

An Update of Demographic Estimates for the Northern Spotted
Owls (*Strix occidentalis caurina*) from Oregon's Central Coast Ranges

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Abstract.—Demographic characteristics of the Northern Spotted Owl (*Strix occidentalis caurina*) were studied on the Eugene District Bureau of Land Management, central Oregon Coast Ranges from 1989-1995. Survival rates were estimated from capture histories of banded owls using Cormack-Jolly-Seber open population models. We banded 233 owls, including 119 that were ≥ 3 years old, 15 that were 1 or 2 years old, and 99 juveniles. Among year variation in the proportion of pairs nesting and fecundity of females was significant ($P < 0.001$). Estimates of apparent annual survival from the selected capture-recapture models were 0.306 (SE = 0.064) for juveniles and 0.875 (SE = 0.018) for subadult and adult owls combined. The estimated annual rate of population change (0.939, SE = 0.045) was < 1.00 ($P = 0.005$) over the 6 years of study, suggesting an average population decline of 6.1 percent per year. Counts of territorial owls decreased by 37 percent from 1990-1995 on the Wolf Creek density study area, a smaller area within the larger surrounding study area. We suggest the owl population decline was due to the reduction of spotted owl habitat.

In 1990 we initiated a demographic study of Northern Spotted Owls (*Strix occidentalis caurina*) on the western half of the Eugene District of the Bureau of Land Management (BLM) which is located in the central portion of the Oregon Coast Ranges. Anderson et al. (1990) identified the central Coast Ranges of Oregon as an "Area of Special Concern" because this region has been heavily impacted by timber harvest reducing both the quantity and quality of owl habitat. Thomas et al. (1990) argued for the use of demographic parameter estimates to infer the rate and direction of population change for spotted owls. The primary purpose of the study was to provide information on demographic performance and population trends of Northern Spotted Owls in a highly modified forest environment. We also believed that this project would provide information on the effects of forest management practices on the species (Thomas et al. 1993a).

At the request of the United State Secretaries of Agriculture and Interior, a workshop was convened in Fort Collins, Colorado in December 1993 to examine all existing demographic data on the Northern Spotted Owl. A main objective of the workshop was to review the demographic information from 11 study areas located throughout the range of the owl before implementation of Option 9 of the President's Northwest Forest Plan (Thomas et al. 1993b). The results were subsequently provided to the U.S. Forest Service (USFS) and BLM for inclusion in their planning documents. In addition, results from the individual study areas and a meta-analysis of the entire data set form the basis of chapters that comprise the publication *Studies in Avian Biology* No. 17.

Following the Fort Collins workshop, most of the spotted owl demography studies continued, as per one of the recommendations of the workshop. Specifically, the Eugene District BLM study continued for 2 additional years and was completed in 1995. The purpose of this paper is to provide an update of the Eugene BLM owl demographic estimates incorporating the 2 additional years of data and also to include results of analyses conducted on parameters (i.e., movements and turnover) not incorporated in our earlier work. Specific

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METHODS

Field Data Collection

objectives of the study were to estimate age-specific survival, birth, and reproductive rates of territorial spotted owls. We also provide information on trend in numbers of territorial owls detected within a smaller portion of the area, the Wolf Creek Density Study Area.

STUDY AREA

The 1,432 km² study area is located in the central Coast Ranges, 30 km west of Eugene, Oregon (fig. 1). Contained within the larger general study area is the Wolf Creek Density Study Area (DSA) (425 km²). Throughout the study area, intermingled land ownership produces a checkerboard pattern of alternating square mile sections (1.6 km²) that are administered by BLM (43.0 per cent), State of Oregon (5.0 per cent), private industrial timber companies and "other" ownerships (52.0 per cent) (fig. 1). Historically, the majority of both federal and privately owned lands were managed for timber production, with clear cutting of late-successional forest (>80 years old) being the major harvest method (Thraill et al. 1997). Topography is characterized by steep mountain slopes with narrow ridges and elevations ranging from 120 to 870 m. Climate is moderate maritime with most precipitation falling as rain during October-May. The study area is bounded on the north, west, and south by four other spotted owl demographic study areas (Franklin et al. 1996), which facilitated the reobservation of dispersing owls. East of the study area is the southern terminus of the Willamette Valley, a non-forested agricultural and urban/suburban valley.

Located within the western hemlock (*Tsuga heterophylla*) vegetation zone, the study area is dominated by forests of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (Franklin and Dyrness 1973). Through field inspections and interpretation of 1990 aerial photography, polygons were delineated that represented suitable, dispersal, and unsuitable spotted owl habitat, 22, 28, and 50 per cent respectively (Thraill et al. 1996). Old forest, in which the dominant overstory trees are >200 years old, comprises 11 per cent of the suitable habitat on the study area (fig. 2). Thomas et al. (1990) considered old forest as "superior" owl habitat. Suitable habitat within the DSA (24 per cent) was similar to the surrounding general study area (21 per cent). Please refer to Thraill et al. (1996) for a complete description of the habitat cover-types and study area.

Personnel on the Eugene BLM District began a spotted owl monitoring and banding program in 1986. Although our study did not formally begin until 1990, we included the cohort of owls banded by district personnel in 1989 (28 percent of our total sample) in our estimates of survival and fecundity. In 1990 we began systematic annual surveys (March-August) across the checkerboard ownership pattern of BLM, State of Oregon, and privately owned industrial forest lands to capture and mark unbanded owls and re-observe previously banded owls. Field methods used for surveying, locating, determining sex, capturing, reobserving, and banding spotted owls followed Forsman (1983), Miller et al. (1990), Franklin et al. (1996), and Thraill et al. (1996). Four spotted owl age-classes were distinguished: juveniles (J), subadults (1-year-old [S1] and 2-year-old [S2] owls) and adults (≥ 3 -yr-old) (Forsman 1981, Moen et al. 1991).

Survey effort on the Wolf Creek Density Study Area was consistent from 1990-1995 and consisted of complete coverage of the area with six replicate nighttime surveys each year during the nesting season (March-August). Within this area we attempted to confirm and band any owls that were encountered and determine their reproductive status (i.e., nesting status and number of young fledged).

Within the general study area (DSA excluded), we surveyed all known (historic) owl territories each year, to confirm presence of banded owls, band unbanded owls, and determine their reproductive status. Surveys of the territories were consistent each year and included six replicate nighttime surveys before concluding a territory (territory analogous to an owl site) was unoccupied in a given year. We defined an owl territory as a 2.4 km (1.5 mi) radius centered on an owl nest tree (or principal day roost site). This distance corresponded to the median annual home range size of an owl pair within this province as computed by the minimum convex polygon algorithm (Thomas et al. 1990:193-200). Surveys were also conducted in suitable owl habitat located between territories with the number of replicate surveys differing by year (1990:0-3 nighttime surveys, 1991-1995:5-6 nighttime surveys).



