

# A Dynamic Analysis of Northern Spotted Owl Viability in a Fragmented Forest Landscape\*

ROLAND H. LAMBERSON

Department of Mathematics  
Humboldt State University  
Arcata, CA 95521, U.S.A.

ROBERT McKELVEY

Department of Mathematical Sciences  
University of Montana  
Missoula, MT 59812, U.S.A.

BARRY R. NOON

CURTIS VOSS

Redwood Sciences Laboratory  
U.S. Forest Service  
1700 Bayview Drive  
Arcata, CA 95521, U.S.A.

**Abstract:** *The Northern Spotted Owl (Strix occidentalis caurina) is closely associated with mature and old-growth coniferous forests in the Pacific Northwest. There has been a rapid loss and fragmentation of this habitat over the last half century, which may jeopardize the long-term survival of the species through reduction of dispersal success. In this paper we report results of a population model for the Northern Spotted Owl that incorporates both juvenile dispersal and search for mates. We analyze both deterministic and stochastic versions of the model in search of thresholds for population persistence related to search efficiency, population density, and amount of suitable habitat. In addition, we analyze the model under the nonequilibrium conditions that currently exist due to timber harvest in the owls' preferred habitat. Our results predict a sharp threshold below which populations cannot persist, and suggest that inferences from population models that incorporate equilibrium assumptions may be highly misleading.*

*Paper submitted January 18, 1991; revised manuscript accepted November 15, 1991.*

*\* The model described in this paper is the individual territory model from the conservation plan for Northern Spotted Owls (Thomas et al. 1990).*

Análisis dinámico de la viabilidad del búo moteado del norte en un paisaje de bosque fragmentado

**Resumen:** *El búo moteado del norte (Strix occidentalis caurina) está estrechamente asociado con bosques maduros y de antiguo crecimiento de coníferas en el Noroeste Pacífico. A lo largo de la última media centuria, ha ocurrido una rápida pérdida y fragmentación de este hábitat que podría poner en peligro la supervivencia a largo plazo de las especies a través de la reducción del éxito en la dispersión. En este trabajo, presentamos resultados de un modelo poblacional para el búo moteado del norte que incorpora tanto la dispersión juvenil como la búsqueda de pareja. Analizamos el modelo tanto en su versión determinística como estocástica en la búsqueda de umbrales para la persistencia de la población en relación con la eficiencia en la búsqueda, densidad poblacional y cantidad de hábitat apropiado. También analizamos el modelo bajo condiciones de desequilibrio que son las que existen actualmente debido a la explotación maderera en el hábitat preferido por el búo. Nuestros resultados predicen un umbral pronunciado por debajo del cual las poblaciones no pueden persistir y sugieren que inferencias obtenidas a partir de modelos poblacionales que incorporan supuestos de equilibrio pueden ser sumamente engañosos.*

## Introduction

The decline in the population of Northern Spotted Owls (*Strix occidentalis caurina*) in the Pacific Northwest has been widely chronicled in both the scientific literature (Franklin et al. 1990; Thomas et al. 1990) and the popular press. It is generally conceded that this decline is primarily due to the rapid loss and fragmentation of its preferred habitat, mature and old-growth coniferous forest in the Pacific Northwest (USFWS 1990). The decline of suitable habitat began about forty years ago but has been most pronounced during the past fifteen years, and it is expected to continue well into the future (see Fig. 1). In addition to a decline in the amount of older forest, the landscape in the Pacific Northwest has been altered by the practice of dispersed clearcut logging on national forest lands. As a consequence, stands of mature and old-growth coniferous forest have become increasingly patchy in their distribution. The resulting fragmentation may jeopardize the long-term survival of the species through a reduction in the dispersal success of both juveniles searching for their own home range and older owls displaced by timber harvest. In addition, the disequilibrium in the ecosystem caused by extensive logging may continue long after the harvest has ended and may lead to misinterpretation of both the current state and future trends of the system.

Previous analyses of the demography of the Spotted Owl (Lande 1988; Noon & Biles 1990) have suggested that the growth of the population is strongly affected by changes in adult survival rates and, less strongly, by changes in juvenile survival rates. Field data shows little variation in adult survival rates (Franklin & Gutierrez 1987, 1988; Franklin et al. 1989) but suggest the possibility of much wider variation in juvenile survival rates. Since the Northern Spotted Owl is strongly territorial,

the likelihood of juveniles successfully dispersing to suitable habitat areas will decrease as suitable habitat becomes more patchy in its distribution. Failure to disperse successfully will be an additional cause of mortality, especially for juveniles and to some extent for all age classes.

