

# MODELING DEMOGRAPHIC PERFORMANCE OF NORTHERN SPOTTED OWLS RELATIVE TO FOREST HABITAT IN OREGON

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**Abstract:** Northern spotted owls (*Strix occidentalis caurina*) are known to be associated with late-successional forests in the Pacific Northwest of the United States, but the effects of habitat on their demographic performance are relatively unknown. We developed statistical models relating owl survival and productivity to forest cover types within the Roseburg Study Area in the Oregon Coast Range of Oregon, USA. We further combined these demographic parameters using a Leslie-type matrix to obtain an estimate of habitat fitness potential for each owl territory ( $n = 94$ ). We used mark-recapture methods to develop models for survival and linear mixed models for productivity. We measured forest composition and landscape patterns at 3 landscape scales centered on nest and activity sites within owl territories using an aerial photo-based map and a Geographic Information System (GIS). We also considered additional covariates such as age, sex, and presence of barred owls (*Strix varia*), and seasonal climate variables (temperature and precipitation) in our models. We used Akaike's Information Criterion (AIC) to rank and compare models. Survival had a quadratic relationship with the amount of late- and mid-seral forests within 1,500 m of nesting centers. Survival also was influenced by the amount of precipitation during the nesting season. Only 16% of the variability in survival was accounted for by our best model, but 85% of this was due to the habitat variable. Reproductive rates fluctuated biennially and were positively related to the amount of edge between late- and mid-seral forests and other habitat classes. Reproductive rates also were influenced by parent age, amount of precipitation during nesting season, and presence of barred owls. Our best model accounted for 84% of the variability in productivity, but only 3% of that was due to the habitat variable. Estimates of habitat fitness potential (which may range from 0 to infinity) for the 94 territories ranged from 0.74 to 1.15 ( $\bar{x} = 1.05$ ,  $SE = 0.07$ ). All but 1 territory had 95% confidence intervals overlapping 1.0, indicating a potentially stable population based on habitat pattern. Our results seem to indicate that while mid- and late-seral forests are important to owls, a mixture of these forest types with younger forest and nonforest may be best for owl survival and reproduction. Our results are consistent with those of researchers in northern California, USA, who used similar methods in their analyses. However, we believe that given the low variability in survival and productivity attributed to habitat, further study is needed to confirm our conclusions before they can be used to guide forest management actions for spotted owls.

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In 1990, the northern spotted owl was listed as a federally threatened species based on declining amounts of suitable habitat throughout their range, declining population trends, and lack of existing regulatory methods to protect the species (Gutiérrez et al. 1996). Northern spotted owls generally are associated with mature or late-seral forests in the Pacific Northwest (Forsman et al. 1984, Carey et al. 1990, Thomas et al. 1990), and numerous studies have documented selec-

tion of late-seral forests by spotted owls for nesting, foraging, and roosting (see reviews in Thomas et al. 1990). In 1994, the U.S. Forest Service and Bureau of Land Management (BLM) adopted a regionwide plan for management of late-successional forests in the Pacific Northwest. A primary goal of this plan (referred to as the Northwest Forest Plan) was to protect and enhance habitat for northern spotted owls (U.S. Department of Agriculture and U.S. Department of the Interior 1994). To monitor progress toward reaching this goal, the U.S. Forest Service and BLM developed an Effectiveness Monitoring Plan for

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northern spotted owls in 1999 (Lint et al. 1999). This plan relies on long-term (since the mid-1980s) mark-recapture surveys to monitor owls within large demographic study areas (Forsman et al. 1996, Lint et al. 1999, Franklin et al. 1999).

Demographic studies of spotted owls are expensive, labor intensive, and involve the capture and handling of large numbers of owls every year. Therefore, the Effectiveness Monitoring Plan included a proposal to explore the possibility of using statistical models to predict the occurrence and vital rates of spotted owls based on remotely sensed (aerial photograph or satellite imagery) habitat features. This proposal assumed that both habitat quality and quantity affect survival and productivity rates of individual owls at the home-range scale, and that consequences of habitat change at the scale of an individual owl territory can be assessed directly by measuring demographic rates (e.g., survival, fecundity). Therefore, the proposal called for an analysis of available demographic data to determine whether the occurrence and vital rates of spotted owls could be predicted using vegetation characteristics obtained from remotely sensed maps. An expected outcome of this analysis was that, if the habitat-based models could reliably predict owl occupancy and demographic rates, trends in habitat could be used to predict trends in owl abundance as opposed to labor-intensive studies of owl demography (Lint et al. 1999).

We designed our study to address the following question raised in the Effectiveness Monitoring Plan: "Can the relation between owl occurrence and demographic performance be reliably predicted given a set of habitat characteristics at the landscape scale?" (Lint et al. 1999:3). We used an aerial photo-based, forest cover-type map to measure habitat characteristics around spotted owl territories on the Roseburg District of the BLM in western Oregon. We recognized that forest cover types are a subset of the "habitat characteristics" that may influence owl demographic performance, but we felt they included most of the factors found to be important in previous studies, such as amount of old conifer forest (Forsman et al. 1984, Ripple et al. 1997) and forest patch metrics (Lehmkuhl and Raphael 1993, Franklin et al. 2000), and were measurable at the landscape scale. Hereafter, references to habitat are restricted to components related to these forest cover types measured at the landscape scale.

We focused on the question of demographic performance. For this, we analyzed 2 measures of performance: annual survival rates and annual

productivity. We also combined these parameters into a single measure of habitat fitness potential (see Franklin et al. 2000). This approach is relatively rare in research relating spotted owls to habitat; most previous studies have used presence/absence of owls (or occupancy) as the response variable (Bart and Forsman 1992, Meyer et al. 1998, McComb et al. 2002). Although important for establishing the link between northern spotted owls and late-successional forest, these studies fall short of establishing whether qualitative differences in habitat composition and pattern influence population vital rates. The link between habitat characteristics and demographic traits in northern spotted owls is still unclear for a variety of reasons (Franklin et al. 2000). Studies that only examine 1 component of fitness (e.g., survival or fecundity) would not detect potential trade-offs that maximize lifetime fitness. Although a few studies have investigated habitat effects on productivity (Bart 1995, Ripple et al. 1997, Thome et al. 1999), only Franklin et al. (2000) and our study also have modeled survival rates and estimated habitat fitness potential for northern spotted owls. Likewise, none of the studies of other spotted owl subspecies (California [*S. o. occidentalis*] and Mexican [*S.o. lucida*]) have taken this approach; although Seamans et al. (2001) used similar methods to estimate survival and productivity for a general demographic analysis of California spotted owls.

## METHODS

### Study Area

The 1,011-km<sup>2</sup> Roseburg Study Area was located in the southern half of the Oregon Coast Range (Fig. 1). The area is characterized by mountainous terrain covered by forests of Dou-



Fig. 1. Map of Oregon illustrating the Roseburg Bureau of Land Management (BLM) northern spotted owl study area.

glas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Elevations ranged from 24 to 900 m. South-facing slopes often included variable amounts of incense cedar (*Calocedrus decurrens*), golden chinquapin (*Castanopsis chrysophylla*), grand fir (*Abies grandis*), and Oregon white oak (*Quercus garryana*). Land ownership consisted of a checkerboard pattern of square-mile sections of nonfederal lands alternating with square-mile sections of federal land administered by the BLM. Forests on nonfederal lands were mostly young stands (<80 yr old), whereas forests on BLM lands included a diverse mix of young forests and older, unlogged forests that were 80–450 years old.

### Demographic Variables

Northern spotted owls have been monitored annually in the Roseburg Study Area since the mid-1980s. Each year, teams of biologists survey established sites to determine owl occupancy, presence of banded birds, reproductive status, and number of young fledged. These items are determined by established protocols (Lint et al. 1999: Appendices A–C) based on a series of visits (usually 4–8 visits/yr) to each site from April to September.

For survival analyses, we included only owls  $\geq 1$  year old (nonjuveniles). Owls banded as juveniles and recaptured when they were  $\geq 1$  year old were treated as though the initial (nonjuvenile) recapture was their first capture. We assigned owls to 1 of 3 age classes when they were first captured or visually confirmed on a territory (1 yr old, 2 yr old, or adult). In the case of owls not banded as juveniles, we estimated age based on plumage characteristics (Forsman 1981). Visual confirmations were based on resightings of unique color bands (Forsman et al. 1996).

