A Simulation Analysis of Population Dynamics of the Northern Spotted owl in Relation to Forest Management Alternatives

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Introduction

A recent demographic analysis indicates that the population of the northern spotted owl has declined over large portions of its range (Burnham et al. 1994), but this report does not relate rates of population change to variation in habitat quality over the species' range. The alternatives under consideration in the Final Supplemental environmental impact Statement on Management of Habitat for late-Successional and Old-Growth Forest Related Species Within the Range of the Northern Spotted Owl allow varying levels of harvest of remaining nesting, roosting, or foraging (NRF) habitat of the owl. Because of the Burnham et al. (1994) finding that the owl population has declined over the past 10 years, likely in response to habitat loss (Murphy and Noon 1992), the effect of further harvest of habitat is of great interest. Some argue that the owl is approaching a demographic threshold below which population recover is unlikely. Over the long term, the habitat reserve design that is part of each of the alternatives will likely support stable and well-distributed populations of owls when unsuitable habitat within the reserves has matured (Thomas et al. 1990, USDI 1992, Murphy and Noon 1992, Thomas et al. 1993, Thomas and Raphael 1993). It is less certain whether harvest of owl habitat over the short term (say, the next 50 years) will nonetheless maintain owl populations or will cause unacceptable risk to recovery of the owl population during this transition to the future habitat equilibrium.

To evaluate the relative likelihood of persistence of the northern spotted owl on federal lands under various alternative, especially during this transition period, we used a spatially explicit life-history simulator (McKlevey et al. 1992). This model is a single organism simulator that is based largely on models developed by Lande (Lande 1987, 1988) and Lamberson (Thomas et al. 1990, Lamberson et al. 1992, Lamberson et al. in press) and is similar to Pulliam's BACHMAP model (Pulliam et al. 1991). The model is sensitive to the shape and location of high-quality habitat, which we mapped using information assembled by the Northern Spotted Owl Recovery Team and incorporated into the FEMAT databases. The model should be viewed as a tool for landscape design that allows a logical framework in which to assess qualitative differences in various land management plans in regard to population dynamics of the northern spotted owl.

We analyzed four harvest-rate scenarios, three of which are modeled from FEMAT and SEIS. First, we evaluated a no-cut scenario, where all current suitable habitat would be retained into the future-none would be lost or gained. This alternative provided a baseline condition upon which to compare the SEIS alternatives. Second, we modeled the harvest rate of Alternative 1 from the SEIS, an alternative in which nearly all of the currently suitable habitat would be retained within large reserves (about 398,900 acres of suitable habitat is available for harvest, out of a total
of 7,409,500 acres of suitable habitat). Third, we modeled the harvest rate of Alternative 9, the preferred alternative in the SEIS. In this alternative, about 1,311,000 acres of suitable NRF habitat are available for harvest in the matrix between reserves and in the available portion of adaptive management areas. Finally, we modeled the harvest rate of Alternative 7, an alternative based on the Final draft Recovery plan for the northern Spotted Owl in which about 2,401,700 acres of currently suitable NRF habitat is available for harvest. These four alternatives gave the widest range of harvest levels upon which to base our simulation studies. Other alternatives presented in the SEIS have intermediate levels of harvest and retention that are so similar to those of Alternative 9 that we did not believe the simulation model could distinguish among them.

Methods

Development of Habitat Maps

Current Conditions.—A Geographic Information System (GIS) was used to prepare habitat maps and other spatial data for input into the model. All of the GIS-based data for the model were drawn from the FEMAT database; other spatial data were generated or recoded from this base data. Because of operational limitations in the total number of owls that could be analyzed at one time by the simulation software, we divided the owl's range into three regions and conducted separate analyses within each region. In addition, because of the larger home range area used by owls on the Olympic Peninsula, we analyzed that province separately. Thus, we conducted separate simulations within a total of four geographic regions: Olympic Peninsula; Washington western and eastern Cascades; Oregon Coast and Oregon western and eastern Cascades; and the Oregon Klamath, California Klamath, California Coast, and California Cascades (Figure 1). These areas represent environmentally similar groupings of physiographic provinces used in the FEMAT effort.

