

## DEMOGRAPHY OF NORTHERN SPOTTED OWLS IN THE SOUTHERN CASCADES AND SISKIYOU MOUNTAINS, OREGON

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### INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) occurs widely within the forests of the interior mountains of southwestern Oregon, which are characterized by the regular occurrence of tanoak (*Lithocarpus densiflorus*), white fir (*Abies concolor*), or Shasta red fir (*A. magnifica shastensis*) within forest stand composition. These forests are northern extensions of forest formations of the Sierra Nevada and coastal northern California (Franklin and Dyrness 1973), and are transitional to forests within the Western Hemlock (*Tsuga heterophylla*) and Pacific Silver Fir (*Abies amabilis*) zones of western Oregon and Washington. Habitat for Northern Spotted Owls within these forests occurs as complex mosaics of forest types and age because of complex geologic, soil, and climatic patterns. Additionally, because of past natural fire events and the prevalence of selective logging methods, forest stand development and structure is often uneven-aged (USDA and USDI 1994).

In 1985 we initiated a cooperative effort among Oregon State University, the Bureau of Land Management (BLM), and the U.S. Forest Service to gather demographic data on the Northern Spotted Owl within the southern Cascades and Siskiyou Mountains. Because forest types, natural fire regimes, and timber harvest systems differ from much of the remainder of the Northern Spotted Owl's range, our objective was to obtain estimates of vital rates and population trend that were representative of the region.

For this study, we used capture-recapture and empirical methods to estimate age-specific survival and fecundity rates and rate of population change for the period 1985-1993 for the watersheds of the interior Rogue River basin, upper South Umpqua River, and a portion of the upper Klamath River basin. Because controversy exists in interpreting model-based estimates of population trend when these results differ from trend based on empirical counts of owls (Thomas et al. 1993a, Raphael et al. *this volume*), we report annual count results and trend from bounded density study areas for 1990-1993. We also compare vital rates measured within the density study areas to the study area as a whole. Because un-

detected emigration from the study area may negatively bias survival rates, we developed estimates for adult and juvenile emigration rates. Our interest here was to assess our confidence in the direction of the estimated population trend. Additionally, we explored the relationship between precipitation patterns and estimates of annual fecundity.

### STUDY AREA

Data collection was initiated on the Southern Cascades and Siskiyou Mountains Study Area in 1985. Initial efforts centered on the Medford District of the BLM but were subsequently expanded during 1987-88 to include the Klamath Resource Area of the Lakeview District, the Rogue River National Forest, the Galice and Illinois Valley Ranger Districts of the Siskiyou National Forest, the Tiller Ranger District of the Umpqua National Forest, and the Klamath Ranger District of the Winema National Forest (Fig. 1). Lands administered by the BLM are typically intermingled with private forest lands, often producing a checkerboard pattern of alternating square mile sections. Timber harvest on private lands has often occurred at an earlier date and more completely than on adjacent Federal lands (USDI 1995). The study area encompasses approximately 15,216 km<sup>2</sup> with about 25% of the area occupied by large non-forested areas, open subalpine forest, and foothill woodlands that do not normally provide habitat for Northern Spotted Owls.

Climate is moderate and maritime influenced. Summers are characteristically hot and dry, and winters are cool and moist (Baldwin 1973), with persistent winter snow cover at elevations >1500 m. Precipitation occurs primarily during October-May with local amounts varying widely in response to topographical effects and rain shadows. Average annual precipitation ranges from 89-175 cm over most of the study area, but reaches 250 cm near the western boundary (Anon. 1982). Data collection for the study coincided with persistent drought conditions. As measured at Medford Oregon, annual precipitation during the study averaged approximately 70% of amounts recorded for the preceding 30 years

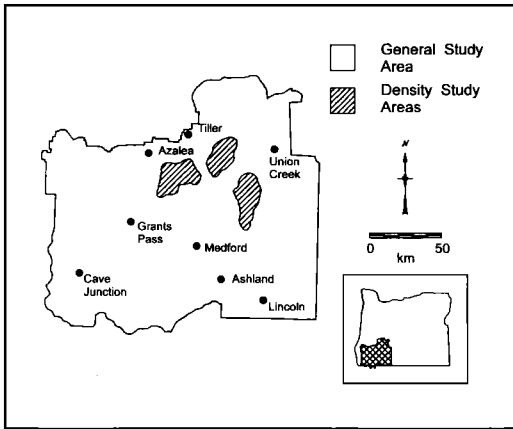


FIGURE 1. The Southern Cascades and Siskiyou Mountains Study Area in southwestern Oregon, 1985–1993. Hatched areas indicate locations of three sub-areas (Density Study Areas) within which we attempted to estimate the number of resident Northern Spotted Owls each year.

(National Weather Service, Medford Oregon, personal communication).

The study area includes portions of the Mixed-Evergreen, Mixed-Conifer, and True Fir vegetation zones (Franklin and Dyrness 1973). Important plant series (Atzet and Wheeler 1984, Atzet and McCrimmen 1990) for Northern Spotted Owl habitat include the Douglas-fir (*Pseudotsuga menziesii*), White Fir, Tanoak, Shasta Red Fir, and Western Hemlock series.