We constructed capture histories for each individual that were both year and site specific, based on the approach used by Franklin et al. (2000). Any resighting of a banded bird within a year was considered a capture for that year. If a bird moved to a new site (permanent movements only), then a new capture history record was constructed. We then used the “losses on capture” notation (Jolly 1965) on the initial capture history to account for the movement and known continued survival of the bird. This treatment resulted in some loss of information but allowed for the correct identification of birds that were known to have survived while using a territory

versus those whose fates were unknown or presumed to have died.

For productivity modeling, we used the number of fledglings produced per pair per year. We assumed that detectability of fledglings by the survey teams was 1.0 after a minimum of 2 visits to each site known to have a nesting pair. By restricting the analysis to sites occupied by nesting pairs, we did not consider variables that may have precluded birds from nesting on other sites. This was due to our desire to include age covariates that we thought would be an important determinant of owl productivity.

### Climate Variables

Although the focus of our research was to assess the influence of habitat, we included climate variables in our models for several reasons: (1) to reduce the random variability in our demographic parameters and possibly better detect habitat effects, (2) to gain insight into how climate may be influencing these parameters that could be used for further research, and (3) to compare the relative magnitude of climate and habitat effects. We chose to use the same set of climate variables used by Franklin et al. (2000) because we hypothesized that climate would similarly affect spotted owls in our study area. These variables were temperature and precipitation for 5 periods within a year: (1) early nesting (Mar–Apr), (2) late nesting (May–Jun), (3) heat stress (Jul–Aug), (4) dispersal (Sep–Oct), and (5) winter stress (Nov–Feb). Temperature variables were calculated as daily degree hours (DDH; Allen 1976), and precipitation was measured as the proportion of days within a season with  $>0.03$  cm of rain.

We obtained data for computing these variables from National Oceanic and Atmospheric Administration (NOAA) U.S. Weather Service Cooperative stations within or adjacent to the study area. The period-specific daily degree models used to compute temperature variables were developed from a single NOAA station (Eugene Airport) that had a complete set of hourly temperature data for the years of our study. We used daily minimum and maximum temperatures from 2 stations (Drain and Elkton 3 SW) near the study area to calculate year- and period-specific DDH, which we averaged across stations to obtain an annual estimate for each period. We used proportion for precipitation rather than absolute numbers because several values were missing in the database. We decided that at least 30 days of recorded values within a period were needed to estimate

Table 1. Summary of forest cover types used to classify habitat within northern spotted owl territories in the Roseburg study area, Oregon, USA, 1985–1999. Original classifications are the vegetation type classes from an aerial photo-based map used as the basis for our habitat variables. Proportion of 1,500-m circles is the proportion of each cover type within all 1,500-m radius circles centered on spotted owl activity centers for each territory.

Forest cover-type category		Original classification	DBH <sup>a</sup> (cm)	Proportion of 1,500-m circle	
Composition	Pattern			Mean (SE)	Range
Nonforest	Nonforest	Agriculture, clearcut, open-sapling	0–24.1	0.30 (0.01)	0.02–0.65
Mid-seral conifer	Mid-seral forest	Pole conifer, young conifer, early mature forest	24.2–80.0	0.38 (0.02)	0.01–0.85
Broadleaf	Mid-seral forest	Hardwood	N/A	0.01 (0.00)	0.00–0.11
Late-seral conifer	Late-seral conifer	Mature, old conifer	>80.1	0.31 (0.02)	0.02–0.81

<sup>a</sup> Diameter at breast height.

the proportion of days with rain, assuming that the missing days had the same relative frequency as the recorded days. Although amount of precipitation may have been a more biologically relevant covariate than proportion of days with rain, we felt that we could not make assumptions regarding the days when amounts were unknown and thus these measures could be highly inaccurate. Data from 3 weather stations (Sutherlin 4 NE in addition to the 2 used for temperature variables) were averaged to compute the year- and period-specific precipitation variables. For all climate variables, we verified that precision for means across stations (spatial variability) was high relative to the variability among years.

### Habitat Variables

*Forest Cover Map.*—We used a digitized forest cover map prepared for previous spotted owl studies (E. D. Forsman and J. A. Reid, unpublished data) to characterize the distribution of forest cover types within owl territories. Forest cover types were identified at the stand level using 1:12,000 scale orthophotos (1998) and color aerial photographs (from 1968 to 1998). Harvest and other disturbances were updated through 1992, after which time logging on federal lands was greatly curtailed. We classified 8 cover types based on age of dominant (>50% of canopy) overstory trees (Table 1). Field checks of a random sample of vegetation polygons indicated that overall accuracy of the map was 76%. Age was overestimated on 11% of the map and underestimated on 13% of the map. The conifer age groups had the following accuracy values (with amounts overestimated or underestimated): young conifer 75% (10% over, 15% under), early mature conifer 70% (30% under), mature conifer 85% (10% over, 5% under), and old conifer 75% (25% over).

We combined the 8 original cover types into 4 categories for assessment of habitat composition and 3 categories for assessment of habitat pattern

(Table 1). Given the available cover-type classes on our map, we considered these combinations of cover types to be most relevant to spotted owls based on literature of habitat selection by spotted owls (cf. Forsman et al. 1984, Carey et al. 1990, Glenn et al. 2004) and on our personal experience. The late-seral conifer category contained cover types generally associated with high-quality nesting, roosting, and foraging habitat in western Oregon (Forsman et al. 1984), while the mid-seral conifer and broadleaf categories represented forest that receive occasional use by owls (Carey et al. 1990). The nonforest and open category contained areas not considered to be spotted owl habitat. As is frequently the case with maps constructed from remotely sensed imagery, our digital map contained little information about forest structure. The original 8 cover types were identified based on overstory composition, and consequently we were unable to use factors such as understory composition, snag density, and fire history to further refine the cover-type categories. In particular, some mid-seral conifer stands with abundant understory and high snag densities likely provided better spotted owl habitat than mid-seral conifer stands lacking in structure; however, we were unable to identify these areas on our map. Forest structure is important to spotted owls for providing nest structures and protection from predators. Furthermore, the amount of structure can affect the densities of small mammals that are the basis of spotted owls' diets. We acknowledge that the lack of forest structure data is a limitation of using remotely sensed imagery for assessing spotted owl habitat.

*Determination of Habitat Composition and Pattern.*—We evaluated habitat attributes within nested circles centered on 298 nest sites or primary roost areas (hereafter, activity centers) in 94 owl territories. If nest sites or primary roost areas were unknown, we based activity centers on locations where owls responded at night. We estimat-

Table 2. Description of habitat variables used in demographic parameter modeling of northern spotted owls in the Roseburg Study Area, Oregon, USA, 1985–1999.

Acronym <sup>a</sup>	Description	Units
LSAMT	Amount of late-seral forest	Proportion of circle area
MFAMT	Amount of mid-seral forest (includes broadleaf)	Proportion of circle area
NOAMT	Amount of nonforest	Proportion of circle area
BLAMT	Amount of broadleaf	Proportion of circle area
LSMCAMT	Amount of late-seral and mid-seral conifer	Proportion of circle area
LSR1, LSR2	Amount of late-seral conifer in the first (601–1,500 m) and second (1,501–2,400 m) rings around the 600-m circle	Proportion of ring area
LSMCR1, LSMCR2	Amount of late-seral and mid-seral conifer in the first (601–1,500 m) and second (1,501–2,400 m) rings around the 600-m circle	Proportion of ring area
LSCORE*	Amount of late-seral forest core habitat	Proportion of circle area
LSMFCORE*	Amount of late-seral or mid-seral forest core	Proportion of circle area
LSNP*	Number of late-seral forest patches	
TOTNP*	Total number of habitat patches	
LSLPS*	Largest late-seral conifer patch size	Proportion of circle area
LSMPS*	Mean of late-seral patch sizes	Proportion of circle area
LSNND*	Mean distance between nearest neighboring late-seral patches	Meters
NOEDGE*	Amount of nonforest edge	Meters

<sup>a</sup> When the suffix of the landscape variable acronym ends in AMT, a separate variable is generated for each of the 3 circle sizes, with the radius of the circle (i.e., 600, 1,500, or 2,400 m) replacing AMT in the acronym name. All landscape pattern variables (designated with an asterisk) were measured only within 1,500-m radius circles.

ed Universal Transverse Mercator (UTM) coordinates of activity centers to the nearest meter with a Global Positioning System or by visual reference to terrain and vegetation features on maps and aerial photos.