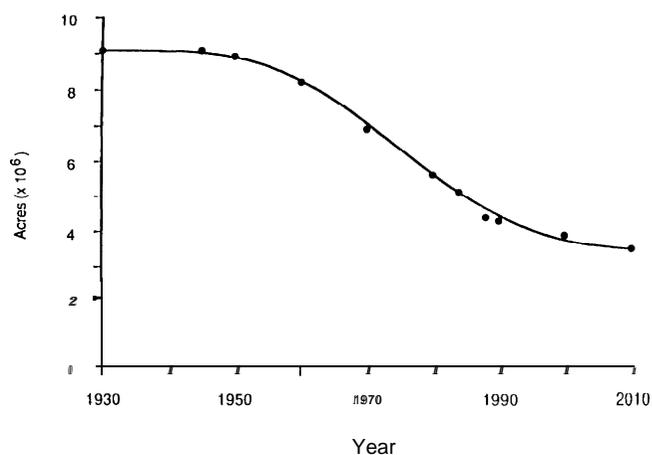
In response to the decline of the owl population, the United States Forest Service put in place a network of protected Spotted Owl habitat areas (SOHAs) selected to include the home range of an individual pair of owls or clusters of up to three owl territories. In this paper we model a region where home ranges for individual Spotted Owl pairs are distributed randomly across the landscape, similar to the pattern of the SOHA network. In a sequel to this paper we consider the optimal size for larger clusters of suitable habitat similar to those in the current proposal for a network of much larger habitat conservation areas (HCAs; Thomas et al. 1990).

Here we first describe the model then examine the results for both deterministic and stochastic simulations. We analyze the model under both equilibrium and nonequilibrium conditions. In these runs we search for thresholds that might lead to extinction for the population either due to low numbers of owls or to reduced area of suitable habitat. We also study the relationship between the ongoing reduction of suitable habitat and the expected density of owl pairs.

## Survey of Prior Models

Both of the initial efforts at modeling the population dynamics of the Northern Spotted Owl incorporated linear, single-sex, Leslie matrix models (Marcot and Holthausen 1987; USDA 1988). Marcot and Holthausen assessed individually the impact of a list of management alternatives on the viability of the species and produced a table of risks for various management options. The Forest Service (USDA 1988) developed a 15-by-15 Leslie matrix model as part of their original Spotted Owl viability analysis. Both of these models are basically exponential growth models and were criticized by Boyce (1987) for not including density dependence. In addition, the linear structure of these models can produce unrealistic, even pathological, stochastic output. Neither of these models contained any spatial component.

The third model is that of Boyce (1987). Boyce argued (correctly, we believe) for the need to incorporate density dependence and spatial effects into population models. He also discussed at some length the Allee effect (Allee 1938; Dennis 1989). He illustrated his ideas through a standard stage-structured, single-sex Leslie model, with life history structure collapsed into three stages: juvenile, subadult, and adult. In addition, he made fecundity and juvenile survival rates density dependent. However, the compensatory fecundity function



**Figure 1.** Trend in suitable Northern Spotted Owl habitat on US Forest Service lands beginning in 1930 and including projected timber sales through 2010.

he chose for his illustration turns out to be too mild for the Allee effect to become operative.

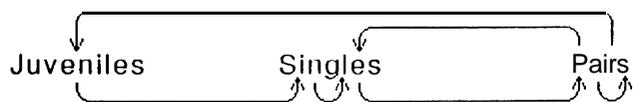
Lande (1987, 1988) developed models that incorporated a stage structure similar to Boyce, and he included a nonlinear search function for dispersing owls. The search function was dependent on both the density of owls and the density of suitable habitat. We have adopted a similar stage structure in our model and patterned our search functions after Lande's. Lande drew his inference from a deterministic, equilibrium analysis of the model, while we extend the analysis to include both nonequilibrium situations (ongoing reduction of the habitat due to timber harvest) and allow for environmental stochasticity.

Doak (1989) introduced spatial structure and environmental stochasticity into a dynamic, all-female model. He simplified the stage structure to juveniles and adults. However, he enhanced the spatial structure by considering clusters of suitable home ranges. The dispersal process became a two-step procedure, dispersal within the natal cluster followed by dispersal to distant clusters. Both of these searches are based on density-dependent logistic functions. A sequel to this paper (Lamberson & Noon, unpublished data) will be comparable to Doak's work.

