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MONITORING THE POPULATION ECOLOGY OF SPOTTED OWLS
(*Strix occidentalis caurina*)
IN NORTHWESTERN CALIFORNIA: ANNUAL RESULTS, 2011

by

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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). 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 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 km² (3,861 mi²) 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 km² (688 mi²). 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 km² (113 mi²) 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

Northern Spotted Owls. — 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.

Barred Owls. — 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 the detectability of barred owls (Roberts 2009). Therefore, in 2009 we began barred owl-specific surveys for most of the WCSA, including 53 historic spotted owl territories and 7 matrix areas (forested areas not occupied by spotted owls). Barred owl surveys were conducted between dusk and 2400 hours (Pacific Standard Time) and were similar to spotted owl point surveys except recorded barred owl calls were broadcast and the length of each survey was increased to at least 15 minutes. We attempted to conduct follow up surveys of 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. In the RSA we continued to document barred owl detections in response 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. Geological Survey Bird Banding Laboratory (USGS) 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 USGS leg bands in previous years required recapturing to check band numbers. Loss of USGS 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 young fledged 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 activity, 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 on reproductive output and productivity and PROC GLIMMIX in SAS (mixed logistic regression, Schabenberger 2005) to analyze binomial data to examine annual trends in proportion of pairs that nested, pairs that nested and fledged young, and pairs that fledged young. 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 examined appropriate variance structures for the error covariance matrix following 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) of reproductive output. 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.

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} . Δ QAICc 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 ($\phi_{\ln T}$), a quadratic trend (ϕ_{TT}), no trend (a means model, ϕ_{\cdot}), 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 and RSA 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 monitored 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 (2009-2010) 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 2008-2009 for the WCSA and 1989-90 through 2008-2009 for the WCSA+RSA. We used program MARK to perform the analyses (see Franklin et al. 2002).

RESULTS

Surveys

We conducted 1,478 surveys within our study areas in 2011 (Table 1); 17.5% of these were daytime surveys. Ninety-four territories previously occupied by northern spotted owls were surveyed on the RSA and WCSA in 2011 (Table 2, Figure 1). Owls were detected at 41 (43.6%) and reproduction was assessed at 33 (35.1%) of the 94 territories surveyed (Table 2). We assumed that 52 (55.3%) of the territories were unoccupied. Thus, we were able to assess reproduction to protocol at 80.5% of the territories found occupied. We identified (captured, recaptured or resighted) 71 individual owls in 2011 (Table 3). We found a total of 7 juvenile spotted owls that had fledged; 5 on the WCSA and 2 on the RSA. We captured and banded all of the juveniles located. A total of 3,766 identifications of individuals have been made on the

WCSA and RSA from 1985 through 2011 (Table 3), not including multiple recaptures and re-sightings of individuals within the same year.

Sex and Age-Class Distribution

The 2011 age-class distribution for northern spotted owls between sexes was not different (Fisher's Exact $P = 0.96$). If juveniles were included as an age-class in the age-class distribution, 12.9% of the 70 owls identified and sexed were subadults (Table 4). If juveniles were excluded, subadults were 14.1% of the adult/subadult age-classes. Of the 538 juveniles sexed from 1992 through 2011, 264 were females and 280 were males. There was no apparent deviation from a 1:1 sex ratio among the 19 years (Fisher's Exact $P = 0.66$), although males seemed to predominate, especially in 1996 (35 males:20 females), 2007 (8 males:3 females), and 2010 (12 males:6 females), while females seemed to predominate in 2009 (15 females:8 males).

Reproduction

Reproductive activity.— Temporal trends in the proportion of pairs checked annually for reproduction which nested and the proportion of pairs which fledged young from 1985 through 2011 (Table 5) were best explained by a good vs bad year model (Table A1 in Appendix A) where the years 1993, 1995, 1999, 2003, 2007, and 2011 had lower proportions nesting and lower proportions fledging young. This model estimated 60.1% (95% CI = 56.8%, 63.4%) of the pairs nesting in good years and 21.6% (95% CI = 16.0%, 27.2%) of pairs nesting in bad years. Overall, an average of 52.5% of the pairs nested annually during the 27 years of study (Table 5). The good vs bad year model estimated 44.2% (95% CI = 41.3%, 47.0%) of the pairs checked for reproduction fledged young in good years and 17.8% (95% CI = 10.0%, 17.8%) of pairs fledged young in bad years. Overall, 37.8% of the pairs successfully checked for reproduction fledged young during the 27 years of the study (Table 5).

Temporal trends in the proportion of pairs nesting and fledging young was best explained by a means model (Table A2 in Appendix A), suggesting no evidence for an annual trend in these data (Table 5). This was also supported by considerable uncertainty in model selection (Table A2). Overall, the proportion of nesting pairs which fledged young on both study areas was 77.1% for the 27 years (Table 5), which can be considered a crude measure of nest success.

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 using a 3-banded heterogeneous Toeplitz variance-covariance structure (Tables A4 and A5 in Appendix A). In these models, we examined the data for linear time trends (model R_T), no time trends (model R_{\cdot}), 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 $R_{G\ vs\ B}$). The latter model was based, *a priori*, on observations of low reproduction in 1993, 1995, 1999, 2003, 2007 and 2011, which were categorized as “bad” years with the other years categorized as “good” years. Based on minimum AICc, model $R_{G\ vs\ B}$ was selected (Table A5) and was heavily weighted (Akaike weight = 1.00) indicating that none of the other models explained the variation in the data as well as model $R_{G\ vs\ B}$. Estimates of the number of young

