

Reserve Design for Territorial Species: The Effects of Patch Size and Spacing on the Viability of the Northern Spotted Owl*

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Abstract: *Designing a reserve system for a threatened territorial species such as the Northern Spotted Owl requires the balancing of biological necessity against economic reality. The Spotted Owl conservation plan and the Pacific Northwest timber industry are in conflict because both demand large areas of mature and old-growth coniferous forests. The primary focus of this paper is the efficient design of a reserve system for territorial species with obligate juvenile dispersal. We examine the relationship between the degree of aggregation of suitable owl habitat, the level of occupancy of that habitat by pairs of Spotted Owls, and the likelihood of owl persistence given different amounts and spatial arrangements of suitable habitat across the landscape. We develop a population model for Spotted Owls that includes an abstracted forest landscape where suitable owl habitat is arrayed in clusters embedded in a matrix not suitable for owl habitation. We conclude from our study of this model that, for any given fraction of the landscape set aside in reserves, the level of occupancy (efficiency of use) of that area will increase as the aggregation of suitable habitat increases. After the reserves reach a size that includes territories for 20 to*

Diseño de reservas para especies territoriales: El efecto del **tamaño** de parche y del espacio en la viabilidad del **Búho** moteado del norte

Resumen: *El diseño de un sistema de reservas para especies territoriales en peligro de extinción, tales como el búho moteado del norte, requiere del balance entre necesidad biológica y realidad económica. El plan de conservación del búho moteado y la industria maderera del Pacífico Noroeste están en conflicto debido a la demanda de grandes áreas de bosques de coníferas maduros y de crecimiento antiguo. El principal foco de este trabajo es el diseño eficiente de un sistema de reservas para especies territoriales con dispersión juvenil obligatoria. A los efectos de alcanzar este logro nosotros examinamos la relación entre el grado de agregación de hábitats adecuados para el búho, el nivel de ocupación de tales hábitats por parejas de búhos moteados y la probabilidad de la persistencia de búhos bajo diferentes cantidades y ordenamientos de hábitats adecuados a lo largo del paisaje. Desarrollamos un modelo poblacional para búhos moteados que incluye un paisaje forestal abstracto, donde hábitats adecuados para el búho se ordenan en grupos enclavados en una matriz que no es adecuada para el búho. A partir de nuestro estudio de este modelo concluimos que, para cualquier fracción del paisaje destinado a reservas, el nivel de ocupación (eficiencia de uso) de dichas áreas aumentará*

* The model described in this paper is an extension of the territory-cluster model from the conservation plan for Northern Spotted Owls (Thomas et al. 1990).

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25 owl pairs, however, there are diminishing returns from further increases. Preserving connectivity and increasing the geographical extent of the reserve begin to outweigh increased size in importance in insuring the long-term viability of the species.

Introduction

To be both effective and acceptable for implementation, a conservation strategy must address two basic objectives: first, the strategy must provide for a high likelihood of long-term persistence of the species and, second, it must do so with a minimal impact on resources that have competing economic values. In this paper we address these requirements in the context of conservation planning for the Northern Spotted Owl (*Strix occidentalis caurina*). In many ways the timber industry and the Northern Spotted Owl are in direct conflict because they both demand incompatible access to the same habitat—mature and old-growth coniferous forests in the Pacific Northwest. The practical questions concern to what extent and in what spatial configuration can the timber resource be exploited without endangering the future existence of the Northern Spotted Owl.

It is apparent from earlier work on the viability of the Northern Spotted Owl that there may be sharp thresholds in habitat availability below which the long-term existence of this subspecies is threatened (Lande 1988a; Doak 1989; Lamberson et al. 1992; Carroll & Lamberson 1993). Further, it has recently become apparent that the distribution and shape of contiguous areas of suitable habitat can be nearly as important as the total amount of suitable habitat when it comes to insuring the stability of local populations of a threatened species (McKelvey et al. 1993; Carroll & Lamberson 1993).

In this paper we examine the relationship between the degree of aggregation of suitable habitat, the level of occupancy of that habitat by pairs of Spotted Owls, and the likelihood of owl persistence given different amounts and spatial arrangements of suitable habitat across the landscape. By suitable, we mean habitat utilized for nesting, with associated expected birth and death rates that allow for a stable or growing population. We are particularly interested in the efficient allocation of suitable habitat in preserving the owl, that is, an acceptable minimum number of hectares required to maintain a given number of owls with a high likelihood of persistence for the next century. We approach this

a medida que la **agregación** de habitats adecuados incrementemente. Sin embargo, existe un rendimiento decreciente para aumentos que incrementen el **tamaño** de las reservas **más allá** de territorios que alberguen de 20 a 25 parejas de **búhos**. La **preservación** de la conectividad y el incremento de la **extensión geográfica** de la reserva, comienza a superar el aumento en **tamaño** de la reserva en cuanto a su importancia para asegurar la viabilidad a largo plazo de la especie.

problem by building a model that incorporates spotted owl population dynamics and, in addition, contains a stylized model of landscape pattern where the suitable habitat is arranged in clusters within a matrix of habitat that is not suitable. We believe the general inferences drawn from our analyses of Spotted Owl populations may be applicable to other territorial species with obligate juvenile dispersal.

Other Models

Most of the earlier attempts at modeling populations of Spotted Owls have either used models that contained no spatial structure (Boyce 1987; Marcot & Holthausen 1987; Noon & Biles 1990) or simply assumed that the suitable habitat was arranged uniformly or distributed randomly across the landscape (Lande 1987, 1988a; Lamberson et al. 1992). Other authors who have considered clusters of suitable habitat include Doak (1989), Carroll and Lamberson (1993), McKelvey et al. (1993), and ourselves in an earlier version of this model (described in Thomas et al. 1990: Appendix M).