Figure 1.—Northern Spotted Owl (*Strix occidentalis caurina*) demography study area on the Eugene District Bureau of Land Management, central Oregon Coast Ranges, 1990-1995. Shaded sub-plot indicates location of the Wolf Creek density study area (DSA) within the larger surrounding general study area. BLM ownership is represented by black sections interspersed with white sections of non-federal ownership.

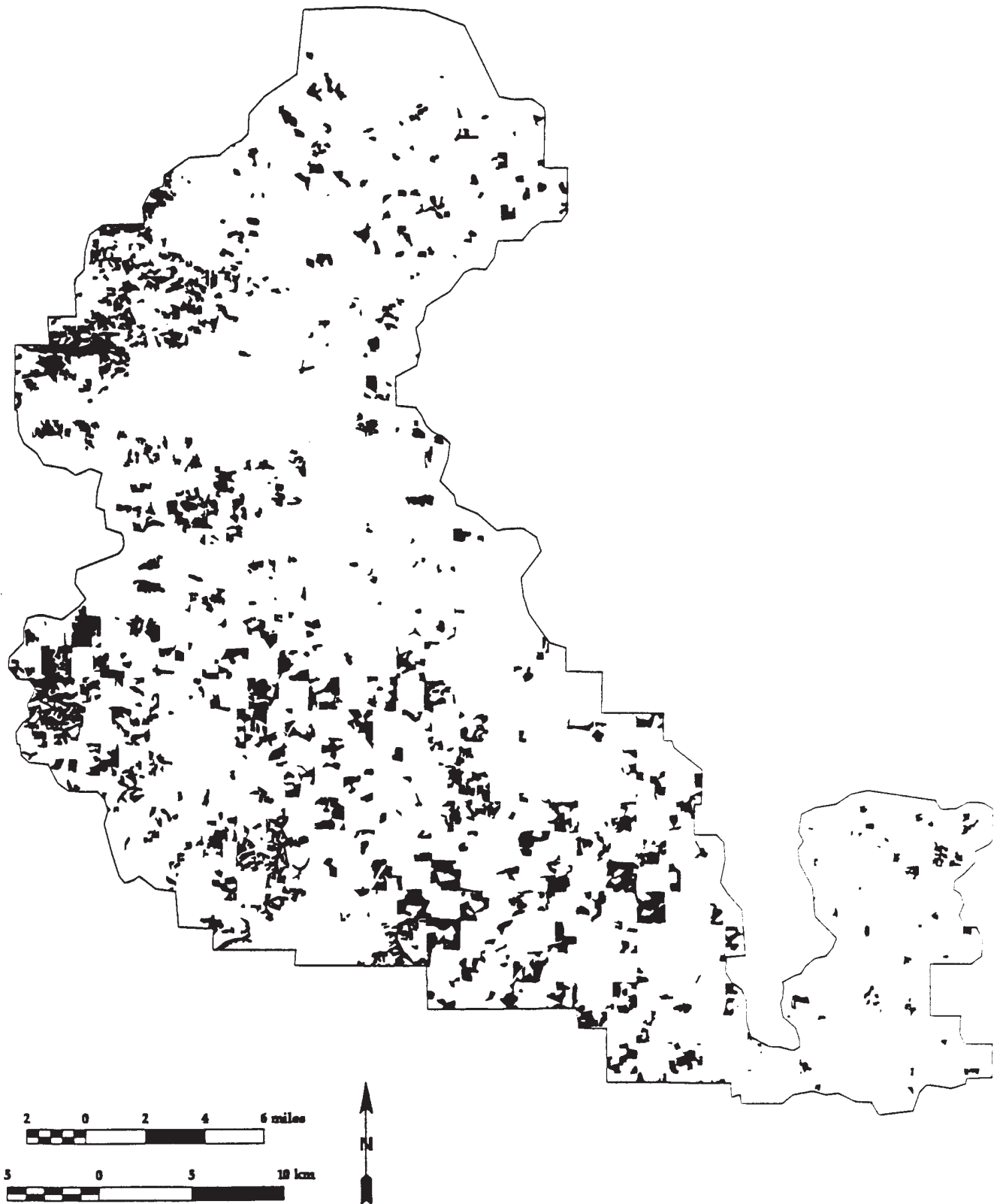


Figure 2.—Old and mature forest (> 80 years old) habitat patches on the Eugene District BLM Northern Spotted Owl (*Strix occidentalis caurina*) demography study area, central Oregon Coast Ranges, 1990.

Data Analysis

We used simple linear regression to assess annual trends in the number of owls detected in the Wolf Creek Density Study Area. Turnover rates were calculated as the proportion of marked territorial adult and subadult owls replaced by another individual or found missing from their territories for at least 1 year (Thraill et al. 1997). Annual turnover rates were a function of adult and subadult mortality, movements of banded birds between territories, and reoccupation and abandonment of territories.

Annual variation in proportions of pairs nesting and pairs checked for reproductive activity were analyzed using chi-square tests. Confidence intervals (95 percent) around mean proportions were calculated following Zar (1984:378-379). Mean fecundity ($\bar{b}_x$) was estimated for each age-class as the average number of female young produced per female each year. We assumed a 1:1 sex ratio and included all young located during the breeding period in fecundity estimates (Franklin et al. 1996). Annual variation in fecundity was analyzed using an ANOVA (Zar 1984:162-170).

Distance of owl inter-territorial movements and emigration (owls that moved off the study area and were re-observed) by age-class was examined. A movement was defined as a territorial owl relocating for at least 1 breeding season ≥ 2.4 km from their previous nest/activity area. A minimum emigration rate for the adult/subadult cohort was computed by dividing the number of emigrated owls by the total number of banded territorial owls.

Goodness-of-fit tests 2 and 3 in program RELEASE were used to determine if the capture-recapture data met the assumptions of the Cormack-Jolly-Seber capture-recapture model (Burnham et al. 1987, Franklin et al. 1996, Pollock et al. 1985). Survival and recapture rates were estimated using program SURGE (Lebreton et al. 1992). Notation of capture-recapture models included subscripts that indicated if a particular model included sex effects (s), age effects (a), non-linear time effects (t), or linear time trends (T). Akaike's Information Criterion (AIC) (Akaike 1973) was used to identify the most parsimonious model (Burnham and Anderson 1992, Franklin et al. 1996, Lebreton et al. 1992).

