

POPULATION VIABILITY ANALYSIS NORTHERN SPOTTED OWL

Introduction

The northern spotted owl (*Strix occidentalis caurina*) is a monogamous, territorial subspecies that inhabits old-growth coniferous forests in western Washington, Oregon, and northern California. Throughout its range, it is closely associated with old, dense, large-diameter forest stands that provide forage, cover, and suitable nest sites. Each breeding pair uses about one to three square miles of forest more than 250 years old and below an elevation of approximately 4000 feet. Timber harvest, fire, and clearing for agricultural and urban development have reduced spotted owl habitats to less than 10% of their original area, mostly since 1950. In considering plans for its conservation, several questions arise:

1. Is the northern spotted owl different enough from other spotted owls to warrant protection?
2. If so, what are the prospects for its long term survival?
3. What must be done to prevent extinction of the northern spotted owl?¹

Distinctiveness of the northern spotted owl

The northern spotted owl is one of three recognized subspecies of spotted owl (*Strix caurina*). Populations of the California spotted owl (*S. occidentalis occidentalis*) are geographically adjacent to those of the northern spotted owl, occurring in mature forests at mid-elevations

¹I'll preach here again about the difference between the *scientific* question and the *value* question. If you think about things the way I do, this question is a scientific question. It requires only experimentally collected data and ecological/genetic theory to determine what the requirements are for long-term persistence of the species. The question of whether to meet those requirements is a values question. It involves weighing the desire to prevent extinction of the northern spotted owl against the desire to provide an economic livelihood who depend on lumber extraction from old-growth forests for the livelihood and well-being (among other tradeoffs).

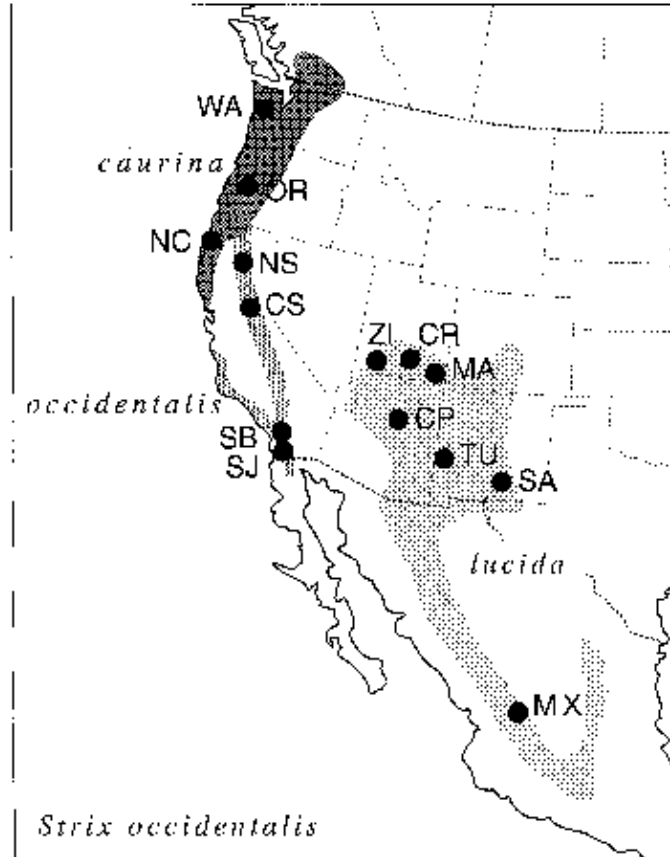


Figure 1: Distribution of spotted owl subspecies in western North America (from [1]).

in the Sierra Nevada and southern Coast Range of California. Populations of the Mexican spotted owl (*S. occidentalis lucida*) are geographically disjunct, occurring in the mountains of southern Utah, southern Colorado, western New Mexico, eastern Arizona, and north-central Mexico (Figure 1). The three subspecies have been recognized as distinct by ornithologists for at least forty years.

