DEMOGRAPHY OF THE NORTHERN SPOTTED OWL ON THE OLYMPIC PENINSULA AND EAST SLOPE OF THE CASCADE RANGE, WASHINGTON

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INTRODUCTION

Research on the Northern Spotted Owl (*Strix occidentalis caurina*) in Washington State began in the late 1970s, and has included a variety of topics, including response rates in different forest types (Mills et al. 1993), ecological relationships with the Barred Owl (*Strix varia*) (Hamer 1988), home range and habitat use (Hamer 1988, Thomas et al. 1990, North 1993), diet (Richards 1989, Thomas et al. 1990, Sovern et al. 1994), nest site characteristics (Buchannan 1991, Buchannan et al. 1993), prey populations (Carey et al. 1992, Forsman et al. 1994), behavior (Sovern et al. 1994), landscape features around nests (Lemkuhl and Raphael 1993), and distribution (Garcia 1979, Thomas et al. 1990). Although most of these studies emphasized importance of particular types of forest habitat for Spotted Owls, none produced quantitative data on population trends or on underlying parameters that determine population growth rates (e.g., age-specific birth and death rates).

Because information on survival and reproductive rates is critical for assessing the health of any animal population, we investigated age-specific birth and death rates and annual rates of population change of Spotted Owls on two study areas in Washington. Our objective was to provide information that would help clarify the status of the owl in Washington, and that could be used in ancillary studies of Spotted Owl habitat relationships (e.g., Lemkuhl and Raphael 1993).

STUDY AREAS

The two study areas were the Cle Elum Ranger District (1,803 km²) on the east slope of the Cascade Range in central Washington (Fig. 1), and an 8,145 km² area that encompassed most of the Olympic Peninsula in northwestern Washington (Fig. 2). On the Olympic Peninsula the study was initially focused on lands administered by the U.S. Forest Service and Washington Department of Natural Resources, which surrounded the Olympic National Park. The study was expanded to include the Olympic National Park in 1989, after the National Park Service began to survey and band Spotted Owls. The Olympic Peninsula Study Area was characterized by mountainous terrain and a wet, relatively warm maritime climate. The area was deeply dissected by numerous large river valleys emanating from the Olympic Range at the center of the peninsula. Precipitation occurred mainly as rain, and was particularly heavy on the western slopes of the Olympic Mountains, where it averaged 365 cm/year from 1987–1993 (USDI National Park Service records, Port Angeles, WA). Elevations ranged from sea level to 2,428 m.

The Cle Elum Study Area included the Cle Elum Ranger District on the Wenatchee National Forest, plus inholdings of private land within the district boundary (Fig. 2). This area was also mountainous, but slopes tended to be gentler than on the Olympic Peninsula, and climate was much drier. Mean annual precipitation during 1989–92 was 64 cm (NOAA 1990–1994). Summers were typically warm and dry, and winters were relatively cold with much of the winter precipitation occurring as snow. Elevations ranged from 670–2,084 m.

Vegetation on the Olympic Peninsula was typical of the humid coastal region of western Washington (Franklin and Dyrness 1973, Henderson et al. 1989). Forests of western hemlock (*Tsuga heterophylla*) western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), pacific silver fir (*Abies amabilis*) and Douglas-fir (*Pseudotsuga menziesii*) covered most of the area, except on recently harvested areas. Areas above about 1,400 m elevation were mostly covered by non-forest subalpine or alpine vegetation. Because of a long history of clear-cut logging and natural events such as fire and windstorms, most areas administered by the Forest Service and Department of Natural Resources were characterized by a mosaic of shrubs or young trees on cutover areas and mixed-age stands of older trees on unharvested areas. In contrast, most forests within Olympic National Park had never been harvested and were characterized by natural variation in age, species, and structure resulting from wildfire, windstorms, and differences in elevation.

Vegetation on Cle Elum was dominated by mixed conifer stands of Douglas-fir, grand fir (*Abies grandis*), and ponderosa pine (*Pinus pon-*
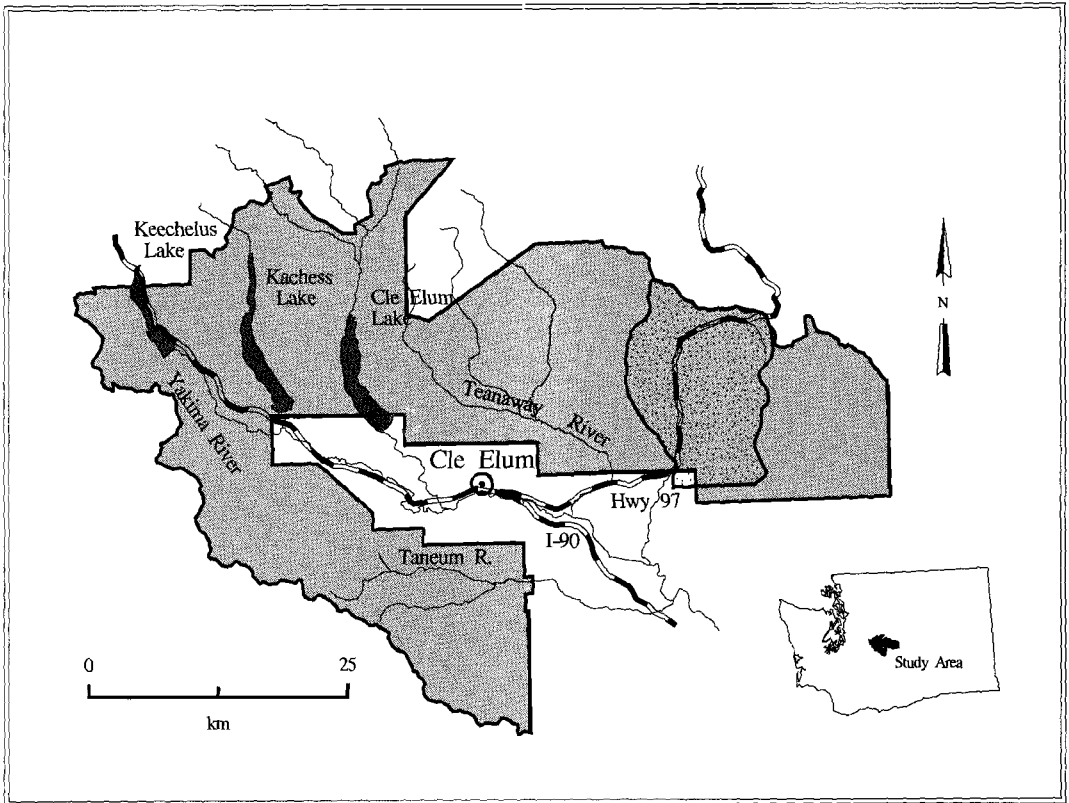
FIGURE 1.   Cle Elum Study Area, WA. 1989–1993. Stippled area indicates location of the Density Study Area, a subplot within the larger study area that was completely surveyed each year to estimate numbers of territorial owls.