We used activity centers as the center point for measuring landscape composition within 3 circle sizes (600, 1,500, and 2,400-m radius) for each owl territory. We selected circles to examine habitat at 3 spatial scales that we believed were important to owls: nest core area (600-m radius), home range (1,500-m radius), and a larger area including more distant winter foraging sites (2,400-m radius). We chose to use circles for 3 reasons: (1) we did not have sufficient information on owl use in each territory to use more exact measures of habitat use; (2) owls are known to be central place foragers that use habitat with declining distance from activity centers (Rosenberg and McKelvey 1999); and (3) circles have most commonly been used in studies relating owls to habitat (cf. Lehmkuhl and Raphael 1993, Meyer et al. 1998, Swindle et al. 1999, Franklin et al. 2000), thus making our results more comparable to past work. Size of the circles was based on home-range data collected from radiomarked owls in the Oregon Coast Ranges (Carey et al. 1990, Glenn et al. 2004). We measured the area (ha) of each cover type (broadleaf, nonhabitat, mid-seral conifer, late-seral conifer) around each activity center using ARC/INFO GIS software (Environmental Systems Research Institute 1998). We used program

FRAGSTATS (McGarigal and Marks 1995) to evaluate 6 landscape pattern variables within the 1,500-m (707 ha) circles at each territory (Table 2).

In a few cases, portions of circles centered around activity centers fell outside of the map coverage. To retain as much of this information as possible without potentially biasing our analyses, we eliminated territories with >10% of the largest circle area unclassified. All variables measured in area were converted to proportions of the total circle area, including all composition and some pattern variables.

### Modeling Strategy

Although statistical modeling methods for survival and productivity differed, we used a similar strategy to develop models for each analysis. First, we constructed a base model consisting of demographic and temporal covariates that were found to be important in explaining variability in the demographic response variables. Demographic covariates included age, sex, and presence of barred owls. Temporal covariates included various functional relationships related to time (i.e., survey year) and the climate variables. The latter were examined based on specific hypotheses regarding their relation with the demographic parameter (Table 3). The base model was selected from among these candidates using an information-theoretic approach (Burnham and Anderson 2002).

We next developed a set of biological hypotheses regarding relationships between demographic

Table 3. Hypothesized relationships between climate covariates and demographic parameters (designated as  $\phi$  for survival, R for productivity, or  $\theta$  for both) of northern spotted owls in the Roseburg study area, Oregon, USA, 1985–1999. All climate effects were assumed to be linear and additive.

Model <sup>a</sup>	Hypothesis
$\theta_{TE + PE}$	$\beta_{TE} < 0, \beta_{PE} < 0$
$\theta_{TL + PL}$	$\beta_{TL} < 0, \beta_{PL} < 0$
$\theta_{PE + PL}$	$\beta_{PE} < 0, \beta_{PL} < 0$
$\phi_{TH}$	$\beta_{TH} < 0$
$\phi_{PH}$	$\beta_{PH} > 0$
$\theta_{TW + PW}$	$\beta_{TW} < 0, \beta_{PW} < 0$
$\theta_{TE + PE + TL + PL}$	$\beta_{TE} < 0, \beta_{PE} < 0, \beta_{TL} < 0, \beta_{PL} < 0$
$\theta_{PD'}$	$\beta_{PD'} > 0$
$\theta_{PE + TE + PL + TL + PW + TW}$	$\beta_{TE} < 0, \beta_{PE} < 0, \beta_{TL} < 0, \beta_{PL} < 0, \beta_{TW} < 0, \beta_{PW} < 0$
$\theta_{PE + TE + PW + TW}$	$\beta_{TE} < 0, \beta_{PE} < 0, \beta_{TW} < 0, \beta_{PW} < 0$
$R_{PE}$	$\beta_{PE} < 0$
$R_{PL}$	$\beta_{PL} < 0$

<sup>a</sup> Precipitation covariates (denoted by P) are the proportion of sample days with measurable precipitation within a period. Temperature covariates (T) are the total daily degree hours within a period. The second letter of the climate variable acronym refers to 1 of 5 periods within a year: E = early nesting, L = late nesting, H = heat stress, D = dispersal, and W = winter stress. A prime (') indicates a lag effect where the demographic parameter in 1 year is affected by the climate variable from the previous year.

response variables and habitat variables (Table 4). We first considered the hypotheses developed by Franklin et al. (2000) and included any that we believed were applicable to our study area, and then added new hypotheses. We also expected that relationships between demographic and landscape variables might not be linear; therefore, for most hypotheses, we developed linear, log-linear (pseudo-threshold), and quadratic models. For quadratic models, we used squared differences of the covariate values from the mean (i.e.,  $[x_i - \bar{x}]^2$ , where  $x_i$  is the covariate value for site  $i$ , and  $\bar{x}$  is the mean of the covariate over all sites). This transformation produces a model with a quadratic structure that is constrained to be symmetric about the mean, but has the advantage of using 1 fewer parameter than an unconstrained quadratic model (see Franklin et al. 2000). If we found that models with a curvilinear structure (log-linear or mean-centered quadratic) were better for a specific habitat covariate than the linear model, we ran an additional unconstrained quadratic model for that covariate. Thus, we developed 2–4 models for each habitat hypothesis.

**Model Selection**

In all cases where model selection was required, we used Akaike’s Information Criterion corrected for small samples ( $AIC_c$ ; Burnham and Anderson

2002) to rank models within each step of the modeling process; models with the lowest  $AIC_c$  were considered the most likely models, given the data. For the base model, we selected the model with the lowest  $AIC_c$  (i.e., most likely) unless we had reason to select a closely competing model (i.e., within 1  $AIC_c$  unit of the best model). At this point in the modeling process, we were more concerned with accounting for variability in the data prior to adding landscape covariates and not concerned about making a model-selection error.

For habitat modeling, we first ranked all models from lowest to highest  $AIC_c$ . The model list was then reduced by eliminating redundant models and retaining only 1 structural form among the same set of landscape variables. Redundancies occurred because of high correlation among some covariates ( $r > 0.95$ ). We also kept only the best model among sets of models representing the same concept at the same spatial scale (i.e., 600, 1,500, or 2,400-m radius circles). For instance, a model including a single variable for amount of late-seral conifer in the 1,500-m radius circle (LF1500) was considered to convey the same concept as the 2-variable model with amount of late-seral conifer in the 600-m radius circle plus the amount of late-seral conifer in the 600–1,500-m ring (LF600 + LSR1). We then computed Akaike weights (Burnham and Anderson 2002) for each model in the reduced set. These weights may be considered as the weight of evidence that a given model is the “best” model (i.e., best supported by the data) from the set of models being compared. The relative degree of support for a specific model as compared to another model can be computed as the ratio of the Akaike weights of the 2 models, with the larger weight in the numerator.

**Variance Components Analysis**

To assess the relative contribution of habitat variables to the amount of variability explained by the best models for survival and productivity, we conducted variance components analyses (VCA). The differing analytical methods used for each parameter model required a different VCA approach. When feasible and appropriate, we followed the methods used by Franklin et al. (2000) because we wanted to compare our results to theirs, although in theory any unbiased VCA methods should be comparable.

The general approach we used was to first separate process variance ( $\sigma^2$ ) from sampling variability ( $\text{Var}(\hat{\phi}|\phi)$ ), and then to separate  $\sigma^2$  into model components. Our process variance includ-

Table 4. Hypothesized relationships between landscape covariates and demographic parameters (designated as N for survival, R for productivity, or 2 for both) of northern spotted owls in the Roseburg study area, Oregon, USA, 1985–1999. Acronyms for landscape variables are given in Tables 1 and 2. The predicted relation is given as the predicted value of regression coefficients ( $\beta$ s). For quadratic relations,  $\beta$ s are given for both linear and quadratic variables. If a structure was not deemed biologically plausible, no model was generated.

