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DEMOGRAPHY OF NORTHERN SPOTTED OWLS IN SOUTHWESTERN OREGON

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INTRODUCTION

Northern Spotted Owls *(Strix occidentalis caurina) are* associated with lower elevation, commercially valuable, late-successional coniferous forests in the Pacific Northwest. Meta-analyses of demographic parameters indicate that Northern Spotted Owl populations are declining throughout their range (Anderson and Burnham 1992, Burnham et al. *this volume).* Recent research has attempted to determine whether management activities have affected the viability of Spotted Owl populations, and results have led to development of conservation plans for the species (Dawson et al. 1987, Thomas et al. 1990, Murphy and Noon 1992, USDI 1992, Thomas et al. 1993b).

In the Recovery Plan for the Northern Spotted Owl (USDI 1992b) threats to the species were identified as small population sizes, declining populations, limited amounts of habitat, continued loss and fragmentation of habitat, geographically isolated populations, and predation and competition from other avian species. Weather and fire are natural processes that also may affect reproductive success of Spotted Owls. Weather may be a factor in the high annual variability in fecundity of Spotted Owls, as has been suggested for other predatory bird species (Newton, 1979, 1986). However, these factors have not been addressed in previous studies of Spotted Owls.

Our objectives were to estimate survival, fecundity, and annual rates of population change (λ) for resident, territorial female Spotted Owls at two study areas in the coastal mountains of southwestern Oregon. We tested if the amount of rainfall was correlated with reproduction of Spotted Owls. While surveying for Spotted Owls, we documented the increased presence of Barred Owls *(Strix varia),* a potential competitor of Spotted Owls.

STUDY AREAS

Coos BAY STUDY AREA

The 2,477 km^2 Coos Bay Study Area included most of the Coos Bay BLM District as well as some adjacent private lands. Most of the Coos Bay Study Area was within the Oregon Coast Ranges Province, which is characterized by high rainfall and steep, mountainous terrain with deep soils. Elevations range from just above sea level to 900 m. The study area was surrounded by five other Spotted Owl demographic study areas and the Pacific Ocean (Franklin et al. *this volume).* Land ownership is intermingled public and private lands forming a checkerboard landscape of alternating square-mile sections. Large amounts of forest have been harvested within the past 20-30 years, especially on private lands. This has resulted in a highly fragmented landscape with obvious structural boundaries between different-aged stands.

Forests in this area are in the western hemlock *(Tsuga heterophylla)* Zone (Franklin and Dyrness 1973). Douglas-fir *(Pseudotsuga menziesii)* dominates the canopy. Western hemlock and western redcedar *(Thuja plicata)* form secondary components of the overstory in most stands. The southern portion of the Coos Bay Study Area extended into the Klamath Province, which is drier with shallower soils (Franklin and Dymess 1973). In the latter province, Douglas-fir is the dominant species, but western hemlock becomes uncommon and Port-Orford-cedar *(Chamaecyparis lawsoniana)* is common.

SISKIYOU STUDY AREA

The 1,262 km^2 Siskiyou Study Area included most of the Chetco and Gold Beach Ranger Districts on the Siskiyou National Forest, and small amounts of adjacent state and private land. This study area was within the coastal region of the Siskiyou Mountains, the most northern range in the Klamath Province. The Siskiyou mountains are steep and elevations range from sea level to 1060 m. Soils are often moderately shallow and unstable, with inclusions of ultra-mafic serpentine soils that are unproductive and not capable of producing closed canopy forests used by Spotted Owls.

Vegetation within the Siskiyou Study Area is in the Mixed-Evergreen Zone (Franklin and Dyrness 1973), and is dominated by Douglas-fir forests with Port-Orford-cedar a common secondary component. On most sites the overstory is relatively open with a dense mid-canopy of tanoak *(Lithocarpus densiflorus)* and other broad-leaved evergreen trees, and a dense shrub layer dominated by evergreen huckleberry *(Vaccinium ovattrm).* The northern tip of the California Coast Province, where coastal redwood *(Sequoia sempervirens)* dominates the overstory, extends into

