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MONITORING THE POPULATION ECOLOGY OF SPOTTED OWLS
(*Strix occidentalis caurina*)
IN NORTHWESTERN CALIFORNIA: ANNUAL RESULTS, 2016

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 \geq 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 a combination of vocal imitations and broadcasts 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). With implementation of the barred owl removal experiment in the fall of 2013, which includes the Hoopa Valley Reservation study area as a treatment area with the Willow Creek Study Area acting as the control (U. S. Fish and Wildlife Service 2013), we initiated a hexagon-grid based survey protocol for barred owl specific surveys. The intent is to survey the whole study area for barred owl occupancy and be consistent with other studies involved in the removal experiment. Each barred owl survey was conducted between dusk and approximately 2400 hours (Pacific Standard Time) and was similar to spotted owl point surveys except recorded barred owl calls were broadcast and the length of each survey was increased to a minimum of 15 minutes. 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 confirmed 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 Antech Diagnostics (Irvine, 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 ($\sigma_{temporal}^2$) 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 from 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} . 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 ($\phi_{G \text{ vs } B}$) where “bad” years were years with very low reproductive output (see *Reproductive Output* section in *Results*). Because of recent concerns about the effects of barred owls (*Strix varia*) on northern spotted owl survival (U.S. Fish and Wildlife Service 2013), we also included a barred owl covariate (BO) that was the number of northern spotted owl territories where a barred owl had been detected at least once. 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 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 data for the WCSA only because 1) it represented an area that was thoroughly surveyed for northern spotted owls throughout its entire extent as a density study area, and 2) we had more complete information on barred owls within the WCSA. 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). The last estimate of λ (2015-2016) 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 2014-2015 for the WCSA. We used program MARK to perform the analyses (see Franklin et al. 2002).

RESULTS

Surveys

We conducted 1,616 surveys within our study areas in 2016 (Table 1); 11.7% of these were daytime surveys. Ninety-five territories previously occupied by northern spotted owls were surveyed on the RSA and WCSA in 2016 (Table 2, Figure 1). Northern spotted owls were detected at 27 (28.4%) and reproduction was assessed at 24 (25.2%) of the 95 territories

surveyed (Table 2). We assumed that 68 (71.6%) of the territories were unoccupied. Thus, we were able to assess reproduction to protocol at 88.9% of the territories found occupied. We identified (captured, recaptured or resighted) 63 individual owls in 2016 (Table 3). We found a total of 17 juvenile spotted owls that had fledged, 6 of which were on the RSA and 11 on the WCSA. We captured and banded 16 (94.1%) of the juveniles located. A total of 4,106 identifications of individuals have been made on the WCSA and RSA from 1985 through 2016 (Table 3), not including multiple recaptures and re-sightings of individuals within the same year.

Sex and Age-Class Distribution

The 2016 age-class distribution for northern spotted owls between sexes was not different (Fisher's Exact $P = 0.38$, Table 4). If juveniles were included as an age-class in the age-class distribution, 11.3% of the 62 owls identified and sexed were subadults (Table 4). If juveniles were excluded, subadults were 14.9% of the adult/subadult age-classes. Of the 615 juveniles sexed from 1992 through 2016, 298 were females and 317 were males. There was no apparent deviation from a 1:1 sex ratio among the 24 years (Fisher's Exact $P = 0.65$), although males seemed to predominate, especially in 1996 (35 males:20 females), 2007 (8 males:3 females), 2010 (12 males:6 females) and 2016 (10 males:5 females), while females seemed to predominate in 2009 (15 females:8 males) and 2012 (5 females, 1 male).

Reproduction

Reproductive activity.— Temporal trends in the proportion of pairs checked annually for reproduction which nested from 1985 through 2016 (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, 2011, and 2012 had lower proportions nesting and lower proportions fledging young. This model estimated 60.4% (95% CI = 57.2%, 63.6%) of the pairs nesting in good years and 22.5% (95% CI = 17.0%, 27.9%) of pairs nesting in bad years. Overall, an average of 52.9% of the pairs nested annually during the 32 years of 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 77.8% for the 32 years (Table 5), which can be considered a crude measure of nest success.

