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# DEMOGRAPHIC CHARACTERISTICS AND TRENDS OF NORTHERN SPOTTED OWL POPULATIONS IN NORTHWESTERN CALIFORNIA

ALAN B. FRANKLIN, R. J. GUTIÉRREZ, BARRY R. NOON, AND JAMES P. WARD, JR.

## INTRODUCTION

In California, research on the distribution and numbers of Northern Spotted Owls (*Strix occidentalis caurina*) began in the early 1970's (Gould 1977). Early indications that the owl population could be declining in California received little attention until the early 1980's when focused ecological research on the owl began in northwestern California (Gutiérrez et al. 1984). Debate over trends in Northern Spotted Owl populations in California recently culminated in a petition to remove the owl in California from the federal list of threatened and endangered species (California Forestry Association 1993). Much of this recent debate has centered around predictive modeling approaches which lacked supporting empirical data (Harrison et al. 1993). In 1985, we began a long-term study on the population ecology of the Northern Spotted Owl in northwestern California (Franklin et al. 1990). Our study followed five years of previous studies in the same region that established baseline information on Spotted Owl habitat and dispersal ecology (Gutiérrez et al. 1985, LaHaye 1988, Sisco 1990, Solis and Gutiérrez 1990). Objectives of our long-term demographic research have been to document life history characteristics of Northern Spotted Owls, monitor long-term population trends on public lands in northwestern California, and to relate estimates of fitness with measures of habitat structure and composition.

In this paper, we present estimates of age- and sex-specific survival probabilities, fecundity rates, and trends in those estimates over a 9-year period. In addition, we test the null hypothesis that the population of Spotted Owls in northwest California was stationary or increasing against the alternative that the population was declining during the period of our study. Throughout this paper, we use the term *stationary* when referring to constant population size over time and *stable* when referring to constant demographic parameters over time (Seber 1982:400).

## STUDY AREA

We studied Spotted Owls within a 10,000-km$^2$ area of northwest California (Fig. 1) that included portions of the Six Rivers, Klamath and Shasta-Trinity National Forests and isolated parcels administered by the Bureau of Land Management. The area was located in the Klamath physiographic province where Mixed Evergreen, Klamath Montane, Oregon Oak and Tan Oak vegetation types predominate (Küchler 1977). Elevations ranged from 200 to 1,700 m. Within this area, we established a 292-km$^2$ study area, near Willow Creek, Humboldt Co., California, which was systematically surveyed each year to estimate density of Spotted Owls (Franklin et al. 1990, Ward et al. 1991). This Willow Creek study area contained 49 Spotted Owl sites. We also selected 12 satellite areas, each 10–30 km$^2$ in size and each containing 2–5 Spotted Owl sites. These satellite areas contained a total of 41 Spotted Owl sites and were selected to increase sample size over a wider geographic area. We conducted surveys for Spotted Owls from 1985–1993 on the Willow Creek study area and 1987–1993 on the satellite areas.

Two additional demographic studies began in 1990 west of our study area on lands owned by Simpson Timber Company (L. Diller, personal communication) and Louisiana-Pacific Corporation (M. Pious, personal communication). A large portion of the area surrounding our study area was surveyed each year for Spotted Owls by the U.S. Forest Service, Bureau of Land Management and private land-holders. These adjacent demographic studies and surveys were useful for detecting movements of banded birds outside areas we surveyed.

## METHODS

Spotted owl sites within the study areas were surveyed on multiple occasions between April and August each year to locate and mark resident owls, and to assess reproductive output. The Willow Creek study area was entirely surveyed at least twice each year. Field methods used for surveying, capturing, marking, and estimating reproductive output are detailed in Franklin et al. (*this volume*). Individuals were uniquely identified, through capture, recapture, or resighting of color bands. In this paper, we defined "capture" either as initial capture of unmarked individuals or as recapture or resighting of previously marked individuals. Marked individuals were used to estimate survival probabilities while measures of reproductive output were used to estimate fe-

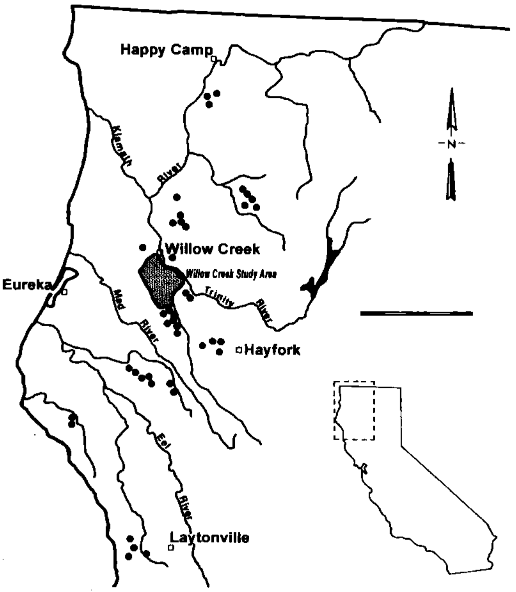

FIGURE 1. Locations of the Willow Creek study area (shaded area) and satellite sites occupied by Northern Spotted Owls for ≥ 1 year (dots) in northwestern California.

cundity (see Franklin et al. *this volume*). We recognized four age-classes of birds when estimating survival and fecundity: juvenile (J), 1-year old (S1), 2-year old (S2) and ≥3-year old (A) (see Franklin et al., *this volume*).

