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DEMOGRAPHY OF NORTHERN SPOTTED OWLS ON THE SIUSLAW NATIONAL FOREST, OREGON

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INTRODUCTION

Historically, the coastal mountains of northwestern Oregon were covered by forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*), including extensive areas of trees that were 100–300-years old. Most of these mature or "old-growth" forests were clear-cut or burned between 1860 and 1990. As a result, the Coast Ranges Province is often identified as an area where wildlife that are associated with mature or old-growth forests may be declining in numbers (Forsman et al. 1976, Forsman 1986, Thomas et al. 1990, 1993a, USDI 1992b). Studies within this region have revealed particularly low numbers of Northern Spotted Owls (*Strix occidentalis caurina*), at least within areas where the majority of older forests have been removed by harvest or wildfires (Forsman et al. 1976, Forsman 1986).

In 1990 we initiated a demographic study of Spotted Owls on the Siuslaw National Forest, which is centrally located within the Oregon Coast Ranges Province. The primary objectives of the study were to document trends in birth, death, and population growth rates of Spotted Owls in the Coast Ranges. In addition, we used annual surveys on a portion of the study area to track changes in numbers of territorial Spotted Owls.

STUDY AREA

The 2,749 km² study area included most of the Siuslaw National Forest, as well as intermixed areas of private, municipal and state-owned lands that were located within the National Forest boundary (Fig. 1). The study area was characterized by a moderate maritime climate, with most precipitation falling as rain during October-May. Average annual precipitation was 196 cm from 1990–1993 (U.S. Forest Service, Mapleton Ranger District, unpublished records). Elevations ranged from sea level to 1,352 m.

Forests within the study area were dominated by Douglas-fir, western hemlock, and western redcedar. Deciduous hardwoods such as red alder (*Alnus rubra*), vine maple (*Acer circinatum*) and bigleaf maple (*Acer macrophylum*) also were common on many sites, particularly in riparian zones. As a result of extensive clear-cutting after 1930, the landscape was characterized by a mixture of older forests on uncut areas, dense stands of shrubs and herbs on recently cutover areas, and dense stands of younger trees on older clearcuts.

Prior to implementation of a systematic program of fire control in the 1950s, periodic wildfires burned extensive areas in the Oregon Coast Ranges. On sites where wildfires were relatively cool, many trees survived. Today, these stands typically consist of a mixture of large old, fire-scarred trees with understories of younger trees. On sites subjected to very hot crown fires in the 1800s and early 1900s, forests are typically dominated by relatively even-aged stands of 80 to 140-year-old Douglas-fir.

Vegetation and land management patterns on the Siuslaw Study Area were typical of the Oregon Coast Ranges Province. Little of the area was reserved in Wilderness or Roadless status, and, until the 1990s, the vast majority of the area was managed with timber production as the primary goal. This pattern changed dramatically during the 1990s as harvest on federal lands was sharply curtailed to protect extensive areas of forest for Spotted Owls, Marbled Murrelets (*Brachyramphus marmoratum*), fisheries enhancement, and other ecosystem goals (Thomas et al. 1990, 1993a,b).

METHODS

We use capture-recapture methodology to estimate population parameters, as described in Franklin et al. (*this volume*). Surveys were conducted each year from 1990–1993 between 1 March–1 September to search for and identify owls banded in previous years and to band any new owls detected. All owls detected were banded with a U. S. Fish and Wildlife Service band on one leg and a plastic color band on the other leg. Sex of owls was determined from differences in vocalizations and behavior, and age was determined from plumage characteristics (see Franklin et al. *this volume*).

Estimates of annual survival rates were calculated from capture-recapture data using Cormack-Jolly-Seber open population models in Program SURGE as described in Pollock et al. (1990), Lebreton et al. (1992), Burnham et al. (1995), and Franklin et al. (*this volume*). Akaike's Information Criterion (AIC) was used to identify