derosa). Less common species that were frequently associated with these stands included western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*) and western hemlock. Although mixed conifer stands predominated in most areas, stands dominated by ponderosa pine and open grassy areas were also common on dry south-facing slopes.

Much of the forest on Cle Elum had been selectively logged or burned one or more times since the early 1900s. Historically, most harvest consisted of partial cutting or selective cutting, in which some overstory trees were removed, leaving much of the stand intact. Small patches of old trees were often left standing. Historic wildfires also played a dominant role in determining species composition and forest structure in Cle Elum. After the initiation of a systematic program of fire suppression in the 1930s, fire-dependent forest types like ponderosa pine generally declined, whereas fire sensitive types like grand fir flourished.

METHODS

The Olympic and Cle Elum studies were started in 1987 and 1989 respectively, and continued through 1993. In both studies we used mark-recapture techniques to estimate survival of banded owls, as described in Franklin et al. *this volume*. Mean annual fecundity (# of female young produced per female owl) was estimated by repeatedly locating pairs of owls during the breeding season and counting the number of young that left the nest (Franklin et al. *this volume*). To find young owls after they left the nest we placed live mice in front of adult owls and then followed them when they captured the mice and carried them to their offspring (Franklin et al. *this volume*).

Both study areas included a subplot that was referred to as a "Density Study Area" (DSA), within which we attempted to monitor annual changes in the number of resident owls (Figs. 1, 2). Survey routes within DSAs were laid out to insure complete coverage of the area, and were surveyed a minimum of 3 times each year during
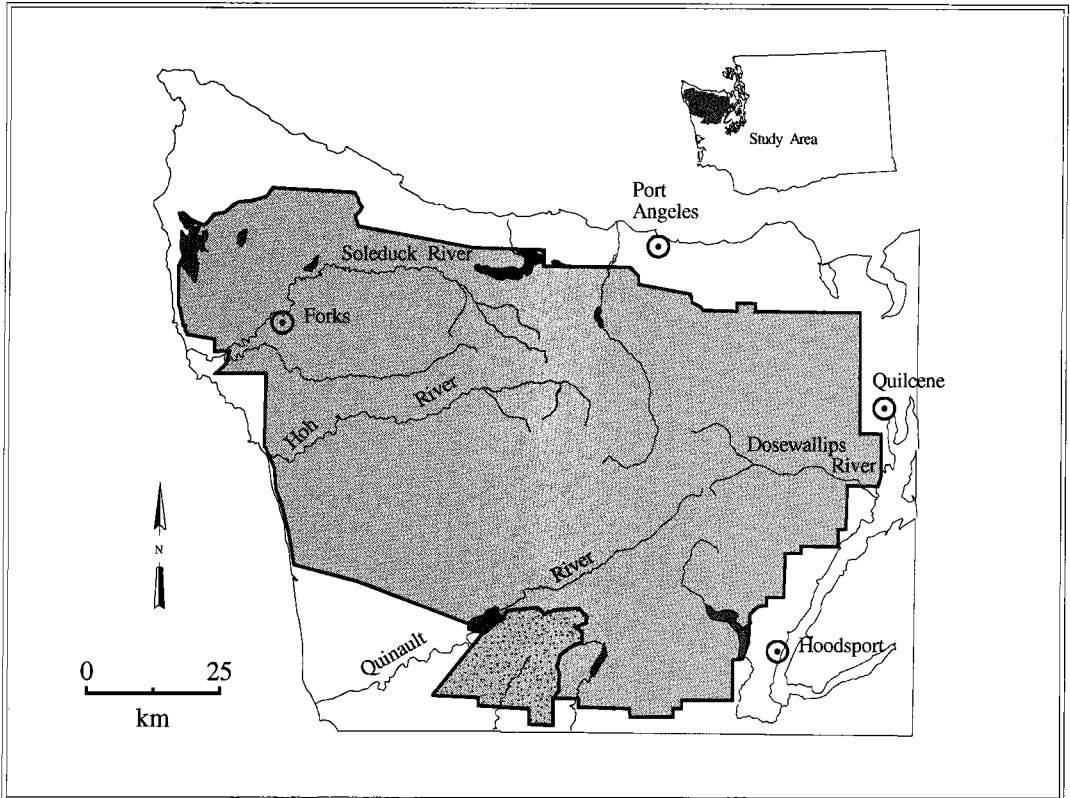
FIGURE 2. Olympic Peninsula Study Area, WA. 1987–1993. Stippled area indicates location of the Density Study Area, a subplot within the larger study area that was completely surveyed each year to estimate numbers of territorial owls.

spring and summer, using techniques described in Forsman (1983) and Franklin et al. *this volume.* Size of DSAs on the Olympic and Cle Elum Study Areas was 355 and 204 km², respectively. In areas outside of DSAs, surveys and banding were conducted on selected areas with a history of owl occupancy, but no attempt was made to survey the entire study area.

