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Assessing Human Impact Despite Uncertainty: Viability of the Northern Spotted Owl Metapopulation in the Northwestern U.S.

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Summary

We demonstrate the effect of uncertainty (resulting from lack of information or measurement error) on the assessment of human impact, with an analysis of the viability of the Northern Spotted Owl throughout its range in the United States. We developed a spatially-explicit, stage-structured, stochastic metapopulation model of the Northern Spotted Owl throughout its range in the United States. We evaluated the viability of the metapopulation using measures such as risk of decline and time to extinction. We incorporated uncertainty in the form of parameter ranges, and used them to estimate upper and lower bounds on the estimated viability of the species. We analyzed the effect of this type of uncertainty on the assessment of human impact by comparing the species' viability under current conditions, and under an assumed loss of spotted owl habitat in the next 100 years. The ranges of parameters were quite large, and resulted in wide range of risks of extinction. Despite this uncertainty, the results were sensitive to parameters related to habitat loss: under all assumptions and combinations of parameters, the model predicted that habitat loss results in substantially higher risks of metapopulation decline. This result demonstrated that even with relatively large uncertainties, risk-based model results can be used to reliably assess human impact.

Introduction

Assessment of human impact on endangered and threatened species increasingly relies on population viability analyses, which use demographic models incorporating various aspects of the ecology and behavior of the species. Most parameters, as well as structural characteristics of these models are estimated based on insufficient data, and sometimes even guessed based on "expert opinion", resulting in large uncertainties. These uncertainties are often ignored when the results of a model are presented. When they are not ignored, they often are used to "demonstrate" the lack of human impact, or as excuses for not taking conservation action. Therefore it is important to determine the ability of models to detect or assess human impact under uncertainty.

Our goal in this analysis was to demonstrate the effect of uncertainty (resulting from lack of information or measurement error) on the assessment of human impact on species viability. For this demonstration, we analyzed the viability of the Northern Spotted Owl *Strix occidentalis caurina* throughout its range in the United States using a metapopulation model. We incorporated two sources of variability in determining the likelihood of species persistence: natural variation and uncertainty. We modeled natural variation (resulting from temporal fluctuations in environmental factors) in the form of randomly distributed vital rates (survivals and fecundities). In addition we added demographic stochasticity to model chance variations in reproduction, survival and dispersal. We used these types of natural variation (environmental and demographic) to express the model results in probabilistic terms such as the viability of the species (for example in terms of the chance of survival or risk of extinction).

We incorporated uncertainty in the form of parameter ranges, and used them to estimate upper and lower bounds on the estimated viability of the species. We analyzed the effect of this type of uncertainty on the assesment of human impact by comparing the species' viability under current conditions, and under an assumed loss of spotted owl habitat in the next 100 years.

Earlier models for the northern spotted owl that have considered spatial structure have either modeled a collection of territories or territory clusters without explicit spatial structure (Lande 1988, Doak 1989), or used hypothetical landscapes as the spatial basis of the model (Lamberson et al. 1992, 1994). More recent studies (e.g., Raphael et al. 1994; Holthausen et al. 1995) were based on the actual habitat of the northern spotted owl. These studies used an individual-based model based on McKelvey et al. (1992) and Lamberson et al. (1994), and analyzed the dynamics in separate regions of the spotted owl's range, such as the Olympic peninsula, Washington, Oregon and California.

One important difference of the current model is that it is a stage-structured metapopulation model, and simulates the dynamics of populations inhabiting individual habitat patches, instead of simulating the behavior of individual owls. As a consequence of this difference, the model we describe in this paper makes different assumptions about population characteristics such as dispersal and density dependence. The major difference of the current model is use of the risk

language, and explicit incorporation of uncertainties. Our goal in this analysis was not the estimation of the viability of a specific metapopulation, or a comparison of model outcomes with those of other models, but the demonstration of the effect of uncertainty in making predictions about human impact.

Methods

We developed a spatially-explicit, stage-structured, stochastic metapopulation model of the Northern Spotted Owl, based on data from Thomas et al. (1990), McKelvey et al. (1992), Raphael et al. (1994), Holthausen et al. (1995), and Burnham et al. (1996). In developing the model, we used the program RAMAS GIS, which is designed to link landscape data from a geographic information system with a metapopulation model (Akçakaya 1997; see also Akçakaya et al. 1995, Akçakaya and Atwood 1997 for other applications; Kingston 1995 and Boyce 1996 for reviews). We used data on the current distribution of spotted owl habitat on federal lands to find the spatial structure of the metapopulation, i.e., to identify the location, size and shape of habitat patches in which (sub)populations of the metapopulation exist.

In addition to spatial structure, the metapopulation model can incorporate parameters related to demography, such as carrying capacities, initial abundances and vital rates of each population, the amount of year-to-year variability in vital rates, as well as the rate of dispersal between patches, and the degree of similarity of environmental fluctuations that different populations experience. The estimations of some of these demographic parameters are also based on the information from the habitat data (see below). In the following sections, we describe the estimation of each of these parameters for the metapopulation of the Northern Spotted Owl in the northwestern U.S.