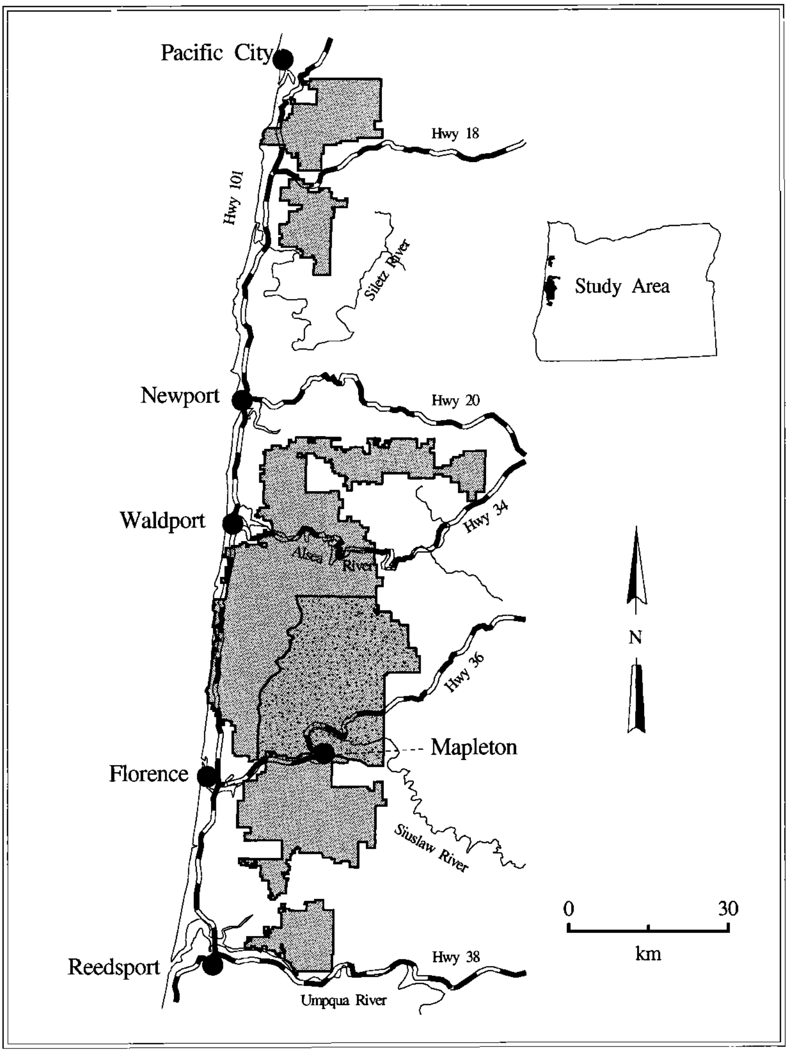

FIGURE 1. Siuslaw National Forest Study Area, Oregon, 1990–1993. Information on survival and fecundity of Northern Spotted Owls was collected from locations scattered throughout the study area. The shaded area with stippling indicates location of a 676 km^2 Density Study Area, within which we attempted to estimate annual changes in the number of territorial owls.

models that best fit the data (Akaike 1973, Burnham and Anderson 1992, Anderson et al. 1994, Franklin et al. *this volume*). Goodness-of-fit tests (Tests 1–3 in program RELEASE) were used to evaluate how well the data met the assumptions in the capture-recapture models (Pollock et al. 1985, Burnham et al. 1987).

Age-specific fecundity of females was estimated from the sample of all females located each year. Fecundity was defined as the number of female young produced per female, and was calculated by dividing the number of young that left the nest by 2, which assumed a 50:50 sex ratio (Franklin et al. *this volume*). Methods for locating and counting juveniles after they left the nest are described in Franklin et al. (*this volume*). Among-year variation in fecundity was examined with ANOVA in program SPSS (Norušis 1990).

Estimates of the annual rate of population change (λ) were derived from average estimates of age-specific annual survival and fecundity. We computed λ by solving the characteristic polynomial of a Leslie-Lefkovitch matrix (Noon and Sauer 1992, Franklin et al. *this volume*).

A 676 km^2 subplot located in the southern half of the study area was designated as a Density Study Area (Fig. 1). This area was completely

TABLE 1. NUMBER OF NORTHERN SPOTTED OWLS BANDED ON THE SIUSLAW NATIONAL FOREST STUDY AREA, OREGON, 1990–1993

Year	≥3-yr-old birds		1–2-yr-old birds		
	Males	Females	Males	Females	Juveniles
1990	37	27	6	2	24
1991	13	13	1	2	3
1992	23	22	2	4	35
1993	4	5	1		10
Total	77	67	10	8	72

TABLE 2. RESULTS OF GOODNESS-OF-FIT TESTS (PROGRAM RELEASE, BURNHAM ET AL. 1987) CONDUCTED ON CAPTURE-RECAPTURE DATA FROM ≥3-YR-OLD NORTHERN SPOTTED OWLS ON THE SIUSLAW NATIONAL FOREST STUDY AREA, OREGON, 1990–1993