Prior to fire suppression efforts beginning during the 1920s, forests at moderate to low elevations developed under conditions of relatively frequent fires of low intensity (Agee 1993). This fire history tended to create uneven-aged forests that are now harvested by both selective methods and clear-cutting (USDA and USDI 1994). Intermediate-aged forest stands derived from selective harvest methods predominate over much of the study area, and these stands typically exhibit greater structural complexity than stands which developed under dense even-aged conditions following clear-cutting or high intensity fire. Because of the prevalence of selective timber harvest methods including overstory removal, shelterwoods, and diameter-limit cuts, extensive stands of unharvested mature and old-growth conifer forest are relatively scarce and largely restricted to remaining remote areas. For example, approximately 17% of commercial forestland administered by BLM contained at least 10% stocking of old-growth trees. Of this proportion, only 30% of the acres were unharvested or lightly harvested by selective cutting, and the

remainder was moderately to heavily harvested by selective methods (USDI 1995).

The study area is adjacent to other spotted owl demography study areas to the north and west (Franklin et al. *this volume*). These neighboring study areas facilitate the reobservation of banded owls that subsequently emigrate out of our study area. Additionally, the eastern and southeast boundaries of the study area are near the known range limits of the Northern Spotted Owl. These areas are characterized by open forests of lodgepole pine (*Pinus contorta*), ponderosa pine (*P. ponderosa*), or western juniper (*Juniperus occidentalis*) that may act as filters discouraging emigration by Spotted Owls.

## METHODS

### FIELD DATA COLLECTION

Methods used for locating, capturing and banding of owls, determining sex and age class, reobservation of marked owls, and determining fecundity are described in Franklin et al. (*this volume*). We used capture-recapture methods to estimate survival rates. During 1985–1993, we uniquely color-marked owls of known age class and sex, and conducted annual surveys to reobserve previously banded owls. We recognized four age classes: fledged juveniles (J), 1-yr-old owls (S1), 2-yr-old owls (S2), and owls  $\geq 3$  yrs old (A). We estimated fecundity from direct counts of the number of young fledged by each territorial female owl or by confirming non-reproduction.

Because the study area is large and characterized by diverse forest types, we established four categories of plant-series groupings to facilitate comparison of survival rates within the study area. We examined the area within a 2.4 km radius around individual owl sites by ground reconnaissance, and classified sites dominated by (1) the Douglas-fir series as the Douglas-fir Group, (2) the White Fir series and/or Shasta Red Fir series as the True Fir Group, (3) mosaics of the Douglas-fir series, White Fir series, and the Western Hemlock series as the Mixed Conifer Group, or (4) mosaics of the Douglas-fir series and the Tanoak series as the Douglas-fir/Tanoak Group.

The study area was partitioned into a General Study Area (GSA) and three smaller Density Study Areas (DSAs). We selected the DSAs to be representative of the range of plant series and timber harvest methods occurring within the study area. DSAs were 273 km<sup>2</sup>, 310 km<sup>2</sup>, and 316 km<sup>2</sup> in size. We used vocal lure surveys to systematically search the DSAs for territorial owls each year from 1990–1993 (Franklin et al. *this volume*). Six replicate surveys during the breeding season (March–August) were required before

concluding an area was unoccupied for a given year. Boundaries and calling points for surveys were established *a priori* and remained the same each year. Survey effort was thus constant for all years.

Individual sites with a known history of owl occupancy were surveyed annually within the GSA, but areas between sampled sites were generally not surveyed each year. The number of sites surveyed and the number of marked owls increased annually during the first half of the study before leveling off. Based on a search radius of > 1.5 km around owl sites, we estimate that survey coverage exceeded 50% of the available owl habitat within the study area during 1990–1993. Additionally, Federal agencies and private timber companies conducted large scale surveys each year for timber sale evaluations and other monitoring purposes. Resightings of previously banded owls from these efforts were shared with us. Data from the GSA and known sites within the DSAs were collected from 1985–1993 and were combined for estimates of fecundity, survival, and rate of population change.

#### DATA ANALYSIS

Notation and methods used for analysis of capture-recapture data are described in Franklin et al. (*this volume*). We summarized capture history data and assessed goodness-of-fit to Cormack-Jolly-Seber models with TESTs 2 and 3 in program RELEASE (Burnham et al. 1987). These tests were used to examine capture histories for independence and heterogeneity across and within capture occasions (Burnham et al. 1987, Pollock et al. 1990). Survival and recapture rates were estimated from Cormack-Jolly-Seber models for open populations in program SURGE (Lebreton et al. 1992).

Modeling procedures started with general models that allowed survival ( $\phi$ ) and recapture ( $p$ ) probabilities to vary by sex ( $s$ ), age ( $a$ ), non-linear time ( $t$ ), linear time ( $T$ ), or group effects. We then used Akaike's Information Criterion (AIC) (Akaike 1973) to identify the most parsimonious model that adequately fit the data (Burnham and Anderson 1992, Lebreton et al. 1992). Likelihood ratio tests were used to further examine the most parsimonious model and competing models with similar AIC values (Burnham et al. 1987). Modeling included two main efforts: (1) data from owls  $\geq 3$  yrs old were used in models to examine sex- and time-specific relationships, and (2) multiple age-class models examined age-, sex-, and time-specific effects or interactions.

Age-specific fecundity was estimated as the average number of female fledglings produced per territorial female of known age-class (Caughley

1977). Because fledged young were of unknown sex when observed, we assumed a 1:1 sex ratio.

The annual rate of population change during the time period of the study ( $\lambda$ , Lambda) was computed from age-specific survival and female fecundity estimates by solving the characteristic equation for a stage-based Leslie-Lefkovich matrix (Noon and Biles 1990, Franklin et al. *this volume*). The calculation of  $\lambda$  used juvenile and non-juvenile ( $\geq 1$ -yr-old owls) survival estimates from the best 2-age class model, and fecundity estimates from three age classes (S1, S2, and A) of territorial females.

