Annual Progress Report (Contract#06-CR-11052007-173) to Region 5, USDA Forest Service
Colorado State University

1 April 2010

MONITORING THE POPULATION ECOLOGY OF SPOTTED OWLS (*Strix occidentalis caurina*) IN NORTHWESTERN CALIFORNIA: ANNUAL RESULTS, 2009

by

Alan B. Franklin[1], Peter C. Carlson[2], Jeremy T. Rockweit [2], Krista Lewicki[2], Maria Immel[2], Andy Van Lanen[2], Heather Hareza[2], Robert Wise[2], Vanessa Schipani[2], and Kenneth Wilson[3]

[1]National Wildlife Research Center, Fort Collins, CO 80521
[2] Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523
[3]Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523

INTRODUCTION

The northern spotted owl (*Strix occidentalis caurina*) is closely associated with old-growth Douglas-fir (*Pseudotsuga menziesii*) forests on public lands in northwestern California (Gould 1974, Gutiérrez et al. 1984, Solis and Gutiérrez 1990, Sisco 1990, Blakesley et al. 1992, Hunter et al. 1995, Franklin et al. 2000). Logging of these old-growth forests was considered to be a major factor in the decline of spotted owl populations which subsequently led to the listing of this species as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1990). Recently, Franklin et al. (2000) found that ecotones between older forest and other habitats may be additional important components of northern spotted owl habitat in northwestern California.

Basic demographic data has been useful for assessing the status and management of spotted owl populations (see Burnham et al. 1996). Our study was initiated in 1985 as a long-term monitoring study of the population dynamics of northern spotted owls with the primary objectives of:

1. Estimating life-history parameters such as reproductive output, annual survival, and longevity,

2. Assessing the effects of environmental variation (such as habitat configuration and climate) on life-history parameters,

3. Estimating rates of change in the population over time, and

4. Understanding population behavioral and regulatory mechanisms.

Information has been collected and disseminated for all these objectives. This report provides additional information on estimates and trends in life-history parameters and population rates of change for the northern spotted owl in northwestern California. In this report, we used a different approach to estimate rates of population change than in previous reports prior to 2002 (e.g., Franklin et al. 2001) because of problems in estimating juvenile survival using mark-recapture estimators. Since 2002, we have used a reverse-time mark-recapture estimator developed by Pradel (1996) and further refined by Nichols and Hines (2002). In addition, we also relied on a random-effects modeling approach to examine trends in both survival and rates of population change (Franklin et al. 2002). In past reports, we had used this approach only in estimating reproductive output. The results of this monitoring study meet the intent and structure of the Effectiveness Monitoring Plan of the Northwest Forest Plan for monitoring northern spotted owl populations (Lint et al. 1999).

STUDY AREA

We studied spotted owls in two areas of northwestern California (Figure 1): a regional study area (RSA) and the Willow Creek Study Area (WCSA). The RSA encompasses approximately 10,000 km^2 (3,861 mi^2) and includes portions of the Six Rivers, Klamath and Shasta-Trinity National Forests and lands administered by the U.S. Bureau of Land Management. The area actually surveyed for northern spotted owls within the RSA is approximately 1,784 km^2 (688 mi^2). Territories in the RSA were selected based on where spotted owls were banded during previous studies (e.g., Gutiérrez et al. 1985) for the purpose of providing a wider geographic sample for estimating demographic parameters.

The Willow Creek study area (WCSA) is a "density" study area encompassing 292 km^2 (113 mi^2) where the entire area is surveyed each year. The WCSA is located just south of Willow Creek, Humboldt Co., California in the central portion of the RSA. The WCSA was selected originally in 1985 for intensive study because (1) the study area was easily delineated by geographic boundaries, (2) the history of occupation by spotted owls was well known through previous surveys and research, and (3) the area was accessible by roads. The WCSA is managed primarily by the Lower Trinity Ranger District, Six Rivers National Forest with a small portion managed by the Big Bar Ranger District, Shasta-Trinity National Forest. Elevations range from 200 m (650 ft) to 1700 m (5580 ft).

Climate within the study areas is characterized by cool, wet winters and hot, dry summers. The dominant land use in the WCSA was timber production with clearcutting being the principal method of logging. However, logging declined, and then ceased, on public land within our study areas over the course of the study. The vegetation is Mixed Evergreen, Klamath Montane, Oregon Oak and Tan Oak forest types (Küchler 1977). Additional description of the climate, physiography, and vegetation of the study area was presented by Franklin et al. (1986). Six vegetative cover types occurred on the WCSA; four represented different seral stages of coniferous forest (CF) (Franklin et al. 1990, Hunter 1994). These cover types were described as follows: CF1 - nonvegetated or grass and forbs associated with seedling conifers <2.5 cm diameter at breast height (dbh); CF2 - brush associated with sapling conifers ranging from 2.5-12.6 cm dbh; CF3 - pole and medium conifers ranging from 12.7-53.2 cm dbh; CF4 - mature and old-growth conifers ≥53.3 cm dbh; HDW - hardwood trees comprising >80% of basal area; and Water. Based on analysis of 1992 LANDSAT imagery, 35.3% of the WCSA was covered by CF4, 12.8% by CF3, 14.4% by CF2, 8.9% by CF1, 28.3% by HDW and 0.3% by Water (Hunter 1994).

METHODS

We attempted to locate and identify all individual spotted owls in the WCSA and the RSA. Spotted owls were located using vocal imitations of their calls to elicit responses (Forsman 1983). Individuals were identified by initial capture, marking and subsequent recapture or resighting colored leg bands. Most of our methods were either adapted from Forsman (1983) or developed during previous research projects (Gutiérrez et al. 1984, Gutiérrez et al. 1985, Franklin et al. 1986, Franklin et al. 1990). Methods for recording data collected in the field were described in Franklin et al. (1986, 1996).

Surveys

Both day and night surveys were used to locate spotted owls. Night surveys were conducted between dusk and 0200 hours (Pacific Standard Time) and consisted primarily of point surveys. A minimum of 10 minutes was devoted to each call station during point surveys. Day surveys were used to locate roosting owls and consisted of walk-in surveys and cruise surveys. Walk-in surveys were initiated during the day at sites where owls had been located previously. Cruise surveys were 1) conducted in habitat considered potentially occupied, or areas presumed occupied based on night surveys and 2) conducted in areas known to contain owls but where no owls were detected during the survey. The two types of surveys differed in that walk-in surveys were successful in detecting owls whereas cruise surveys were unsuccessful in detecting owls.

Once located, owls were checked for reproductive activity by feeding live mice to individuals (Forsman 1983). Breeding spotted owls take prey and fly to the nest or fledged young; non-reproductive owls either eat or cache the mice. Lack of reproductive activity was

inferred if (1) an owl took ≥ 2 offered mice, and cached the last mouse taken, (2) a female did not have a well-developed brood patch during the incubation period, or (3) a combination of the above 2 criteria. We attempted to visit owls at least twice during the sampling period to determine the number of fledged young or to confirm lack of reproductive activity. Reproductive activity of each owl visited was characterized as having 0, 1, 2, or (rarely) 3 fledged young. A territory was assumed unoccupied if spotted owls were not detected after five night surveys which completely covered the territory. Occupancy of territories by single birds was assumed if an additional occupant was not found after (1) at least 1 daytime visit where mice were fed to the occupant and (2) at least 4 additional night-time surveys of the territory.