fledged per pair from model $R_{G \text{ vs } B}$ were 0.188 (SE = 0.038) for years 1993, 1995, 1999, 2003, 2007, and 2011 combined (“bad” years) and 0.683 (SE = 0.029) 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 of 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 ($R_{[G \text{ vs } B] * [fS1 + fS2 \text{ vs } fA]}$) was selected as the best model (Table A6 in Appendix A), with 47.7% of the Akaike weight. This model had separate estimates for the pooled subadult (S1 and S2) females, which varied differently from adult females; these age class groups in turn varied differently between “good” and “bad” (1993, 1995, 1999, 2003, 2007, and 2011) years (Figure 2). Model ($R_{[G \text{ vs } B] * [fS1 \text{ vs } fS2 \text{ vs } fA]}$) was a competitive model, with 45.0% of the Akaike weight but differed only from model ($R_{[G \text{ vs } B] * [fS1 + fS2 \text{ vs } fA]}$) by having the subadult age classes separate. The estimates from model ($R_{[G \text{ vs } B] * [fS1 + fS2 \text{ vs } fA]}$) 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 0.582 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 ($R_{[G \text{ vs } B] * [fS1 + fS2 \text{ vs } fA]}$) explained 94.3% 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. However, we used a compound symmetric variance-covariance structure in the random effect models (Table A7 in Appendix A). Based on minimum AICc, the model P. (Akaike weight = 0.075; Table A8 in Appendix A) suggested that there was no discernible variation in productivity over years. However, models $P_{[fS1 + fS2, fA]}$, $P_{G \text{ vs } B}$, and P_{InT} were almost equally likely (Akaike weights = 0.060, 0.057 and 0.052, respectively; Table A8 in Appendix A). Model $P_{[fS1 + fS2, fA]}$ suggested productivity differed between subadult and adult age classes with no time effect ($\hat{\beta}_1 = 0.131$, 95% CI = -0.065, 0.328) while model $P_{G \text{ vs } B}$ suggested that productivity varied by good versus bad years ($\hat{\beta}_1 = 0.120$, 95% CI = -0.069, 0.310). However, neither of these competing models were useful models because 1) the 95% confidence intervals for parameters of interest overlapped zero, and 2) the variation explained by the two competing models was only 0.3 to 6.8%. 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 1.57 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 ($\hat{c} = 0.921$). We initially examined 4 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) (Table A9 in Appendix A). From this initial set of models, model (ϕ_t ,

p_t) best approximated the data (Table A9 in Appendix A). The last estimates of ϕ (for the interval 2010-2011) and p (for 2011) 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 = 0.533; Table A9 in Appendix A), which suggested that annual survival varied according to good and bad ($\hat{\beta} = -0.048$, SE=0.021) reproductive years (Figure 3). This model explained 53.0% of the temporal process variation and was more than three times as likely as models $\{\phi_{lnT}\}$ and $\{\phi\}$ (Akaike weights = 0.152 and 0.123, respectively; Table A9 in Appendix A). Based on the random-effects means model, annual apparent survival for territory holders averaged 0.852 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_T (Akaike weight = 0.372; Table A10 in Appendix A), suggesting a linear decline in $\hat{\lambda}$ over time (Figure 4; $\hat{\beta}_1 = -0.002$, 95% CI = -0.006, 0.001). However, this time trend was not different than zero and model λ_T was similarly weighted as model λ . (Akaike weight = 0.226), which suggested that $\hat{\lambda}$ did not vary over time. In addition, estimated temporal process variation for $\hat{\lambda}$ was zero (Table 7), which suggested little evidence for any time trends, especially when combined with the high degree of model uncertainty. For the WCSA and RSA data combined (WCSA+RSA), model λ . was the best approximating model (Akaike weight = 0.273; Table A10 in Appendix A), with models λ_T (Akaike weight = 0.236) and λ_{lnT} (Akaike weight = 0.194) as competitive models. Again, lack of estimable temporal process variation and uncertainty in model selection results suggest that these data could not support a time trend in $\hat{\lambda}$. The estimate of λ from 1985 through the interval 2009-2010 (the interval 2010-2011 was not estimable using random effects models) was 0.984 (95% CI = 0.967, 1.001) on the WCSA and 0.982 (95% CI = 0.969, 0.995) on the WCSA+RSA. For the WCSA data the 95% confidence interval for the estimate of λ barely included $\lambda = 1$ (a stationary population) but λ was < 1 for the WCSA+RSA data set, suggesting a declining population for the study population.

Barred Owls

Barred owls were first detected in the WCSA in 1991 and in the RSA in 1992 (Table 8). In 1994, a male barred \times spotted hybrid was detected in Bee Tree Creek in the WCSA, but hybrids have remained rare in the study area. The first nesting pair of barred owls was found in 1999.

Since 1991, we have observed a gradual increase in the number of territories with barred owl detections (Table 8). We suspect the large increase in 2008 was due in part to our implementation of barred owl-specific surveys (See *Barred Owl-Specific Surveys* above). The proportion of surveyed spotted owl territories with barred owl detections in 2011 was 0.38,

higher than previous years; given similar survey effort in 2010 and 2011, this likely represents an annual increase in barred owls. To document long term trends, we also estimated the number of barred owl “sites” in the study area. Prior to 2009, when study area-wide barred owl surveys began, we estimated this number 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”. Beginning in 2009 we were able to confirm the number of sites with occupancy surveys. We estimated 21 barred owl “sites” in 2011, 17 of which occurred in the WCSA (Table 8). We confirmed reproductive status for three barred owl pairs, one of which fledged at least one 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 2011 was considered a below average (or “bad”) year, which is the sixth such year of very low reproduction (Table 6) observed during the 27 years of the study. In general, productivity and the proportion of nests that fledged young have remained relatively stable while the proportion of birds nesting each year is primarily responsible for low reproductive output. That is, very few birds nested in 1993, 1995, 1999, 2003, 2007, and 2011 which was primarily responsible for low reproductive output in those years. Annual weather variation may be one factor in determining this trend because cold, wet springs have been associated with low reproduction on our study area (Franklin et al. 2000). However, 5 of these 6 events have occurred at regular 4-year intervals, which suggest some other extrinsic factor may be operating, such as seed production governing small mammal populations.

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). Estimates of survival have remained near average the last few years.

