, there will be source locations that produce an excess of young, and sink locations into which some of these juveniles travel. When the possibility of nesting in the sink locations exists, populations will occur exterior to the designated reserve network, even though the vital rates from these areas do not provide for a self-supporting population (compare Figures 13 and 14). These results suggest that the presence of sink areas adjacent to habitat clusters may have a negative impact on the stability of the reserve. Even though the mean population size of the entire landscape is higher in the source-sink system, the mean occupancy of the reserve clusters is lower and the variability of the system increases with time.

DISCUSSION

Inferences from the deterministic analyses

The analyses of Lande (1988) and Noon and Biles (1990) demonstrate that λ shows an extreme sensitivity to variation in adult survival rate and a relative insensitivity to fecundity or preadult survival rates. Two types of information, however, are relevant to a species' population growth rate. One is the sensitivity of λ to variation in life history characters; the other concerns life history attributes showing the most natural variation. Varia-

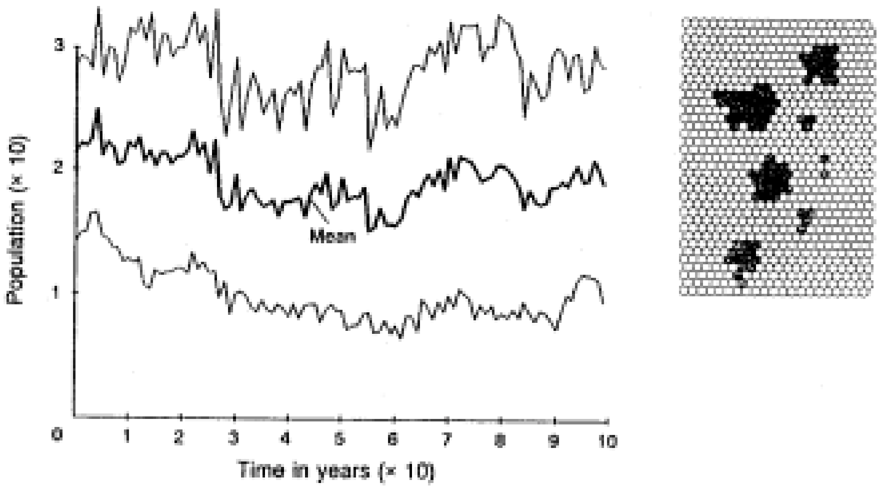

FIGURE 14. Landscape simulation with a reserve system consisting of clusters of suitable habitat surrounded by unsuitable habitat. The population was initialized with owl pairs occupying all suitable sites. The results are based on 30 simulations. Shading is based on mean pair occupancy.

tions in growth rate (λ) may be associated more closely with attributes showing extensive natural variation. In the case of the northern spotted owl, the effects of landscape pattern on survival during dispersal may induce high levels of both spatial and temporal variation in first-year survival rate. As habitat fragmentation continues, the uncertainty of successful dispersal will become progressively more relevant to the likelihood of persistence. The effects of landscape pattern on demographics are difficult to track analytically, but can be addressed through computer simulation.

Shifts in life history parameters

Because the static stage-projection model is a single-sex, nonspatial model, its extrapolation to population dynamics in real landscapes is limited. The simulation models diverge from this structure by including the dynamics of both sexes and the effects of search efficiency-as, for example, in the individual territory model (Figure 15). In this model, juvenile survival, dependent on finding a suitable site, is largely defined by search efficiency. Similarly, search efficiency regulates the movement between a pool of singles and the reproductive adult class. Pair survival occurs only when both members survive with probability s^2 rather than s, for a single-sex model (Figure 15). Therefore, if the probability of pair formation is low, the number of reproductive females will decline more quickly than indicated by the stage matrix model.

