

Demographic models of the northern spotted owl (*Strix occidentalis caurina*)

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Summary. Classical demographic methods applied to life history data on the northern spotted owl yield an estimate of the annual geometric rate of increase for the population of $\lambda = 0.96 \pm 0.03$, which is not significantly different from that for a stable population ($\lambda = 1.00$). Sensitivity analysis indicates that adult annual survivorship has by far the largest influence on λ , followed by the probability that juveniles survive dispersal, and the adult annual fecundity. Substantial temporal fluctuations in demographic parameters have little effect on the long-run growth rate of the population because of the long adult life expectancy. A model of dispersal and territory occupancy that assumes demographic equilibrium is evaluated using data on the amount of old forest habitat remaining in the Pacific Northwest and the current occupancy of this habitat by northern spotted owls. This model is employed to predict the effect of future habitat loss and fragmentation on the population, implying that extinction will result if the old forest is reduced to less than a proportion 0.21 ± 0.02 of the total area in a large region. The estimated minimum habitat requirement for the population is greater than that allowed in management plans by the USDA Forest Service.

Key words: Demography – Territoriality – Dispersal – Colonization – Extinction

The northern spotted owl (*Strix occidentalis caurina*) is a monogamous, territorial subspecies that inhabits old coniferous forests in western Washington, Oregon and northern California. Each pair utilizes about one to three square miles of forest more than about 250 years old and below an elevation of roughly 4000 ft., nesting in hollow trees and preying on small mammals, birds and insects (Forsman et al. 1984; Gutiérrez 1985). Heavy logging, especially on private land, in recent decades has destroyed most of the old forest upon which these owls depend, and the great majority of that remaining is concentrated in areas managed by the U.S. Forest Service, the National Park Service, and the Bureau of Land Management (Society of American Foresters 1984). The total population of the northern spotted owl in the Pacific Northwest region was recently estimated to be about 2500 pairs (USDI Fish and Wildlife Service 1982; Dawson et al. 1987).

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The National Forest Management Act of 1976 (16 U.S.C. §1600 et seq.) and its implementing regulations 36 C.F.R. §219) require that viable populations of all native species of vertebrates be maintained well-distributed through their range. Under opposing pressures from conservationists and the timber industry, the U.S. Forest Service formulated guidelines for the management of spotted owl habitat. The management plan, as originally proposed (USDA Forest Service 1984), suggested preservation of enough old-forest habitat to maintain a population of the minimum size that has been thought sufficient to ensure long-term persistence on population genetic grounds (Franklin 1980). Recognizing that demographic factors also need to be considered, later management recommendations have been based on extensive computer simulations of population growth models (USDA Forest Service 1986).

Here I apply simple analytical models to (1) estimate the geometric growth rate of the northern spotted owl population, and (2) predict the effect of future habitat loss and fragmentation on the equilibrium occupancy of suitable territory. The first model uses a standard demographic method for projecting the growth of a population from age-specific fecundity and mortality rates (Lotka 1956; Keyfitz 1977). The second model generalizes Levins' (1969, 1970) analysis of a metapopulation maintained through a balance of local extinction and colonization, by incorporating life history, territoriality and dispersal behavior in a patchy environment (Lande 1987).

Geometric growth rate of the population

Characteristic equation

In a population with overlapping generations, reproducing at discrete yearly intervals, the annual geometric growth rate of the population, λ , is the (unique) positive real solution of the Euler-Lotka or characteristic equation,

$$\sum_{x=0}^{\infty} \lambda^{-x} l_x b_x = 1. \quad (1)$$

Here l_x is the probability of survival from birth or fledging to age x . Letting s_i be the probability of survival from ages i to $i+1$, define $l_x = s_0 s_1 \dots s_{x-1}$, and b_x as the rate of production of female offspring per female of age x (Leslie 1966; Mertz 1971). If these parameters do not change with time,

Table 1. Basic demographic statistics for the northern spotted owl

Parameter estimate	Sample size	Reference
Fledgling survival probability (pre dispersal), $s'_0=0.60$	$N_0=135$	Marcot and Holthausen (1987)
Probability of successful dispersal, $s_d=0.18$	$N_d=44$	Marcot and Holthausen (1987)
Subadult annual survival probability, $s_1=0.71$	$N_1=7$	Franklin et al. (1986)
Adult annual survival probability, $s=0.942$	$N_s=69$	Franklin et al. (1986)
Adult female ave. annual fecundity, $b=0.24$	$N_b=438$	Marcot and Holthausen (1987)
Age at first breeding (in years), $\alpha=3$	general observations	Forsman et al. (1984); Gutiérrez (1985)

and there is a constant sex-ratio at fledging, the size of the total population at year t can be predicted approximately from the geometric formula, $N(t)=\lambda^t N(0)$, apart from fluctuations in age structure during the first few generations (Keyfitz 1977).