Habitat maps were developed from interpretations by U.S.D.A. Forest Service, Regions 5 and 6, and BLM District biologists and are identical to the spotted owl habitat maps used for the FEMAT effort in 1993. These are binary maps that depict presence or absence of suitable NRF habitat for northern spotted owls on federal lands in Washington, Oregon, and Northern California. These maps were originally digitized in a vector (line) format but were generalized into a raster (grid) format for our analysis. The minimum resolution of the gridded maps (cell size) is 400 m², or approximately 16 hectares. This data resolution is equal to the Spatial Unified Database used in the FEMAT effort. A comparison of the original line maps to their gridded equivalents showed an overall difference of less than 0.3 percent in areas of habitat (Table 1). Each cell on the resulting grid map was coded as suitable if half or more of the underlying map was suitable, and as unsuitable otherwise.

Boundaries of FEMAT alternatives from the FEMAT database were provided in GIS format by Region 6 personnel. The boundaries used were the latest update to the alternatives (after January 15, 1994). This map was used to code areas as either reserve or matrix to project habitat loss over the next 50 years. Areas coded as matrix or Adaptive Management Area (AMA) were assumed...
to be available for harvest in our analysis. We also coded areas in matrix or AMA with a riparian reserve factor based on percent of matrix in stream buffers (Thomas and Raphael 1993: Appendix V-G). These factors were provided by the SEIS team and vary by alternative and physiographic province. Factors for Riparian Reserve scenario 1 buffers were applied for Alternatives 1 and 9, and agency plan buffers were applied for Alternative 7.

Before inputting habitat maps into the owl model, and elevation screen was generated to remove areas that would likely be unsuitable for spotted owls. The FEMAT database contains a U.S. Geological Survey 1:250,000 scale Digital Elevation Model (DEM) for Washington, Oregon, and California coded into 500-foot elevation zones. We used this map to screen out areas over 4,500 feet in Washington, over 5,000 feet in Oregon, and over 6,000 feet in northern California (E. Forsman, pers. comm.). During model runs, these screened areas would be avoided by owls as a "reflecting" boundary. Similar screens were developed for ocean areas and lands outside the owl's range.

After screening for elevation, maps of suitable habitat were overlain with a map of hexagons (simulating an owl home range) generated for in put to the owl model. The individual hexagon sizes were 3,500 hectares for the Olympic Peninsula and 1,500 hectares elsewhere (see discussion below on parameterizing the model). The percent of each hexagon in suitable habitat was calculated by counting the number of 16-ha cells coded as suitable in each hexagonal cell and dividing by the hex cell's area. Percent suitable habitat by hexagonal cell was then output to the model for each region for current conditions.

**Future Conditions.**—To project future habitat conditions, we developed a generalized harvest simulation in GIS by using the macro programming capabilities of ARC/INFO (ESRI, Redlands, CA). A series of operations was carried out on maps of suitable habitat in a recursive fashion to simulate removal of habitat in matrix areas at 10-year intervals (Figure 2). For each 10-year interval, calculations were made to determine the amount of habitat available for harvest in the matrix and amount of habitat remaining after a simulated harvest was performed. This was added to the amount of habitat in reserves, which remained fixed over time. At successive time-steps, the amount of habitat available from the previous time step was used as input. The available matrix habitat at the new time-step was then harvested and total remaining habitat was determined. Each alternative and the no-cut baseline were run once for each of four regions and once for each of five 10-year time steps, producing a total of 64 habitat maps.

We calculated harvest as a percent of matrix area in each administrative unit likely to be harvested each year under Alternatives 1, 7, and 9 in the SEIS based on projections by Johnson et al. (1993). Therefore, the suitable habitat in each 16-ha cell in matrix or AMA was reduced by a percentage factor each year to simulate harvest (Table 2). This had the effect of distributing harvest evenly across the matrix. We projected harvest at five consecutive 10-year intervals by using these assumptions. No allowance was made for regrowth of habitat during the 50-year time interval. In reality, some areas undoubtedly will move from unsuitable to suitable over the next 50 years. However, we do not currently have the necessary data to support reliable estimates of
habitat growth in specific locations. Habitat reserved in riparian reserves was added back to cells reduced by harvesting to simulate reservation of buffer areas around streams. Therefore, cells in the matrix were not allowed to fall below the riparian reserve factor due to harvesting.

At the end of the simulation for each 10-year increment, the remaining habitat at that year was overlain with a map of hexagons, and percent suitable habitat by hexagonal cell was calculated and output for a model run (as described above).

