

DEMOGRAPHY OF NORTHERN SPOTTED OWLS ON THE H. J. ANDREWS STUDY AREA IN THE CENTRAL CASCADE MOUNTAINS, OREGON

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INTRODUCTION

We initiated intensive monitoring of a Northern Spotted Owl (*Strix occidentalis caurina*) population in the central Cascade Mountains of western Oregon in 1987. Our study was established to collect long-term demographic trend information in order to better understand the current status of the Northern Spotted Owl population in the western Oregon Cascades. In particular, we wanted to determine if concerns about gradual population declines in conjunction with habitat loss were well-founded (Thomas et al. 1990, 1993a; USDI 1990).

The H. J. Andrews Study Area (HJA) was an ideal location to examine these issues. Vegetation on the area is typical of much of the forest and land-use conditions on the west slope of the Cascade range in Oregon. The area also has a long history of Spotted Owl research. The first intensive study of Spotted Owl ecology, including home range size and habitat use, occurred on the HJA area and began in the early 1970s (Forsman 1980, Forsman et al. 1984). Several owl nest sites have been monitored periodically since that time. With this work came some of the first banded Spotted Owls, providing insights into the species' longevity. In addition, the first study of dispersal of juvenile Spotted Owls in Oregon was conducted on the HJA (Miller 1989), along with research on Spotted Owl prey species (Rosenberg 1991) and the influence of habitat fragmentation on owl populations (Johnson 1992).

Our objectives for this long-term monitoring study were to estimate survival based on capture-recapture methods, estimate age-specific fecundity based on direct observations of number of young fledged, and to use this information to calculate rate of population change (λ) for the period 1987–1993. We also compared these results to empirical counts of territorial owls, and discuss owl population dynamics in light of remaining amounts of late seral stage forest on our study area.

STUDY AREA

The 1,474 km² HJA Study Area is located on the west slope of the Cascade Mountain Range

in western Oregon, and includes the H. J. Andrews Experimental Forest plus adjacent lands on the Willamette National Forest, and some interspersed private holdings (Fig. 1). The study area is bounded on the east by wilderness and on the west by private lands and lands administered by the Bureau of Land Management. Topography is typical of the Western Cascades Province (Franklin and Dyrness 1973), with mountainous terrain deeply dissected by rivers and streams. Elevations range from 400–1,500m. Climate is maritime, with relatively dry summers and wet winters. Winter precipitation is often in the form of snow at higher elevations.

The study area is within the Western Hemlock (*Tsuga heterophylla*) Zone, the most extensive vegetation zone in western Oregon (Munger 1930, Franklin and Dyrness 1973). Subclimax forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western redcedar (*Thuja plicata*) dominate most of the area. Although about 52% of the study area has been harvested or is not considered Spotted Owl habitat, extensive stands of older forest are present on much of the area, with most stands being either older than 200 years of age or younger than 40 years of age. Late seral stage forest (≥ 80 yr-old) and younger forest (< 80 yr-old) accounted for 48% and 15%, respectively, of the area of the DSA, and 63% and 16% of the Experimental Forest (Table 1). The remaining land base was comprised of habitats that we believed were not suitable for spotted owls. We did not have estimates for cover types for the GSA.

The study area includes a central, 31,700-ha Density Study Area (DSA), nested within a larger 147,400-ha General Study Area (GSA). The 6,395-ha Experimental Forest is located within the boundaries of the DSA, and makes up 4% of the land area of the GSA (Fig. 1). Hereafter, reference to either GSA or HJA includes the DSA.

METHODS

FIELD METHODS

We monitored Spotted Owl demographic performance and territory occupation from 1987 to 1993. In general, calling surveys to locate Spotted