Temporal trends in the overall proportion of pairs fledging young was also best explained by a good vs bad year model (Table A3 in Appendix A), which estimated 44.4% (95% CI = 41.6%, 47.2%) of the pairs checked for reproduction fledged young in good years and 14.2% (95% CI = 10.1%, 18.2%) of pairs fledged young in bad years. Overall, 38.1% of the pairs successfully checked for reproduction fledged young during the 32 years of the study (Table 5).

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, 2011, and 2012, 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 in Appendix A) 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 $R_{G vs B}$ were 0.196 (SE = 0.038) for years 1993, 1995, 1999, 2003, 2007, 2011, and 2012 combined (“bad” years) and 0.691 (SE = 0.038) 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 ($R_{[GvsB]*[fS1vsfS2vsfA]}$) was selected as the best model (Table A6 in Appendix A), with 48.6% of the Akaike weight. This model had separate estimates for subadults (S1 and S2) and adult females; these age class groups in turn varied differently between “good” and “bad” (1993, 1995, 1999, 2003, 2007, 2011, and 2012) years (Figure 2). Model ($R_{[GvsB]*[fS1+fS2vsfA]}$) was almost equally weighted with 44.6% of the Akaike weight but differed only from model ($R_{[GvsB]*[fS1vsfS2vsfA]}$) by having the subadult age classes pooled. The estimates from model ($R_{[GvsB]*[fS1vsfS2vsfA]}$) 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 0.594 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 ($R_{[GvsB]*[fS1vsfS2vsfA]}$) explained 94.0% 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 = 0.092; Table A8 in Appendix A) suggested that there was no discernible variation in productivity over years or age classes. However, models $P_{[fS1+fS2vsfA]}$ was almost equally likely (Akaike weights = 0.090; Table A8 in Appendix A). Model $P_{[fS1+fS2vsfA]}$ suggested productivity differed between subadult and adult age classes with no time effect ($\hat{\beta}_1 = 0.135$, 95% CI = -0.054, 0.323). However, none of the 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 <1%. 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 1.593 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 time. Based on the goodness-of-fit, the global mark-recapture model $\{\phi_{s*t}, p_{s*t}\}$ exhibited little

overdispersion ($\hat{c} = 0.952$). We initially examined 4 models that included combinations of 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 $\{\phi_t, p_t\}$ best approximated the data (Table A9 in Appendix A). The last estimates of ϕ (for the interval 2015-2016) and p (for 2016) 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 $\{\phi_{G \text{ vs } B + BO}\}$ (Akaike weight = 0.467; Table A9 in Appendix A), which suggested that annual survival varied according to good and bad ($\hat{\beta} = -0.056$, 95% CI = -0.092, -0.019) reproductive years and a negative effect due to increasing numbers of spotted owl sites with barred owl detections ($\hat{\beta} = -0.001$, 95% CI = -0.003, 0.0001) (Figure 3). This model explained 83.7% of the temporal process variation. Model $\{\phi_{G \text{ vs } B * BO}\}$ was the second-ranked model (Akaike weight = 0.242; Table A9 in Appendix A), which was similar to model $\{\phi_{G \text{ vs } B + BO}\}$ but included an interaction term. According to the random-effects means model, annual apparent survival for territory holders averaged 0.846 (95% CI = 0.829, 0.863), which did exhibit annual variation based on the coefficient of temporal process variation but at a much lower level than the reproduction parameters (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 (density study area) using random effects models examining no change over time (e.g., model λ_{\cdot}), linear time trends (e.g., model λ_T), log-linear time trends (e.g., $\lambda_{\ln T}$), quadratic time trends (e.g., model λ_{TT}), difference in “good” versus “bad” years based on reproductive output models (e.g., model $\lambda_{G \text{ vs } B}$), and numbers of spotted owl territories on the WCSA with barred owl detections (e.g., model λ_{BO}).