In many avian species the expected mortality and reproductive rates of adults are nearly constant and independent of age (Deevey 1947). Denoting the age of first reproduction as α , and the adult annual survivorship as s , for such species we can write $l_x=l_\alpha s^{x-\alpha}$ and $b_x=b$ for $x \geq \alpha$ (with $b_x=0$ for $x < \alpha$). The series in the characteristic equation can then be summed to give

$$\lambda^\alpha(1-s/\lambda)=l_\alpha b. \quad (2)$$

Because $l_\alpha b \geq 0$, the positive real solution of this equation must be such that $\lambda \geq s$.

Field data indicate that northern spotted owls usually start breeding at an age of $\alpha=3$ years (Forsman et al. 1984; Gutiérrez 1985). In this case, the characteristic equation is cubic and can be easily solved numerically. The probability of survival through the first year of adulthood can be written as $l_3=s'_0 s_d s_1 s$, where the first year survivorship, s'_0 , has been expressed as the probability of successful dispersal, s_d , times that of surviving the first year excluding the risk of dispersal s'_0 . Estimates of the demographic parameters in Table 1 give the probability of survival to reproductive age as $l_3=0.0722$, the adult annual survivorship as $s=0.942$, and the average reproductive rate of $b=0.24$ female offspring fledged per adult female per year. From these data and formula (2) it can readily be found that $\lambda=0.961$.

Sensitivity analysis

The sensitivities (or partial derivatives) of λ with respect to small changes in the life history parameters indicate which of the parameters has the largest impact on the geometric growth rate of the population; they also are important in calculating the standard error of λ and in determining the effect of stochastic variation in life history parameters on the long-run growth rate of the population. The sensitivities are found by implicit differentiation of the characteristic Eq. (2), as in Goodman (1971),

Table 2. Sensitivity of λ to changes in estimated demographic parameters of the northern spotted owl, and their contributions to the sampling variance in λ , from Eqs. (3), (4) and Table 1

Parameter	Sensitivity of λ	Contribution to $\sigma_\lambda^2 (\times 10^4)$
s'_0	0.030	0.016
s_d	0.102	0.349
s_1	0.026	0.199
s	0.981	7.620
b	0.076	0.041
α	-0.000	0.000
Total		8.225×10^{-4}

$$\begin{aligned} \partial \lambda / \partial \pi &= \lambda / (\pi T), & \partial \lambda / \partial s &= \lambda (T - \alpha + 1) / (s T), \\ \partial \lambda / \partial \alpha &= -\lambda [\ln(\lambda/s)] / T \end{aligned} \quad (3)$$

where π represents any of the statistics s'_0, s_d, s_1 , or b , and $T = \alpha + s/(\lambda - s)$ is the generation time of the population, defined as the average age of mothers of newborn individuals in a population with a stable age distribution (Leslie 1966; Mertz 1971).

Using the data on the northern spotted owl, the sensitivity coefficients are evaluated in Table 2. The geometric growth rate of the population is by far most sensitive to changes in the probability of adult annual survival, and is next most sensitive to the probability of finding a territory and the average reproductive rate. However, adult survivorship is already quite high, and may have little possibility of further improvement. The age of first reproduction is relatively unimportant because increasing the reproductive age by 1 year would decrease the geometric growth rate of the population by less than 0.1%.

Standard error of λ

The sensitivities in equations (3) appear in the approximate formula for the sampling variance of an estimated value of λ ,

$$\sigma_\lambda^2 = \sum_{\pi} (\partial \lambda / \partial \pi)^2 \sigma_\pi^2 \quad (4)$$

where π here represents each of the parameters, and σ_π^2 is the sampling variance of π estimated from N_π individuals in the population (Kendall and Stuart 1977, Ch. 10.6). Most of the parameters are survival probabilities with binomial sampling distributions for which $\sigma_\pi^2 = \pi(1-\pi)/N_\pi$; for estimates of b or α the sampling variance is the variance of annual fecundity or age at first reproduction among females in the population divided by the appropriate sample size. Formula (4) omits possible covariances between the sample statistics which could arise for example if some of the parameters are estimated from the same individuals, or are measured on genetic relatives. It also neglects sampling variance caused by spatial and temporal inhomogeneity of the population, and possible biases such as increased mortality of dispersing juveniles carrying radio transmitters.

Components of the sampling variance of λ were calculated from formula (4), using the demographic statistics in Table 1 and the sensitivity coefficients in Table 2. Following

the analytical statistics of other variables among the tributaries of λ . It is observed (Forsman et al. 1984) that the square of the estimated value of λ is 0.961 and is therefore stable population. The estimate of λ is 0.961 and is therefore stable population. The estimate of λ is 0.961 and is therefore stable population.