Parameterizing the Model

To link the population of spotted owls to the actual landscape as portrayed by our GIS maps of habitat, relationships were developed between the amount and distribution of habitat and the survival and reproductive performance of the owl. The model allows for input of parameter estimates relating these vital rates to six classes of habitat. Our analysis was meant to compare the relative effects of the different harvest rates of these plans, not to predict the precise number of owls over time. Because there are such great uncertainties in such comparisons, it was advantageous to compare results under varying sets of assumptions. For this analysis, we developed three "Rule Sets," that is, three different sets of vital rates based on different assumptions concerning the effects of such rates based on the proportion of habitat within each hexagonal cell. The first rule set was derived from earlier work completed by McKelvey and others in cooperation with members of the Northern Spotted Owl Recovery Team, in particular Jon Bart (McKelvey 1992; McKelvey and Crocker, unpublished). For Rule Set 2, we shifted the parameters for >60% suitable habitat to the 41-60% level. For Rule Set 3, parameters were shifted again to the 31-40% level.

We modified these rules for application to the larger area of interest in this analysis after consultation with additional biologists (E. Forsman, R. Holthausen; pers. comm..) (Table 3). Our primary modification was to make subadult (Stage 1) survival equal to adult (Stage 2) survival. The vital rates can be used to calculate $\lambda$, the finite rate of population change in relation to proportion of habitat under each of the three rule sets (Figure 3).

We conducted a series of tests to evaluate the performance of the model under varying initial conditions. First, we calculated an appropriate hexagonal-cell size from estimates of median home range area in each province. We assumed 60% overlap among pairs based on comparisons of density of owls in relation to home range area (Raphael and Marcot, unpublished data). Based on this assumption, we calculated the median annual exclusive area for a pair of owls within each physiographic province from data in the Final Recovery Plan (USDI 1992). For the Olympic Peninsula, this value was about 3,500 ha. The estimate varied between about 1,000 and 2,000 ha among the other provinces. We averaged the estimate for all other provinces, which came to 1,500 ha.

To start the model, an initial population level must be set. one option is to manually place owls over the landscape. We considered using the locations of all known activity centers, but this
would have left gaps where owls have not been fully surveyed. Another option is to assume an owl occurs everywhere where the amount of habitat exceeds some proportion of a cell. We experimented with this option and found the simulated initial population size was highly sensitive to the proportion used. For example, in a test in the Washington Cascades, we found that the initial simulated population varied from 500 to 1,600 to 2,250 depending on whether pairs were assigned to cells with greater than 60%, 40%, or 30% habitat, respectively (Figure 4).

After experimenting with these values, we selected the greater than 40% habitat level to initialize the owl population. This level seemed to best match expected population size within each regional area, although without more thorough survey work it is not possible to project the current population with much certainty. If the initial simulated population was too large relative to the rule set used, the model generally required 20 to 30 years before the simulated population settled down to an equilibrium level. If the initial simulated population is too low relative to the rule set, the model "grows" owls over the for 20 to 30 years to fill unoccupied suitable areas for essentially converse reasons. This, the model results for the first decade or two are not as useful as those from later years.

Population trend.—We examined 4 harvest scenarios: (1) Assume no harvest (all currently suitable habitat remains so and no additional habitat is produced; (2) Alternative 1 (nearly all habitat is reserved, but some harvest is allowed in matrix lands); (3) Alternative 9 (most habitat is reserved, but harvest is allowed in matrix and available AMA lands as described above); and (4) Alternative 7 (based on the Final Draft Recovery Plan for the Northern Spotted Owl and existing agency plans). For each of these alternatives, the model was run for 100 years. For the harvest simulations, five habitat maps were developed (see methods above) representing the estimated amounts of habitat at years 10, 20, 30, 40, and 50. Simulations were conducted so that each map was inserted into the analysis at the appropriate year during the 100-year run. Each run was repeated 10 times to derive an estimate of variability of results. We summarized several results for this analysis, including estimates for mean total population size and its 95% confidence interval, and mean occupancy of each cell in the landscape. For each run, a cell was scored as "occupied" if a pair was present in that cell at the end of a year. Mean occupancy was the total occupied cell-years divided by the products of total cells times years times replications. We also calculated $\lambda$ for each simulation run using mean population size for each year from year 20 through year 30 by dividing the mean for the current year by the mean from the previous year. We started with year 21 to reduce the effects of initial simulated population size. These 10 yearly estimates were averaged to estimate $\lambda$ for that population. Some of the other assumptions we used in our analyses and their consequences are summarized in Table 4. To summarize occupancy, we identified those cells where occupancy was 70% or greater. This is a high occupancy rate and we used it as an indicator of the best-quality (or "source") habitat. The value 70% is just under expected turnover if adult survival rates are on the order of 0.90 (turnover = 0.9 x 0.9 = 0.81).
Results