To increase our knowledge about the occurrence and potential effect of barred owls, we implemented a pilot study in 2008 to survey a portion of the WCSA using barred owl-specific surveys. These surveys were successful in increasing our detections of barred owls (Roberts 2009). Thus in 2009 we began barred owl surveys for most of the WCSA, including 53 historic spotted owl territories and 7 matrix areas (areas where no spotted owls have been located, but could be inhabited by barred owls). Each barred owl survey was conducted between dusk and 2400 hours (Pacific Standard Time) and was similar to spotted owl point surveys except that recorded barred owl calls were broadcast and the length of each survey was a minimum of 15 minutes. We attempted to do follow up surveys for barred owl detections to confirm occupancy and reproductive status, following similar methods as for spotted owls. This allowed us to confirm resident barred owls in most cases. On the RSA we continued to document barred owl detections to spotted owl surveys only.

Capture

Owls were typically captured and marked after their reproductive status had been determined. Several capture techniques were used, including a snare pole, noose pole (Forsman 1983), baited mist net, dip net and, occasionally, by hand. Handling of captured owls was usually less than 20 minutes. Locking aluminum bands provided by the U.S. Fish and Wildlife Service (USFWS) were placed on the tarso-metatarsus of each captured spotted owl to verify the identity of individual owls during recaptures. Colored plastic leg bands with colored flexible tabs were placed on the opposing tarso-metatarsus in order to identify individuals without physical recapture (Forsman et al. 1996).

Identifying individual owls marked with only USFWS leg bands in previous years required recapturing to check band numbers. Loss of USFWS leg bands was assumed to be zero. The identity of owls detected at night was either inferred by the position of the owl relative to known spotted owl territories or by sight identification of color-marked individuals.

Determining Sex and Age

The sexes of adult and subadult spotted owls were distinguished by calls and general behavior. Males produce lower-pitched calls than females (Forsman et al. 1984). However, fledglings could not be accurately sexed until 1992 when we began collecting blood samples from juveniles to determine sex (Dvořák et al. 1992, Fleming et al. 1996). Blood samples taken from juveniles were analyzed by Zoogen, Inc. (Davis, California).

Spotted owls were aged by plumage characteristics (Forsman 1981, Moen et al. 1991). Four age-classes were used: juvenile (J; fledged young of the year); first-year subadults (S1; one year old); second-year subadult (S2; two years old) and adults (A; at least 3 years old). We could not differentiate age beyond the adult age-class.

Data Analysis

Direct inferences from analysis of our data can, at most, be extended to the resident, territorial population of owls on public lands within the scope of the RSA and, at the least, to specific spotted owl sites sampled within the RSA because selection of study areas and spotted owl sites within the RSA were not random. In both cases, inferences are limited to the years when data were collected and temporal trends should not be extrapolated beyond the study period.

Reproduction. —We defined *reproductive output* as the number of young fledged per spotted owl pair, *productivity* as the number of fledged young per pair producing young and *fecundity* as the number of young fledged of a given sex by a parent of the same sex (e.g., female young fledged per female; Franklin 1992). Trends in reproductive output and productivity were examined using mixed-effects (random effects) models where age was considered a fixed effect, and both year and northern spotted owl territories were considered random effects. We used PROC MIXED in program SAS (SAS Institute 1997) to perform analyses. Models were examined for both time trends and age effects with inferences limited to the portion of the population that were paired (i.e., single birds were not included). We used a log-linear variance structure for the error covariance matrix (Littell et al. 1996:295) because the annual variances of mean number of young fledged was proportional to the mean (Franklin et al. 1990, 1999a, 2000). We used a version of Akaike's Information Criterion corrected for sample size (AICc; Hurvich and Tsai 1995) for model selection where minimum AICc values indicated the best approximating model for the data. We obtained maximum likelihood estimates of annual reproductive output and productivity using a random-effect means model with the ESTIMATE statement in SAS (Littell et al. 1996:141). This model also provided estimates of temporal process variation ($\sigma^2_{temporal}$) from which sampling variation had been removed.

We tested for a 1:1 sex ratio using Fisher's Exact Test (Sokal and Rohlf 1981) in fledged young of known sex where sex was determined by chromosomal analysis of blood samples. Differences in proportions estimated for reproductive activity were tested using chi-square tests of homogeneity (Sokal and Rohlf 1981:724; Zar 1984:49) on the raw counts used to calculate the proportions.

Survival. —We examined mark-recapture data for goodness-of-fit to the global Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965) using program RELEASE (Burnham et al. 1987). We also estimated overdispersion (c) using the median $\hat{c}$ procedure in program MARK. We used the estimate of c to correct for any violations of assumptions that resulted in overdispersion (see Franklin et al. 1999a for details). In previous reports, we used a parametric bootstrap algorithm (White and Burnham 1999). However, further simulations suggested that this algorithm underestimated c.

We used a random-effects modeling approach (Burnham and White 2002) to examine trends in survival of non-juvenile territory holders (S1, S2, and A age-classes). We included the S1, S2, and A portion of capture histories for birds initially captured as juveniles and later recaptured. We modeled survival probabilities using model nomenclature and selection outlined in Lebreton et al. (1992). We used the model selection approach based on QAICc (see Lebreton et al. 1990, Franklin et al. 1996, Franklin et al. 1999a) that incorporated $\hat{c}$. ΔQAICc and Akaike weights were used to evaluate the degree to which different models were competitive (Burnham and Anderson 2002). We initially examined time-specific models $\{\phi_t, p_t\}$, $\{\phi_{a*t}, p_{a*t}\}$, $\{\phi_{a*t}, p_t\}$, $\{\phi_{s*t}, p_{s*t}\}$, $\{\phi_{s*t}, p_t\}$, $\{\phi_{a*s*t}, p_{a*s*t}\}$, $\{\phi_{a*s*t}, p_{s*t}\}$, and $\{\phi_{a*s*t}, p_t\}$ selecting the most appropriate model from this set using lowest QAICc. We then used the annual estimates from the selected time-specific model as the basis for examining trends over time using random effects models (see Franklin et al. 2002). We examined 5 types of trends over time: a linear trend (ϕ_T), a log-

linear trend (ϕ_{lnT}), a quadratic trend (ϕ_{TT}), no trend (a means model, $\phi_{\bullet}$), and a "good" year versus "bad" year model where "bad" years were years with very low reproductive output (see *Reproductive Output* section in *Results*). The random effects models were implemented directly in program MARK (White and Burnham 1999).

Population trends. — We examined population trends by estimating the finite rate of population change (λ) directly from the mark-recapture data from the WCSA using the reparameterized Jolly-Seber estimator (Pradel 1996, Nichols and Hines 2002). This avoided the potential biases in estimating λ from the modified stage-based Leslie matrix that we had used previously. The predominant bias in estimating λ from the Leslie matrix approach was the negative bias in estimates of juvenile survival obtained from mark-recapture estimators. Estimates of λ were a function of apparent survival (accounting for death and emigration) and recruitment (accounting for local births and immigration). Thus, estimates of λ represented the change in the WCSA population on an annual basis. We used a random effects approach similar to that used for estimating trends in survival, with the model $\{\phi_t, p_t, \lambda_t\}$ providing annual estimates for the random effects models. We examined two data sets. The first was for the WCSA only. In this data set, we eliminated the first two years of the study (1985 and 1986) in the random effects models because of a potential learning effect by observers that could bias estimates of λ (Hines and Nichols 2002). In the second data set, we combined the data from the WCSA with data from 28 sites on the RSA which had been consistently surveyed since 1988. We referred to this data set as the WCSA+RSA. In both cases, the last estimate of λ (2008-2009) was not estimable in model $\{\phi_t, p_t, \lambda_t\}$ because the last estimate of λ was confounded with the last estimate of p. Therefore, we were only able to examine estimates from 1987-88 through 2007-2008 for the WCSA and 1989-90 through 2007-2008 for the WCSA+RSA. We used program MARK to perform the analyses (see Franklin et al. 2002).