Capture-recapture (CR) analyses were conducted on the complete data set for each study area. Survival rates for each sex and age class were calculated from CR data using Cormack-Jolly-Seber open population models in Program SURGE as described in Pollock et al. (1990), Lebreton et al. (1992), Burnham et al. (1995), and Franklin et al. (*this volume*). Akaike's Information Criterion (AIC) (Akaike 1973, Burnham and Anderson 1992, Anderson et al. 1994) was used to identify models that best fit the data. Goodness-of-fit to the statistical assumptions in the CR models was evaluated using tests 1–3 in program RELEASE (Pollock et al. 1985, Burnham et al. 1987).

Juvenile Spotted Owls disperse from their natal territories in their first year, often moving beyond the boundaries of a given study area (i.e., they emigrate). Because emigration is usually indistinguishable from mortality in CR data, juvenile survival estimates from CR analyses may be biased low. To estimate emigration rates of juvenile owls (E_J) we installed 5-gram radio transmitters on the rectrices of a subset of the 1991–1992 juvenile cohorts on both study areas. Emigration was defined as any case in which a radio-marked bird moved into an area not normally searched during our annual calling surveys, survived its first year, and was not detected by our normal calling surveys (Burnham et al. *this volume*). This definition was adopted because: (1) a bird that moves within the original study area is still susceptible to recapture and will be correctly treated by CR models; (2) a bird that leaves the original study area but is captured elsewhere will be reported to the original study area and treated as a recapture; and (3) only birds that emigrate and survive remain in the popu-

TABLE 1. SAMPLE SIZE[a] AND NUMBER OF OWLS BANDED FOR CAPTURE-RECAPTURE STUDIES OF NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA AND CLE ELUM STUDY AREAS, WASHINGTON

	Olympic Peninsula	Cle Elum
Years of study	1987–1993	1989–1993
Sample size[a]		
≥3-yr-old males	295	131
≥3-yr-old females	278	96
Number owls banded		
≥3-yr-old males	127	60
≥3-yr-old females	129	56
1- or 2-yr-old males	27	12
1- or 2-yr-old females	15	18
1–2-yr-old, sex undet.	1	
Juveniles	249	186
Total	548	332

[a] Sample size was the sum of the birds captured and released on i occasions $(R_1 + R_2 + ... + R_{k-1})$ in the capture-recapture m-array (Lebreton et al. 1992).

lation; a bird that emigrates and dies has the same effect on the population as one that dies without emigrating. Clearly, the emigration rate defined here will be specific to the study area in which it is estimated.

Estimates of E_J from the radio-marked juveniles were used to adjust estimates of juvenile survival from CR data $(\hat{\phi}_J)$ using the formula:

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

where $\hat{S}_J$ = the adjusted estimate of survival. We assumed that annual survival probabilities were the same for emigrating and non-emigrating individuals and that tail-mounted radio-transmitters had no effect on emigration rates of juvenile Spotted Owls. Only juveniles that survived at least through March of the year following hatching were used.

The annual rate of population change (λ) was estimated by solving the characteristic equation

resulting from a modified stage-based Leslie matrix (Franklin et al. *this volume*). We made two estimates of λ, one of which was based on the unadjusted survival estimates for juveniles and non-juveniles from the best age-class models, and estimates of fecundity from two age classes (1 and 2-yr-old birds and ≥3-yr-old birds). The second estimate of λ was based on the same parameter estimates as the first, except that we substituted the estimate of juvenile survival that was adjusted for emigration. Estimates of fecundity for 1 and 2-yr-old birds were pooled because of small sample size.

Trends in the total number of territorial birds detected each year within DSAs were assessed using regression analysis in SPSS (Norušis 1990) to test the null hypothesis that there was no change in population size. Years examined were 1988–1993 on the Olympic Peninsula and 1991–1993 on Cle Elum. Data from the first year of study on the Olympic Peninsula DSA (1987) were excluded because some portions of the DSA were not surveyed in that year. A power analysis of the regression (Gerrodette 1987) was conducted using Program TRENDS (T. Gerrodette, personal communication). For all statistical tests, P values ≤ 0.05 were considered significant.

RESULTS

SAMPLE SIZE AND GOODNESS OF FIT

Capture-recapture data were collected from 548 owls on the Olympic Peninsula and 332 owls on Cle Elum (Table 1). Results of TEST 1 in program RELEASE (Burnham et al. 1987) indicated no differences in survival or recapture rates of ≥3-yr-old males and females on either study area (Olympic Peninsula $\chi^2 = 3.50$, df = 11, P = 0.982; Cle Elum $\chi^2 = 6.81$, df = 7, P = 0.530) (Table 2). TEST 1 was not conducted on juveniles because the sex of most juveniles was not known.

For ≥3-yr-old birds, the combined results of TEST 2 and 3 from Program RELEASE revealed no lack of fit for CR data for either males or

TABLE 2. GOODNESS-OF-FIT TEST RESULTS FROM PROGRAM RELEASE (BURNHAM ET AL. 1987) FOR CAPTURE-RECAPTURE DATA FROM ≥3-YR-OLD NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA (OLY) AND CLE ELUM (CLE) STUDY AREAS, WASHINGTON

Study area	Sex	TEST 2 P	TEST 3 P	TEST 2 + 3[a]		
				χ^2	df	P
OLY	Males	0.3937	0.0499	19.89	12	0.0691
	Females	0.2021	0.0008	34.36	13	0.0011
CLE	Males	0.3280	0.7185	5.11	7	0.6466
	Females	0.0612	0.9942	6.03	7	0.5368

[a] TEST 2 tests for statistical independence among age and sex cohorts and individuals (Burnham et al. 1987). TEST 3 tests whether previously released individuals have the same future fates as newly released individuals.