The best approximating model was model $\lambda_{G \text{ vs } B + BO}$ (Akaike weight = 0.346; Table A10 in Appendix A), which included the additive effects “good” versus “bad” years and the number of spotted owl sites with barred owl detections observed on the WCSA. This model explained 94.2% of the variation in the data. The next best approximating models were $\lambda_{G \text{ vs } B * BO}$ and $\lambda_{G \text{ vs } B}$, which were almost equally weighted and included the same effects as model $\lambda_{G \text{ vs } B + BO}$. These three models accounted for 70.0% of the Akaike weight for the model set examined. Model $\lambda_{G \text{ vs } B + BO}$ suggested that $\hat{\lambda}$ was negatively affected by “bad” years that resulted in low reproduction ($\hat{\beta}_1 = -0.075$, 95% CI = -0.148, -0.002) and negatively affected by increasing numbers of spotted owl sites with barred owl detections observed on the WCSA ($\hat{\beta}_1 = -0.002$, 95% CI = -0.005, -0.0003) (Figure 4). Estimates of λ exhibited temporal process variation similar to those observed for annual estimates of ϕ (Table 7). The estimate of λ from 1985 through the interval 2014-2015 (the interval 2015-2016 was not estimable using random effects models) was 0.977 (95% CI = 0.960, 0.993) on the WCSA, suggesting a declining population because the 95% confidence interval for the estimate of λ did not include $\lambda = 1$ (a stationary 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). However, 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 2016 was 0.41, which was increased substantially from the past 3 years. 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. In 2016, we estimated 33 barred owl “sites”, 26 of which occurred in the WCSA, a slight decrease from last year (Table 8).

DISCUSSION

Reproductive patterns in northern spotted owls on our study area continue to follow a pattern of low reproductive output in “bad” years and average or, occasionally, high reproductive output in “good” years. In 2016, reproductive output by spotted owls maintained a relatively high level, similar to 2014 and 2015 (Table 6). In general, productivity and the proportion of nests that fledge young have remained relatively stable while the proportion of birds nesting each year is primarily responsible for variation in reproductive output. For example, very few birds nested in 1993, 1995, 1999, 2003, 2007, 2011, and 2012, 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 7 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. In general, there has been little evidence for an overall decline in reproduction despite the fact that the number of pairs detected has declined from a high of 74 in 1992 (Table 6) to 27 in 2016 while survey effort has been relatively constant (Table 1).

During the course of this study, we have had five years where apparent survival was substantially below average, 1990-1991, 1994-1995, 1998-1999, 2010-2011, and 2011-2012 (Figure 3). Although apparent survival seemed to increase from 2012-2013, it declined again in 2013-2014 (Figure 3). Two of the five periods of decline in survival 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) but the increasing number of barred owl sites has become an important factor as well; models including both good versus bad years and the number of spotted owl sites where barred owls have been detected dominated the top models. As with reproduction, apparent survival can be affected by annual weather variation (Franklin et al 2000), which may explain the good versus bad year effect observed in these models. The number of barred owl sites has increased dramatically in the last few years; barred owls are currently detected on almost 75% of the WCSA (Franklin et al. 2015). Thus, the effects on survival from interference competition by barred owls (Van Lanen et al. 2011) may finally have become expressed on our study area. A

model with barred owls as an additive effect fit our data better than one with an interaction, which suggests that barred owls on spotted owl sites may be an added pressure on spotted owl survival beyond normal background pressures, such as climate and habitat variation. Thus, northern spotted owl survival on our study area appears to be a function of multiple stressors.