The estimated mean annual rate of population change (λ) during the period of study was computed from age-class estimates of annual survival (juvenile and non-juvenile) and the mean estimate of fecundity for all females ≥ 1 year old (Franklin et al. 1996). Estimates of the rate of population change refer to the resident territorial population, which contained several age classes.

RESULTS

Territory Occupancy and Turnover Rates

A sample of 44 territories was known and monitored in 1990. The cumulative number of territories monitored increased by 55 percent through 1995 and approached an asymptotic level in 1994 (fig. 3). The greatest increase in the number of territories occurred between 1991 and 1992 where we recorded a 26.5 percent gain by the end of the season. We attribute this increase in known territories to an increase in the number of field biologists, increase in survey effort, and an enlargement of the study area by 181 km² (+ 3 territories); it was not due to an increase in the number of owls on the study area. We attribute the observed increase during the last 2 years to internal emigration (owls abandoning old territories and inhabiting new territories within the study area), not to a population increase.

Among the last 4 years of study (1992-1995), the total number of occupied territories remained relatively stationary (1990:50, 1991:60,

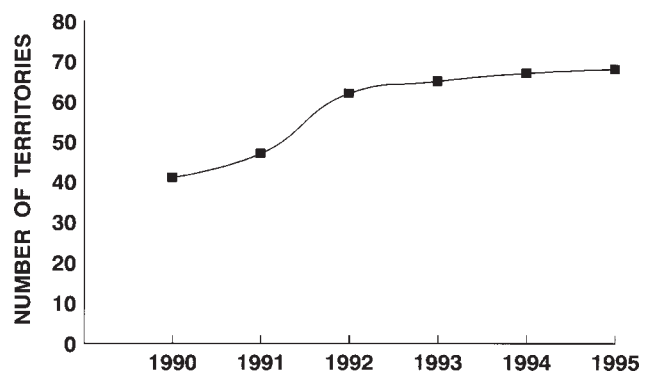


Figure 3.—Cumulative number of Northern Spotted Owl (*Strix occidentalis caurina*) territories monitored within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995.



1992:56, 1993:54, 1994:53, 1995:53). For both 1994 and 1995 the proportion of unoccupied territories was similar at 0.34 and 0.35, respectively. Annual composition of territories was dominated by pairs (range 1990:0.52-1994:0.78) and secondarily by owls classified as "social status unknown" (fig. 4). The proportion of resident single males was consistently greater than resident single females (fig. 4).

For all years and sexes combined, mean annual turnover rate for individual territorial owls was 25.8 percent. Overall, the frequency of female turnover rates (30.5 per cent) was significantly higher than for males (21.2 per cent) ($X^2 = 156$, $df = 1$, $P = 0.01$). Annually, the percentage of female turnover events was consistently greater than for males (fig. 5).

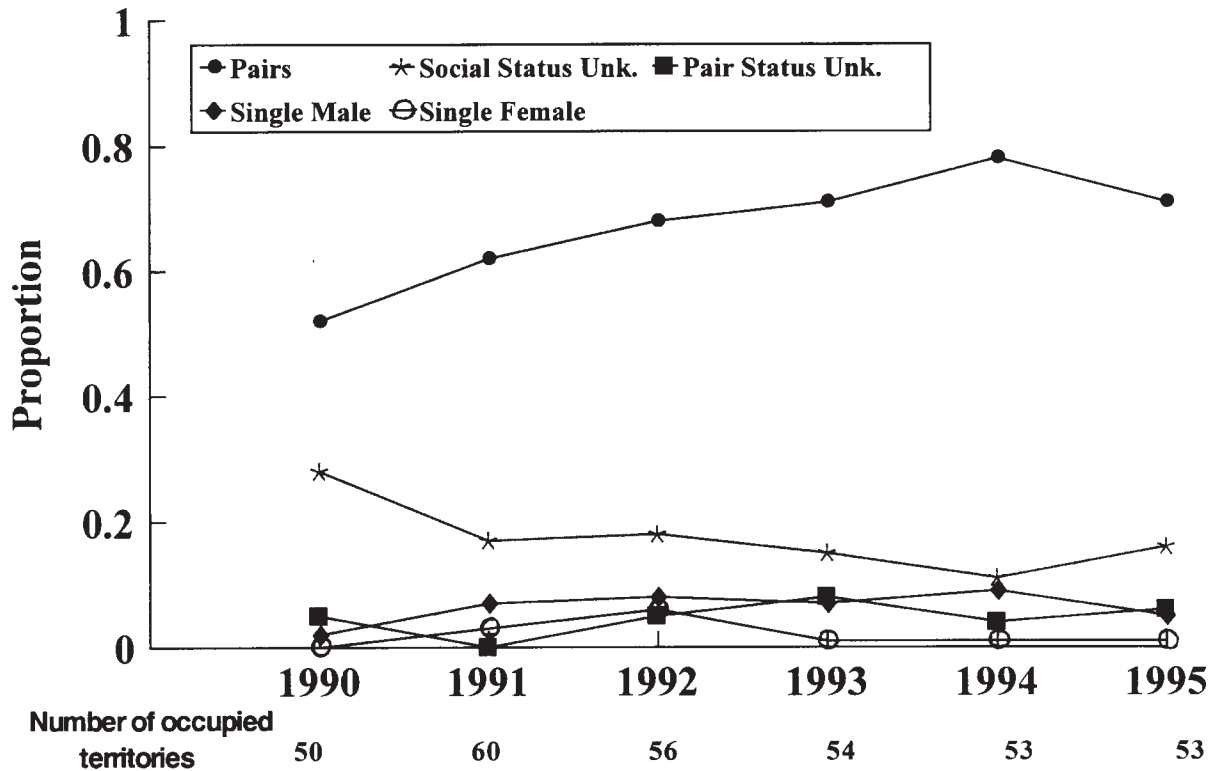


Figure 4.—Social status of occupied Northern Spotted Owl (*Strix occidentalis caurina*) territories located within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995.