## The Model

The model focuses on a landscape of fixed spatial extent and contains a number of potential home-range territories (or "sites," which we imagine to contain roughly 1000 ha). However, only a fraction of these sites are assumed to be stocked with suitable habitat. A suitable site is one which, in a probabilistic sense, allows for survival, mate attraction, and reproductive success.

The life history in this model follows the stage structured pattern shown in Figure 2. A nesting pair will annually produce young according to either some fixed fecundity (deterministic) or a fluctuating fecundity (stochastic). These juvenile birds will disperse at the end of the breeding season, males seeking an unoccupied site and females seeking a site occupied by a solitary male. Dispersal success is patterned after Lande's model (Lande 1987, 1988); it is density dependent and is calculated by assuming random search of accessible sites:



**Figure 2.** Stage-structured life history pattern for Northern Spotted Owls as implemented in the model.

Probability of Success =

$$1 - (1 - \text{unoccupied suitable sites}/\text{total sites})^m$$

Various assumptions can be made about the bird's search efficiency, which is measured by  $m$ , the number of sites it is capable of searching prior to experiencing mortality. Search capabilities, together with the occupancy ratio of searched sites, determine the bird's potential for successful dispersal.

In our simulation runs we have assumed that juvenile females and redispersing adults were more efficient searchers than juvenile males: juvenile females may get aid through vocalizations from males with sites but no mate, and adults should be more efficient because of their additional experience. In both cases we have assumed a doubling of efficiency over the juvenile male (the model seems to be insensitive to further increases in efficiency).

Birds are first allowed to breed in their third year of life. Adult birds older than one year are subject to mortality, and adults occupying territories are subject to site disturbance (such as timber harvest); consequently, some surviving adults will also be forced to disperse. Juvenile birds are also subject to mortality; in particular, it is assumed that all male birds unsuccessful in dispersal to suitable sites perish. To condense the model it is assumed that the number of male and female solitaires remains equal, with the single females retained as a floater population (this effectively has half of the singles occupying suitable home territories and half being a floating population, but gives all of them the same vital rates). This assumption allows considerable simplification without-to our present state of empirical knowledge-any significant loss of accuracy.

The state variables in the model, which are 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 occupied by nesting pairs; and (3) the number,  $S$ , of suitable sites occupied by single males.

## Model Parameterization

The model is parameterized based on the demographic studies of Franklin et al. (Franklin & Gutierrez 1987, 1988; Franklin et al. 1989) and values published by Marcot and Holthausen (1987). We assume an annual adult survival probability of 0.94, a juvenile predispersal survival probability of 0.60, fecundity (number of young fledged/adult females) of 0.66, and a 1:1 sex ratio at birth. Single birds were assumed to survive at the estimated annual subadult survival rate of 0.71.

## Modeling Results

We ran the model under a number of alternative assumptions, varying the proportion of the landscape that

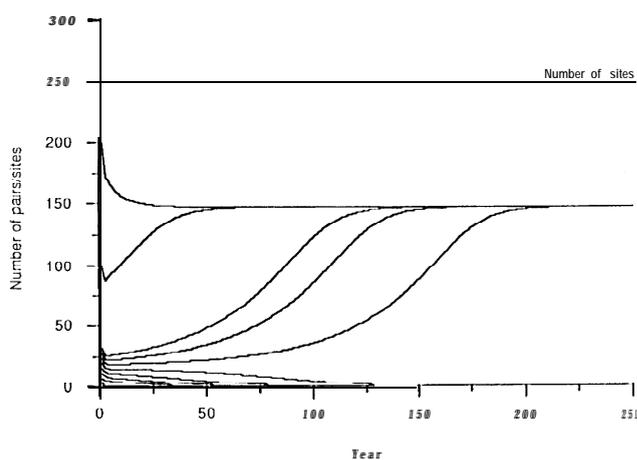
was suitable habitat, aspects of the owl's biology, initial population sizes, and environmental conditions. We examined changes in the landscape by specifying differing fractions of the forest as suitable habitat during various runs of the model or by allowing the amount of suitable habitat to vary with time during the course of the simulation. We incorporated key aspects of the owl's biology and behavior by specifying survival and fecundity parameters and the efficiency of its search for a home range and a mate. We also varied the amount of environmental stochasticity, primarily through a fluctuating fecundity, to reflect variability in food supply (such as small rodents).

