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Spotted owl metapopulation dynamics in Southern California

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Summary

1. The California spotted owl *Strix occidentalis occidentalis* is found in the Sierra
Nevada and in a series of isolated populations in the mountains of southern California.
2. We developed a model to assess the risk of decline of the southern California
spotted owl metapopulation. We modelled the spatial structure of this metapopulation
by incorporating distance-dependent dispersal and correlation among the population
growth rates.
3. Demographic characteristics of the largest insular population were estimated from
colour-ringing the majority of the territorial population. This owl population declined
dramatically during the study period, 1987–93.
4. If the observed decline continues and similar declines are occurring in the other
populations, our viability analysis predicts that this metapopulation has a high risk
of going extinct in the next 30–40 years.
5. If the observed decline is due to naturally occurring environmental fluctuations
(drought), and thus temporary, the model results indicate substantial decline, but a
low probability of total metapopulation extinction.
6. Our results indicate that the risk of decline is quite sensitive to the correlations
among population growth rates. Increased correlation increased the risk of decline.

Key-words: California spotted owl, extinction risk, metapopulation dynamics, spatial
autocorrelation, *Strix occidentalis occidentalis*.

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Introduction

The spotted owl inhabits the forested mountains of
western North America from central Mexico to south-
ern British Columbia, Canada. The northern sub-
species *Strix occidentalis caurina* (Merriam) and the
Mexican subspecies *Strix occidentalis lucida* (Nelson)
were declared threatened under the provisions of the
Endangered Species Act (US Department of Interior
1990, 1993). However, the California spotted owl
Strix occidentalis occidentalis (Xantus), a subspecies
found in the Sierra Nevada and in approximately 20
relatively isolated populations in the mountains of
southern California, has not received similar status
even though the largest insular owl population has
declined dramatically in recent years (LaHaye, Gut-
iérrez & Call 1992).

There have been numerous studies of the Northern
spotted owl (e.g. Forsman, Meslow & Wight 1984;
Gutiérrez & Carey 1985; Thomas *et al.* 1990 and refer-
ences therein) and the Sierra Nevada populations of
the California spotted owl (e.g. Laymon 1989; Lutz
1992; Bias & Gutiérrez 1992; Call, Gutiérrez & Verner
1992; Verner *et al.* 1992). These studies have shown
that the spotted owl is closely associated with late
seral stage and primary (old-growth) forests. In
addition, some populations of northern spotted owls
appear to be declining (Thomas *et al.* 1990; US
Department of Interior 1992). The status of the Sierra
Nevada population is not clear (Verner *et al.* 1992).

There is much less information on the spotted owl
populations occupying the mountain ranges of south-
ern California (Gould, Roberts & Roberts 1987; Gut-
iérrez & Pritchard 1990; LaHaye *et al.* 1992). One of
the primary differences between these populations and
populations further north is that southern California
populations are relatively small and isolated from
each other by non-forested habitat.

In this paper we present an analysis of the spotted
owl metapopulation that inhabits the mountains of
southern California (Fig. 1). We have studied the
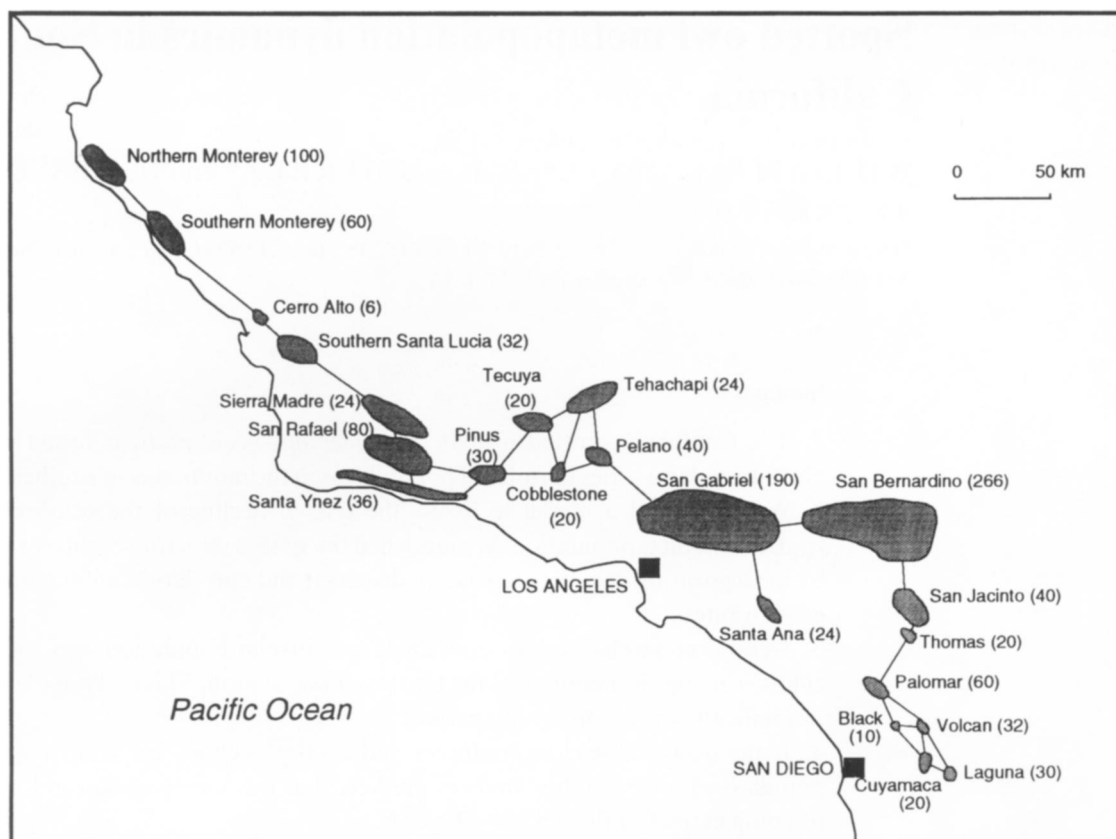demography of the largest of these owl populations