The effect of barred owls affecting survival also dominated models examining annual trends in population rates of change (λ), with the same negative effects on λ as observed with apparent survival. The average rate of population change for the WCSA population was 0.977, suggesting the WCSA population was declining at a rate of 2.3% per year. Based on 95% confidence interval, this estimate was different than a stationary population. However, this average rate of decline does not reflect the fairly dramatic loss in the population observed in 2011 and 2012 (Figure 4). Although there was no apparent loss in 2013, there was another decline in λ from 2013 to 2014, which appeared to rebound in 2015.

It appears that barred owls are having a discernible effect on the northern spotted owl population, at least in the WCSA. While anecdotal and correlative evidence (e.g., Van Lanen et al 2011) 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 2016, there appears to be a continued 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; Franklin et al. 2015). We recommend that continued monitoring of both species is necessary to evaluate the extent that barred owls are impacting the spotted owl population on our study area.

Of immediate concern are the current effects of multiple stressors on northern spotted owl populations. While one, environmental conditions, is uncontrollable, the other (barred owls) could be managed. Experimental manipulations of barred owl populations through culling of barred owl populations have recently been implemented (U.S. Fish and Wildlife Service 2013). Until these studies have been completed, it is difficult to understand how barred owls are affecting northern spotted owls in our study area.

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Table 1. Annual number of surveys conducted to detect northern spotted owls in northwestern California, from 1985 through 2016.

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
2012	1271	98	120	1489
2013	1320	108	114	1542
2014	1277	125	88	1490
2015	1320	119	68	1507
2016	1427	107	82	1616

Table 2. Number of northern spotted owl territories surveyed, occupied and checked for reproduction in 2016 in northwestern California.

No. Territories	Study Area		
	WCSA	RSA	Combined
<i>Surveyed</i>	61	34	95
<i>With Unknown Status</i>	0	0	0
<i>Assumed Unoccupied</i>	45	23	68
<i>Found Occupied By:</i>			
Pairs	13	10	23
Males	3	1	4
Females	0	0	0
Total	16	11	27
<i>Checked For Reproduction Where Occupied By:</i>			
Pairs	12	10	22
Males	1	1	2
Females	0	0	0
Total	13	11	24

Table 3. Number of northern spotted owls identified in northwestern California from 1985 through 2016. 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
2012	8	6	14	5	43	48	62
2013	5	13	18	4	41	45	63
2014	6	18	24	4	39	43	67
2015	15	20	35	1	49	50	85
2016	7	16	23	1	39	40	63
Total	506	847	1353	427	2326	2753	4106

Table 4. Age-class distribution, by sex, in 2016 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	
	n	P	n	P	n	P
Adult	21	0.62	19	0.68	40	0.64
2nd-yr Subadult	3	0.09	2	0.07	5	0.08
1 st -yr Subadult	0	0	2	0.07	2	0.03
Juvenile	10	0.29	5	0.18	15	0.24

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 2016. 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)
2012	19	0.32 (0.107)	5	0.80 (0.179)	23	0.17 (0.079)
2013	20	0.55 (0.111)	11	0.91 (0.087)	24	0.41 (0.101)
2014	21	0.76 (0.093)	16	0.75 (0.108)	24	0.50 (0.102)
2015	24	0.63 (0.099)	15	0.87 (0.088)	26	0.50 (0.098)
2016	19	0.58 (0.113)	11	0.91 (0.087)	22	0.45 (0.106)
Overall ^d	1154	0.53 (0.015)	609	0.78 (0.017)	1567	0.38 (0.012)

^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 2016. 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
2012	4	2.000	0.000	23	0.348	0.162
2013	10	1.500	0.167	24	0.625	0.168
2014	12	1.917	0.149	24	0.958	0.213
2015	13	1.692	0.133	26	0.846	0.181
2016	10	1.700	0.153	22	0.773	0.197

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 2016. Estimates are from random effects means models.