Habitat Trends

There is an estimated 7,409,500 acres of northern spotted owl NRF habitat that currently occurs on federal lands within the species' range. The amount of this habitat that would essentially be reserved from cutting varies among the three alternatives considered in this analysis: Alternatives 1, 9, and 7 would reserve 95%, 82%, and 68% of owl habitat, respectively. We projected the likely annual rate of harvest for 50 years and calculated the percentage of habitat within each hexagonal cell as used in the owl model. Subtracting these percentages across pairs of alternatives (Figure 5) showed that because the majority of harvest falls in a relatively small number of cells, most cells will not be affected significantly (differences of < 10%) through the harvest projected to occur over the next 50 years. Regional differences in the amount of habitat harvested are more apparent. For example, a comparison of differences between Alternatives 1 and 7 (Figure 5A) shows few cells with a greater than 25% change of habitat on the Olympic Peninsula and Washington Cascades but relatively more cells exceeding 25% change in California and Oregon, areas with higher projected harvest levels. A similar comparison between Alternatives 9 and 7 (Figure 5B) shows a narrow spread of differences and shows greater differences in the California and Oregon regions than elsewhere. Again, such comparisons do not account for the transition of currently unsuitable habitat to suitable condition during this period.

Simulated Population Dynamics of the Northern Spotted Owl

No Cutting.—Under the scenario that no habitat would be harvested and none would be grown over the next 100 years, simulated populations in each region either declined, were stable, or grew, depending on the rule set selected (Figure 6). Although simulated population sizes varied, the pattern and trend over time were generally similar among regions. In Oregon, however, populations seemed stable under Rule Set 2, whereas populations were projected to continue to decline under this rule set in the other regions.

The simulated population sizes, set through initial model conditions, totaled about 5,200 birds on federal lands across the four regions. The Northern Spotted Owl Recovery Team estimated 2,825 known pairs on federal lands (USDI 1992:40) or about 5,650 birds (not including single birds and juveniles). This number is greater than the initial condition of our simulation, and the recovery team's estimate includes only known birds. Thus, the number of owls in the simulated initial condition is probably low.

SEIS Alternatives.—The results of the harvest simulations varied among regions, based primarily upon the relative level of cutting of habitat in each region (Figure 7). On the Olympic Peninsula, relatively little land is available for timber harvest under the alternatives, and this is reflected in the simulation results (Figure 7A). All alternatives and the no-cut scenario show virtually identical population trends over time, under each of the three rule sets. Mean occupancy within
cells was also similar among the four simulations (Figure 8), as was the number of cells with > 70% occupancy (Figure 9).

In the Cascades of Washington, estimated population trends were similar for the no-cut scenario, Alternative 1, and Alternative 9 harvest simulations, especially over the first 50 years (Figure 7B). Considering the confidence intervals around these means (see Figure 6), these three trends do not differ. The trend for Alternative 7 is lower than that of the other simulations under Rule Sets 2 and 3, especially from year 30 on. The greater harvest rate allowed under this Alternative is reflected in this trend. Mean occupancy was most similar between the no-cut scenario and Alternative 1, somewhat lower for Alternative 9, and much lower for Alternative 7 (Figures 8, 9).

In the Oregon region (which excludes the Oregon Klamath province for this analysis), harvest levels are the highest of the regions, which results in greater estimated effects on simulated owl populations. Under each of the rule sets, the no-cut scenario and Alternative 1, simulations were quite similar, but simulations for Alternative 7 showed lower expected populations than those of the low-harvest alternatives after year 30 (Figure 7C). The simulation for Alternative 9 was intermediate, reflecting the fact that its projected level of harvest falls between Alternative 1 and 7. Under Rule Set 2, simulated populations are projected to decline; simulated populations are projected to stabilize under Rule Set 3 and to remain relatively high throughout the 50 years of simulated harvest. None of the simulations, including those from Rule Set 1, predict extirpation. Mean occupancy patterns among the harvest simulations showed the same trends, with occupancy greatest under the no-cut scenario, slightly lower under Alternative 1, much lower under Alternative 7 and intermediate under Alternative 9 (Figures 8, 9). Few cells were occupied with 70% or greater frequency in the Eastern Cascades province, and no cells were occupied at that rate in the Coast Range province (Figure 9).