### Deterministic Analyses

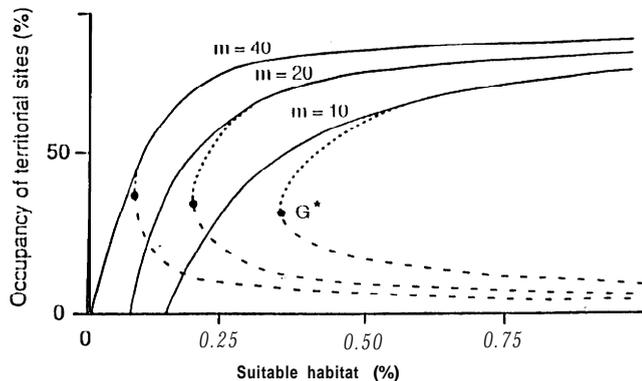
First we ran the model deterministically (with no environmental fluctuations) while varying the initial population size (initial  $S$  and  $P$  being kept in fixed proportion). Owl biology (demographic parameters) and the proportion of the landscape that was suitable habitat were held constant during this exercise.

If the initial population size was sufficiently large and the search efficiency was relatively high, the population tended to a stable equilibrium level (Fig. 3). An initially small population crashed even when the search efficiency was relatively high. If search efficiency was low, however, even very large initial populations crashed. The system had two stable equilibria, one being extinction. The trajectories that tended to the two different stable equilibria were separated by an unstable equilibrium.

The location of the stable and unstable equilibria depended on the quality of the habitat, as measured by the fraction that was suitable. This dependence is depicted



**Figure 3.** Trend in number of pairs of Spotted Owls based on a 250-year simulation. Each curve was initialized at a different population size. We assumed that 25% of the landscape was suitable owl habitat, and that juvenile owls could search 30 sites.



**Figure 4.** Percentage occupancy of Spotted Owl territorial sites (pairs and singles) against the proportion of the landscape that was suitable Spotted Owl habitat. Solid curves resulted from an all-female version of the model (no search for mates). Dotted and dashed curves include mate search and show stable and unstable equilibria, respectively, resulting from the Allee effect. Three sets of curves correspond to various juvenile search abilities (10, 20, and 40 sites).

in Figure 4. (The variable on the vertical axis is occupancy of suitable habitat,  $[S + P]/T$ .) The various curves correspond to alternative assumptions about the owl's search efficiency (the number of sites searched,  $m$ , prior to death). The solid curves represent the equilibrium occupancy when females are not required to search for a mate. On each curve, where the mate search routine is employed, the dotted line shows the stable equilibrium and the dashed line the unstable equilibrium. At the left of each curve, the solid and dashed lines meet at a point ( $G^*$ ) that has a specific value for the proportion of the landscape that is suitable habitat ( $G$ ). For  $G < G^*$ , the two nontrivial equilibria have disappeared: only the (0,0) equilibrium remains. Thus, for  $G < G^*$  all populations go extinct, regardless of initial population levels. Figure 4 is qualitatively the same as Lande's equilibrium configuration (Lande 1987:629), though he obtained the result using quite different numerical techniques.

Figures 3 and 4 demonstrate an "Allee effect": As the population becomes smaller and more scattered or the habitat more fragmented, dispersing males experience diminishing success in finding suitable home ranges and females experience increasing difficulty in finding a mate. Note that, in this two-sex model, the Allee effect arises from an explicit nonlinear mating search-success probability function. (Alternative hypotheses of search are explored by Dennis [1989]).

### Stochastic Analyses

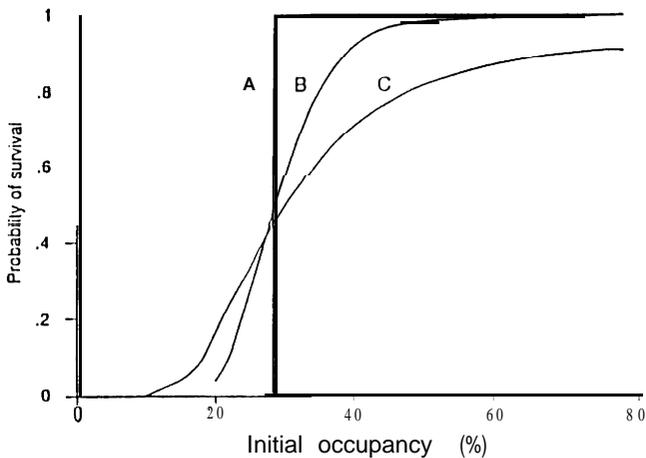
The effects of environmental stochasticity can be addressed in a number of ways. For example, we com-

pared stochastic simulation runs with different initial population sizes directly to the similar deterministic simulations shown in Figure 3. Adding environmental stochasticity slowed the rate of increase to the stable equilibrium when initial populations were above the unstable equilibrium, and it decreased the time to extinction for declining populations (those initialized below the unstable threshold). Qualitatively, however, the results were the same for both models.