Barrowclough et al. [1] collected small amounts of blood from five or ten individuals in each of thirteen widely separated geographical localities that span the geographical range of the species as a whole. Nucleotide sequences of the mitochondrial control region were used

to assess patterns of genetic divergence within and among the subspecies.²

They identified 37 distinct haplotypes, but phylogenetic analysis shows that they fall naturally into three distinct clades corresponding with the northern, the Californian, and the Mexican Spotted Owl. In only one case was a haplotype belonging to one of these clades collected in the “wrong” population.³ This suggests that populations of the three subspecies have been evolutionarily independent for some time.

Within each subspecies, however, there is no apparent relationship between geographical location and the phylogeny of haplotypes present within populations. This suggests that there has been considerable movement among populations *within* subspecies, i.e., that there are probably not evolutionarily independent entities below the level of taxonomically recognized subspecies.

The combination of these two pieces of evidence suggests that it is reasonable to treat each subspecies as an evolutionarily significant unit⁴ and that it is reasonable for conservationists to be concerned about protecting any of these subspecies if they are endangered.⁵

A Leslie matrix approach for viability analysis

Recall our parameter definitions for a Leslie matrix model:⁶

$$\begin{aligned} p_i &= && \text{probability of surviving from age } i \text{ to age } i + 1 \\ f_i &= && \text{number of offspring per individual of age } i \\ n_i^{(t)} &= && \text{number of individuals in age class } i \text{ at time } t \end{aligned}$$

Given these definitions the probability of surviving from birth to age x , l_x , is

²The control region of animal mitochondrial DNA is usually the most rapidly evolving part of the molecule, and is often more useful for analysis of diversity within species than are other parts of the molecule.

³A Californian haplotype was collected from the southernmost population of northern spotted owls sampled. The nine other haplotypes found in this population were northern haplotypes.

⁴We’ll talk about ESUs in a couple of weeks. For now the context probably provides you with a reasonable understanding. The idea is that the northern spotted owl is an entity distinct from others and worthy of conservation concern.

⁵Don’t forget our discussion about whether or not ESUs are the appropriate criterion for determining whether populations are worthy of protection. I’m assuming, and I think it’s reasonable to make this assumption, that everyone agrees that ESUs are worthy of concern. The debate about the relationship between ESUs and endangered species protection concerns whether populations segments that are *not* ESUs deserve some protection, too, and whether all ESUs are equally worthy of protection.

⁶This section is based on Lande [6].

$$\begin{aligned}
l_1 &= p_0 \\
l_2 &= p_0 p_1 \\
&\vdots \\
l_x &= \prod_{k=0}^{x-1} p_k
\end{aligned}$$

For a Leslie matrix model, the leading eigenvalue⁷ is given by the unique, positive solution of the Euler-Lotka equation

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

We can use this equation and some observations about avian biology to calculate λ from a few simple life-history observations (and assumptions).

1. Constant probability of survival for adults, s .
2. Constant fecundity for adults, f , where f is the number of offspring successfully fledged.
3. Reproduction begins at age α .
4. Probability of survival to adulthood, l_α , given that an individual successfully fledges.

Using these assumptions we can rewrite the Euler-Lotka equation and solve for λ .

$$\sum_{x=\alpha}^{\infty} \lambda^{-x} (l_\alpha s^{x-\alpha}) f = 1$$

because $f = 0$ for $x < \alpha$ and $l_x = l_\alpha s^{x-\alpha}$ for $x > \alpha$. Now a little bit of rearranging makes things considerably simpler.

$$\begin{aligned}
(l_\alpha f) \lambda^{-\alpha} \sum_{x=\alpha}^{\infty} \lambda^{-x+\alpha} s^{x-\alpha} &= 1 \\
(l_\alpha f) \left(\frac{1}{1 - \frac{s}{\lambda}} \right) &= \lambda^\alpha \\
\lambda^\alpha \left(1 - \frac{s}{\lambda} \right) &= l_\alpha f
\end{aligned}$$

⁷Recall that the leading eigenvalue gives (asymptotically) the geometric growth rate of the population.

This equation can be solved numerically for λ once we have estimates for s , l_α , and f .