Habitat map

The habitat map was developed by the Forest Ecosystem Management Assessment Team (Thomas and Raphael 1993). This raster (grid) map consisted of 3156 rows and 1036 columns. Each cell was 400 m \times 400 m (0.16 km²), and had a value of 0 (no habitat) or 1 (habitat). There were 190,929 cells $(30,548 \text{ km}^2)$ with a value of 1. The habitat map was developed by Forest Service and Bureau of Land Management biologists to depict suitable nesting, roosting, and foraging habitat, defined as "forest vegetation with the age class, species of trees, structure, sufficient area, and adequate food source to meet some or all of the life needs of the northern spotted owl" (Thomas and Raphael 1993, p.IX-22). Habitat designations were based on interpretations of aerial photography and ground-based stand examinations. This map only includes habitat that is on federally administered lands, which occupy about 50% of the owl's range.

We contracted this map by aggregating a region of 6 cells by 6 cells into one. The resulting habitat map had 2.4 km \times 2.4 km (5.76 km²) cells, each of which now had a value ranging from 0 to 36. These values will be referred to as "habitat values".

Thomas et al. (1990, p. 197) reported an annual median pair home range of 3000 to 5000 acres (12 to 20 km²). Thus, the cell size of 5.76 km² corresponds to a resolution of about 2.1 to 3.5 cells per median pair home range. It is necessary to have a resolution that is substantially greater than 1 cell per home range, in order not to lose significant information as a result of map contraction (see below).

Habitat threshold value

This parameter is the minimum habitat value below which the habitat is not suitable for reproduction and/or survival. It is assumed that the species may disperse or migrate through habitat that has a lower value than this threshold, but cannot reproduce. We used 10% (i.e., 3.6/36) as the threshold; only those cells that had a habitat value of 4 or above were considered when habitat patches were analyzed (see below). If a cell had a value of 4 or higher, it was considered suitable, regardless of the distribution of the habitat within the cell. This assumption does not decrease the precision of the model, because the model operates at the population, not at the individual level. In addition, the spatial resolution of the model was high enough even at the individual level that an average owl would use several cells (there are 2-4 cells per median home range), and thus would be affected by the total habitat quality more than the distribution of habitat within each cell that makes up a small portion of its home range. Note that the "suitable" designation does not necessarily indicate the presence of an owl or a pair. The number of owls in a habitat patch (which is different from a cell or a home range; see below) is determined by many factors, including the size of the patch and the quality of habitat (which determine its carrying capacity), and by demographic factors. These are discussed below.

Neighborhood distance

This parameter is used to identify nearby cells that belong to the same patch. Suitable cells (as defined by the habitat threshold parameter) that are separated by a distance less than or equal to the neighborhood distance are regarded to be in the same patch. This parameter may represent, for example, the foraging distance of adults in their home ranges, and is expressed in terms of number of cells. In this model, we used a neighborhood distance of 1.5 cells. This means that if the cell marked by an "X" in Figure 1 is a suitable habitat cell, then any suitable cells within the shaded region are assumed to belong to the same *habitat patch* as the marked cell. This corresponds to assuming that any two suitable locations within about 4 km of each other are in the same habitat patch. The patches are identified by aggregating all of those cells that are sufficiently close to each other, and that also have sufficiently high habitat values. Given the

same habitat map, a higher habitat threshold and/or a smaller neighborhood distance would result in a greater number of smaller patches, i.e., a more patchy landscape. Note that each habitat patch may contain several to several hundred home ranges.

Carrying capacities and initial abundances

We used carrying capacities to model ceiling-type of density dependence (see below). The program allows the calculation of carrying capacities and initial number of individuals in each habitat patch, based on the total habitat value in each patch. For this calculation, the habitat values (which range from 4 to 36) of all cells that are included in a patch are summed up, and multiplied by a constant to calculate the carrying capacity of that patch. We estimated this constant (number of owls per unit habitat value) as follows. The average habitat value was 14.5 (out of a maximum of 36) per cell. Assuming that the median home range is about 2.8 cells (about 16 km² or 4000 acres), it would have a total habitat value of $2.8 \cdot 14.5 = 40.6$. Thomas et al. (1990, p. 196) report a mean overlap of 18% among home ranges of neighboring pairs. This amount of overlap would correspond to about 2.36 territorial owls per home range. With these assumptions, the number of owls per unit habitat value would be 2.36/40.6 (number of owls per average home range, divided by the total habitat value for an average home range), or 0.058, giving the constant to be used. The carrying capacity is thus calculated by multiplying the total habitat value of each patch with the constant 0.058 (see *Results*). Because we used the total habitat value instead of the total area, each patch has a carrying capacity (*K*) determined both by its size, and by the quality of habitat it has. Thus a patch with a high proportion of habitat would have a higher carrying capacity than a patch with the same total area but with a lower proporiton of habitat. Patches with *K*≤8 were not considered as populations, because only larger populations would have ≥1 juvenile at stable stage distribution (see next section). We made two assumptions about the initial abundance, *N*(0): we assumed that *N*(0) in each patch was equal to the carrying capacity, *K*, or to 80% of *K*.