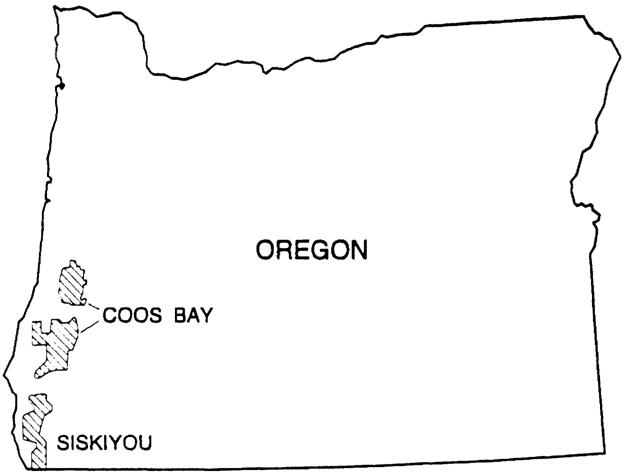

FIGURE 1. Coos Bay and Siskiyou Study Areas in southwestern Oregon, 1990-1993.

TABLE 1. GOODNESS-OF-FITTEST RESULTS FOR CAPTURE - RECAPTURE DATA ON ≥ 3 -YEAR-OLD SPOTTED OWLS IN THE COOS BAY AND SISKIYOU STUDY AREAS, OREGON, 1990-1993. RESULTS ARE FOR TESTS 1-3 IN PROGRAM RELEASE (BURNHAM ET AL. 1987)

	Coos Bay			Siskiyou		
Test	x^2	df	P	x^2	df	P
TEST 1	5.97	5	0.31	1.22	4	0.88
TEST 2 + 3						
Males	2.98	4	0.56	0.50	3	0.92
Females	6.47	3	0.09	0.23	3	0.97
Total	9.45	7	0.22	0.72	6	0.99

the southern edge of the study area. Serpentine areas are characterized by open forests (<40% canopy closure) of Jeffrey pine *(Pinus jeffreyi),* Douglas-fir, incense-cedar *(Calocedrus decurrens),* and knobcone pine *(P. attenuata)* with dense shrub layers of evergreen huckleberry and manzanita *(Arctostaphylos* spp.).

METHODS

The Coos Bay and Siskiyou demography studies were initiated in March 1990. In the Siskiyou Study Area, efforts were concentrated in Chetco Ranger District for most of the first season, but subsequently expanded late in 1990 to include the Gold Beach Ranger District.

Methods used to determine reproduction and survival of Spotted Owls followed those described by Franklin et al. *(this volume).* Programs RELEASE (Burnham et al. 1987) and SURGE (Pradel et al. 1990) were used for analyses of capture-recapture data. Choice of the best capture-recapture model to estimate survival for each study area was based on Akaike's Information Criterion (AIC), as described in Franklin et al. *(this volume).* We tested 64 models on data from owls that were ≥3 yrs old. Numerous age class models were tested on the data from all owls.

Fecundity was defined as the number of female young fledged per female (Franklin et al. *this volume*) for which we determined reproductive success by 15 July. Means and variances for fecundity were calculated using formulae for a discrete frequency distribution. Confidence limits were calculated using a relationship between the F distribution and the binomial distribution (Zar 1984). Mann-Whitney U tests were used for comparisons among age groups. Due to small sample sizes, a nonparamctric Kruskall-Wallis ANOVA (Zar 1984) was used to test for annual differences in fecundity.

Weather data, provided by the state of Oregon climatologist's office, were averaged across five weather stations on the Coos Bay Study Area and three weather stations on the Siskiyou Study Area. We used linear regression to compare fecundity to the total amount of precipitation within the breeding season (1 March-30 June). To compare amounts of precipitation that occurred during our studies to a long term average, we calculated 30-year averages from monthly rainfall records published by the National Oceanic and Atmospheric Administration. *t*-tests were used to compare differences between observed rainfall (from 1990-l993) and 30-year averages, using data from 1 March to 30 June.

RESULTS

NUMBER OF OWLS BANDED

We banded 376 owls on the Coos Bay Study Area and 110 owls on the Siskiyou Study Area. At Coos Bay this included 191 owls ≥3 yrs old (93 females and 98 males), 49 1- and 2-yr-old owls (26 females and 23 males), and 136 juveniles. The sample also included nine owls ≥3 yrs old and 13 l- or 2-yr-old owls that were marked by researchers on adjacent study areas and subsequently immigrated into our study area. Owls banded at Siskiyou included 69 ≥3-yr-old owls (31 females and 38 males), 10 1- or 2-yr-old owls (5 females and 5 males), and 31 juveniles. The sample also included one immigrant from another study area.