The model by Doak considers dispersal both within and outside of clusters of suitable habitat, but both are treated somewhat differently than in ours. His model assumes that each cluster is equally accessible when the dispersing juvenile leaves its natal cluster. Doak's dispersal equations for successful dispersal within and between clusters do not incorporate specific geometry for the landscape, but instead he evaluates coefficients that reflect the ease with which dispersing owls may penetrate the landscape. Our model is more realistic in that between-cluster dispersal success is a function of the size of clusters, the distance between clusters, and the costs of locating them.

Carroll and Lamberson (1993) developed an analytic model in which they considered spatial structure, but they were only able to do an equilibrium analysis. Their results are completely compatible with ours even though their approach is entirely different. Both models establish a persistence threshold related to the amount of suitable habitat available and observe that the threshold is lowered (occurs at a lower density of suitable habitat) by increased aggregation of the suitable habitat.

Model Description

In the territory-cluster model, the landscape is portrayed as a rectangular array of identical circular clusters containing potential owl habitat (Fig. 1). Each cluster contains a variable number of owl home ranges (territories or sites), all of identical size (for example, 1000 ha). There is no interstitial space between sites within a cluster. The landscape matrix between clusters was assumed to be entirely unsuitable for owl territories, while the clusters were either partially or totally suitable. Thus, a cluster was a collection of territories with all sites, or only a subset of the sites, within a cluster being suitable owl habitat. The carrying capacity of a cluster, measured in terms of owl pairs, was equal to its number of suitable sites.

The life-history model was an all-female stage projection model with the stage-classes being juveniles, subadults, and adults. This structure was similar to that of Boyce (1987 unpublished data), Lande (1987, 19884, and Noon and Biles (1990). Survival rates were treated as binomial random variables, and fecundity in our model was stochastic, with each year's fecundity drawn from a beta distribution. (The model also permits fecundity to be deterministic or to have a good year/bad year form.) Before dispersal, the number of juvenile owls was reduced by predispersal mortality (Table 1). These deaths were assigned at random to juvenile owls throughout the array of clusters. The mean values of the birth and survival rates used were chosen to approximate current estimates from field data (Table 1) but adjusted to allow the possibility of stable or growing populations.

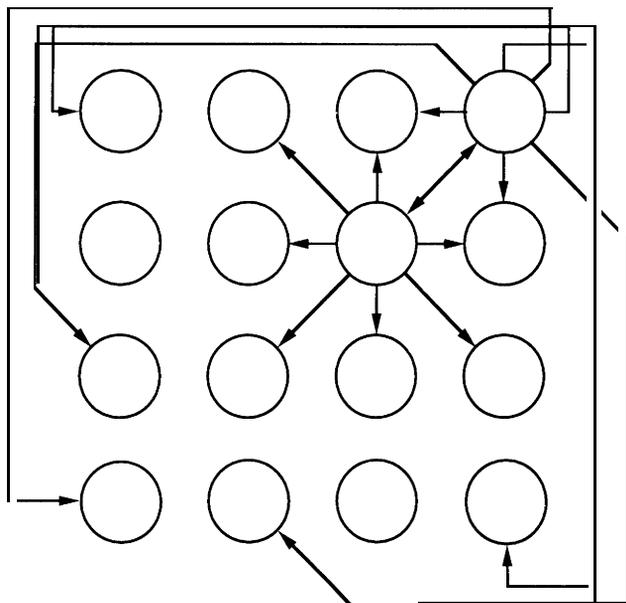


Figure 1. Example of a stylized landscape with a fixed array of circular clusters. Accessibility between clusters with wraparound effect is shown

Table 1. Estimates of survival and fecundity based on Franklin et al. (1990), and values used in model simulations.

Parameter	Franklin et al. Estimate	Model Values
Juvenile survival	0.159	—
Predispersal survival	—	0.60, 0.69
Subadult survival	0.83	0.83
Adult survival	0.84	0.92
Fecundity*	0.38	0.38

* Number of female young per territorial adult female.

Each cluster was composed of an assigned number of sites, with a given number (or percentage) of them considered suitable habitat. The population status of a cluster was measured in terms of adult female owls (age ≥ 2 years old), subadult ($1 \leq \text{age} < 2$ years), and postdispersal juveniles (age < 1 year). The total population for a cluster (exclusive of predispersal juveniles) was never allowed to exceed the carrying capacity of that cluster.

Because little is known of the behavior of Spotted Owls as they search for a suitable site, we chose to model this process as simply as possible. The model distinguished between dispersal within a cluster and dispersal between clusters (compare with Doak 1989). The dispersal within a cluster followed Lande (1987) with each dispersing owl allowed to sample with replacement a given number, m , of sites within the cluster. The probability of successful dispersal within the cluster was computed as 1 minus the probability of failing to find a suitable, unoccupied site within the given number of trials:

$$Prob(\text{success}) = 1 - \left[1 - \frac{\text{no. available suitable sites}}{\text{total no. sites}} \right]^m \quad (1)$$

No further mortality was assigned to juveniles that succeeded in finding a site within their natal cluster (see Carroll and Lamberson 1993 for a treatment of the cost of dispersal both within and outside of the clusters).

To determine the allocation of search effort within a cluster, we assumed a random walk. The assumption was that an owl could traverse one site in a single time step. We estimated, by simulation, the expected number of steps taken before crossing the boundary of a circular cluster, given a random starting point within the cluster. Based on 10,000 simulations for various sized clusters and regressing the number of steps taken before crossing the boundary, we estimated the following relationship:

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

For a cluster of size 20 sites, for example, on the average 8 sites are searched before the cluster was exited. The total number of sites sampled (searched) across all clusters was based on the upper bound of the 90th percentile of the maximum straight-line dispersal distances of

radio-tagged juvenile Spotted Owls (Thomas et al. 1990: 305) and the assumption that each site had a diameter of about 3.6 km.