We tested for differences in survival and recapture probabilities across capture-history data sets for the 4 plant-series groups with TEST 1 of program RELEASE (Burnham et al. 1987). Owls  $\geq 1$  yr old of both sexes were pooled for this test, and the sample of marked and released owls totaled 555, 462, 640, and 344 respectively for the Douglas-fir, True Fir, Mixed Conifer, and Douglas-fir/Tanoak groups.

We used Chi-square tests to assess annual variation in fecundity of owls  $\geq 1$  yr old. We compared annual fecundity between owls  $\geq 3$  yrs old and owls 1–2 yrs old (pooled S1 and S2) with ANOVA. Linear regression was used to compare annual fecundity to the amount of annual precipitation from September through April. We used precipitation amounts recorded at Medford, Oregon (U.S. Dep. Commerce 1994) as an index for the study area as a whole.

To evaluate the trend of owl abundance within DSAs against time, we used linear regression of the natural log of annual counts. We then converted the growth rate, expressed as the slope of the fitted line, to an empirical estimate of the annual rate of population change ( $\lambda = r^e$ ) (Caughley and Sinclair 1994). Because modeling indicated that recapture probabilities within the study area were not significantly affected by annual variation, we used unadjusted annual counts to assess trend. A power analysis of the regression (Gerrodette 1987) was conducted using program TRENDS (T. Gerrodette, personal communication).

We compiled capture-recapture data sets and estimates of annual fecundity for the DSAs and GSA separately. We used TEST 1 of program RELEASE to test for differences in survival and recapture probabilities between the DSAs and GSA. Owls  $\geq 1$  yr old were pooled and totaled 1422 (GSA) and 289 (DSAs) marked and released owls. We compared fecundity between the GSA and DSAs and among years using ANOVA.

#### EMIGRATION ESTIMATES

To assess the potential of emigration to negatively bias survival probabilities, we construct-

ed estimates of emigration rates for juveniles and non-juveniles separately. For bias from emigration to occur, owls must leave the study area, live through the first year of emigration, remain undetected, and not return (Anderson et al. 1990). From this definition, we identified 6 components of the overall probability that an owl would emigrate from the study area: (1) the annual probability that a banded owl would leave its territory and relocate elsewhere ( $P_1$ ), (2) the probability that an owl would move a distance sufficient to leave the study area ( $P_{ds}$ ), (3) the probability that an owl would move in a suitable direction to leave the study area ( $P_{dr}$ ), (4) the probability that an owl would remain alive through the first year of emigration ( $P_\phi$ ), (5) the probability that an owl would remain undetected after emigration ( $P_{nd}$ ), and (6) the probability that an owl would not return after emigrating ( $P_{nr}$ ). We estimated permanent emigration as the sum of the product of these probabilities for each owl banded within the study area:

$$P(\hat{E}) = \sum P(\hat{E}_i) = (P_1)(P_{ds})(P_{dr})(P_\phi)(P_{nd})(P_{nr})$$

We estimated  $P_1$  for non-juveniles from radio-marked owls that were observed within the study area (F. Wagner, unpublished data) during 1985–93 for a total of 136 owl-years. We assumed that all non-juveniles would move permanently to new territories at the same rate as radio-marked owls. Territorial relocations were defined as those occurring outside of an estimated home-range area (generally  $\geq 2.4$  km radius) and persisting for  $\geq 1$  year. We assumed that all juveniles dispersed from their natal site.

We estimated  $P_{ds}$  based on 2 sets of distances: (1) for banded owls that were recaptured as residents after moving to a new territory, the observed straight-line distance between the old and new territories (non-juvenile territorial-relocation distance) or the distance between the natal site and the new territory (juvenile dispersal distance); and (2) for all banded owls, the shortest distance between the location they were banded and the study area boundary in 2-km intervals. For territorial-relocation and juvenile dispersal distances, we derived separate cumulative frequency distributions in 2-km intervals based on the straight-line distances observed for those owls that moved permanently to another territory. We computed  $P_{ds}$  as the product of the proportion of owls banded at a given distance from the study area boundary and the probability that an owl would move as far or farther than that distance based on the cumulative frequency distributions. Because male and female juvenile owls exhibit different mean distances of dispersal (Miller 1989), we estimated juvenile emigration separately by sex and assumed a 1:1 sex ratio.

For estimates of  $P_{dr}$ , we assumed that territorial relocations and dispersal were random in direction and that these movements occurred with equal probability either towards the study area boundary or towards the interior of the study area.

Because our model-based estimates of survival include some level of bias due to emigration, we estimated  $P_\phi$  with a range of survival probabilities. Hence we attempted to bracket the true survival for juveniles and non-juveniles ( $S_j$  and  $S_{NJ}$ ). The lower limit of this range was set equal to the survival probabilities from the selected age-specific model, and the upper limit was set at what we considered to be optimistic but biologically feasible rates: 0.55 for juveniles, 0.88 for non-juveniles. We assumed that survival was not affected either by the occurrence or distance of a movement.

For  $P_{nd}$  and  $P_{nr}$ , we assumed that all emigrating owls would neither return to the study area nor be detected outside the study area. These assumptions would cause emigration to be overestimated, especially for dispersing juveniles. Of those owls originally banded on our study area, a significant proportion of the recaptures of dispersing owls has occurred in adjacent study areas. Our calculations may also overestimate potential juvenile emigration because they are based on the shortest distance to the study area boundary rather than the average distance. Alternately, our estimates, which are based on recaptures of banded owls, may underestimate true rates because recapture may vary with distance of dispersal. Therefore we calculated an additional estimate of emigration using the dispersal distances from telemetry-marked owls observed by Miller (1989).