GOODNESS-OF-FIT TESTS

Goodness-of-fit tests generated with program RELEASE (Burnham et al. 1987) indicated no lack of fit to the assumptions in the capture-recapture models for the ≥3-yr-old age group on either study area (Table 1). TEST 1 results indicated that overall survival and recapture probabilities did not differ between males and females at either study area (Table 1). However, for Coos

TABLE 2. CAPTURE-RECAPTURE MODELS USED TO ESTIMATE SURVIVAL OF SPOTTED OWLS ON THE COOS BAY STUDY AREA, OREGON. MODELS FOR ≥ 3 - YEAR - OLD OWLS AND 2-AGE-CLASSES (JUVENILES AND NON-JUVENILES) ARE PRESENTED. MODELS SHOWN ARE THOSE WITH THE LOWEST AIC (AKAIKE 1973) VALUES. RESULTS OF LIKELIHOOD-RATIO TESTS BETWEEN EACH MODEL AND THE BEST MODEL ARE INDICATED. K = NUMBER OF PARAMETERS IN MODEL; $D_S - D_G$ = (DEVIANCE OF SIMPLE MODEL) - (DEVIANCE OF MORE GENERAL MODEL) = LIKELIHOOD-RATIO TEST RESULT; DF = ($K_G - K_S$)

Model	K	AIC	D_S-D_G	df	P
Time and sex specific models on ≥3-year-old owls					
$\{\varphi_t, P_{s+t}\}$	6	390.027			
$\{\phi_t, PA$	5	390.037	2.010	1	0.18
$\{\phi_t, p_{s+T}\}$	6	390.221		0	
$\{\phi_t, p_{s \cdot T}\}$	7	390.728	1.299	1	0.23
$\{\phi_{s \cdot T}, p_{s \cdot T}\}$	8	390.849	3.178	2	0.22
2-age-class models					
$\{\phi_{2a+t}, p_{2a+s}\}$	7	599.444			
$\{\phi_{2a+t}, p_{2a \cdot s}\}$	8	600.154	1.290	1	0.26
$\{\phi_{2a \cdot t}, p_{2a+s}\}$	9	602.999	0.445	2	0.80
$\{\phi_{2a+t}, p_{2a+s+t}\}$	9	603.091	0.353	2	0.84
$\{\phi_{2a \cdot t}, p_{2a \cdot s}\}$	10	603.798	1.646	3	0.68

TABLE 3. CAPTURE-RECAPTURE MODELS USED TO ESTIMATE SURVIVAL OF SPOTTED OWLS ON THE SISKIYOU STUDY AREA, OREGON. MODELS SHOWN ARE THOSE WITH THE LOWEST AIC (AKAIKE 1973) VALUES. RESULTS OF LIKELIHOOD-RATIO TESTS BETWEEN EACH MODEL AND THE BEST MODEL ARE INDICATED. K = NUMBER OF PARAMETERS IN MODEL; $D_S - D_G$ = (DEVIANCE OF SIMPLE MODEL) - (DEVIANCE OF MORE GENERAL MODEL) = LIKELIHOOD-RATIO TEST RESULT; DF = ($K_G - K_S$)

Model	K	AIC	D_S-D_G	df	P
Time and sex specific models on ≥3-year-old owls					
$\{\varphi, P_T\}$	3	180.814			
$\{\phi_T, p_T\}$	4	181.127	1.687	1	0.22
$\{\varphi, p_{s+T}\}$	4	181.490	1.324	1	0.25
$\{\varphi, p_t\}$	4	181.836	0.978	1	0.36
$\{\phi_s, P_T\}$	4	181.859	0.955	1	0.37
Time and sex specific models on ≥ 1-yr-old owls					
$\{\phi_T, P_T\}$	4	207.854			
$\{\varphi, p_T\}$	3	207.909	2.055	1	0.17
$\{\varphi_{s+T}, p_T\}$	5	209.439	0.415	1	0.53
$\{\phi_T, p_t\}$	5	209.848	0.006	1	0.94
$\{\phi_t, p_t\}$	5	209.848	0.006	1	0.94

Bay, component 1.T2 (which tests differences between groups by year; Burnham et al. 1987: 128) indicated that recapture probabilities differed significantly between males and females in 1991 (x^2 = 3.89, P < 0.05). This was consistent with results from the model selection process in Program SURGE indicating that the best model for Coos Bay had sex-specific recapture probabilities.