### ESTIMATING DEMOGRAPHIC PARAMETERS

We examined mark-recapture data for goodness-of-fit to a global model using TEST 2 and TEST 3 in program RELEASE (Burnham et al. 1987:71–77). Goodness-of-fit for reduced models was assessed by computing likelihood ratio tests between global and reduced models and then adding the $\chi^2$ values and degrees of freedom from these tests to the values obtained from the goodness-of-fit tests for the global models (Lebreton et al. 1992). To examine the assumption that captures occurred in a brief sampling period, we tested for differences in median capture dates between years (Smith and Anderson 1987) using Kruskal-Wallis tests (Sokal and Rohlf 1981). We initially tested for differences in median capture dates between years for ≥1-year old owls and juveniles separately, to determine if pooling across years within each age-class was appropriate, and then tested for differences between ≥1-year olds and juveniles. Nonparametric multiple comparisons were used to test all possible pairs of years with $\alpha$ adjusted by the number of tests performed (Dixon et al. 1990). Smith and Anderson (1987) provided a formula for adjusting survival rates to a 12-month interval if intervals between capture occasions did not equal 1 year:

$$\tilde{\phi} = \hat{\phi}^{12/x}$$

where $\tilde{\phi}$ was the adjusted survival estimate, $\hat{\phi}$ the unadjusted mark-recapture survival estimate and $x$ is the difference in months between medians.

We modeled survival probabilities using model nomenclature, selection and testing procedures outlined in Franklin et al. (*this volume*). Akaike's Information Criterion (AIC) was used primarily in model selection; models with lowest AIC were selected as the best models explaining the mark-recapture data. Models within 1 unit of AIC were considered to be competing models and were examined more closely with likelihood ratio tests (Lebreton et al. 1992) that tested $H_O$: reduced models best fit the data, versus $H_A$: the more complex model best fit the data. We examined trends in survival using two sets of capture-history matrices. The first set consisted of owls which were initially captured when they were ≥3-years old, separated by sexes. The second data set included 8 subsets partitioned by sex and the four age-classes when owls were first captured (J, S1, S2 and A). We tested the null hypothesis that survival probabilities were constant over time (model $\phi$) versus alternatives that survival was time-dependent without a linear trend (model $\phi_t$) and with a linear trend (model $\phi_T$). Sex effects were considered in all hypotheses tested.

We initially modeled the ≥3-year old data with all 64 possible combinations of effect: no sex ($s$) effect, no time ($t$) effect, $t$, $s$, $s+t$, $s*t$, $s+T$, and $s*T$ for both $\phi$ and $p$. In addition, we examined models where recapture probabilities were structured on methodological constraints ($p_c$) as follows. During the first three years of the study (1985–1987) birds were physically recaptured each year to read their USFWS bands. During the rest of the study (1988–1993), owls were resighted through the use of color bands (Franklin et al. 1990). We, therefore, included models with $p_c$ which represented a single estimate of $p$ for 1986 and 1987 and one for 1988 through 1993.

Juvenile Northern Spotted Owls are capable of dispersing considerable distances (Gutiérrez et al. 1985). Therefore, we suspected that estimates of juvenile survival could be biased low because of permanent emigration of juveniles from our study area. Without the use of radio-telemetry, we were unable to quantitatively estimate this bias (e.g., Burnham et al. *this volume*). However, we examined this bias qualitatively by examining (1) distances moved by each age-class estimated from observed movements of banded birds between sites, and (2) the percentages of recaptures for each age-class which would have been missed if additional surveys had not been conducted by others outside the boundaries of areas we surveyed.

Estimates of age-specific fecundity ($b_x$, where $x$ = age-class; number of female young fledged per female) were estimated according to Franklin et al. (*this volume*). In estimating fecundity, a 1:1 sex ratio was assumed. We tested this assumption using Fisher's Exact Test (Sokal and Rohlf 1981) on fledged young of known sex for 1992 (N = 48 young) and 1993 (N = 9 young) where sex was determined by chromosomal analysis of blood samples (Dvořák et al. 1992). Blood samples were analyzed by Zoogen, Inc., Davis, California. Trends in fecundity were examined using mixed-effect analysis of variance (ANOVA) models. We used PROC MIXED in program SAS (SAS Institute 1993) where age and time were fixed effects and occupied sites were random block effects (C. J. Schwarz, personal communication) because of possible lack of independence between years at a particular site. Using a linear contrast, we also tested an *a priori* hypothesis of $H_O:\mu$ for all years was equal versus $H_A:\mu_{1985-92} = \mu_{1993}$, based on the observation of a substantial decline in reproductive output in 1993.

### ESTIMATING POPULATION TRENDS

We examined population trends by estimating the annual rate of population change ($\lambda$) as (1) a function of age- and sex-specific survival and fecundity (denoted as $\lambda_d$ based on demographic parameters) and (2) changes in annual abundance (denoted as $\lambda_n$ based on estimated annual counts of owls). We estimated $\lambda_d$ by solving the characteristic equation resulting from a modified stage-based Leslie matrix (see Franklin et al. *this volume*). Size of the matrix was determined by the number of age-class groupings resulting from parameter estimation procedures for survival probabilities and fecundity.