In applying assumptions for this analysis, we attempted to use a realistic but conservative approach that approximated or exceeded true emigration rates. We used our estimates of emigration ( $\hat{E}$ ) to produce less biased survival estimates and to assess our confidence in the direction of the model-based estimate of population trend ( $\hat{\lambda}$ ). We estimated a range of true survival rates, not confounded by emigration, for juveniles ( $\hat{S}_j$ ) and non-juveniles ( $\hat{S}_{NJ}$ ) with the relationship (Burnham et al. *this volume*, Franklin et al. *this volume*):

$$\hat{S} = \frac{\hat{\phi}}{1 - \hat{E}}$$

We compared our results to the  $S_j$  and  $E_j$  rates necessary to obtain a rate of population change ( $\lambda$ ) = 1.0 (Franklin et al. *this volume*). We used  $\hat{S}_j$  to interpolate a  $\hat{\lambda}$  between the model based  $\hat{\lambda}$  and  $\lambda = 1$ . We tested  $H_0: \lambda < 1$  vs.  $H_a: \lambda \geq 1$  with a 1-tailed z-test (Franklin et al. *this volume*)

using the SE derived from the original model-based estimate  $\hat{\lambda}$ :

$$z = \frac{1 - \hat{\lambda}}{\text{SE}(\hat{\lambda})}$$

## RESULTS

### CAPTURE-RECAPTURE DATA

We captured and banded 1,897 owls (Table 1) and captured 23 additional owls that were initially marked on other study areas and subsequently immigrated into our study area. The latter birds, primarily dispersing juveniles, were treated as newly banded owls with their age class determined at the time of first observation following immigration. The sample size of captured and released owls used in capture-recapture analysis was 823 females  $\geq 3$  yrs old, 1,032 males  $\geq 3$  yrs old, 121 1–2-yr-old females, 142 1–2-yr-old males, and 680 juveniles. These totals include individual birds that were captured (or reobserved) and released multiple times, and are equal to the  $R$  totals in the capture-recapture  $m$ -array (Burnham et al. 1987)

### GOODNESS-OF-FIT

We found no significant lack of fit (TEST 3, program RELEASE) within adult cohorts (females:  $\chi^2 = 10.98$ , 12 df,  $P = 0.53$ ; males:  $\chi^2 = 10.50$ , 12 df,  $P = 0.57$ ), indicating that owl capture histories within a released cohort had similar survival and recapture probabilities. However, expected future fates differed between cohorts (TEST 2, program RELEASE) released at different occasions (females:  $\chi^2 = 29.55$ , 5 df,  $P < 0.001$ ; males:  $\chi^2 = 21.18$ , 3 df,  $P < 0.001$ ) and for the combined results of TEST 2 and 3 (females:  $\chi^2 = 40.54$ , 17 df,  $P = 0.001$ ; males:  $\chi^2 = 31.692$ , 15 df,  $P = 0.007$ ). We examined the partitioned test components of TEST 2 and isolated most of the lack of fit to 5 females and 5 males exhibiting temporary emigration. TEST 2 is sensitive to temporary emigration (Burnham et al. 1987), but because the lack of fit was not systematic and stemmed from only a few individuals within relatively large samples, we concluded that the test results did not indicate an overall lack of fit of the data and that Cormack-Jolly-Seber models were appropriate for use.

### MODEL SELECTION

The time- and sex-specific model that provided the best fit to the adult data,  $\{\phi_T, p_s\}$ , showed a negative linear time effect ( $T$ ) (Fig. 2) on annual survival probabilities ( $\phi$ ) with no time effects on recapture probabilities ( $p$ ). There was a sex effect on recapture rates but not on survival. In com-

TABLE 1. NUMBER OF NORTHERN SPOTTED OWLS BANDED 1985–1993 ON THE SOUTHERN CASCADE AND SISKIYOU MOUNTAINS STUDY AREA, OREGON

Year	Owls $\geq 3$ yrs old		Owls 1 & 2 yrs old		Juveniles
	Male	Female	Male	Female	
1985	11	11	1	0	5
1986	14	8	2	0	8
1987	17	14	4	2	9
1988	38	33	13	6	50
1989	31	30	6	9	27
1990	122	92	11	13	108
1991	116	100	19	10	137
1992	122	110	16	15	284
1993 <sup>a</sup>	85	86	25	25	51
Total	556	484	97	80	680

<sup>a</sup> Owls banded in 1993 are not reflected in capture-recapture analyses because they were not released until the last capture occasion.

mon with the selected model, competing models (Table 2) consistently had a sex effect on recapture rates (males had higher rates than females) and usually included a time effect on annual survival probabilities.

The best fitting age-specific model,  $\{\phi_{a2}, p_{a4'+s}\}$ , indicated that survival and recapture probabilities varied across age-classes and that recapture rates also differed between males and females. This model indicated no time effects on either survival or recapture probabilities (Fig. 2). Age structure on  $\phi$  was reduced to 2 classes (juveniles and non-juveniles). Comparison with competing models in Table 2 indicated that increasing age structure on recapture probabilities improved AIC values up through 4 age classes, and additive sex effects had a secondary but consistent effect on recapture probabilities.

### ESTIMATED SURVIVAL RATES

Estimated survival and recapture rates of owls did not differ among plant-series groups (Test 1:  $\chi^2 = 28.14$ , 23 df,  $P = 0.211$ ). Therefore, data from the entire study area were combined for estimates of survival and recapture rates.

Estimated annual survival for  $\geq 3$ -yr-old owls from the selected sex- and time-specific model,  $\{\phi_T, p_s\}$ , averaged 0.840 (SE = 0.010) (Fig. 2). Because standard errors could not be estimated from models with time effects on  $\phi$ , the standard error was approximated from the closest model in AIC value,  $\{\phi, p_s\}$ , without a time effect on  $\phi$ .