If the juvenile female owl did not succeed in finding a territory within her natal cluster (based on a fixed number of searches), she 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, death resulted if a juvenile female moved in a direction that did not intersect a neighboring cluster. As an example, when suitable habitat accounted for 31% of the landscape, juvenile mortality from this source occurred in about 45% of the cases where juveniles were forced to disperse between clusters. Restricting the likelihood of selecting the correct direction to the immediate neighborhood slightly underestimated juvenile survival for small clusters. For a cluster of size 5 with 60% suitable habitat, for example, the maximum bias was an underestimate of 0.02 in mean occupancy rate.

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

$$\text{Prob}(\text{success}) = \exp(-k * d). \quad (3)$$

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 ($r^2 = 0.97$).

The overall between-cluster dispersal success probability is given by

$$\text{Prob}(\text{success}) = \text{Prob}(\text{intersects neighboring cluster}) * \exp(-k * \text{distance between clusters in km}). \quad (4)$$

Based on an average cluster size of 20 sites occupying 31% of the landscape, when $k = 0.035$, about 53% of juveniles that chose a direction that intersected one of the nearest neighbor clusters successfully arrived at that cluster (about 6.7 km away, edge to edge), which gives an overall success rate of about 24%. Because search begins in the natal cluster and moves through adjacent clusters, the search success in the model, as in nature, is a function of the condition of the landscape near the bird's natal site, as well as the forest matrix.

We envision that most conservation plans will reflect a compromise between the size of reserve areas and the distance between them. Assuming a constant percentage of the landscape as potentially suitable owl habitat and restricting that habitat to the clusters had two im-

portant consequences. First, as average cluster size increased, the distance between adjacent clusters increased in a predictable way (Fig. 2). We believe this consequence accurately reflects real-world constraints encountered when developing a species' conservation strategy. Second, the dispersal angle and the probability associated with selecting this angle were constant regardless of the average cluster size (as long as the fraction of the landscape included in clusters remained fixed).

Once a juvenile had successfully traveled to an adjacent cluster, she repeated the within-cluster search process as in the m possible searches of the natal cluster (Equation 1). The number of clusters searched could be systematically varied and was based on the total number of sites in the cluster. If m searches were unsuccessful in the first cluster, travel to additional clusters was allowed until the maximum number of sites to be sampled was exhausted. Dispersing owls were chosen sequentially, and the occupancy data within each cluster were updated after each dispersal.

For the results reported here, the landscape simulated by the model had a "wrap-around" structure to exclude possible anomalous output that might result from edge effects (Fig. 1). The clusters on the right side of the grid were treated within the model 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 similar fashion. The effect is to equate immigration and emigration rates, and to assure that all clusters have exactly the same number of neighboring clusters.

Unless otherwise noted, the model was initialized at approximately 90% of a fixed carrying capacity with the age-structure near that expected at equilibrium (stable age-structure about 13% juveniles, 8% subadults, 79% adults). All simulations were initialized with approxi-

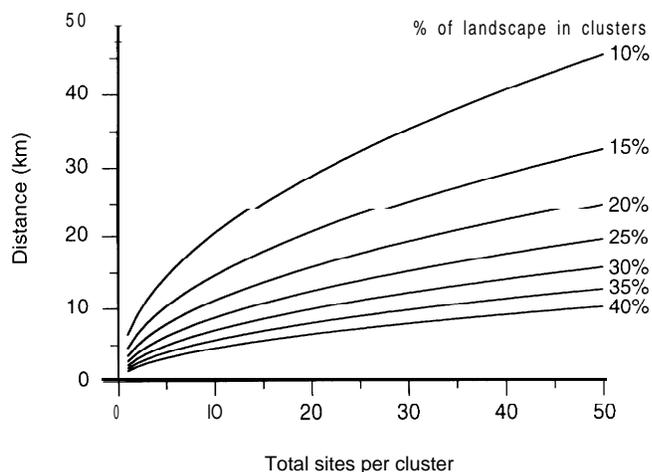


Figure 2. Edge-to-edge distance to nearest neighbor versus total sites per cluster for various percentages of landscape in clusters.

mately the same number of owls—thus, the array size (Fig. 1) was larger for smaller clusters than for larger clusters. The owls were distributed to the clusters at random, with care that none of the clusters exceeded its carrying capacity. All simulations were stochastic, with 50 replications per simulation.

Model Parameterization

The life-history component of the model was parameterized based on the demographic studies of Franklin et al. (1990), except that adult female survival was increased to allow for a stable or increasing population (Table 1). We assumed an annual adult and subadult survival probability of 0.92 and 0.83, a juvenile dispersal survival of 0.60 and 0.69 (both produce overall juvenile survival rates greater than those reported by field studies), fecundity (number of young fledged/adult female) of 0.76, and a 1:1 sex ratio at birth (see Table 1). Reproduction first occurred at age two years.

The standard search pattern used in these simulations was to have a dispersing owl choose, with replacement, a random sample of sites. The number of sites chosen (m) was equal to 0.4 times total sites within a cluster. If the sample chosen from the first cluster did not result in finding a suitable unoccupied site, the owl attempted to disperse to a randomly chosen adjacent cluster where the sampling process was repeated until successful, or until the total number of sites sampled equalled 22. For example, assuming successful movement between clusters, if the clusters were each 20 total sites, the sample from the first cluster would consist of 8 sites and the sample from the second cluster would again include 8 sites; if necessary, a final sample of 6 sites from a third cluster was chosen to complete the 22 allowed. The value for maximum number of searches (22) was based on the dispersal distances of radio-transmitted juveniles (above) and the fact that a 1000-ha site has a diameter of approximately 3.6 km.