Sex	TEST 2 + 3[a]			TEST 2	TEST 3
	χ^2	df	P	P	P
Males	3.83	4	0.430	1.000	0.280
Females	1.15	4	0.886	1.000	0.764

[a] TEST 2 tests whether different cohorts have different future fates. TEST 3 tests whether previously released individuals have the same future fates as newly released individuals (Burnham et al. 1987).

surveyed three times each year during the breeding season (March–August) to estimate the number of territorial owls. Within the remainder of the study area we conducted three or more annual surveys of all areas where we had banded owls in previous years, but we did not do a complete coverage survey of all intervening areas between sites that were historically occupied by owls.

Changes in numbers of territorial owls counted on the Density Study Area were assessed using linear regression to test the null hypothesis H_O: number of territorial owls was stationary or increasing, against the alternative hypothesis H_A: number of territorial owls was declining. A power analysis of the linear regression analysis (Gerrodette 1987) was conducted using Program TRENDS (Gerrodette, personal communication). For all statistical tests, P values ≤0.05 were considered significant.

RESULTS

During 1990–1993 we banded 234 owls on the study area, including 144 birds that were ≥3 yrs old, 18 birds that were 1 or 2 yrs old, and 72 juveniles (Table 1). In addition, the total sample included eight 1- or 2-yr-old birds and 10 ≥3-yr-old birds that immigrated into our study area after they were marked by researchers on adjacent study areas.

GOODNESS-OF-FIT

Examination of capture histories from ≥3-yr-old birds indicated that the data met the assumptions underlying the capture-recapture models (Table 2). Results of TEST 1 in program RELEASE indicated no differences in survival or recapture rates of males and females (χ^2 = 5.843, df = 5, P = 0.322). Numbers of recaptures of juveniles and 1- and 2-yr-old owls were so small that meaningful goodness of fit tests could not be conducted on those age classes.

MODEL SELECTION

Sixty-four models were constructed for owls that were ≥3 years old. The model that fit the data best was one in which there was no sex- or time-effect on survival (model $\{\phi, p_{s+t}\}$)(Table 3). Likelihood ratio tests indicated no difference between the best model and several competing models that included sex-effects or linear time-effects on survival (Table 3).

The model that best fit the data from all age and sex cohorts was a simple model that included no sex-effects or time-effects on survival or recapture and that lumped estimates of survival into 2 age classes (juveniles and ≥1-yr-old birds)(model $\{\phi_{a2}, p_{a2}\}$, Table 3). Likelihood ratio tests indicated no difference between the best model and several competing models (Table 3).

FECUNDITY

The average number of female young produced per female per year was 0.231 (SE = 0.043) for ≥3-yr-old females, and 0.071 (SE = 0.101) for 1- and 2-yr-old birds. Samples of 1- and 2-yr-old birds were too small to estimate fecundity separately for each age class. Mean fecundity of ≥3-yr-old females varied among years (F = 11.04, df = 3, P < 0.001), ranging from a low of 0.037 to a high of 0.457 (Fig. 2). Among-year variation in fecundity was due primarily to variation in the proportion of females that attempted to nest, which also varied among years (χ^2 = 32.407, df = 3, P < 0.001)(Fig. 2).

POPULATION GROWTH RATE

Estimates of survival from the best 2-age-class model were 0.2430 (SE = 0.0924) for juveniles and 0.822 (SE = 0.027) for ≥1-yr-old birds. Based on these estimates and the age-specific estimates of fecundity, the estimated annual rate of population change ($\hat{\lambda}$) was 0.874 (SE = 0.031), suggesting an average annual population decline of 12.6% per year during the period of study.

POPULATION CHANGE ON THE DENSITY STUDY AREA

The number of owls detected on the Density Study Area ranged from 46–58 during the 4 years of survey (Fig. 3). Because there were no time-

TABLE 3. CAPTURE-RECAPTURE MODELS THAT BEST FIT THE DATA FOR NORTHERN SPOTTED OWLS ON THE SIUSLAW NATIONAL FOREST STUDY AREA, 1990–1993. MODELS ARE LISTED IN ORDER OF INCREASING AIC (AKAIKE'S INFORMATION CRITERION) VALUES (AKAIKE 1973) FOR EACH DATA SET. ONE SET OF MODELS INCLUDED ≥3-YR-OLD BIRDS ONLY. THE OTHER SET INCLUDED TWO AGE CLASSES (JUVENILES AND ≥1-YR-OLD OWLS)