Stage matrix

We modeled the dynamics within each patch with a stage-structured, stochastic matrix model with three stages (juveniles, subadults, adults). Juveniles are defined here as owls just under 12 months old, subadults are those that are just under 24 months old, and adults are all older birds. We defined the following parameters:

- *S*₀ : juvenile survival rate; the proportion of fledglings that survive to become one-year old (subadults),
- *S*₁ : subadult survival rate, proportion of one-year old owls that become two-year old,
- *S*_a : adult survival rate, proportion of older owls that survive one year,
- b_1 , b_2 , and b_3 : maternities (number of fledglins produced per owl) of one-year old, two-year old and older owls, respectively.

We parameterized the model assuming pre-breeding census (a census immediately before breeding). In this model, fecundity is the number of fledglings that survive until the next census per individual counted in the current census. Various reports call the parameters b_1 , b_2 , and b_3 fecundities. In this paper, we call these parameters "maternities" in order to differentiate them from the fecundities (such as $S_0 \cdot b_3$) as defined for a Leslie or stage matrix model (see Jenkins 1988, Caswell 1989). With these definitions, the stage matrix is

The parameters of the stage matrix were based on Burnham et al. (1996), and Bart (1995). We assumed $S_1 = S_a$, and that $S_0 = 0.38$, a value that incorporates correction for juvenile emigration (Burnham et al. 1996). Following Raphael et al. (1994) and Holthausen et al. (1995), we specified a different stage matrix for each population, based on percent habitat in the patch that the population occupies. The stage matrices for different patches differed in terms of the parameters S_1 , S_2 , b_1 , b_2 , and b_3 . These parameters were assigned as functions of percent habitat as follows. We set each parameter to its mean value as estimated by Burnham et al. (1996) for a hypothetical patch of average habitat suitability. To predict the parameters for each patch based on its habitat, we used the survival-habitat and fecundity-habitat functions calculated by Bart (1995). Thus for adult and subadult survival rates (see the solid line in Figure 2), we used the slope (0.39) reported by Bart (1995), and adjusted the intercept so that for the average habitat (40%), the survival rate was 0.884 (mean adult survival for all regions from Burnham et al.). For fecundities (solid line in Figure 3), we used half the slope reported by Bart (1995), since the unit in our case is number of fledglings per owl (not per pair). We adjusted the intercept so that for the average habitat (40%), the adult maternity (b_3) was 0.339 (mean for all regions from Burnham et al.). Burnham et al. report b_1 and b_2 as 0.068 and 0.205, respectively. We used these values for average habitat, and assigned a different set of b_1 and b_2 to each population, as 20.06% (0.068/0.339) and 60.5% (0.205/0.339) of *b*₃, respectively. The range of percent habitat in these two figures $(20 - 47%)$ corresponds to the range of percent habitat in the patches identified by the model (see *Results*).

We incorporated uncertainty in vital rates by specifying three sets of fecundities and survivals, low (dashed lines in Figures 2 and 3), medium (solid lines), and high (dotted lines). We used ±0.0409 for survival rates, and ±0.0466 for maternities, based on the approximate standard deviation around the predicted values in figure 1 of Bart (1995). This value is close to the empirical standard error (SE) calculated by Burnham et al. (1996) for juveniles (0.036), but higher than the SE for adults (0.005). To avoid unrealistically high survival rates, we truncated survival rates >0.92 (the dotted line in Figure 2). The low, medium and high values of fecundities and survival rates for an average patch of 40% habitat are given in Table 1, with fecundities expressed as $S_0 \cdot b$ (0.38 $\cdot b$).

Initial stage distribution

For most simulations, we assumed stable initial distribution of individuals to stages, and set the initial distribution of each population to its stable distribution based on the stage matrix for that population. After adding the stage abundances in all populations, the overall stable distribution consisted of 11%, 10% and 79% juveniles, subadults and adults, respectively. We also ran two simulations with different initial distributions: a juvenile-heavy distribution with 10% more juveniles, preserving the ratio of subadults to adults, and an adult-heavy distribution with 10% more adults, preserving the ratio of juveniles to subadults. These two simulations started with 21%, 9%, 70% (juvenile-heavy), and 6%, 5%, 89% (adult-heavy) juveniles, subadults and adults, respectively.

Standard deviations (environmental stochasticity)

We modeled environmental stochasticity by sampling the set of vital rates used to project the dynamics of each population from random (lognormal) distributions. The sampling was done at each time step (in this case each year), thus the required standard deviation for the lognormal distributions is one among years. We estimated these standard deviations based on the variability of survival rates and fecundities from Burnham et al. (1996) as follows. We calculated the coefficient of deviation (CV) of adult survival rates based on data read from their Fig.1. The coefficient of variation of these data was 5.75% (Table 2). For each vital rate set, the standard deviation of adult survival was calculated using the mean value for that set (at 40% habitat) and this coefficient of variation.