The landscape parameters, based on the best estimates of the current status of lands of the U.S. Forest Service and Bureau of Land Management in the Northern Spotted Owl range, are variable and imprecise. Estimates of the percentage of the landscape within the proposed habitat conservation areas (HCAs; Thomas et al. 1990) range from 18% to 31% in different regions (Noon, unpublished data). Estimates of the percentage of the habitat within HCAs that is currently suitable range from less than 30% in the Oregon Coast Range to about 60% in northwestern California. Thomas et al. (1990) recommended that HCAs contain enough area to support at least 20 pairs of owls when suitable habitat has regrown. HCA sizes are variable, however, because among other things home range size is variable (Thomas et al. 1990: Appendix I). Given this variability, for most analyses we selected default settings for parameters of

25% of the forested landscape in clusters, of which 60% was suitable, with 20,000 ha (20 potential owl sites) in each cluster.

Results

The number of model parameters, their range of values, and their possible combinations were immense (Table 2). We examined model behavior using two different techniques. First, to incorporate the full range of potential variability in the model, we performed Monte Carlo sensitivity analyses. These allowed each parameter, for each simulation, to vary independently within some reasonable range of variation (Table 2). Because of the complete randomization of parameter values, we performed a large number of simulations (10,000), sampling from a uniform distribution over each parameter interval. For each 100 year simulation, we recorded three response variables: mean occupancy per suitable site, average population size in the last 30 years of the simulation, and whether the population had persisted or gone extinct (0, 1 binary variable). The parameter values, selected during the randomization process for each simulation, served as predictor variables. We used two statistical models to examine response variable sensitivities: multiple regression (mean occupancy and average population size as dependent variables) and two-group discriminant function analysis (population persists or goes extinct). The interpretation of the sensitivities were very similar among the statistical models, so we report only the discriminant results.

Model output is a multi-dimensional, nonlinear surface. Sensitivity changes depending on the region of space over which parameters are allowed to vary. Knowledge of the reaction surface of each parameter when varied independently allowed us to determine those regions in which the model response was mostly linear. Thus, for the Monte Carlo simulations, we restricted the range of some parameter values in order to more clearly interpret the results of the linear statistical models.

We also performed a more restricted set of analyses varying selected model parameters one at a time, holding all others constant. This allowed us to explore in

Table 2. Values of model parameters used in the simulations.

<i>Parameter</i>	<i>Range of Variation</i>
Percentage of the landscape within the clusters	5-40
Cluster size	5-45
Percentage of sites within clusters that are suitable	20-100
Number of sites searched per cluster	0.2, 0.4, and 0.8 times cluster size
Dispersal coefficient	0.0004-0.30

Table 3. Two-group discriminant analysis contrasting populations that went extinct (E) or persisted (P) over 100-year simulations.*

Variable	Variable Range	Group Means (SD)		Structure Coefficients
		E	P	
Cluster size (CS)	5-20	11.18 (4.46)	12.93 (3.99)	0.300
Percent of suitable sites per cluster	10-40	21.22 (8.48)	29.59 (7.62)	0.683
Total number of searches (TS)	3-20	9.71 (5.36)	13.60 (4.22)	0.552
Dispersal coefficient	0.0-0.1	0.05 (0.03)	0.04 (0.03)	-0.195
CS by TS interaction		102.52 (65.65)	178.52 (82.43)	0.680
Sample size		5332	4668	
Wilk's lambda			0.549	
Approximate F-statistic			1639.00**	

* Summary statistics and group means and standard deviations of variables included in the model are presented
 Proportion of the landscape within clusters = 0.20.

** Significant at $p < 0.001$.

more detail the nonlinear relationships between occupancy rate and various parameter values. Specifically, we explored the effects of varying cluster size and spacing, key components common to any reserve design, under the assumption that the majority of sites within clusters were suitable and static.

Monte Carlo Sensitivities

Based on the randomized parameter values and their interactions, we observed significant discrimination between simulated populations that persisted and those that went extinct (Table 3). Interpreting the discriminant model on the basis of total structure coefficients (Green 1978:271-273), the most important variables were cluster size, total searches and their interaction, the proportion of the cluster that was suitable habitat, and the costs of dispersal between clusters (Table 3). Based on these variables, the a posteriori probability of correct classification of each simulation into either the persistent or extinct group exceeded 80%.

INDIVIDUAL PARAMETER SENSITIVITIES

The cluster size at which mean occupancy stabilized was affected by the number of sites that were searched within the natal cluster before dispersal into the surrounding matrix (Equation 1). To explore the sensitivity of mean occupancy to variation in search, we fixed the total number of sites sampled but systematically varied the number of sites searched in the natal and subsequent clusters (Fig. 3). Assuming 20 sites per cluster, 60% suitable, mean occupancy was moderately sensitive to variation of within-cluster search efficiency. For example, the difference in equilibrium occupancy between 4 sites and 16 sites searched per cluster was roughly 20 percent (Fig. 3). The sensitivity to within-cluster search efficiency increased as clusters became smaller. In contrast, increasing the total number of searches beyond about 22 had little effect on mean occupancy for any of the within-cluster search allocations we examined.

VARYING BETWEEN-CLUSTER DISPERSAL RISKS

We assumed that juvenile owls search systematically within their natal cluster for a vacant site before entering the forest matrix to search for another cluster. If dispersing juveniles allocate less search effort to their natal cluster, they will leave that cluster sooner and spend more time moving through the matrix. As the nature of the matrix changes, however, dispersal risks may increase and affect overall occupancy rates. To investigate the effect of increased dispersal costs, we varied the dispersal parameter k (Equation 4) but fixed the total number of searches. The general result was a reduction in equilibrium mean occupancy (Fig. 4). For clusters of size 20, for example, the reduction due to increasing k was about 20%. If less search is allocated to each cluster and dispersal risks are higher, mean occupancy is reduced even further.