Hypothesized model	Structure of predicted effects		
	Linear	Pseudo-threshold	Quadratic
1. $\theta_{LSAMT}$	$\beta_{LSAMT} > 0$	$\beta_{In(LSAMT)} > 0$	$\beta_{LSAMT} > 0, \beta_{(LSAMT)^2} < 0$
2. $\theta_{NOAMT}$	$\beta_{NOAMT} < 0$	$\beta_{In(NOAMT)} < 0$	$\beta_{NOAMT} > 0, \beta_{(NOAMT)^2} < 0$
3. $\theta_{LSAMT+LFAMT}$	$\beta_{LSAMT} > 0,$ $\beta_{LFAMT} > 0$	$\beta_{In(LSAMT)} > 0,$ $\beta_{In(LFAMT)} > 0$	$\beta_{LSAMT} > 0, \beta_{(LFAMT)^2} < 0$ $\beta_{LFAMT} > 0, \beta_{(LFAMT)^2} < 0$
4. $\theta_{LSAMT+BLAMT}$	$\beta_{LSAMT} > 0,$ $\beta_{BLAMT} > 0$	$\beta_{In(LSAMT)} > 0,$ $\beta_{In(BLAMT)} > 0$	$\beta_{LSAMT} > 0, \beta_{(LSAMT)^2} < 0$ $\beta_{BLAMT} > 0, \beta_{(BLAMT)^2} < 0$
5. $\theta_{TOTNP}$	$\beta_{TOTNP} < 0$	$\beta_{In(TOTNP)} < 0$	
6. $\theta_{LSNP}$	$\beta_{LSNP} > 0$	$\beta_{In(LSNP)} > 0$	$\beta_{LSNP} > 0, \beta_{(LSNP)^2} < 0$
7. $\theta_{NOEDGE}$	$\beta_{NOEDGE} < 0$	$\beta_{In(NOEDGE)} < 0$	
8. $\theta_{LSNND}$	$\beta_{LSNND} < 0$	$\beta_{In(LSNND)} < 0$	
9. $\theta_{LSCORE}$	$\beta_{LSCORE} > 0$	$\beta_{In(LSCORE)} > 0$	$\beta_{LSCORE} > 0, \beta_{(LSCORE)^2} < 0$
10. $\theta_{LSMFCORE}$	$\beta_{LSMFCORE} > 0$	$\beta_{In(LSMFCORE)} > 0$	$\beta_{LSMFCORE} > 0, \beta_{(LSMFCORE)^2} < 0$
11. $\theta_{NO1500 + NOEDGE}$	$\beta_{NO1500} < 0,$ $\beta_{NOEDGE} < 0$	$\beta_{In(NO1500)} < 0,$ $\beta_{In(NOEDGE)} < 0$	
12. $\theta_{LSMPS}$	$\beta_{LSMPS} > 0$	$\beta_{In(LSMPS)} > 0$	$\beta_{LSMPS} > 0, \beta_{(LSMPS)^2} < 0$
13. $\theta_{LSLPS}$	$\beta_{LSLPS} > 0$	$\beta_{In(LSLPS)} > 0$	$\beta_{LSLPS} > 0, \beta_{(LSLPS)^2} < 0$
14. $\theta_{LSMCAMT}$	$\beta_{LSMCAMT} > 0$	$\beta_{In(LSMCAMT)} > 0$	$\beta_{LSMCAMT} > 0, \beta_{(LSMCAMT)^2} < 0$
15. $\theta_{LS600+LSR1}$	$\beta_{LS600} > 0,$ $\beta_{LSR1} > 0$	$\beta_{In(LS600)} > 0,$ $\beta_{In(LSR1)} > 0$	$\beta_{LS600} > 0, \beta_{(LS600)^2} < 0$ $\beta_{LSR1} > 0, \beta_{(LSR1)^2} < 0$
16. $\theta_{LS600+LSR1+LSR2}$	$\beta_{LS600} > 0,$ $\beta_{LSR1} > 0,$ $\beta_{LSR2} > 0$	$\beta_{In(LS600)} > 0,$ $\beta_{In(LSR1)} > 0,$ $\beta_{In(LSR2)} > 0$	
17. $\theta_{LSMC600+LSMCR1}$	$\beta_{LSMC600} > 0,$ $\beta_{LSMCR1} > 0$	$\beta_{In(LSMC600)} > 0,$ $\beta_{In(LSMCR1)} > 0$	$\beta_{LSMC600} > 0, \beta_{(LSMC600)^2} < 0$ $\beta_{LSMCR1} > 0, \beta_{(LSMCR1)^2} < 0$
18. $\theta_{LSMC600+LSMCR1+LSMCR2}$	$\beta_{LSMC600} > 0,$ $\beta_{LSMCR1} > 0,$ $\beta_{LSMCR2} > 0$	$\beta_{In(LSMC600)} > 0,$ $\beta_{In(LSMCR1)} > 0,$ $\beta_{In(LSMCR2)} > 0$	
19. $R_{LS1500+LSNND}$	$\beta_{LS1500} > 0,$ $\beta_{LSNND} < 0$	$\beta_{In(LS1500)} > 0,$ $\beta_{In(LSNND)} < 0$	
20. $R_{LS1500+LSNND+LS1500*LSNND}$	$\beta_{LS1500} > 0,$ $\beta_{LSNND} < 0,$ $\beta_{LS1500*LSNND} \neq 0$	$\beta_{In(LS1500)} > 0,$ $\beta_{In(LSNND)} < 0,$ $\beta_{In(LS1500*LSNND)} \neq 0$	

ed variability from all sources, whether explicitly accounted for or not, and thus could be partitioned as  $\sigma^2 = \sigma^2_{MODEL} + \sigma^2_{RESIDUAL}$ . The proportion of variability explained by the model (expressed as a percentage) was estimated as  $\hat{\sigma}^2_{MODEL} / \hat{\sigma}^2 \times 100$ . We then further partitioned  $\sigma^2_{MODEL}$  into the specific model components and estimated their relative contributions (again as a percentage) as  $\hat{\sigma}^2_{\theta} / \hat{\sigma}^2_{MODEL} \times 100$ , where  $\theta$  refers to a specific component. In all cases, we assumed that no covariance was associated with model components, and hence variance components were considered additive.

**Survival Modeling**

We used Cormack-Jolly-Seber open population methods (cf. Pollock et al. 1990, Lebreton et al. 1992) and program MARK (White and Burnham 1999) to develop survival models from our a pri-

ori hypotheses. Our first step was to find a parsimonious model for capture probabilities. We developed candidate models for capture probabilities based on age class (subadult vs. adult), sex, and time. We considered 3 general time structures—time-specific, time trend, and time trend with threshold—as well as an even-odd year effect that reflected trends in productivity noted during previous analyses of spotted owl data for several study areas, including ours (Franklin et al. 1999). Interactions between some effects were considered. After we identified suitable models for capture probabilities, we developed our base model as described earlier. For the habitat modeling, we computed territory-specific habitat covariates by taking weighted means of the year-specific data for each territory, in which the weights were the number of years that each site center appeared in the data file.

*Variance Components Analysis*—For survival rates ( $\hat{\phi}$ ), we used a random-effects model approach (Franklin et al. 2000, Burnham and White 2002) to estimate variance components. First, temporal variability ( $\sigma^2_{TEMPORAL}$ ) was estimated from an intercept-only model with time-specific survival estimates using program MARK (the structure on capture probabilities was from the best capture probability model). The amount of temporal variability attributable to climate ( $\sigma^2_{CLIMATE}$ ) was estimated by including the climate variables from the best model in the random-effects model, then subtracting the residual variance from this model from the residual variance computed in the intercept-only model.

We estimated spatial variability in survival rates ( $\sigma^2_{SPATIAL}$ ) from the intercept-only, random-effects model and territory-specific survival estimates from model  $\{\phi_H, p_B\}$ , where the subscript  $H$  denotes territory and  $B$  the best model from capture probability modeling. In some cases,  $SE(\hat{\phi}_H) = 0$ , which were undoubtedly an underestimate of the true sampling error of these estimates. We handled these cases as in Franklin et al. (2000:Appendix B) by using a regression model approach in which sampling error was estimated relative to estimated territory-specific survival. The amount of spatial variability attributed to habitat was estimated as the empirical variance of the predicted estimates of survival ( $\hat{\phi}_H$ ) from the model containing only the habitat covariate (Franklin et al. 2000):

$$\hat{\sigma}^2_{HABITAT} = \frac{\sum_{i=1}^n (\hat{\phi}_i - \bar{\hat{\phi}})^2}{n-1},$$

where  $n$  = number of territories (94).