Estimates of annual survival from the selected age-specific model,  $\{\phi_{a2}, p_{a4'+s}\}$ , were 0.320 (SE = 0.038) for juveniles ( $\phi_j$ ) and 0.824 (SE = 0.009) for non-juveniles ( $\phi_{NJ}$ ) (Fig. 2). Estimates of annual survival from the selected model and several competing models varied  $\leq 1\%$  for juveniles and  $\leq 1.4\%$  for non-juveniles. This indicated that

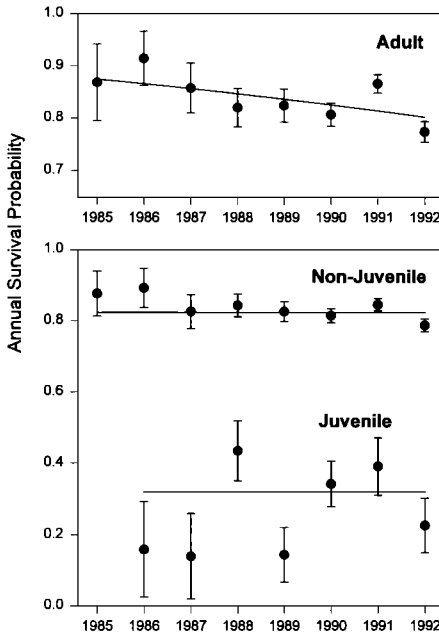


FIGURE 2. Estimates of survival for Northern Spotted Owls on the Southern Cascades and Siskiyou Mountains Study Area, Oregon, 1985–1993. The solid line in the upper graph indicates a nearly linear negative time trend in annual survival for  $\geq 3$ -yr-old owls from the selected model  $\{\phi_T, p_s\}$ . Point estimates of annual survival ( $\pm 1$  SE) from the next most parsimonious model with variable time effects  $\{\phi_t, p_s\}$  on  $\phi$  are shown for comparison. Solid lines in the lower graph represent constant survival estimates for non-juveniles ( $\geq 1$  yr old) and juveniles from the selected age-specific model  $\{\phi_{a2}, p_{a4+s}\}$ . Point estimates of annual survival ( $\pm 1$  SE) from the next most parsimonious model with variable time effects  $\{\phi_{a2+t}, p_{a4+s}\}$  are shown for comparison.

survival estimates were not greatly affected by model selection.

#### FECUNDITY

Annual fecundity of territorial females averaged 0.013 (SE = 0.019) for 1-yr-old owls, 0.145 (SE = 0.056) for 2-yr-old owls, and 0.313 (SE = 0.016) for owls  $\geq 3$  yrs old. Estimated annual fecundity for  $\geq 3$ -yr-old owls (Fig. 3) was higher than for 1 and 2-yr-old owls ( $F = 40.241$ , 1 df,  $P < 0.001$ ). Fecundity of owls  $\geq 1$  yr old varied among yrs ( $\chi^2 = 315.48$ , 24 df,  $P < 0.001$ ), ranging from 0.075 in 1993 to 0.524 in 1992). Annual variation in mean fecundity rates was negatively correlated with both the amount of precipitation during September–April ( $r = 0.81$ ,  $P = 0.004$ ) (Fig. 4), and with mean fecundity from the previous year ( $r = 0.81$ ,  $P < 0.001$ ).

TABLE 2. SUMMARY OF CAPTURE-RECAPTURE MODELS FOR THE NORTHERN SPOTTED OWL ON THE SOUTHERN CASCADES AND SISKIYOU MOUNTAINS STUDY AREA, OREGON, 1985–1993. MODELS ARE LISTED IN ORDER OF INCREASING AIC (AKAIKE'S INFORMATION CRITERION) VALUES (AKAIKE 1973). TIME AND SEX SPECIFIC MODELS INCLUDED ONLY THOSE OWLS INITIALLY MARKED WHEN THEY WERE  $\geq 3$  YRS OLD. AGE-SPECIFIC MODELS INCLUDED OWLS INITIALLY MARKED AS TWO AGE CLASSES: NON-JUVENILES ( $\geq 1$  YR OLD) OR JUVENILES. MODEL SUBSCRIPTS DENOTE AGE CLASSES (E.G., A2), SEX (S), LINEAR TIME (T), NON-LINEAR TIME (T), OR ADDITIVE (+) EFFECTS

Model	Deviance ( $-2 \ln[L]$ )	K*	AIC
Time and sex specific models on owls $\geq 3$ yrs old			
$\{\phi_T, p_s\}$	2292.969	4	2300.969
$\{\phi_t, p_s\}$	2282.350	10	2302.350
$\{\phi, p_s\}$	2296.458	3	2302.458
$\{\phi_{T+s}, p_s\}$	2292.482	5	2302.482
$\{\phi_T, p_{s+T}\}$	2292.663	5	2302.663
Age, sex, and time specific models			
$\{\phi_{a2}, p_{a4+s}\}$	3441.966	7	3455.966
$\{\phi_{a2}, p_{a4}\}$	3444.904	6	3456.904
$\{\phi_{a2}, p_{a5+s}\}$	3441.010	8	3457.010
$\{\phi_{a2+T}, p_{a4+s}\}$	3439.020	9	3457.020
$\{\phi_{a2}, p_{a3+s}\}$	3454.646	6	3466.646

\* Number of estimable parameters.