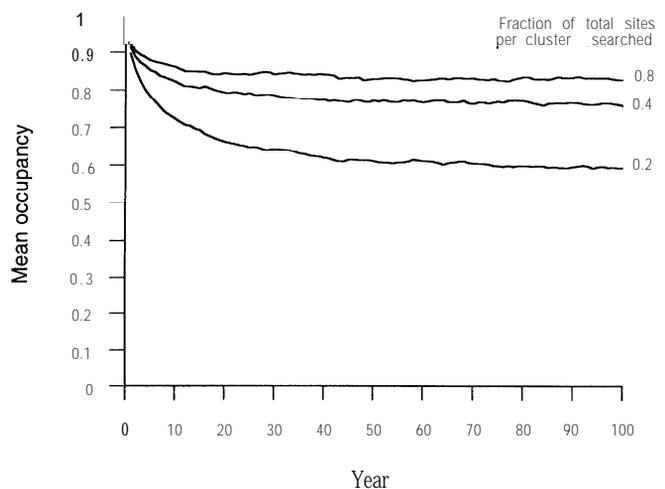


Figure 3. Mean occupancy versus time for various numbers of sites sampled per cluster during the search process. Sample sizes were 0.2, 0.4, and 0.8 times the total number of sites per cluster. All clusters had 20 sites, with 60% of the sites suitable.

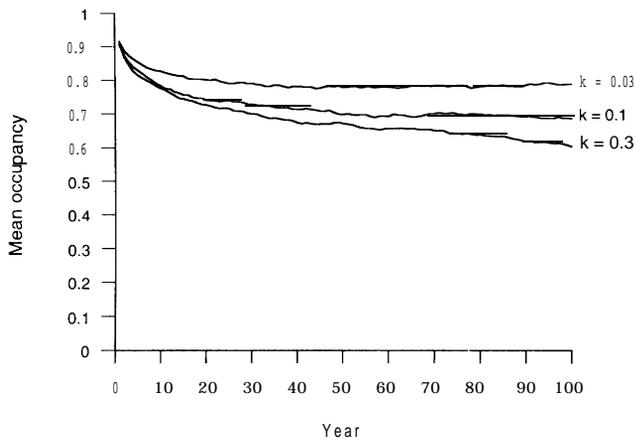


Figure 4. Mean occupancy versus time for various values of the exponential coefficient in Equation 3. All clusters had 20 sites, with 60% of the sites suitable

VARIATION IN CLUSTER SIZE

The most significant results of this study pertain to the relationship between mean occupancy and the number of sites per cluster. Assuming 60% of the sites in each cluster to be suitable (approximately the current condition), the number of sites sampled per cluster to be 40% of cluster size, and a maximum of 22 sites searched, we did not observe a stabilization of mean occupancy within 100 years until each cluster contained at least 15 sites (Fig. 5). Clusters of 20 sites stabilized at approximately 77% occupancy, while clusters of 45 stabilized at near 90%. Once clusters contained 30 sites, however, increasing cluster size had little effect

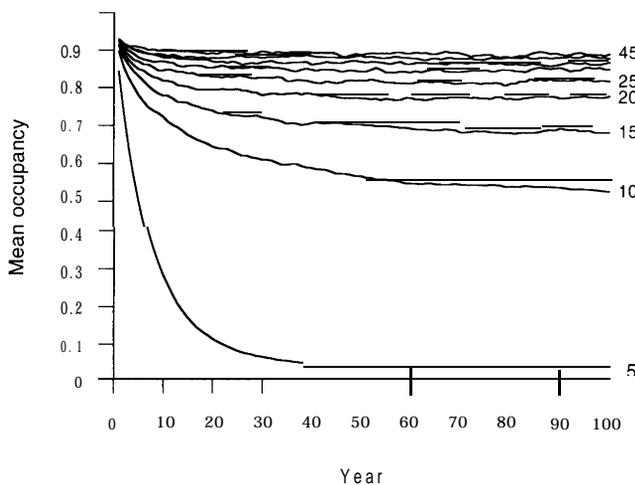


Figure 5. Mean occupancy versus time for various cluster sizes with 60% suitable within cluster. Total sites per cluster = 5, 10, 15, 20, 25, 30, 35, 40, and 45, with the lowest curve representing 5 sites per cluster and moving progressively upward to the top curve, which represents 45 sites per cluster.

on the equilibrium level of mean occupancy (Fig. 5), with larger clusters stabilizing between 85% and 90% occupancy.

The sensitivity analyses suggest that the equilibrium mean occupancy would depend on the percentage of suitable sites within a cluster. Assuming that 80% of the sites within a cluster are suitable, mean occupancy increased beyond that observed at a level of 60% suitable (compare Figs. 5 and 6). Occupancy rate for clusters of 5-10 sites, however, remained well below those with 15 or more sites per cluster.

Another approach to choosing an optimal cluster size is to compute the number of owls expected to occupy a fixed amount of suitable habitat. Based on mean occupancies at 100 years (Fig. 5), we plotted mean occupancy versus cluster size as a measure of the efficiency of land use. For a fixed allocation of land in a reserve system, larger clusters support larger equilibrium population sizes (Fig. 7).

VARIATION IN THE FRACTION OF LANDSCAPE IN RESERVES

Variation in the percentage of the landscape within clusters interacted with cluster size to affect mean occupancy. We investigated the strength of this interaction through a series of simulations. Assuming that 60% of the sites in each cluster were suitable, we systematically varied the percentage of landscape in clusters and cluster size. For a given cluster size, increasing the percentage of the landscape in clusters increased mean occupancy (Fig. 8). The increase, however, was much more dramatic for small clusters (5-10 sites) than for large clusters (20 or more sites).