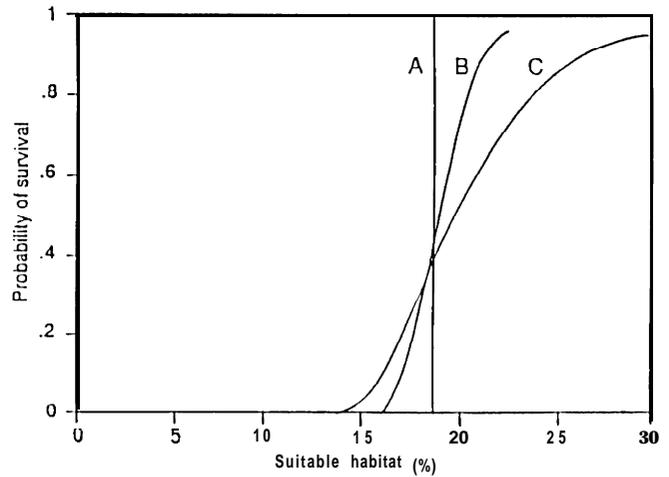
A better means of comparison is to run a large number of both deterministic and stochastic simulations and compare the fraction of sample runs that lead to extinction within a fixed time span. In Figure 5 we plot the probability,  $p$ , of population survival for 250 years as a function of initial population size. The three curves correspond to the three alternative assumptions about environmental stochasticity. When there is no stochasticity,  $p$  is a stairstep function, rising abruptly from 0 to 1 at the unstable equilibrium levels of Figures 3 and 4. Adding environmental stochasticity smooths out the stairstep, as shown in the two curves for low and high environmental variance. Note that for a given high probability of survival,  $p$ , an increase in environmental variance will increase the initial occupancy needed to guarantee  $p$ ; for a given low probability  $p$ , an increase in variance will decrease the needed initial occupancy. Thus, increasing environmental variance broadens the band of occupancy across which  $p$  rises from 0 to 1; that is, the extinction threshold becomes less abrupt.

### Amount of Suitable Habitat

It is of interest to examine how survival probability depends on the percent of the landscape that is suitable



**Figure 5.** The 250-year survival probability against the initial percentage of the sites occupied by pairs of Spotted Owls. Curves represent three conditions: no (A), low (B), and high (C) environmental variance. We assumed 18% of the landscape was suitable habitat and that adults could search 40 sites (juveniles could search 20 sites).

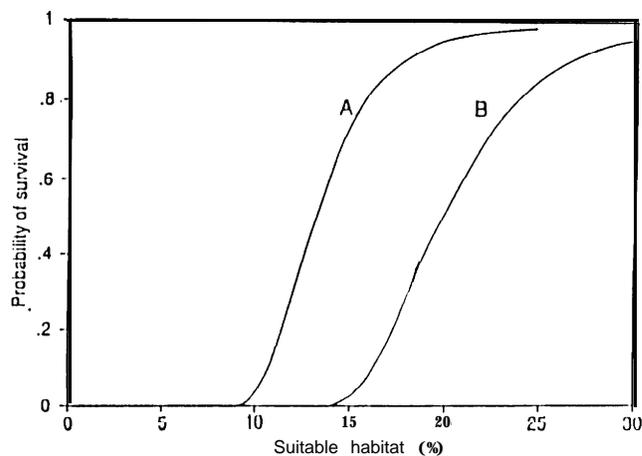


**Figure 6.** The 250-year survival probability against the percentage of landscape that was suitable habitat. Curves are shown for three conditions: no (A), low (B), and high (C) environmental variance. We assumed adult owls could search 26 sites. All simulations were initialized with the same number of owls.

habitat,  $G$ , and to determine how it might be affected by environmental stochasticity. To illustrate this dependency, the 250-year survival probability,  $p$ , is plotted as a function of  $G$  (Fig. 6). Once again, the deterministic case shows a stairstep function, with the jump from 0 to 1 occurring at the point  $G^*$  (Fig. 4). As before, adding environmental variance smooths out the stairstep. If we demand a high  $p$  (such as 90% probability of survival for 250 years), then the greater the environmental variance the higher the proportion of suitable habitat required to guarantee it. On the other hand, greater environmental variance also means a less abrupt threshold into the high-risk zone.