#### RATE OF POPULATION CHANGE

Based on the age-specific estimates of survival from model  $\{\phi_{a2}, p_{a4+s}\}$  and the age-specific estimates of annual fecundity, the estimate of the finite rate of population change ( $\lambda$ ) was 0.9105 (SE = 0.0121), which is significantly  $< 1.0$  ( $z = 7.39$ ,  $P < 0.001$ ). This estimate of  $\lambda$  suggests an average annual decline in the territorial population of 0.0895 during the period of study. Assuming that all other parameters are estimated accurately, values necessary for the true rate of juvenile survival (survival not confounded by emigration) ( $S_j$ ) or juvenile emigration ( $E_j$ ) to force  $\lambda = 1.0$  were 0.746 and 0.75 (Burnham et al. *this volume*).

#### CHANGES IN ABUNDANCE WITHIN DENSITY STUDY AREAS

The annual trend in owl abundance within the combined DSAs during 1990–1993 (Table 3) was 0.959. This estimated rate of change did not differ ( $r = 0.83$ ,  $P = 0.168$ ) from a stationary rate ( $\lambda = 1.0$ ). However, statistical power to detect an average annual decline of 4.1% over three occasions was low (0.31), and a lack of significance would not be unexpected regardless of actual trends.

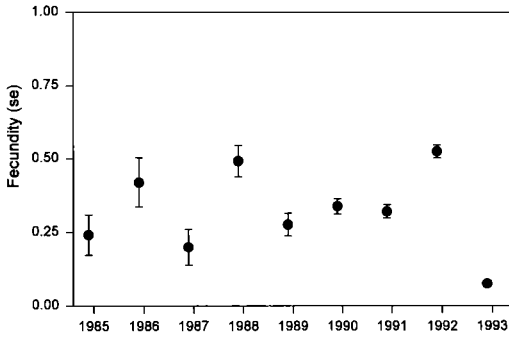


FIGURE 3. Annual variation in fecundity of  $\geq 3$ -yr-old female Northern Spotted Owls. Annual means and standard errors are expressed as the number of female young fledged per female.

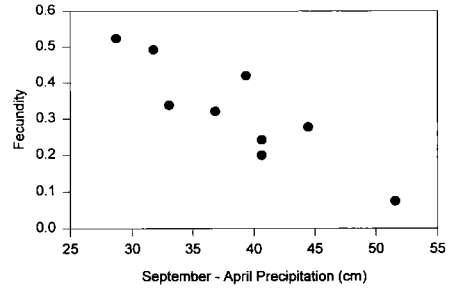


FIGURE 4. Relationship between precipitation during September–April and fecundity of Northern Spotted Owls on the Southern Cascades and Siskiyou Mountains Study Area, Oregon, 1985–1993. Fecundity is the mean number of female young fledged per  $\geq 1$ -yr-old female.

Most of the decline in owl abundance occurred in the single occasion from 1990 to 1991. Of the 23 owls which occupied sites in 1990 and subsequently were absent without replacement in 1991, 16 owls (69%) were associated with sites that had significant timber harvest within or adjacent to the center of activity. After 1990, most timber harvest within DSAs was administratively directed away from sites occupied by owls.

Estimated annual survival probabilities for 1990–93 were 0.813 (SE = 0.020) within DSAs and 0.843 (SE = 0.016) within the GSA. Neither survival probabilities or recapture probabilities were significantly different (Test 1:  $\chi^2 = 4.97$ , 5 df,  $P = 0.419$ ). Mean annual fecundity of  $\geq 1$ -yr-old females during the same period was lower ( $F = 20.151$ , 1 df,  $P < 0.001$ ) within the DSAs (fecundity = 0.184, SE = 0.024) than in the GSA (fecundity = 0.303, SE = 0.010).

#### ESTIMATES OF EMIGRATION

The annual rate that non-juvenile owls relocated to new territories was 0.0147 (SE = 0.010). This rate was similar to rates for other samples of radio-marked Northern Spotted Owls in Oregon and northern California (Thomas et al. 1990). The mean territorial-relocation distance observed for recaptured non-juvenile owls was 6.74 km ( $N = 41$ ,  $SD = 5.16$ ). Mean dispersal distances observed for recaptured juveniles averaged 17.23 km for males ( $N = 48$ ,  $SD = 16.54$ ) and 26.13 km for females ( $N = 52$ ,  $SD = 13.82$ ). Given the distribution of banded owls relative to the study area boundary (Fig. 5), the cumulative annual probability that owls would move far enough in a suitable direction to leave the study area was 0.084 for non-juveniles, 0.292 for

juvenile males, 0.384 for juvenile females, and 0.338 for pooled juveniles.

Based on these values, the estimated annual rate of emigration ( $\hat{E}$ ) for non-juveniles was 0.001 when  $P_\phi$  was set at 0.88. The annual rate of  $\hat{E}$  for juveniles surviving their first year ranged from 0.108 based on  $P_\phi$  set at 0.32 from the 2-age-class model to 0.1859 based on  $P_\phi$  set at 0.55. The juvenile  $\hat{E}$  based on  $\hat{\phi}_J = 0.55$  was 25% of the rate needed for  $\lambda = 1.0$ . The corresponding estimate of true survival ( $\hat{S}_J$ ) was 0.394, which is 53% of the rate necessary for  $\lambda = 1.0$ . Using  $\hat{S}_J = 0.394$ , we interpolated an adjusted  $\hat{\lambda}$  of 0.9577, which is significantly less than  $\lambda = 1.0$  ( $z = 3.65$ ,  $P < .001$ ).