Given the relationship between the landscape frac-

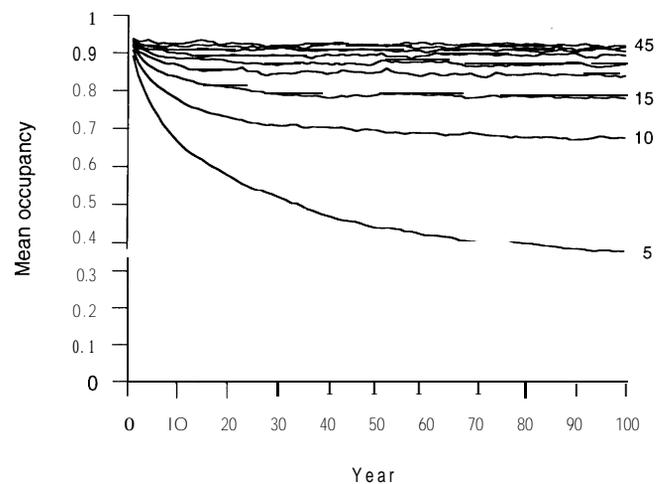


Figure 6 Mean occupancy versus total sites per cluster, with 80% suitable within cluster. Total sites per cluster = 5, 10, 15, 20, 25, 30, 35, 40, and 45, moving progressively upward with increasing sites per cluster:

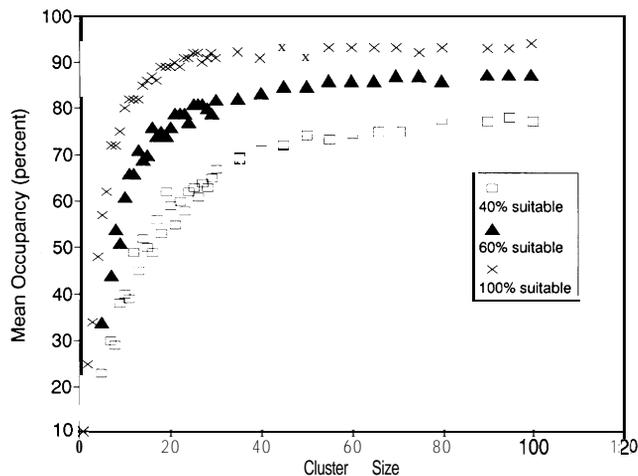


Figure 7. Mean occupancy versus total sites per cluster for 40%, 60%, and 100% of the sites suitable within each cluster. Occupancies are averaged over the last 10 years of each simulation.

tion within clusters and cluster spacing (Fig. 2), different levels of allocation to a reserve system can also be viewed in terms of the distance between clusters. For clusters with less than 20 sites, we found mean occupancy to be strongly affected by increased spacing between clusters (Fig. 9). In contrast, clusters with more than 25 sites showed minimal distance effects beyond about 30 km spacing (Fig. 9). Including low levels of environmental variation in the survival rates lowered occupancy rates 3-7%. This suggests that in reality

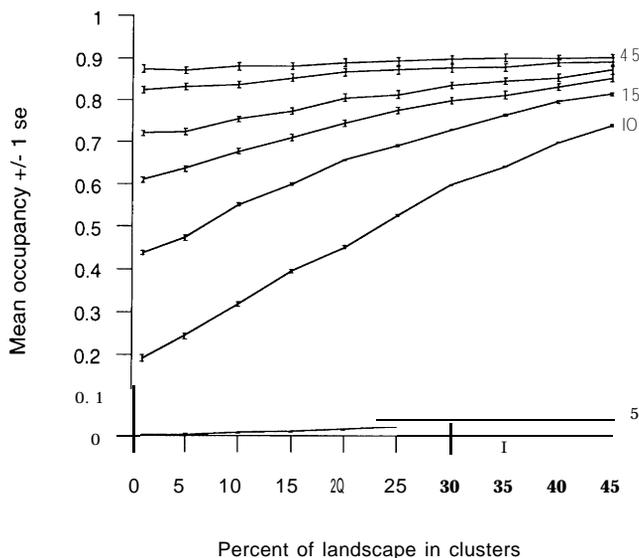


Figure 8. Mean occupancy \pm 1 S.E. versus percentage of landscape in clusters, for various total sites per cluster. Occupancy rates represent the last 10 years of each simulation. Total sites per cluster = 5, 10, 15, 20, 25, 30, 35, and 45, of which 60% were suitable sites.

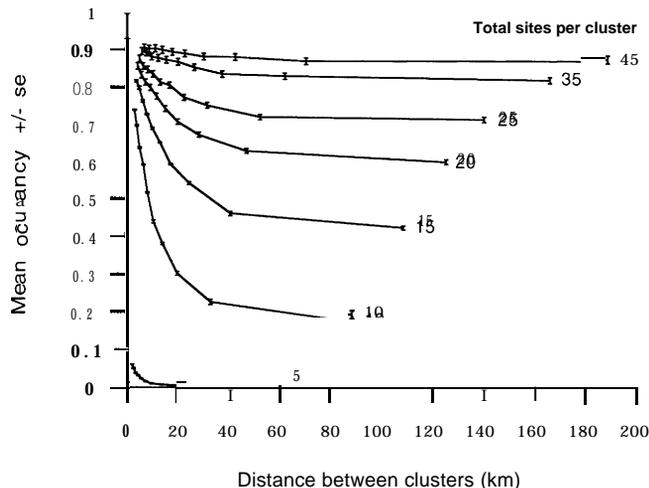


Figure 9. Mean occupancy \pm 1 S.E. versus edge-to-edge distance to nearest cluster, for various total sites per cluster. Occupancy rates represent the last 10 years of each simulation. Total sites per cluster = 5, 10, 15, 20, 25, 35, and 45, of which 60% were suitable sites.

slightly larger cluster sizes are needed for the same levels of occupancy.

In general, mean occupancy increased with cluster size, percentage of suitable sites, and percentage of the landscape in clusters. With clusters of more than 25 sites, however, changes in landscape percentage had little effect on mean occupancy. This result was a consequence of our assumptions about the behavior of dispersing juveniles. With about 35 sites per cluster, a successful dispersal event usually occurred within the natal cluster. With fewer suitable sites, or smaller clusters, birds were frequently forced to leave their natal cluster and enter the surrounding matrix (Table 4). As a consequence, they had decreased dispersal success. Thus, to the extent that our within- and between-cluster dispersal equations reflect reality, cluster size is more important than cluster spacing.