Fig. 1. Southern California spotted owl metapopulation. Lines show the possible dispersal routes. Numbers in parentheses are the estimated carrying capacities.

which inhabits the San Bernardino Mountains (SBM) as well as one of the smallest of these insular populations found in the San Jacinto Mountains (SJM) for 6 and 5 years, respectively (Gutiérrez & Pritchard 1990; LaHaye *et al.* 1992). We combined the demographic data from the SBM study with information on size and distribution of the other spotted owl populations in the region (Gould *et al.* 1987; Gutiérrez & Pritchard 1990; Stephenson 1991) to define the characteristics of the southern California spotted owl metapopulation. We then modelled this system to assess its dynamics, the demographic characteristics that most strongly influence the dynamics and its risks of decline under a set of alternative assumptions.

Study area

SOUTHERN CALIFORNIA

Southern California is dominated by low elevation desert and semi-desert habitats (Hanes 1988; Mooney 1988; Heady 1988; Vasek & Barbour 1988; Burk 1988). Most areas average less than 40 cm of rainfall per year (Kahrl 1978). However, the higher peaks and ridges of many of these mountain ranges average more than 100 cm of annual precipitation and often support well-structured conifer and hardwood forests (Griffin 1988; Thorne 1988). These relatively isolated forested mountain tops support spotted owl populations. This

metapopulation is found within an area of approximately 34 000 km².

SAN BERNARDINO MOUNTAINS

The San Bernardino Mountains (lat. 34°15′N; long. 117°55′E) are located approximately 140 km east of Los Angeles, California. Elevations range from 800 to 3500 m. Suitable habitat is contained within an area of approximately 1900 km² (LaHaye *et al.* 1992). Average annual rainfall within the study area varies from less than 20 cm to more than 100 cm and is greatly affected by elevation and topography (Minnich 1988). The climate is Mediterranean, with most precipitation falling as rain below 2000 m and as snow above this elevation (Minnich 1988). The vegetation forms a continuum from Mojave Desert scrub to alpine (Barbour & Major 1988) and is a complex mosaic of forest, chaparral, grass and wetland communities influenced by climate, elevation, aspect, edaphic and human (e.g. urbanization, mines, wildfires, firewood cutting and silviculture treatments) factors. The forest types occupied by spotted owls range in elevation from 800 m to 2600 m and are mixed conifer, big-cone fir (*Pseudotsuga macrocarpa*)/canyon live oak (*Quercus chrysolepis*) or forests which are transitional between these two forest types.

Methods

ESTIMATING DEMOGRAPHIC CHARACTERISTICS

We surveyed all forested habitat within a 535 km² area beginning in 1987 in the SBM. In 1989, we expanded this study area to include all forested habitats in the mountain range (1900 km²). Survey, capture and owl social status assessment techniques followed Forsman (1983). All owls captured were ringed with United States Fish and Wildlife Service locking aluminum leg rings. In addition, we colour-ringed each adult and subadult to facilitate individual identification. We resighted ('recaptured') colour-rings on ringed birds using binoculars.

Survivorship was estimated from capture–recapture data for owls in their first year of life and for all owls greater than 1 year in age using the program SURGE (Pradel & Lebreton 1991). Fecundity was computed by dividing the number of fledged young by the number of pairs checked for fledging. We assumed an equal sex ratio in the offspring and then divided the average number of fledged young per pair by two to estimate the number of female offspring per paired female in the population. The finite annual rate of population increase was estimated using a two-stage Leslie projection matrix (LaHaye *et al.* 1992).