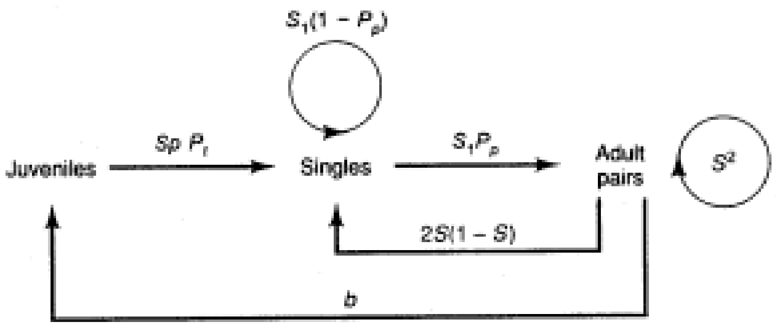

FIGURE 15. A flow diagram of the life history structure used in the individual territory model. P_t is the probability of finding a territory, P_p is the probability of pairing.

The territory cluster model has a simpler life history structure than the individual territory model, but more complex spatial dynamics. The only demographic parameter affected by search is s_0 (= $s_p s_d$). Being a single-sex model, it underestimates pair turnover rates, particularly in small isolated clusters, and contains no Allee effect. These two features lead to optimistic predictions regarding the fate of owl populations.

The landscape model is a two-sex model that maintains a strict stage structure but allows for movement between reproductive and nonreproductive classes (Figure 16). In this model, survival rates are differentially affected by search to the extent they are explicitly linked to properties of a landscape map. For example, survival may decrease in poor-quality habitat. In contrast to the previous two models, in the landscape model juveniles that fail to locate a suitable site do not die. As a consequence, search efficiency has less of a direct effect on s_0, but has a strong effect on the dynamic movement between the reproductive and non-reproductive stages. To the extent that search inefficiency prevents pair formation, fecundity (*b*) declines and λ decreases accordingly.

The role of clusters

In a spatial model with search, a system composed of clusters is more stable than a diffuse system because clusters produce regions where search efficiency is maximized. In a cluster of suitable territories, a population can recover from low occupancy because search efficiency will remain high. Dispersing males have a high probability of finding habitats immediately adjacent to existing pairs. Dispersing females will more easily find territorial males because of their adjacency. The key to stable populations within clusters is that they be large enough to avoid frequent local extinction due

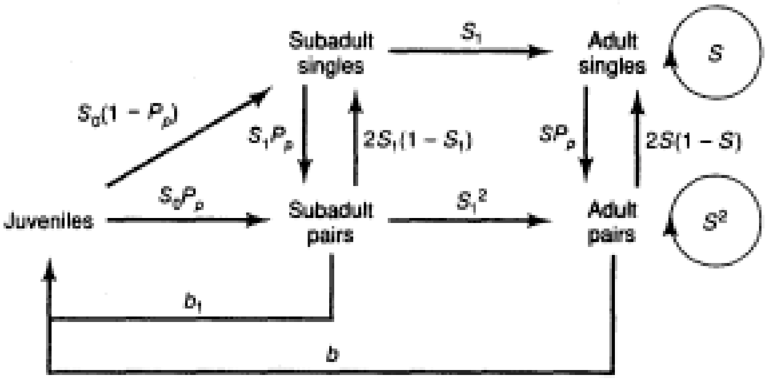

FIGURE 16. A How diagram of the life history structure used in the landscape model. P_p is the probability of pairing.

to stochastic demographic events. Based primarily on demographic uncertainty, this suggests a minimum cluster population size of about 20 breeding pairs (see also Richter-Dyn and Goel, 1972). Even in a diffuse system with a large number of 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. As the density of reproductive pairs decreases, the probability of new pair formation at isolated sites also decreases due to a decreased density of dispersing owls.

The effects of shape

The negative effects, of cluster irregularity can also be explained through the effect of shape on search efficiency. Circular clusters are the most stable because the density of suitable habitat is locally maximized. All other geometric forms will have reduced search efficiency when compared with a circular cluster. The effects of cluster irregularity are, in fact, probably more pronounced than is indicated by Figures 10-12. In these simulations, the risks associated with crossing poor-quality habitat were identical to those encountered in suitable habitat. If greater risks were encountered in the poor habitat, the effects of irregular cluster shape would be accentuated.