Discussion

In keeping with the findings of Doak (1989) and Carroll and Lamberson (1993), we conclude that a conserva-

Table 4. Dispersal success rates for a range of cluster sizes.

Cluster Size	Found Site in Natal Cluster (%)	Found Site Outside Natal Cluster (%)	Successfully Dispersal Between (%)
5	43.0	13.6	37.3
10	52.1	11.6	29.4
15	55.0	6.1	25.0
20	55.8	5.4	21.6
25	59.6	2.3	18.6

tion plan that provides for clusters of territories above some minimal size should greatly increase the persistence likelihood of Spotted Owls, primarily by facilitating juvenile dispersal. Because of the uncertainties associated with environmental variation, precisely estimating a critical cluster size for a specified likelihood of persistence is very difficult at this time. Within the structure of our model simulation-60% of the sites suitable, moderate connectivity among clusters (Table 4), preferential search within the natal cluster before dispersal, equilibrium conditions, and no edge effect-clusters with 20 or more sites appear to support stable populations. As a member of a large, clustered population, an individual Spotted Owl becomes less susceptible to the uncertainties of between-cluster dispersal and the character of the landscape matrix.

Cluster size and the percentage of suitable sites were highly interdependent. On average, suitable territories are less contiguous in clusters below their potential, habitat-determined carrying capacities. Therefore, within-cluster dispersal becomes more uncertain, rates of territorial replacement when birds die are decreased, and birds spend more time traveling through the surrounding matrix. Collectively, these factors all contribute to lower survival and fecundity rates and increase the risks to long-term viability.

Of interest was the observation that once a minimum number of searches was allowed, the probability of finding a suitable site became largely independent of the number of searches. For the Spotted Owl life history and associated parameter values (Table 1), that value occurred at about 20 sites sampled (see Carroll and Lamberson 1993 for an analytical derivation).

Further, our results suggest that a reserve design that provides only for individual pairs or small clusters of pairs has a low likelihood of sustaining the species. In fact, even relatively large clusters for Spotted Owls have uncertain fates if they currently hold far less suitable habitat than their eventual carrying capacity. Such areas will need to be closely monitored until habitat within them has had time to recover. One way to increase their short-term occupancy rate is to increase their current effective size by preserving adjacent, suitable habitat.

We emphasize the fact that ours is an all-female model. This simplification eliminated the complications of mate finding, an additional source of uncertainty for dispersing birds. Consequences of mate finding difficulties are most pronounced for small clusters, or when the population is very diffuse relative to the amount of suitable habitat (Lamberson et al. 1992). Thus, the inclusion of search for mates will further reduce mean occupancies when cluster sizes are small, certainly when they contain less than 20 sites.

Models of the population dynamics of long-lived vertebrates are difficult to validate. Further, the output and inferences drawn from a model are always a reflection of

the model's structure. The patterns we observed in our simulations reflect the model's structure and the assumptions we made about Spotted Owl behavior. We have structured our model to reflect our current understanding of owl behavior and life history. In some aspects of model structure, however, such as basic life-history patterns and the values of birth and death rates, we have more certainty than in others. For example, our model and its results are clearly the consequence of assumptions we have made about the dispersal behavior of juvenile owls within and between territory clusters. Unfortunately, little is known of Spotted Owl dispersal costs and how juvenile birds move through heterogeneous landscapes.

One inference drawn from our results-the positive effect of increasing cluster size-has much stronger support in both empirical and theoretical studies. Populations quickly escape from the dangers of demographic stochasticity with even slight increases in population size (see Goodman 1987). Populations also gain security from environmental uncertainty with increasing numbers, but at a slower rate than from demographic effects (Shaffer 1987). Therefore, this model result was not surprising. Of interest, however, was the fact that marginal gains in mean occupancy were not constant with incremental increases in cluster size. Rather, large gains occurred in moving from clusters of 5 to clusters of 20 sites; much smaller gains were made in moving from 20 to 45 sites per cluster.

In their individual territory model, Lamberson et al. (1992) assumed all sites were equally likely to be searched until a suitable site was located or search capabilities were exhausted (that is, the owl died). The probabilities of finding a suitable site, or an individual of the opposite sex, became insurmountable when suitable habitat was less than about 15% of the landscape, or the population density was too low. In the current model, we invoked the concept of clusters, groups of two or more adjacent suitable sites. If a single very large cluster is created with reflecting boundaries, however, model behavior is similar to the individual territory model. Clusters did not have reflecting boundaries, but owls searched preferentially within their natal cluster before searching the matrix for another cluster. With a finite number of searches and a sufficiently large cluster (of more than 40 sites), search seldom occurred outside the natal cluster. For very large clusters, the model behaves as if the cluster boundaries are reflecting-little between-cluster movement occurs, and occupancy rate is insensitive to dispersal costs or the distance between clusters. In general, large clusters become very stable if the proportion of suitable sites within the cluster lies above the threshold value derived in Lamberson et al. (1992).

If Spotted Owls do not preferentially search within clusters, the costs associated with moving through the

matrix become considerably more important. Assuming a fixed search effort and less preference for within-cluster search, more effort is spent searching among clusters. Therefore, the necessary cluster size to achieve a given level of occupancy is increased proportional to the distance traveled in the matrix.

We assumed that the risks to owl viability were more pronounced for demographic than genetic factors (see Lande 1988b). There may be some long-term genetic consequences, however, if dispersing owls preferentially search their natal cluster before entering the matrix. The general effect of subdividing the owl population into a number of clusters may be to slightly increase the total genetic variation among clusters (Lande & Barrowclough 1987). Widely spaced but very large clusters would have local demographic stability but may eventually lead to a decline in genetic variation due to inbreeding. This is more likely if we have overestimated the vagility of dispersing owls. Smaller clusters more closely spaced promote higher dispersal rates between clusters but may lead to local demographic instability. Therefore, there may be an optimal size for a cluster that achieves a balance between these two processes.