In an attempt to estimate dispersal between SBM and SJM, we annually censused and colour-ringed all owls that we could locate in the San Jacinto Mountains between 1988 and 1993. Since we colour-ringed the majority of birds on each mountain range, the number of birds moving between ranges would be directly proportional to the dispersal rate between the two ranges.

METAPOPULATION ANALYSIS

We used RAMAS/space, a spatially structured metapopulation model (Akçakaya & Ferson 1992), that simulates the growth of each population by a stochastic growth model and provides for the interaction between the populations by incorporating information on the number, size and geographic configuration of habitat patches, dispersal patterns and the correlation of environmental fluctuations.

In this model, each population may have a different stochastic model which can incorporate density dependence (e.g. logistic growth or Allee effects). Since independent estimates of the population growth rate and its variance were not available for each population, we used the data from the SBM spotted owl population to model the internal dynamics of all populations. However, for each population, we used initial population sizes and carrying capacities based on the best available information for each population (Stephenson 1991; see Fig. 1). We only modelled territorial owls because almost no information exists on non-territorial spotted owls (Franklin 1992). We

assumed the current territory occupancy rate by pairs to be 0·70 (LaHaye *et al.* 1992) and, therefore, we set the initial abundance of each population to 70% of its carrying capacity. We simulated environmental stochasticity by using information on population growth rate variability from the SBM population. The variability in population growth rate was calculated from the output of a stochastic, age-structured, single-population model (Ferson & Akçakaya 1990), using data from the SBM population. Demographic stochasticity was simulated by sampling the number of survivors from a binomial distribution and fecundity from a Poisson distribution (Akçakaya 1991; Akçakaya & Ferson 1992).

The least known parameters of the southern California spotted owl metapopulation pertain to two important aspects of spatial structure. The first aspect is dispersal among populations. If there is no dispersal, habitat patches that go extinct will not have the opportunity to be recolonized. The lower the dispersal rate, the greater will be the risk of extinction or decline of the metapopulation. The rate of dispersal between populations may depend on the distance between populations, and the size and number of geographic barriers.

Thus far, we have recorded no owls dispersing between the SBM and SJM. Given the number of owls ringed and the number of years of observation, this result indicated that the dispersal rate was probably quite low, if not zero. Therefore, we modelled a relatively large range of values for dispersal rates to make sure that the range included the true dispersal rate. We assumed that dispersals were most likely to occur between populations that show connections in Fig. 1. For these populations, we assigned the dispersal rate (mean percentage of individuals migrating between populations per year) as a function of distance (Table 1).

The second aspect of the spatial structure of the southern California metapopulation was the correlation among the dynamics of its populations, resulting from the similarity of the environmental fluctuations they experience. This aspect of metapopulation dynamics was first pointed out by den Boer (1968), who noted that when fluctuations were spread over a number of separate populations, the overall risk faced by the metapopulation was reduced.

Table 1. Dispersal rates (percentage of individuals migrating in each direction per year) at four assumptions of degree of dispersal

Distance (km)	Degree of dispersal			
	None	Low	Med	High
7–14	0	1·0	2·0	4·0
15–29	0	0·5	1·0	2·0
30–60	0	0	0·5	1·0

If the fluctuations in the environment were at least partially independent, so would be fluctuations in population growth rates. Thus, it would be less likely that all populations would go extinct at the same time, compared to a case where the fluctuations were dependent, i.e. synchronous. Conversely, if the fluctuations were partially synchronous, then models based on an assumption of independent population dynamics among patches would underestimate extinction risk. The effect of correlated environmental fluctuations has been discussed by Gilpin (1988, 1990), Forney & Gilpin (1989), Harrison & Quinn (1989), Akçakaya & Ginzburg (1991), and Burgman, Ferson & Akçakaya (1993).

Dynamics of the SBM spotted owl population could have been affected by rainfall (see below). If this was the case, any spatial correlation among different locations in terms of their rainfall patterns would also be reflected as a correlation among the population dynamics at those locations. Since there is substantial uncertainty in the estimation of this factor, we repeated our analysis with three different assumptions. In the first set of simulations, we assumed that there is no correlation among growth rates of different populations (i.e. their dynamics are independent). In second and third sets of simulations, we used two different levels of correlation. Thus, as we did for dispersal, we analysed the metapopulation dynamics with a wide range of correlations, from none to 'high'. We assumed that correlation in growth rates is a function of distance and assigned the correlation coefficients using the three functions given in Fig. 2. We assumed that the observed correlations among rainfall patterns (Table 2; squares in Fig. 2) represented an upper limit to the correlation among population dynamics. The reason for this assumption was that the correlation in the growth rates among populations would be a function of the product of two correlations, i.e. the correlation in the underlying environmental factors (such as rainfall) among populations and the correlation between the environmental factor(s) and population growth rates. Since the
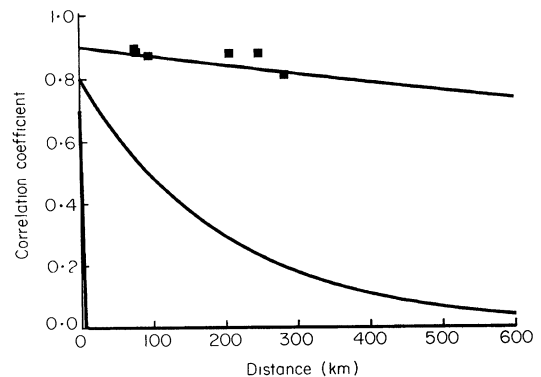
Table 2. Correlation of rainfall among four localities in southern California with spotted owl populations