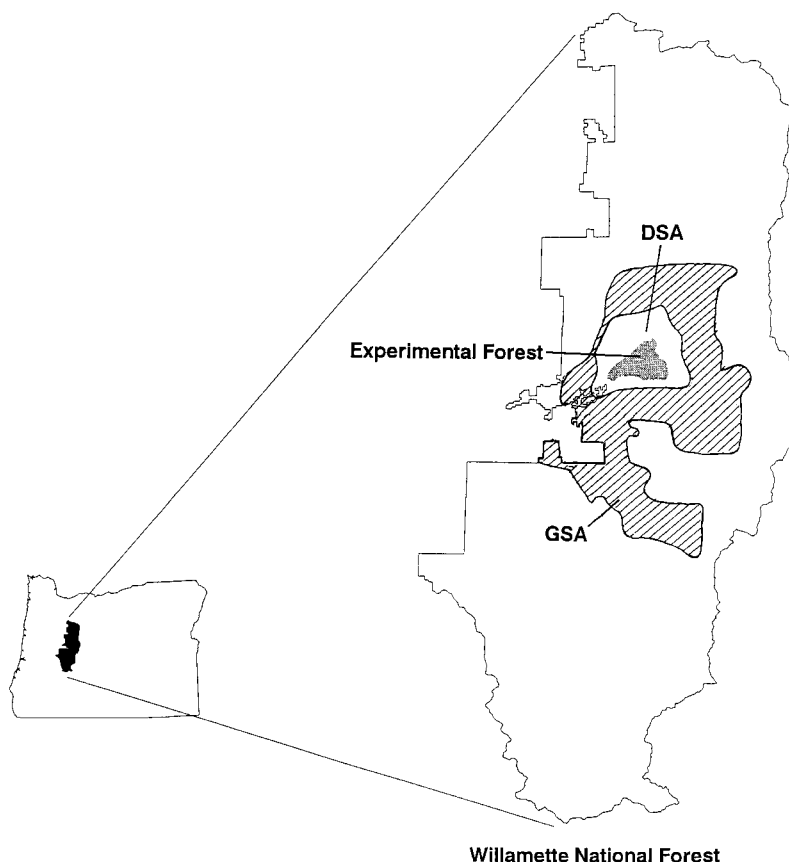


FIGURE 1. The H. J. Andrews Study Area (HJA) on the Willamette National Forest, west slope of the Cascade Mountain Range, Oregon. The study area included a 31,700-ha Density Study Area (DSA) that was nested within a larger 1,474 km² General Study Area (GSA) (diagonal-lined area). The 6,395-ha H. J. Andrews Experimental Forest (dark area) was part of the DSA.

Owls and capture and banding techniques followed Forsman (1983) and Franklin et al. (*this volume*).

Within the DSA, we did complete-coverage surveys, using both night and day calling, to locate owls. Within the GSA, we surveyed for owls in and around areas where we had banded pairs of owls, but we did not attempt to attain complete coverage of the entire area. Surveys were conducted from March–August. Each year, we first searched locations where pairs or single individuals had been located in previous years; historic nest sites and known roost sites were searched first. When there was no response by an owl, adjacent areas were searched. Area searches were initially conducted during the day for those sites with previous information on Spotted Owl use, and at night for those sites with no known history of Spotted Owl use. During day searches, observers walked sites systemati-

cally and used vocal imitations or taped calls to elicit responses from owls (Forsman 1983). In most cases, if owls were present they responded to the observer and could then be located visually at their roost. If day searches were unsuccessful on several occasions at the same site, night calling was initiated in hopes of obtaining a response. Late in the summer, night calling was conducted in the early morning hours, 1–2 hours prior to sunrise, providing the potential to contact owls just before they went to roost. If a response occurred, we had the opportunity to walk into the site as soon as it was light and locate owls on their roosts.

Owls were captured using a noose pole (Forsman 1983). U. S. Fish and Wildlife Service lock-on leg bands and colored plastic leg bands were placed on all owls captured. Owls ≥ 1 yr old were marked with unique color band combinations. Juvenile owls were all marked with the same

TABLE 1. AREA AND PERCENT COVERAGE OF FOUR MAJOR FOREST COVER TYPES ON THE DENSITY STUDY AREA (TOTAL AREA = 31,700 HA) AND EXPERIMENTAL FOREST (TOTAL AREA = 6,395 HA) ON THE H. J. ANDREWS STUDY AREA, WESTERN CASCADE MOUNTAINS, OREGON, 1987–1993. THE EXPERIMENTAL FOREST WAS A SUBSET OF THE DSA AND WAS LOCATED ENTIRELY WITHIN THE BOUNDARIES OF THE DSA. AREA ESTIMATE OF THE DSA INCLUDES THE EXPERIMENTAL FOREST. CLASSIFICATION OF COVER TYPES WAS BASED ON LANDSAT IMAGERY (SEE COHEN ET AL. 1995)

Area	Cover type	Area (ha)	% area
Density Study Area (DSA)	Water	148.2	0.5
	Non-habitat*	11,677.1	36.8
	≤80-yr-old forest	4,641.3	14.6
	≥80-yr-old forest	15,282.2	48.1
Experimental Forest	Water	0.4	<0.01
	Non-habitat	1,376.4	21.5
	≤80-yr-old forest	1,004.8	15.7
	≥80-yr-old forest	4,012.9	62.7

* Non-habitat included areas not suitable for Northern Spotted Owls, such as non-forested areas (e.g., agricultural fields, natural meadows), open and semi-open hardwood and conifer forest, and lava and rock.

color leg bands. If juveniles were encountered in subsequent years, they were recaptured and re-banded with unique color combinations.

We conducted complete annual counts of non-juvenile (≥ 1 yr old) territorial owls, which included pairs and resident singles, on the DSA. An owl was defined as a territorial individual if ≥ 2 visual or auditory detections were recorded, based on an established protocol (Franklin et al. *this volume*). We excluded owls whose territories straddled DSA boundaries or were in relatively inaccessible areas and thus were not surveyed on a consistent basis during each year of the study—we called these “adjusted” counts. For comparative purposes, we also report “unadjusted” counts, where unadjusted refers to inclusion of all owls on the DSA, regardless of whether or not they were included consistently in our annual counts.

We defined annual survey effort as the time spent by all crew members in field activities related to research, including night surveys, daytime follow-ups, and capture and banding. Total survey effort was recorded for the DSA and the GSA. We used linear regression and multiple regression (Ryan et al. 1980, SAS 1990b) to test for trends in density after accounting for differences in survey effort over time. Our ability to detect trends in numbers of owls over time, given our data, was examined with program TRENDS (Gerodette 1987).