The assumption of Thomas et al. (1990) that risks to owl viability were more pronounced from demographic than genetic factors could be significant if they have overestimated the vagility of dispersing owls in the forest matrix. If the assumption is false, there may be possible deleterious genetic effects from inbreeding within the large clusters at some future time. To have a higher degree of confidence in the generality of our model results, however, will require a considerably deeper understanding of how Spotted Owls move through their environment and respond to habitat heterogeneity at a variety of spatial scales.

The question of reserve design for Spotted Owls concerns both how big the clusters should be and how much of the landscape should be in clusters (thus controlling spacing). For an all female model, clusters with 15 or more sites appear stable but are still quite sensitive to cluster spacing (Fig. 9). To assure successful mate finding in a real reserve system subject to environmental variation and irregular spacing, this number should be increased to at least 20-25. With clusters of 20 sites, the number of owls that will be protected in the same amount of reserve land is more than three times that for clusters of 5 sites. Thus, to protect the same number of owls in smaller clusters would require a substantial increase in the amount of land that would have to be set aside.

Given some minimum criteria for cluster size and spacing, the next concern is the number of clusters required for a stable reserve system (the percentage of the landscape within the species range to include within clusters). To address this question requires knowledge

of the frequency and magnitude of catastrophic events. Our model did not include these effects because, at this time, we do not know how to reliably model them. Several theoretical studies, however, have demonstrated that metapopulation extinction times increase exponentially with the number of local populations (see Nisbet & Gurney 1982), largely as a consequence of reducing the probability that local populations simultaneously experience major environmental perturbations (Goodman 1987; Harrison & Quinn 1989). Thus, the risk of stochastic failure of the reserve system is greatly diminished by increasing the number of large clusters and spreading them widely across the landscape.

The proposed cluster structure for the Northern Spotted Owl—the system of habitat conservation areas (HCAs) would reserve roughly 15-30% of the forested landscape on public lands in the owls' range (Thomas et al. 1990). Most of the conservation areas will have an eventual capacity of 15 to 25 pairs of owls, and they will be established throughout the species' current range (Thomas et al. 1990: Appendix Q). In addition, Thomas et al. (1990) proposed specific minimum habitat requirements for the forest matrix in order to facilitate owl dispersal. Our model results, assuming 60% suitable habitat within clusters with 20 or more sites, suggest a high likelihood for long-term stability. Given implementation of their conservation strategy, and assuming rapid recovery of habitat within those HCAs that currently contain little suitable habitat, Thomas et al. (1990) speculated that the strategy would have a moderate to high likelihood of providing for long-term stability and at the same time the connectivity necessary to avert genetic difficulties in future owl populations.

The greatest uncertainty with the owl conservation strategy (Thomas et al. 1990), and a limitation of the equilibrium model used here, is our ignorance of the transient behavior of a recovering population while its habitat is regenerating. Several of the HCAs, particularly those on Bureau of Land Management lands in the northern coast range of Oregon, have far less than 60% suitable habitat. In these HCAs, we expect population instability in the near term. Given many alternative ways to attain the future steady-state reserve structure, preventing the population trajectory from passing through zero during the transition may depend critically on the pattern and rate of recovery of critical habitat within the reserve.

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Literature Cited

- Boyce, M. S. 1987. A review of the U.S. Forest Service's viability analysis for the spotted owl. Final report to the National Council of the Paper Industry for Air and Stream Improvement. Unpublished.
- Carroll, J. E., and R. H. Lamberson. 1993. A continuous model for the dispersal of territorial species. *SIAM. Journal of Applied Mathematics* 53(1):205-218.
- Dennis, B. 1989. Allee effects: Population growth, critical density, and the chance of extinction. *Natural Resources Modeling* 3:481-538.
- Doak, D. 1989. Spotted owls and old growth logging in the Pacific Northwest. *Conservation Biology* 3:389-396.
- Franklin, A. B., J. A. Blakesley, and R. J. Gutierrez. 1990. Population ecology of the northern spotted owl in northwestern California: preliminary results. 1989. Final report submitted to the Forest Service and the California Department of Fish and Game. Unpublished.
- Goodman, D. 1987. The demography of chance extinction. Pages 11-34 in M. E. Soule, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, England.
- Green, P. E. 1978. *Analyzing multivariate data*. Dryden Press, Hinsdale, Illinois.
- Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. *Oikos* 56:293-298.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. The effects of varying dispersal capabilities on the population dynamics of the northern spotted owl. *Conservation Biology* 6:505-512.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130:624-635.
- Lande, R. 1988a. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601-607.
- Lande, R. 1988b. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Lande, R. and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87-123 in *Viable populations for conservation*. M. E. Soulé (ed.). Cambridge University Press, Cambridge. 189 pp.
- Marcot, B. B., and R. Holthausen. 1987. Analyzing population viability of the spotted owl in the Pacific Northwest. *Transactions of the Conference on North American Wildlife and Natural Resources* 52:333-347.
- McKelvey, K. B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: The case of the northern spotted owl. Pages 424-450 in P. Kareiva, J. Kingsolver, and R. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts.
- Nisbet, R. M., and W. S. C. Gurney. 1982. *Modelling fluctuating populations*. John Wiley & Sons, New York.
- Noon, B. R., and C. M. Biles. 1990. The mathematical demography of the spotted owl in the Pacific Northwest. *Journal of Wildlife Management* 54:18-27.
- Shaffer, M. 1987. Minimum viable populations: Coping with uncertainty. Pages 69-86 in M. E. Soule, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, England.
- 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*. 1990-791-171/20026. U.S. Government Printing Office, Washington, D.C.
- USDA Forest Service. 1988. Final supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide. 2 vols. U.S. Department of Agriculture, Forest Service, Portland, Oregon.