The average rate of population change for the WCSA population was not quite distinguishable from a stationary population ($\lambda = 1$) with a point estimate of 0.984. The point estimate for the WCSA+RSA population was < 1 (0.982), indicating the combined populations were declining at a rate of 1.8% per year. This difference in point estimates and confidence intervals is likely a result of sample size, which increases with each year of data. We were still 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, including recent declines from 2007-2010 (Figure 4). The results from both data sets suggest that the northern spotted owl population in our study area is, on average, likely declining slowly (Figure 4).

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. 2011). The number of barred owl detections in a year is influenced by survey effort and methodology, which have not been consistent across all years. We do not know if the increase in barred owl detections in the WCSA prior to 2009 (Table 8) represents an actual increase in barred owl numbers in the WCSA. However, with consistent barred owl surveys in 2009 through 2011, there appears to be continued recent increase in the numbers of barred owls on our study area and an increase in the number of northern spotted owl territories where barred owls have been detected (Table 8). We cannot predict what effect such an increase may have on the spotted owl population but recommend that continued monitoring of both species is necessary to evaluate whether barred owls are impacting the spotted owl population on our study area. It may take several more years to reliably estimate barred owl effects on northern spotted owl population parameters.

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Table 1. Annual number of surveys conducted to detect northern spotted owls in northwestern California, from 1985 through 2011.

Year	Survey Type			Total
	Point	Walk-in	Cruise	
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
2010	1255	152	147	1554
2011	1219	115	144	1478

Table 2. Number of northern spotted owl territories surveyed, occupied and checked for reproduction in 2011 in northwestern California.

No. Territories	Study Area		
	WCSA	RSA	Combined
<i>Surveyed</i>	60	34	94
<i>With Unknown Status</i>	0	1	1
<i>Assumed Unoccupied</i>	37	15	52
<i>Found Occupied By:</i>			
Pairs	16	16	32
Males	5	2	7
Females	2	0	2
Total	23	18	41
<i>Checked For Reproduction Where Occupied By:</i>			
Pairs	15	13	28
Males	4	1	5
Females	0	0	0
Total	19	14	33

Table 3. Number of northern spotted owls identified in northwestern California from 1985 through 2011. New birds were owls that had not been previously banded; old birds were owls that had been previously banded.

Year	No. new birds captured as:			No. old birds which were:			Grand Total
	Adult & Subadult	Juvenile	Total	Recaptured	Resighted	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	101	121
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
2010	8	21	29	3	68	71	100
2011	6	7	13	7	51	58	71
Total	465	774	1239	412	2115	2527	3766

Table 4. Age-class distribution, by sex, in 2011 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*.

Age-Class	Male		Female		Both Sexes	
	<i>n</i>	<i>p</i>	<i>n</i>	<i>p</i>	<i>n</i>	<i>P</i>
Adult	28	.78	27	.79	55	.79
2nd-yr Subadult	3	.08	3	.09	6	.09
1 st -yr Subadult	2	.06	1	.03	3	.04
Juvenile ^a	3	.08	3	.09	6	.09

^a Estimates do not include 1 juvenile that was of 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 2011. Standard errors are in parentheses.

Year	Proportion of pairs which:					
	Nested		Nested and fledged young		Fledged young	
	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)
2010	29	0.66 (0.088)	19	0.89 (0.070)	38	0.45 (0.081)
2011	17	0.35 (0.116)	6	0.83 (0.153)	28	0.18 (0.072)
Overall ^d	1051	0.53 (0.015)	551	0.77 (0.018)	1448	0.38 (0.013)

^aTotal number of pairs checked each year before 31 May.

^bTotal number of nesting pairs found each year before 31 May.

^cTotal number of pairs checked throughout the entire sampling period in each year.

^dEstimate 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 2011. Pairs are number of pairs checked for reproductive activity.

Year	Productivity			No. young fledged per pair		
	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	0.612	0.097
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	58	0.603	0.107
2003	4	1.250	0.250	53	0.094	0.049
2004	27	1.667	0.092	56	0.804	0.121
2005	21	1.381	0.109	53	0.547	0.103
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
2010	17	1.294	0.114	38	0.579	0.117
2011	5	1.400	0.245	28	0.250	0.111

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 2011. Estimates are from random effects means models.

Parameter	Mean	SE	$\hat{\sigma}_{temporal}$	CV _{temporal}
R	0.582	0.050	0.231	0.396
P	1.574	0.034	0.113	0.071
ϕ	0.852	0.008	0.024	0.028
λ (WCSA)	0.984	0.009	0.000	0.000
λ (WCSA+RSA)	0.982	0.007	0.000	0.000

Table 8. Number of barred owls detected in the WCSA and RSA from 1991 through 2011.

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
2010	29	15	2	15	2
2011	36	17	4	17	4

^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.