Parameter	Mean	SE	$\hat{\sigma}_{temporal}$	CV _{temporal}
R	0.594	0.047	0.227	0.382
P	1.593	0.033	0.112	0.070
ϕ	0.846	0.009	0.031	0.037
λ (WCSA)	0.977	0.008	0.017	0.018

Table 8. Number of sites with barred owl detections in the WCSA and RSA from 1991 through 2016.

Year	Spotted Owl Territories With Detections	Number of Barred Owl Sites ^a	
		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
2009	21	9	1
2010	29	15	2
2011	36	17	4
2012	33	21	4
2013	37	21	6
2014	33	22	4
2015	46	29	7
2016	39	26	7

^a Estimated using the spatial clustering of detections. This number should be considered an approximate number of barred owl sites.

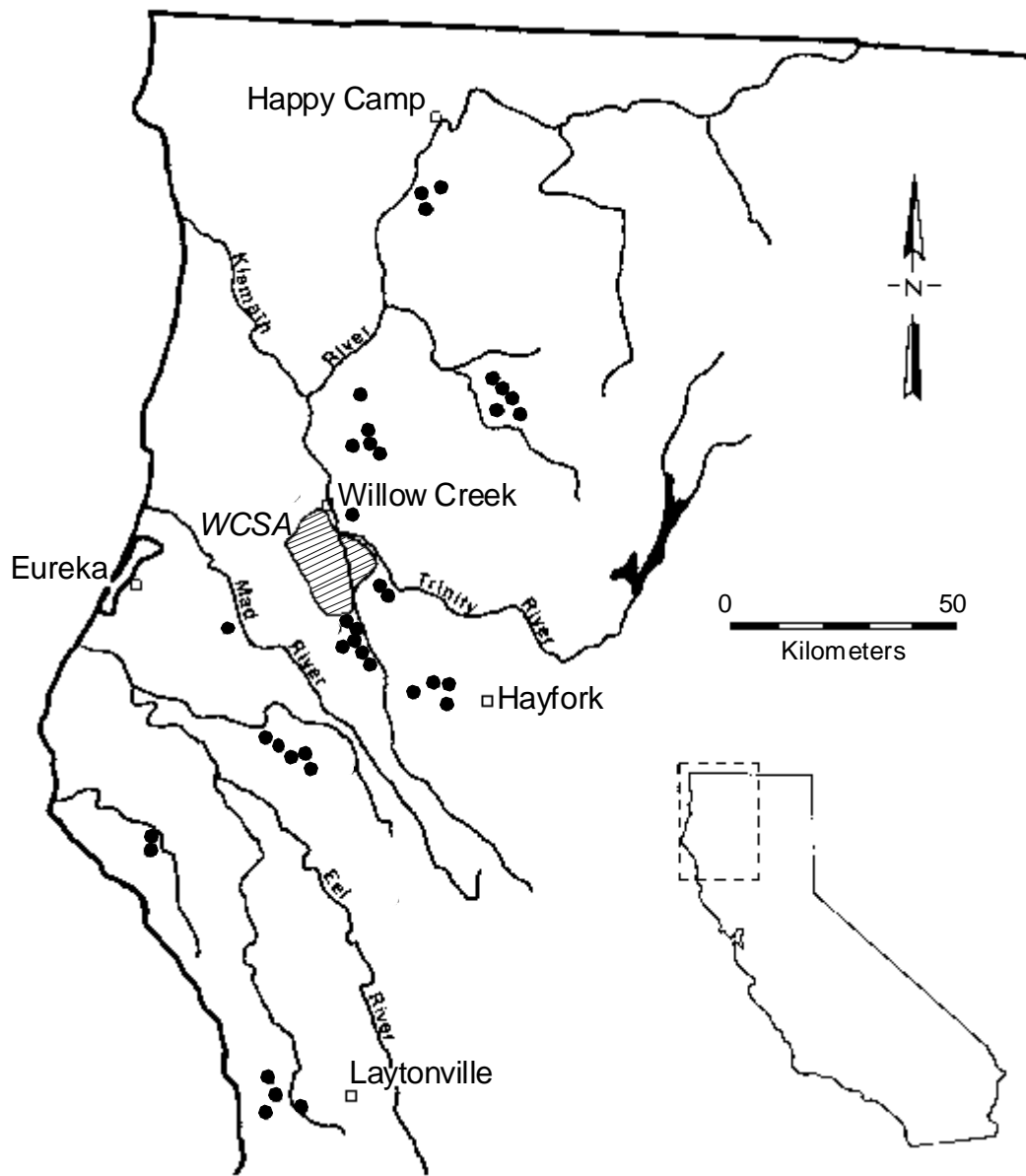


Figure 1. Map of northern spotted owl territories (dots) surveyed in the Regional Study Area, northwestern California. Shaded area represents the Willow Creek Study Area.

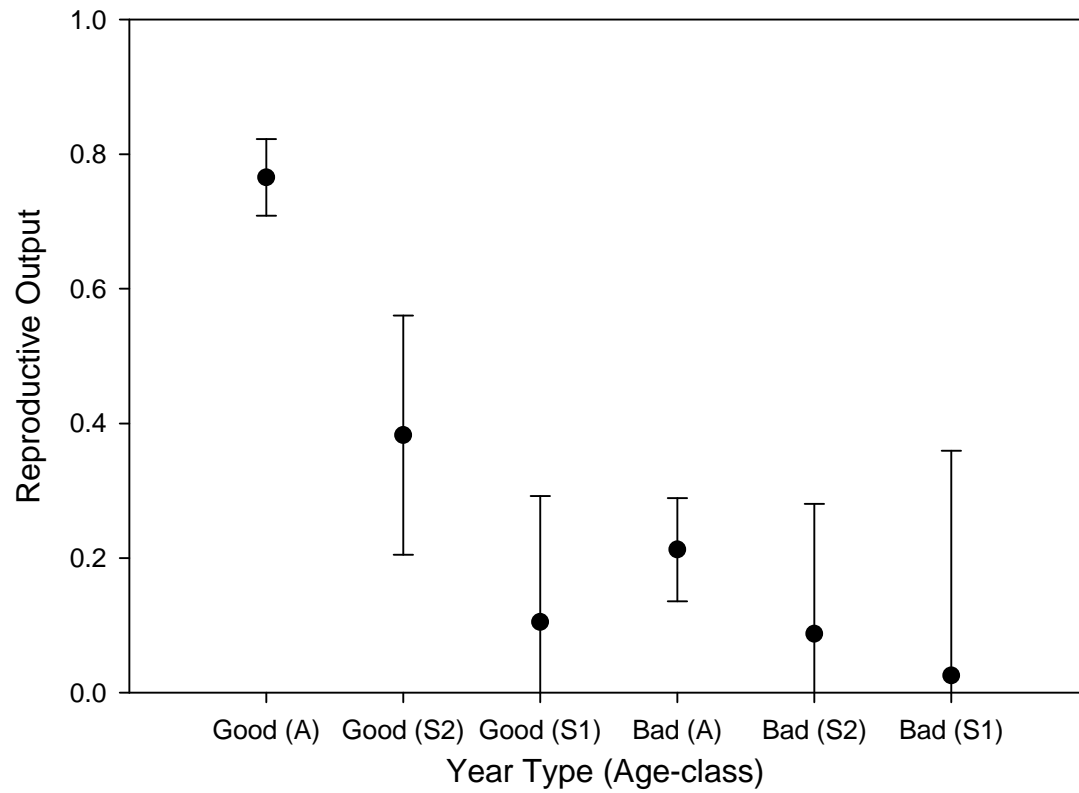


Figure 2. Mean reproductive output for S1, S2, and adult northern spotted owls in “good” and “bad” years in northwestern California from 1985 through 2016. Bars are 95% confidence intervals.