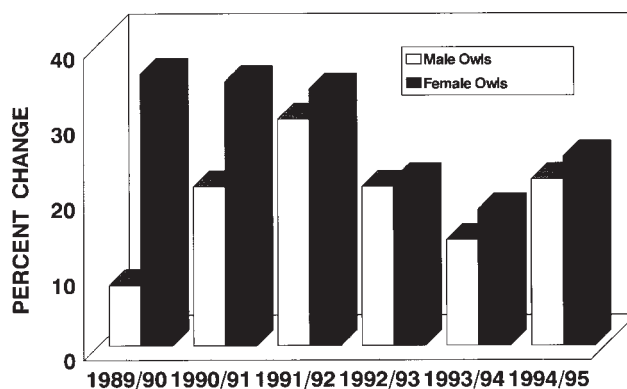


Figure 5.—Turnover rates of Northern Spotted Owls (*Strix occidentalis caurina*) within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1989-1995. Overall, the frequency of female turnover rates was significantly higher than for males ($X^2 = 156$, $df = 1$, $P = 0.01$).

Owl Density Within the Wolf Creek Density Study Area

The number of territorial owls detected on the Wolf Creek DSA declined ($r^2 = 0.885$, $df = 4$, $P = 0.003$) by 37 percent from 1990 through 1995 (fig. 6). Approximately two-thirds (64 percent) of the decline was attributed to owls relocating to territories outside of the DSA. The number of occupied territories also declined significantly ($r^2 = 0.869$, $df = 4$, $P = 0.007$) by 36 percent during the study period (fig. 6).

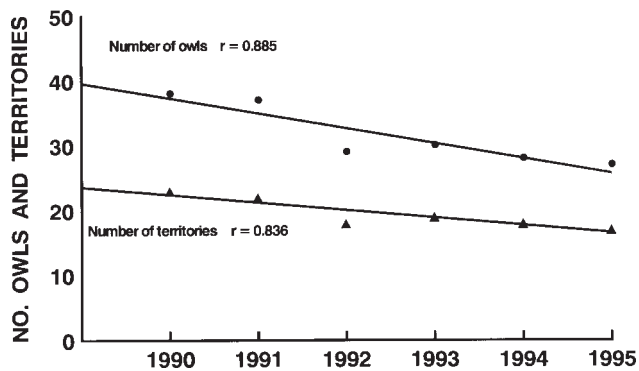


Figure 6.—Crude density estimates of the number of Northern Spotted Owls (*Strix occidentalis caurina*) and territories within the Wolf Creek DSA (425 km²), Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. Both the number of territorial owls and occupied territories declined significantly.

Sex and Age Composition

The male:female sex ratio for all age classes (adults, subadults, and age unknown) was skewed towards males annually. Male owls comprised the greatest proportion of the adult age-class annually, except in 1992. Conversely, for the subadult age-class, females comprised an increasingly greater proportion of this age-class annually except in 1991, whereas, male composition gradually decreased. The number and composition of owls identified as subadults declined during the study (subadult numbers 1990:10, 1991:7, 1992:7, 1993:5, 1994:6, 1995:3). ($r^2 = 0.836$, $df = 4$, $P = 0.011$) (fig. 7). The highest ratio of subadults (18.5 percent) to adults (81.5 percent) occurred in 1990, whereas the lowest ratio occurred in 1995 (3.7 percent subadults

vs 96.3 percent adults) (fig. 7). Within the age unknown category, the male:female ratio was skewed towards males every year except in 1993 and 1994 when the ratio was 1:1.

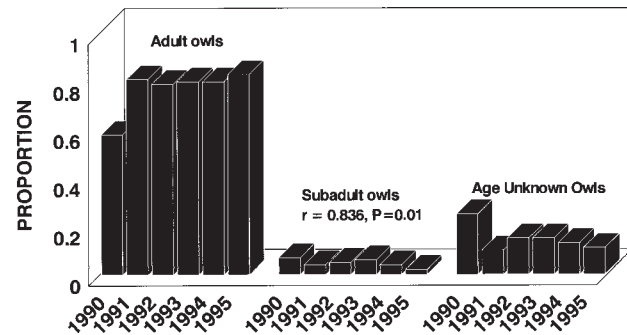


Figure 7.—Age composition of Northern Spotted Owls (*Strix occidentalis caurina*) detected on the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. The number of subadult owls declined significantly during the study.

Nesting Attempts, Success, and Fecundity

For the 6 years combined, the mean proportion of pairs nesting was 0.44 ($n = 177$, 95 percent CI = 0.03 - 0.94). However, the proportion of pairs determined to be nesting varied significantly among years ($X^2 = 41.6$, $df = 4$, $P = 0.0001$) (fig. 8). The probability of nesting in an

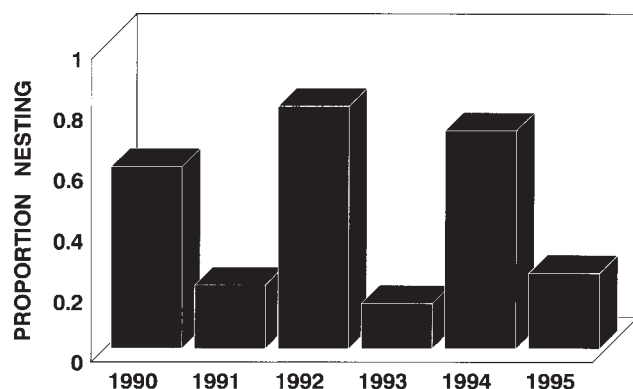


Figure 8.—Annual proportion of Northern Spotted Owl (*Strix occidentalis caurina*) pairs nesting on the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. The proportion of pairs determined to be nesting varied significantly among years ($X^2 = 41.6$, $df = 4$, $P = 0.0001$).



even year was nearly 10 times greater (odds ratio = 9.8) than in an odd year (odds ratio = 1.0) ($X^2 = 48.9$, $df = 1$, $P = 0.001$). The mean proportion of nesting pairs fledging young for the six years combined was 0.64. Conversely, a mean proportion nest failure rate for the 6 years combined was 0.36. This included a low failure rate of 0.04 in 1992 and a high of 0.60 in 1993.

Fecundity, defined as the average number of female young produced per female (assume a 1:1 sex ratio), averaged 0.240 (SE = 0.030) for adult females, 0.068 (SE = 0.050) for subadult females, and 0.223 (SE = 0.028) for all females combined. Successful reproduction by subadult females occurred only two times during this study and each time by a 2-year-old (S2) owl. Fecundity of all females combined varied significantly among years ($F = 28.29$, 4 df , $P < 0.001$), ranging from a high of 0.512 in 1992 to a low of 0.039 in 1993 (fig. 9), but no trend with time was evident.