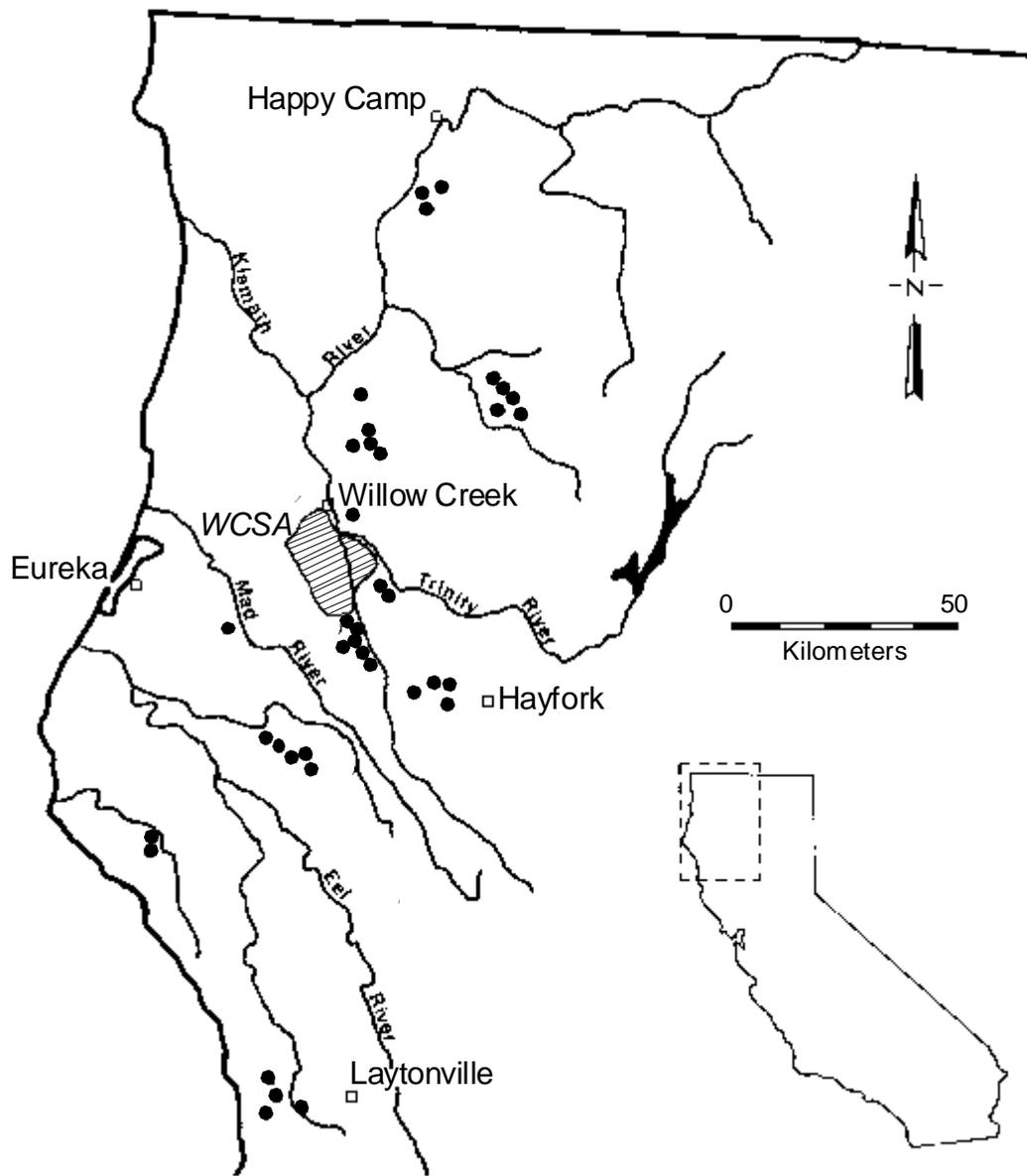


Figure 1. Map of northern spotted owl territories (dots) surveyed in the Regional Study Area, northwestern California. Shaded area represents the Willow Creek Study Area.

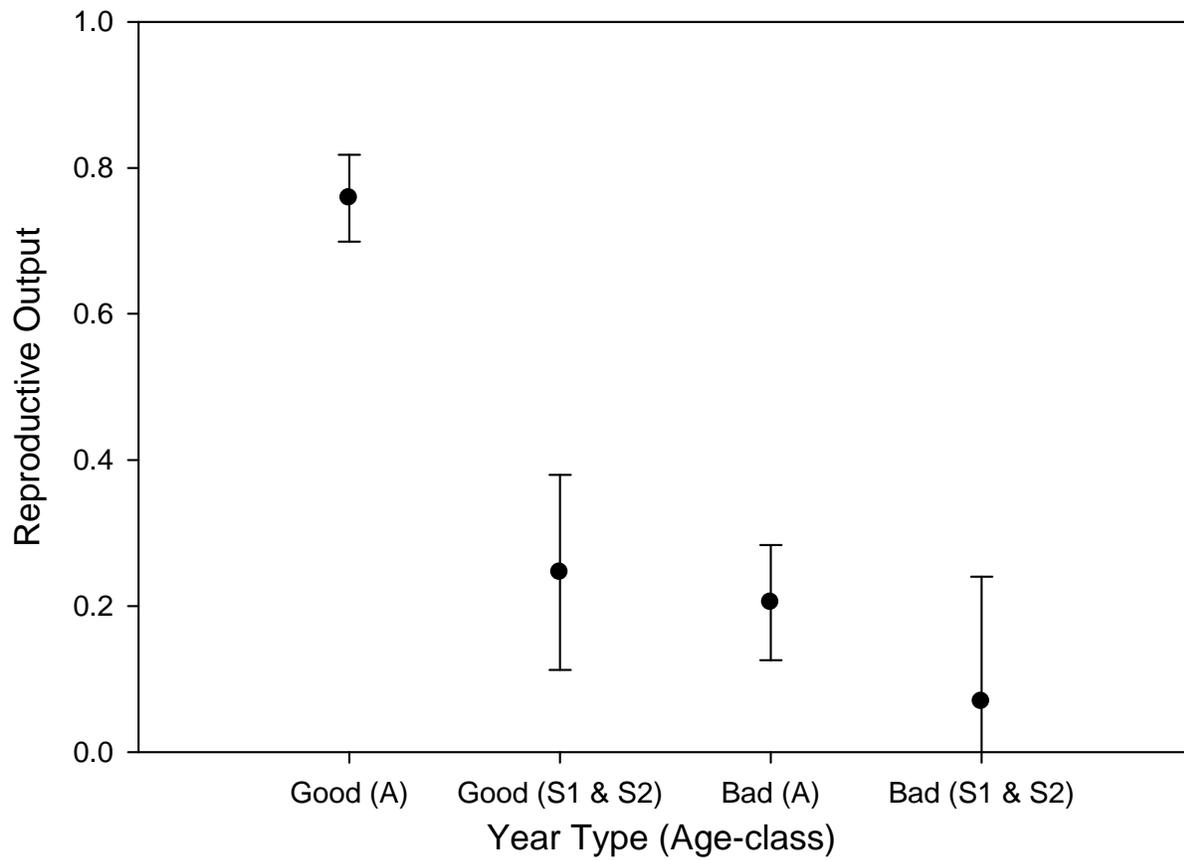


Figure 2. Mean reproductive output for S1, S2, and adult northern spotted owls in “good” and “bad” years in northwestern California from 1985 through 2011. Bars are 95% confidence intervals.