Northern spotted owls start breeding at age 3 ($\alpha = 3$); their annual adult survivorship is $s = 0.942$; their annual reproductive rate, i.e., the average number of fledged offspring per individual, is $f = 0.24$; and their probability of survival to age 3 is $l_3 = 0.0722$. Thus,

$$\lambda^3 \left(1 - \frac{0.942}{\lambda}\right) = 0.0722 \times 0.24 \quad .$$

Solving this equation gives us an estimate of $\lambda = 0.961$. After some more manipulations, the standard error of this estimate can be calculated as 0.029. Thus, the approximate 95% confidence interval for λ is [0.903,1.019]. It is also possible to do some sophisticated calculations that include the effects of demographic stochasticity and (mild) environmental stochasticity. The long-run population growth rate calculated including these effects is only 2% smaller than the growth rate calculated when ignoring them.

In short, projecting population dynamics based on the data available in 1988 (after almost 15 years of conservation concern) suggests a 4% annual decline in abundance, plus or minus 5.8%. The observed decline based on long-term surveys is only about 1%. Both observations seem to suggest that populations are currently near a demographic equilibrium. Why, then, all the fuss? Why is this species listed as threatened under the Endangered Species Act?

First, Taylor and Gerrodette [11] remind us that what we've just shown is that we cannot reject the null hypothesis of no population decline.⁸ That's not the same thing as saying that the population is "near demographic equilibrium." We could have said just as legitimately that we cannot reject the null hypothesis that the population is declining at a rate of almost 10% per year (3.9% + 5.8%). The calculations Taylor and Gerrodette present suggest that even if the population were *actually* declining at 4% per year, there might have been as little as a 13% chance of detecting it with the data available in Lande's analysis.

Second, let's look at that leading eigenvalue a bit more closely, especially how it's affected by changes in juvenile survival and individual fecundity.

⁸This is, or should be, an elementary statistical point. In classical statistics, we often test a null hypothesis. When we do and we fail to reject the null hypothesis, we should *not* conclude that the null hypothesis is true. We should conclude only that the evidence we have is not sufficient to reject it, which is not the same thing.

To see why, consider a simple example: Suppose I assert that the average height of human beings is 2 meters. Now let's suppose we pick a couple of people at random from this room and see how tall they are. I don't think anyone would be surprised if one of those picked was about 1.8 meters (5 feet, 11 inches) and the other was about 1.6 meters (5 feet, 3 inches) tall. Would that be enough evidence to reject the null hypothesis that the average height in humans is 2 meters? No. The 95% confidence interval on the mean is 0.43-2.97 meters.

We may fail to reject a null hypothesis that is "obviously" false simply because we didn't collect enough data.

l_α	f	λ	
0.0722	0.24	0.961	baseline
0.14	0.24	0.977	
0.25	0.24	1.002	
0.0722	0.50	0.980	
0.0722	0.90	1.006	
0.14	0.50	1.011	

If fledging success were the only life-history stage amenable to manipulation, it would have to be increased more almost four-fold for the leading eigenvalue to be greater than 1, i.e., for the projection to be for an *increasing* population. Doubling both the fledging success and survivorship from fledgling to adult, while not easy, may be achievable. These analyses suggest that we need to pay attention to both life history stages *and* that the population cannot be overly stable if doubling survivorship and fledging success barely bumps the leading eigenvalue above 1.

The leading eigenvalue is close to 1 (and the population appears to be stable) only because of high adult survivorship — mean adult lifetime is $\frac{1}{1-s} \approx 17$ years. Because adults die off so slowly and constitute most of the population, the population size changes relatively little from one year to the next. Even if all reproduction stopped now, the rate of decline would be about $1 - s$ per year or 6%.

Third, a leading eigenvalue of 0.961 suggests a slow population decline, 4% per year. In fact, it can't be statistically distinguished from an eigenvalue of 1, which would mean the population size is stable. Recall, however, that this is a *linear* model leading to a *geometric* rate of population size change.