TABLE 3. CAPTURE-RECAPTURE MODELS USED TO ESTIMATE SURVIVAL OF NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA STUDY AREA, WASHINGTON: 1987–1993. MODELS ARE SHOWN IN ORDER OF INCREASING AKAIKE'S INFORMATION CRITERION (AIC) VALUES (AKAIKE 1973). K = THE NUMBER OF ESTIMABLE PARAMETERS

Model[a]	Deviance	K	AIC
≥3-yr-old owls			
$\{\phi_s, p_T\}$	786.615	4	794.615
$\{\phi, p_{s+T}\}$	787.540	4	795.540
$\{\phi, p_T\}$	789.584	3	795.585
$\{\phi_{s+T}, p_T\}$	785.622	5	795.622
$\{\phi_s, p_{s+T}\}$	785.822	5	795.822
2-age-class models			
$\{\phi_{a2}, p_{a5+T}\}$	1171.903	8	1187.903
$\{\phi_{a2}, p_{a4+T}\}$	1173.960	7	1187.960
$\{\phi_{a2'+s}, p_{a5+T}\}$	1170.058	9	1188.058
$\{\phi_{a2+s}, p_{a3+T}\}$	1181.509	7	1195.509
$\{\phi_{a2+T}, p_{a3+T}\}$	1181.629	7	1195.629

[a] Model subscripts indicate age (a), sex (s), or time (t, T) effects on survival (ϕ) or recapture (p). An upper case T in a subscript indicates a linear time-effect in the subscripted parameter. Numbers indicate number of age-groups. The subscript a2′ + s indicates 2 age groups with sex effects on non-juveniles, but not on juveniles. An * indicates full age, sex, or time-effects, whereas a + sign indicates a reduced model in which age, sex, or time-effects are additive.

TABLE 4. CAPTURE-RECAPTURE MODELS USED TO ESTIMATE SURVIVAL OF NORTHERN SPOTTED OWLS ON THE CLE ELUM STUDY AREA, WASHINGTON: 1989–1993. MODELS ARE SHOWN IN ORDER OF INCREASING AKAIKE'S INFORMATION CRITERION (AIC) VALUES (AKAIKE 1973). K = NUMBER OF ESTIMABLE PARAMETERS

Model[a]	Deviance	K	AIC
≥3-yr-old owls			
$\{\phi_T, p_s\}$	317.177	4	325.177
$\{\phi_T, p_{s+T}\}$	315.181	5	325.181
$\{\phi, p_{s+t}\}$	313.714	6	325.714
$\{\phi, p_s\}$	320.152	3	326.152
$\{\phi_T, p_{s*T}\}$	314.496	6	326.496
2-age-class models			
$\{\phi_{a2+T}, p_{s+T}\}$	533.349	6	545.349
$\{\phi_{a2+T}, p_{a2+s+T}\}$	532.671	7	546.671
$\{\phi_{a2+T}, p_{a2+s}\}$	537.459	6	549.459
$\{\phi_{a2*s}, p_{a2*t}\}$	526.553	12	550.553
$\{\phi_{a2+T}, p_{a3+s}\}$	537.054	7	551.054

[a] Subscripts indicate age (a), sex (s), or time (t, T) effects on survival (ϕ) or recapture (p). Numbers indicate number of age groups. Time effects were either linear (T) or non-linear (t). An * indicates full age, sex, or time-effects. A + sign indicates a reduced model with additive age, sex or time-effects.

females on Cle Elum (Table 2). On the Olympic Peninsula, combined results of TEST 2+3 indicated some lack of fit for both males and females (Table 2). Closer inspection of the data revealed that over 75% of the χ^2 value for TEST 3.SR was contributed by 32 birds banded in 1992. Only six of those individuals were recaptured in 1993. When we excluded the 1992 cohort and ran RELEASE on the first five years of data, Tests 2+3 indicated no lack of fit for males (χ^2 = 16.572, df = 10, P = 0.084), females (χ^2 = 7.715, df = 10, P = 0.657), or for males and females combined (χ^2 = 24.286, df = 20, P = 0.230). The winter of 1992–93 was apparently a particularly difficult one for Spotted Owls on the Olympic Peninsula, because none of the pairs located there in 1993 nested (see FECUNDITY below). This could explain why the adult cohort banded in 1992 had a different future fate than cohorts banded in previous years. Because the sample of birds banded in 1992 was small compared to the total sample for all years, we believe that the resulting lack of fit was not a serious concern in the overall analysis.

CAPTURE-RECAPTURE MODEL SELECTION

For the Olympic Peninsula, the CR model that best fit the data from ≥3-yr-old birds was one in which survival (ϕ) differed by sex, and recapture probability (p) varied linearly over time (symbolized as $\{\phi_s, p_T\}$)(Table 3, Fig. 3). For Cle

the model that best fit the data from ≥3-yr-old birds was one in which ϕ varied linearly over time, and p varied by sex ($\{\phi_T, p_s\}$)(Table 4, Fig. 4).

The best age-class model for the Olympic Peninsula was $\{\phi_{a2}, p_{a5+T}\}$, indicating that ϕ differed by age (juvenile vs. non-juvenile), but did not differ by sex or year (Table 3, Fig. 3). For Cle Elum the best age-class model was $\{\phi_{a2+T}, p_{s+T}\}$, indicating an age and linear time effect on ϕ, but no sex effect (Table 4, Fig. 4). Thus, age-class models indicated no difference in survival of males and females on either study area. Examination of model output for Cle Elum indicated that the linear time trend on survival was negative (Fig. 4).