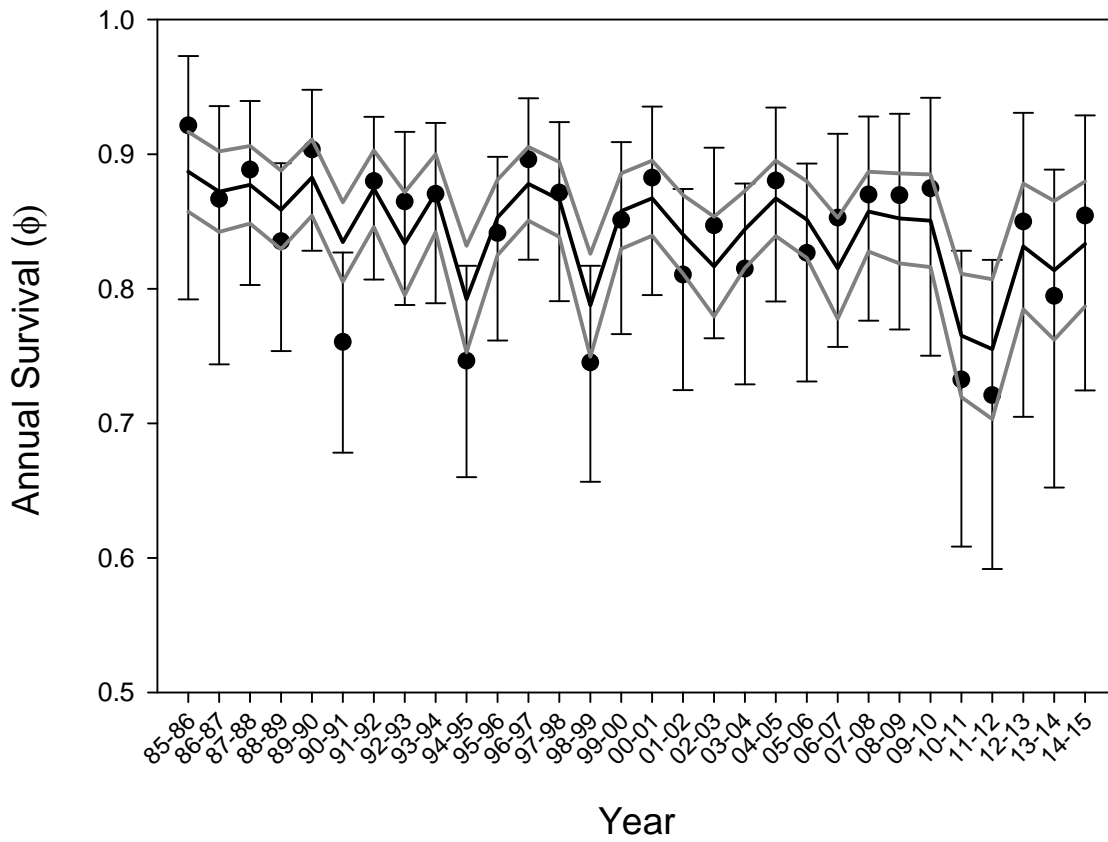


Figure 3. Trends in apparent survival for subadult and adult northern spotted owls in northwestern California from 1985 through 2016. Trend estimates are from random effects model $\{\phi_{G \text{ vs } B + BO}\}$ with gray lines representing 95% confidence intervals. Estimates of individual values (solid dots) \pm 95% confidence intervals are from model $\{\phi_i, p_i\}$ for comparison. The estimate for 2015-2016 was not estimable.