We examined trends in abundance for females from (1) the Willow Creek study area combined with 21 selected sites that were consistently surveyed on the satellite areas from 1987 through 1993, and (2) both sexes on the Willow Creek study area only from 1985 through 1993. These two data sets were chosen *a priori* to achieve greatest possible statistical power. Abundance was estimated using open mark-recapture estimators (Pollock et al. 1990). We used the recapture probabilities ($p$) estimated from the analysis of survival probabilities to estimate numbers of individuals ($N$) in each year ($t$) as:

$$\hat{N}_t = \frac{(n_t + 1)\hat{M}_t}{m_t + 1} \quad \text{where} \quad \hat{M}_t = \frac{m_t}{\hat{p}_t}$$

and $n_t$ (number of marked and unmarked owls captured on occasion $t$) and $m_t$ (number of marked owls captured on occasion $t$) were treated as constants (Pollock et al. 1990). Sampling variances for $\hat{M}_t$ and $\hat{N}_t$ were estimated using the delta method (Oehlert 1992). We felt estimating numbers in this manner was more reliable because we had more confidence in estimating $\hat{p}_t$ from the flexible modeling approach discussed in Franklin et al. (*this volume*) than using existing software (e.g., JOLLY and JOLLYAGE; Pollock et al. 1990). An annual change in population size ($\lambda_i$) between years $t$ and $t + 1$ can be estimated as:

$$\hat{\lambda}_i = \frac{\hat{N}_{t+1}}{\hat{N}_t}$$

Estimates of SE($\lambda_i$) tend to be negatively correlated because the numerator of one time interval becomes the denominator of the next time interval (Eberhardt 1970). For this reason, we regressed ln($\hat{N}_t$) on time (Caughley and Birch 1971, Eberhardt 1985):

$$\ln(\hat{N}_t) = a + \beta t + \epsilon_t$$

where the slope of the regression ($\beta$) estimates r, and $\epsilon$ the error term is assumed N(0, $\sigma^2$). We used weighted regression in PROC GLM to estimate r and SE(r) where the inverse of SE($\hat{N}_t$) was used to weight $\hat{N}_t$ (SAS Institute 1990). The annual rate of change ($\lambda_n$) can then be estimated for a birth pulse population (Eberhardt 1985) as:

$$\hat{\lambda}_n = 1 + \hat{r} \qquad \text{and} \qquad \widehat{\text{SE}}(\hat{\lambda}_n) = \widehat{\text{SE}}(\hat{r})$$

We used a 1-tailed t-test of $H_0$: $r \geq 0$ versus $H_A$: $r < 0$, which was equivalent to $H_A$: $\lambda < 1$.

We used the approach for estimating power from trends in abundance described by Gerrodette (1987). In the power calculations, we used parameters representative of the trends observed on the Willow Creek study area. These parameters represented the best-case scenario for detecting trends given our data and included an 8-year sampling period, an initial CV of 4.9% for the first estimate of abundance, and $\alpha = 0.05$. We assumed a 1-tailed t-test to detect a negative rate of change and that precision of the abundance estimates was relatively constant over time.

## RESULTS

### TRENDS IN SURVIVAL PROBABILITIES

From 1985 through 1993, we individually marked 274 juveniles, 46 1-year old birds (27 females, 19 males), 38 2-year old birds (19 females and 19 males), and 197 ≥3-year old birds (97 females and 100 males). Results of goodness-of-fit tests indicated the mark-recapture data adequately fit the global model for each data set (Table 1).

TABLE 1. RESULTS OF GOODNESS-OF-FIT TESTS FROM TESTs 2 AND 3 IN PROGRAM RELEASE FOR MARK-RECAPTURE DATA ON NORTHERN SPOTTED OWLS IN NORTHWESTERN CALIFORNIA FROM 1985 THROUGH 1993. GLOBAL MODELS CONTAIN ALL EFFECTS CONSIDERED WITHIN EACH DATA SET. REDUCED MODELS ARE MODELS SELECTED WITHIN EACH DATA SET BASED ON AIC AND LIKELIHOOD RATIO TESTS

| Data set | Model | TEST 2 + 3 | | | TEST 2 | TEST 3 |
|---|---|---|---|---|---|---|
| | | $\chi^2$ | df | P | P | P |
| ≥3-year-olds | Global $\{\phi_{s*t}, p_{s*t}\}$ | 15.97 | 28 | 0.966 | 0.600 | 0.972 |
| | Reduced $\{\phi_{s+T}, p_c\}$ | 36.18 | 55 | 0.977 | 0.846 | 0.976 |
| Age-class | Global $\{\phi_{a*s*t}, p_{a*s*t}\}$[a] | 40.53 | 50 | 0.828 | 0.451 | 0.875 |
| | Reduced $\{\phi_t, p_c\}$[a] | 7.16 | 16 | 0.970 | 0.985 | 0.994 |

[a] Juvenile age-class not included (see text for explanation).