On both areas there were one or more alternative models that fit the data nearly as well as the preferred adult models and age-class models (Tables 3, 4). Examination of the alternative models revealed none that seemed more biologically reasonable than the models with lowest AIC values, so all subsequent calculations were based on estimates from the age-class models with the lowest AIC values.

SURVIVAL ESTIMATES FROM CAPTURE-RECAPTURE MODELS

Estimates of mean annual survival from the best age-class model on the Olympic Peninsula were 0.245 (SE = 0.064) for juveniles and 0.862 (SE = 0.017) for non-juveniles (Fig. 3). On Cle Elum, estimates of survival from the best age-
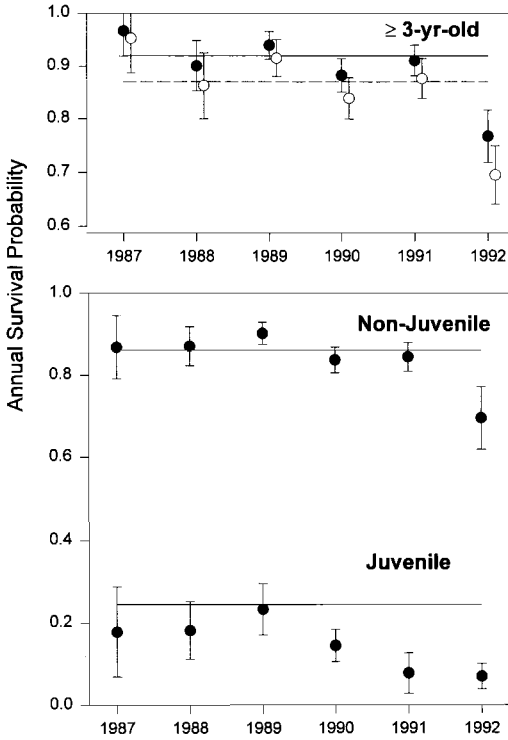
FIGURE 3. Estimates of annual survival for ≥3-yr-old, ≥1-yr-old, and juvenile Northern Spotted Owls on the Olympic Peninsula, WA: 1987–1993. Horizontal lines in top graph represent constant survival estimates for males (solid line, $\bar{\phi}_\delta = 0.920$, SE =0.0201) and females (dashed line, $\bar{\phi}_\circ$ =0.870, SE = 0.0236) from the best adult CR model ($\{\phi_s, p_T\}$). Annual estimates of survival and SEs for ≥3-yr-old males (solid dots) and females (open dots) from a variable time model ($\{\phi_{t+s}, p\}$) are shown for comparison. In the lower graph, horizontal lines indicate constant survival estimates for ≥1-yr-old owls ($\phi_{NJ} = 0.862$, SE = 0.017) and juveniles ($\phi_J = 0.245$, SE = 0.064) from the best age-class model ($\{\phi_{a2}, p_{a5+T}\}$); dots with SEs indicate yearly survival estimates from a variable time model ($\{\phi_{a2+t}, p_{a3+t}\}$).
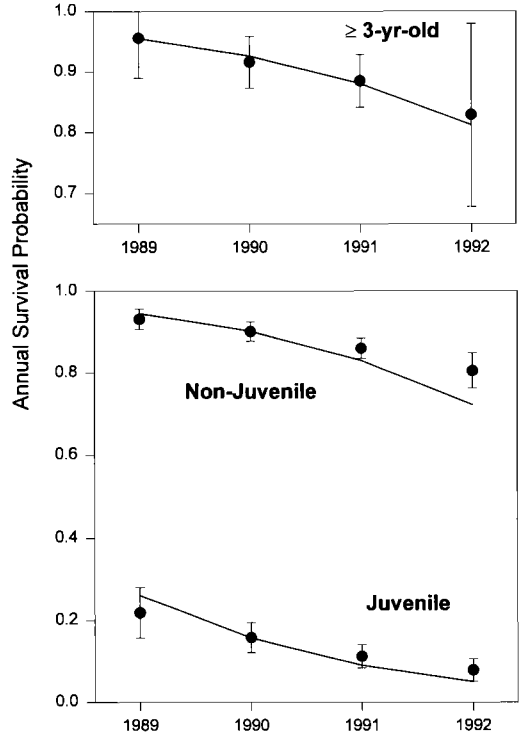

FIGURE 4. Estimates of annual survival for ≥3-yr-old, ≥1-yr-old, and juvenile Northern Spotted Owls on the Cle Elum Study Area, WA: 1989–1993. Line in top graph represents the nearly linear time trend in survival estimates from the best model for ≥3-yr-old owls (ϕ_T, p_s), with average SE = 0.0351. Annual estimates and associated SEs from a variable time model ($\{\phi_t, p_{s+t}\}$) are shown for comparison. Lines in lower graph represent the nearly linear time trends in survival estimates from the best 2-age-class model (ϕ_{a2+T}, p_{s+T}), with average SEs of 0.0280 and 0.0353 for ≥1-yr-old birds and juveniles, respectively. Annual estimates and associated SEs from a variable time model ($\{\phi_{a2·t}, p_{a2·s}\}$) are shown for comparison.

class model were 0.140 (SE = 0.026) for juveniles and 0.850 (SE = 0.0312) for non-juveniles (Fig. 4). Because standard errors could not be calculated on estimates from models that included a year effect on ϕ, standard errors for survival rates from model $\{\phi_{a2+T}, p_{s+T}\}$ were approximated from the model with the next closest AIC, but no year effect on ϕ (model $\{\phi_{a2}, p_{a2+T}\}$)(Franklin et al. *this volume*).