Inter-territorial Movements/Emigration and Dispersal

From 1990-1995, we documented 31 adult/subadult movements ≥ 2.4 km. On average, subadults moved significantly farther than the

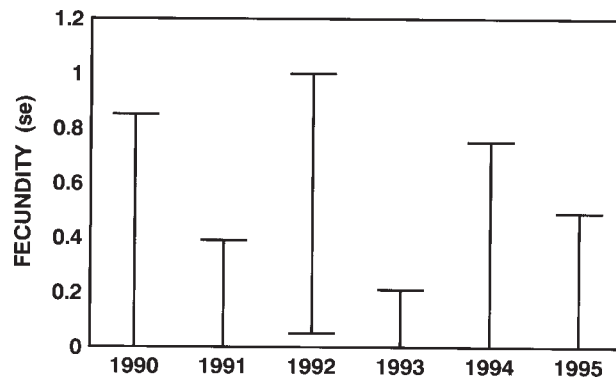


Figure 9.—Mean annual fecundity of female Northern Spotted Owls on the Eugene District BLM Northern Spotted Owl (*Strix occidentalis caurina*) demography study area, central Oregon Coast Ranges, 1990-1995. Fecundity is defined as the number of female young produced per female owl and assuming a 1:1 sex ratio of young. Fecundity of all females combined varied significantly among years ($F = 28.29$, $df = 4$, $P < 0.001$).

adults (sexes combined) ($t = 4.190$, $df = 7$, $P = 0.004$) (fig. 10). Within each of the 3 age cohorts, there were no significant differences in the mean distances moved between the sexes ($P > 0.05$). We recorded a total of 20 dispersals for the juvenile cohort, with the mean dispersal distance being significantly greater than that for adults and subadults ($t = 3.797$, $df = 19$, $P = 0.001$) (fig. 10). The range of dispersal distances (4.8-66.0 km) for all age cohorts of owls was most varied in the juvenile cohort in comparison to either the adults or subadults.

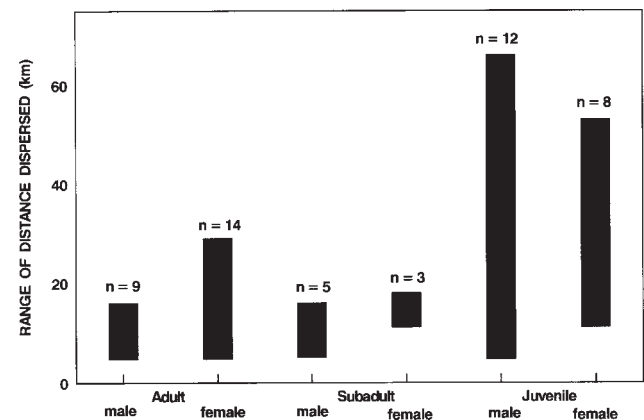


Figure 10.—Range of distances dispersed by sex and age class for Northern Spotted Owls (*Strix occidentalis caurina*) originally banded within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. On average, subadults moved significantly farther than the adults (sexes combined) ($t = 4.190$, $df = 7$, $P = 0.004$); mean distances moved between the sexes was not significantly different ($P > 0.05$); juveniles dispersed significantly farther than adults and subadults ($t = 3.79$, $df = 19$, $P = 0.001$).

Of the adults and subadults that dispersed, 67.7 percent were reobserved within the Eugene study area, whereas 32.2 percent were reobserved by biologists on adjacent study areas (fig. 11). We recorded a greater percentage of dispersing females (55 percent) compared to males (45 percent). From 1989-1994 approximately 23.1 percent of the 124 territorial adults and subadults moved to other territories (includes movements both within and outside the study area). Of this total, 6.5 percent relocated to adjacent study areas. Of

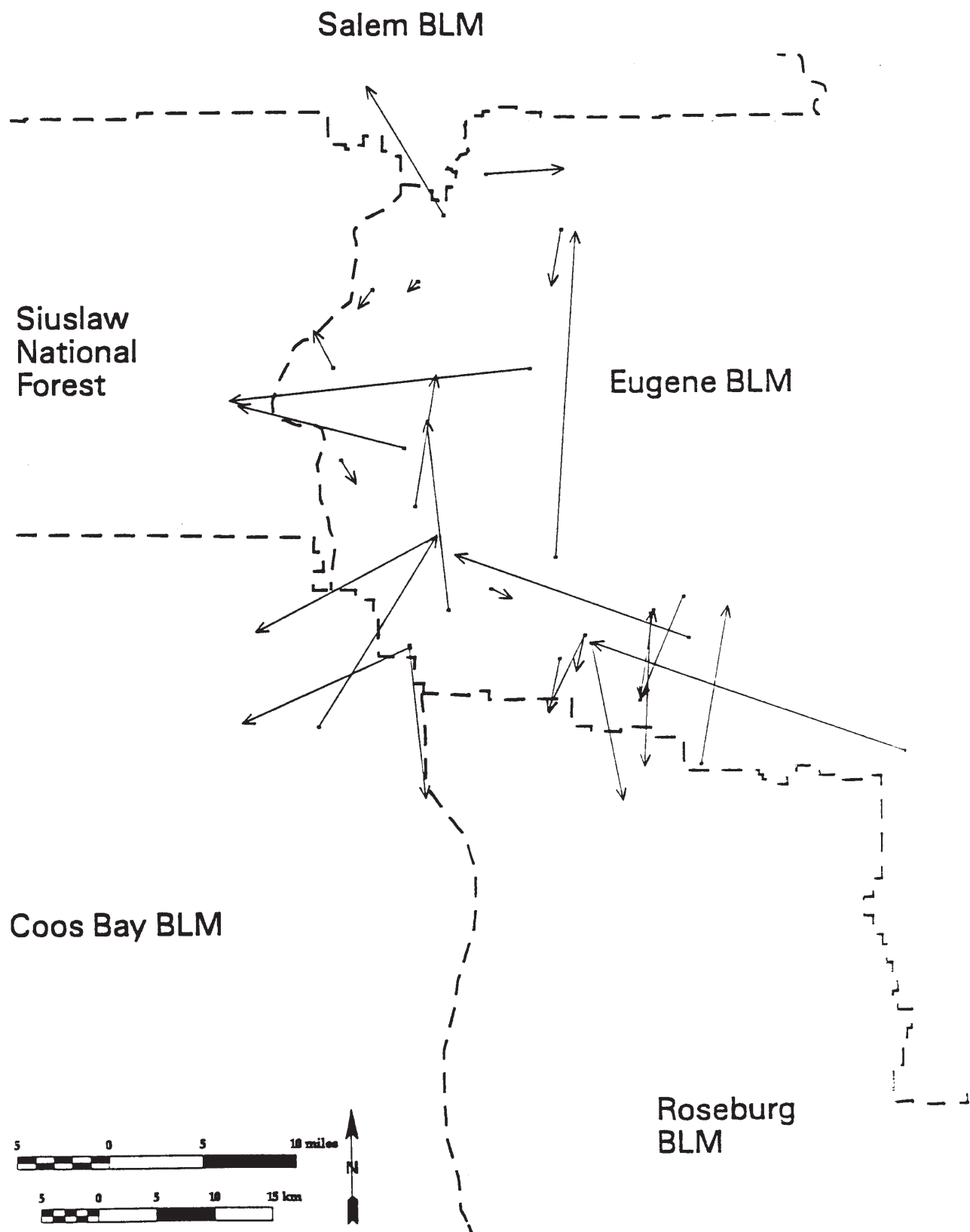


Figure 11.—Adult and subadult Northern Spotted Owl (*Strix occidentalis caurina*) movements recorded through color-band reobservations, Eugene BLM District Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995.



juvenile owls originally banded within our Eugene study area and encountered 1 or more years later, 30 percent were reobserved within

our study area whereas 70 percent were reobserved on adjacent areas (fig. 12).