MODEL SELECTION-COOS BAY

Because we had small numbers of owls banded as l- or 2-yr-olds, we could not justify using models with l- or 2-yr-old owls as a separate age class. Therefore, we compared one set of models for ≥ 3-yr-old owls, and another set of 2-age class models that included juveniles and non-juveniles (≥ 1-yr-old). The most parsimonious model for ≥ 3-yr-old owls indicated that survival varied among years, and that recapture rates varied with sex and year (Table 2). Likelihood ratio tests indicated several other models did not differ from the model with the lowest AIC value (Table 2). Males had a higher recapture probabilities than females. The most parsimonious 2-age-class model indicated that survival differed between juveniles and non-juveniles and among years (Table 2).

MODEL SELECTION-SISKIYOU

Thirty one juveniles wcrc banded at the Siskiyou Study Area, but none were recaptured. Because a juvenile survival estimate of zero could distort survival models, we used only models that examined ≥ 3-yr-old owls and ≥ 1-yr-old owls. Likelihood-ratio tests indicated no difference between the five best models at Siskiyou, regardless of whether we included only ≥3-yr-old owls, or all non-juvenile owls (Table 3). The most parsimonious model for ≥3-yr-old owls indicated survival was independent of time and sex, and recapture probability was decreasing linearly with time (Table 3). When all owls ≥ l-yr-old were included in the analysis, the best model included a linear time trend on survival and recapture (Table 3).

DEMOGRAPHIC PARAMETER ESTIMATES

Estimates of apparent annual survival (Fig. 2) from the best 2-age-class model at Coos Bay ($\{\varphi_{2a+t}, P_{2a+s}\}$) (notation follows Lebreton et al. 1992) were 0.86 (SE = 0.02) for non-juveniles and 0.22 (SE = 0.045) for juveniles. Standard errors for mean survival estimates from this time-dependent model were approximated from the best time-independent model since SES could not be calculated directly from models with time-dependent survival. The survival estimate for ≥3-yr-old owls from the most parsimonious model at Siskiyou ($\{\varphi, p_T\}$) was 0.83 (SE = 0.045) (Fig. 2).

Fecundity varied among years at both study areas (H = 65.4, 3 df, P = 0.0001 at Coos Bay; H = 13.0, 3 df, P = 0.005 at Siskiyou) (Fig. 3). On average, 1- and 2-yr-old owls at Coos Bay had significantly lower fecundity ($\bar{X}$= 0.16, SE =

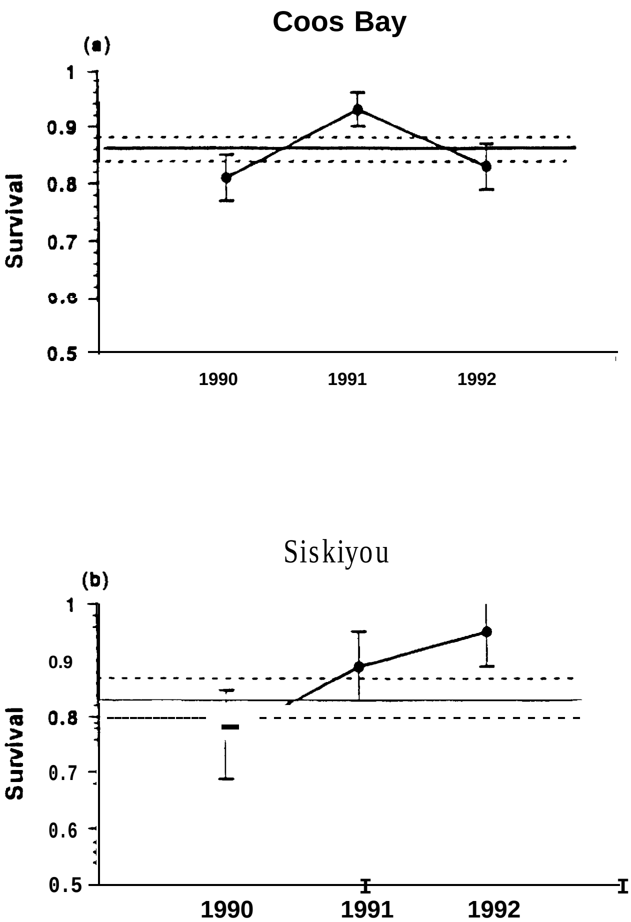

FIGURE 2. Estimates of survival for Northern Spotted Owls at Coos Bay and Siskiyou Study Areas, Oregon, 1990-1993. Point estimates (± 1 SE) are from the most parsimonious time-dependent capture-recapture models. Solid, horizontal lines indicate constant survival estimates from the best time-independent models (dashed lines indicate 1 SE).