JUVENILE EMIGRATION RATES

The proportion of radio-marked juveniles that emigrated each year ($\hat{E}_J$) was 0.579 (SE = 0.113) on the Olympic Peninsula and 0.625 (SE = 0.121) on Cle Elum (Table 5). Logistic regression indicated no year or area effects on emigration rates ($\chi^2 = 2.065$, df = 1, P = 0.151), so the data from both areas were pooled to produce a single estimate of $\hat{E}_J = 21/35 = 0.600$ (SE = 0.083) (Table 5). Based on this estimate of E_J, the adjusted juvenile survival estimate ($\hat{S}_J$) was 0.611 (SE = 0.204) for the Olympic Peninsula and 0.349 (SE = 0.098) for Cle Elum.

FECUNDITY

Fecundity of females that were ≥3 yrs old averaged 0.380 (SE = 0.036) on the Olympic Peninsula and 0.565 (SE = 0.061) on Cle Elum. Sam-

TABLE 5. PROPORTION OF RADIO-MARKED JUVENILE NORTHERN SPOTTED OWLS THAT EMIGRATED FROM THE OLYMPIC PENINSULA AND CLE ELUM STUDY AREAS, WA: 1991 AND 1992 COHORTS.

Area/cohort	n	Proportion emigrating[a] ($\hat{E}$)	SE ($\hat{E}$)
Olympic Peninsula			
1991	11	0.727	
1992	8	0.375	
1991 & 1992	19	0.579	0.113
Cle Elum			
1991	12	0.583	
1992	4	0.750	
1991 & 1992	16	0.625	0.121
Combined areas			
1991	23	0.652	
1992	12	0.500	
1991 & 1992	35	0.600	0.083

[a] Emigration was defined as a bird that dispersed into an area not normally searched during annual calling surveys, survived until at least 30 March of the year after birth, and was not detected using normal calling surveys (i.e., that would have gone undetected without the use of radio telemetry).
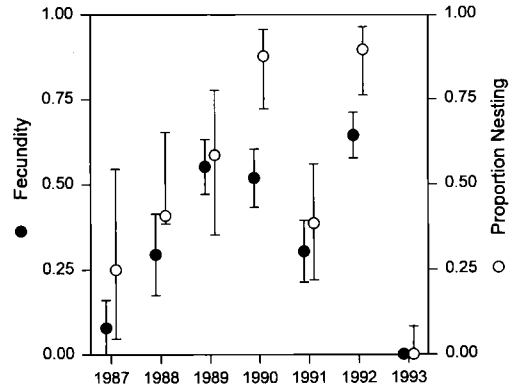

FIGURE 5. Annual fecundity and proportion of ≥3-yr-old female Northern Spotted Owls nesting on the Olympic Peninsula Study Area, WA: 1987–1993. (●) with associated SEs indicates fecundity, defined as the number of female young fledged per female owl. (O) with associated 95% confidence intervals indicates proportion of females nesting.

ples for 1- and 2-yr-old birds were too small to calculate separate estimates for each age class, so we used a pooled estimate for those age classes (Olympic Peninsula $\bar{x} = 0.206$, SE = 0.106; Cle Elum $\bar{x} = 0.379$, SE = 0.120).

Fecundity varied among years on both study areas (Olympic Peninsula F = 20.834, df = 6, P < 0.001; Cle Elum F = 20.033, df = 4, P < 0.001) (Figs. 5, 6). Among-year variation in fecundity was due primarily to variation in the proportion of females that attempted to nest, which also varied among years (Olympic Peninsula $\chi^2 = 123.16$, df = 6, P < 0.001; Cle Elum $\chi^2 = 67.074$, df = 4, P < 0.001) (Figs. 5, 6). However, some of the variation in fecundity was also explained by among-year variation in rates of nest failure.

POPULATION RATE OF CHANGE

Survival estimates from the best age-class CR models produced $\hat{\lambda} = 0.947$ (SE = 0.026) for the Olympic Peninsula and $\hat{\lambda} = 0.924$ (SE = 0.032) for Cle Elum. Thus, the point estimates of $\hat{\lambda}$ indicated average annual declines in the territorial population of 5.3% on the peninsula and 7.6% on Cle Elum during the respective study periods. Estimates of λ were less than 1 on both areas (one-tailed test, H_o: $\lambda \geq 1$, Olympic Peninsula z = 2.07, P = 0.019; Cle Elum z = 2.35, P = 0.009). Substituting $\hat{S}_J$ for $\hat{\phi}_J$ in the population growth rate equation produced $\hat{\lambda} = 1.058$ (SE = 0.065) on the Olympic Peninsula and 1.024 (SE = 0.058) on Cle Elum. These estimates of λ were not dif-

ferent from 1.0 (one-tailed test, H_o: $\lambda \leq 1.0$, Olympic Peninsula z = −0.898, P = 0.815; Cle Elum z = −0.424, P = 0.664). However, power tests indicated that the chance of detecting a difference between the estimated rates of change and $\lambda = 1.0$ was low (10.9% on Cle Elum and 22.6% on the Olympic Peninsula).