| Locality | Locality | | |
	Palomar	Santa Ana	Santa Ynez
San Bernardino	0·873	0·885	0·842
Santa Ynez	0·811	0·880	
Santa Ana	0·896		

second correlation was not likely to be perfect, the correlations among growth rates of different populations were likely to be less than those among rainfall patterns.

The empirical observations of population change, as well as estimates of vital rates (see *Parameter estimation* overleaf) indicated that the population we modelled was declining. Since the cause of this decline was unknown to us, we modelled the dynamics of this population under two different hypotheses, 'deterministic decline' and 'environmental fluctuations'. Under the deterministic decline hypothesis, we assumed that for some unknown reason the population has entered into an irreversible decline and the population growth rate will never increase to the point that the population will recover (similar to 'systemic decline' as defined by Shaffer 1981). Under the environmental fluctuations hypothesis, we assumed that the population is exhibiting a temporary negative growth rate from which the population will recover once the environmental conditions improve (see *Population decline hypotheses* overleaf for details). The model was composed of 22 linked equations, each describing the dynamics of one population:

$$N_i(t+1) = N_i(t) R_i(t) - \sum_{j=1}^{n} m_{ij}N_i + \sum_{j=1}^{n} m_{ji}N_j$$

where n is the number of populations, $N_i(t)$ is the number of individuals in population i at time t, $R_i(t)$ is the growth rate of population i at time t, m_{ij} is the proportion of individuals emigrating (dispersing) from population i to population j. At each time step, the growth rates, $R_i(t)$, were selected from a multivariate lognormal distribution defined by the mean and standard deviation of the growth rate of each population and by the matrix of correlations among growth rates. These random variables were used to represent environmental stochasticity. In addition, demographic stochasticity was modelled by sampling the number of dispersers from a binomial distribution, and by decomposing the growth rate into components of survivorship and fecundity and sampling the number of survivors from a binomial and the number of young from a Poisson distribution (see Akçakaya & Ferson 1992; Akçakaya 1991; Lamberson 1992). The above equation shows that the dynamics of each population was modelled with a scalar (unstructured) model. The available data that we used to par-

Fig. 2. Functions used to assign correlation among growth rates of populations as a function of the distance between them. Squares are the observed correlations among rainfall patterns from Table 2.

ameterize this model came from only one of the populations and were limited to the territorial population. Therefore, a more detailed, age- or stage-structured model for the whole metapopulation was not justified.

For each of the two hypotheses outlined above, we performed simulations using four levels of dispersal and three levels of correlation (see above), and with four different durations (10-, 20-, 30- or 40-year time periods). For each combination, we performed 1000 replications of each simulation to obtain estimates of risk of decline. For each replication, the model started with the initial population sizes as described above. At each (yearly) time step, the growth rate of each population and the dispersal between populations were calculated, and the sizes of each population as well as the total metapopulation size were recorded. The results were summarized in terms of the probability of decline as a function of the amount of decline in the total metapopulation size in the next 10–40 years.

Results

PARAMETER ESTIMATION

Estimates of vital rates and annual rate of population change

Survivorship estimates were 0·344 (95% CI = 0·249–0·453) and 0·767 (95% CI = 0·728–0·802) for first year birds and owls greater than 1 year old, respectively. All ages greater than one year, sexes and time (years) categories were combined because either no significant differences in survivorship and recapture probabilities existed between the groups, or the data would not support these models at this time. We estimated fecundity to be 0·304 female offspring per territorial female over the study period.

The Leslie matrix analysis indicated that the SBM spotted owl population had an annual finite rate of increase of 0·860. The results of the stochastic simulations with an age-structured single-population model (Ferson & Akçakaya 1990) showed that the variation observed in survivorships and fecundities translated to a standard deviation of 0·11 for the finite rate of increase.