There were no comparable data on juvenile survival variation. For this parameter, we used the standard errors for juvenile survival rate for 11 sites, reported by Burnham et al. in their table 4. These standard errors include temporal variation as well as measurement (sampling) error. The standard error for juveniles is about 3 times the standard error for adults for most sites. Assuming that the sampling error is similar for adults and juveniles, we set the temporal standard deviation of juvenile survival as 3 times the temporal standard deviation of adult survival.

The standard deviations of maternities (*b*) were calculated from table 6 of Burnham et al. (1996; see Table 3). Since the sample size in each year was different, we calculated the mean and the standard deviation using sample sizes given in this table as weights (see Sokal and Rohlf 1981, p.57). The coefficient of variation of these data was 49.55%. Calculation of the standard deviation of fecundities based on this CV is more complicated, since fecundity is maternity multiplied by juvenile survival $(b·S₀)$. The approximate variance of the product of two random numbers ($Var_{1\times2}$) is a function of their means ($Mean_1$, $Mean_2$), variances (Var_1 , Var_2) and covariance (Cov_{12}) , given by Kendall and Stuart (1958):

$$
Var_{1\times 2} = Var_1 (Mean_2)^2 + Var_2 (Mean_1)^2 + 2 Mean_1 Mean_2 Cov_{12}.
$$

For each vital rate set, we calculated the standard deviation of fecundities (the first row of the matrix) based on this formula, assuming that maternity and juvenile survival are perfectly correlated (among years). We also assumed that all other vital rates within the same population were perfectly correlated, although they may have intermediate degree of correlation among different populations (see below). The standard deviation for each vital rate (Table 1) is based on mean value of the vital rates for average (40%) habitat. During a simulation of the model, the matrix elements are sampled from lognormal distributions with means and standard deviations, based on the amount of habitat and the vital rate set. After sampling, fecundities were truncated to be ≥0, and survivals were truncated to [0,1]. Thus although the *average* adult survival was truncated at 0.92, the adult survival for a particular population at a particular time step might be >0.92 . To reduce truncation bias for survival rates with mean > 0.5 , we sampled lognormally distributed mortality rates (instead of survival rates).

Correlation-distance function

If the variation in vital rates is correlated among populations, this may increase the overall variability of the total abundance and decrease the viability of the metapopulation (by den Boer 1968; Gilpin 1988; Harrison and Quinn 1989; Akçakaya and Ginzburg 1991; Burgman et al. 1993; LaHaye et al. 1994). In the current model, we used three different estimates of correlation of vital rates among populations. The high estimate is perfect correlation among all patches, and the low estimate is zero correlation. A third (medium) estimate is based on distances among patches: since correlation of vital rates is expected to be related to correlation among environmental factors, which in turn can be functions of the geographic distance between populations, we specified the correlation coefficients (*C*) between any two patches as a negative exponential function of distance (*d*, in km) between them, with the function $C = e^{(-d/300)}$. This function was selected because it gives almost complete correlation between the closest populations, and almost zero correlation between the most distant pairs of populations.

Demographic stochasticity

In this model, demographic stochasticity is incorporated by sampling the number of survivors from a binomial distribution and number of offspring from a Poisson distribution (Akçakaya 1991). For example, if the survival rate of juveniles at time *t* is sampled (see above) as 0.856, and the number of juveniles is 7, then a binomial deviate with sample size 7 and probability 0.856 [binomial($p=0.856$, $k=7$)] is used to calculate the number that survive to the next time step, instead of a simple matrix multiplication. Similarly, the number of juveniles are calculated by sampling the fecundity from a Poisson distribution. In addition, we incorporated demographic stochasticity in dispersal (see next section).

Dispersal

In this model, dispersal refers to the movement of owls among habitat patches; dispersal among home ranges within a habitat patch is not explicitly modeled. Dispersal rate (proportion dispersing from target population to source population) may depend on the distance between source and target populations, and the stage of the owl. We assumed that adults and subadults have negligible dispersal among populations (they can disperse within the same patch), and used dispersal parameters discussed above only for the juvenile stage.

We estimated the distance dependence of dispersal based on data from Table P1 of Thomas et al. (1990; p.305, "Final dispersal distances"). The table gives the number of radio-tagged juveniles that dispersed different distances, and is based on several studies of dispersing juvenile spotted owls. We divided the number of dispersing juvenile owls in each distance class by the total sample size (50) to obtain proportion dispersing, and used this as the dependent variable. We used the mid-point of each distance class (in km) as the independent variable. We fitted the following exponential model to these data:

$$
M = a \cdot \exp\left(-\frac{d}{b}\right).
$$

In this model, *M* is the dispersal rate, *d* is the minimum (edge-to-edge) distance (in km) between the two populations, and *a* and *b* are model parameters. The model was fitted with $a=0.24$ and $b=34.85$ ($R^2 = 0.823$; see Figure 4). In addition, the above equation was modified to reflect a maximum dispersal distance of 200 km. The parameter *b* determines the rate of decline in the number of dispersers as distance increases. The parameter *a* must be scaled according to the total proportion of dispersers from one population to another. In the absence of such information, we used different values of *a* : for simulating "high" and "medium" dispersal, we used the dispersal distance function with $a=0.5$ and 0.24, respectively. We also ran a simulation with no dispersal (*a*=0).