The harvest simulation results in the California region (which included the Oregon Klamath province in our analysis) were similar to those of Oregon, except that trends for Alternative 9 were closer to those of Alternative 1 and to the no-cut scenario than to Alternative 7 (Figure 7d). Occupancy trends (Figure 8, 9) showed the same relative rankings of the alternatives. Note that the California Cascades province, which has little federal land and little suitable habitat, has no cells with greater than 70% occupancy (Figure 9). In this region, our assumption of no habitat (and, consequently, no owls) on nonfederal lands certainly results in an underestimation of population size. For example, the Northern Spotted owl Recovery Team estimated that 414 pairs of owls occur on private lands (USDI 1992:40).

**Discussion**

The predicted power of the model is untested (and fundamentally not testable, at least in the short term). It provides a more quantitative tool through which we can assess the relative merits of a variety of plans assuming the basic validity of the underlying assumptions about habitat relationships. Actual prediction of population levels during a transitional period is extremely
unlikely to be reliable - even if the model were perfect - because these levels are very dependent on the start-up population and estimates of current population are still fairly crude. Here, the best approach is probably to allow the habitat to change for a period of time (perhaps 50 years, as in our study) and then hold it stable until the population equilibrates. This, again, allows for ordinal ranking of the alternatives.

The ability of the model to differentiate between various alternatives is dependent on how different those alternatives are (in terms of both quantity and geometry of habitat). Some of the SEIS alternatives are not significantly different with respect to the scale at which the model operates. This is why we chose to focus on Alternatives 1, 7, and 9. We did not believe the model would differentiate in any meaningful way between, say, Alternative 9 and 5.

McKelvey et al. (1992) described some of their major findings for the model used here. They found that the model was very sensitive to the shape, size, and distance between areas of "source" habitat - that is, habitat which, if it covered the entire map, would support a stable or increasing population. The model is also sensitive to simulated behavioral patterns - in particular the ability of the owls to determine when they are in source habitat and become territorial. In irregular habitat configurations in which there is a great deal of edge between the source areas and sink area, poor choices can destabilize the modeled population. In large, blocky habitat designs, the ability to differentiate between source and sink habitat is less important.

Results of this analysis do not purport to represent actual population trends; rather, its major purpose is to shed light on the sensitivity of owl population dynamics to varying degrees of habitat change over time and to compare the qualitative similarity of trends among alternatives. There are simply too many unknowns to be confident that any model will predict the actual population of a species many decades into the future.

Because we did not attempt to model growth of habitat within reserves over time, and because we did not model habitat conditions on nonfederal lands, our simulations must be considered conservative, especially over the long term. Therefore, our results do not directly address the issue of whether owls will eventually achieve a stable equilibrium, at least in part on the basis of regrowth of suitable habitat within the reserves. Our simulations can reveal likelihoods of population stability or decline on federal lands, but the simulations are not able to show recovery or growth of populations because no habitat recovery is included. In fact, our simulations, under the most likely set of assumptions (Rule Set 2), indicate that populations under a no-cut scenario and under Alternative 1 will stabilize or decline very slowly over the four regions we analyzed. For Alternative 9, our simulations suggest a slightly greater rate of decline than under the no-cut scenario or Alternative 1 in the Western Cascades of Oregon.

It is important to note that relative differences in simulated population sizes and occupancy rates among scenarios are swamped by differences caused by using different Rule Sets. If Rule Set 1 is correct, populations might be expected to decline under all scenarios. If Rule Sets 2 or 3 are
correct, then populations can be expected to stabilize under any of the scenarios (though at lower levels under Alternative 7).

Our results support the conclusions reach by the FEMAT in assessing likelihood of habitat conditions to provide for stable and well-distributed populations (measured against the owl's historic range on federal lands over both the short and long term. The FEMAT presented habitat likelihood outcomes of 89%, 71%, and 83% for Alternatives 1, 7, and 9 respectively (Thomas and Raphael 1993:IV-93). These rankings compare with the relative rankings of the alternatives one might derive from the simulated population trends under these alternatives (Figure 7). The FEMAT based their ratings on an assumption that the amount and distribution of habitat would be sufficient to support a large enough population of owls to prevent passing an extinction threshold. Our simulation results do not prove this assumption correct (nor could they), but they do lend support to it for Alternatives 1 and 9 under the most likely model rule sets.