Empirical observations of population change

Territory occupancy declined in the SBM owl population between 1987 and 1993 (Fig. 3). The largest decline in this figure corresponded to an annual finite rate of population change of about 0·923. This decline was smaller than the estimate based on vital rates, and seemed to be leveling off towards the end of the study period. In addition, the proportion of subadults in the territorial population increased from 2% in 1987 to 23% in 1991 and declined back to 14% in 1992 (Fig. 4).
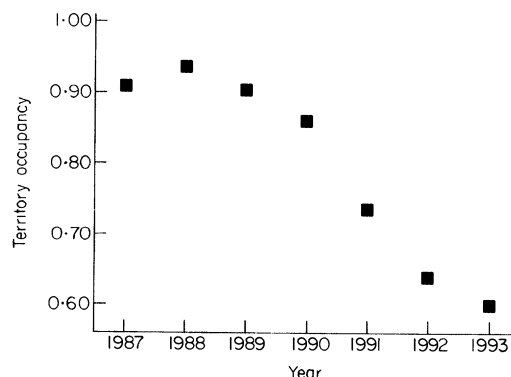

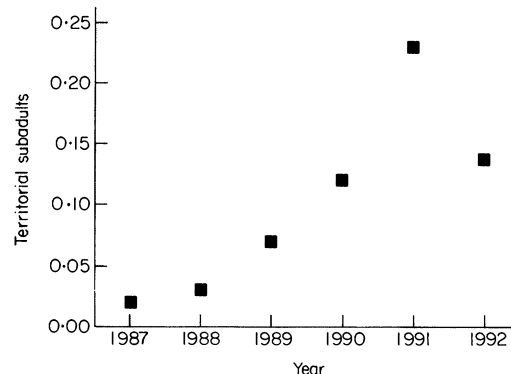**Fig. 3.** Territory occupancy in the San Bernardino Mountains population.

Fig. 4. Proportion of territorial population that was subadult in the San Bernardino Mountains population.

Environmental correlations

From 1985 to 1991, the SBM received below average rainfall. We explored the relationship between fecundity in year t and annual rainfall between June of year t-2 and May t-1 (Fig. 5). There was a positive linear relationship, significant at $P < 0·10$ level, that explained 52% of the variation in fecundity. The data (in Fig. 5) suggested that the relationship was nonlinear, but the small number of data points precluded a non-linear regression analysis.

The coefficients of correlation in total annual rainfall among four localities in southern California were
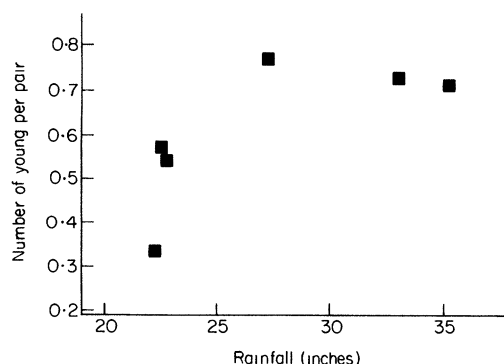

Fig. 5. Fecundity (number of young per pair) in year t as a function of annual rainfall between June t-2 and May t-1 in the San Bernardino Mountains population.

all significant ($P < 0.001$; Table 2). These annual rainfall correlations corresponded to the yearly time scale used in the metapopulation model.

The results demonstrated strong spatial correlation across large distances in an environmental variable, which may influence small mammal (i.e. the owl's prey) populations. Because this environmental variable might be correlated with fecundity, we decided to analyse the consequences of correlated growth rates among populations. To do this we used three levels of correlation as a function of distance (Fig. 2) as described above (see Methods).

RESULTS WITH NO DISPERSAL AND UNCORRELATED POPULATION GROWTH RATES

Deterministic decline hypothesis

We infer from this analysis that there is a moderate probability that the metapopulation will go extinct in the next 30 years (Fig. 6). However, this number by itself may be misleading if the whole decline curve is not taken into account: the rest of the 30-year risk curve indicates that it is very likely that only 1% of the metapopulation will remain at the end of 30 years. The last curve indicates that the metapopulation almost certainly will go extinct within the next 40 years under this hypothesis.

Environmental fluctuations hypothesis

Our analysis under this hypothesis showed that there may be a substantial decline in the southern California spotted owl metapopulation in the next 30–40 years (Fig. 7). However, total metapopulation extinction under this hypothesis is unlikely.

EFFECT OF DISPERSAL AND CORRELATED DYNAMICS

We evaluated the effect of dispersal on the risk of decline by comparing risk curves from simulations with different assumptions about the rate of dispersal.
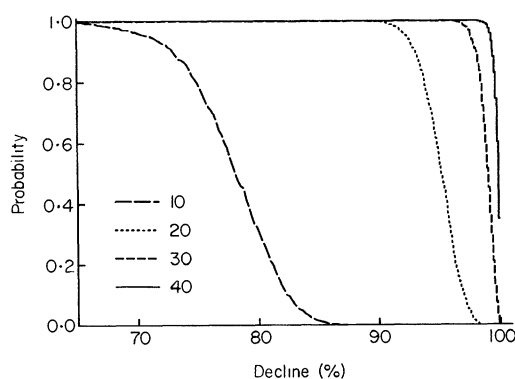

Fig. 7. Risk of decline under the environmental fluctuations hypothesis as a function of amount of decline and time (10–40 years). Dispersal and correlation are assumed to be zero.