Median date of capture for juveniles was not significantly different among years ($\chi^2 = 12.01$, df = 8, P = 0.15) suggesting that annual distributions of capture dates were similar from year to year. For birds ≥1 year old, median capture dates significantly differed ($\chi^2 = 37.01$, df = 1, P < 0.001) by 19 days in only two of the nine years (from 1987 to 1988 and from 1992 to 1993). Median capture dates for birds captured when ≥1-year old and birds captured as juveniles significantly differed by 37 days ($\chi^2 = 215.07$, df = 1, P < 0.001). We examined the effect of this bias in estimating annual rates of population change ($\lambda_d$).

Three competing models resulted from the analysis of the data containing owls first captured as ≥3-year olds, $\{\phi_{s+t}, p_c\}$, $\{\phi_{s*T}, p_c\}$, and $\{\phi_{s+T}, p_c\}$, which were all within one AIC unit of each other (Table 2). The structure of the recapture probabilities constrained by capture methods ($p_c$) yielded the lowest AIC models without sex or other time effects. Although $\{\phi_{s*T}, p_c\}$ had the lowest AIC, it was not significantly different from $\{\phi_{s+T}, p_c\}$ (Table 2) and the slope parameter for the interaction term was not significantly different from zero (Wald test: $\chi^2 = 2.02$, df = 1, P = 0.154). Therefore, we selected $\{\phi_{s+T}, p_c\}$ as the model which best explained the mark-recapture data because the interaction term in $\{\phi_{s*T}, p_c\}$ was not supported. Model $\{\phi_{s+T}, p_c\}$ had significant time and sex effects (Table 2), still adequately fit the data based on goodness-of-fit tests (Table 1) and estimated slopes for sex ($\hat{\beta}_1 = 0.5126$, $\widehat{SE}(\hat{\beta}_1) = 0.2298$; $\chi^2 = 4.98$, df = 1, P = 0.03) and time ($\hat{\beta}_2 = -0.1307$, $\widehat{SE}(\hat{\beta}_2 = 0.0537$, $\chi^2 = 5.91$, df = 1, P = 0.02) that were significantly different from zero. Thus, we concluded that survival of owls first captured when ≥3-years old declined in a linear fashion, the trend differed according to sex, but survival in both sexes declined at the same rate (i.e., slopes were the same for both sexes; Fig. 2). The slope parameter for time ($\hat{\beta}_2$) was in terms of logit-transformed variables (Lebreton et al. 1992) which did not reflect a meaningful rate of decline. Therefore, we regressed the transformed estimates of annual survival against year to obtain the appropriate estimate (K. P. Burnham, personal communication) of $\hat{\beta}_2 = -0.0182$ ($\widehat{SE}(\hat{\beta}_2) = 0.004$), which indicated a 1.82% annual decline.

Based on analysis of 45 models that included all age-classes, model $\{\phi_{J,At}, p_{a4',c}\}$ had the lowest AIC (Table 2) where A included all birds ≥1 year old. Models that included separate estimates for 1-year, 2-year, and ≥3-year old age-classes had higher AICs (>1636) and were not considered further. Model $\{\phi_{J,At}, p_{a4',c}\}$ had significant variable time effects in adult survival estimates but sex or linear time effects were not supported (Table 2). Sex and time effects were not supported in estimating juvenile survival (Table 2). Therefore, model $\{\phi_{J,At}, p_{a4',c}\}$ was selected as the most parsimonious explanation of our mark-recapture data. This model indicated that (1) survival of owls >1-year old varied over time, (2) juvenile survival was constant over time, (3) there was no difference in survival by sex for any age-class, (4) recapture probabilities were different for the three years following initial capture as a juvenile, and (5) adults and subadults had similar capture probabilities regardless of sex but differed according to the method of capture during the study (Table 3, Fig. 2). We were unable to assess goodness-of-fit for this model because of the lack of identifiability of parameters when juveniles were treated as separate groups in TESTs 2 and 3 of RELEASE. However, an assessment of the portion of this model that included owls ≥1-year old indicated adequate goodness-of-fit (Table 1).

### TRENDS IN FECUNDITY

Based on chromosomal analysis, the sex ratio of juveniles captured in 1992–1993 (28 males: 29 females) was not significantly different from a 1:1 sex ratio (Fisher's exact P = 1.00) which