RESULTS

Surveys

We conducted 1402 surveys within our study areas in 2009 (Table 1); 19.1% of these were daytime surveys. Ninety-four territories previously occupied by northern spotted owls were surveyed on the RSA and WCSA in 2009 (Table 2, Figure 1). Owls were detected at 48 (51.1%) and reproduction was assessed at 45 (47.9.7%) of the 94 territories surveyed (Table 2). We assumed that 46 (48.9%) of the territories were unoccupied. Thus, we were able to assess reproduction to protocol at 93.8% of the territories found occupied. We identified (captured, recaptured or resighted) 105 individual owls in 2009 (Table 3). We found a total of 24 juvenile spotted owls that had fledged; 21 on the WCSA and 3 on the RSA. Of the 24 juveniles located, we captured and banded 23 of these juveniles (1 juvenile died during capture). A total of 3,593 identifications of individuals have been made on the WCSA and RSA from 1985 through 2009 (Table 3), not including multiple recaptures and re-sightings of individuals within the same year.

Sex and Age-Class Distribution

The 2009 age-class distribution for northern spotted owls between sexes was different (Fisher's Exact $P = 0.02$) with more female subadults than male subadults. If juveniles were included as an age-class in the age-class distribution, 3.8% of the 106 owls identified were subadults (Table 4). If juveniles were excluded, subadults were 4.9% of the adult/subadult age-classes. Of the 520 juveniles sexed from 1992 through 2009, 255 were females and 265 were males. There was no apparent deviation from a 1:1 sex ratio among the 17 years (Fisher's Exact $P = 0.65$), although males seemed to predominate, especially in 1996 (35 males:20 females) and

2007 (8 males:3 females), while females seemed to predominate in 2009 (15 females:8 males).

Reproduction

Reproductive activity.— The proportion of pairs checked annually for reproduction which nested from 1985 through 2009 (Table 5) were different among years (χ^2 = 120.1, 24 df, P < 0.001). We used only those pairs checked for reproduction before 31 May, which we considered the end of the nesting period. The years 1993, 1995, 1999, 2003, and 2007 were responsible for the difference (χ^2 = 6.4, 1 df, P < 0.011 when 1993, 1995, 1999, 2003, and 2007 were tested against the other years combined). When data for 1993, 1995, 1999, 2003, and 2007 were omitted, the remaining years were not different (χ^2 = 21.5, 19 df, P = 0.31). Overall, an average of 52.4% of the pairs nested annually during the 25 years of study (Table 5).

The proportion of pairs which nested and subsequently fledged young from 1985 through 2009 (Table 5) was also different among years (χ^2 = 39.6, 24 df, P = 0.02). Based on cell contributions to the overall χ^2 value, the years 1992, 2001, and 2003 contributed most to the difference (χ^2 = 5.3, 1 df, P = 0.02 when 1992, 2001, and 2003 were tested against the other years combined). When data for 1992, 2001, and 2003 were omitted, the data did not support differences between years (χ^2 = 20.5, 21 df, P = 0.49). In two years (1992 and 2001), the proportion of pairs nesting and fledging young was higher than average and in one year (2003), it was lower than average (Table 5). Overall, the proportion of nesting pairs which fledged young on both study areas was 76.6% for the 25 years. This can be considered a crude measure of nest success. The proportion of pairs checked which fledged young from 1985 through 2009 (Table 5) was different among years (χ^2 = 108.4, 24 df, P < 0.001). This difference was attributed to years 1993, 1995, 1999, 2003, and 2007 (χ^2 = 10.2, 1 df, P = 0.001 when 1993, 1995, 1999, 2003, and 2007 were tested against the other years combined; χ^2 = 18.2, 19 df, P = 0.51 when 1993, 1995, 1999, 2003, and 2007 were omitted from the analysis). For the 25 years combined, 38.1% of the pairs checked successfully fledged young.

Reproductive output.— We modeled reproductive output using two data sets: one which included all pairs, and one which included only pairs where females were of known age-class. We analyzed the first data set to compare reproductive output with reproductive activity in terms of time trends and we analyzed the second data set to estimate age-specific and sex-specific fecundity rates.

Using data on pairs only (regardless of whether both members had been aged), we analyzed 7 mixed-effects models. In these models, we examined the data for linear time trends (model R_T), no time trends (model R **.**), quadratic time trends (R_{TT}), time trends with a threshold (R_{lnT}), an even-odd year trend (R_{EO}), an even-odd year trend which increased or decreased (R_{EO+T}), and for "good" and "bad" years represented as a categorical variable (model R_g). The latter model was based, *a priori*, on observations of low reproduction in 1993, 1995, 1999, 2003, and 2007, which were categorized as "bad" years with the other years categorized as "good" years. Based on minimum AICc, model R_g was selected (AICc = 3227.90, K = 29 parameters). This model was heavily weighted (Akaike weight = 1.00) indicating that none of the other models explained the variation in the data as well as model R_g. Estimates of the number of young fledged per pair from model R_g were 0.179 (SE = 0.038) for years 1993, 1995, 1999, 2003, and 2007 combined ("bad" years) and 0.508 (SE = 0.046) for the other years combined ("good" years). Annual estimates for reproductive output for pairs are shown in Table 6 for comparison.

To estimate the effects of age on reproductive output for females, we used data for individuals of known age-class only. We examined 46 random-effects models which included combinations of time and age effects, and their interactions. Of these 46 models, model ($R_{g*[fS1,fS2,fA]}$) was selected as the best model (AICc = 3076.0, K = 35, Akaike weight = 0.999). This

model had separate estimates for S1, S2 and adult females which varied differently between "good" and "bad" (1993, 1995, 1999, 2003, and 2007) years. No other models were competitive. Estimates of reproductive output in "good" and "bad" years for each age-class are shown in Figure 2. These estimates suggested that adults had better reproductive output than subadults during "good" years but this advantage diminished during "bad" years. These results were similar to those reported in previous years. Based on a random-effects means model, northern spotted owl pairs of known age fledged an average of 0.596 young per year (Table 7). This parameter had substantial annual variation, based on the coefficient of temporal process variation ($CV_{temporal}$; Table 7). The model ($R_{g*\,[fS1,fS2,fA]}$) explained 98.6% of this process variation.

We investigated effects on productivity in pairs and individuals of known age with 46 mixed-effects models similar to those used to describe reproductive output. Based on minimum AICc, the model selected (P**.**; AICc = 806.9, K = 28, Akaike weight = 0.165) suggested that productivity varied little over years. However, models P_g and P_{lnT}, were almost equally likely (Akaike weights = 0.103 and 0.080, respectively). Model P_g suggested productivity was higher in "good" years (1.602, 95% CI = 1.532, 1.673) than in "bad" years (1.482, 95% CI = 1.292, 1.671) while model P_{lnT} suggested there was a log-linear decline in productivity over time ($\hat{\beta}_1$ = -0.04, 95% CI = -0.112, 0.041). However, neither of these competing models were useful models because 1) the lack of precision in the estimates of productivity for the "bad" years indicated that the "good" versus "bad" year effect was very weak, 2) the 95% confidence intervals for the slope in model P_{lnT} overlapped zero, and 3) the variation explained by the two competing models was only 5.2 to 5.7%. The uncertainty in model selection was primarily due to lack of trends and relatively low process variation in the annual estimates (Table 7). Based on model P**.**, northern spotted owl pairs of known age that fledged young fledged an average of 1.59 young per year (Table 7). This parameter exhibited little annual variation, relative to reproductive output, based on the coefficient of temporal process variation (Table 7). Annual estimates are shown in Table 6 for comparison.