The risk of decline was not sensitive to the degree of dispersal under the deterministic decline hypothesis. This was also true for the environmental fluctuation hypothesis for all but the highest degree of dispersal (Fig. 8). We assessed the effect of correlated growth rates among populations and found that increased correlations lead to increased risk of decline. This effect was quite large under the environmental fluctuations hypothesis (Fig. 9), but it was small under the deterministic decline hypothesis.
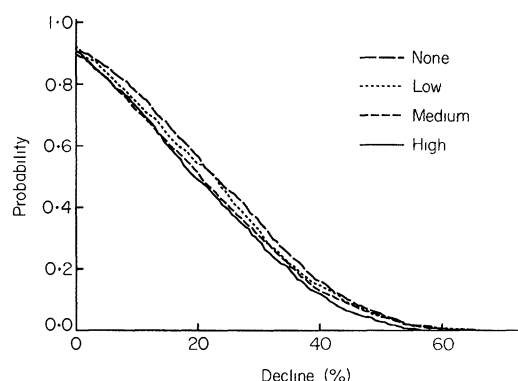
Fig. 8. Effect of dispersal on risk of decline in 20 years under the environmental fluctuations hypothesis and assumption of uncorrelated fluctuations.

Fig. 6. Risk of decline under the deterministic decline hypothesis as a function of amount of decline and time (10–40 years). Dispersal and correlation are assumed to be zero.
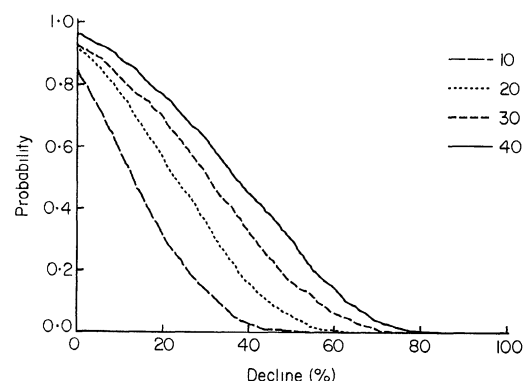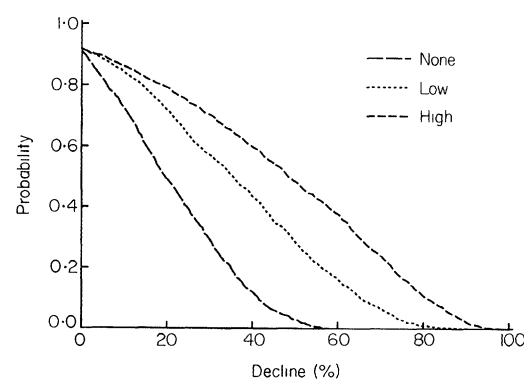

Fig. 9. Effect of correlation among population growth rates on risk of decline in 20 years under the environmental fluctuations hypothesis and assumption of high dispersal.

Discussion

SURVIVORSHIP AND FECUNDITY

Both survivorship and fecundities observed in this population were lower than those that have been estimated for the threatened Northern spotted owl (Thomas *et al.* 1990). Gutiérrez & Pritchard (1990) also found fecundity and adult survivorship of two other southern California owl populations to be lower than those estimated for the Northern spotted owl.

The two estimates of population growth rate from the SBM population, one based on demographic parameters, and the other based on territory occupancy, were different. An underestimation of vital rates, especially juvenile survivorship, could have accounted for this difference. However, a more likely scenario was that the decline in territory occupancy lags behind the decline in total population size because of the presence of 'floaters' in the population (Franklin 1992). Floaters are a non-territorial component of this owl population that we know exists, but that cannot be monitored because of their lack of typical, territorial behaviour. Floaters regularly fill territory vacancies. This buffers the predicted decline that is based on demographic characteristics of the observed territorial population. This scenario seemed especially plausible since the largest declines in territory occupancy occurred between 1990 and 1992 (Fig. 3). This suggested that the pool of floaters was diminishing. This notion of a floater population was strengthened by the increasing proportion of subadult owls occupying territories during the study period (see also Gutiérrez & Pritchard 1990). As the territorial and floater populations (composed mainly of adults) decline, subadult owls have increased access to territory vacancies.

POPULATION DECLINE HYPOTHESES

The cause of the decline in the SBM spotted owl population was not known. This population as well as others in southern California was not experiencing the level of habitat loss and fragmentation that threatens the Northern spotted owl and the California subspecies in the Sierra Nevada (US Department of the Interior 1992; Verner *et al.* 1992). Nevertheless, there was evidence that the SBM population may be declining even faster than spotted owl populations further north. The cause of this decline will have important implications for modelling the future persistence of this population. The cause of decline, or demonstration of a long-term decline was beyond the scope of the present study. In this study our aim was to investigate the metapopulation dynamics and to analyse the effects of spatial factors on the persistence of this metapopulation. For this analysis, we used a metapopulation model that we parameterized with the available data. Since the data may be interpreted differently to address the questions about the cause

(or even the existence) of population decline, we chose to perform our metapopulation analyses with different hypotheses. Below we provide several hypotheses for this decline and discuss their implications for model selection.