CHANGES IN NUMBERS OF OWLS ON DENSITY STUDY AREAS

On the Olympic Peninsula Density Study Area the regression of the annual number of territorial
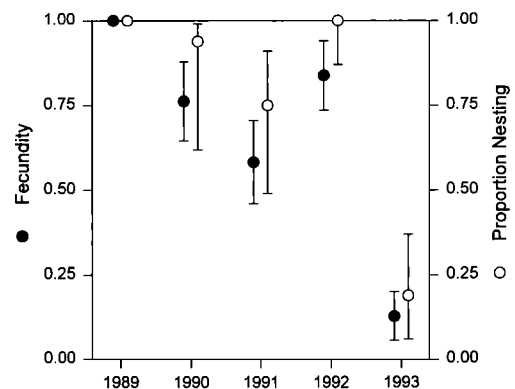

FIGURE 6. Annual fecundity and proportion of ≥3-yr-old female Northern Spotted Owls nesting on the Cle Elum Study Area, Washington, 1989–1993. (●) with associated SEs indicates fecundity, defined as the number of female young fledged per female owl. (O) with associated 95% confidence intervals indicates proportion of adult females nesting.
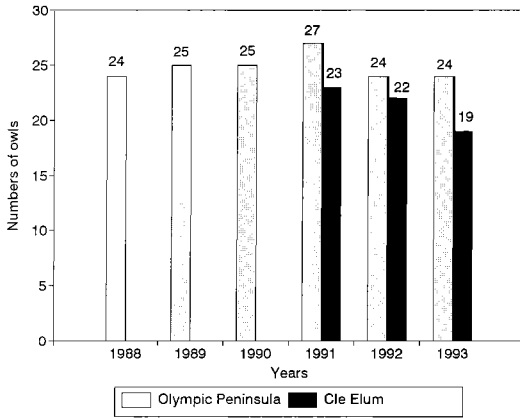
FIGURE 7.   Numbers of territorial Northern Spotted Owls detected during annual surveys on the Olympic Peninsula and Cle Elum Density Study Areas, WA.

owls detected on time (year) indicated no change in numbers from 1988–1993 (H_o: stable population, slope = -0.029, r = -0.04572, P = 0.932, Fig. 7). On the Cle Elum Density Study Area there was a slight (but non-significant) downward trend in the number of owls detected from 1991–1993 (H_o: stationary population, slope = -2.000, r = -0.961, P = 0.179, Fig. 7).

Although no trends were indicated on either study area, the power of the tests used to examine the null hypothesis that the population was stable was only 0.05 for the Olympic Peninsula and 0.06 for Cle Elum. With such low statistical power, it would take a minimum of 10–20 years of monitoring before significant trends could be detected if the annual rate of change was less than 5% per year.

DISCUSSION

SURVIVAL

Capture-recapture models that best fit the data indicated strikingly different patterns in the Olympic and Cle Elum Study Areas. The models that best fit the Cle Elum data indicated decreasing adult survival over time, whereas survival rates on the Olympic Peninsula did not vary among years. These differences were consistent regardless of whether we used models that included all birds divided into two age groups or models that included only birds that were ≥ 3 yrs old. We do not know why the two study populations should have differed regarding time effects on survival. A variety of possible explanations are possible, including small sample size, slight differences in timing of the two studies, local or temporal differences in climate, differ-

ences in prey populations, or differences in rates of habitat alteration.

In addition to emigration (discussed below) a variety of factors could have biased survival estimates. For example, broods of juveniles were often not banded until after they had been outside the nest for 1–6 weeks. As a result, owlets that left the nest, but died before we located and banded the remaining young were not included in the capture-recapture analysis. This should have caused a positive bias in survival estimates of juveniles, which were estimated from the date that juveniles left the nest. Another factor that may have caused a positive bias in juvenile survival estimates is that the capture interval during the first year of life was typically less than a year, again because many juveniles were not banded until they were out of the nest for some time (Franklin et al. *this volume*). While these positive biases are probably not large, they may at least partially compensate for the negative bias on survival estimates caused by emigration of juveniles.

EMIGRATION RATES

Our estimate of E_J was based on a much smaller data set than was used in the capture-recapture analysis, and only two cohorts were radio-marked for emigration estimates. If the sampled years were anomalous in any way, the results may be misleading. However, in the absence of more complete data, we believe it is reasonable to use the existing information to examine the possible influence of emigration on survival estimates of juvenile owls from capture-recapture studies like ours. This analysis indicates that emigration had a considerable effect on estimates of juvenile survival from CR data, as suggested in Bart (1995) and Burnham et al. (*this volume*).

FECUNDITY

Estimates of fecundity could have been positively biased if non-nesting females were less detectable than nesting females, or negatively biased if some juveniles died after they left the nest but before we estimated brood size. These biases were probably compensatory to some degree, but we had no way to assess them.

Reasons for the considerable annual variation in the proportion of females breeding were unknown, but a number of hypotheses have been proposed for this behavior in owls and other birds of prey, including annual or cyclic variation in prey populations and weather conditions (Pitelka et al. 1955, Southern 1970, Rusch et al. 1972, Adamcik et al. 1978, Newton 1979, Nero 1980, Forsman et al. 1984).

Estimates of adult fecundity on our study areas were higher than for most other study areas

(Burnham et al. *this volume*). Why owls near the northern limits of the range of the species should have higher average fecundity than owls in study areas closer to the center of the range is unclear. We do not believe this was due to biases in sampling procedure, because we used the same techniques on our study areas in Washington that were used on other study areas in Oregon and California. The comparatively higher fecundity on our study areas is particularly interesting in light of evidence that prey biomass on the Olympic Peninsula may be lower than in western Oregon (Carey et al. 1992).

POPULATION GROWTH RATES

Initial estimates of λ, without adjustment of $\hat{\phi}_J$ for emigration, indicated rapidly declining populations of Spotted Owls on both study areas. Estimates of λ based on $\hat{S}_J$ indicated non-declining populations in both study areas. However, we are reluctant to conclude that populations on either of our study areas were stationary, because our adjusted estimate of juvenile survival was based on small samples from only two years, and because there are a variety of other factors that can cause positive and negative biases in estimates of λ, as discussed earlier and in Bart (1995) and Raphael et al. (*this volume*). In addition, power to detect population trends based on only a few years of data is low (Taylor and Gerrodette 1993).

It is unclear how to reduce the effect of juvenile emigration on λ based on banding studies of Spotted Owls. The adjustment we performed relies on the assumption that survival of emigrants is equal to that of non-emigrants. However, if emigrants have a different survival than non-emigrants the adjusted survival rate could be biased either high or low.