Our observed dispersal distances from banding data were somewhat shorter than dispersal distances observed with radio-marked juveniles in western Oregon (Miller 1989). Substituting telemetry data from Miller (1989) resulted in an  $\hat{E}$  of 0.240 when  $P_\phi$  was set at 0.55; and a  $\hat{S}_J$  of 0.42. Use of these data gave similar results as

TABLE 3. NUMBER OF NON-JUVENILE NORTHERN SPOTTED OWLS COUNTED ANNUALLY BY AGE AND SEX CLASS WITHIN THE 899 KM<sup>2</sup> COMBINED DENSITY STUDY AREAS ON THE SOUTHERN CASCADES AND SISKIYOU MOUNTAINS STUDY AREA, OREGON, 1990–1993

	1990	1991	1992	1993
Males $\geq 3$ yrs old*	76	68	69	64
Females $\geq 3$ yrs old*	60	57	54	53
Males 1–2 yrs old	6	3	2	7
Females 1–2 yrs old	5	2	4	4
Total	147	130	129	128

\* Includes non-juvenile owls of unknown age.

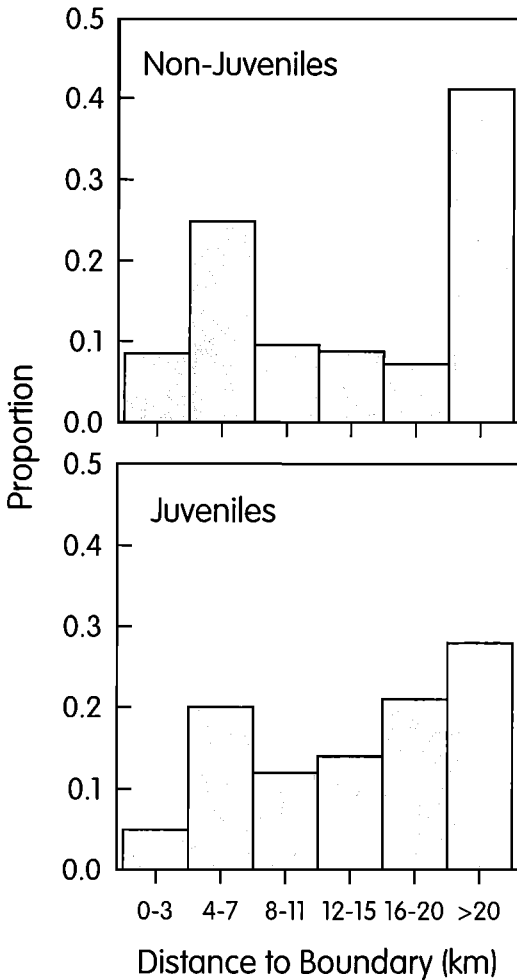


FIGURE 5. Proportion of juvenile and non-juvenile ( $\geq 1$ -yr-old) Northern Spotted Owls that were banded at various distances from the boundary of the Southern Cascades and Siskiyou Mountains Study Area, Oregon, 1985-1992.

those from data from banded owls and did not alter our conclusions about the direction of  $\hat{\lambda}$ .

## DISCUSSION

### MODEL SELECTION AND CALCULATED LAMBDA ESTIMATE

Three major results emerge from the estimates of population trend, survival probabilities, and fecundity. The calculated  $\hat{\lambda}$  indicates that the territorial population within the interior mountains of southwest Oregon underwent a significant decline, averaging 8.9% per year during 1985-93. This estimated rate of decline was greater than estimates reported for most other contemporary demographic studies (Burnham et al. *this vol-*

*ume*). Second, the most parsimonious model for owls  $\geq 3$  yrs old included a negative linear time trend in survival rates. This result is common to several other contemporary studies and the meta-analysis (Burnham et al. *this volume*). Third, the negative correlation between fecundity and total precipitation during September-April suggests that the prevailing drought conditions within the study area may have provided more favorable conditions for reproduction compared to average (wetter) conditions. If so, this implies that the estimated decline in population occurred in spite of relatively favorable weather conditions for reproduction.

In examining potential biases from emigration and changes in abundance within DSAs (below), we found no compelling evidence leading us to question the direction or significance of the model-based  $\hat{\lambda}$ . Enough potential juvenile emigration likely exists to reduce the magnitude of actual decline, however. If our estimates of juvenile emigration are reasonable, then  $\hat{\lambda}$  is likely to be negatively biased, perhaps as much as 0.03-0.05. Given this corrected rate of decline,  $\hat{\lambda}$  would still be significantly  $< 1.0$ . Thus, based on the negative population trend estimated over the 9-year period of study and the negative linear time trend on survival rates, we believe a conservative approach to the management of the Northern Spotted Owl and its habitat should be taken within the interior mountains of southwestern Oregon.

Because the demography and habitat of the Spotted Owl are dynamic, results from current studies cannot be used to predict future population trends (Burnham et al. *this volume*, Raphael et al. *this volume*). Thus, there is a need for continued data collection and analysis. We suggest that study design should emphasize minimizing potential bias and acquiring a sufficient data set to support model structure and adequate estimation of parameters. These design objectives are largely controlled by the size of the study area, intensity and duration of sampling, and the proximity to other study areas. Even with a large study area, our analysis suggested that emigration may cause a significant negative bias in estimates of juvenile survival. Estimates of this parameter could be improved with radio-telemetry data.

### CHANGES IN ABUNDANCE WITHIN DENSITY STUDY AREAS

The pattern of change in owl abundance within the DSAs appeared to reflect recent timber harvest history and does not offer evidence that supports either the negative linear time effect on survival probabilities or the substantial decline in population resulting from model-based estimates. This disparity between trends estimated



from empirical counts and model-based trends may be due to several factors.

Empirical estimates of owl numbers within bounded areas may reflect site specific factors or spatial or temporal stochastic events occurring either within or outside the bounded area. DSAs are therefore subject to various biases in estimates of population trend (e.g., Franklin 1992), and these biases may be largely unknown and difficult to estimate (Van Horne 1983).