Survival probability is sensitive to model assumptions, both biological and environmental. The curves in Figure 7 illustrate 250-year survival probability under high environmental variance, with two different assumptions of search efficiency, both consistent with the present state of knowledge of the owl's biology. Note that in both cases the threshold into the high-risk zone is quite steep, and that these threshold curves bracket levels of suitable habitat preservation advocated by various parties to the current policy dispute (see Thomas et al. 1990).

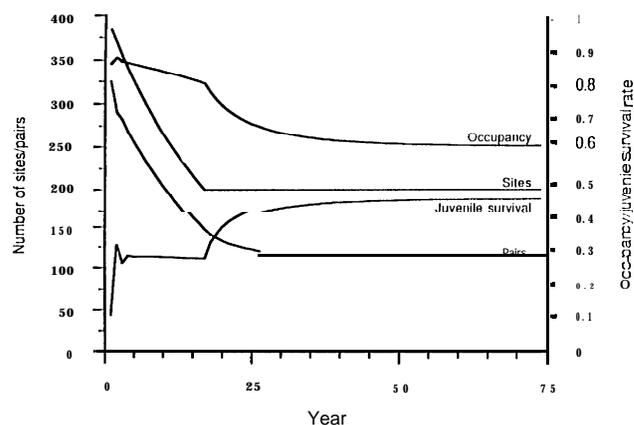
For specified amounts of suitable habitat and given assumptions about environmental variance, we computed the population survival probability,  $p$ , as a function of time. In all cases that we tested, this probability departs from 1 at roughly 200 years. This is because it is essentially impossible for a relatively abundant population of long-lived animals to go extinct in a shorter period of time, regardless of how harsh the conditions may be, as long as we exclude the possibility of a population-wide catastrophe.



**Figure 7.** The 250-year survival probability against the percentage of landscape that was suitable habitat. Curves are shown for two conditions: high environmental variance with adults searching 40 and 26 sites (A and B, respectively). All simulations were initialized with the same number of owls.

### Introducing Landscape Dynamics

We simulated a dynamic landscape, both deterministically and stochastically, by allowing the proportion of the landscape that was suitable Spotted Owl habitat to be diminished by, for example, timber harvest. The inclusion of timber harvest meant that we no longer had a system at equilibrium, since the extent of suitable habitat (carrying capacity) was declining. We tracked the proportion of the landscape that remained as suitable habitat,  $T$  as a function of time (Fig. 8). But for this case we assumed that the suitable habitat was being cut at a



**Figure 8.** Trend in number of pairs of Spotted Owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. We assumed that 4% of the suitable owl habitat was lost per year until 20% remained, and that juvenile male owls could search 20 sites (adults and juvenile females could search 40).

rate of 4% of the remainder per year, until cutting ceased with 20% of the landscape remaining as suitable habitat. At the same time, we tracked the occupancy level for the remaining suitable habitat.

Here a critical result appeared that was directly related to the fact that the system was dynamic-subjected to declining habitat. The occupancy curve (Fig. 8) represents the percent of suitable habitat occupied at any given time. Note that the level of occupancy remained virtually unchanged during the period when timber harvest was taking place. This is the result of a crowding effect in the remaining suitable habitat. The owls currently holding home ranges found their territories when the amount of suitable habitat was greater and unoccupied sites were easier to secure. As mature and old-growth timber continued to be cut, the amount of suitable habitat was further reduced and, at the same time, some adult pairs of owls were displaced from their home ranges. These displaced adults were now in competition with dispersing juveniles for the smaller amount of unoccupied suitable habitat remaining. Being inexperienced, the juveniles in our model (and probably in reality) were less likely to be successful in their quest for a suitable territory. Thus, what remained of the suitable habitat was more densely occupied than we would expect in an equilibrium setting. Also, it was crowded with owls that were somewhat older than we would expect at equilibrium. Simultaneously, we saw unusually low juvenile survival rates because of the excessively difficult time the juveniles had finding the few remaining home ranges (note the juvenile survival curve in Fig. 8).

Beyond the period of diminishing habitat, the population began to come into equilibrium with a landscape that contained less and more dispersed suitable habitat. The population age structure gradually returned to a more stable configuration, less dominated by an overabundance of older owls. The juvenile survival rate increased rapidly because of the reduced competition for unoccupied sites, resulting from the fact that older owls were no longer being displaced by logging and the fact that there were new territories opening up when the older owls died.