Stochastic

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where λ is calculated from Table 1) and the equation and $r_{s,\pi}$ is To get suppose

the analysis by Barrowclough and Coats (1985) of reproductive statistics for the northern spotted owl, and various other owl species, I assumed that the variance in fecundity among adult females is 1.3 times its mean value shown in Table 1. The sensitivity coefficient of the age at first reproduction is so small that intrapopulation variation in α contributes a negligible amount to the sampling variance in λ . It is therefore sufficient to use $\alpha=3$, based on general observations that breeding usually begins in the third year (Forsman et al. 1984; Gutiérrez 1985), and to ignore variation in this parameter, i.e. occasional observations of breeding in the second year (Gutiérrez 1985), or that many females must first successfully fledge female offspring in their fourth or fifth year (which is implied by the low mean fecundity, $b \ll 1$).

The standard error of the estimate of λ , obtained as the square root of the sampling variance in formula (4), for the spotted owl is ± 0.029 . The estimated value of $\lambda=0.961$ is less than twice its standard error from 1.000 and is therefore not significantly different from that for a stable population, supporting the contention that the population currently may be near a demographic equilibrium. The estimated rate of change in population size, representing an annual increment of $\lambda-1 = -4\%$, also is not significantly different from the approximate 1% annual decline estimated from long-term surveys in Oregon (Forsman et al. 1984; Forsman 1986).

Stochastic variation in demographic parameters

So far the analysis has dealt only with the average demographic parameters in the population. The conclusion that the population is nearly stable may be overly optimistic because it does not account for temporal fluctuation in age-specific fecundity and mortality rates around their average values (the "environmental stochasticity" of Shaffer [1981]), which tends to diminish the long-run growth rate of the population, if there is no serial correlation (autocorrelation) in the fluctuations (Tuljapurkar 1982). In species with long-lived adults, the population may be maintained by occasional good years for reproduction and juvenile survival. Long-term weather records in the continental United States show very little autocorrelation on a yearly time scale (Nambias 1978; Nicholls 1980). For species that reproduce at annual intervals, such as the spotted owl, this justifies in part the assumption of no autocorrelation in demographic parameters, although long-term fluctuations or cycles in prey abundance may cause some autocorrelation.

According to a general formula of Tuljapurkar (1982), the long-run (geometric average) growth rate of a population, A , subject to small fluctuations in demographic parameters with no serial correlation is approximately

$$A = \lambda \exp \left\{ -\frac{1}{2} \lambda^{-2} \left[(\partial \lambda / \partial s)^2 v_s^2 + (\partial \lambda / \partial \pi)^2 v_\pi^2 + 2(\partial \lambda / \partial s)(\partial \lambda / \partial \pi) v_s v_\pi r_{s,\pi} \right] \right\} \quad (5)$$

where λ is the geometric growth rate of the population calculated from the average demographic statistics (Eq. 2 and Table 1). v_s^2 is the yearly variance in adult annual survival, and the sensitivity coefficients have the forms shown in equations (3), but here $\pi = l_2 b$ with the yearly variance v_π^2 , and $r_{s,\pi}$ is the correlation between s and π .

To gain some impression of the magnitude of this effect, suppose that adult annual survivorship has a coefficient

of variation among years of 10%, $v_s/s=0.1$ (which indicates roughly the range of values used in different models), that $\pi = l_2 b$ undergoes much larger fluctuations with a coefficient of variation of $v_\pi/\pi = 5$ representing frequent poor years and occasional good years for reproduction and juvenile survival (Forsman et al. 1984; Barrows 1985), and that fluctuations in s and π are highly correlated, $r_{s,\pi} = 1$. Utilizing the information in Tables 1 and 2, the long-run growth rate of the population, $A = (0.98)\lambda$, is only slightly smaller than in a constant environment with the average demographic parameters. Because of the long life expectancy of adults, $1/(1-s) \cong 17\frac{1}{4}$ years, substantial yearly fluctuations in demographic parameters have little effect on the long-run growth rate of the population, at least in the absence of serial correlation.

Truncation of the life table

Demographic models of the northern spotted owl population constructed by the USDA Forest Service (1986, Appendix B) and by Marcot and Holthausen (1987) assumed a maximum age for survival and reproduction of 10 or 15 years. The amount by which truncation of the life table, without changing the other life history parameters, decreases λ can be seen by including in the present model a maximum age for survival, ω , as done by Mertz (1971), so that the characteristic equation becomes

$$\lambda^\alpha (1-s/\lambda) / [1 - (s/\lambda)^{\omega-\alpha+1}] = l_\alpha b. \quad (6)$$

With truncation of the life table, λ may be less than s .