Dispersal rates based on the distance between patches results in symmetric dispersal (i.e., the same rate at both directions between two populations). If dispersal rate is the same between a large and a small population in both directions, the number of dispersers from the large to the small population would be much larger than the number in the other direction. Although this may be realistic in some cases, it may also give the result that increased rate of dispersal decreases the viability of the metapopulation as a whole. This is because, on average, the large number of migrants from a large to a small population will overshoot the small population's ceiling or carrying capacity (and thus not contribute much to its persistence), whereas the small number of migrants from the small population to large population will not compensate for the number that leaves the large population (Akçakaya and Baur 1996).

This effect would not occur if the migration rates in the two directions are unequal, which may be the case when there is a large difference in the areas of the two patches. Consider a large and a small habitat patch close to each other, and assume an equal dispersal rate in both directions, say 10%. If the large patch has 1000 owls and the small patch only 10, the expected number of migrants would be 100 owls from the large to small patch, and 1 owl from the small to the large patch. However, it is not realistic to assume that dispersal rate would be the same in both directions, since most of the large patch lies quite far away from the small patch, whereas all of the small patch is about the same distance from the edge of the large patch. Another reason is that the dispersers from the large to the small patch are more likely to "miss" the target and disperse in other directions. Such unequal dispersal can be simulated with an individual-based model, if dispersal behavior of individuals within and between patches is explicitly modeled. In a metapopulation model, one way to model unequal dispersal is to change one of the two dispersal rates in relation to relative carrying capacities of the two populations. Thus we changed the dispersal rate M_{ji} from the large population i to the small population *j* by multiplying it with K_j/K_i , the ratio of the two carrying capacities. Obviously, it would be better to have direct estimates of dispersal among different-sized populations. In the absence of such detailed data, we combined the available data with the arbitrary modification outlined above, to estimate dispersal rates between each pair of populations.

We incorporated demographic stochasticity in dispersal among populations by sampling the number of dispersers from a binomial distribution with sample size equal to the number of juveniles in the source population, and probability equal to the dispersal rate based on distance. Thus the number of dispersers from population *i* to population *j* is equal to binomial($p=M_{ji}$, $k=J_i$), where M_{ji} is the dispersal rate based on the dispersal-distance function, and J_j is the number of juveniles in the source population *i*. On average the number of dispersers equals $M_{ji} J_i$, with variance equal to $M_{ji} (1-M_{ji}) J_i$.

Density dependence

At this time there are no studies on density dependence of vital rates in spotted owl populations. Because of this, we assumed a ceiling-type density dependence model for each population, and used the carrying capacities calculated based on habitat data as population ceilings. This model allows the populations to fluctuate independently of the population density, according to the stage matrix and the standard deviations matrix, until the population reaches the ceiling. The population then remains at this level until a population decline takes it below the ceiling.

Allee effects, which may cause a reduction in vital rates when population size becomes very small, are not well-studied for the northern spotted owl. In the current model, we incorporated Allee effects by specifying two types of extinction thresholds: one for the whole metapopulation, and one for each population.

Once any population falls to or below its local threshold, the model assumes the population to be extinct by setting its abundance to zero. The patch then remains unoccupied, unless it is colonized by dispersers from another patch. We set the local thresholds at 0%, 5% and 10% of the carrying capacity (ceiling population size) of the patch. By considering a population to be extinct once it reaches or falls below its threshold, the model need not accurately predict the dynamics of the metapopulation at these low abundance levels.

In addition, we expressed the risk results as the risk of a 90% decline from the initial abundance (or falling below 1038 individuals). However, once the abundance did fall below this level, we did not set the abundance to zero (unlike for the local thresholds). This allows the representation of results as a function of thresholds (or as a function of percent decline) in the risk of decline curves.

Habitat loss

We modeled habitat loss by reducing the amount of habitat 10% in 100 years. This resulted in a gradual decline in the carrying capacities, survival rates and fecundities of all populations. The relative decline in these parameters was not the same for each population, as it depended on the initial size and habitat quality of the patch. We ran all simulations twice, with and without habitat loss, and compared the results with respect to the increase in risk of decline in the owl metapopulation that is attributable to the simulated habitat loss.

Raphael et al. (1994) found that habitat might decrease by 25% over a 100-year period, assuming no regrowth. Much of the currently unsuitable habitat within protected areas may become habitat over the next 100 years, so that total habitat may actually increase. Thus the real change in habitat may range from a 25% decrease to an increase. The number (10%) we used is strictly for illustrative purposes and is not intended to simulate actual habitat change in the next 100 years. Because the habitat loss modeled is arbitrary, our focus is not the absolute magnitude of the impact of habitat loss, but rather the reliability of assessing this impact under uncertainties present in the model. We selected a modest amount of decline (only 0.1% per year on average) in order to demonstrate the ability of a modeling approach to detect an impact even when the expected habitat losses are small and the model uncertainties are large.