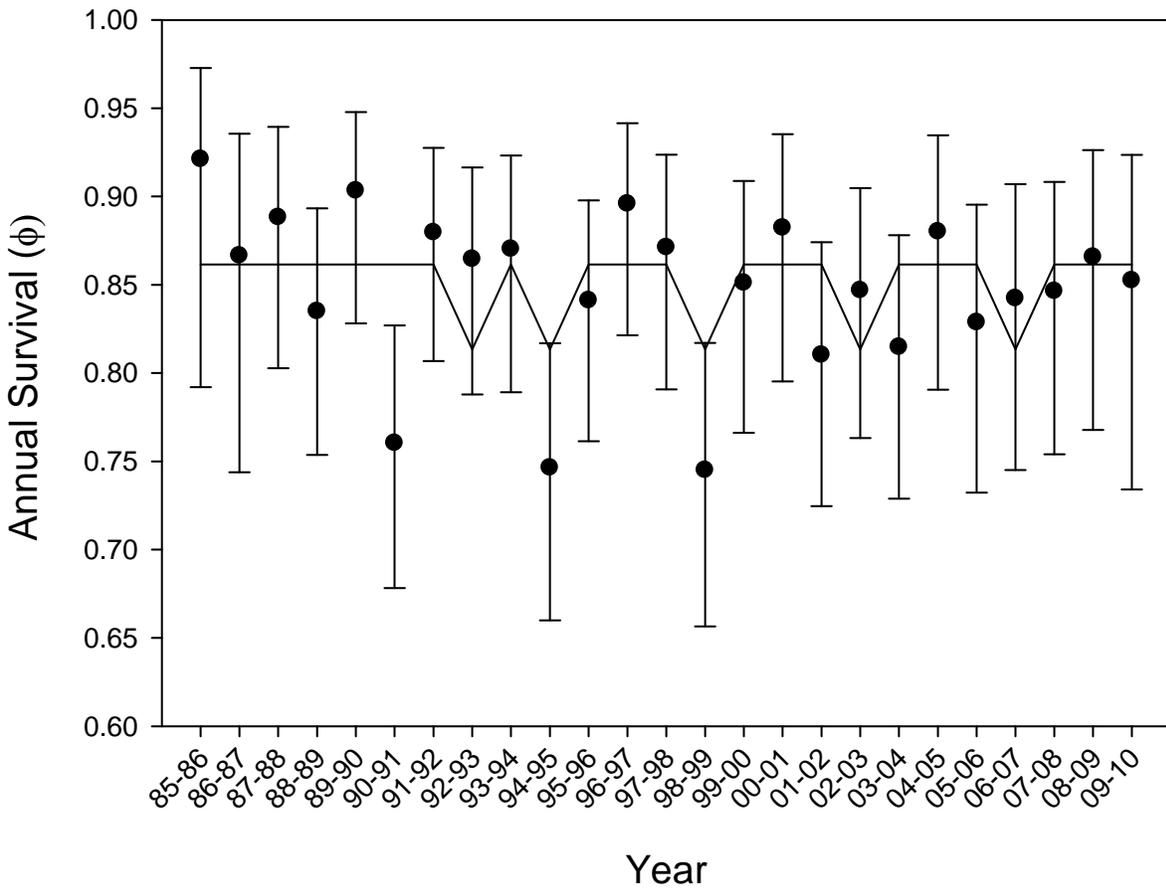


Figure 3. Trends in apparent survival for subadult and adult northern spotted owls in northwestern California from 1985 through 2011. Trend estimates are from random effects model $\{\phi_{G \text{ vs } B}\}$. Estimates of individual values (solid dots) \pm 95% confidence intervals are from model $\{\phi, p_i\}$ for comparison. The estimate for 2010-2011 was not estimable.

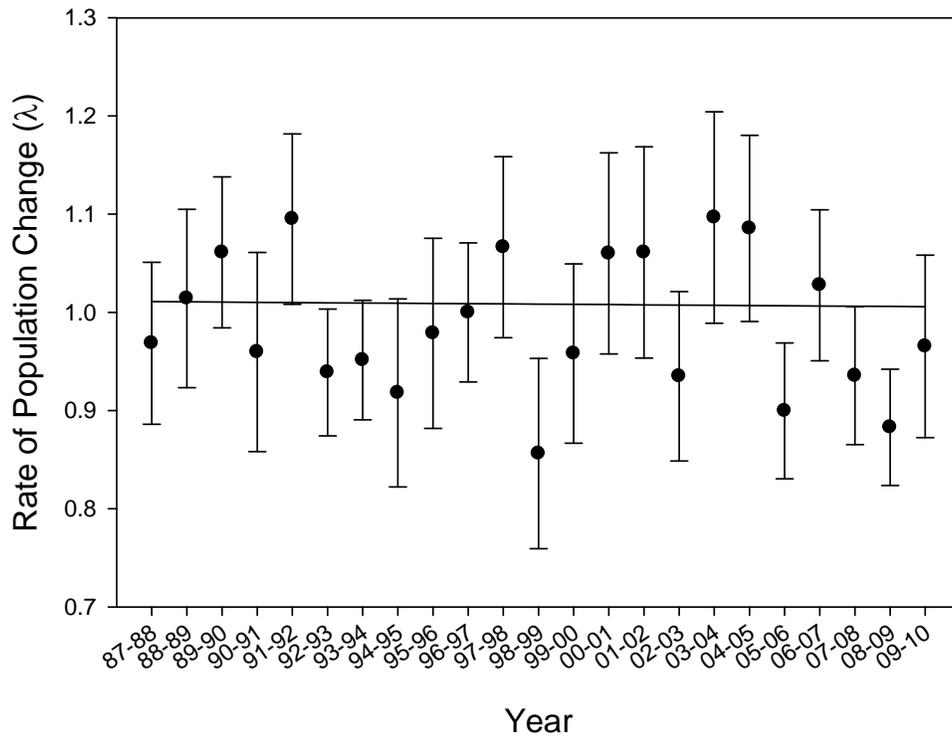


Figure 4. Annual estimates of λ (dots \pm 95% confidence intervals) from the reverse-time Jolly-Seber estimator for the Willow Creek Study Area (WCSA). Solid line indicates estimate from random effects model $\hat{\lambda}_T$.