Acknowledgements

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Literature Cited


Table 1. Relationship between original estimate of amount of suitable habitat (hectares) and generalized (grid-based) data used for model runs.

<table>
<thead>
<tr>
<th>Province</th>
<th>Original habitat estimated (polygon-based)</th>
<th>Generalized habitat (grid-based 16-ha grid)</th>
<th>Difference (%)</th>
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<tr>
<td>Olympic Peninsula</td>
<td>257,696</td>
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<td>W. Washington Lowlands</td>
<td>0</td>
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<td>W. Washington Cascades</td>
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<td>Oregon Coast Range</td>
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<td>Willamette Valley</td>
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<td>TOTAL</td>
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a FEMAT Physiographic Provinces

b Original polygon data from FEMAT data (nesting, roosting, and foraging habitat).

c Amount of suitable habitat generalized to 16-ha grid cells.
Table 2. Estimated harvest of spotted owl habitat by administrative unit and by Alternative.

<table>
<thead>
<tr>
<th>Dist.</th>
<th>Matrix habitat (ha)&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Predicted annual harvest (ha)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Proportion cut&lt;sup&gt;c&lt;/sup&gt;</th>
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<td></td>
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<td>Alter. 9</td>
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<td>7,824</td>
</tr>
<tr>
<td>SHT</td>
<td>7,888</td>
<td>27,888</td>
<td>20,336</td>
</tr>
<tr>
<td>Total</td>
<td>301,680</td>
<td>1,052,768</td>
<td>879,760</td>
</tr>
</tbody>
</table>

<sup>a</sup> Calculated from FEMAT database using GIS.
<sup>b</sup> Estimated from Johnson et al. (1993: Table 12), and from C. Hamilton (Pers. Comm., Jan. 21, 1994, memo).
<sup>c</sup> Predicted harvest divided by area in matrix.
Table 3. Summary of parameters under three sets of rules used to simulate population dynamics of the northern spotted owl.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Start up parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rule Set 1</td>
<td>OFF</td>
</tr>
<tr>
<td>Mean survival probabilities&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Stage 0 (Juvenile)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 1 (Subadult)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 2 (Adult)</td>
<td>0</td>
</tr>
<tr>
<td>Rule Set 2</td>
<td></td>
</tr>
<tr>
<td>Mean survival probabilities&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Stage 0 (Juvenile)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 1 (Subadult)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 2 (Adult)</td>
<td>0</td>
</tr>
<tr>
<td>Rule Set 3</td>
<td></td>
</tr>
<tr>
<td>Mean survival probabilities&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Stage 0 (Juvenile)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 1 (Subadult)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 2 (Adult)</td>
<td>0</td>
</tr>
<tr>
<td>Rule Sets 1, 2 &amp; 3</td>
<td></td>
</tr>
<tr>
<td>Mean survival probabilities&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Stage 0 (Juvenile)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 1 (Subadult)</td>
<td>0</td>
</tr>
<tr>
<td>Stage 2 (Adult)</td>
<td>0</td>
</tr>
<tr>
<td>Fledge Number = 2&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Male Prob. of Fledging = 0.50&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Movement&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Nesting OK</td>
<td>0</td>
</tr>
<tr>
<td>Aversion</td>
<td>0</td>
</tr>
<tr>
<td>Prob. Female Finds Male = 0.50&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Male territorial Aversion = 0.50&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Directional Weighting = 2.00&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>WanderL&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0</td>
</tr>
<tr>
<td>Boundary Condition = Absorbing&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Time series</td>
<td></td>
</tr>
<tr>
<td>Total number of runs = 10 Total run length = 100 Years</td>
<td></td>
</tr>
<tr>
<td>Delta-t = 20 (Olympic Peninsula = 15)</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Variance of survival probabilities is 0 for all three rule sets and stages.

<sup>b</sup>See McKelvey at al. (1992) for explanation of these factors.
Table 4. Summary of major operating assumptions used in simulation runs.