λ	Time to 50% population size
0.99	69
0.98	34
0.97	23
0.96	17

Rule of 69: doubling time $\approx \frac{69}{r}$, where $r = 1 - \lambda$.

$$\begin{aligned}
 N_t &= N_0 e^{rt} \\
 \frac{N_t}{N_0} &= e^{rt} \\
 \ln\left(\frac{N_t}{N_0}\right) &= rt \\
 t &= \frac{\ln\left(\frac{N_t}{N_0}\right)}{r}
 \end{aligned}$$

So the time it takes for population size to double, i.e., for $N_t = 2N_0$ is

$$\begin{aligned} t_d &= \frac{\ln(2)}{r} \\ &\approx \frac{0.69}{r} \end{aligned}$$

If we take the linear analysis as a *forecast* rather than a *projection*, then we would predict that the population size could be half of what it is now in as little as 7 years (using the lower 95% confidence bound on λ) or it could be double what it is now in about 35 years (using the upper 95% confidence bound on λ).

A More Detailed Analysis

The previous analysis is based on some extreme simplifying assumptions. There is good evidence that survivorship and fecundity differ among three classes: juveniles, subadults (1–2 year olds), and adults. Using an approach similar to the one above,⁹ let

$$\begin{aligned} f_1 &= \text{fecundity of juveniles} \\ f_2 &= \text{fecundity of subadults} \\ f_a &= \text{fecundity of adults} \\ s_j &= \text{survivorship of juveniles} \\ s_a &= \text{survivorship of subadults and adults} \end{aligned}$$

Then λ is found as the solution to the following equation

$$1 = f_1 \left(\frac{s_j}{\lambda} \right) + f_2 \left(\frac{s_j s_a}{\lambda^2} \right) + f_a \left(\frac{s_j s_a^2}{\lambda^3} \right) \left(\frac{1}{1 - s_a/\lambda} \right) .$$

Data from fourteen demographic study areas that had at least four years and as many as nine years of capture-recapture data found substantial differences in λ among sites: range 0.83–1.02, mean 0.93. Noon and Blakesley [7] point out that more recent analyses provide an estimate of $\lambda = 0.976 \pm 0.014$ for eight study areas on federal lands and an estimate of $\lambda = 0.942$ for five study areas on non-federal lands.

We now have five additional years of data and a more detailed model and we discover that the spotted-owl is even worse off than we initially imagined. Why?

⁹From Burnham et al. [2]. See [8] for a summary.

Parameter	Value	Sensitivity	Elasticity
f_1	0.068	0.020	0.00147
f_2	0.205	0.018	0.00400
f_a	0.339	0.196	0.07200
s_j	0.258	0.278	0.07773
s_a	0.844	1.008	0.92193
λ	0.923		

As argued above, population dynamics are predominantly determined by adult survivorship.

These estimates are biased by the underestimate of juvenile survivorship due to individuals that migrate outside the study area and survive. When this is accounted for $\lambda = 0.95 \pm 0.02$.

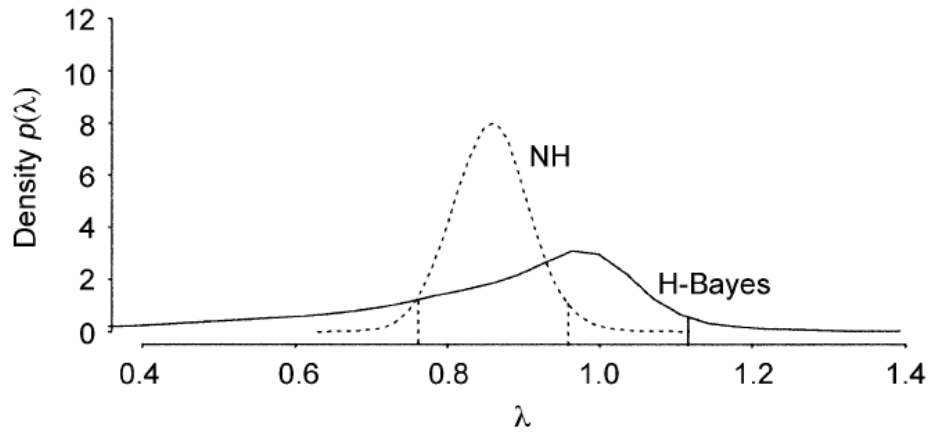
Juvenile survivorship is 0.38 ± 0.06 and emigration is 0.32 ± 0.05 . For $\lambda > 1$ we would require juvenile survivorship > 0.57 and emigration > 0.51 . In addition to this, we have other strong reasons for thinking the decline is very real.