APPENDIX A. Tables of model selection results from analyses on reproductive activity, reproductive output, annual survival, and population trends of northern spotted owls in northwestern California from 1985 through 2011.

Table A1. Model selection results for random effects models estimating the proportion of pairs nesting.

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
PN.	1454.32	2	1458.32	1458.33	99.323	0.000
PN _t	1323.79	29	1381.79	1383.49	24.486	0.000
PN _T	1452.48	3	1458.48	1458.50	99.495	0.000
PN _{TT}	1445.86	4	1453.86	1453.90	94.890	0.000
PN _{lnT}	1451.14	3	1457.14	1457.16	98.155	0.000
PN_{G vs B}	1350.97	4	1358.97	1359.01	0.000	1.000
PN _{EO}	1426.67	4	1434.67	1434.71	75.700	0.000
PN _{EO+T}	1424.35	5	1434.35	1434.41	75.399	0.000

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, G vs B = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend

Table A2. Model selection results for random effects models estimating the proportion of pairs nesting and fledging young.

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
PNF.	385.36	2	389.36	389.38	0.000	0.454
PNF _t	Not estimable					
PNF _T	385.31	3	391.31	391.35	1.972	0.169
PNF _{TT}	385.27	4	393.27	393.34	3.961	0.063
PNF _{lnT}	385.29	3	391.29	391.33	1.952	0.171
PNF _{G vs B}	385.34	4	393.34	393.41	4.031	0.061
PNF _{EO}	385.36	4	393.36	393.43	4.051	0.060
PNF _{EO+T}	385.30	5	395.30	395.41	6.028	0.022

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, G vs B = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend

Table A3. Model selection results for random effects models estimating the proportion of pairs fledging young.

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
PF _.	1920.92	2	1924.92	1924.93	102.342	0.000
PF _t	1793.89	29	1851.89	1853.12	30.530	0.000
PF _T	1917.26	3	1923.26	1923.28	100.690	0.000
PF _{TT}	1917.24	4	1925.24	1925.27	102.681	0.000
PF _{lnT}	1917.20	3	1923.20	1923.22	100.630	0.000
PF_{G vs B}	1816.57	3	1822.57	1822.59	0.000	1.000
PF _{EO}	1898.06	3	1904.06	1904.08	81.490	0.000
PF _{EO+T}	1894.03	4	1902.03	1902.06	79.471	0.000

^aModel notation: . = means (intercept-only) model, t = varies by year, T = linear trend, TT = quadratic trend, lnT = log-linear trend, G vs B = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend

Table A4. Model selection results for covariance structures examined for random effects modeling of reproductive output in northern spotted owls.

Covariance Structure	q	-2logL	AIC	AICc	ΔAICc	Akaike Weight
Exp(Yr)	4	3527.30	3535.30	3535.33	76.83	0.000
AR(1)	4	3516.70	3524.70	3524.73	66.23	0.000
AR(1) w/ EXP(Yr)	6	3506.80	3518.80	3518.86	60.36	0.000
CS	3	3532.30	3538.30	3538.32	79.82	0.000
CSH	29	3412.40	3470.40	3471.63	13.13	0.001
ARH(1)	30	3401.00	3461.00	3462.31	3.81	0.129
TOEP	29	3471.00	3529.00	3530.23	71.73	0.000
TOEPH(3)	31	3395.10	3457.10	3458.50	0.00	0.869
UN	Unable to converge					

Table A5. Model selection results for random effects models estimating the number fledged young per pair of northern spotted owls (without age effects).

Model^a	-2lnL	K	AIC	AICc	ΔAICc	Akaike Weight
R _T	3377.20	33	3443.20	3444.82	35.400	0.000
R _{TT}	3377.20	34	3445.20	3446.92	37.499	0.000
R _{lnT}	3377.10	33	3443.10	3444.72	35.300	0.000
R _.	3378.70	32	3442.70	3444.22	34.804	0.000
R_[GvsB]	3341.80	33	3407.80	3409.42	0.000	1.000
R _{EO}	3374.70	33	3440.70	3442.32	32.900	0.000
R _{EO+T}	3373.00	34	3441.00	3442.72	33.299	0.000

^aModel notation: . = means (intercept-only) model, t = varies by year, T = linear trend, TT = quadratic trend, lnT = log-linear trend, [GvsB] = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend

Table A6. Model selection results for random effects models estimating the number of fledged young per pair that had been aged.