Total process variance ( $\hat{\sigma}^2$ ) for survival was estimated as  $\hat{\sigma}^2_{SPATIAL} + \hat{\sigma}^2_{TEMPORAL}$  (assuming no covariance between the 2), and  $\hat{\sigma}^2_{MODEL}$  was estimated as  $\hat{\sigma}^2_{CLIMATE} + \hat{\sigma}^2_{HABITAT}$ , since no other effects were in the model.

### Productivity Modeling

For productivity modeling, we used a linear mixed-model approach (SAS<sup>®</sup> Proc Mixed; SAS Institute 1997) similar to that used by Franklin et al. (1999) in which territories and years were treated as random effects to broaden the scope of inference. This method allowed us to specify a covariance structure that reflected the lack of independence among the random effects. It also allowed a log-linear error structure that account-

ed for the fact that both the mean and variance of the response variable tended to increase with increasing values of the explanatory effects (based on plots of the data). The latter structure had been used previously by Franklin et al. (1999) for modeling productivity of spotted owls. Our application was similar with the exception that we investigated more fixed effects in our analyses. We used restricted maximum-likelihood (REML) methods and a single well-parameterized means model to determine the fixed effects to be retained in the variance model. Although SAS<sup>®</sup> Proc Mixed allows for separate specification of mean and variance effects, we believed that—in general—effects not included as mean effects should not be considered as variance effects. Also, habitat covariates were not included as variance effects because we found no support for this relation based on the plots. The variance model used for subsequent means modeling was chosen based on lowest AIC<sub>c</sub>.

The main covariates we examined to construct a base model were female age, male age, pair age, presence of barred owls, the cyclic nature of the reproductive success (even-odd year effect), and interactions between some of these effects. For comparisons among models based on AIC<sub>c</sub>, we required a standardized data set with no missing values for covariates. Therefore, we deleted any records with unknown covariate values. We also included data only from sites with  $\geq 3$  years of data because we felt that was a minimum sample size needed to estimate random year effects. We then added climate effects to the best demographic model. The climate hypotheses and predicted relations developed with respect to productivity were mostly the same as for survival, with some additional models (Table 3).

We believed that most of the same hypotheses regarding the influence of habitat covariates on survival also applied to productivity. Therefore, with a few exceptions, we examined the same set of models in the productivity analysis (Table 4).

*Variance Components Analysis*.—We used estimates of residual variance for each model, produced by SAS<sup>®</sup> Proc Mixed (SAS Institute 1997), to estimate variance components by sequentially including model variables and computing the reduction in residual variance. We used REML methods for variance components analysis because maximum-likelihood variance estimates from the mixed model are biased (Rao 1997). The residual variance from the intercept-only model (including year and territory as random

effects) was considered the total process variance. Model variance ( $\sigma^2_{MODEL}$ ) was estimated as the difference in residual variance of the intercept-only model and the final best model with all effects specified.

### Habitat Fitness Potential

Franklin et al. (2000:558) defined habitat fitness potential ( $\lambda_H$ ) as "...the fitness conferred on an individual occupying a territory of certain habitat characteristics." We followed their methods and estimated  $\lambda_H$  as the dominant, real eigenvalue of the stage-based Leslie matrix, computed for each territory:

$$\begin{bmatrix} \hat{\phi}_{1,2}\hat{m}_{1,3} & \hat{\phi}_{1,2}\hat{m}_3 & \hat{\phi}_3\hat{m}_3 \\ \hat{\phi}_{1,2} & 0 & 0 \\ 0 & \hat{\phi}_{1,2} & \hat{\phi}_3 \end{bmatrix}$$

where  $\hat{\phi}$  was apparent survival,  $\hat{m}$  fecundity, and the subscripts refer to age (1,2 represents 1- and 2-yr-old owls [subadults], and 3 refers to owls  $\geq 3$  yr old [adults]). Age-specific estimates of  $\hat{\phi}$  and  $\hat{m}$  were computed from the best models for survival and productivity, respectively, with fecundity computed as  $\hat{m} = \hat{R}/2$  (i.e., the number of female fledged per female, assuming a 1:1 sex ratio at fledging). Thus,  $\lambda_H$  is expressed in terms of female fitness only.

We estimated the territory-specific components of  $\lambda_H$  using the best-approximating models for survival and productivity as described above. Temporal effects in these models were averaged over the years of data collection. We calculated  $\lambda_H$  for each of the 94 Roseburg territories and estimated their sampling variances using the Delta method (Bajpai et al. 1978).

## RESULTS

### Survival Modeling

We used only data from 1988–1999 for survival modeling because we had few captures of owls <2 years old in prior years, especially of females. The base model selected for survival models included the effects of early- and late-nesting season precipitation on survival, and age, sex, and time-trend effects on capture probabilities (model  $\{\phi_{Pe} + P_e, \phi_{a+s+T}\}$ ). The best capture probability model was similar to models selected previously for spotted owls (Franklin et al. 1999). Capture probabilities were greater for older owls (adults vs. subadults) and for males, and they increased linearly

Table 5. Ten best models relating survival and habitat variables for northern spotted owls in Roseburg study area, Oregon, USA, 1988–1999, ranked using Akaike's Information Criterion adjusted for sample size ( $AIC_c$ ) and Akaike weight ( $w_i$ ). Model names given are the variables added to the base model consisting of early- and late-nesting season precipitation effects on survival probabilities and additive effects of age, sex, and time trend on capture probabilities. Habitat variable acronyms are from Table 2. Suffixes to landscape variables indicate the form of the relationship: ln = linear, pt = pseudo-threshold, qm = mean-centered quadratic, and q2 = unconstrained quadratic. Sign refers to the regression coefficients corresponding to the habitat variables, given as positive (+) or negative (-) if 95% confidence intervals do not overlap zero, and zero otherwise.

Model name	Sign	$AIC_c$	$\Delta AIC_c$	$w_i$
LSMC1500qm	-	1,358.02	0.00	0.64
LS2400qm + MF2400qm	0,-	1,361.03	3.01	0.14
LSMC600pt	0	1,363.37	5.35	0.04
LSMPSln	0	1,363.61	5.60	0.04
LSNNDln	0	1,363.90	5.88	0.03
LSNPln	0	1,364.42	6.40	0.03
base model only		1,364.46	6.44	0.02
LS2400ln	0	1,365.09	7.08	0.02
TOTNPln	0	1,365.34	7.32	0.02
base model + age		1,365.37	7.35	0.02

through time. Survival had a negative relationship with early-nesting season precipitation but a positive relationship with late-nesting season precipitation. Model selection resulted in 2 potentially competing models ( $\Delta AIC_c < 2.0$ ), 1 with an age effect on survival added  $\{\phi_{a+Pe+Pl}\}$  and 1 that included temperature effects on survival  $\{\phi_{Pe+Te+Pl+Tl}\}$ . We selected the simpler model as a basis for habitat analyses, however, because 95% confidence intervals on the regression coefficients for all of the additional variables (age,  $T_e$ , and  $T_l$ ) overlapped zero.

We ran 89 models in the habitat analyses (Table 5 shows results after redundant models were eliminated). Only the top third of these models had regression coefficients for habitat variables with 95% confidence intervals not overlapping zero.

In general, increases in late-seral forest had a positive effect on survival, whereas increases in early seral and nonforest had a negative effect. However, the best model indicated a nonlinear relationship between late- and mid-seral forest and survival, with a slight decrease in survival when proportions of these cover types in the 1,500-m radius circle were high (Fig. 2).

*Variance Components Analysis.*—Most of the variability in survival rates was spatial (92.3%) rather than temporal (17.7%; Table 6). However, only 15.9% of the total variance was accounted for by the best survival model. Of this, 14.8% was due to the climate variables and 85.1% due to the habitat variable. Climate variables accounted for

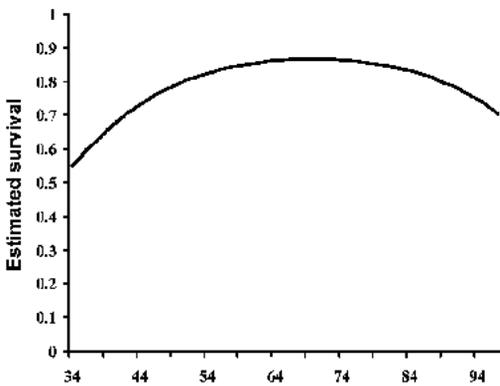


Fig. 2. Estimated survival for northern spotted owls on the Roseburg study area, Oregon, USA, 1988–1999, from the landscape pattern model with percentage of old and mid-seral conifer within a 1,500-m circle centered on owl activity centers.