- Average adult female survivorship declined from approximately 0.88 in 1985 to 0.80 in 1994.
- λ calculated using average adult survivorship of 0.84.¹⁰ If declining trend were included, λ would be even smaller.
- Although adult survival has the highest elasticity coefficient, there may be little that can be done to improve it, since it's already relatively high. Focusing on improving juvenile establishment is likely to have greater returns.

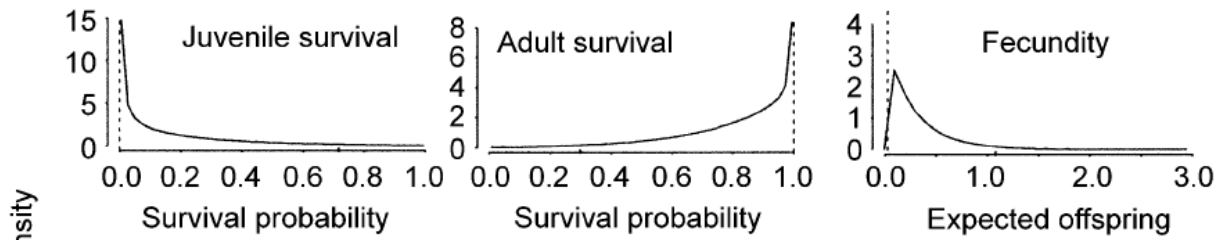
Note: 14 demographic study areas with a minimum of four years capture-recapture data. Approximately 50 biologists spent two weeks collating and analyzing the data to reach these conclusions. λ barely distinguishable from 1, i.e., barely demonstrable that population is declining. In fact, the results in [3] suggest that it's even worse than that (Figure 2). The results we've presented so far pretend (a) that we know the values of each demographic parameter without error and (b) that the values of those parameters do not vary among individuals or populations. Both of those assumptions are wrong. As a result, the projections underestimate both the *process* error, i.e., the probabilistic uncertainty of outcomes because of the intrinsic stochasticity of the underlying processes (demographic and environmental stochasticity), and the *parameter* error, i.e., the uncertainty about the correct values of the demographic parameters. The result is that the results overstate the degree to which we can be confident about the projections.

¹⁰Recall that Lande used 0.94 in his 1988 calculations.

a) Predictive distribution for population growth rate



b) Marginalized parameter posteriors



c) Hyperparameter posteriors

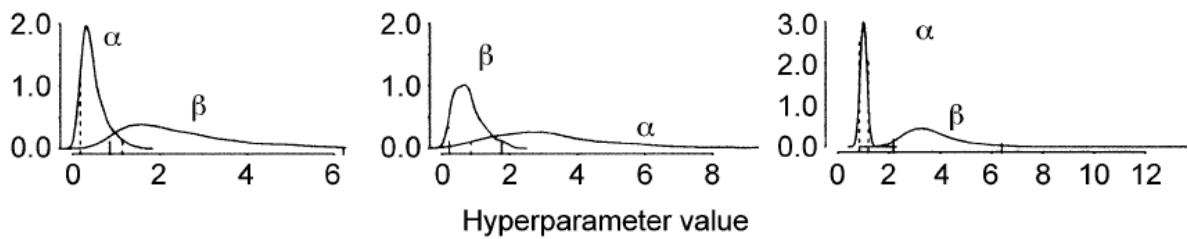


Figure 2: Comparison of projection uncertainty with (H-Bayes) and without (NH) parameter uncertainty (from [3]).