We conducted nesting status surveys between 1 April and 1 June each year from 1988–1993. Once a pair was determined to be nesting, the nest site was visited during late May to mid-June to count fledglings. We made ≥ 2 visits to the site to find and count the number of young fledged, timing the visits so that young were observed as soon as possible after leaving the nest. A mini-

num of 4 mice were offered to one or both members of the pair during each visit, with visits separated by at least one week, to determine the reproductive status of the adult pair and to assist in locating the young (Forsman 1983, Franklin et al. *this volume*). Annual fecundity was defined as the number of female young produced per female owl, and was based on the number of young leaving the nest (fledging) (Franklin et al. *this volume*). Fecundity was estimated separately for 1–2-yr-old owls and for owls ≥ 3 yrs old (“adults”).

DATA ANALYSIS

We used capture-recapture models to estimate age- and sex-specific survival of color-marked owls (Franklin et al. *this volume*). Capture histories (Burnham et al. 1987:28–36) that spanned the 7-yr period (1987–1993) were developed for each marked owl. Owls were grouped according to sex and age (juveniles were < 1 yr old, non-juveniles were ≥ 1 yr old, adults were ≥ 3 yrs old).

We used program RELEASE to summarize our capture-release data, to conduct goodness-of-fit tests (GOF) to assess the fit of our data to the Cormack-Jolly-Seber (CJS) model (Pollock et al. 1990, Burnham et al. 1987), and to compare survival rates of adult males and adult females. In RELEASE, GOF tests consist of 2 components, which Burnham et al. (1987:71–77) refer to as TEST 2 and TEST 3. TEST 2 tests several of the requisite assumptions of the CJS model (Franklin et al. *this volume*), but focuses on cohorts of owls (i.e., groups of birds rereleased during the same year). TEST 3 focuses on subcohorts (i.e., individuals with the same capture histories) and tests whether previously released individuals have the same future fates as newly released individ-

TABLE 2. NUMBERS OF NORTHERN SPOTTED OWLS BANDED ON THE H. J. ANDREWS STUDY AREA (HJA) IN THE CENTRAL CASCADES OF WESTERN OREGON DURING 1987-1993

Year	Adult (≥3 yrs) females	Adult (≥3 yrs) males	1-2-yr-old females	1-2-yr-old males	Juveniles
1987	17	20	3	2	12
1988	24	22	3	10	37
1989	26	30	4	7	24
1990	15	11	8	1	29
1991	7	15	3	4	26
1992	17	17	5	3	98
1993	3	8	1	3	0
Totals	109	123	27	30	226

uals. Both TEST 2 and 3 consist of a series of χ^2 contingency tables, the results of which are additive and can be reported as TEST 2 + 3 (Burnham et al. 1987). A P-value that was not significant (>0.1) indicated that there were no differences in estimates of survival and recapture probabilities among cohorts or in the future fates of subcohorts of owls, and thus the data examined fit the CJS model.

Program RELEASE will also compare 2 groups and calculate a survival ratio (\hat{s}) where $\hat{s} = \hat{\phi}_t / \hat{\phi}_c$, t is treatment effect, and c is control (Burnham et al. 1987:56-71). An s -ratio $\neq 1.0$ indicates a treatment effect on survival. We compared survival in adult males and adult females, where our "treatment effect" was sex.

We used program SURGE for model building and selection and to produce estimates and variances of survival rates ($\hat{\phi}$) and capture probabilities (\hat{p}) (Clobert et al. 1987, Lebreton et al. 1992). Model parameterization followed Franklin et al. (*this volume*) and included considerations for age, sex, and time (years) (see Appendix for notation and subscripts). Model selection philosophy followed the principle of parsimony (Burnham and Anderson 1992) and used Akaike's Information Criteria (AIC) as the basis to select the most appropriate or best model (i.e., the model with the fewest parameters that fit the data and was, in our judgment, biologically realistic) (Akaike 1973, Anderson et al. 1994, Burnham et al. 1995a, Franklin et al. *this volume*). Models with the lowest AIC value are considered the most appropriate, and those that differed from the best model by an AIC value of ≤ 2 are presented for comparative purposes. Likelihood ratio tests (McCullough and Nelder 1983) were used to compare models with similar AIC values.

We examined two groups of models based on age of owls: (1) adult and (2) age-class (juvenile-nonjuvenile) models. Not all owls that are 1 or 2 yrs old breed, but our sample of marked owls

in this age range was small. We thus combined data for all owls ≥ 1 yr old (i.e., nonjuveniles) for the age-class models. We did suspect, however, that adults (i.e., owls ≥ 3 yrs old) had different survival rates than 1-2-yr-old birds, and so we ran survival models that considered only owls ≥ 3 yrs old.

We computed lambda (λ), the finite rate of population change, from our age-specific survival and fecundity estimates for the time period 1987-1993 (Franklin et al. *this volume*). Calculation of λ is based on the matrix theory developed by Leslie (1945, 1948) and Lefkovich (1965), and is explained more fully by Franklin et al. (*this volume*). We used the 1-tailed form of the t-test to test the null hypothesis that $\lambda < 1$, which would indicate a declining population during 1987-1993 for the resident Spotted Owl population on the HJA Study Area.