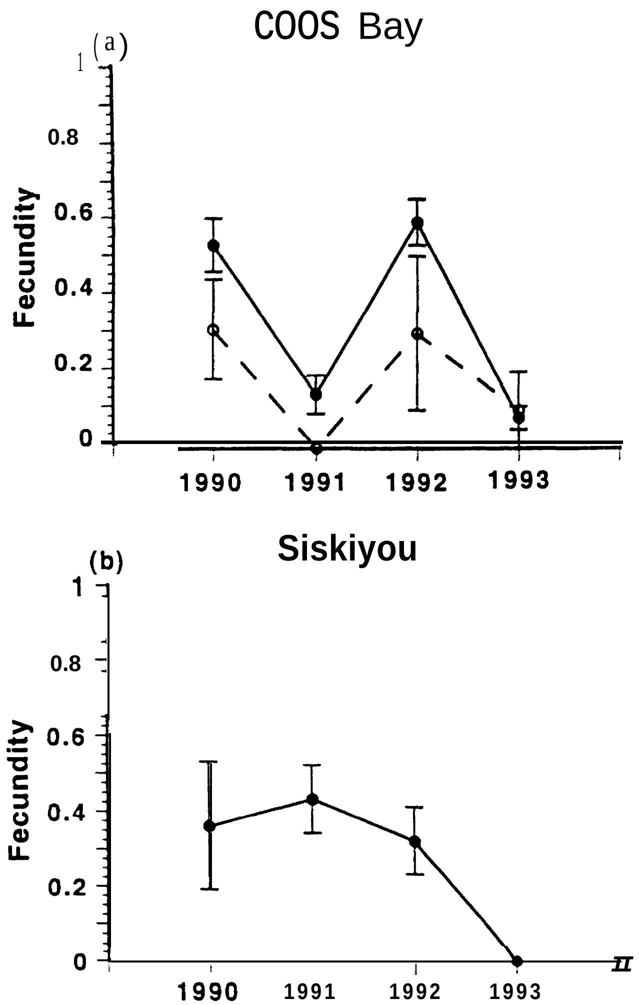

FIGURE 3. Estimates of fecundity (± 1 SE) for Northern Spotted Owls at Coos Bay and Siskiyou Study Areas, Oregon, 1990-1993. Solid circles represent data for ≥ 3-yr-old owls. Open circles represent 1- and 2-yr-old owls. No 1- or 2-yr-old owls nested at Siskiyou during these years.

0 06) than ≥3-yr-old owls ($\bar{X}$ = 0.33, SE = 0.03) (Z = 2.0, P = 0.05). At Siskiyou, no 1- or 2-yr old owls nested at sites we surveyed; mean adult fecundity was 0.30 (SE = 0.05).

The estimated finite rate of annual population change for ≥3-yr-old females at Coos Bay was 0.93 (SE = 0.02), which was significantly < 1.0 (t = 3.25, P = 0.0006). In the Siskiyou data, λ reduces to simply survival of non-juvenile owls (0.83), because a juvenile survival rate of zero cancels all other terms (see Noon and Biles 1990: 21). Also, no standard error could be computed for λ in the Siskiyou data because the juvenile survival estimate was $\varphi_J = 0$.

PRECIPITATION AND FECUNDITY

Fecundity was negatively correlated with total precipitation during the nesting season at both study areas (r = -0.93, 3 df, P = 0.04 for Coos Bay; r = -0.92, 3 df, P = 0.04 for Siskiyou)(Fig. 4). The index of precipitation explained 86% and 85% of the variance in fecundity from the respective study areas. Precipitation during the nesting season was 24% below the 30-year average in 1990 (t = -5.0, P = 0.02), normal in 1991 (t = 1.9, P = 0.16) and 1992 (t = -1.9, P = 0.16), and 92% above normal in 1993 (t = 4.4, P = 0.02).