30.8% of all temporal variability, but the habitat variable in the best model accounted for only 14.6% of spatial variance.

**Productivity Modeling**

The base model selected for productivity was quite complex. The fixed effects in this model included female age (subadult vs. adult), male age, the even–odd year effect, interactions between each age and the even–odd year effect, early- and late-nesting season precipitation, and presence of barred owls. The variance model contained all of these effects except barred owl presence. Model selection identified 2 other closely competing models ( $\Delta AIC_c < 1.0$ ): 1 without the barred owl effect, and the other without the female age  $\times$  even–odd year effect in the variance model. Since all effects appeared to be significant (95% CI on parameters did not overlap 0), we chose the more complex model as our base model. Age, in general, had a positive effect on productivity, and productivity of all owls was greater in even than in odd years. However, adult owls showed greater declines in productivity be-

tween even and odd years than did subadult owls. As with survival, we found a negative relationship between early-nesting season precipitation and reproduction, but a positive relationship with late-nesting season precipitation. The presence of barred owls had a negative effect on productivity.

We ran 74 habitat models and report results from the top 10 (Table 7). For half of the models listed, a significant relationship existed between habitat and productivity. However, the nature of these relations was unexpected, with productivity apparently declining with increases in mid- and late-seral forest and increasing with increases in early seral and nonforest. Most of these models were linear; some included a pseudo-threshold structure that was linear for a large portion of the range of the covariates. The model with the greatest Akaike weight (0.91) included a positive linear relationship between productivity and the amount of edge between the early seral and nonforest class and the other classes combined (Table 7, Fig. 3). Post hoc analyses that included interactions among climate and habitat variables did not produce better models than the additive models.

*Variance Components Analysis.*—Unlike Franklin et al. (2000), we simultaneously modeled both spatial and temporal factors in our productivity analyses, as well as demographic variables such as age and barred owl presence. Interactions between age and the even–odd year effect prevented us

Table 6. Estimated variance components of the best survival model developed for northern spotted owls in the Roseburg study area, Oregon, USA, 1988–1999.

Variance component	Estimate
$\sigma^2_{temporal}$	0.0013
$\sigma^2_{climate}$	0.0004
$\sigma^2_{spatial}$	0.0157
$\sigma^2_{habitat}$	0.0023
$\sigma^2_{model}$	0.0027
$\sigma^2_{total}$	0.0170

Table 7. Ten best models relating productivity and habitat variables for northern spotted owls in the Roseburg study area, Oregon, USA, 1985–1999, ranked using Akaike’s Information Criterion adjusted for sample size ( $AIC_c$ ) and Akaike weight ( $w_i$ ). Model names given are the variables added to the base model, in which mean effects are barred owl presence, early- and late-nesting season precipitation, female age, male age, even–odd year indicator, and interactions between each age variable and the even–odd indicator. Variance effects are the same, except that the barred owl indicator is not included. Suffixes to landscape variables indicate the form of the relationship: ln = linear, pt = pseudo-threshold (log-linear), qm = mean-centered quadratic, and q2 = unconstrained quadratic. Sign refers to the regression coefficient corresponding to the landscape variable, given as positive (+) or negative (–) if 95% confidence intervals for the coefficient do not overlap zero, and zero otherwise.

Model name	Sign	$AIC_c$	$\Delta AIC_c$	$w_i$
NOEDGEln	+	1,395.53	0.00	0.91
LS2400ln + MS2400ln	–,–	1,402.17	6.64	0.03
NO1500pt	+	1,403.53	8.00	0.02
LSMCCOREpt	–	1,404.90	9.37	0.01
LS1500ln +MC1500ln	–,–	1,405.32	9.79	0.01
TOTNPpt	+	1,405.66	10.13	0.01
LS2400ln	–	1,405.82	10.29	0.01
LS600ln	0	1,406.71	11.18	0.00
LS1500pt	0	1,406.91	11.38	0.00
LSCOREln	0	1,407.00	11.47	0.00

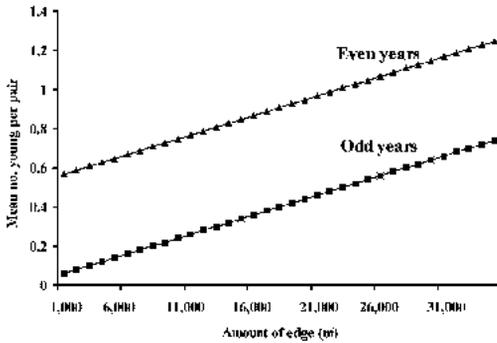


Fig. 3. Estimated productivity for northern spotted owls on the Roseburg study area, Oregon, USA, 1985–1999, from the habitat pattern model with amount of edge between mid- and late-seral conifer and other landscape vegetation types within a 1,500-m circle centered on owl activity centers.

from cleanly separating these components. Further, the covariance structure we used for the mixed model was complex, including many of the same factors specified as fixed effects. Consequently, specific estimation of spatial and temporal variance as intermediate components would be difficult. However, these components were not necessary to estimate total variability, model variability, and the relative contribution of model effects (estimates are given in Table 8). The best productivity model accounted for 83.6% of the total variability, 38.4% of which was explained by climate variables and 59.1% by other temporal and demographic factors. Only 2.6% of model variability was attributed to the habitat covariate.

### Habitat Fitness Potential

We encountered complications in estimating habitat fitness potential because our best models for both survival and productivity included temporal covariates, and the productivity model included male age as a covariate. Temporal covariates (climate variables and the even–odd year effect) were accounted for by using average precipitation values for

Table 8. Estimated variance components for productivity models developed for northern spotted owls in the Roseburg study area, Oregon, USA, 1985–1999.

Variance component	Estimate
$\sigma^2_{\text{age} \times \text{even-odd year}}$	0.2708
$\sigma^2_{\text{climate}}$	0.1814
$\sigma^2_{\text{barred owl}}$	0.0083
$\sigma^2_{\text{habitat}}$	0.0123
$\sigma^2_{\text{model}}$	0.4728
$\sigma^2_{\text{total}}$	0.5655

1988–1999 and using 0.5 for the even–odd year effect, thus computing an average for this effect as well. Male age was accounted for by estimating  $\hat{R}_{1,2}$  and  $\hat{R}_3$  using the proportion of adult males associated with subadult and adult females, respectively.

The estimates of  $\lambda_H$  for all 94 Roseburg territories (Fig. 4) ranged from 0.74 to 1.15 with a mean of 1.05 and variance 0.005. All but 1 of the 95% confidence intervals overlapped 1.00, suggesting that habitat within these territories was potentially sufficient for owl reproduction and survival.

### DISCUSSION

Our modeling results for both survival and productivity were somewhat unexpected. While we anticipated that amount of mid- and late-seral forest would be important to northern spotted owls, we found that a mixture of these forests with

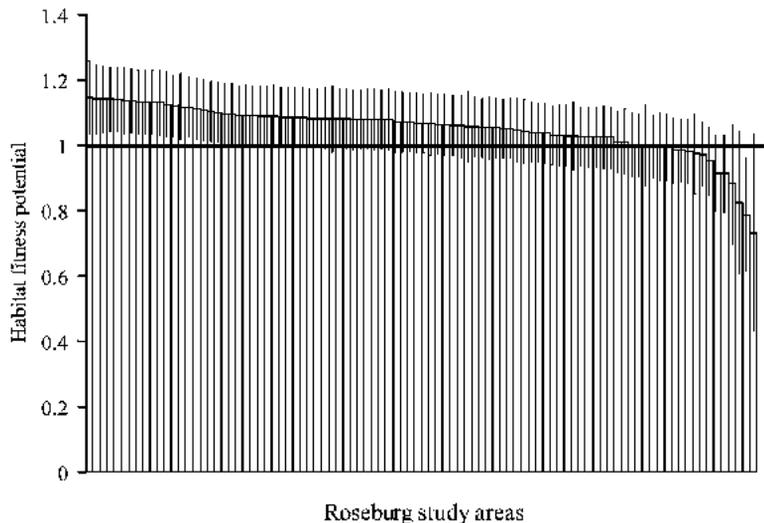


Fig. 4. Estimated habitat fitness potential (with 95% CI) for 94 northern spotted owl territories in the Roseburg study area, Oregon, USA. Estimates are derived from territory- and year-specific (1988–1999) Leslie matrices with age-specific survival and fecundity estimated from the best models developed during model analyses. Landscape values for each territory and temporal values for each year were used to estimate survival and fecundity, and the overall estimated territory-specific habitat fitness potential was computed as the geometric mean of the annual values.