Calculations of λ are based on age-specific survival and do not account for permanent emigration. Emigration of marked juvenile owls off of the HJA Study Area undoubtedly occurred, but because the HJA was relatively isolated (i.e., there was only one other demography study nearby), the probability of detecting an owl that moved off the area was low. Therefore, we asked the question, "what would juvenile emigration rate have to be in order for λ to equal 1?" We also asked this same question with regards to juvenile survival, i.e., "what would juvenile survival rate have to be in order for λ to equal 1?" The equation used for answering these questions is given by Franklin et al. (*this volume*).

We used LANDSAT information to categorize types of habitat within the boundaries of the Experimental Forest and the larger DSA (LANDSAT data on cover types were not available for the entire GSA). Original LANDSAT landform classifications were developed by Cohen et al. (1995). We pooled Cohen et al.'s 12 classifications to 4 cover types, based on their potential suitability as Spotted Owl habitat. These categories were water, non-habitat, closed-canopy forest < 80 years old, and forests 80 years or older. Non-habitat included land areas not suitable for owls such as non-forested areas (e.g., agricultural fields, natural meadows), open and semi-open hardwood and conifer forest, and lava and rock. We calculated total land area (ha) and percent coverage for each category.

RESULTS

NUMBER OF OWLS MARKED AND RESIGHTED

During 1987-1993, we color-marked 515 spotted owls, including 226 fledglings, 57 1- or 2-yr-old birds, and 232 adults (≥ 3 yrs old) (Table 2). Recapture or resighting rates as defined by

TABLE 3. MARK-RECAPTURE DATA DISPLAYED IN *M*-ARRAY FORMAT FOR FEMALE AND MALE NORTHERN SPOTTED OWLS INITIALLY CAPTURED AS JUVENILES (<1 yr old), 1- or 2-year-olds, and adults (≥ 3 yr old) in the central cascade range of Oregon, 1987–1993. R_i IS THE NUMBER OF ANIMALS MARKED AND RELEASED ON THE *I*TH OCCASION, m_{ij} THE NUMBER OF ANIMALS MARKED AND RELEASED ON OCCASION *I* WHICH WERE RECAPTURED (OR RESIGHTED) ON OCCASION *J*, AND r_i THE TOTAL NUMBER OF ANIMALS MARKED AND RELEASED ON OCCASION *I* WHICH WERE LATER RECAPTURED ($= \sum m_{ij}$) (BURNHAM ET AL. 1987)

Cohort	i	R_i	m_{ij} for j =							r_i
			2	3	4	5	6	7		
Juveniles (sexes combined)	1	12	0	2	1	2	0	0	5	
	2	37		2	0	2	0	0	4	
	3	28			2	3	2	1	8	
	4	32				3	1	1	5	
	5	36					6	3	9	
	6	106						7	7	
1–2-yr-old females	1	3	2	0	0	0	0	0	2	
	2	5		4	0	0	1	0	5	
	3	8			6	0	0	0	6	
	4	14				6	2	1	9	
	5	9					7	1	8	
	6	15						9	9	
1–2-yr-old males	1	2	2	0	0	0	0	0	2	
	2	12		10	0	0	0	0	10	
	3	17			13	0	1	0	14	
	4	14				12	0	0	12	
	5	16					14	0	14	
	6	18						11	11	
≥ 3 -yr-old females	1	17	15	1	0	0	0	0	16	
	2	39		27	3	1	1	0	32	
	3	54			37	6	0	1	44	
	4	55				43	4	0	47	
	5	57					42	5	47	
	6	64						28	28	
≥ 3 -yr-old males	1	22	20	0	0	0	0	0	20	
	2	40		27	0	0	0	1	28	
	3	57			43	3	1	0	47	
	4	54				40	3	0	43	
	5	58					42	6	48	
	6	63						40	40	

Burnham et al. (1987:28–36) were 72–80% for owls ≥ 1 yr old (Table 3). No differences in resighting rates were detected between females and males ($\chi^2 \leq 1.0$, $df = 1$, $P \geq 0.31$). Resighting rate for juveniles (birds <1 yr old), however, was 15%, and was lower than those for other age cohorts ($\chi^2 \geq 142$, $df = 1$, $P < 0.001$), probably because juveniles experienced lower rates of survival and higher rates of emigration from our study area than nonjuveniles.

NUMBERS OF TERRITORIAL OWLS ON DSA

Our adjusted counts of number of territorial owls on the DSA were lower than the unadjusted counts for each year during 1988–1993 (1987 was not included because a complete survey of the entire DSA was not conducted that year). This is understandable because the adjusted counts excluded some owls, i.e., those whose territories straddled the DSA boundary or were in

relatively inaccessible areas and thus were not consistently included in annual surveys. However, both the unadjusted and adjusted annual estimates of owl numbers within the DSA showed similar trends over time (Fig. 2).

Adjusted counts of owls on the DSA varied by year, but we did not detect an increasing or decreasing trend over time ($r = 0.22$, slope = 0.06, $t = 0.04$, $df = 4$, $P = 0.97$). The power to detect a trend, either increasing or decreasing, however, was low ($1 - \beta = 0.46$) (Gerrodette 1987, Peterman 1990). The proportion of owls detected in the DSA that were banded in a previous year increased from 0.40 in 1988 to a mean of 0.80 (SE = 0.02) per year for the remaining years of the study (1989–1993) (Fig. 3).