BARRED OWLS

We made no deliberate attempt to survey for Barred Owls at either study area. However, during regular surveys for Spotted Owls, Barred Owls sometimes responded. The number of sites where Barred Owls were detected at Coos Bay was 1 in 1990, 0 in 1991, 12 in 1992, and 11 in 1993. Because our survey effort (number of people doing surveys and length of field season) and technique were essentially constant from 1990-l 993, we assumed this reflected a real increase in number of Barred Owls. On the Siskiyou Study Area, three Barred Owls were detected from 1990-l993.

DISCUSSION

Four years of data from the Coos Bay and Siskiyou Study Areas provide only first estimates of survival, fecundity, and rates of population change for Spotted Owls at these sites; however, our estimates of adult survival and fecundity were similar to those from other studies of longer duration (Burnham et al. *this volume).* The estimate of population change for Coos Bay during 1990-1993 indicated that this population was declining at a rate of 7% per year. Having no estimate for juvenile survival in the Siskiyou data made estimating λ problematic. However, if we assume our non-juvenile survival and fecundity estimates were accurate, the juvenile survival rate would have to be 0.6 1 in order for this population to be stationary (i.e., λ = 1.0) (Burnham et al. this *volume).* This is 1.5 times larger than the highest juvenile survival rate reported for 11 Spotted Owl demography study areas. Similarly, for the Coos Bay population to be stationary, the juvenile survival rate would need to be 0.49. This is also higher than any reported estimate from other Spotted Owl demography studies (Burnham et al. *this volume*), but not higher than estimates derived from radio telemetry data (Forsman et al. *this volume,* Reid et al. *this volume).*

Potential sources of bias in λ have been discussed (Bart 1995, Burnham et al. *this volume,* Raphael et al. *this volume).* Factors other than juvenile survival estimates that may have exaggerated the rate of decline were particularly a problem for the Siskiyou data. The Siskiyou Study Area was isolated from any other demography study, increasing the likelihood that emigrating owls were undetected. It was long and narrow, which may exacerbate emigration biases (Raphael et al. *this volume).* Survey effort on the Siskiyou Study Area declined after two years when the budget was reduced by 65%. Therefore, no new sites were surveyed, and banded juveniles that survived were not likely to be reobserved. Finally, both the Siskiyou and Coos Bay studies were of short duration. All of these factors could effect estimates of survival and lead to greater uncertainty about the true rate of population change.

Reproduction varied greatly between 1990 and 1993 at both study areas. Similar variation in reproduction was reported in other studies (e.g., see Forsman et al. *this volume,* Reid et al. *this volume,* Thrailkill et al. *this volume).* The negative correlation between fecundity and precipitation indicated that weather affected variability in reproduction of Spotted Owls at our study areas. Reproduction was lowest in 1993, the only year during our study when rainfall during the nesting season was significantly greater than average. Similar associations bctwccn precipitation and fecundity were found just east of the Siskiyou Study Area (Wagner et al. *this volume).* Heavy rainfall has adversely affected breeding success in many other predatory bird species, including Buzzards *(Buteo buteo)* and Goshawks *(Accipiter gentilis)* (Kostrzewa and Kostrzewa 1990), Kestrels *(Falco sparverius)* (Newton 1979), Peregrine Falcons *(Falco peregrinus)* (Meams and Newton 1988, Olsen and Olsen 1989a, 1989b) and Sparrowhawks *(Accipiter nisus)* (Newton et al. 1993). Rain may lower the hunting success of birds and increase their energy requirements, thus reducing their ability to reproduce successfully (Newton 1979, 1986).

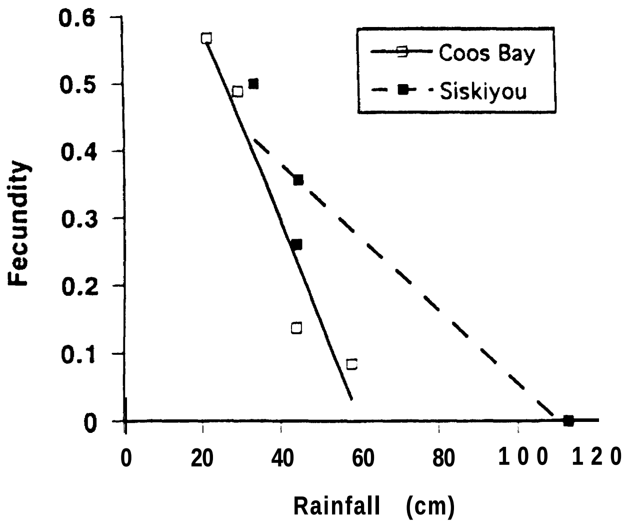

FIGURE 4. Correlation between precipitation during the breeding season (1 March-30 June) and fecundity of Northern Spotted Owls at the Coos Bay and Siskiyou Study Areas, Oregon, 1990-1993.