Analysis and types of viability measures used

Following Raphael et al., we used the model to project the dynamics for 100 years. We set the number of replications as 1000, in contrast to 10 replications (runs) by Raphael et al., and 50 used by Holthausen et al. The reason for the larger number of replications is the different types of viability measures that we used to express the results of the study (see below).

The analysis of the dynamics of the northern spotted owl metapopulation with the model described above consisted of a series of simulations. Each simulation consisted of 1,000 replications, and each replication projected the abundance of each population for 100 time steps (years). At each time step, the number of juveniles, subadults and adults at each population were projected using a set of vital rates, drawn from a random (lognormal) distribution (also see "Demographic stochasticity" above).

The mean values of these vital rates (survival and fecundity) were taken from a patch-specific stage matrix, depending on the amount of habitat in the patch occupied by that population, and the vital rate set used in the simulation. The standard deviation of vital rates are those given by the standard deviation matrix for that vital rate set, as described above. The number of individuals in each stage of each population, as well as the number of dispersers were always integer numbers. These calculations followed the algorithm described by Akçakaya (1997, pp. 213-220).

We summarized the predictions of the models with four types of graphs: (1) total metapopulation abundance through time, (2) metapopulation occupancy (number of occupied patches, or extant populations) through time, (3) risk of decline (within the simulated time horizon) as a function of amount of decline, and (4) time to fall below the metapopulation extinction threshold.

The risk of decline was calculated as the proportion of replicates that declined by a given amount (from the initial abundance) anytime within the simulated time period, and was reported as a function of percent decline from the initial total abundance (Akçakaya 1992). Time to fall was calculated as the distribution of time steps (years) it took each replicate to reach the metapopulation threshold for the first time, and was reported as a cumulative probability distribution.

The risk curves are given with their 95% confidence interval, based on Kolmogorov-Smirnov test statistic, *D* (Sokal and Rohlf 1981, page 721). The confidence interval is for the whole curve (thus conservative for the risk of falling by a given percentage), and its width is a function of the number of replications (1000 in this case). For comparing risks of decline to a specific level, we used confidence limits for percentages (Rohlf and Sokal 1981, page 156).

Results

Patch structure

Given the habitat map, the habitat threshold value, and the neighborhood distance described in *Methods*, the program found 18 habitat patches, which are clusters or groups of suitable cells within the neighborhood distance of each other. Suitable cells are those that had habitat values higher than or equal to the threshold value. The 4 largest patches made up about 96% of the total area of all patches, and the 7 largest made up about 98% (Table 4). The amount of habitat within a patch ranged from 20% to 47%, with an overall average of 40%.

Based on this patch structure, the program then calculated the carrying capacities and initial abundances of each population, by multiplying the total habitat value with the constant 0.058 (see *Methods*). The estimated total initial abundance was 10,383 owls.

Initial abundance and distribution

All results discussed in the following sections are based on models with an initial abundance of 10,383 owls, which was also the total carrying capacity of all populations. We also ran a simulation with an initial abundance equal to 80% of the carrying capacity, or 8,306 owls. Initial abundance did not change any of the result appreciably. Changing the initial distribution of owls among the three stages (juvenile, subadult, adult) from stable distribution to juvenile-heavy or adult-heavy distributions caused only negligible differences in the metapopulation's abundance, occupancy and viability.

Dispersal rates

The metapopulation as a whole had an average of 152 juvenile dispersers in the first year of the simulation, 68 of them from the largest population (see Table 4). In subsequent years the numbers changed since they are proportional to the number of juveniles.

The major effect of dispersal was on metapopulation abundance and occupancy (number of extant populations, or occupied patches). At the end of 100-year simulations, the numbers of occupied patches were 10.1 ± 3.3 (mean \pm s.d.) with high dispersal, 7.8 ± 2.4 with medium dispersal and 5.0 ± 1.2 without dispersal. However most of this difference was due to increased occupancy of smaller patches with dispersal, and neither the total abundance nor the viability of the population was sensitive to the rate of dispersal.

Correlation

The degree of correlation among the fluctuations of vital rates of different populations had a more substantial effect on the risk of decline. Under the assumption of medium values for all other parameters, the risk of 90% decline (falling below 1038 owls) was 0.021, 0.039 and 0.1152, for no, distance-dependent, and full correlation, respectively. These percentages are significantly different from each other at $P=0.01$.

Allee effects

Changing the local extinction threshold from 5% of carrying capacity (medium Allee effects) to 0% (no Allee effects) and 10% (strong Allee effects) caused considerable difference in metapopulation occupancy, and slight difference in metapopulation abundance. At the end of 100-year simulations, the numbers of occupied patches were 13.3 ± 2.5 (mean \pm s.d.) with no Allee effects, and 5.6 ± 2.1 for strong Allee effects. The risk of a 90% decline was 0.024, 0.039 and 0.130 for no, low and high thresholds, respectively. These percentages are significantly different from each other at $P=0.01$.