For a population with the parameters used by the USDA Forest Service (1986, p. B-24), $s_0 = 0.20$, $s_1 = s = 0.85$, $b = 0.275$, $\alpha = 3$ and $\omega = 10$, the positive real solution of Eq. (6) is $\lambda = 0.77$. At this rate of decline, starting from the current estimated population size of 2500 pairs (USDI Fish and Wildlife Service 1982; Dawson et al. 1987) or $N = 5000$ individuals, the population is expected to become extinct (reduced to a single individual) in roughly $\tau = -\ln N / \ln \lambda$ years, or about 33 years. This agrees with the precipitous population crash forecast by the USDA Forest Service (1986, p. B-25). Using the same statistics, but without truncating the life table, $\omega = \infty$, Eq. (2) yields $\lambda = 0.90$, which is close to my initial estimate of 0.92 from similar data (Lande 1985).

For the demographic parameters used by Marcot and Holthausen (1987), $s_0 = 0.11$, $s_1 = s = 0.96$, $b = 0.24$, $\alpha = 3$ and $\omega = 15$, the geometric growth rate of the population becomes $\lambda = 0.86$, indicating extinction of the present population in about 56 years. If their life table is not truncated, $\omega = \infty$, Eq. (2) gives the more realistic growth rate of $\lambda = 0.985$, nearly identical to the approximate long-term trend (Forsman et al. 1984; Forsman 1986).

Dispersal and territory occupancy

Basic theory

Utilizing the concept of a metapopulation maintained by a balance between local extinction and colonization, Levins (1969, 1970) pointed out that a species may not occupy all of the habitat available to it, and a population may go extinct in the presence of suitable patches of habitat. Shaffer (1985) discussed the relevance of these ideas for conservation of the northern spotted owl. Lande (1987) ex-

tended the metapopulation concept to a territorial population by identifying the individual territory as the unit of local extinction and colonization, and incorporating life history and the dispersal behavior of individuals in a patchy environment. On the assumption that environmental patches suitable for survival and reproduction of the species are randomly or evenly distributed across a large region, interspersed with uninhabitable patches, the model predicts the equilibrium occupancy of suitable habitat by females, \hat{p} , as a function of the proportion of the region that is suitable (habitable), h , and the demographic potential of the population, k , which is determined by the life history and dispersal behavior. k is called the demographic potential because it gives the equilibrium proportion of territories that would be occupied by females in a completely suitable region. Knowing the amount of suitable habitat in a large region, h , and estimating the proportion of it currently occupied by females, p , assuming the population is at a demographic equilibrium, the structure of the model allows us to estimate k and to predict the effect of future environmental alterations on the equilibrium occupancy of suitable habitat, \hat{p} .

Let the probability that a juvenile (female) inherits the home territory of its (female) parent be ε , which is assumed to be constant. If the natal territory is not inherited, juveniles disperse and are assumed capable of searching m territories to find a suitable unoccupied patch of habitat, before perishing from predation, starvation, etc. Then the probability of not inheriting the home territory, and upon dispersal not finding a suitable unoccupied territory in m trials is $(1-\varepsilon)(ph+1-h)^m$. The characteristic equation for a territorial population at demographic equilibrium ($\lambda=1$) can thus be written by separating from the other parameters the probability of successful dispersal, i.e. inheriting or finding a suitable unoccupied territory,

$$[1-(1-\varepsilon)(\hat{p}h+1-h)^m]R'_0=1 \quad (7)$$

where

$$R'_0 = \sum_{x=0}^{\infty} l'_x b_x \quad (8)$$

is the mean lifetime production of female offspring per female, conditional on the mother finding a suitable territory, with l'_x denoting the probability of survival until age x under the same condition. For the avian life history given above (without truncation of the life table) $R'_0 = l'_x b / (1-s)$. This model encompasses a range of possible density-dependent population dynamics, from $m=1$ as in Levins' model involving logistic growth, to $m=\infty$ which allows density-independent exponential growth up to a ceiling ($\hat{p}=1$).

Solving Eq. (7) for the equilibrium occupancy of territories by females gives

$$\hat{p} = \begin{cases} 1-(1-k)/h & \text{for } h > 1-k \\ 0 & \text{for } h \leq 1-k \end{cases} \quad (9)$$

where the demographic potential of the population is

$$k = [(1-1/R'_0)/(1-\varepsilon)]^{1/m} \quad (10)$$

Assuming that $0 < k < 1$, Eq. (9) describes the equilibrium occupancy of suitable habitat in a large region. The demographic potential then gives the equilibrium occupancy of suitable territories by females in a large region

that is completely habitable ($\hat{p}=k$ when $h=1$). The population can persist only if the proportion of suitable habitat in the region, h , is greater than $1-k$. The minimum proportion of suitable habitat in a large region is termed the extinction threshold for the population (Lande 1987).

From current estimates of p and h in the population, assuming it is at a demographic equilibrium, Eq. (9) can be solved for the demographic potential containing all of the (unknown) demographic parameters, $k=1-(1-\hat{p})h$. This procedure allows k to be estimated directly from p and h without detailed information on the parameters of life history and dispersal behavior in Eq. (10). If h is known exactly, the sampling variance of an estimate of k is approximately $\sigma_k^2 = h^2 \sigma_p^2$ where $\sigma_p^2 = p(1-p)/N_p$ and N_p is the number of suitable territories sampled for occupancy. Having estimated k , and supposing it is constant, past and future values of the equilibrium occupancy of suitable habitat can be estimated from Eq. (9) for regions in which h was, or will be, different from its present value.