Annual Survival

We modeled the survival of territory holders using data partitioned by sex and the three age-classes (S1, S2 and A). Based on the goodness-of-fit, the global mark-recapture model $\{\phi_{a*s*t}, p_{a*s*t}\}$ exhibited no overdispersion ($\hat{c}$ = 0.896). We initially examined 6 models that included combinations of age-class, sex and time effects with no constraints on time (e.g., ϕ and p always varied by year, t). From this initial set of models, model (ϕ_t, p_t) best approximated the data. The last estimates of ϕ (for the interval 2008-2009) and p (for 2009) were confounded and therefore not estimable. We then used the annual estimates from this model for the random effects modeling process. The random effects model with the lowest QAICc was $\{\phi_{G\ vs\ B}\}$ (Akaike weight = 0.381), which suggested that annual survival varied according to good and bad ($\hat{\beta}$ = -0.051, SE=0.024) reproductive years (Figure 3). This model explained 42.9% of the temporal process variation and was more than twice as likely as model $\{\phi_{lnT}\}$ and $\{\phi_T\}$ (Akaike weights = 0.190 and 0.120, respectively). Based on the random-effects means model, annual apparent survival for territory holders averaged 0.848 which did not vary substantially from year to year, based on the coefficient of temporal process variation (Table 7).

Population Trends

We used annual estimates for λ from the reverse-time Jolly-Seber model $\{\phi_t, p_t, \lambda_t\}$ to estimate trends in λ over time on the WCSA and the WCSA combined with 28 territories on the RSA (WCSA+RSA), using the random effects models. In each data set, we examined 5 random

effects models: λ. (no change over time), λ_T (linear time trend), λ_{lnT} (log-linear time trend), λ_{TT} (quadratic time trend), and $\lambda_{G\ vs\ B}$ (difference in "good" versus "bad" years based on reproductive output model). In the WCSA data set, the best approximating model was model {λ.} (Akaike weight = 0.495), suggesting that none of the trend models adequately explained annual variation in λ. This model was twice as likely model $\lambda_{G\ vs\ B}$ (Akaike weight = 0.261), which was the second-ranked model. For the WCSA and RSA data combined (WCSA+RSA), model {λ.} was also the best approximating model (Akaike weight = 0.413) with model {$\lambda_{G\ vs\ B}$} as a competitive model (Akaike weight = 0.213). Because model {λ.} had the lowest AICc and was twice as likely as model {$\lambda_{G\ vs\ B}$} in the WCSA+RSA data, we concluded that these data could not support a time trend in λ. This difference was supported by the lack of estimable temporal process variation (Table 7, Figure 4). The estimate of λ from 1985 through the interval 2007-2008 (the interval 2008-2009 was not estimable using random effects models) was 0.989 (95% CI = 0.970, 1.007) on the WCSA and 0.986 (95% CI = 0.972, 1.001) on the WCSA+RSA, which were not different from $\lambda = 1$ (a stationary population) based on 95% confidence intervals.

Barred Owls

Barred owls were first detected in the WCSA in 1991 (Table 8). The first barred owl detection in the RSA occurred in Big Slide Creek the following year: this detection was also our first documented interaction between a spotted owl and a barred owl, with two males calling simultaneously. In 1994, a male barred × spotted hybrid was detected in Bee Tree Creek in the WCSA. The first nesting pair of barred owls was confirmed in 1999.

Since 1991, we have observed a gradual increase in the number of barred owl detections in the study areas (Table 8). The proportion of surveyed spotted owl territories with barred owl detections in 2009 was 0.22. To document long term trends, we also estimated the number of barred owl "sites" in the study area using an estimate of barred owl home range size from Washington (Hamer 1988), and topographic features (e.g., ridges) that may act as natural boundaries between sites. At least 2 barred owl detections (either within a year or between 2 or more consecutive years) were needed to define a barred owl "site". We estimated 10 barred owl "sites" in 2009, 9 of which occurred in the WCSA (Table 8).

We confirmed 13 barred owl territories in the WCSA with barred owl specific survey (Table 8; note that full barred owl surveys were not done in 2008, so this does not indicate an increase in barred owl occupied territories). We had only 1 barred owl detection in the RSA, a drop in the number of such detections from 2008. In the WCSA we confirmed 11 pairs of barred owls, 10 within historic spotted owl territories. Both species of owl were found occupying 2 territories. Four of the barred owl pairs nested and fledged young for a total of 8 young.

DISCUSSION

Reproductive patterns in northern spotted owls on our study area continues to follow a pattern of low reproductive output in "bad" years and average or, occasionally, high reproductive output in "good" years. Reproduction by spotted owls in 2009 was considered one of these "good", or average, years. We have observed five years of very low reproduction (Table 6) during the 25 years of the study which are mostly responsible for this variation. While productivity and the proportion of nests that fledge young have remained relatively stable, the proportion of birds nesting each year is primarily responsible for the low reproductive output. That is, very few birds nested in 1993, 1995, 1999, 2003, and 2007, which was primarily responsible for low reproductive output in those years. Annual weather variation is suspected to

be a strong factor in determining this trend with low reproduction during cold, wet springs (Franklin et al. 2000).

We have had three years of below average apparent survival, 1990-1991, 1994-1995, and 1998-1999 (Figure 3). Two of these periods correspond to years that also had low reproductive output. Our analysis suggested that trends in annual survival of territory holders were partially explained by the "good" versus "bad" year model used for reproductive output (Figure 3). As with reproduction, apparent survival can be affected by annual weather variation (Franklin et al 2000). The average rate of population change for the WCSA and the WCSA+RSA population was not different from a stationary population ($\lambda = 1$) and point estimates (0.989 and 0.986, respectively) were indistinguishable from a stationary population ($\lambda = 1$) in both cases. We were unable to estimate temporal process variation because annual sampling variation was large relative to the differences in $\hat{\lambda}$. Estimates of average $\hat{\lambda}$ were nearly identical between the two data sets, the WCSA alone and the WCSA combined with the RSA. In both cases, the annual estimates suggested that there were periods when the population declined followed by periods of increase (Figure 4). The results from both data sets suggest that the northern spotted owl population in our study area is, on average, stationary. However, a population with a stationary λ estimated using the reverse-time Jolly-Seber approach could be a self-sustaining population, a population maintained solely from outside immigration, or a combination of both.

In order to document the status of barred owls (*Strix varia*) in the WCSA and the RSA, we continue to include an additional section into the results of this report. While anecdotal and correlative evidence suggests that barred owls may out-compete spotted owls for resources, it remains unclear what the full impact of barred owls will be on spotted owls (Forsman et al. 2010). The number of barred owl detections in a year is influenced by the number of surveys done in the area and should not be viewed as a reliable indicator of a barred owl range expansion. Because of this, we also include the number of spotted owl territories with barred owl detections and attempted to estimate the approximate number of barred owl activity centers. We do not know if the increase in barred owl territories in the WCSA (Table 8) is a result of our increased barred owl survey efforts, or if it represents an actual increase in barred owl numbers in the WCSA.

ACKNOWLEDGMENTS

We thank Patricia Krueger of the U. S. Forest Service Region 5 for her assistance in financial and logistical support. Bill Rice and the rest of the staff of the Lower Trinity Ranger District, Six Rivers National Forest were generous with their time and access. Christine Moen, John Hunter and Jennifer Blakesley contributed greatly to the success of this project over the years. We extend our gratitude to Sam Cuenca, Lowell Diller, Dennis Garrison, Keith Hamm, Tony Hacking, Mark Higley, Amy Krause, Kary Schlick, Peter Steele, Joel Thompson, and Mark Williams for their assistance and willingness to share information.