Model^a	K	AICc	ΔAICc	Akaike Weight
R _{[GvsB]*[fS1+fS2vsfA]}	35	3253.95	0.00	0.4767
R _{[GvsB]*[fS1vsfS2vsfA]}	37	3254.07	0.12	0.4496
R _{[GvsB]+[fS1vsfS2vsfA]}	35	3257.95	4.00	0.0645
R _{[GvsB]+[fS1+fS2vsfA]}	34	3262.24	8.30	0.0075
R _{[GvsB]*[fS1vsfS2+fA]}	35	3265.65	11.70	0.0014
R _{[GvsB]+[fS1vsfS2+fA]}	34	3268.64	14.70	0.0003
R _{EO*[fS1vsfS2vsfA]+T}	38	3290.68	36.73	0.0000
R _{EO*[fS1vsfS2vsfA]}	37	3290.77	36.82	0.0000
R _{EO*[fS1+fS2vsfA]+T}	36	3290.86	36.91	0.0000
R _{EO*[fS1+fS2vsfA]}	35	3291.05	37.10	0.0000
R _{EO+T+[fS1vsfS2vsfA]}	36	3292.16	38.21	0.0000
R _{EO+[fS1vsfS2vsfA]}	35	3292.35	38.40	0.0000
R _[fS1vsfS2vsfA]	34	3294.24	40.30	0.0000
R _{lnT+[fS1vsfS2vsfA]}	35	3294.25	40.30	0.0000
R _{T+[fS1vsfS2vsfA]}	35	3294.35	40.40	0.0000
R _{EO+T+[fS1+fS2vsfA]}	35	3295.65	41.70	0.0000
R _{EO+[fS1+fS2vsfA]}	34	3295.84	41.90	0.0000
R _{TT+[fS1vsfS2vsfA]}	36	3296.46	42.51	0.0000
R _{lnT+[fS1+fS2vsfA]}	34	3297.44	43.50	0.0000
R _[fS1+fS2vsfA]	33	3297.54	43.60	0.0000
R _{T+[fS1+fS2vsfA]}	34	3297.64	43.70	0.0000
R _{T*[fS1vsfS2vsfA]}	37	3298.37	44.42	0.0000
R _{lnT*[fS1vsfS2vsfA]}	37	3298.37	44.42	0.0000
R _{lnT[fS1+fS2vsfA]}	35	3299.55	45.60	0.0000
R _{T*[fS1+fS2vsfA]}	35	3299.65	45.70	0.0000
R _{TT+[fS1+fS2vsfA]}	35	3299.75	45.80	0.0000
R _{EO*[fS1vsfS2+fA]}	35	3300.05	46.10	0.0000
R _{EO*[fS1vsfS2+fA]+T}	36	3300.06	46.11	0.0000
R _[GvsB]	33	3301.94	48.00	0.0000
R _{TT*[fS1vsfS2vsfA]}	40	3302.42	48.47	0.0000
R _{EO+[fS1vsfS2+fA]}	34	3302.64	48.70	0.0000
R _{EO+T+[fS1vsfS2+fA]}	35	3302.65	48.70	0.0000
R _{TT*[fS1+fS2vsfA]}	37	3303.27	49.32	0.0000
R _[fS1vsfS2+fA]	33	3304.84	50.90	0.0000
R _{T+[fS1vsfS2+fA]}	34	3305.14	51.20	0.0000
R _{lnT+[fS1vsfS2+fA]}	34	3305.14	51.20	0.0000
R _{lnT*[fS1vsfS2+fA]}	35	3307.15	53.20	0.0000
R _{T*[fS1vsfS2+fA]}	35	3307.25	53.30	0.0000
R _{TT+[fS1vsfS2+fA]}	35	3307.25	53.30	0.0000
R _{TT*[fS1vsfS2+fA]}	37	3310.97	57.02	0.0000
R _{EO}	33	3333.44	79.50	0.0000
R _{EO+T}	34	3333.44	79.50	0.0000
R _.	32	3335.25	81.30	0.0000
R _{lnT}	33	3335.44	81.50	0.0000
R _T	33	3335.54	81.60	0.0000
R _{TT}	34	3337.64	83.70	0.0000

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, [GvsB] = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend, [fS1vsfS2vsfA] = female S1 vs female S2 vs female adult ages, [fS1+fS2vsfA] = female subadult vs female adult ages, [fS1vsfS2+fA] = female S1 vs combined female S2 and adult ages.

Table A7. Model selection results for covariance structures examined for random effects modeling of productivity.

Structure	q	-2logL	AIC	AICc	ΔAICc	Akaike Weight
Exp(Yr)	4	846.70	854.70	854.73	1.21	0.211
AR(1)	4	846.50	854.50	854.53	1.01	0.233
AR(1) w/ EXP(Yr)	6	843.10	855.10	855.16	1.64	0.170
CS	3	847.50	853.50	853.52	0.00	0.386
CSH	29	836.50	894.50	895.75	42.23	0.000
ARH(1)	30	836.10	896.10	897.44	43.92	0.000
TOEP	28	Unable to make hessian positive definite				
TOEPH(3)	31	835.50	897.50	898.93	45.41	0.000
UN	Unable to converge					

Table A8. Model selection results for random effects models estimating productivity of northern spotted owls that had been aged.