The habitat occupancy model depends strongly on the assumption of a random or even distribution of suitable territories in a region, but is largely independent of the dispersal strategy of individuals, provided they are capable of moving much farther than the average distance between their natal territory and the nearest suitable site. Since dispersing individuals may settle on the first suitable unoccupied territory they encounter, while the parameter m describes the number of potential territories that a dispersing individual can search, the model allows for adjustment of realized dispersal patterns and changes in the probability of successful dispersal with changes in the amount of suitable habitat and its occupancy. This type of mass action model (like Levins') does not account for the detailed spatial distribution of suitable habitat, or chance clumping of individuals as a result of dispersal, mating and reproduction, but it should be valid as long as the population density is not so low that demographic and environmental stochasticity are likely to cause rapid extinction (cf. Lande 1987).

Application to the northern spotted owl

Before 1800, roughly 60% to 70% of the forested regions of the Pacific Northwest consisted of coniferous forest more than 200 years old, with the remaining areas in younger age categories due to fire and other natural catastrophes (Franklin and Spies 1984). National forests in the Douglas-fir region of western Washington and Oregon currently contain about 38% old forest greater than 200 years old (Society of American Foresters 1984), thus $h \cong 0.38$. Although there is some ambiguity in the Forest Service guidelines (USDA Forest Service 1984, 1986), they appear to call for 550 pairs of owls distributed on one-pair and three-pair Spotted Owl Management Areas (SOMAs) spaced respectively within 6 and 12 miles apart in 12 national forests in Washington and Oregon, with a minimum of 1000 acres and a maximum of 2200 acres of (nearly) contiguous old forest per pair. (Among six pairs studied by radiotelemetry in northwestern Oregon, 1008 acres was the smallest amount of old growth included in a home range, with the average being 2264 acres of old growth [Forsman and Mellow 1985].) This totals a minimum of 0.55 million acres and a maximum of 1.21 million acres of old forest in about 7.6 million acres of forested land (Society of American Foresters 1984). Under the guidelines the future proportion of

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suitable habitat for northern spotted owls in national forests would be in the range of about 7% to 16%.

Young spotted owls are fledged in the summer and disperse long distances in the fall (dozens of kilometers) (Gutiérrez 1985; Gutiérrez et al. 1985), so there may seem to be no difficulty for juveniles searching for potential territories up to 6 to 12 miles away during dispersal. However, the low density of suitable habitats in the future may pose serious problems for dispersing juvenile spotted owls searching for a suitable unoccupied territory.

Surveys of 46 SOMAs designated by the Forest Service on national forests in western Washington during the three years 1984–1986 (giving $N_p = 138$) indicate that on average each year 22% of SOMAs were confirmed occupied by a pair of owls and an additional 22% of SOMAs were confirmed occupied by single owls (Allen et al. 1987), giving an average annual occupancy of $p \cong 0.44 \pm 0.04$. (43% of the SOMAs were confirmed occupied by a pair of spotted owls in at least one of the three years.) SOMAs were confirmed to be occupied through daytime visual sighting after day or night response(s) to artificial calls. This figure probably overestimates female occupancy because some of the single owls may have been males; in northern California, most of the single owls occupying territories were males (Franklin et al. 1986, Table 7).

From current estimates of $h \cong 0.38$ and $\hat{p} \cong 0.44$, assuming the population is stable, the demographic potential estimated from the above formulas is $k = 0.79 \pm 0.02$. The model of Eq. (9) then suggests that under primitive conditions with $h = 0.6$ to 0.7 the proportion of suitable habitat occupied by females was high, $\hat{p} \cong 0.7$. Furthermore, it appears that in large regions where a proportion less than $1 - k = 0.21 \pm 0.02$ of the area is composed of suitable habitat (coniferous forest more than 200 years old) northern spotted owls can not persist. This model therefore predicts that the effect of implementing Forest Service guidelines and recommendations (USDA Forest Service 1984, 1986), with future $h \cong 0.07$ to 0.16 , will be to cause the extinction of spotted owls from the region. Even a plan that would double or triple the number of SOMAs, assuming these to consist each of 1000 acres of old growth (Shaffer 1985), would be likely to rapidly extinguish the population. The predicted extinction of the population is robust to substantial error in estimating the current occupancy, for if $\hat{p} = 0.60$ then $k = 0.85$, or if $\hat{p} = 0.25$ then $k = 0.72$, and in either case the population is still likely to become extinct under the proposed plan.