LITERATURE CITED

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, second edition. Springer-Verlag, New York, New York

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5, Bethesda, Maryland.

Burnham, K. P., D. R. Anderson and G. C. White. 1996. Meta-analysis of vital rates of the northern spotted owl. Studies in Avian Biology 17:92-101.

Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ring data. Journal of Applied Statistics 29:245-264.

Blakesley, J. A., A. B. Franklin, and R. J. Gutiérrez. 1992. Spotted owl roost and nest site selection in northwestern California. Journal of Wildlife Management 56:388-392.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-438

Dvořák, J., J. L. Halverson, P. Gulick, K. A. Rauen, U. K. Abbott, B. J. Kelley, and F. T. Shultz. 1992. cDNA cloning of a Z- and W-linked gene in gallinaceous birds. *Journal of Heredity* 83:22-25.

Fleming, T. L., J. L. Halverson, and J. B. Buchanan. 1996. Use of DNA analysis to identify sex of northern spotted owls (Strix occidentalis caurina). *Journal of Raptor Research* 30:118-122.

Forsman, E. D. 1981. Molt of the Spotted Owl. *Auk* 98: 735-742.

Forsman, E. D. 1983. Methods and materials for locating and studying Spotted Owls. U.S. Forest Service General Technical Report PNW-12.

Forsman, E. D., E. C. Meslow and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monograph* 87:1-64.

Forsman, E.D, A.B. Franklin, F.M. Oliver, and J.P. Ward, Jr. 1996. A color band for spotted owls. *Journal of Field Ornithology* 67:507-510.

Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, J. E. Hines, J. B. Lint, R. J. Davis, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, S. A. Gremel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. Schaberel, T. J. Snetsinger, and S. G. Sovern. 2010. Demographic trends of northern spotted owls: a meta-analysis, 1985–2008. Final Report Interagency Regional Monitoring Program, USDA Forest Service, Portland, Oregon.

Franklin, A. B. 1992. Population regulation in northern spotted owls: theoretical implications for management. Pages 815-827 *In* D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: populations. Elsevier Applied Science, London, England.

Franklin, A. B., D. R. Anderson, and K. P. Burnham. 2002. Estimation of long-term trends and variation in avian survival probabilities using random effects models. *Journal of Applied Statistics* 29:267-287.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12-20.

Franklin, A. B., K. P. Burnham, G. C. White, R. G. Anthony, E. D. Forsman, C. Schwarz, J. D. Nichols, and J. Hines. 1999a. Range-wide status and trends in northern spotted owl populations. U. S. Geological Survey - Biological Resources Division, Colorado and Oregon Cooperative Fish and Wildlife Research Units, Fort Collins, CO and Corvallis, OR.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539-590.

Franklin, A. B., R.J. Gutiérrez, and P. C. Carlson. 1996. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northwestern California: annual results, 1995. Progress report, U. S. Forest Service, Region 5, San Francisco, CA. 18pp.

Franklin, A. B., R.J. Gutiérrez, and P. C. Carlson. 2001. Population ecology of the northern spotted owl (*Strix*

occidentalis caurina) in northwestern California: annual results, 2000. Progress report, U. S. Forest Service, Region 5, San Francisco, CA. 18pp.

Franklin, A., J.P. Ward, and R.J. Gutiérrez. 1986. Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northwestern California: preliminary results, 1985. Unpubl. Prog. Rep. Project Work No. W_65_R_3 (554). Calif. Dept. Fish & Game. Sacramento, CA. 42pp.

Franklin, A., J.P. Ward, R.J. Gutiérrez and G.I. Gould. 1990. Density of northern spotted owls in northwest California. *Journal of Wildlife Management* 54:1-10.

Gould, G.I., Jr. 1974. The status of the Spotted Owl in California. Unpubl. Tech. Rep., Calif. Dept. Fish and Game and USDA Forest Service, Region 5. 34pp.

Gutiérrez, R.J., D.M. Solis and C. Sisco. 1984. Habitat ecology of the Spotted Owl in northwestern California: implications for management. Pages 368-373 *in* Proc. Soc. Amer. Foresters Natl. Conv., 16_20 Oct., 1983.

Gutiérrez, R.J., J.P. Ward, A.B. Franklin, W. LaHaye and V. Meretsky. 1985. Dispersal ecology of juvenile northern spotted owls (*Strix occidentalis caurina*) in northwestern California. Unpubl. Tech. Rep., USDA _ Forest Serv., Pacific NW Forest and Range Exper. Sta., Olympia, WA. 48pp.

Hamer T. E. 1988. Home range size of the northern barred owl and northern spotted owl in western Washington. MS thesis, Western Washington University, Washington, USA.

Hines, J. E., and J. D. Nichols. 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture-recapture data. *Journal of Applied Statistics* 29:573-587.

Hunter, J. E. 1994. Habitat configuration around spotted owl nest and roost sites in northwestern California. M.S. Thesis, Humboldt State University, Arcata, California.

Hunter, J. E., R. J. Gutiérrez, and A. B. Franklin. 1995. Habitat configuration around spotted owl sites in northwestern California. Condor 97:684-693.

Hurvich, C. M., and C-L. Tsai. 1995. Model selection for extended quasi-likelihood models in small samples. *Biometrics* 51:1077-1084.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247.

Küchler, A.W. 1977. The map of the natural vegetation of California. Pages 909-938 *in* M. Barbor and J. Majors, eds. Terrestrial vegetation of California. John Wiley and Sons, New York, New York.

Lebreton, J-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecolological Monograph* 62:67-118.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS® sytem for mixed models. SAS Institute, Inc., Cary, North Carolina, USA.

Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. U. S. Forest Service General Technical Report PNW-GTR-440, Portland, Oregon.

Moen, C. A., A. B. Franklin, and R. J. Gutiérrez. 1991. Age determination of subadult northern spotted owls in northwest California. *Wildlife Society Bulletin* 19:489-493.

Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ and demographic contributions to λ, using capture-recapture data. *Journal of Applied Statistics* 29:539-568.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703-709.

SAS Institute. 1997. SAS/STAT® software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.

Seber, G.A.F. 1965. The multi-sample single recapture census. *Biometrika* 49:330-349.

Sisco, C. L. 1990. Seasonal home range and habitat ecology of spotted owls in northwestern California. M.S. Thesis, Humboldt State University, Arcata, California.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., San Francisco.

Solis, D. M. and R. J. Gutiérrez. 1990. Summer habitat ecology of northern spotted owls in northwestern California. *Condor* 92:739-748.

U.S. Fish and Wildlife Service. 1990. 50 CFR Part 17 Endangered and threatened wildlife and plants; determination of threatened status for the northern spotted owl; final rule. *Federal Register* 55:26114-26194.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (suppl.): S120-S139.

Zar, J.H. 1984. Biostatistical analysis. Prentice_Hall, Englewood, N.J. 718pp.