Finally, given that sufficiently large numbers of owls remained and an adequate amount of suitable habitat was still intact, the model came to equilibrium. The equilibrium population was substantially smaller than that observed near the end of the period of timber harvest even though that population, if estimated using levels of occupancy, may have appeared to be stable. We believe that it may be very difficult, based on data collected during the course of active timber harvest, to distinguish a collapsing population from one that will reach some long-term stable equilibrium. If, in the simulation run displayed in Figure 8, we continued the timber harvest until only 13% of the landscape was suitable

habitat, then the population became extinct after about 250 years. The output in the two cases was identical while harvesting went on in both, and it was similar until well beyond the end of harvest in the second. In the second case, however, the population decline never ended.

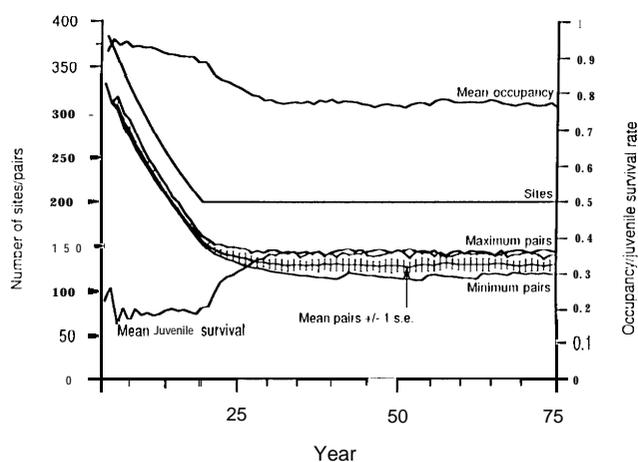
When environmental stochasticity was introduced, all of the characteristics that we observed in the deterministic case again appeared in the stochastic model (Fig. 9).

## Discussion

In the following discussion, we confine our remarks to a comparison of our results with those from earlier models.

The model developed by Lande (1987) is essentially the same as ours when we restrict it to a deterministic equilibrium configuration. Our Figure 4 is basically the same as his Figure 3 (and with appropriate assumptions our model reproduces his Fig. 1). Lande's deterministic analysis can be thought of as leading to the staircase threshold functions in our Figures 5 and 6. The exact locus of the step-break depends on the assumptions about parameter values. Thus, the real difference between our analysis and Lande's is that we examine the effects of nonequilibrium conditions resulting from ongoing timber harvests and provide for environmental stochasticity.

If we incorporate into Boyce's model (1987) a search effectiveness function such as ours (or Lande's), we find that the Allee effect is operative, with results consistent with our own.



**Figure 9.** Trend in number of pairs of Spotted Owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year stochastic simulation. We assumed that 4% of the suitable owl habitat was lost per year until 20% remained, and that juvenile male owls could search 20 sites (adults and juvenile females could search 40).

## Conclusions

Two major conclusions can be drawn from this modeling effort. First, in a fixed landscape, the model predicts a sharp threshold below which Spotted Owl viability plunges. The underlying cause is dispersal failure (the recolonization rate of pair-sites is less than their extinction rate), due to a scarcity of suitable habitat or a scarcity of available mates in suitable habitat (the so-called Allee effect). The location and steepness of this threshold depends on the parameters of the model: on the initial number of owl pairs, on the density of suitable habitat, on assumptions concerning the owl's biology—particularly its life history characteristics and its dispersal search strategy and efficiency—and finally on assumptions made regarding the quality and stability of the owl's environment. Other than refining our knowledge of these factors, there is currently no way to pinpoint the locus of the threshold, and no direct empirical means to ascertain whether the population is currently at high risk of crossing a threshold point.

Second, the fact that the system we examined was dynamic played a crucial role in its analysis. The crowding of older owls into remaining suitable habitat as timber harvest continues is likely to produce very high occupancy rates—much higher than would be expected under long-term stable conditions. As a result, we should be very careful in using occupancy data to predict long-term abundance, since the equilibrium occupancy levels predicted by the model are well below those seen while logging of suitable owl habitat is continuing. In fact, if we extend the harvest for the case shown in Figure 8 just nine more years (leaving everything else as before), the simulation leads to extinction in approximately 250 years. In this case, the occupancy levels during habitat loss are virtually unchanged, but the population crashes long after timber harvest has ceased. Also, the juvenile survival rate is substantially depressed during the logging phase (Fig. 8). This may explain the very low juvenile survival rates that have been estimated from current field data (Thomas et al. 1990, Appendix L). It may also distort any computations of long-term growth rates for the owl population that use data collected while habitat decline continues. This model may be overly optimistic with regard to the long-term survival of the owl. The long-term growth rate of this population is nearly an order of magnitude more sensitive to adult survival rate than any other parameter (Lande 1988), and our simulations have used a relatively high estimate of adult survival rate.