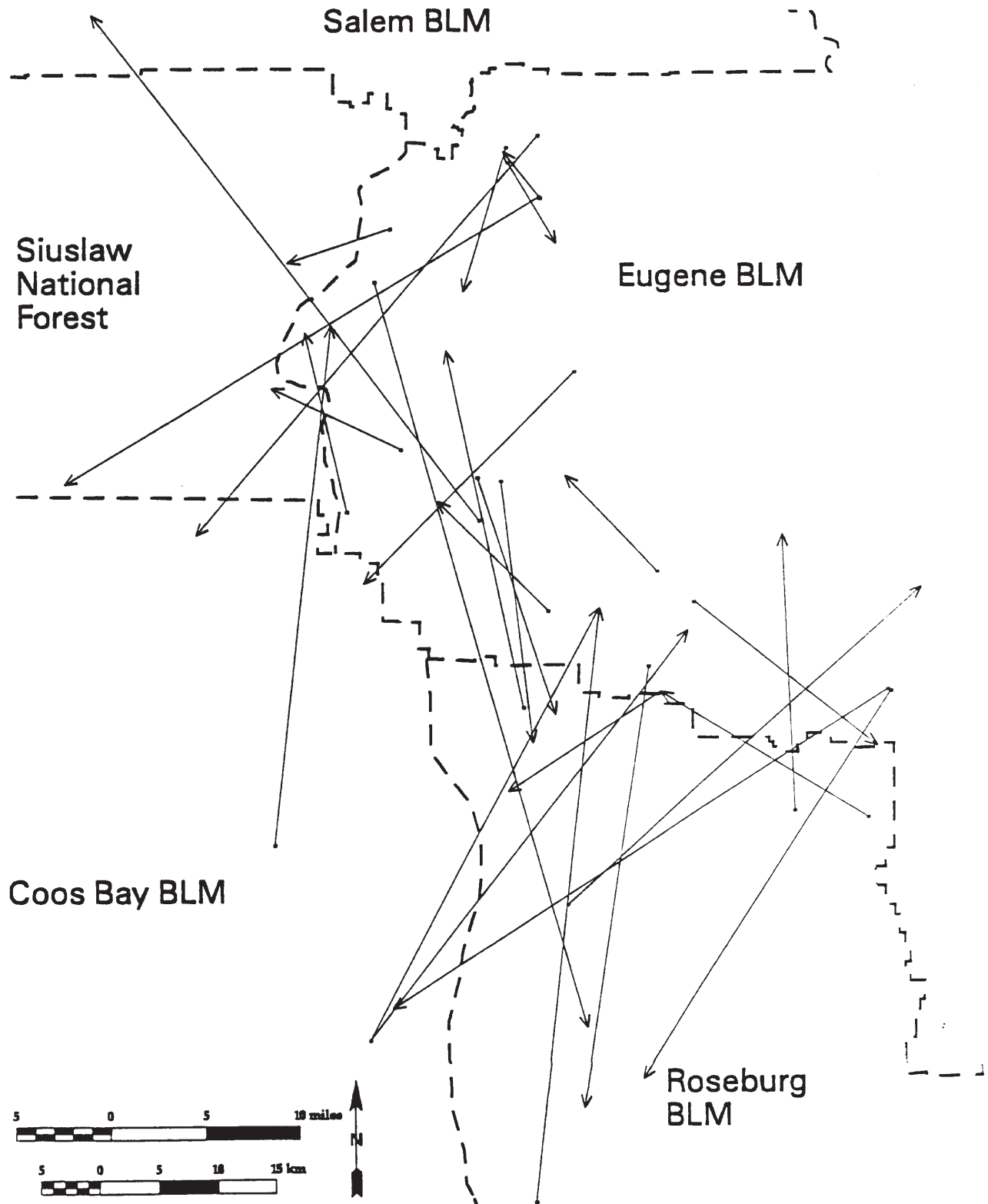


Figure 12.—Dispersal of juvenile (young of the year) Northern Spotted Owls (*Strix occidentalis caurina*) recorded through color-band reobservations within the Eugene District BLM study area and immigrants from adjacent study areas, central Oregon Coast Ranges, 1986-1995.

Capture-Recapture Population

We banded 233 owls from 1989-1995, including 119 adults, 15 subadults, and 99 juveniles (table 1). The sample also included 10 owls (7 females and 3 males) that were banded on adjacent study areas and subsequently immigrated to our study area. The straight-line distance moved by immigrant adults ranged from 3.2-43 km.

Goodness-of-Fit and Model Selection

Goodness-of-fit tests 2 and 3 in the program RELEASE indicated good fit of the capture history data for adult owls (males $X^2 = 9.32$, 13 df, $P = 0.744$; females $X^2 = 8.99$, 10 df, $P = 0.532$); therefore the Cormack-Jolly-Seber open population models were appropriate for the data. The results for Test 3 indicated that owls had similar future expected fates. Results from Test 2 indicated that data for the various age and sex classes were statistically independent. We had so few recaptures of owls banded as juveniles or as subadults that we could not conduct meaningful goodness-of-fit tests for those age groups.

Because of our previous results (Thraill et al. 1996), we chose to construct models with two age classes, rather than just adults. The most parsimonious model that provided the "best fit" for the two age classes (juveniles and non-juveniles [1-, 2-, and ≥ 3 -year-old owls]) was a more "basic" model (ϕ_{a2}, p_{a2}) that held survival and recapture probabilities constant and that did not have time or sex effects. A likelihood

ratio test indicated that a competing model (ϕ_{a2+t}, p_{a2}) with the next lowest AIC value ($X^2 = 0.559$, df = 1, $P = 0.454$) also fit the data (table 2).