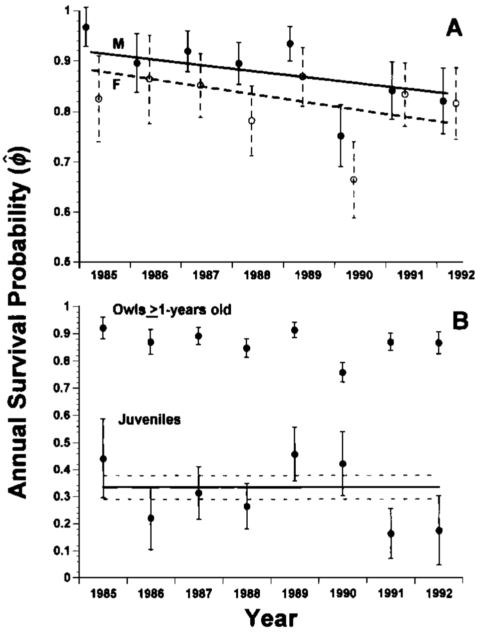

FIGURE 2. Estimates of juvenile and nonjuvenile survival (±1 SE) for Northern Spotted Owls in northwestern California, 1985–1993. **A.** Estimates for birds first captured when ≥3-years old. Lines for males (solid) and females (dashed) represent linear time trends in estimates under model $\{\phi_{s+T}, p_c\}$ with an average standard error of 0.0301 for females and 0.0207 for males. Solid (males) and open (females) dots with 1 standard error are estimates under the variable time model $\{\phi_{s*t}, p_c\}$. **B.** Estimates (±1 SE) for juveniles and birds ≥1-year old under model $\{\phi_{J,At}, p_{a4',c}\}$. Estimates for juveniles is solid line with 1 SE represented by dashed lines under model $\{\phi_{J,At}, p_{a4',c}\}$ and dots under the variable time model $\{\phi_{Jt,At}, p_{a4',c}\}$.

supported our assumption of a 1:1 sex ratio in estimating fecundity. Fecundity differed significantly by age-class ( F = 8.54; df = 2, 392; P = 0.0002) and time ( F = 3.92; df = 8, 392; P = 0.0001), but the interaction between the two was not significant (F = 1.00; df = 15, 377; P = 0.45). Site effects were about 5% of the residual error for both sexes and were not significantly different from zero (z = 1.51, P = 0.13) which suggested that observations at a particular site were independent from year to year. Based on the *a priori* contrast, there was a significant difference (F = df = 22.35; 1, 444; P > 0.0001) in fecundity between 1993 and the other years combined (Fig. 3). We, therefore, concluded that fecundity differed by age-class (Table 4) but was relatively constant for all years except 1993 when fecundity declined significantly (Fig. 3).

TABLE 2. RESULTS OF LIKELIHOOD RATIO TESTS BETWEEN NESTED MARK-RECAPTURE MODELS USED TO ESTIMATE SURVIVAL PROBABILITIES. HYPOTHESES TESTED ARE $H_O$: REDUCED MODEL BEST EXPLAINS DATA, VERSUS $H_A$: MORE GENERAL MODEL BEST EXPLAINS DATA

| $H_O$ | | | $H_A$ | | | Test | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Model | K[a] | AIC[b] | Model | K[a] | AIC[b] | $\chi^2$ | df | P | Effect tested | Decision |
| Owls banded as ≥3-year olds | | | | | | | | | | |
| $\{\phi_{s+T}, p_c\}$ | 5 | 728.043 | $\{\phi_{s+t}, p_c\}$ | 11 | 728.968 | 11.08 | 6 | 0.086 | Variable time | |
| | | | $\{\phi_{s*T}, p_c\}$ | 6 | 728.018 | 2.03 | 1 | 0.155 | Interaction term | Do not reject $H_O$ |
| $\{\phi_s, p_c\}$ | 4 | 732.073 | $\{\phi_{s+T}, p_c\}$ | 5 | 728.043 | 6.03 | 1 | 0.014 | Linear time | Do not reject $H_O$ |
| $\{\phi_T, p_c\}$ | 4 | 731.350 | $\{\phi_{s+T}, p_c\}$ | 5 | 728.043 | 5.31 | 1 | 0.021 | Sex | Reject $H_O$ |
| Owls banded in all age-classes | | | | | | | | | | |
| $\{\phi_{J,AT}, p_{a4'c}\}$ | 8 | 1633.976 | $\{\phi_{J,At}, p_{a4'c}\}$ | 14 | 1633.611 | 12.37 | 6 | 0.054 | Linear time in A | Reject $H_O$ |
| $\{\phi_{J,At}, p_{a4'c}\}$ | 14 | 1633.611 | $\{\phi_{J,As+t}, p_{a4'c}\}$ | 15 | 1634.525 | 1.09 | 1 | 0.297 | Sex in A | Do not reject $H_O$ |
| $\{\phi_{J,A}, p_{a4'c}\}$ | 7 | 1634.878 | $\{\phi_{J,At}, p_{a4'c}\}$ | 14 | 1633.611 | 15.26 | 7 | 0.033 | Variable time in A | Reject $H_O$ |
| $\{\phi_{J,At}, p_{a4',c}\}$ | 14 | 1633.611 | $\{\phi_{JT,At}, p_{a4',c}\}$ | 15 | 1635.495 | 0.12 | 1 | 0.733 | Linear time in J | Do not reject $H_O$ |
| | | | $\{\phi_{Jt,At}, p_{a4',c}\}$ | 21 | 1639.151 | 8.46 | 7 | 0.294 | Variable time in J | Do not reject $H_O$ |
| | | | $\{\phi_{Js,At}, p_{a4',c}\}$ | 15 | 1635.105 | 0.51 | 1 | 0.477 | Sex in J | Do not reject $H_O$ |

[a] Number of estimate parameters.

[b] Akaike's information criterion.