DISTRIBUTION OF SURVEY EFFORT

Survey effort for all owl-related research activities on the DSA increased during 1987–1993

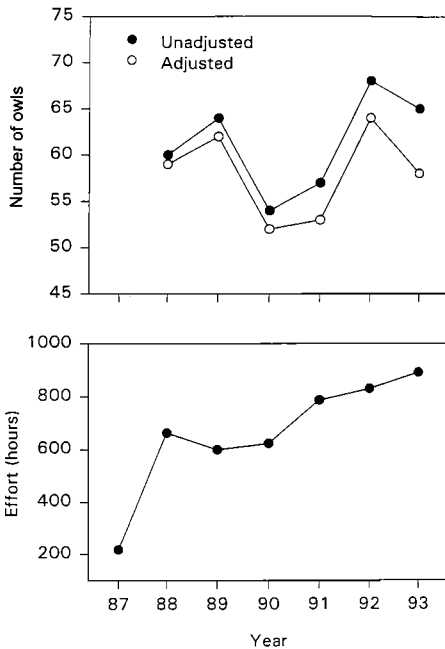


FIGURE 2. Trend in numbers of Northern Spotted Owls detected and survey effort for demographic studies on the H. J. Andrews Density Study Area in the central Cascades of western Oregon, 1988–1993. Survey effort was measured as number of hours expended to conduct all field activities related to research on Spotted Owls, including surveys, searches for nests, capture and banding, and observation of banded individuals. The trend in numbers of owls detected was not different from 0 when corrected for survey effort.

($r = 0.88$, slope = 90.9, $t = 4.12$, $df = 5$, $P = 0.009$, Fig. 2). A similar, somewhat weaker, trend was observed for the GSA ($r = 0.78$, slope = 130, $t = 2.77$, $df = 5$, $P = 0.04$). The largest increase in effort occurred between the first and second years (1987–1988) because field work began later in 1987 compared to other years. Effort appeared to approach an asymptote, which is common for long-term field studies (Franklin et al. 1990, *this volume*). After accounting for the increase in survey effort over time, the trend in annual owl counts did not differ from 0 during 1988–1993 (slope = -1.1 , $t = -0.36$, $P = 0.74$). Numbers of owls varied among years, but there was no obvious increasing or decreasing long-term trend.

FECUNDITY ESTIMATES

Estimated mean annual fecundity was 0.35 (SE = 0.03) for ≥ 3 -yr-old females and 0.15 (SE = 0.10) for 1–2-yr-old owls. Fecundity was consistently higher for adults than younger owls ($t = 6.14$, $df = 63$, $P < 0.001$, $N = 377$ adults and

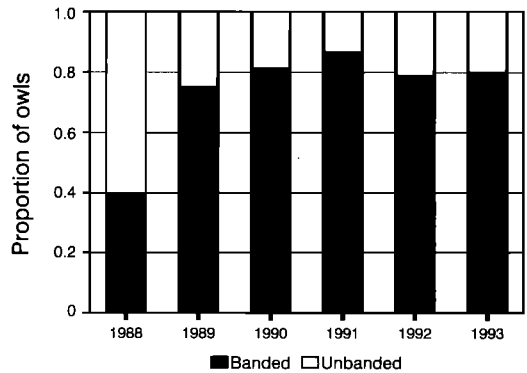


FIGURE 3. Proportion of Northern Spotted Owls detected each year within the 31,700-ha H. J. Andrews Density Study Area that had been banded in previous years, 1988–1993.

30 1–2-yr-old owls). In addition, fecundity and proportion of adult females nesting were high in 1988, 1990, and 1992, and low during alternate years (1987, 1989, 1991, and 1993) (Fig. 4). No successful reproductive activity was detected among the 50 pairs of owls monitored during 1993.

MODEL SELECTION AND ESTIMATES OF SURVIVAL

The combined results for Tests 2 and 3 in Program RELEASE indicated that the data from adult males fit the Cormack-Jolly-Seber model (i.e., no differences in survival rates and recapture probabilities among cohorts [annual releases of marked birds] or in future fates among individual males were detected, $\chi^2 = 16.2$, $df = 12$, $P = 0.18$ for Tests 2 + 3). This was not the case for adult females, however, at least at a probability level of 0.10 ($\chi^2 = 19.9$, $df = 13$, $P = 0.10$ for Tests 2 + 3). Any problems with lack of fit in the adult female data came from the TEST 3 component of the GOF test, indicating that, in a given year, newly banded and released individuals may have had different future fates than previously banded and released individuals ($\chi^2 = 17.0$, $df = 9$, $P = 0.05$ for TEST 3). TEST 2 indicated that fit was adequate for this component of GOF testing (i.e., no differences detected in survival rates and capture probabilities among cohorts, $\chi^2 = 2.8$, $df = 4$, $P = 0.59$ for TEST 2). Sample sizes and recapture rates were inadequate to test goodness-of-fit for juveniles and 1–2-yr-old owls. Despite evidence that there may have been some lack of fit to the assumptions in the Cormack-Jolly-Seber models, we proceeded with model testing, assuming that estimates would not be greatly influenced by some lack of fit.