Table 1. *Annual number of surveys conducted to detect northern spotted owls in northwestern California, from 1985 through 2009.*

	Survey Type			
Year	Point	Walk-in	Cruise	Total
1985	521	149	36	706
1986	318	156	20	494
1987	726	219	161	1106
1988	1067	212	107	1386
1989	1387	215	89	1691
1990	1425	199	64	1688
1991	1305	244	84	1633
1992	904	207	55	1166
1993	934	170	104	1208
1994	1020	242	96	1358
1995	1129	202	132	1463
1996	1172	249	123	1544
1997	861	224	107	1192
1998	965	216	113	1294
1999	968	170	120	1258
2000	1129	183	127	1439
2001	1031	228	114	1373
2002	1004	210	126	1340
2003	1035	196	108	1339
2004	905	181	93	1179
2005	1014	206	97	1317
2006	1014	162	110	1286
2007	1121	172	113	1406
2008	982	165	109	1256
2009	1134	167	101	1402

Table 2. *Number of northern spotted owl territories surveyed, occupied and checked for reproduction in 2009 in northwestern California.*

	Study Area		
No. Territories	WCSA	RSA	Combined
Surveyed	60	34	94
With Unknown Status	0	0	0
Assumed Unoccupied	31	15	46
Found Occupied By:			
Pairs	25	17	42
Males	3	2	5
Females	1	0	1
Total	29	19	48
Checked For Reproduction Where Occupied By:			
Pairs	23	17	40
Males	2	1	3
Females	1	0	1
Total	27	18	45

Table 3. *Number of northern spotted owls identified in northwestern California from 1985 through 2009. New birds were owls that had not been previously banded; old birds were owls that had been previously banded.*

	No. new birds captured as:			No. old birds which were:			
Year	Adult & Subadult	Juvenile	Total	Recaptured	Resighted	Total	Grand Total
1985	54	16	70	22	0	22	92
1986	8	17	25	55	0	55	80
1987	48	31	79	42	18	60	139
1988	18	36	54	13	86	99	153
1989	26	39	65	21	87	108	173
1990	25	35	60	14	104	118	178
1991	24	37	61	28	87	115	176
1992	20	49	69	12	114	126	195
1993	12	9	21	13	105	118	139
1994	9	48	57	19	105	124	181
1995	21	15	36	22	83	105	141
1996	11	58	69	17	95	112	181
1997	11	43	54	7	105	112	166
1998	12	32	44	16	93	109	153
1999	17	11	28	10	87	97	125
2000	13	39	52	7	86	93	145
2001	17	51	68	11	85	96	164
2002	21	34	55	13	90	103	158
2003	16	4	20	8	93	99	119
2004	16	41	57	13	87	100	157
2005	16	24	40	11	84	95	135
2006	11	21	32	11	70	81	113
2007	13	11	24	5	83	88	112
2008	9	22	31	5	77	82	113
2009	3	23	26	7	72	79	105
Total	451	746	1197	402	1996	2396	3593

Table 4. *Age-class distribution, by sex, in 2009 for northern spotted owls in northwestern California. The number observed is represented by n and the proportion of each age-class within sex by p.*

	Male		Female		Both Sexes	
Age-Class	*n*	p	*n*	p	*n*	P
Adult	42	0.84	36	0.65	78	0.74
2nd-yr Subadult	0	0.0	4	0.07	4	0.04
1st-yr Subadult	0	0.0	0	0.0	0	0.0
Juvenile[a]	8	0.16	15	0.27	24	0.23

[a]Sex-specific juvenile estimates exclude 1 juvenile with unknown sex.

Table 5. *Proportion of northern spotted owl pairs checked for reproductive activity (n) which nested, which nested and successfully fledged young, and which fledged young in northwestern California from 1985 through 2009. Standard errors are in parentheses.*

	Proportion of pairs which:					
	Nested		Nested and fledged young		Fledged young	
Year	n[a]	Proportion	n[b]	Proportion	n[c]	Proportion
1985	32	0.50 (0.088)	16	0.81 (0.098)	42	0.45 (0.077)
1986	25	0.64 (0.096)	16	0.56 (0.124)	37	0.38 (0.080)
1987	31	0.65 (0.086)	20	0.70 (0.102)	57	0.42 (0.065)
1988	36	0.64 (0.080)	23	0.87 (0.070)	62	0.47 (0.063)
1989	52	0.60 (0.068)	31	0.74 (0.078)	65	0.42 (0.061)
1990	53	0.66 (0.065)	35	0.63 (0.082)	67	0.40 (0.060)
1991	58	0.64 (0.063)	37	0.70 (0.075)	67	0.42 (0.060)
1992	49	0.45 (0.071)	22	1.00 (0.000)	74	0.42 (0.057)
1993	25	0.16 (0.073)	4	0.75 (0.217)	59	0.10 (0.039)
1994	50	0.62 (0.069)	31	0.68 (0.084)	62	0.44 (0.063)
1995	49	0.16 (0.053)	8	0.88 (0.117)	59	0.19 (0.051)
1996	40	0.70 (0.072)	28	0.93 (0.049)	57	0.65 (0.063)
1997	49	0.55 (0.071)	27	0.81 (0.075)	61	0.46 (0.064)
1998	47	0.64 (0.070)	30	0.73 (0.080)	56	0.43 (0.066)
1999	42	0.17 (0.058)	7	0.86 (0.132)	54	0.15 (0.048)
2000	40	0.63 (0.077)	25	0.76 (0.085)	52	0.46 (0.069)
2001	35	0.54 (0.084)	19	1.00 (0.000)	53	0.55 (0.068)
2002	45	0.58 (0.074)	26	0.77 (0.083)	58	0.40 (0.064)
2003	40	0.23 (0.066)	9	0.44 (0.166)	53	0.08 (0.036)
2004	39	0.62 (0.078)	24	0.83 (0.076)	56	0.48 (0.067)
2005	36	0.58 (0.082)	20	0.65 (0.107)	53	0.40 (0.067)
2006	29	0.34 (0.088)	10	0.90 (0.095)	44	0.34 (0.071)
2007	35	0.31 (0.078)	11	0.73 (0.134)	49	0.16 (0.053)
2008	35	0.71 (0.076)	25	0.68 (0.093)	45	0.38 (0.072)
2009	33	0.67 (0.082)	22	0.82 (0.082)	40	0.45 (0.079)
Overall[d]	1005	0.52 (0.016)	526	0.77 (0.018)	1382	0.38 (0.013)

[a]Total number of pairs checked each year before 31 May.
[b]Total number of nesting pairs found each year before 31 May.
[c]Total number of pairs checked throughout the entire sampling period in each year.
[d]Estimate represents overall outcomes rather than pairs because same pairs often measured across years.

Table 6. *Mean productivity and mean number of young fledged per pair for northern spotted owl pairs in northwestern California, from 1985 through 2009. Pairs are number of pairs checked for reproductive activity*.

	Productivity			No. young fledged per pair		
Year	Pairs	Mean	SE	Pairs	Mean	SE
1985	19	1.789	0.123	42	0.810	0.149
1986	14	1.571	0.137	37	0.595	0.137
1987	24	1.708	0.095	57	0.719	0.119
1988	29	1.414	0.105	62	0.661	0.103
1989	27	1.741	0.114	65	0.723	0.117
1990	27	1.407	0.096	67	0.567	0.093
1991	28	1.464	0.096	67	0.597	0.095
1992	31	1.742	0.080	74	0.730	0.106
1993	6	1.500	0.224	59	0.153	0.063
1994	27	1.815	0.076	62	0.790	0.120
1995	11	1.455	0.157	59	0.271	0.080
1996	37	1.703	0.102	57	1.105	0.127
1997	28	1.571	0.095	61	0.721	0.110
1998	24	1.333	0.098	56	0.571	0.098
1999	8	1.375	0.183	54	0.204	0.072
2000	24	1.667	0.098	52	0.769	0.125
2001	29	1.759	0.081	53	0.962	0.129
2002	23	1.522	0.107	59	0.593	0.106
2003	4	1.250	0.250	53	0.111	0.049
2004	27	1.667	0.092	56	0.804	0.121
2005	21	1.381	0.109	51	0.569	0.106
2006	15	1.467	0.133	44	0.500	0.115
2007	8	1.750	0.164	49	0.286	0.097
2008	17	1.588	0.123	45	0.600	0.125
2009	18	1.667	0.114	40	0.750	0.142