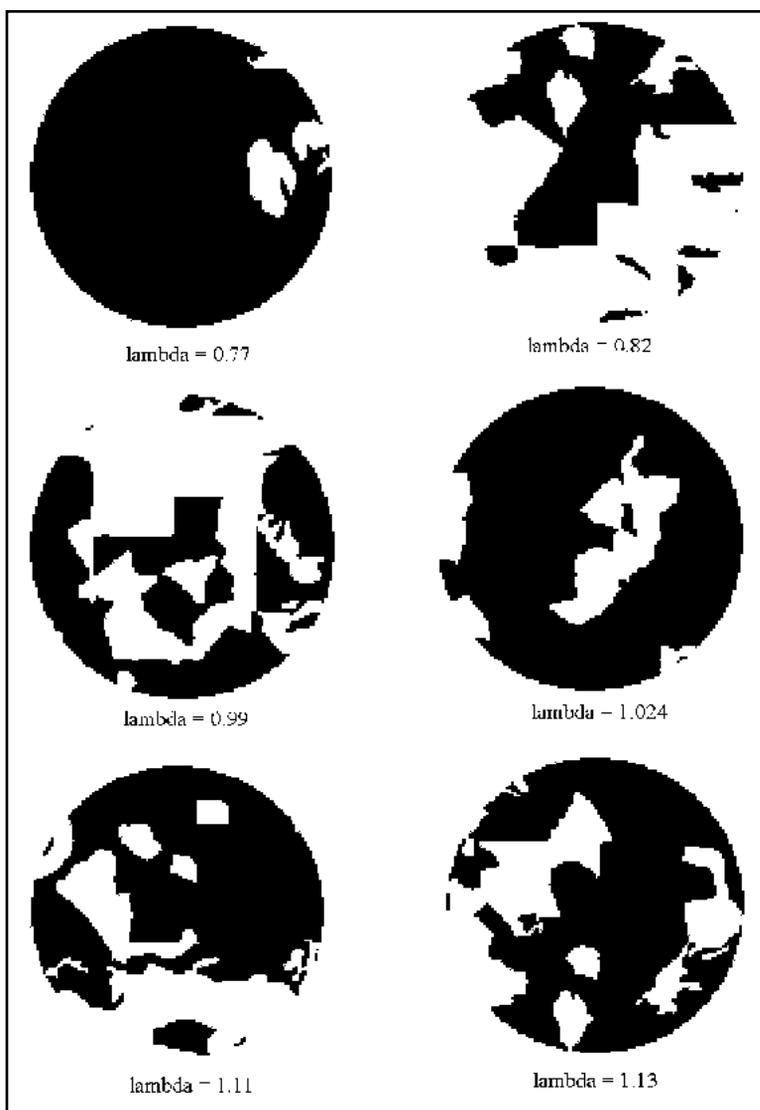


Fig. 5. Comparison of habitat composition as measured from aerial photographs (dark = broadleaf, mid-seral, and late-seral forest; light = nonforest and open) around northern spotted owl activity centers (1,500-m radius circle) across the range of  $\lambda$  values (averaged over 1988–1999) for spotted owls on the Roseburg study area, Oregon, USA.

early seral and nonforest improved owl productivity and survival. The same habitat factors did not appear to be most important for both survival and productivity. Survival was highest at the mean amount of mid- and late-seral forest (approx 70%), whereas productivity increased linearly as the amount of edge between these forest types and other habitats increased (within 1,500-m radius circles). To achieve maximum fitness potential, spotted owls should select territories where both factors are optimal, yet simply increasing amount

of mid- and late-seral forests could not achieve that goal. Our modeling exercise indicates that the pattern of forest type within territories is important. Since habitat fitness potential is a combination of survival and productivity, territories with the greatest  $\lambda_H$  should have the type of forest distribution that best combines the competing factors important to these fitness parameters. Figure 5 shows examples of territories from our study area where model estimated  $\lambda_H$  are  $>1.0$ ,  $\approx 1.0$ , and  $<1.0$ . These examples illustrate that large expanses of mid- and late-seral forests may not be optimal for spotted owls, but neither are territories with small amounts of these forest types.

Our results are similar to those found by Franklin et al. (2000) for northern spotted owls in northern California, although their habitat variables were defined somewhat differently than ours. The habitat patterns seen in their Fig. 10 of selected  $\lambda_H$  estimates (Franklin et al. 2000:573) are remarkably similar to those in our Fig. 5.

Although we found a positive relationship between the amount of edge and productivity of spotted owls, we agree with Franklin et al. (2000) that the importance of edge for this species is not well understood. Northern spotted owls are forest owls and, in our study area, they fed primarily on forest mammals such as flying squirrels (*Glaucomys sabrinus*) and red tree voles (*Arborimus longicaudus*; Forsman et al. 1984; E. D. Forsman, unpublished data). Radiotelemetry studies provide considerable evidence that owls forage pri-

marily in forests, generally selecting for the oldest available forest (Forsman et al. 1984, Carey et al. 1992, Irwin et al. 2000). With the exception of areas where their diet is dominated by woodrats (*Neotoma* spp.; Zabel et al. 1995, Ward et al. 1998), little evidence suggests that they forage disproportionately along edges (Glenn et al. 2004). The possibility exists that, in some regions, forests adjacent to edge may have higher biomass of prey that are important to spotted owls, such as woodrats or brush rabbit (*Sylvilagus bachmani*), or may provide alternative sources of prey during periods when populations of the primary prey (flying squirrels) are low. For example, Ward et al. (1998) found that dusky-footed woodrats (*N. fuscipes*) were most abundant in brushy clearcuts in northwestern California. Whether this translates into higher biomass of suitable and available prey in forests adjacent to openings is less clear, especially in regions where woodrats are uncommon, and flying squirrels are the primary source of food for spotted owls.

Prior to settlement by Europeans, forest areas in the Pacific Northwest were regularly impacted by wildfires, windstorms, and disease, thus creating a dynamic patchwork of different forest age classes and openings. Ripple et al. (2000) estimated that these landscapes included about 10% open and early-seral forest and 63% late-seral conifers. Considering that spotted owls evolved under these conditions, we can reasonably assume that they are adapted to living in landscapes that include a patchwork of old forests and openings. Franklin and Gutiérrez (2002), in a review of numerous spotted owl studies at several scales, concluded that no clear consensus exists on the effects of habitat fragmentation or habitat heterogeneity on spotted owls. Bart (1995) suggested that spotted owls need at least 35–50% of the landscape in suitable habitat to maintain nondeclining populations.

We were disappointed with the amount of variability in survival explained by our models. Factors included in our models seemed less important than factors we did not consider, as only 16% of the variability was explained by our best model. In contrast, the survival model developed by Franklin et al. (2000) explained >70% of variability in survival from their study site in northern California. Franklin et al.'s (2000) estimate of annual survival was nearly 2.5 times less variable than ours (variance = 0.0070 vs. 0.0170), which could explain why their model explained a much higher amount of the total variation in survival.

Most of this difference was in spatial variability (ours was 0.0157 and Franklin et al.'s [2000] was 0.0057), as temporal variability was identical between the 2 study areas (0.0013). The large amount of spatial variability in survival indicates that differences among territories, or owls on territories, have a strong influence on survival, but we did not adequately account for these factors in our model. Some of these factors may have been forest characteristics that we were unable to quantify with our cover-type map. Using remotely sensed imagery, we were able to quantify vegetation characteristics over a large landscape; however, a major limitation of this type of map is the lack of information about forest structure. Because our map did not include forest structure data, we could not include covariates for structural components likely to be important to spotted owls (e.g., snag density, shrub cover) in our models. In addition, we did not have year-by-year cover-type data that documented changes in forest composition during our study. Finally, our use of circles to measure habitat use probably was inaccurate for some owl territories, further reducing our ability to account for more of the variability in survival due to habitat.