So we are left with a dilemma. It is clear from first principles that populations of northern spotted owls will continue to decline if their habitat continues to become less common. It is also clear from first principles that at some point the amount of habitat remaining will be insufficient to support a self-sustaining wild population. But after all these years of effort, it is still very difficult to provide clear, quantitative advice that would allow land managers to determine whether the amount of remaining old-growth is sufficient or whether forests must be managed to provide even more in the future. Moreover, “[t]he causal factors of spotted owl declines from 1990 to 2003 are poorly known,” and invasion of the barred owl into the region appears to pose a new threat to persistence of the northern spotted owl [7]. The recent controversy over whether forest management practices should be changed to account for losses to wildfire in dry provinces of the region further illustrates that professional biologists can come to dramatically different conclusions [4, 5, 9, 10].

Major research question: Is there a way to reach management conclusions more rapidly? Are there reliable rules of thumb that we can use?

A Metapopulation Approach

The analysis we’ve done so far presumes that we can treat this geographically widespread species as a single, homogeneous population. This clearly doesn’t make a lot of sense. Instead, it may make more sense to treat it as a metapopulation.¹¹ Lande [6] showed how the metapopulation approach, which we’ll see applied in a different way to the bay checkerspot butterfly, can be applied to territorial animals by treating the individual territory as the unit of extinction and colonization.

Parameter	Definition
ϵ	probability that a juvenile female inherits the territory of its mother
m	number of territories a juvenile can disperse through before dying from predation, starvation, etc.
h	proportion of the region that is habitable
p	proportion of habitable sites that are occupied

The probability of *not* finding a suitable unoccupied territory in m trials is $(1 - \epsilon)(ph + 1 - h)^m$. Thus, for a population in demographic equilibrium

¹¹*metapopulation*—A set of partially interacting populations connected by (1) exchange of individuals among existing populations, (2) extinction of existing populations, and (3) founding/re-colonization of populations.

$$[1 - (1 - \epsilon)(ph + 1 - h)^m]R'_0 = 1 \quad ,$$

where

$$R'_0 = \sum_{x=0}^{\infty} l'_x f_x$$

is the mean lifetime production of offspring per female, given that she finds a territory, and l'_x is the probability of survival to age x , given that she finds a territory. For our model $R'_0 = l'_\alpha b / (1 - s)$.

We can solve the above equation for the equilibrium number of patches occupied.

$$\hat{p} = \begin{cases} 1 - \frac{1-k}{h} & \text{for } h > 1 - k \\ 0 & \text{for } h \leq 1 - k \end{cases}$$

where

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

k is the equilibrium occupancy of patches when the entire region is habitable ($h = 1$). The population can persist only if $h > 1 - k$.

National forests in the Douglas-fir region of Washington and Oregon contained about 38% forest greater than 200 years old in 1987. Thus, $h \approx 0.38$. Recent surveys have suggested that about 44% of the appropriate sites are currently occupied, i.e., $p \approx 0.44$. Assuming that the population is demographically stable, as suggested by the Leslie matrix model, then we can solve for k as

$$\begin{aligned} k &= 1 - h(1 - p) \\ &\approx 0.79 \end{aligned}$$

Future Forest Service plans suggest leaving 7% to 16% of forest in stands older than 200 years. $1 - k = 0.21 > 0.07 - 0.16$. Therefore, this course of action seems likely to doom spotted owls to extinction. Note: Even if habitat occupancy estimates are highly inaccurate, this conclusion does not change much. Suppose 60% of all suitable habitat is occupied. Then $k \approx 0.85$, $1 - k \approx 0.15$

These estimates for k may be optimistic because older owls are likely to pack more densely into existing habitat as harvest continues. Thus, recent estimates of habitat occupancy may be overestimates. If equilibrium occupancy rates are 50% lower than those currently seen (not unreasonable given the long life-span of these birds), then $k = 0.70$.

Moreover, these calculations are overly optimistic about the persistence possibilities. They are, after all, based on the assumption that the population is demographically stable, which it is not.

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