Deterministic decline

The decline could be due to an irreversible change in vital rates (lower than they were in the past). If this is the case, the appropriate model for evaluating metapopulation dynamics and predicting future trends would be the density-independent model using the observed growth rate. In other words, this hypothesis assumes that the population abundance will continue the trend observed between 1988 and 1992. Under these circumstances, the metapopulation would be expected to decline until it went extinct.

Density-dependent decline

A more optimistic scenario would be that the metapopulation had temporarily exceeded its carrying capacity and is currently in the process of returning to equilibrium. A temporary increase of metapopulation abundance above normal levels during favourable years may allow lower quality habitats to become temporarily occupied. These territories would be expected to become vacant as the population returned to normal levels. Conversely, a temporary increase above normal densities could be caused by loss of suitable habitat. The Palomar Mountain population (San Diego County) appeared to have an unusually high density of spotted owls in 1988 (Gutiérrez & Pritchard 1990). This increased density may have been caused by loss of suitable habitat by wildfire in 1987 (Gutiérrez & Pritchard 1990).

If the observed vital rates are low due to an overcrowding effect, they would be expected to return to normal levels once the population returns to normal densities. In this situation, the population should be modelled using a density-dependent model with a population growth rate greater than 1·0 and an equilibrium (or long-term average) population size equal to the currently estimated population size. This would lead to a greater probability of persistence than the previous model. However, there is no evidence of compaction or that the SBM spotted owl population is above an equilibrium or carrying capacity. We conclude that there is no evidence to support this hypothesis.

A previous viability analysis produced by the United States Forest Service (1988) for the northern spotted owl was criticized for being based on a model that lacked density dependence (Boyce 1987). However, in the case of the SBM population, the data did not suggest that the currently observed decline was towards an equilibrium determined by density-dependent relationships. This did not mean that the

population was never subject to density-dependent constraints. It only suggested that the current decline will probably not be stopped by the action of such constraints. Thus, it would not change the predictions of decline whether or not such constraints were included in the model.

Environmental fluctuations

A third explanation of the observed decline could be based on the effect of environmental factors. One environmental factor that could affect spotted owl population dynamics is precipitation. Precipitation's effect on primary productivity and thus prey densities could be an important determinant of spotted owl population growth rates. Southern California experienced a series of dry years during the period that the demographic study was conducted in the SBM. If this hypothesis is correct, estimates of fecundity or survivorship collected after several years of above average precipitation could be high enough to produce population growth rate estimates indicating a stable or increasing population.

If the 7-year dry period was the reason for the observed population decline, our models should have taken into account the possibility that the growth rate could approach 1·0 in the long term. Since the growth rate of the population has been observed only during dry years, the variation of growth rate, in addition to its average, will be expected to be higher in the long run. If the long-term growth rate is 1·0, one would have been as likely to observe an increase similar in magnitude to the observed decline. This would have doubled the amount of variation observed. For this reason, we assumed that the standard deviation of the growth rate could be twice the observed value of 0·11 in the long run. This scenario also required an estimate of the average population growth rate at low densities (when effects of overcrowding are not significant). We would have expected this to be more than 1·0, allowing the population to recover. The value of this parameter will determine how fast the modelled population will increase and how strong the density-dependent relationship is. When data are not available to estimate this parameter, one option is to use a density-independent model with a growth rate of 1·0. This approach provides more conservative estimates of risk of decline than a density-dependent model (Ginzburg, Ferson & Akçakaya 1990). In addition, it will still be a more optimistic scenario compared to the deterministic decline scenario discussed above. Consequently, we decided to perform risk assessment and metapopulation viability analysis with models based on these two scenarios. The names we have given these two hypotheses, 'deterministic decline' and 'environmental fluctuations', were chosen for convenience. They did not imply that there were no environmental fluctuations in the first hypothesis or that the second hypothesis will not lead to a population decline.

METAPOPULATION MODEL

Our aim in modelling the dynamics of the southern California spotted owl metapopulation was to evaluate the effect of spatial structure on the persistence of these populations. This evaluation was based on the two important components of spatial structure discussed above, dispersal and correlation of environmentally induced fluctuation among populations.