TABLE 3. ESTIMATES OF RECAPTURE PROBABILITIES ($p$) FOR THE SELECTED MARK-RECAPTURE MODEL {$\phi_{J,At}$, $p_{A4',c}$} DESCRIBING AGE- AND SEX-SPECIFIC SURVIVAL PROBABILITIES FOR NORTHERN SPOTTED OWLS IN NORTHWESTERN CALIFORNIA FROM 1985–1993.

| Class | Recapture probability | |
|---|---|---|
| | $\hat{p}$ | $\widehat{SE}(\hat{p})$ |
| Juveniles first recaptured as 1-year olds | 0.2028 | 0.0467 |
| Juveniles first recaptured as 2-year olds | 0.3962 | 0.0693 |
| J first recapture as ≥3-year olds | 0.5654 | 0.0844 |
| Owls ≥1-year old first recaptured in 1986–1987 | 0.7766 | 0.0379 |
| Owls ≥1-year old first recaptured in 1988–1993 | 0.9182 | 0.0124 |

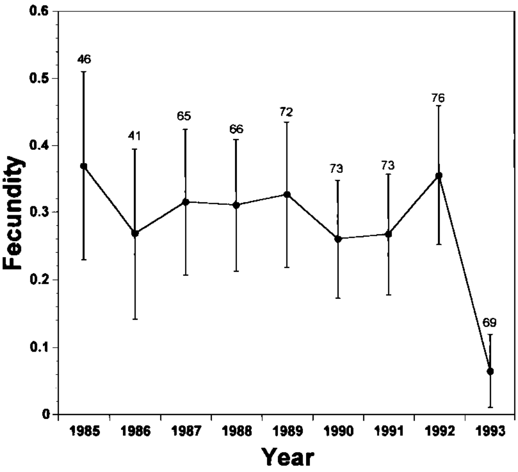

FIGURE 3. Estimates of fecundity (±1 SE) for Northern Spotted Owls ≥1 year old in northwestern California, 1985–1993. Numbers above estimates represent sample sizes.

## ESTIMATES OF POPULATION CHANGE

### *Trends based on demographic parameters*

To estimate the annual rate of change based solely on demographic parameters ($\lambda_d$), we used estimates of fecundity and survival averaged over the period 1985–1993 (Table 4). For fecundity, we used the age-specific estimates from the ANOVA models and, for survival, we used the estimates of $\phi$ from model {$\phi_{J,At}$, $p_{a4',c}$} of the mark-recapture analyses. Average survival of birds ≥1-year old was calculated by averaging the annual estimates from the variable time portion of the model with a standard error estimated using the delta method, which incorporated the annual standard error estimates and the covariances between years. Using our estimates of average demographic parameters, and their standard errors, in a 3-stage Leslie matrix, $\hat{\lambda}_d$ was 0.9656 ($\widehat{SE}(\hat{\lambda}_d)$ = 0.0138) which was significantly different from a stationary population (1-tailed z = 2.08, P = 0.019 ). Values for partial derivatives of each parameter estimate with respect to $\hat{\lambda}_d$ suggested that model sensitivity was highest for ≥1-year old survival followed by juvenile survival and adult fecundity which had roughly similar sensitivities (Table 4).

Our estimate of juvenile survival was probably biased low because of permanent emigration from our study area. Inter-site distances moved by 56 juveniles ($\bar{X}$ = 19.61 km, SE = 2.70) were significantly higher (t-test with unequal variances: t = −5.32, df = 63, P = 0.0001) than the relatively short, with respect to study area size, distances moved by 45 ≥1-year old owls ($\bar{X}$ = 4.75 km, SE = 0.73). We never observed marked juveniles on their natal sites, indicating they always

TABLE 4. AGE-SPECIFIC ESTIMATES AND STANDARD ERRORS OF DEMOGRAPHIC PARAMETERS, PARTIAL DERIVATIVES ($\delta\hat{\lambda}_d/\delta\hat{\theta}$) FOR DEMOGRAPHIC PARAMETERS, AND ESTIMATES OF DEMOGRAPHIC PARAMETERS REQUIRED TO ACHIEVE A STATIONARY POPULATION ($\theta_{|\lambda=1}$) FOR FEMALE NORTHERN SPOTTED OWLS IN NORTHWESTERN CALIFORNIA, 1985–1993. PARAMETER ESTIMATES WERE USED TO CALCULATE THE ANNUAL RATE OF POPULATION CHANGE ($\hat{\lambda}_d$).

| Parameter ($\theta$) | $\hat{\theta}$ | $\widehat{SE}(\hat{\theta})$ | $\delta\hat{\lambda}_d/\delta\hat{\theta}$ | $\theta_{\vert\lambda=1}$ |
|---|---|---|---|---|
| Fecundity | | | | |
| 1-year old | 0.0938 | 0.0669 | 0.0302 | 0.9613 |
| 2-year old | 0.2046 | 0.0773 | 0.0272 | 1.2044 |
| ≥3-year old | 0.3333 | 0.0292 | 0.2408 | 0.4858 |
| Survival | | | | |
| Juvenile | 0.3295 | 0.0489 | 0.2690 | 0.4614 |
| 1-year old | 0.8677 | 0.0115 | 0.0989 | >1.0000 |
| ≥2-year old | 0.8677 | 0.0115 | 0.9118 | 0.9053 |

moved. However, movements for owls ≥1-year old were relatively rare; they moved only 6.6% of the time based on number of movements detected divided by the number of their recaptures (45/685; Table 5). In terms of recaptures outside of our study areas, we would have missed 20.8% of juvenile recaptures, if other observers had not located them during their surveys (Table 5). In contrast, <1% of owls ≥1-year old were detected outside of the study area suggesting that emigration of these age-classes from our study area was very low. Regardless, juvenile survival would have to increase by 40.0% to achieve a stationary population (i.e., $\lambda = 1$) under the Leslie matrix model, given that all other parameter estimates remained the same (Table 4). Adult survival would have to increase by 4.3% to achieve the same effect.