Model ^a	K	AICc	ΔAICc	Akaike Weight
P.	5	800.315	0.00	0.0748
P _[fS1+fS2vsfA]	6	800.762	0.45	0.0598
P _[GvsB]	6	800.862	0.55	0.0569
P _{lnT}	6	801.062	0.75	0.0515
P _{lnT+[fS1+fS2vsfA]}	7	801.116	0.80	0.0501
P _{[GvsB]⁺[fS1+fS2vsfA]}	7	801.116	0.80	0.0501
P _T	6	801.262	0.95	0.0466
P _{T+[fS1+fS2vsfA]}	7	801.316	1.00	0.0454
P _{T*[fS1+fS2vsfA]}	8	801.778	1.46	0.0360
P _{EO}	6	802.262	1.95	0.0283
P _{lnT*[fS1+fS2vsfA]}	8	802.278	1.96	0.0280
P _[fS1vsfS2vsfA]	7	802.316	2.00	0.0275
P _[fS1vsfS2+fA]	6	802.362	2.05	0.0269
P _{EO*[fS1vsfS2+fA]}	8	802.378	2.06	0.0267
P _{[GvsB]*[fS1+fS2vsfA]}	8	802.578	2.26	0.0241
P _{EO+[fS1+fS2vsfA]}	7	802.616	2.30	0.0237
P _{lnT+[fS1vsfS2vsfA]}	8	802.778	2.46	0.0218
P _{[GvsB]+[fS1vsfS2vsfA]}	8	802.778	2.46	0.0218
P _{[GvsB]+[fS1vsfS2+fA]}	7	802.916	2.60	0.0204
P _{T+[fS1vsfS2vsfA]}	8	802.978	2.66	0.0198
P _{lnT+[fS1vsfS2+fA]}	7	803.116	2.80	0.0184
P _{EO+T}	7	803.216	2.90	0.0175
P _{TT+[fS1+fS2vsfA]}	8	803.278	2.96	0.0170
P _{EO+T+[fS1+fS2vsfA]}	8	803.278	2.96	0.0170
P _{TT}	7	803.316	3.00	0.0167
P _{T+[fS1vsfS2+fA]}	7	803.316	3.00	0.0167
P _{EO*[fS1vsfS2+fA]+T}	9	803.448	3.13	0.0156
P _{EO*[fS1vsfS2vsfA]}	10	803.726	3.41	0.0136
P _{T*[fS1vsfS2+fA]}	8	804.178	3.86	0.0108
P _{EO+[fS1vsfS2vsfA]}	8	804.278	3.96	0.0103
P _{lnT*[fS1vsfS2+fA]}	8	804.278	3.96	0.0103
P _{EO+[fS1vsfS2+fA]}	7	804.316	4.00	0.0101
P _{[GvsB]*[fS1vsfS2vsfA]}	9	804.348	4.03	0.0100
P _{EO*[fS1vsfS2vsfA]+T}	11	804.413	4.10	0.0096
P _{EO*[fS1+fS2vsfA]}	8	804.678	4.36	0.0084
P _{EO+T+[fS1vsfS2vsfA]}	9	804.948	4.63	0.0074
P _{[GvsB]*[fS1vsfS2+fA]}	8	804.978	4.66	0.0073
P _{TT+[fS1vsfS2vsfA]}	9	805.048	4.73	0.0070
P _{EO*[fS1vsfS2+fA]+T}	9	805.248	4.93	0.0063
P _{EO+T+[fS1vsfS2+fA]}	8	805.278	4.96	0.0063
P _{T*[fS1vsfS2vsfA]}	10	805.326	5.01	0.0061
P _{TT+[fS1vsfS2+fA]}	8	805.378	5.06	0.0060
P _{TT*[fS1+fS2vsfA]}	10	805.826	5.51	0.0048
P _{lnT*[fS1vsfS2vsfA]}	10	805.926	5.61	0.0045
P _{TT*[fS1vsfS2+fA]}	10	808.026	7.71	0.0016
P _{TT*[fS1vsfS2vsfA]}	13	811.31	10.99	0.0003

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, [GvsB] = good versus bad years, EO = even-odd years, EO+T = even-odd year plus linear trend, [fS1vsfS2vsfA] = female S1 vs female S2 vs female adult ages, [fS1+fS2vsfA] = female subadult vs female adult ages, [fS1vsfS2+fA] = female S1 vs combined female S2 and adult ages.

Table A9. Model selection results for fixed and random effects models estimating apparent survival of northern spotted owls.

Model^a	K	AICc	ΔAICc	Akaike Weight
ϕ_t, p_t : RE GvsB	37.5	4049.4483	0	0.53283
ϕ_t, p_t : RE lnT	39.5	4051.9552	2.5069	0.15213
ϕ_t, p_t : RE Mean	40.2	4052.3837	2.9354	0.12279
ϕ_t, p_t : RE TT	40.3	4052.7072	3.2589	0.10446
ϕ_t, p_t : RE T	40.5	4053.0567	3.6084	0.08771
ϕ_t, p_t	51	4067.1405	17.6922	0.00008
ϕ_{s*t}, p_{s*t}	102	4129.0122	79.5639	0
ϕ_{a*t}, p_{a*t}	150	4161.0923	111.644	0
ϕ_{a*s*t}, p_{a*s*t}	282	4320.9311	271.4828	0

^aModel notation: “*” indicates full additive effects and interactions; RE = random effects model, a = age effects, s = sex effects, Mean = intercept-only, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, GvsB = good versus bad years,

Table A10. Model selection results for fixed and random effects models estimating population rate of change (λ) for WCSA only data and WCSA & RSA data combined.

Model ^a	K	QAICc	Δ QAICc	Akaike Weight
WCSA data				
ϕ_t, p_t, λ_t RE T	56	3166.5375	0	0.37168
ϕ_t, p_t, λ_t RE Mean	56	3167.5316	0.9941	0.2261
ϕ_t, p_t, λ_t RE TT	57	3168.1398	1.6023	0.16681
ϕ_t, p_t, λ_t RE GvsB	57	3168.6914	2.1539	0.12661
ϕ_t, p_t, λ_t RE lnT	57	3168.9944	2.4569	0.10881
ϕ_t, p_t, λ_t	77	3197.3303	30.7928	0
$\phi_{s^*t}, p_t, \lambda_t$	103	3211.5746	45.0371	0
$\phi_t, p_{s^*t}, \lambda_t$	104	3237.6700	71.1325	0
$\phi_{s^*t}, p_{s^*t}, \lambda_t$	131	3251.3122	84.7747	0
$\phi_{s^*t}, p_{s^*t}, \lambda_{s^*t}$	Did not converge			
WCSA & RSA data				
ϕ_t, p_t, λ_t RE Mean	48	5300.7365	0	0.27312
ϕ_t, p_t, λ_t RE T	49	5301.0224	0.2859	0.23674
ϕ_t, p_t, λ_t RE lnT	49	5301.4185	0.682	0.1942
ϕ_t, p_t, λ_t RE TT	50	5301.7433	1.0068	0.16509
ϕ_t, p_t, λ_t RE GvsB	49	5302.2081	1.4716	0.13086
ϕ_t, p_t, λ_t	68	5329.1734	28.4369	0
$\phi_{s^*t}, p_t, \lambda_t$	91	5355.6635	54.927	0
$\phi_t, p_{s^*t}, \lambda_t$	92	5358.9246	58.1881	0
$\phi_{s^*t}, p_{s^*t}, \lambda_{s^*t}$	136	5427.4589	126.7224	0

^aModel notation: “*” indicates full additive effects and interactions; RE = random effects model, a = age effects, s =sex effects, Mean = intercept-only, t = varies by year, T= linear trend, TT = quadratic trend, lnT = log-linear trend, GvsB = good versus bad years,