Levins (1969, 1970) developed the first metapopulation model which was based on the balance between rates of local extinction and recolonization of patches. Shaffer (1985) pointed out that the concept of metapopulation may be important in spotted owl population dynamics. Lande (1987, 1988) then developed a metapopulation model for the Northern spotted owl based on the recognition of individual territories as habitat patches where local extinction and recolonization take place. This last model rested on the assumption of random or even distribution of territories. This model was later extended by Lamberson et al. (1992) and used to assist in the design of habitat conservation areas for the Northern spotted owl (Thomas et al. 1990, appendix M, 'individual-territory model').

We believe that the assumption of random or even distribution of territories is not applicable in southern California. Spotted owl territories in southern California have a clumped distribution forming a series of isolated populations. These isolates range in size from one dozen to well over 100 territories. The owls can move much more freely within populations than between them.

Doak (1989) developed another metapopulation model for the Northern spotted owl and recognized groups of clumped territories. However, this model did not have explicit spatial structure and lacked the two important aspects of spatial structure discussed above. Doak assumed that the survival and reproduction probabilities were independent among populations (even within a population). The assumption of independent population dynamics could lead to an underestimation of risks of population decline. He also assumed that the rate of dispersal between all populations was equal. This assumption was relaxed in a similar model applied to both Northern (Thomas et al. 1990, appendix M, 'territory-cluster model') and to California (Noon & McKelvey 1992) spotted owl populations. In our analysis, the distance between populations ranged from 7 km to more than 600 km and these distances were reflected in the dispersal rates between populations in our analysis.

For the correlation among population dynamics, we assume that the similarity of environmental fluctuations between two populations is also a function of distance, i.e. closer populations are more likely to experience similar patterns of environmental fluctuations. In a region such as southern California where weather patterns have strong spatial corre-

lation, we believe this is a more reasonable assumption than complete independence or complete correlation of population dynamics.

RISK ASSESSMENT AND VIABILITY ANALYSIS

The natural variability in population dynamics compounded by the uncertainty in the population parameters, make probabilistic risk analysis with the use of stochastic models a useful tool for assessing the viability of animal populations (Shaffer 1990; Ginzburg *et al.* 1990; Akçakaya 1992). In this study, we express the results of our model in terms of risk of decline as a function of the amount of decline during the simulated time period (Figs 6–9). A decline of 100% corresponds to the total extinction of the metapopulation. Expressing risk as a probability of a partial loss generalizes the case of total extinction. This is particularly useful since in most cases the estimates of the risk of total extinction are less reliable due to complicating demographic and genetic factors such as Allee effects and inbreeding depression that become effective at low population sizes.

Our results show that the spotted owl metapopulation in southern California faces a serious threat of decline if the current demographic trends continue. The SBM spotted owl population has declined dramatically in the last 5 years. If the current demographic trends continue and are representative of the other populations in the region, our analysis indicates that the southern California metapopulation could become extinct within 40 years. Even the more optimistic scenario that the decline is temporary, would result in a substantial decline in this metapopulation before a recovery period begins.

Another important result from our analysis was that dispersal and correlation of growth rates between the populations had little effect on the results when modelled under the deterministic decline hypothesis. However, our results indicated that the risk of decline was quite sensitive to the correlations among population growth rates under the environmental fluctuations hypothesis (Fig. 9). As expected from results of previous theoretical studies, increased correlation of the dynamics of different populations in this metapopulation increased the risk of decline. This was an important result, since some metapopulation models developed for the spotted owl have ignored this factor, thus they have potentially underestimated the risks that the spotted owl metapopulations were facing. Others have made the other extreme assumption that all populations have completely correlated dynamics (e.g. Lamberson *et al.* 1992). This assumption prevents an underestimation of extinction risks, but may be overly conservative (i.e. pessimistic in prediction of risks) for species with widespread geographic distributions. The results of our sensitivity analysis suggested that correlation of population growth rates needs to be estimated more accurately.

Our simulation results were not very sensitive to the rate of dispersal. This result suggested that unless the actual dispersal rates between populations were higher than the maximum rates we assumed (4% per year between the closest populations), the populations can be considered effectively isolated. However, we have assumed density-independent dispersal in our model. Making the dispersal rate an increasing function of density may make the results (risks of decline) more sensitive to changes in dispersal rates.

Distinguishing natural population fluctuations from human-induced declines can be difficult and require long-term demographic data (Pechmann *et al.* 1991). Clearly, the two hypotheses we use make very different predictions about the future of this metapopulation. If increased rainfall increases fecundity or survival, it would validate the use of the environmental fluctuations hypothesis for evaluating this metapopulation. However, if increased rainfall has little or no effect on fecundity, the deterministic decline hypothesis would be the correct model to use when modelling the southern California spotted owl metapopulation.

We conclude that continued monitoring of the SBM spotted owl population would provide important information on the population dynamics of spotted owls in southern California. In addition, similar information collected on other populations in this region are necessary to estimate the variation in and correlation among population dynamics within the metapopulation. The ability to distinguish natural fluctuations from human-caused changes is critical to developing appropriate conservation strategies for endangered species.

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