In addition, the effect of emigration on $\hat{\lambda}$ for a given study area will depend in part on the rate of immigration, which is unknown. For the purpose of our analysis we assumed that there were no appreciable biases in any other parameter estimates, and addressed only the effects of emigration on juvenile survival estimates. If there is no immigration, then λ based on the CR estimate of ϕ_J will correctly reflect the population trend on the study site. If immigration exactly equals emigration, then λ based on $\hat{\phi}_J$ will underestimate the rate of population change, and λ based on $\hat{S}_J$ will be closer to the actual trend. If immigration is between 0 and the emigration rate, then the actual population trend will be somewhere between those two values of λ. If immigration exceeds emigration, then the actual population growth rate will exceed any of the estimates of λ.

From this discussion it should be clear that adjustments of parameter values to compensate for suspected bias can indicate a potential range for λ, but should not be taken as definitive measures of population trend. It does appear, however, that if there is any immigration at all, then population declines on the Olympic Peninsula and Cle Elum Study Areas are not as drastic as indicated by the unadjusted CR data.

Because adult emigration appears to be infrequent, and is difficult to document, we have ignored it, assuming $\phi_A = S_A$. An analysis of data from 37 radio-marked owls on the Olympic and Cle Elum Study Areas indicated that, although some movement occurred within the study areas, none of the owls left the study area during a two year period of study, with the exception of one bird that underwent temporary emigration (E. Forsman, unpublished data) Nevertheless, estimates of λ are highly sensitive to adult survival rates (Noon and Biles 1990), and a few percent bias in this parameter caused by occasional adult emigration could cause a negative bias of similar magnitude in λ, as suggested by Bart (1995).

CHANGES IN OWL NUMBERS

Regression analysis showed no change in the number of resident territorial owls on either of our Density Study Areas. However, a gradual decline (e.g., 1–5%/year) in the number of resident owls could easily go undetected by this analysis, because the regressions had low statistical power. Additionally, even if the total population were declining, there might be no change in the number of territorial birds during early years of the decline if the territorial birds that died were replaced by floaters (birds without territories). Thus, changes in density of territorial birds might not become apparent for many years, especially if the rate of population decline was small (e.g., 1–2% per year). If the rate of population decline was relatively large (e.g., 5–10% per year), declines in density should become apparent sooner. In either case, our studies are of short duration relative to the time needed to observe such changes.

Because Spotted Owls are relatively long-lived, occur at low densities, and have considerable annual variation in fecundity, it takes many years to get a sufficient sample size for estimation of vital rates and population trends. Our studies were of relatively short duration (Olympic Peninsula = 7 years, Cle Elum = 5 years). Power to detect trends in vital rates and annual rates of population change should improve as more years of data are collected.

SUMMARY

Examination of demographic trends in survival and reproduction is one of the most reliable methods of assessing the health of a population.

To evaluate the performance of Spotted Owl populations in Washington, we examined age-specific birth and death rates and population growth rates on two study areas, the Olympic Peninsula in northwestern Washington, and the Cle Elum Ranger District on the east slope of the Cascade Range. Duration of studies was 1987–1993 on the Olympic Peninsula and 1989–1993 on Cle Elum. The analysis indicated that annual adult survival was declining on Cle Elum. No trends in adult survival were apparent on the Olympic Peninsula. Fecundity of ≥ 3-yr-old females, expressed as the number of female young produced per female owl per year, averaged 0.380 (SE = 0.106) on the Olympic Peninsula and 0.565 (SE = 0.061) on Cle Elum. Fecundity of 1 and 2-yr-old females averaged 0.206 (SE = 0.106) on the Olympic Peninsula and 0.379 (SE = 0.120) on Cle Elum. Fecundity varied among years on both study areas (P < 0.001), primarily due to variation in the proportion of females that attempted to nest. Estimates of non-juvenile survival rates ($\hat{\phi}_{NJ}$) from the best 2-age-class capture-recapture models were 0.862 (SE = 0.017) on the Olympic Peninsula and 0.850 (SE = 0.031) on Cle Elum. Juvenile survival estimates ($\hat{\phi}_J$) from the same models were 0.245 (SE = 0.064) and 0.140 (SE = 0.046) on the Olympic and Cle Elum study areas, respectively. Emigration rates of radio-marked juveniles averaged 0.579 (SE = 0.113) on Cle Elum and 0.625 (SE = 0.121) on the Olympic Peninsula. Adjusting the mark-recapture estimates of $\hat{\phi}_J$ to account for emigration produced an adjusted estimate of juvenile survival ($\hat{S}_J$) of 0.611 (SE = 0.204) on the Olympic Peninsula and 0.349 (SE = 0.098) on Cle Elum. Without the adjustment for juvenile emigration, estimated annual rates of population change ($\hat{\lambda}$) were < 1 on both study areas (Olympic P = 0.019, Cle Elum P = 0.009), with the Olympic Peninsula and Cle Elum populations declining at 5.3 and 7.6% per year, respectively. With the adjustment for juvenile emigration, λ did not differ from 1.0 in either area (Olympic Peninsula P = 0.815, Cle Elum P = 0.664). However, statistical power to detect the estimated rate of change was low. Because small samples were used to estimate average rates of emigration, and because of other factors that could cause positive or negative biases in estimates of λ (Bart 1995), we stress that our analysis should not be interpreted as evidence of a non-declining population. However, the analysis does suggest that estimates of λ based on banding data alone are likely to underestimate λ. Annual counts of owls within two areas that were completely surveyed each year did not indicate a change in owl numbers on either area during the study (P > 0.05), although in both cases the estimated trends were negative. Statistical power of the regression used to test the null hypothesis (H_0: no change in owl numbers over time) was low (0.05–0.06), indicating that the ability to detect trends, even if they were present, was poor.