Table 7. *Mean estimates, standard errors (SE) and process standard deviation ($\hat{\sigma}_{temporal}$) of reproductive output (R), productivity (P), survival (ϕ), and rates of population change (λ) for northern spotted owls in northwestern California from 1985 through 2009. Estimates are from random effects means models.*

Parameter	Mean	SE	$\hat{\sigma}_{temporal}$	$CV_{temporal}$
R	0.596	0.053	0.233	0.390
P	1.586	0.033	0.117	0.068
ϕ	0.848	0.009	0.027	0.032
λ (WCSA)	0.989	0.009	0.000	0.000
λ (WCSA+RSA)	0.986	0.007	0.000	0.000

Table 8. *Number of barred owls detected on the WCSA and RSA from 1991 through 2009.*

Year	Spotted Owl Territories With Detections	Number of Barred Owl Sites[a]		Number of Barred Owl Territories[b]	
		WCSA	RSA	WCSA	RSA
1991	0	1	0	-	-
1992	1	0	1	-	-
1993	0	0	0	-	-
1994	1	1	0	-	-
1995	8	3	2	-	-
1996	4	2	0	-	-
1997	5	4	0	-	-
1998	6	4	0	-	-
1999	7	3	2	-	-
2000	8	5	0	-	-
2001	12	6	1	-	-
2002	10	5	0	-	-
2003	10	5	3	-	-
2004	7	5	1	-	-
2005	8	6	1	-	-
2006	12	7	1	-	-
2007	13	9	1	-	-
2008	20	9	4	8	3
2009	21	9	1	13	1

[a] Estimated using the spatial clustering of detections. This number should be considered an approximate number of barred owl sites.
[b] Confirmed territories based on spotted and barred owl survey effort.

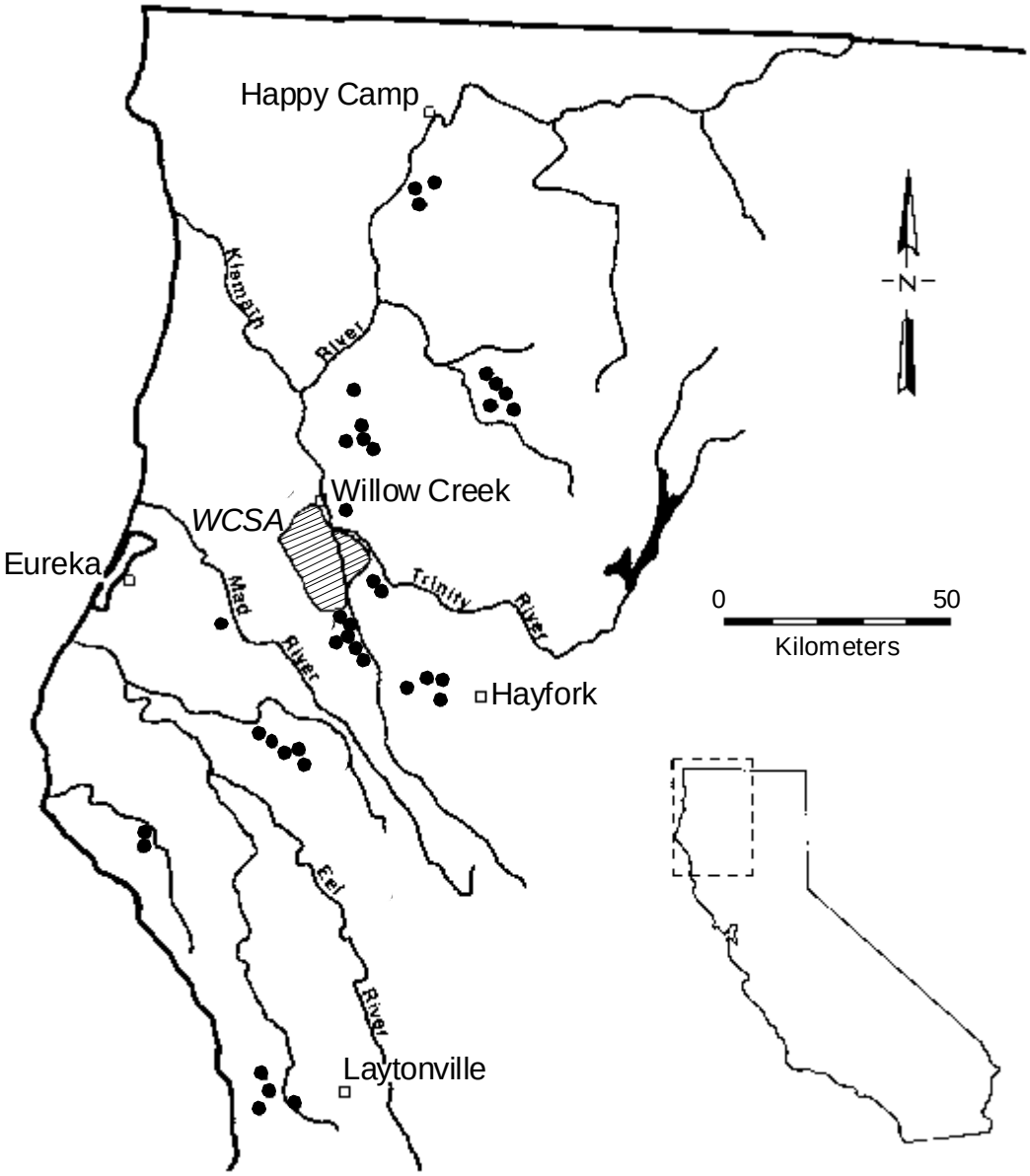

Figure 1. *Map of northern spotted owl territories (dots) surveyed in the Regional Study Area, northwestern California. Shaded area represents the Willow Creek Study Area.*