Fecundities and survival rates

The viability of the metapopulation was very sensitive to the set of vital rates used. The average total abundance declined slightly, and then stabilized under high vital rates, declined steadily under medium vital rates, and declined exponentially under low vital rates. Risk of falling by 90% from the initial abundance during the simulated 100-year period was small, 0.005 with high survival and 0.006 with high fecundity. The risk was substantial, 0.995 and 0.331, with low survival and fecundity respectively.

Viability of the spotted owl

The predicted abundance of owls was quite variable, with about 50% coefficient of variation for the total abundance at the end of the simulation. The simulated viability of the metapopulation according to this model was most sensitive to the set of vital rates used (especially survival), and also sensitive to the degree of spatial correlation among vital rates of the populations, and to the local extinction thresholds (Allee effects). In addition, metapopulation occupancy was sensitive to vital rates, Allee effects and dispersal. Combining these results, an optimistic scenario corresponds to a model with high vital rates, no environmental correlation and no Allee effects. Such a model predicted that the risk of 90% decline was less than 0.005 in the next 100 years (99% upper confidence limit for 0% for a sample size of 1000). The risk of a 90% decline in 100 years was about 0.04 with a model in which we used the mid-range estimates of all parameters.

A pessimistic scenario would be a model with low vital rates, high correlation, strong Allee effects, and low initial abundances. Such a model predicted that the median time to a 90% decline was about 34 years (Figure 5). This time horizon corresponds to about 3.5 owl generations. According to the newly revised IUCN (International Union for Conservation of Nature) threatened species criteria (Mace and Stuart 1994), this level of risk is classified as ENDANGERED (\leq 50% risk of extinction in 3 generations; $>$ 20% risk in 5 generations). This and other IUCN threatened species categories are represented by circles in the figure. Thus the range of possible outcomes includes three categories according to IUCN criteria: LOWER RISK, VULNERABLE, and ENDANGERED.

Uncertainty and the effect of habitat loss

We estimated the effect of habitat loss in terms of the increase in risk of decline. Under medium parameters, the risk of a 90% decline (from initial abundance) within the next 100 years increased by 0.267 from 0.039 with no habitat loss to 0.306 with assumed habitat loss. In other words, the increased risk attributable to the simulated habitat loss was about 27%.

Because the habitat loss modeled was arbitrary, our focus is not the absolute magnitude of this increase in risk, but its reliability under uncertainty. Given the uncertainty in parameter values, and the resulting uncertainty in risk of decline, it may seem that the model cannot reliably assess the impact of habitat loss. However, the change in risk of decline as a result of habitat

loss was similar under most assumptions of the model (Table 5): habitat loss increased the risk of a 90% decline by 0.22 to 0.45 for different assumptions. The only exceptions were assumptions related to survival and fecundity, the parameters to which the results were most sensitive. The increase in risk due to habitat loss is much less for low survival rate (because the risk is close to 1.0 regardless of whether there is habitat loss or not), and also much less for high survival and high fecundity (because the risk is close to zero regardless of whether there is habitat loss or not). As mentioned above (in "Stage matrix"), the uncertainty we assumed for adult survival (± 0.04) based on Bart's (1995) data is substantially higher than the SE of adult survival (± 0.005) calculated by Burnham et al. (1996). This assumption may be responsible for the high sensitivity to survival (and low sensitivity to habitat loss under the assumption of low or high survival). In addition, all of these risks were calculated for 100 years. The increase in risk due to habitat loss under low survival was again substantial when risks are computed for a shorter time horizon (40 years).

The above risks were computed for a 90% decline from initial abundances. However, different comparisons give the maximum change in risk at different levels of decline. For example, under an assumption of low fecundity, both no-habitat-loss and habitat-loss scenarios give higher risks, and the maximum difference in risk (attributable to habitat loss) is 0.45 for a 90% decline (Figure 6a), whereas under an assumption of medium fecundity the maximum increase in risk due to habitat loss is 0.44 for a 78% decline (Figure 6b), and under an assumption of high fecundity, the maximum increase in risk due to habitat loss is 0.37 for a 69% decline (Figure 6c). Note that "maximum difference in risk" here refers to the risk of percentage decline for which the difference between no-habitat-loss and habitat-loss scenarios is largest. This level of decline is given by the x-value of the vertical bar in Figure 6, wherease the maximum difference in risk (0.44 in the case of medium parameters) is indicated by the height of the bar. Overall, the maximum increase in risk due to habitat loss ranged from 0.33 to 0.52, for substnatial declines (≥42% of initial abundance; Table 5).

Discussion: Uncertainty and risk assessment

The results presented above do not depict what the population of the Northern Spotted Owl will actually do in the next 100 years. Rather, they represent *the range of probable outcomes*, subject to the numerous assumptions and simplifications we had to make. The range of outcomes was quite wide, covering three categories of threat according to IUCN criteria: LOWER RISK, VULNERABLE, ENDANGERED (Figure 5).