Estimated Survival Rates

Mean annual survival estimates for the two age classes (ϕ_{a2}, p_{a2}) were 0.306 (SE = 0.064) for juveniles and 0.875 (SE = 0.018) for non-juveniles (fig. 13). Estimates of annual survival from a variable time model (ϕ_{a2+t}, p_{a2}) are presented here for comparison and generally show a decreasing, although not significant, trend in adult survival (1989:0.98, 1990:0.95, 1991:0.77, 1992:0.84, 1993:0.90, 1994:0.89) ($r^2 = 0.14$, df = 4, $P = 0.465$) (fig. 13). Estimates of annual survival from the selected model and several competing models varied ≥ 2.5 percent for non-juveniles indicating that survival estimates were not greatly affected by model selection (table 2). Estimates of juvenile survival were more variable than for non-juveniles, differing as much as 8 per cent among models. The estimate of juvenile survival from the best model was near the upper end of the range of survival estimates produced by the best two-age-class models.

Annual Rate of Population Change

The estimated annual rate of population change on the study area was 0.939 (SE = 0.045), which was significantly < 1.0 ($P = 0.005$). This suggested an average decline of territorial owls of 6.1 per cent per year over the 6 year study period.

Table 1.—Number of Northern Spotted Owls (*Strix occidentalis caurina*) banded and used in capture-recapture analyses on the Eugene District BLM study area, central Oregon Coast Ranges, 1989-1995.

Year	Adults (> 3 yrs old)		Subadults (1 or 2 yrs old)			Juveniles
	Female	Male	Female	Male	Unknown	
1989	16	22	1	1	0	8
1990	4	5	3	4	1	13
1991	20	15	1	1	0	8
1992	8	3	0	0	0	37
1993	4	4	2	0	0	3
1994	2	7	0	0	0	16
1995	5	4	1	0	0	14
Total	59	60	8	6	1	99



Table 2.—The “best candidate” two-age-class (juvenile and non-juvenile ≥ 1 year old) capture-recapture models for Northern Spotted Owls (*Strix occidentalis caurina*) on the Eugene District BLM study area, central Oregon Coast Ranges, 1989-1995.

Model ¹	Deviance	K ²	AIC ³	ϕ ⁴
$\{\phi_{a2}, p_{a2}\}$	546.453	4	554.453	0.875
$\{\phi_{a2*t}, p_{a2}\}$	528.278	14	556.278	0.888
$\{\phi_{a2*s}, p_{a2}\}$	546.332	5	556.332	0.870
$\{\phi_{a2''}, p_{a2}\}$	546.389	5	556.389	0.887
$\{\phi_{a2}, p_{a2+T}\}$	546.450	5	556.450	0.895
$\{\phi_{a2+t}, p_{a2}\}$	538.709	9	556.709	0.878
$\{\phi_{a2}, p_{a2*T}\}$	545.504	6	557.504	0.895
$\{\phi_{a2}, p_{a2*s}\}$	545.594	6	557.594	0.875
$\{\phi_{a2*T}, p_{a2}\}$	545.873	6	557.873	0.871
$\{\phi_{a2*t}, p_{a2*s}\}$	527.934	15	557.934	0.886

¹ Parameters are subscripted s for sex, t for time (year) with no linear trend, and T for time as a linear trend. An asterisk (*) indicates interactions. Additive effects in models are denoted with a “+”.

² K is the number of estimatable parameters from the model.

³ AIC (Akaike’s Information Criterion) is used to select objectively an appropriate “best” model (Akaike 1973).

⁴ ϕ = estimate of survival for non-juvenile owls; p = probability of resighting individual owls.

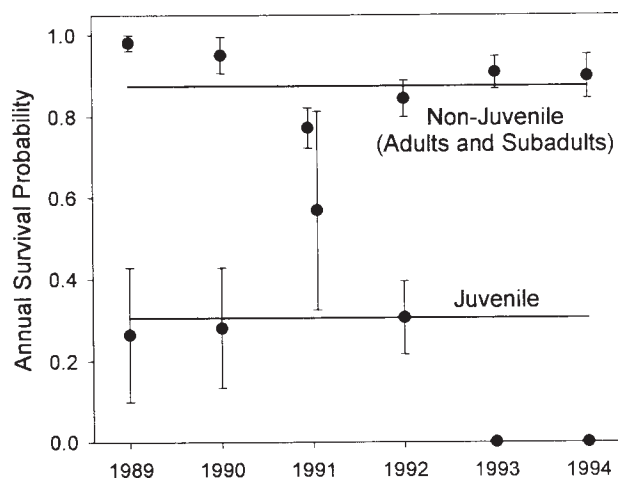


Figure 13.—Estimates of annual survival probabilities for non-juvenile (> 1 year old) and juvenile Northern Spotted Owls (*Strix occidentalis caurina*) on the Eugene District BLM demography study area, central Oregon Coast Ranges, 1989-1995. Solid line represents a constant trend in annual survival estimates for non-juveniles and juveniles from the most parsimonious age-class model (ϕ_{a2}, p_{a2}). Point estimates and SE’s of annual survival from a variable time model (ϕ_{a2*t}, p_{a2}) are shown for comparison.

DISCUSSION

Territory Occupancy and Turnover

The number of occupied territories in the entire study area remained relatively stationary over the last 4 years; however, the population appeared to be constantly undergoing some manner of social change which was reflected by the relatively high turnover rates and proportion of inter-territory movements. This social change occurred within approximately 26 percent of the population while relatively little change occurred among a large proportion of the older owls occupying territories. We believe this social instability is most likely related to low habitat quality within our study area. Only 22 percent of the study area is comprised of suitable owl habitat; of that, only 11 percent is old forest. In contrast, a similar project area in the central Cascades of Oregon is comprised of approximately 55 percent suitable habitat and has relatively lower annual rates of turnover (18 percent, K. Swindle, unpubl. data, 1987-1994). Thomas et al. (1990:266) used population models and showed that when a landscape has < 20 percent suitable habitat, the probability that an owl will find a suitable territory is almost insurmountable. Bart and Forsman (1992) found that site occupancy and productivity were lower in areas with < 40 percent suitable habitat. Similarly, we present results showing a significant increase in the frequency of turnover events and lower rates of territory occupancy in landscapes with greater amounts of early seral forest (Thraillkill et al. 1997).