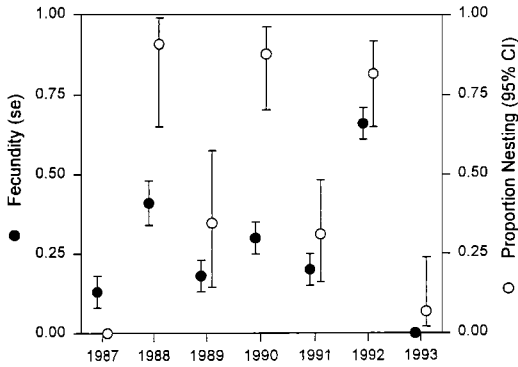


FIGURE 4. Estimated fecundity (± 1 SE) and proportion of females nesting ($\pm 95\%$ CI) for adult female Northern Spotted Owls on the H. J. Andrews Study Area, western Cascade Mountains, Oregon, 1987–1993.

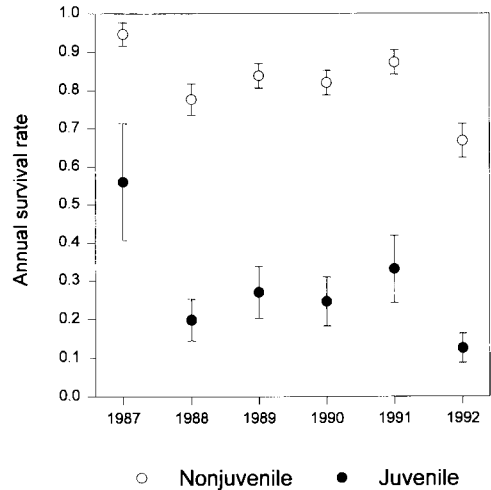


FIGURE 5. Estimates of survival (± 1 SE) for nonjuvenile (≥ 1 yr old) and juveniles (< 1 yr old) Northern Spotted Owls on the H. J. Andrews Study Area, western Cascade Mountains, Oregon, 1987–1993.

Of the 64 adult models examined, the five most parsimonious models (those with the lowest AIC values) all had some form of time variation associated with the capture probabilities, but survival rates appeared constant, with only weak time or sex effects indicated (Table 4). Of the 28 age-class models examined, the model with the lowest AIC value had 11 parameters. This model ($\{\phi_{a2+t}, p_{a3+s}\}$) indicated that survival was a function of two age classes and varied nonlinearly among years, while recapture probability was a function of three age classes and sex. We selected this model as our “best” model, i.e., a biologically reasonable model that followed the principle of parsimony (Franklin et al. *this volume*). The model with the second lowest AIC value (ϕ_{a2+t}, p_{a3+s}) was a 16-parameter model that was not competitive, based on likelihood ratio tests ($\chi^2 = 9.7$, $df = 5$, $P = 0.09$, Table 4).

The annual survival estimate for ≥ 3 -yr-old owls from the best adult model ($\{\phi, p_{s+T}\}$) was 0.848 (SE = 0.018). The remaining top competing adult models provided similar survival estimates for adults (Table 5). In models that treated sexes separately, survival was not different between males and females (TEST 1, $\chi^2 = 11.5$, $df = 11$, $P = 0.4$). Estimates of survival from the best age-class model (ϕ_{a2+t}, p_{a3+s}) averaged 0.821 (SE = 0.016) for nonjuveniles and 0.288 (SE = 0.052) for juveniles (Table 5).

We plotted estimates of survival for nonjuveniles and juveniles, based on our best age-class model over time (Fig. 5) and tested the null hypothesis that there was not a negative trend in survival. Survival rates did decline during 1987–1993 for both nonjuveniles ($r = -0.64$, slope = 3.69, $df = 5$, $t = 2.12$, $P = 0.04$ for 1-tailed test) and juveniles ($r = -0.64$, slope = 4.89, $df = 5$,

$t = 1.78$, $P = 0.07$ for 1-tailed test). In addition, there was a similar pattern in annual variation in survival between nonjuveniles and juveniles (Fig. 5).

POPULATION RATE OF CHANGE

Using the estimates of survival from the best age-class model and our empirical estimates of

TABLE 4. SUMMARY OF CAPTURE-RECAPTURE MODELS EXAMINED FOR ESTIMATING SURVIVAL (ϕ) AND RECAPTURE (p) PROBABILITIES FOR NORTHERN SPOTTED OWLS ON THE H. J. ANDREWS STUDY AREA IN THE CENTRAL CASCADES OF WESTERN OREGON DURING 1987–1993

Model*	Number of parameters	Deviance	AIC*
Adult models			
$\{\phi, p_{s+T}\}$	4	882.2	890.2
$\{\phi_t, p_{s+T}\}$	9	872.5	890.5
$\{\phi_s, p_{s+T}\}$	5	880.6	890.6
$\{\phi_{s+t}, p_{s+t}\}$	13	864.9	890.9
$\{\phi_s, p_{s+t}\}$	8	875.0	891.0
Age-class (juvenile-nonjuvenile) models			
$\{\phi_{a2+t}, p_{a3+s}\}$	11	1325.3	1347.3
$\{\phi_{a2+t}, p_{a3+s}\}$	16	1320.9	1352.9
$\{\phi_{a2+t}, p_{a3+s}\}$	18	1320.9	1356.9
$\{\phi_{a2+T}, p_{a3+s}\}$	7	1343.0	1357.0
$\{\phi_{a3+t}, p_{a3+s}\}$	21	1315.8	1357.8

* Model subscripts include s for sex, t for time as a categorical variable, and T for time as a continuous (linear) value. A + or * between subscripts signifies additive or multiplicative interactions, respectively, between variables.