Most of this uncertainty resulted from the uncertainty about vital rates, combined with the assumption of ceiling-type density dependence (i.e., density *in*dependence below the population ceiling). Density independence under medium or low vital rates (that give a long-term growth rate below 1.0), means that the assumed decline will continue, even if the habitat does not decrease. This is only one of the possible outcomes. Another possibility is that after an initial

decline of several years, the vital rates will improve as a result of a density-dependent feedback (if the habitat does not decrease). Unfortunately, at this time there are no studies on density dependence of vital rates in spotted owl populations.

As a result of these types of uncertainties, results of population viability models such as this one are less reliable if interpreted as absolute predictions than if interpreted as relative to other sets of assumptions or scenarios. Our results demonstrate that even with relatively small impacts (0.1% habitat loss per year, in this case), and relatively large uncertainties, risk-based results are sensitive to parameters related to habitat loss. Even though the model predictions change as a function of parameters and assumptions (i.e., model results are effected by the uncertainties in input), all assumptions still predict that habitat loss results in substantially higher risks of metapopulation decline. Such relative results (expressed, for example as increase in risk of decline) are much more reliable than a prediction of exactly what the population size would be 100 years from now.

A similar argument can be made for ranking or comparing management options. Even if results of a model are sensitive to various model assumptions, it is likely that relative rankings of management options may not be as sensitive, i.e., all assumptions may rank the management options in a similar order.

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Vital rate		Low		Medium	High		
	Mean	S.D.	Mean	S.D.	Mean	S.D.	
$F_1 (= S_0 b_1)$	0.0223	0.0196	0.0258	0.0232	0.0294	0.0268	
$F_2 (=S_0 b_2)$	0.0672	0.0590	0.0779	0.0699	0.0886	0.0809	
$F_3 (=S_0 b_3)$	0.1111	0.0976	0.1288	0.1155	0.1465	0.1338	
S ₁	0.8431	0.0485	0.884	0.0508	0.92	0.0529	
$S_{\rm a}$	0.8431	0.0485	0.884	0.0508	0.92	0.0529	

Table 1. Mean and standard deviation of fecundities (*F*) and survival rates (*S*) under assumptions of low, medium and high vital rates.

(1996).

Table 2. Adult survival rate Table 3. Maternity (*b*) data from (*S*a) data from Burnham et al. Burnham et al. 1996 (*n* is the sample size)

Rank	Area (km^2)	Area as % of all patches	% habitat in patch	K and N_0	Dispersers [®]
	42785	59.6%	40.3%	6241	68.0
$\boldsymbol{2}$	16779	23.4%	40.6%	2469	59.8
3	4764	6.6%	46.6%	804	2.0
4	4504	6.3%	32.7%	534	13.1
$\mathbf 5$	605	0.8%	30.0%	66	1.1
6	432	0.6%	25.4%	40	0.5
7	397	0.6%	42.6%	61	1.8
Total for the 7 largest patches	70266	97.8%	40.1%	10215	146.3
Total for all 18 patches	71798	100.0%	39.9%	10383	152.2

Table 4. Characteristics of the seven largest patches in the model

* Dispersers: Average number of juveniles dispersing to all other populations at the first time step of the simulation (see text for details).

Table 5. Increase in risk of decline due to simulated harvest under different model assumptions. Both difference in risk of a fixed amount of decline (90%) from iniital abundance and the maximum difference in risk of decline are given

* The "%decline" column indicates the amount of decline for which the difference in risk between 'harvest' and 'no harvest' simulations was the largest.

	$\mathbf X$		

Figure 1. Neighborhood distance of 1.5 cells (see text for details).

are adjusted so that $S_a=0.884$ (from Burnham et al., *in press*) for medium vital rate set and average habitat. The amount of habitat within a patch ranged from 14% to 47%, with an overall average of 39.5% (the dotted vertical line).

Figure 3. Adult maternity (b_3 , the number of fleglings per adult owl) as a function of percent habitat, for low, medium and high vital rate sets. The slope is based on Bart (1995), the interceps are adjusted so that *b*3=0.339 (from Burnham et al., *in press*) for medium vital rate set and average habitat (the dotted vertical line).

Figure 4. Proportion of dispersing juveniles as a function of distance (in km). Data from Table P1 (on page 305) of Thomas et al. (1990). See text for model fitting.

Figure 5. Time to extinction with the mid-range parameters (curves close to the x-axis), and with a pessimistic scenario. The thick curves show the cumulative probability that the metapopulation abundance will fall below the extinction threshold (530 owls) at or before a given year. The dotted curves show 95% confidence interval of the risk curve, and the circles indicate IUCN's risk-based criteria for categories of threat (see text).

Figure 6. Risk of decline as a function of the amount of decline with and without habitat loss under three assumptions about fecundities: (A) low, (B) medium, (C) high.