Owl Density Within the Wolf Creek Density Study Area

Because the best two age class models did not indicate any time effects on recapture probabilities, we assumed that the number of owls estimated on the DSA each year could be compared without any correction for year-to-year differences in detectability. The 37 percent decline (two-thirds attributed to movements) in the number of owls detected on the DSA is most likely a response to the rapid harvest of owl habitat in the 1980's. Approximately 45 percent of the DSA was comprised of suitable habitat in 1984; 18 percent was clearcut harvested from 1985-1990 prior to court-imposed harvest restrictions on federally managed lands. Approximately 4 percent of the habitat was harvested during the study

period 1990-1995, with most of the habitat on private lands harvested prior to 1990. What we measured is probably due, in large part, to "lag-effects" of decreasing habitat on both owl abundance and owl demographic parameters. Van Horne (1983) suggested that species densities may reflect conditions in the recent past or temporary present, rather than long-term habitat quality. The combination of declining survival, density, and annual rate of population change, we believe, indicates a non-stationary, declining owl population in response to the rapid removal in suitable habitat in the 1980's.

Reproductive Parameters: Nesting and Fecundity

The significant annual variation in the proportion of territorial females that nested and produced young on our study area could be due to fluctuations in food supply, weather, habitat alteration, or other factors influencing the reproductive physiology or behavior of spotted owls. For example, annual variation in the breeding by Great Gray Owls (*Strix nebulosa*) and Tawny Owls (*Strix aluco*) fluctuates in response to rodent cycles (Duncan 1992, Southern 1970). Preliminary results from a similar spotted owl study in the Oregon Cascades suggests a positive correlation between the proportion of nest attempts and abundance of deer mice (*Peromyscus maniculatus*) (R.G. Anthony, unpubl. data). For a long-lived species like the spotted owl, the population can probably persist through periods of low fecundity as long as they are followed by periods of high fecundity (Noon and Biles 1990).

Juvenile Survival

Our estimates of juvenile survival for the time period of 1989-1995 are 7 percent higher (30 vs 23 percent) than for the previously reported period of 1989-1993 (Thraillkill et al. 1996). A primary factor influencing juvenile recapture rates is the duration of study. Burham et al. (1996) showed that studies conducted between 6-8 years tend to provide higher estimates of juvenile survival than shorter studies because additional years of surveys are available to re-observe owls marked as juveniles. Juvenile survival estimates from adjacent long-term study areas in the Oregon Coast Ranges show survival rates are at least 10 percent higher than ours. For example, Reid et al. (1996), on



a study area immediately to the south of ours, showed a juvenile survival estimate of 42 percent (adjusted with radio-tagged juveniles = 54 percent) over a 8-year study period. Hopkins et al. (1996) showed a juvenile survival estimate of 40 percent on a study area immediately to the north of ours from 1986-1993. A juvenile survival estimate from the central Cascades study population was 0.28 (Miller et al. 1996:1987-1993); this estimate is probably negatively biased due to the lack of adjacent study areas to encounter dispersed juveniles.

Adult Survival

Adult survival increased by 2 percent (87.5 percent) compared to Thrailkill et al. (1996) for 1989-1993 (85.3 percent). Our adult survival probability was similar, but slightly higher relative to adjacent study populations in the Oregon Coast Ranges. Results of Reid et al. (1996) and Hopkins et al. (1996) showed adult survival probabilities of 84.3 and 85.1 percent, respectively. The 2 percent increase we observed is most likely attributed to two factors and does not reflect an actual increase in adult survival. The first factor is our almost "complete survey coverage" of suitable habitat throughout the entire study area, which is in contrast to "site only" monitoring designs utilized in the majority of demographic studies. With our survey design, one is more likely to encounter adult owls that make inter-territorial movements. Second, the juxtaposition of our study area to other study areas enhances the opportunity to record owls that emigrate. A bias in estimates of adult survival may occur with permanent emigration of adults. However, Burnham et al. (1996) stated that permanent emigration of territorial adults seems to be relatively rare and is not a significant concern in estimating survival rates of adults. Thomas et al. (1990) documented only one occurrence of permanent emigration in > 100 radio-marked adult owl years. Based on our recapture data for 1989-1994, 6.5 percent of the territorial adult/subadult owls relocated to adjacent study areas, indicating that this movement would have gone undetected if adjacent studies were not present. This percentage should be considered as a minimum and we suggest that adult emigration in the Coast Ranges possibly occurs to a greater extent than previously documented and also greater than in other areas. For example, a similar study located in the central Oregon Cascades has a relatively lower overall rate of

movement (4 percent). The high proportion of movements we have observed is probably a response to the relatively low amounts of suitable habitat.

When adult owls were recaptured in other study areas, their movements are not considered as permanent emigration in our analysis of survival rates. Therefore, our estimated survival rates are not negatively biased due to these known movements. Future analysis of spotted owl trend estimates should attempt to incorporate the potential bias due to permanent emigration of adults and juveniles (Bart 1995). We believe that methods to estimate this bias could be developed using existing data from demographic study areas sharing common boundaries.

Rate of Population Change

The major finding of this study was the average annual population decline of 6.1 percent. Previously, Thrailkill et al. (1996) showed a 8.7 percent population decline for the 1989-1993 time period. For this earlier period, we indicated that we did not disagree with this finding, but questioned the magnitude of the decline given the short-term duration of the study and potential biases in juvenile and adult survival rates (Thrailkill et al. 1996). The 2.6 percent difference between the study periods is most likely related to the computed increases in both juvenile and adult survival estimates as stated above. Noon and Biles (1990) found that population growth rates are highly sensitive to adult survival rates, with a few percent change in survival causing a similar magnitude of change in population growth estimates. Although the population growth estimate improved, a disturbing declining trend is still evident. The most plausible explanation for the computed population decline, decreased density, declining survival rates, and high proportion of social instability, is the decline in the acreage of suitable habitat. Most likely, the population has been declining slowly for the past 10-15 years, and our findings not only reflect current conditions, but to some degree, account for lag-effects from previous years. At this time, we do not believe it is possible to tell if our findings are indicative of a population that has dropped below a demographic "threshold" (Lamberson et al. 1992).

Because spotted owls are long-lived and vital rates may change, monitoring of demographic

information on occupancy, survival and fecundity in relation to changing habitat conditions should continue. A priority for future research should be to establish relationships between owl demographic performance and habitat conditions measured at different scales (Raphael et al. 1996). In particular, these relationships need to be examined at the scales corresponding to the size of owl breeding and annual home ranges. Consideration should also be given to conducting surveys for spotted owls in habitat outside of demographic areas and among different land use allocations to provide an independent sample for comparison with the demographic area results. This approach would provide a framework for validation monitoring under the President's Northwest Forest Plan.

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