Source-sink dynamics

The increase in the variance of population size observed in landscapes in which breeding occurs in sink locations outside of the clusters (Figure 13) is primarily due to increased variance in adult survival (*s*). If breeding is limited to the clusters, the population will equilibrate with a relatively constant proportion of the population within the clusters and dispersing through the matrix. Changes in λ will be bounded by the levels of demographic and environmental stochastieity, and population variability will remain relatively constant over time. In contrast, when breeding occurs exterior to the clusters, the variability in λ will depend not only on environmental stochasticity but also on the proportion of the population within the clusters. The bounds on λ will be determined by the proportion of the population found outside the clusters ± the impact of environmental stochasticity. Because the simulations reported here were initialized with reproductive pairs restricted to clusters, the divergence from this state increases with time (Figure 13).

The decline in mean occupancy within the clusters in the source sink system (Figure 13) is due to decreased interaction between the clusters. Dispersing juveniles that settle exterior to the clusters would, if this option were not available, continue searching. Some of this search would return owls to clusters, increasing the recolonization rates. Thus a reserve design may be more stable if the boundaries between the reserve and the surrounding landscape are very distinct, since sink areas exterior to the reserve system may lead to suboptimal choices on the part of the dispersing juveniles. In particular, because juveniles settle outside of clusters, reserve systems with adjacent marginal habitat may be more prone to extinction than reserves surrounded by totally hostile habitats (cf. Figure 13 with Figure 14). This effect can arise even though the total population (number in the reserve plus adjacent habitats) is enhanced by marginal habitats.

CONCLUSIONS

The negative consequences associated with unsuccessful search are quailtatively similar in all three models but, due to differences in the mechanics of search, different inferences can be drawn from each model. All of these inferences yield insights into the probable efficacy of particular reserve designs.

The primary inferences drawn from the individual territory model are that the introduction of environmental stochasticity does not change the inflection point for the extinction threshold and that, in landscapes experiencing a high rate of habitat loss, both occupancy and demographic rates may underestimate the risk of extinction. The territory cluster model demonstrated that, for a given area, large clusters spaced farther apart on the landscape were more stable than small clusters that were closer together, and, assuming low to moderate dispersal rates among adjacent clusters, 15-20 suitable territories per cluster represents a likely stability threshold. The landscape model demonstrated that the shape of clusters is nearly as important as their size. Further, it raised the possibility that, in a landscape consisting of a gradient of habitat qualities, the presence of marginal habitat adjacent to a reserve may not help the owl population, and may even increase its risk of extinction. In addition, the landscape model integrates landscape-level vegetation characteristics into a spatially explicit distribution of habitat qualities. This allows one to project the population consequences of current and future landscape patterns.

The models we have described in this chapter are much more than academic exercises. In particular, explicit links between vegetation characteristics and the expected value of the vital rates at the scale of individual territories have been developed for the northern spotted owl in Washington and Oregon (J. Bart pers. comm.). Concurrently, vegetation maps are being drawn based on Forest Service and Bureau of Land Management data which describe all federal lands in western Oregon and Washington in terms of habitat suitability for spotted owls. Merging our landscape models with such detailed habitat maps will allow us to better design old-growth reserves that favor the persistence of the northern spotted owl. In addition, the strategy we develop should be applicable to a wide range of threatened species with narrow habitat requirements.

Allen, H. and L. Brewer. 1985. A progress report for the cooperative administrative study to monitor spotted owl management areas in National Forests in Washington. Washington Department of Fish and Game, Olympia, WA.

Brownie, C. D. R., J. E. Hines, and J. D. Nichols. 1986. Constant parameter capture-recapture models. Biometrics 24:561-574.