To examine the effect of unequal sampling intervals on survival and, hence, estimates of $\lambda_d$, we corrected our single estimate of juvenile survival to obtain $\tilde{\phi}_J = 0.2907$ ($\widehat{SE}(\tilde{\phi}_J) = 0.0421$) and the two years included in average survival of ≥3-year olds to obtain a new average $\tilde{\phi}_A = 0.8661$ ($\widehat{SE}(\tilde{\phi}_A) = 0.0125$). We used these adjusted survival estimates, with the same fecundity estimates used before, to estimate $\tilde{\lambda}_d = 0.9535$ ($\widehat{SE}(\tilde{\lambda}_d) = 0.0169$) which was lower than our previous estimate.

### *Trends based on counts*

Based on annual estimates of population size from counts of owls on the study area, trends for females on the Willow Creek study area plus the selected satellite areas ($\hat{\lambda}_n = 1.000$, $\widehat{SE}(\hat{\lambda}_n) = 0.014$, N = 6 years) was not significantly different (t = 0.02, df = 5, 1-tailed P = 0.491) from a stationary population (i.e., $\lambda = 1$). Trends for both sexes on the Willow Creek study area alone ($\hat{\lambda}_n = 1.009$, $\widehat{SE}(\hat{\lambda}_n) = 0.008$, N = 8 years) was also not significantly different (t = 1.16, df = 7, 1-tailed P = 0.145) from a stationary population. Estimates of $N_t$ ranged from 55 to 62 for females in the larger sample, and 75 to 85 for both sexes on the Willow Creek study area alone, and were precise with CV's ranging from 1.3 to 4.9%. We achieved 100% power for detecting a linear annual decline of r = −0.034 (our point estimate of $\lambda_d - 1$), 80% power if r = −0.020, and 33% power if r = −0.010, given CV($\hat{N}_t$) = 0.049 remaining constant over an 8-year period and a 1-tailed t-test with $\alpha = 0.05$. The latter values of r were both within the upper 95% confidence interval of $\hat{\lambda}_d$. To detect an r = −0.01 with 80% power, would require 4 more years of monitoring.

## DISCUSSION

Direct inferences from analysis of our data can, at most, be extended to the resident, territorial population of owls on public lands within northwestern California and, at the least, to specific Spotted Owl sites sampled within our study area because selection of study areas and Spotted Owl sites within the study area were not random. In both cases, we limited our inferences to the years when data were collected.

TABLE 5. NUMBER OF RECAPTURES BETWEEN 1985 THROUGH 1993 OF NORTHERN SPOTTED OWLS THAT WERE DETECTED WITHIN AND OUTSIDE THE BOUNDARIES OF THE AREAS SURVEYED IN NORTHWESTERN CALIFORNIA. PERCENT MISSED (OUTSIDE ÷ {OUTSIDE + WITHIN}) REPRESENTS THE PERCENTAGE OF RECAPTURES WHICH WOULD HAVE BEEN MISSED IF ADDITIONAL SURVEYS BY OTHER OBSERVERS HAD NOT BEEN CONDUCTED OUTSIDE THE BOUNDARIES OF THE SURVEY AREAS.

| | Number of recaptures | | |
|---|---|---|---|
| Age-class | Within survey area | Outside survey area | Percent missed |
| Juvenile | 80 | 21 | 20.8 |
| 1–2 years old | 156 | 6 | 3.7 |
| ≥3-years old | 523 | 0 | 0 |

### TRENDS IN DEMOGRAPHIC TRAITS

Survival of owls banded as ≥3-year olds decreased significantly over the period of our study. Possible hypotheses for this decrease included (1) a density-dependent response to changes in environmental conditions as the population adjusted to a new, lower carrying capacity; (2) a real decline in survival with the decline continuing to some lower level beyond which it will not recover; (3) a response to some environmental factor related to time; and (4) senescence. The latter hypothesis was partially supported (but not tested) by the fact that the decreasing trend in survival disappeared when younger age-classes were included in the mark-recapture models. If owls ≥3-years old were fairly old when first captured, then time would represent increasing age. This effect may have been masked when younger (1–2 years old) birds were included in the sample. If senescence was occurring, estimates of $\lambda_d$ would be negatively biased (Noon and Biles 1990). The variable survival of owls ≥1-year old over time (based on the age-class models) suggested that external influences, such as weather, may affect survival. The decreasing nature of survival for owls ≥3-years old could, therefore, represent a trend imposed by environmental factors. The alternative hypotheses explaining decreasing survival need to be examined in greater detail and was beyond the scope of this paper. Therefore, we cannot ascribe a specific cause for this decrease in survival for owls ≥3-years old or for the variability of survival for owls $\geq$1-year old during our study period.