This model of dispersal and habitat occupancy is optimistic in several respects because of the assumptions that there is no difficulty in finding a mate, no dispersal out of regions containing suitable habitat, no demographic or environmental stochasticity (including environmental catastrophes – see Forsman 1986), and no loss of fitness from inbreeding depression in small populations. In addition it is assumed that the suitability of SOMAs designated by the Forest Service is now high and will not decline in the future (e.g., due to increasing fragmentation of old forest within individual territories, or local extinction of prey species that are incapable of dispersing between SOMAs). Violation of any of these assumptions would render population persistence more difficult (Levins 1969; Shaffer 1981; Lande 1987), hence this model is likely to underestimate the extinction threshold, or minimum proportion of suitable habitat in a region necessary to sustain the population.

Discussion

The annual geometric growth rate of the northern spotted owl population estimated from currently available demographic data (Table 1) is $\lambda = 0.96 \pm 0.03$, which is statistically not significantly different from that for a stable population ($\lambda = 1.00$) or from the approximate 1% annual decline estimated from long-term surveys by Forsman et al. (1984) and Forsman (1986). This is larger than earlier estimates of the geometric growth rate by Lande (1985), the USDA Forest Service (1986), and Dawson et al. (1987), all of which predicted rapid extinction under current conditions. The discrepancies between the present estimate and previous ones can be explained as follows. My initial estimate of $\lambda = 0.92$ was based on earlier data that indicated higher juvenile survival and adult fecundity, but somewhat lower adult survivorship. The sensitivity coefficients in Table 2 indicate that changes in the latter parameter have the largest effect on λ , which explains why my initial estimate was less than the present one.

Dawson et al. (1987) used data similar to those in Table 1, but with an adult annual survival of only 0.80, which from formula (2) yields $\lambda = 0.83$. Although this would imply rapid extinction of the population, the decline would not be nearly as rapid as they claimed because they incorrectly used R_0 (the mean number of female offspring fledged by females in their lifetime) instead of λ to project future population changes.

The USDA Forest Service (1986) estimated a much more rapid decline under current conditions, based on essentially the same statistics as in my earlier report, but they assumed a maximum longevity of 10 years, which as shown above produces $\lambda = 0.77$. Arbitrary truncation of the life table is largely responsible for their extreme results. The practice of assigning the observed adult annual survival probability, s , to adults up to some age, and setting annual survival to zero thereafter (USDA Forest Service 1986; Marcot and Holthausen 1987), is actually inconsistent with the data since in such a model the average annual survival probability of adults in the population is less than s because of certain death at the maximum age. In the absence of data on the age-specific survivorship of adults, it seems more reasonable to equate s with the observed average annual adult survivorship without truncating the life table. For the purpose of computer simulation it may be convenient to truncate the life table at some age, or to otherwise limit adult longevity (Botkin and Miller 1974), but for avian species there is little biological justification for setting the maximum adult longevity less than four times the average adult longevity in nature (Deevey 1947, Fig. 4). The maximum lifespan should therefore be at least $\alpha + 4/(1 - s)$, which for the northern spotted owl is about 72 years (Table 1). Several eagle owls (*Bubo bubo*) are reported to have lived more than sixty years, and one individual 68 years, in captivity (Pettingill 1970, p. 399; Grzimek 1972, p. 407). Since maximum longevity in animals scales as body weight to the 0.15 power (Blueweiss et al. 1978), and spotted owls weight about one fourth as much as eagle owls (Grzimek 1972, p. 406; Dawson et al. 1987), this suggests a maximum longevity of roughly 55 years for spotted owls. Had the Forest Service not truncated the life table of the northern spotted owl at such an early age, they would not have found it necessary to “recalibrate” their model by increasing juvenile survivorship and adult fecundity beyond what was warranted by the data in order

to achieve a current population growth rate comparable to the 1% annual decline estimated from long-term surveys to investigating a range of management alternatives.

Formal sensitivity analysis provides the best method for planning an efficient sampling program to estimate the life history parameters contributing to population growth. As a general rule, sampling effort to measure the basic demographic statistics should be proportional to their contribution to the sampling variance of λ (or if possible the sampling variance of A , the long-term geometric growth rate). Applying this rule to the present data on the northern spotted owl suggests that future field studies should concentrate most sampling effort on adult survivorship within and between years, since this has by far the largest sensitivity coefficient and accounts for the vast majority of the sampling variance of λ , if the life table is not truncated (Table 2). The second most important parameter in both respects is the probability of successful dispersal. Subadult survival contributes the third largest amount to the sampling variance in λ because of the small sample size, although it has only the fifth largest sensitivity coefficient. The least important parameter is the age at first breeding, which has a sensitivity coefficient so low that its contribution to the sampling variance of λ is negligible. In contrast, previous numerical analyses by the USDA Forest Service (1986, Appendix B) and Marcot and Holthausen (1987) concluded that juvenile survival and adult fecundity are the two most important parameters in determining the growth rate of the population, followed by the ages of first and last reproduction; those results are apparently an artifact of truncation of the life table. Without the benefit of a sensitivity analysis, Dawson et al. (1987) recommended that top priority in future demographic research should be given to pre-adult survival, age at first reproduction, and age-specific reproductive rate, and that relatively low priority should be assigned to adult survivorship.