For a long-lived species such as the Spotted Owl, reproductive activity over the short-term may have little effect on rates of change in population size; populations can probably persist through periods of low fecundity (Noon and Biles 1990). The rate of change in Spotted Owl populations is most affected by variation in adult survival (Lande 1988, Noon and Biles 1990, Anderson and Burnham 1992). Major causes of known mortality among Spotted Owls are starvation and avian predation (Miller 1989, Foster et al. 1992, Paton et al. 1992). It has been suggested that the larger Barred Owl may be displacing Spotted Owls in some areas (Taylor and Forsman 1976, USDA 1988, Dunbar et al. 1991). Barred Owls are distributed throughout the Oregon Coast Ranges and were recorded at 46 sites from 1980-l991 (USDI 1992b). The increase in Barred Owl detections at Coos Bay from 1990-1993 indicates that they could be a threat to Spotted Owls there.

Threats to Spotted Owl populations in the Or-cgon Coast Ranges were rcportcd to bc greater than those in any other Oregon Province (USDI 1992b). Loss of habitat and poor habitat connectivity for dispersal were identified as special concerns within the Oregon Coast Ranges and Klamath Province. Less than 40% of the forests remaining at the Coos Bay and Siskiyou study areas are suitable nesting, roosting, and foraging habitat for Spotted Owls (Raphael et al. *this volume*). Bart and Forsman (1992) reported that areas with <40% suitable owl habitat supported lower densities of Spotted Owls, and pairs had lower reproduction than in areas with >60% suitable owl habitat. Home range sizes, an indication of owl density, were significantly larger at Siskiyou than at two other study areas within the Klamath Province in northwestern California (Zabel et al. 1995). Comparing adult fecundity of Spotted Owls among the 11 study areas, the Siskiyou ranked third lowest and Coos Bay fifth lowest (Burnham et al. *this volume)*. Lack of suitable habitat may be contributing to the apparently declining populations of Spotted Owls at Coos Bay and Siskiyou.

Demographic studies such as ours require many years of data before population trends can accurately be detected. The Siskiyou and Coos Bay studies were terminated after four years due to lack of funding. Problems in interpreting results from these studies have been discussed. It is not cost effective to initiate short term or poorly funded demographic studies. We recommend that demographic studies not be initiated without a long term commitment to fund them adequately.

SUMMARY

Northern Spotted Owls in the Oregon Coast Ranges were identified as being at particular risk due to loss of habitat and poor connectivity of remaining habitat (USDI 1992b). We estimated survival, fecundity, and annual rate of population change (λ) from 1990-1993 for Spotted Owls on the Coos Bay District of the Bureau of Land Management and the Siskiyou National Forest, Oregon. For the Coos Bay Study Area, the estimated survival rates from the best model (ϕ_{a2+t}, p_{a2+s}) were 0.86 (SE = 0.02) for non-juveniles and 0.22 (SE = 0.045) for juveniles; mean fecundity was 0.33 (SE = 0.03) for adults and 0.16 (SE = 0.06) for subadults. These estimates indicated that the population was declining at an annual rate of 7% (P = 0.0006). For the Siskiyou Study Area, non-juvenile survival from the best model ({ϕ, p_T}) was estimated at 0.83 (SE = 0.045), with juvenile survival of 0; mean adult fecundity was 0.30 (SE = 0.05). These estimates indicated that this population was declining at a rate of 17% annually (SE undefined). However, due to several sources of potential bias, was probably underestimated and we were uncertain of the true rate of population change. There was a significant negative correlation (P = 0.04) between fecundity and precipitation during the nesting season at both study areas. Detections of Barred Owls increased from 1990-1993 at one of the study areas. These vital rate estimates were consistent with those from other demographic studies, but they are only preliminary estimates due to the short duration of these studies. We recommend that demographic studies be initiated only when adequate funding is secured for long term studies.

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Key words: Barred Owl, California, demography, fecundity, lambda, Northern Spotted Owl, Oregon, precipitation, *Strix occidentalis caurina, Strix varia,* survival rates.

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