Although fecundity declined significantly in one year, we found it to be stable over the majority of years in this study in contrast to other populations of Northern (Forsman et al. 1984) and California Spotted Owls (*S. o. occidentalis*; Noon et al. 1992).

### POPULATION TRENDS

Based on our estimate of $\lambda_n$, we found no evidence for a rate of change as low as $-0.0334$ ($1 - \hat{\lambda}_d$), or even $-0.02$. We had sufficient statistical power to detect such trends. However, our estimates of $\lambda_d$ and $\lambda_n$ were subject to a number of biases that make estimating the exact rate of change difficult. Several alternatives exist that could explain the discrepancy between our estimate of $\lambda_d$, which indicated a declining population, and $\lambda_n$, which indicated a stationary population. One explanation of the projected decline under $\lambda_d$ was that we underestimated juvenile survival because of permanent emigration from our study area. However, our estimate of juvenile survival would have to be substantially higher to achieve a stationary population. Understanding juvenile survival over the long term may be a key to understanding the demographics of Northern Spotted Owl populations. As estimated under the Leslie matrix model, changes in $\lambda_d$ appear to be most sensitive to adult survival (see also Noon and Biles 1990). However, model sensitivity should not be confused with process sensitivity. Large-scale temporal changes in juvenile survival may be a process that ultimately regulates Spotted Owl populations. We believe this process can be examined best using radio-telemetry to estimate juvenile survival rather than through mark-recapture studies.

Another alternative to explain the discrepancies between our estimates of $\lambda_d$ and $\lambda_n$ was proposed by Franklin (1992), where a non-territorial "floating" population serves to stabilize the observed territorial population through immigration, even though the entire population as a whole may be declining. The Leslie model can include immigration if recruitment is used in lieu of fecundity and juvenile survival (Caswell 1989). Unfortunately, statistical models to estimate recruitment lack the current sophistication of those used to estimate survival and fecundity (see Pollock et al. 1990). True $\lambda_d$ for the female portion of the population lies between 0.9385 and 0.9926 with a 95% probability. Therefore, decline in the female portion of the population could be less than 1% a year. If true $\lambda_d$ was 1%, our study population of about 65 females would decline to 62 females after 5 years. With this magnitude of change, we lacked the power to detect this trend when estimating $\lambda_n$. Additional years of monitoring will be required before such rates will be detectable with sufficient statistical power.

We believe appropriate inferences regarding rates of change of the Spotted Owl population in our study is that this population is currently not declining dramatically. The possibility exists that the population is either stationary or slightly declining. Estimates of $\lambda_n$ are estimates of population change over the sample period only, whereas estimates of $\lambda_d$ are properly interpreted as the rate of change in the population if the conditions during the study period were maintained indefinitely. Therefore, we do not know if estimated declines will continue past the time period when estimates of demographic traits and numbers were measured. We caution against attempts to forecast population trends using our estimates beyond the time period when the population was sampled because of uncertainty concerning the underlying causes of these trends. Even though there is considerable uncertainty in our estimates of population trends, our results suggest it would be prudent to exercise caution with management of Spotted Owl populations. Since our results suggest a slow rate of decline, management actions which may accelerate this decline should be avoided.

We believe that reliable information concerning the effects of land management activities on Northern Spotted Owl populations can be best achieved through well-designed experiments. For example, if logging continues in Spotted Owl habitat on public lands, different harvesting regimes could be applied to randomly selected control and treatment sites to examine the effects of such practices on survival, fecundity, (or their correlates) and, ultimately, fitness. Such a design could be incorporated into existing demographic studies. Demographic studies such as ours provide observational information for establishing the biologically-based hypotheses to be experimentally tested, as well as the initial pre-treatment data.

## SUMMARY

A contentious point in the controversy surrounding Northern Spotted Owls is whether populations are declining or stationary. We estimated age- and sex-specific survival probabilities and fecundity rates from 1985 through 1993 in a population of Northern Spotted Owls on public lands in northwestern California. We used mark-recapture models to estimate survival probabilities and ANOVA models to estimate fecundity rates. We estimated annual rates of population change using average estimates of demographic parameters in a 3-stage Leslie matrix and by estimating counts of owls over time. We found a significant decline in survival for owls ≥3-years old in mark-recapture models which only included this age-class. However, survival of owls ≥1-year old was variable over time when all age-classes were included in the mark-recapture models. Estimates of juvenile survival and fecundity (with the exception of one year) were constant during the study period. Using our estimates of demographic parameters in a Leslie matrix, we estimated an annual rate of population change (λ) of 0.9656, which was significantly different (P = 0.019) from a stationary population. In contrast, trends in numbers of owls (λ = 1.000–1.009) were not different (P = 0.15–49) from a stationary population. A number of biases made estimation of population rates of change problematic and were possible explanations for the discrepancy between our estimates of λ. During the period of study, we concluded that the population of Spotted Owls in our study were not in dramatic decline, but may have been in either slight decline or stationary.

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