The present analysis indicates that substantial yearly fluctuations in demographic statistics have only a small effect in decreasing the long-run growth rate of the population (assuming no serial correlation) because of the long expected adult longevity of $17\frac{1}{4}$ years. In this regard, a coefficient of variation of 10% in adult annual survival probability is almost equivalent to a coefficient of variation of 500% in the product of survival probability through age 2 and adult annual fecundity, because of the relatively large sensitivity coefficient of the former parameter (Eq. 5 and Table 2). In contrast with the present analysis, the USDA Forest Service (1986, p. S-11) concluded that the greatest risks to the northern spotted owl population are "reduction in habitat combined with the low reproductive rate for the species and variations in reproductive rate over time." Marcot and Holthausen (1987) concluded that demographic stochasticity poses the most immediate threat to continued persistence of the northern spotted owl population. The importance these authors place on stochastic variation in demographic parameters may in part be an artifact of their truncation of the life table. Dawson et al. (1987) recognized the prime importance of habitat destruction, but also placed great emphasis on demographic stochasticity in small populations, based on case studies of other species. Long-term surveys in Oregon (Forsman et al. 1984; Forsman 1986) and California (Gould 1985), the present analysis of stochastic demography, and the present deterministic model of territory occupancy, concur that destruction of old-forest habi-

tat by logging constitutes the major threat to the continued existence of the northern spotted owl.

The model employed here to predict the effect of future habitat alteration on the northern spotted owl population extends Levins' (1969, 1970) model of a metapopulation maintained by local extinction and colonization by including life history, territoriality, and dispersal behavior in a patchy environment (Lande 1985, 1987). The fundamental results of these models are that in general a population at demographic equilibrium does not occupy all of the patches of suitable habitat available to it, and that a population may become extinct in the presence of suitable habitat because of the difficulty that dispersing juveniles experience in searching for a territory.

The original plan for preserving the northern spotted owl did not recognize these demographic principles (USDA Forest Service 1984), but was based instead on population genetic considerations which are by themselves of dubious value for the conservation of wild populations (Lande and Barrowclough 1987, pp. 119-120). Subsequent computer simulations incorporated stochastic models of demography and dispersal to quantitatively assess a range of management alternatives (USDA Forest Service 1986; Marcot and Holthausen 1987). The management strategy currently preferred by the USDA Forest Service (1986, pp. S-13, 2-20 to 2-22) closely resembles the original plan, despite their own prediction that under the preferred alternative the probability of persistence of a well-distributed population of the northern spotted owl more than 150 years in the future is "low to very low."

Using current estimates of the proportion of old-growth forest remaining in 12 National Forests in Oregon and Washington, and the occupancy of Spotted Owl Management Areas (SOMAs) designated by the Forest Service in Washington, the model of territory occupancy indicates that the northern spotted owl can not persist in any large region where the proportion of old forest is less than 0.21 ± 0.02 of the total area; this figure is likely to be conservative for several reasons outlined above. At present, less than half of the SOMAs designated by the Forest Service in Washington appear to be occupied annually (Allen et al. 1987). With continued reduction of old forest by logging, from the current proportion of about 38% to something in the range of 7% to 16% under the plan preferred by the Forest Service, it should be expected that occupancy of SOMAs by spotted owls will decline until the population is extirpated from the region. This analysis of territory occupancy indicates that only a plan involving preservation of the great majority of the remaining old-growth forest (e.g. Dawson et al. 1987) is likely to promote long-term persistence of the northern spotted owl population.

The results and conclusions presented here are of course subject to revision as more information becomes available. Ongoing studies in different parts of the subspecies range may eventually provide sufficient data to estimate geometric rates of increase and minimum habitat requirements for populations in particular regions rather than for the subspecies as a whole.