† Akaike's Information Criterion (Akaike 1973; Franklin et al. *this volume*).

TABLE 5. ESTIMATES OF ANNUAL SURVIVAL (ϕ) FOR NORTHERN SPOTTED OWLS CALCULATED FROM SELECTED CAPTURE-RECAPTURE MODELS, H. J. ANDREWS STUDY AREA IN THE CASCADE MOUNTAINS OF WESTERN OREGON, 1987-1993

Model*	Juveniles		Nonjuveniles	
	$\hat{\phi}_j$	SE ($\hat{\phi}_j$)	$\hat{\phi}_\lambda$	SE ($\hat{\phi}_\lambda$)
Adult models (≥ 3 -yr-old owls)				
$\{\phi, p_{s+T}\}$			0.848	0.018
$\{\phi_t, p_{s+T}\}$			0.840 ^b	0.024 ^c
$\{\phi_s, p_{s+T}\}$			δ : 0.872	0.024
			δ : 0.830	0.024
$\{\phi_{s+t}, p_{s+t}\}$			δ : 0.889 ^b	0.017 ^c
			δ : 0.834 ^b	0.017 ^c
$\{\phi, p_{s+1}\}$			0.851	0.017
Age-class models (juvenile-nonjuvenile owls)				
$\{\phi_{a2+t}, p_{a3+s}\}$	0.288 ^b	0.052 ^c	0.821 ^b	0.016 ^c
$\{\phi_{a2+t}, p_{a3+s}\}$	0.337 ^b	0.052 ^c	0.820 ^b	0.016 ^c
$\{\phi_{a2+t}, p_{a3+s}\}$	0.337 ^b	0.052 ^c	0.820 ^b	0.016 ^c
$\{\phi_{a2+T}, p_{a3+s}\}$	0.253 ^b	0.052 ^c	0.822 ^b	0.016 ^c
$\{\phi_{a3+t}, p_{a3+s}\}$	0.385 ^b	0.052 ^c	0.255 ^{b,d}	0.052 ^c
			0.821 ^{b,e}	0.016 ^c

* Model subscripts include s for sex, t for time as a categorical variable, and T for time as a continuous (linear) value. A + or * between subscripts signifies additive or multiplicative interactions, respectively, between variables.

^b Survival estimates averaged over time (years).

^c Standard error is an approximation based on the nearest (in AIC) model with no time effects on survival probability.

^d Survival estimate for second-year owls (1-yr-old).

^e Survival estimate for third-year owls (2-yr-old owls) and adults.

age-specific fecundity, we estimated $\lambda = 0.911$ (SE = 0.012), which was < 1.0 ($z = 7.42$, $P < 0.001$). Among the potential biases that may affect calculations of λ (Bart 1995a), we were particularly interested in the influence of juvenile survival or emigration. We, therefore, asked the question, "assuming that λ is really equal to 1.0, and that all other parameters were estimated accurately, how much undetected emigration by juveniles would have to occur, or what would juvenile survival have to be, to attain a λ equal to 1?" Based on additional calculations carried out during the meta-analysis by Burnham et al. (*this volume*), juvenile dispersal (i.e., young of the year surviving and leaving the study area but not being resighted) would have to be 54% or juvenile survival would have had to be 63% for $\lambda = 1.0$.

DISCUSSION

Empirical counts of Northern Spotted Owls on our Density Study Area indicated that the territorial population was relatively stationary during 1987-1993. However, our ability to detect a change in numbers over time was low ($1 - \beta = 0.46$), even for the relatively long period of our study (7 years). We suspect that several more

years of count data would be needed in order for us to detect a negative or positive trend in numbers, or to be assured that the territorial population is indeed stationary, based on these kinds of data.

Our calculations of rate of population change ($\lambda = 0.91$, SE = 0.02) suggested that the population of Northern Spotted Owls on the HJA was declining at an annual rate of 9% from 1987 to 1993, which at first seems contradictory to our empirical counts. However, we recommend caution when attempting to relate empirical counts of owls to annual rate of change. Our counts of territorial owls were based on a subsample of the population (DSA only), whereas the estimate of λ was based on owls throughout the entire study area. The rate of tree harvest during the period of this study was less within the DSA than on the rest of the study area, in part due to the influence of the Experimental Forest, which has different management objectives than the rest of the Willamette National Forest and thus lower rates of timber harvest. In addition, the proportion of marked owls on the DSA remained constant at about 80% for each year from 1988-1993. This is an indication that there was at least some turnover (i.e., emigration or mortality of marked owls, which were replaced by unmarked owls) of marked owls on the DSA, because one would suspect that the proportion of marked owls would increase over time rather than remain stable. This premise would be especially true when survey effort is high, as occurred on the HJA area during the last several years of the study.