The ultimate conclusion that can be drawn from this work is that we should proceed very cautiously with any management decisions. There are likely to be some very sharp population thresholds which, once passed, can lead to a disaster for the Spotted Owl population. At the same time, none of our numbers should be taken as

exact measures of where these thresholds lie. Our model is of sufficient sophistication to examine the system and to discover the existence of threshold levels, but neither the model nor current knowledge of the vital parameters and behavior of this species are well enough known to allow us to predict with certainty at what population level or at what level of habitat fragmentation the long-term viability of this bird is compromised.

## Acknowledgments

Professor Lamberson's work on this project was supported by United States Forest Service cooperative research agreement PSW-900008CA.

## Literature Cited

- Allee, W. C. 1938. *The social life of animals*. Norton, New York.
- 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.
- Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource 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., and R. J. Gutierrez. 1987. Population ecology of the Northern Spotted Owl in northwestern California: Preliminary results, 1987. California Department of Fish and Game, Sacramento, California.
- Franklin, A. B., and R. J. Gutierrez. 1988. Population ecology of the Northern Spotted Owl in northwestern California: Preliminary results, 1988. California Department of Fish and Game, Sacramento, California.
- Franklin, A. B., J. A. Blakesley, and R. J. Gutierrez. 1989. Population ecology of the Northern Spotted Owl in northwestern California: Preliminary results, 1988. Final report submitted to the U.S. Forest Service and the California Department of Fish and Game.
- 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 California Department of Fish and Game.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130:624-635.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). *Oecologia* 75:601-607.

Marcot, B. G., and R. Holthausen. 1987. Analyzing population viability of the Spotted Owl in the Pacific Northwest. Transactions of the North American Wildlife and Natural Resources Conference 52:333-347.

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.

Thomas, J. W., et al. 1990. A conservation strategy for the Northern Spotted Owl: Report of the interagency scientific committee to address the conservation of the Northern Spotted Owl. Portland, Oregon.

USDA [U.S. Department of Agriculture], Forest Service. 1988. Final supplement to the environmental impact statement for an amendment to the Pacific Northwest Regional Guide. Two volumes. Portland, Oregon.

USFWS [U.S. Fish and Wildlife Service]. 1990 status review: Northern Spotted Owl (*Strix occidentalis caurina*). Washington, D.C.

## Appendix

The dynamic equations (time-specific) used in the model in the case where the number of suitable sites was fixed (no timber harvest) are as follows:<sup>a</sup>

- (1) dispersal survival =  $1 - [1 - \text{available sites } (t) / \text{total sites}]^m$ ;
- (2) available sites ( $t$ ) = suitable sites ( $t$ ) - occupied sites ( $t$ );
- (3) occupied sites ( $t$ ) = pairs ( $t$ ) + male singles ( $t$ );<sup>b</sup>
- (4) mating success =  $1 - [1 - \text{singles } (t) / \text{total sites}]^n$ ;
- (5) male singles ( $t$ ) =  $0.5 * \text{juveniles } (t - 1) * \text{juvenile survival} * \text{dispersal survival} + \text{male singles } (t - 1) * \text{single survival} * (1 - \text{mate}) + \text{pairs } (t - 1) * (\text{probability that male survives and female dies})$ ;
- (6) female singles ( $t$ ) = male singles ( $t$ );
- (7) pairs ( $t$ ) =  $\text{pairs } (t - 1) * (\text{probability of both surviving}) + \text{singles } (t - 1) * \text{single survival} * \text{mating success}$ ;
- (8) juveniles ( $t$ ) =  $\text{pairs } (t) * \text{fecundity}$ .

<sup>a</sup>  $t$  indexes time on an annual basis.  $m$  = number of sites sampled (with replacement) by dispersing juvenile males.  $n$  = number of sites sampled (with replacement) by dispersing juvenile females in search of a single male.

<sup>b</sup> Note that male singles were assumed to occupy a site, while female singles were retained as floaters.