For productivity, we accounted for 85% of the variability, yet only 2.3% of this was attributable to habitat. Parental age and temporal factors accounted for most of the variability in productivity, which is consistent with current knowledge of northern spotted owls. Although we were unable to cleanly separate demographic and temporal variability in our models, temporal variability appeared more prominent to productivity than spatial variability, indicating that differences among territories may be less influential than annual effects.

Our ability to make comparisons with the results of Franklin et al. (2000) are somewhat limited by different methods. However, comparisons of model factors based on percentage of model variance are still appropriate. Much more of the model variability in our study (59 vs. <2%) was explained by factors other than climate or habitat, perhaps because we included some factors that they did not. Climate variables accounted for less variability in productivity in our study (38% vs. 55%). Most striking, however, was the relatively large amount (43%) of variability explained by habitat in Franklin et al.'s (2000) model, as compared to the <3% we found in our best model. To discern whether these differences reflect different relative importance of habitat between the 2 study areas or are due to different

methodologies and habitat classifications would require further study.

Although our analyses were not designed to specifically address relationships among climate factors and fitness parameters, their importance in our results indicates that including them in our analyses was appropriate. Our results partially agree with those of Franklin et al. (2000), who found survival and productivity to be negatively associated with spring-nesting precipitation. Our results differ in that we found late-nesting season to be positively associated with both survival and productivity. Since the timeframe covered in both studies was similar, this indicates that climate effects may vary spatially and thus must be modeled independently for each study area.

### MANAGEMENT IMPLICATIONS

Our study was intended to address the question posed by the Effectiveness Monitoring Plan for northern spotted owls: "Can the relation between owl occurrence and demographic performance be reliably predicted given a set of habitat characteristics at the landscape scale?" (Lint et al. 1999:3). Although no 1 study could definitively address that question, the answer with respect to demographic performance, based on our study, may be "no." Yet, we believe that our results are an important step in determining relationships between northern spotted owl demographic performance and habitat, particularly because they indicate that an intermingled pattern of forest types may be more suited for spotted owls. However, we do not recommend that forest managers use our modeling results as a prescription for managing habitat either within the Oregon Coast Range or elsewhere until other similar studies have been conducted. Likewise, the small amount of variability in fitness parameters attributable to habitat variables in our models should not be used to argue that habitat has little influence on owl demography. The habitat covariates we examined simply may not adequately capture the aspects that are important to spotted owls. Our results do indicate that we have a lot to learn about how habitat affects owl demography, and we continue to believe that examination of habitat influences on fitness parameters are the best way to achieve this knowledge.

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### LITERATURE CITED

- ALLEN, J. C. 1976. A modified sine wave method for calculating degree days. *Environmental Entomology* 5:388–396.
- BAJPAI, A. C., I. M. CALUS, AND J. A. FAIRLEY. 1978. *Statistical methods for engineers and scientists*. John Wiley & Sons, New York, New York, USA.
- BART, J. 1995. Amount of suitable habitat and viability of northern spotted owls. *Conservation Biology* 9:943–946.
- , AND E. D. FORSMAN. 1992. Dependence of northern spotted owls *Strix occidentalis caurina* on old-growth forests in the western United States. *Biological Conservation* 62:95–100.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- , AND G. C. WHITE. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264.
- CAREY, A. B., S. P. HORTON, AND B. L. BISSELL. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- , J. A. REID, AND S. P. HORTON. 1990. Spotted owl home range and habitat use in southern Oregon coast ranges. *Journal of Wildlife Management* 54:1–17.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 1998. ARC/INFO. Version 7.2.1. Environmental Systems Research Institute, Redlands, California, USA.
- FORSMAN, E. D. 1981. Molt of the spotted owl. *Auk* 98:735–742.
- , A. B. FRANKLIN, D. R. ANDERSON, K. P. BURNHAM, AND F. F. WAGNER. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12–20.
- , E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* 87.
- FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIERREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- , K. P. BURNHAM, G. C. WHITE, R. G. ANTHONY, E. D. FORSMAN, C. SCHWARZ, J. D. NICHOLS, AND J. HINES. 1999. Rangewide status and trends in northern spotted owl populations. Final report. Colorado Cooperative Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA, and Oregon Cooperative Fisheries and Wildlife Research Unit, Oregon State University, Corvallis, Oregon, USA.

- , AND R. J. GUTIÉRREZ. 2002. Spotted owls, forest fragmentation, and forest heterogeneity. *Studies in Avian Biology* 25:203–220.
- GLENN, E. M., M. C. HANSEN, AND R. G. ANTHONY. 2004. Spotted owl home range and habitat use in young forests of western Oregon. *Journal of Wildlife Management* 68:33–50.
- GUTIÉRREZ, R. J., E. D. FORSMAN, A. B. FRANKLIN, AND E. C. MESLOW. 1996. History of demographic studies in the management of the northern spotted owl. *Studies in Avian Biology* 17:6–11.
- IRWIN, L. L., D. F. ROCK, AND G. P. MILLER. 2000. Stand structures used by northern spotted owls in managed forests. *Journal of Raptor Research* 34:175–186.
- JOLLY, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration—stochastic model. *Biometrika* 52:225–247.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LEHMKUHL, J. F., AND M. G. RAPHAEL. 1993. Habitat pattern around northern spotted owl locations on the Olympic Peninsula, Washington. *Journal of Wildlife Management* 57:302–315.
- LINT, J., B. NOON, R. ANTHONY, E. FORSMAN, M. RAPHAEL, M. COLLOPY, AND E. STARKEY. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. General Technical Report PNW-GTR-440. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- MCCOMB, W. C., M. T. MCGRATH, T. A. SPIES, AND D. VESELY. 2002. Models for mapping potential habitat at landscape scales: an example using northern spotted owls. *Forest Science* 48:203–216.
- MCGARIGAL, K., AND B. J. MARKS. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- MEYER, J. S., L. L. IRWIN, AND M. S. BOYCE. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. *Wildlife Monographs* 139.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. F. HINES. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107.
- RAO, P. S. R. S. 1997. Variance components estimation: mixed models, methodologies and applications. *Monographs on statistics and applied probability* 78. Chapman & Hall, New York, New York, USA.
- RIPPLE, W. J., K. T. HERSHEY, AND R. G. ANTHONY. 2000. Historical forest patterns of Oregon's central Coast Range. *Biological Conservation* 93:127–133.
- , P. D. LATTIN, K. T. HERSHEY, F. F. WAGNER, AND E. C. MESLOW. 1997. Landscape composition and pattern around northern spotted owl nest sites in southwestern Oregon. *Journal of Wildlife Management* 61:151–158.
- ROSENBERG, D. K., AND K. S. MCKELVEY. 1999. Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management* 63:1028–1038.
- SAS INSTITUTE. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.
- SEAMANS, M. E., R. J. GUTIERREZ, C. A. MOEN, AND M. Z. PEERY. 2001. Spotted owl demography in the central Sierra Nevada. *Journal of Wildlife Management* 65:425–431.
- SWINDLE, K. A., W. J. RIPPLE, E. C. MESLOW, AND D. SCHAFER. 1999. Old-forest distribution around spotted owl nests in the central Cascade Mountains, Oregon. *Journal of Wildlife Management* 63:1212–1221.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. U.S. Government Printing Office, Washington, D.C., USA.
- THOME, D. M., C. J. ZABEL, AND L. V. DILLER. 1999. Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. *Journal of Wildlife Management* 63:44–59.
- U.S. DEPARTMENT OF AGRICULTURE AND U.S. DEPARTMENT OF THE INTERIOR. 1994. 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. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. U.S. Department of Agriculture and U.S. Department of the Interior, Portland, Oregon, USA.
- WARD, J. P., JR., R. J. GUTIERREZ, AND B. R. NOON. 1998. Habitat selection by northern spotted owls: the consequences of prey selection and distribution. *Condor* 100:79–92.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement 1:20–139.
- ZABEL, C. J., K. MCKELVEY, AND J. P. WARD, JR. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* 73:433–439.

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