Model[a]	Deviance	K	AIC	χ^2	df	P
≥3-yr-old owls						
$\{\phi, p_{s+t}\}$	333.482	5	343.482			
$\{\phi_T, p_{s+T}\}$	333.526	5	343.526			
$\{\phi, p_{s+T}\}$	335.891	4	343.526	2.409	1	0.121
$\{\phi_s, p_{s+t}\}$	331.980	6	343.980	1.502	1	0.220
$\{\phi_T, p_T\}$	336.123	4	344.123	2.641	1	0.104
2-age-class models						
$\{\phi_{a2}, p_{a2}\}$	450.527	4	458.527			
$\{\phi_{a2}, p_{a2+s}\}$	448.738	5	458.738	1.789	1	0.181
$\{\phi_{a2+T}, p_{a2+s}\}$	447.804	6	459.804	2.723	2	0.256
$\{\phi_{a2+T}, p_{2+T}\}$	448.639	6	460.639	1.888	2	0.389
$\{\phi_{a2}, p_{a2*s}\}$	448.724	6	460.724	1.803	2	0.406

[a] Subscripts indicate age (a), sex (s), or time (t, T) effects on survival (ϕ) or recapture (p). Lower case or capital t's indicate that ϕ or p varied among years, either in a linear fashion (T) or non-linear fashion (t). Numbers indicate number of age-groups estimated by the model. An * indicates full age, sex or time-effects, whereas a + indicates a reduced model in which age, sex or time-effects are additive.

effects on recapture rates in the most parsimonious age-class CR model ($\{\phi_{a2}, p_{a2}\}$), we concluded that annual counts of owls detected on the Density Study Area could be compared without correction for annual differences in detectability of owls. A linear regression indicated no trend in total numbers (slope = −0.600, r = −0.121, P = 0.879), a finding that did not support the null hypothesis that the population was non-stationary. Power of the regression analysis to detect a trend given the observed rate of population change was extremely low (0.05).

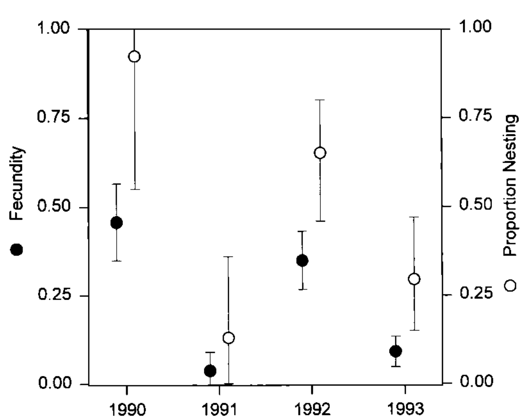

FIGURE 2. Mean annual estimates of fecundity of ≥3-yr-old female Northern Spotted Owls on the Siuslaw National Forest Study Area, Oregon, 1990–1993. Proportion of ≥3-yr-old females breeding each year is also shown. Fecundity was defined as the number of female young produced per female owl, assuming a 50:50 sex ratio in broods observed.

DISCUSSION

Bias in estimates of survival and fecundity can cause bias in estimates of the annual rate of population change. We believe that our estimates of the annual rate of population change on the Siuslaw Study Area are likely to be biased low because of undetected emigration, particularly by juveniles. However, there are many other factors that can cause positive or negative bias in estimates of survival or fecundity (e.g., see Bart 1995, Raphael et al. *this volume*), and we do not know what the combined effect of these biases is on the estimated rate of population change. However, we should be able to better assess the effects of some of these potential biases as more years of data are accumulated.

After three years of study (4 capture occasions), there was no strong indication of time trends on survival in the study area, and variance in fecundity was so large that no trends in that parameter were obvious either. Another approach that may allow detection of trends in demographic parameters with relatively short-term data sets is the use of meta-analyses on data sets from multiple study areas (Burnham et al. *this volume*).

Because this analysis only covered a period of 3 years (4 capture occasions), there is some question whether the results reflect the actual age-specific differences in survival that may exist in the population. In particular, samples were too small to obtain precise estimates of survival for 1- and 2-yr-old birds. More detailed comparisons of age-specific survival should become possible in future years, as the sample of marked individuals increases.