<table>
<thead>
<tr>
<th>Assumptions</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell-size 1500 ha (3500 ha on Olympic Peninsula).</td>
<td>Sets maximum population size. The smaller the cell, the greater the maximum number of owls.</td>
</tr>
<tr>
<td>Initial owl population - owls allocated to any cell with &gt; 40% suitable</td>
<td>Sets initial population size. If proportion suitable is lowered, more owls &quot;populate&quot; the landscape when the run begins, and vice versa. If population is too large, early results of model runs are unreliable.</td>
</tr>
<tr>
<td>habitat.</td>
<td></td>
</tr>
<tr>
<td>Rule set - sets relationship between proportion habitat in up to 6 classes</td>
<td>Greater estimates of survival and fecundity rates in a given habitat class result in faster population growth in landscapes with that class, and vice versa. Model is most sensitive to adult survival.</td>
</tr>
<tr>
<td>and vital rates of population.</td>
<td></td>
</tr>
<tr>
<td>No regrowth of habitat.</td>
<td>Underestimates total habitat, especially in the future when some currently unsuitable forest will likely become suitable habitat. Result is a conservative estimate of habitat quality.</td>
</tr>
<tr>
<td>No habitat on nonfederal land.</td>
<td>Underestimates total habitat within range of owl, as some habitat occurs and will likely continue to occur on state and private land. Result is underestimate of simulated population size.</td>
</tr>
<tr>
<td>Even rate of harvest within administrative units.</td>
<td>Spreads harvest evenly across all acres, thus does not reveal direct effects of fragmentation resulting from patchy cutting pattern. Result is overestimate of habitat quality in the matrix.</td>
</tr>
<tr>
<td>Application of riparian buffer factor across all units.</td>
<td>Spreads retention of habitat evenly across all acres, though does not reveal contiguous patches of habitat along streams. Result is underestimate of habitat quality.</td>
</tr>
<tr>
<td>No allowance for loss of habitat due to catastrophic events (fire, insect</td>
<td>Increases estimate of amount of suitable habitat. Maintains more even distribution of habitat over the landscape.</td>
</tr>
<tr>
<td>infestation).</td>
<td></td>
</tr>
<tr>
<td>No consideration of other viability factors such as weather.</td>
<td>Decreases yearly variability of estimates of fecundity and population size.</td>
</tr>
<tr>
<td>No harvest in reserves.</td>
<td>Under the SEIS alternative, thinning and salvage operations are permitted within reserves. The effects of these actions could be positive or negative, but are likely to be minor at the scale of this analysis.</td>
</tr>
</tbody>
</table>
**Figure Legends**

Figure 1. Location and extent of four regions for which model runs were made to simulate harvest levels and consequent simulated population dynamics of the northern spotted owl. Lines within states indicate the boundaries of physiographic provinces (USDI 1992).

Figure 2. Flow chart depicting the process we used to simulate harvest levels for each alternative. Each alternative has a mapped reserve network in which essentially no harvest takes place, and a matrix where harvest is permitted. In addition, some area within the matrix is protected within unmapped riparian zones. The harvest level within the matrix was adjusted to account for these riparian areas. At each 10-year increment, harvest was accumulated, and a new map was created for the owl simulations.

Figure 3. Finite growth rates ($\lambda$) calculated from three sets of rules (stage-specific rates of survival and fecundity) in relation to habitat suitability (percent of suitable habitat within a 3,500-ha or 1,500-ha hexagonal cell).

Figure 4. Effect of varying simulated initial population size on population trend assuming stable habitat conditions. Initial size was set by automatically placing a pair of owls into any cell that contained greater than 30%, 40% or 60% habitat, respectively.

Figure 5. Projected degree of difference between alternatives in the amount of habitat within a particular hexagonal cell after harvest over a 50-year period, for each of the four large regions. A: Acres of habitat under Alternative 7 subtracted from the respective cell under Alternative 1; B: Acres of habitat under Alternative 7 subtracted from the respective cell under Alternative 9; C: Acres of habitat under Alternative 9 subtracted from the respective cell under Alternative 1.

Figure 6. Simulated population trend of the northern spotted owl over 100 years with no harvest of currently suitable habitat (no-cut scenario) under three Rule Sets (parameter estimates). Values are estimated mean total population size plus or minus the 95% confidence interval. Estimates of $\lambda$ were calculated from the mean of the values calculated for $\lambda$ for each of the 10 years between year 20 and year 30; these estimates are not the same as those calculated directly from the three Rule Sets (Figure 3). A: Olympic Peninsula; B: Washington; C: Oregon; D: California. See Figure 1 for map of regions.