Comparison of fecundity rates clearly indicated that the DSAs were less productive than the GSA. Given the estimated vital rates for the DSAs, the numbers of owls counted annually within DSAs are likely to have been dependent on some level of net immigration. Additionally, although small annual rates of change may be biologically important, statistical power is likely to be insufficient to detect such trends over three occasions. Thus, counts of spotted owls within the DSAs do not provide convincing counter evidence to  $\hat{\lambda}$  or the linear time effect on survival probabilities.

#### POTENTIAL BIAS

There are several sources of bias that may bias  $\hat{\lambda}$  upwards or downward (Anderson et al. 1990, Noon and Biles 1990, Thomas et al. 1990, Bart 1995a, Raphael et al. *this volume*). Of these, we considered juvenile and non-juvenile emigration to be the most important because of the potential to underestimate survival rates (Thomas et al. 1993a). Because rate of population change for the Northern Spotted Owl is most affected by variation in adult survival (Noon and Biles 1990), relatively low rates of adult emigration may be significant. We found the potential for non-juvenile emigration from the study area to be relatively unimportant, however, because few non-juveniles moved, distances of observed movements tended to be short, and many owls occupied territories that were located long distances from study area boundaries.

Juvenile emigration is important because these owls are capable of moving substantial distances during dispersal, and population trend is sensitive to first year survival (Noon and Biles 1990). Our calculations suggest that juvenile emigration occurred at low to moderate levels within the study area. However, bias from juvenile emigration can account for only a portion of the rate of decline shown by  $\hat{\lambda}$ , even when  $S_j$  is set at an optimistic 0.55.

#### FECUNDITY

The mechanisms underlying the inverse relationship between fecundity and total precipitation from September–April are unknown. Winter weather patterns dominated by high-pressure

systems could hypothetically result in higher overwinter survival of prey and lower energetic costs for owls, which may enable owls to be in better physical condition as they enter the breeding season in March and April. The negative correlation of fecundity with the fecundity rate of the previous year may simply reflect the energetic costs of reproduction.

#### HABITAT

The study area is in large part characterized by uneven-aged forest stands derived from past fire events and selective timber harvest methods, and interest exists in the silvicultural use of selective harvest treatments to retain or accelerate development of appropriate habitat structure for Northern Spotted Owls (Thomas et al. 1990). However, the negative population trend estimated for the study area underscores the need to base evaluations of owl habitat and silvicultural treatments on observed demographic performance (Anderson et al. 1990, Thomas et al. 1990). We consider it likely that the region's diverse mosaics of forest habitat comprise a varying range of quality for the owl, and recommend that research be conducted that relates forest landscape and stand structure elements to demographic parameters. Such research is a necessary precursor to both adaptive management of habitat and the investigation of heterogeneous populations (Raphael et al. *this volume*).

#### SUMMARY

We estimated age-specific vital rates and the rate of population change for Northern Spotted Owls within the southern Cascades and Siskiyou Mountains of southwestern Oregon during 1985–1993. Because these forested mountains provide diverse habitats for the owl and occupy a geographic location between the northern and southern portions of the species' range, our objective was to obtain estimates that were representative of the region. We estimated fecundity by direct counts of fledged young. Survival was estimated with capture-recapture methods using Cormack-Jolly-Seber models for open populations. Survival estimates from sex- and time-specific models for owls  $\geq 3$  yrs old included a negative linear time trend. Survival estimates from age-specific models were 0.824 (SE = 0.009) for non-juveniles ( $\geq 1$  yr old) and 0.320 (SE = 0.038) for juveniles. Annual fecundity estimates of territorial females averaged 0.013 (SE = 0.019) female young for 1-yr-old owls, 0.145 (SE = 0.056) for 2-yr-old owls, and 0.313 (SE = 0.016) for owls  $\geq 3$  yrs old. Annual fecundity for 1- and 2-yr-old owls was lower than for owls  $\geq 3$  yrs old ( $P < 0.001$ ). Annual fecundity was inversely correlated with precipitation during the preceding fall and winter

( $P = 0.005$ ). Based on estimates of survival and fecundity, the estimated rate of population change ( $\hat{\lambda}$ ) was 0.9105 ( $SE = 0.0121$ ), which was significantly  $< 1.0$  ( $P < 0.001$ ). We calculated estimates of annual non-juvenile (0.001) and juvenile (0.186) emigration to evaluate these as sources of bias in estimating the population change rate. Our estimates of emigration were insufficient to account for the direction and significance of the estimated rate of population change, but a portion of the magnitude of decline may be explained by juvenile emigration. Based on estimated rates of juvenile emigration, we interpolated an adjusted  $\hat{\lambda}$  of 0.9577, which was significantly less than  $\lambda = 1.0$  ( $P < .001$ ). Counts of territorial owls within density study areas (DSAs) did not differ among years during 1990–1993. However, power to detect trends was low. Comparison of vital rates between the DSAs and the remainder of the study area indicated lower fecundity within DSAs ( $P < 0.001$ ), and suggested that the observed owl abundance within the DSAs was dependent on net immigration. We concluded that owl abundance based on empirical counts within DSAs neither supported or contradicted model-based estimates of population trend. Based on the negative population trend estimated over the 9-year period of study and the negative linear time trend on survival rates, we believe a conservative approach to the management of the Northern Spotted Owl and its habitat should be taken within the interior mountains of southwestern Oregon.

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*Key words:* capture-recapture, demography, emigration, fecundity, Northern Spotted Owl, population rate of change, Siskiyou Mountains, southern Cascades, southwestern Oregon, *Strix occidentalis caurina*, survival.