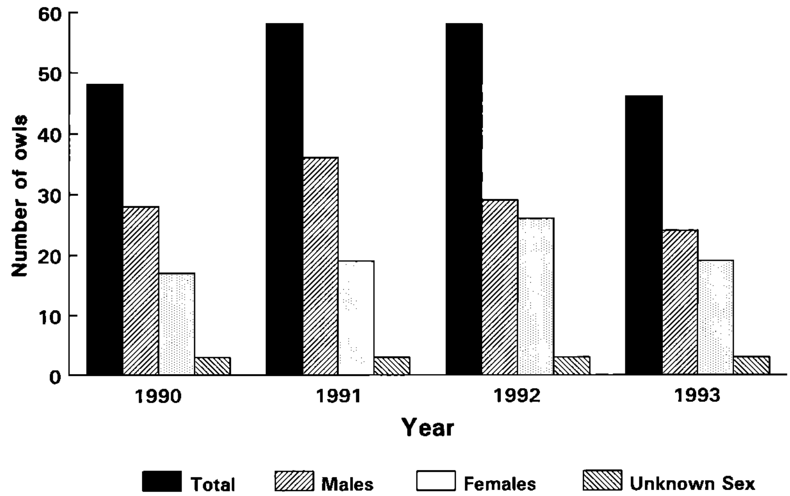

FIGURE 3. Number of territorial Northern Spotted Owls located per year on the 676 km² Density Study Area on the Siuslaw National Forest, Oregon, 1990–1993. Numbers indicate all territorial owls detected by surveys.

The absence of a significant change in owl numbers on the Density Study Area did not necessarily refute or support the estimate of the annual rate of population change calculated from capture-recapture data. The power of the regression of owl numbers on time was so low (0.05) that the test would not have revealed a gradual decline (or increase) even if it was occurring. Statistical power to detect trends will improve as more years of data are collected. In addition to the problem of statistical power, estimates of owl numbers on the Density Study Area may be confounded in such a way that they do not reflect true population trends. For example, it is possible that in a declining population, observed densities of territorial owls might not change during early years of the decline simply because territorial owls that died could be replaced by floaters (owls without territories)(Franklin 1992). Thus, significant changes in density of territorial owls might not become apparent for many years, especially if the rate of population decline was small (e.g., 1–2% per year). However, if the rate of population decline was as large as suggested by the capture-recapture analysis (12.6% per year), then the population of floaters should be rapidly exhausted, and declines in the territorial population should become apparent within a few years. Also, if the rate of decline was 12.6% per year, then that rate of decline must have started only recently. Otherwise, the population of floaters would have been exhausted long ago, and we would be witnessing a rapid decline in the density of territorial owls. Since a rapid decline in numbers was not apparent on the DSA, we conclude that either the rate of decline suggested by the capture-recapture analysis is somewhat exaggerated, or the high rate of decline is a relatively recent phenomenon. These relationships should become clearer, as more years of data are accumulated.

SUMMARY

A capture-recapture study was conducted to assess survival, fecundity and population growth rates of Northern Spotted Owls on the Siuslaw National Forest in the Coast Ranges Province of western Oregon from 1990–1993. The most parsimonious capture-recapture model indicated no sex- or time-effects on survival or recapture rates. Age-specific annual survival estimates were 0.2420 (SE = 0.0924) for juveniles and 0.822 (SE = 0.027) for non-juveniles. Fecundity, defined as the number of female young produced per female owl per year, averaged 0.231 (SE = 0.043) for $\geq$3-yr-old birds and 0.071 (SE = 0.101) for 1- and 2-yr-old birds. Fecundity varied among years, primarily as a result of variability in the proportion of females that nested. The estimated annual rate of population growth ($\hat{\lambda}$) based on age-specific estimates of survival and fecundity was 0.874 (SE = 0.031), suggesting a population decline of 12.6% per year. We suspect that $\hat{\lambda}$ is biased low, primarily because of negative bias in the estimate of juvenile survival due to emigration. However, the extent to which $\hat{\lambda}$ is biased relative to the true rate of population change is unclear, because a variety of other factors could cause positive or negative biases in estimates of vital rates.

In a 676 km²-Density Study Area that was completely searched for owls each year, the num-

ber of territorial owls detected did not change significantly from 1990–1993 (slope = −0.600, r = −0.121, P = 0.879). However, the power of the regression analysis was low (0.05), indicating that more years of data are needed to reliably estimate population trends from the count data. Count data are also subject to a variety of biases that make interpretation difficult.

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Key words: capture-recapture, demography, fecundity, Northern Spotted Owl, Oregon, populations, *Strix occidentalis caurina,* survival.