Caswell, H. 1989. Matrix Population Models. Sinauer, Sunderland, MA.

Caswell, H., R. J. Naiman, and R. Morin. 1984. Evaluating the consequences of reproduction in complex salmonid life cycles. AquaCulture 43:123-134.

Caughley, G. 1977. Analysis of Vertebrate Populations. Wiley, New York.

Doak, D.F. 1989. Spotted owls and old-growth logging in the Pacific Northwest. Conserv. Biol. 3:389-396.

Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. General Technical Report PNW-162, U.S. Department of Agriculture Forestry Service.

Forsman, E. 'D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. 87:1-64.

Franklin, A. B. In press. Population regulation in northern spotted owls: Theoretical implications for management. In Wildlife 2001: Populations, D. McCullough and R.H. Barrett (eds.). Elsevier, New York.

Franklin, A. B., J. A. Blakesley, and R. J. Gutierrez. 1989. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northern California: Preliminary results, 1989. California Fish and Game Department Technical Report 1989-4, Sacramento, CA.

Franklin, A. B., J. A. Blakesley, and R. J. Gutierrez. 1990. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northern California: Preliminary results, 1990. California Fish and Game Department Technical Report 1990-9, Sacramento, CA.

Gutierrez, R. J., A. B. Franklin, W. LeHaye, V. J. Meretsky, and J. P. Ward. 1985. Juvenile spotted owl dispersal in northwestern California: Preliminary results. In Ecology and Management of the Spotted Owl in the Pacific Northwest, R. J. Gutierrez and A. B. Carey (eds.). USDA Forest Service General Technical Report PNW-185. pp. 60-65.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and dilution-stochastic model. Biometrika 52:225-247.

Keyfitz, N. 1968. Introduction to the Mathematics of Populations. Addison-Wesley, Reading, MA.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. In press. The effects of varying dispersal capabilities on the population dynamics of the northern spotted owl. Conserv. Biol.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. Am. Nat. 130:624-635.

Lande, R. 1988a. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia 75:601-607.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18

Levins, R. 1970. Extinction. In Some Mathematical Questions in Biology, Vol. 2. M. Gerstenhaber (ed.). American Mathematical Society, Providence, RI. pp. 77-107.

Lord, J. M. and D. A. Norton. 1990. Scale and spatial concept of fragmentation. Conserv. Biol. 4:197-202.

Mertz, D. B. 1971. The mathematical demography of the California condor population. Am. Nat.105:437-453.

Meslow, E. C. 1985. Dispersal of juvenile northern spotted owls in the Pacific Northwest Douglas-fir region. Annual report, USDA Forest Service Pacific Northwest Experiment Station, Portland, OR.

Miller, G. S. 1989. Dispersal of juvenile northern spotted owls in western Oregon. M.S. Thesis, Oregon State University, Corvallis, OR.

Moen, C. A., A. B. Franklin, R. J. Gutierrez. 1991. Spotted owl age-class determination. Wildl. Soc. Bull. 19:489-493.

Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat conservation planning: Reserve design for the northern spotted owl. Ecol. Appl. 2:3-17.

Nichols, J. D., G. L. Hensler, and P. W. Sykes, Jr. 1980. Demography of the Everglade kite: Implications for population management. Ecol. Model. 9:215-232.

Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in northwest California. J. Wildl. Manage. 54:1-10.

Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. Theoret. Pop. Biol. 3:406-433.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika 52:249-259.

Shaffer, M. L. 1985. The metapopulation and species conservation: The special case of the northern spotted owl. In Ecology and management of the spotted owl in the Pacific Northwest, R. J. Gutierrez and A. B. Carey (eds.). USDA Forest Service General Technical Report PNW-185. pp. 86-99.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A Conservation Strategy for the Northern Spotted Owl. Report to the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. Portland, Oregon.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. In Conservation Biology: The Science of Scarcity and Diversity, M. E. Soule (ed.). Sinauer, Sunderland, MA. pp. 237-256.