The juvenile survival rate necessary to make $\lambda = 1.0$ (0.63) was probably higher than what juvenile owls actually experienced on the HJA, but perhaps not unrealistic. Miller (1989) reported an estimated first-year survival rate of 19% with cohort differences from 5-37%, while Forsman et al. (*this volume*) reported juvenile survival, which they adjusted for emigration, of 35% for central Washington and 61% for the Olympic Peninsula.

The juvenile emigration rate necessary to make $\lambda = 1.0$ (0.54) probably was possible for juvenile Spotted Owls banded on the HJA Study Area. This inference is based on the results of two other studies. In 1983, nine juvenile Spotted Owls were radio-marked on the HJA Study Area and followed through dispersal (Miller 1989). All nine of the juveniles left the HJA area and did not return (although radio contact was lost for three of these individuals). In another study, Forsman et al. (*this volume*) found that about 60% of radio-marked juveniles moved off of their study areas in Washington. These data indicate that, for a relatively isolated study area like ours, a juvenile emigration rate of 50-60% is likely. It is therefore

possible that a relatively large number of marked juveniles left the HJA Study Area, survived, and went undetected.

Reproductive effort was highly variable on an annual basis, with extremes of virtually no successful reproductive output at all (1993) to very high reproductive output (1992). There was also an interesting pattern of alternatively high and low years of both proportion of females nesting and fecundity. We have not identified a mechanism to explain this pattern and the synchrony among female owls, but suspect food resources may play a role.

Our description of remaining late seral stage forest and other cover types that may be used by owls (i.e., forest <80 yrs old) is cursory at best, but it does provide at least some information on the amounts of these cover types on part of the HJA Study Area. This area contains perhaps some of the best remaining owl habitat in the Pacific Northwest (Thomas et al. 1990). We are convinced that Spotted Owls use, and probably depend, on late seral stage forest for most if not all phases of their life history (breeding, roosting, feeding, protection from predators) (Forsman et al. 1984, Bart and Forsman 1992). In light of this fact, and based on the demographic information provided in this paper, we offer the following conclusions: (1) given our estimate of λ (0.91) and the trend of variable but declining survival rates of nonjuveniles and juveniles over time, we doubt that the Spotted Owl population on the HJA Study Area was stable during 1987–1993; (2) we suspect, however, that the rate of decline was lower than the estimated 9% per year decline suggested by λ because juvenile survival was probably higher than we were able to estimate, given the negative influence that permanent emigration can have on estimations of survival; (3) the remaining tracts of late seral stage forest do, however, provide the potential to maintain a stable population of Spotted Owls on the HJA area, if perhaps at lower than historical levels; and (4) retention of large stands of old growth trees and the use of silvicultural techniques to enhance and promote the maintenance of late seral stage forest would probably help to ensure adequate habitat for Spotted Owls and their prey. The latter point is still a viable option on HJA because harvest of old forests has not been as intensive or extensive as many other parts of the Northern Spotted Owl range (Thomas et al. 1990).

It is also clear to us, given the above discussions of empirical count data, annual variability in reproduction, calculations of survival rates, and juvenile survival and emigration, that determining the status of the Spotted Owl population on the HJA is a difficult task, even with 7 years of data. Intensive monitoring of marked

owls on the HJA should be continued, along with increased efforts to document juvenile movements and survival rates. Given the potential life span of a Northern Spotted Owl of perhaps 8–10 yrs (Forsman and Meslow 1986), monitoring and marking should continue for at least 2–4 generations, or about 10–30 additional years.

SUMMARY

We collected demographic trend information on Northern Spotted Owls in the central Cascade Mountains of western Oregon during 1987–1993 in order to better understand the current status of the population and to calculate population rate of change. The H. J. Andrews (HJA) Study Area was an ideal location to examine these issues because the area is typical of much of the forest and land-use conditions on the west slope of the Cascade range in Oregon, and the HJA has a long history of Spotted Owl research, dating back to the early 1970s. We counted numbers of territorial owls, captured and banded 515 owls, collected resightings of marked owls, and determined fecundity (number of female fledglings produced per female) in the field. We then used capture-recapture models to estimate age- and sex-specific survival of color-marked owls and computed λ , the finite rate of population change, from our age-specific survival and fecundity estimates for the time period 1987–1993. Annual adult and juvenile survival rates were 0.82 (SE = 0.02) and 0.29 (SE = 0.05), respectively, and annual age-specific fecundity was 0.35 (SE = 0.03) female young per adult female and 0.15 (SE = 0.10) per 1- or 2-yr old female. Based on these parameters, we estimated an annual rate of population change (λ) of 0.91 (SE = 0.012), which was significantly <1, indicating that the population of resident adults was declining at a rate of about 9% per year. However, this rate of decline was likely an overestimate because juvenile survival and/or emigration was probably higher than our calculations showed. We conclude that the Spotted Owl population probably declined on the HJA area during 1987–1993, but at a rate lower than indicated by λ .

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Key words: demography, fecundity, Northern Spotted Owl, Oregon, *Strix occidentalis*, survival estimation, threatened species.