Figure 7. Simulated population trends (mean population size) of the northern spotted owl with four levels of timber harvest projected under Alternatives 1, 7, and 9 compared with a no-harvest baseline, and under each of three Rule Sets (parameter estimates). Harvest was modeled for the first 50 years for Alternatives 1, 7, and 9. A: Olympic Peninsula; B: Washington; C: Oregon; D: California. See Figure 1 for map of regions.

Figure 8. Number of hexagonal cells that had 70% or greater occupancy by pairs of owls over a 100-year simulation run by Alternative and physiographic province.
Figure 9. Location of cells that had 70% or greater occupancy by pairs of owls over a 100-year simulation run, using Rule Set 2 (Figure 3, Table 3). A: Current condition (no-cut scenario). B: Alternative 1. C: Alternative 7. D: Alternative 9.
Regional Analysis Areas

- Olympic Peninsula
- Washington
- Western Cascades
- Eastern Cascades
- Oregon
- Coast Range
- Western Cascades
- Eastern Cascades
- California
- Oregon Klamath
- California Klamath
- Cascades

Lines within state boundaries denote Physiographic Provinces

Figure 1
GIS Harvest Simulation

begin, seed model at year 0

habitat at year 0 * riparian reserve factor (matrix) = habitat estimated available for harvest in matrix

habitat reserved from estimated harvest (inviolate) = habitat at year 0

simulate harvest at 10-year increments

habitat available for harvest at year n-10 * 1-projected cut (proportion of admin. unit) = habitat remaining in matrix

estimated habitat at year n = reserved from harvest

send to owl model at 10-year increments
Figure 4

Owls assigned to a cell that exceeded a given percent habitat.

Effects of Initial Population Size

Washington Cascades

Total Population

Years

Effect of Initial Population Size
Alternative 1 minus Alternative 7

Olympic Peninsula

California

Washington Cascades

Oregon

Number of Cells

Difference in Habitat (%)
Alternative 9 minus Alternative 7

**Olympic Peninsula**

**California**

**Washington Cascades**

**Oregon**

Difference in Habitat (%)
Alternative 1 minus Alternative 9

Olympic Peninsula

California

Washington Cascades

Oregon

Number of Cells

Difference in Habitat (%)

Figure 5C
Olympic Peninsula - Current Habitat

\[ \lambda = 0.98 \]

Rule Set 1

\[ \lambda = 1.00 \]

Rule Set 2

\[ \lambda = 1.00 \]

Rule Set 3

Years
Washington - Current Habitat

Figure 6B

Rule Set 1

\[ \lambda = 0.98 \]

Rule Set 2

\[ \lambda = 0.99 \]

Rule Set 3

\[ \lambda = 1.00 \]
Oregon - Current Habitat

Rule Set 1

\( \lambda = 0.98 \)

Rule Set 2

\( \lambda = 1.00 \)

Rule Set 3

\( \lambda = 1.01 \)
California - Current Habitat

Rule Set 1

\[ \lambda = 0.96 \]

Rule Set 2

\[ \lambda = 0.99 \]

Rule Set 3

\[ \lambda = 1.01 \]

Figure 6D
Olympic Peninsula
Harvest for 50 years

Rule Set 1

Rule Set 2

Rule Set 3

Figure 7A
Figure 7B

Washington
Harvest for 50 years

Rule Set 1

Rule Set 2

Rule Set 3

Years
Oregon
Harvest for 50 years

Rule Set 1

Alt. 1 Alt. 7 Alt. 9 No Cut

Rule Set 2

Rule Set 3

Figure 7C
California
Harvest for 50 years

Rule Set 1

Mean Population Size

Rule Set 2

Rule Set 3

Years

Figure 7D
Current Condition
Rule Set 2

- Dots represent locations occupied at a rate of 70 percent or greater during simulation runs of 100 years.

Lines within state boundaries denote Physiographic Provinces.
Alternative 1
Rule Set 2

- Dots Represent Locations Occupied at a Rate of 70 Percent or Greater During Simulation Runs of 100 Years

Lines within state boundaries denote Physiographic Provinces

Figure 9B
Alternative 7
Rule Set 2

- Dots Represent Locations Occupied at a Rate of 70 Percent or Greater During Simulation Runs of 100 Years
Alternative 9
Rule Set 2

- Dots Represent Locations Occupied at a Rate of 70 Percent or Greater During Simulation Runs of 100 Years

Lines within state boundaries denote Physiographic Provinces