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References

- Allen HL, Dixon K, Knutson KL, Potter AE (1987) Progress report No. 3. Cooperative administrative study to monitor spotted owl management areas in national forests in Washington. [Unpublished] Washington Dept of Game, Wildlife Management Division, Olympia, Washington, 38 pp
- Barrowclough GF, Coats SL (1985) The demography and population genetics of owls, with special reference to the conservation of the spotted owl (*Strix occidentalis*). In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest. (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 74-85
- Barrows CW (1985) Breeding success relative to fluctuations in diet for spotted owls in California. In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest. (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 50-54
- Blueweiss LH, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. *Oecologia* (Berlin) 37:257-272
- Botkin DB, Miller RS (1974) Mortality rates and survival of birds. *Am Nat* 108:181-192
- Dawson WR, Ligon JD, Murphy JR, Myers JP, Simberloff D, Verner J (1987) Report of the scientific advisory panel on the spotted owl. *Condor* 89:205-229
- Deevey ES (1947) Life tables for natural populations of animals. *Q Rev Biol* 22:283-314
- Forsman ED (1986) The spotted owl: a literature review. In: Draft supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide, vol 2. USDA Forest Service, Portland, Oregon, Appendix C
- Forsman ED, Meslow EC (1985) Old-growth forest retention for spotted owls - how much do they need? In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest. (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 58-59
- Forsman ED, Meslow EC, Wight HM (1984) Distribution and biology of the spotted owl in Oregon. *Wildl Monogr* 87:1-64
- Franklin A, Ward JP, Gutiérrez RJ (1986) Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in Northwestern California: preliminary results. [Unpublished] Report submitted to the Calif Dept of Fish and Game, Sacramento, Calif., 38 pp
- Franklin IR (1980) Evolutionary changes in small populations. In: Soulé ME, Wilcox BA (eds) Conservation biology, an evolutionary-ecological perspective. Sinauer, Sunderland, Mass., pp 135-139
- Franklin JF, Spies TA (1984) Characteristics of old-growth Douglas-fir forests. In: Proc 1983 Conv Soc Am Foresters. Society of American Foresters. Bethesda, Md., pp 328-334
- Goodman LA (1971) On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. *Theoret Popul Biol* 2:339-354
- Gould, GI, Jr (1985) Management of spotted owls by the California Department of Fish and Game. In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest. (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 21-26
- Grzimek B (1972) Animal life encyclopedia (vol 8, Birds II). Van Nostrand Reinhold Co, London Toronto New York
- Gutiérrez RJ (1985) An overview of recent research on the spotted owl. In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 39-49
- Gutiérrez RJ, Franklin AB, Lahaye W, Meretsky VJ, Ward JP (1985) Juvenile spotted owl dispersal in Northwestern California: preliminary results. In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest. (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 60-65
- Kendall M, Stuart A (1977) The advanced theory of statistics, vol 1: Distribution theory, 4th edn. MacMillan, New York
- Keyfitz N (1977) Introduction to the mathematics of population, with revisions. Addison-Wesley, Reading, Mass.
- Lande R (1985) Report on the demography and survival of the northern spotted owl. [Unpublished] National Wildlife Federation, Portland, Oregon, 30 pp
- Lande R (1987) Extinction thresholds in demographic models of territorial populations. *Am Nat* 130:624-635
- Lande R, Barrowclough GF (1987) Effective population size, genetic variation, and their use in population management. In: Soulé, ME (ed) Viable populations for conservation. Cambridge University Press, Cambridge, pp 87-123
- Leslie PH (1966) The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.). *J Anim Ecol* 25:291-301
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237-240
- Levins R (1970) Extinction: In: Gerstenhaber ML (ed) Some mathematical questions in biology. (Lect Math Life Sci, vol 2). Am Math Soc, Providence, Rhode Island, pp 75-107
- Lotka AJ (1956) Elements of mathematical biology, 2nd edn. Dover, New York
- Marcot BG, Holthausen R (1987) Analyzing population viability of the spotted owl in the Pacific Northwest. *Trans N Am Wildl Nat Res Conf* 52:333-347
- Mertz DB (1971) The mathematical demography of the California condor population. *Am Nat* 105:437-453
- Namias J (1978) Persistence of U.S. seasonal temperatures up to one year. *Mon Weather Rev* 106:1557-1567
- Nicholls N (1980) Long-range weather forecasting: value, status and prospects. *Rev Geophys Space Phys* 18:771-788
- Pettingill OS, Jr (1970) Ornithology in laboratory and field, 4th edn. Burgess, Minneapolis
- Shaffer ML (1981) Minimum population sizes for species conservation. *BioScience* 31:131-134
- Shaffer ML (1985) The metapopulation and species conservation: the special case of the northern spotted owl. In: Gutiérrez RJ, Carey B (eds) Ecology and management of the spotted owl in the Pacific Northwest. (Gen Tech Rept PNW-185). USDA Forest Service, Portland, Oregon, Pacific Northwest Forest and Range Expt Station, pp 86-99
- Society of American Foresters (1984) Scheduling the harvest of old growth. Society of American Foresters, Bethesda, Md., 44 pp
- Tuljapurkar SD (1982) Population dynamics in variable environments. III. Evolutionary dynamics of *r*-selection. *Theoret Popul Biol* 21:141-165
- USDA Forest Service (1984) Final regional guide and final environmental impact statement for the Pacific Northwest region. USDA Forest Service, Portland, Oregon, Standard and guideline 8-1, 8-2, Appendices B to F
- USDA Forest Service (1986) Draft supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide, vols 1, 2. USDA Forest Service, Portland, Oregon
- USDI Fish and Wildlife Service (1982) The northern spotted owl: a status review. USDI Fish and Wildlife Service, Washington, DC

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