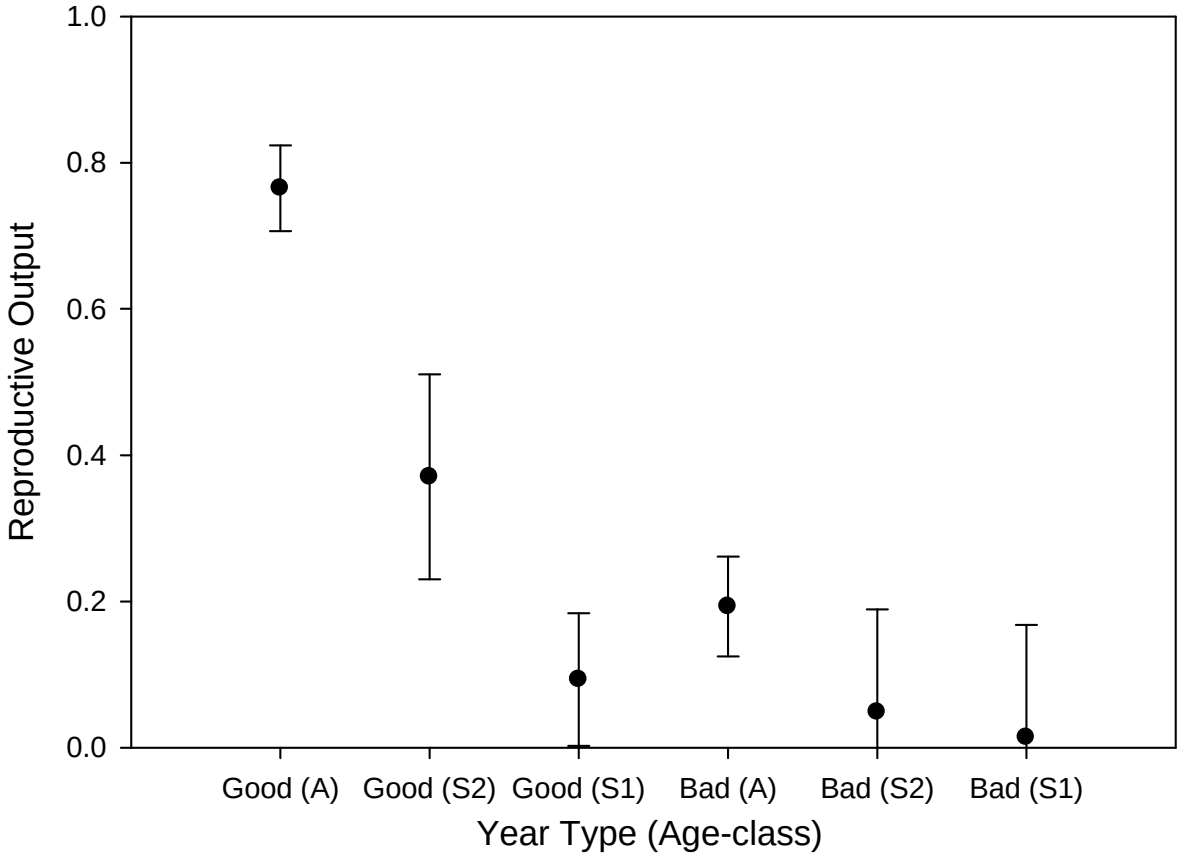

Figure 2. *Mean reproductive output for S1, S2, and adult northern spotted owls in "good" and "bad" years in northwestern California from 1985 through 2009. Bars are 95% confidence intervals.*

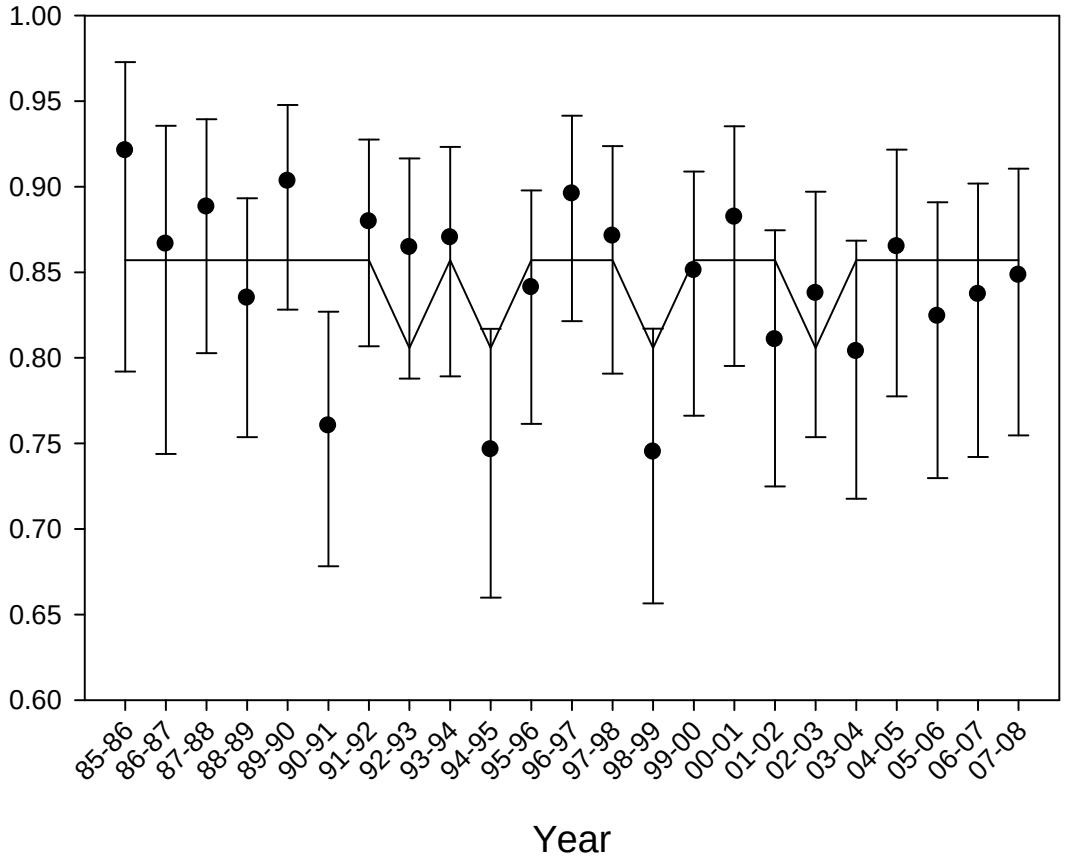

Figure 3. *Trends in apparent survival for subadult and adult northern spotted owls in northwestern California from 1985 through 2009. Trend estimates were from random effects model* $\{\phi_{G\ vs\ B}\}$. *Estimates of individual values (solid dots) ± 95% confidence intervals are from model* $\{\phi_t, p_t\}$ *for comparison. The estimate for 2008-2009 was not estimable.*

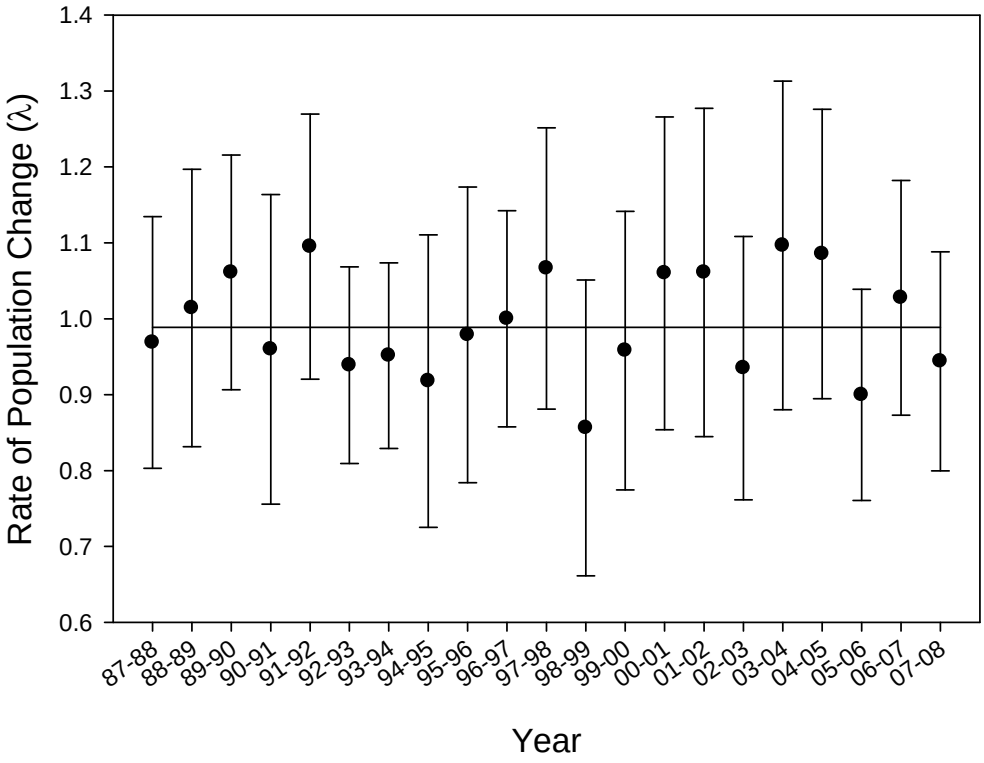

Figure 4. *Annual estimates of λ (dots ± 95% confidence intervals) from the reverse-time Jolly-Seber estimator for the Willow Creek Study Area (WCSA). Solid line indicates estimate from random effects means model.*