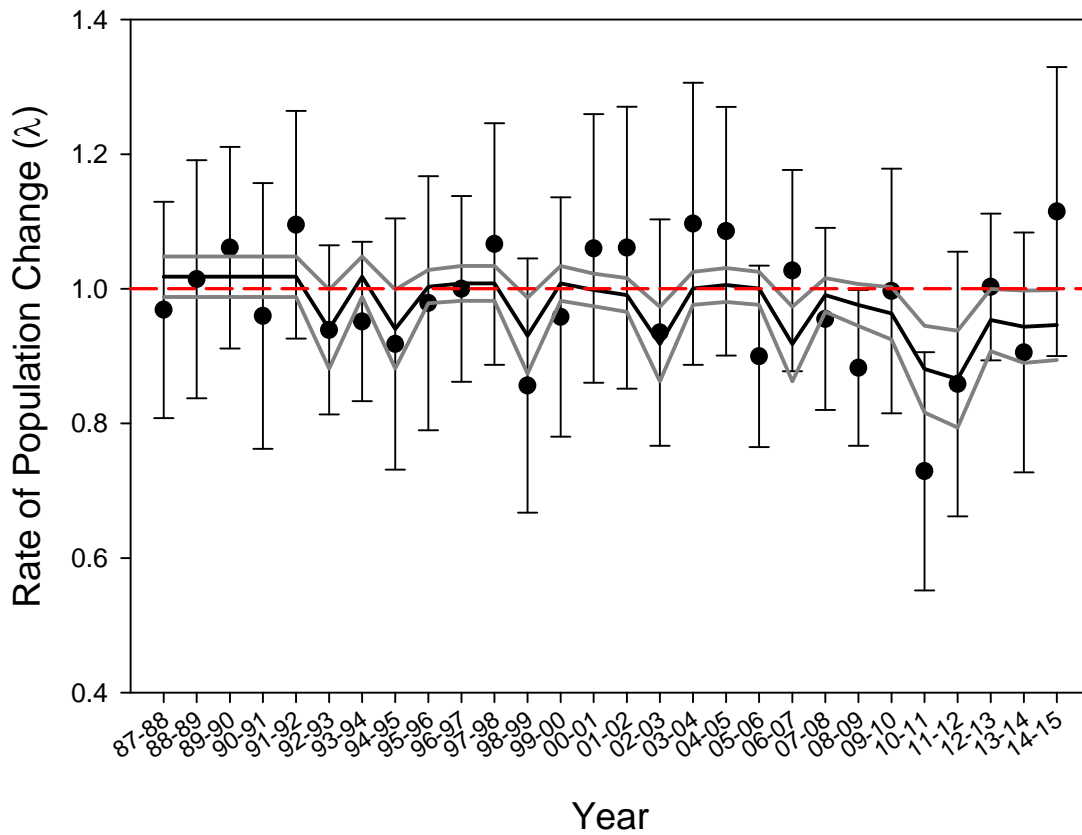


Figure 4. Trends in annual estimates of λ for northern spotted owls on the WCSA in northwestern California from 1987 through 2016. Trend estimates are from random effects model $\{\lambda_{GvSB+BO}\}$ with gray lines representing 95% confidence intervals. Estimates of individual values (solid dots) \pm 95% confidence intervals are from model $\{\phi_t, p_t, \lambda_t\}$ for comparison. Dashed red line indicates $\lambda = 1$ (stationary population). The estimate for 2015-2016 was not estimable.

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 2016.

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.	1595.77	2	1599.77	1599.78	107.270	0.000
PN _t	1455.69	33	1521.69	1523.69	31.183	0.000
PN _T	1595.52	3	1601.52	1601.54	109.030	0.000
PN _{TT}	1585.83	4	1593.83	1593.86	101.354	0.000
PN _{lnT}	1594.15	3	1600.15	1600.17	107.660	0.000
PN_{G vs B}	1486.49	3	1492.49	1492.51	0.000	1.000
PN _{EO}	1571.11	3	1577.11	1577.13	84.620	0.000
PN _{EO+T}	1570.54	4	1578.54	1578.57	86.064	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.	413.28	2	417.28	417.30	0.000	0.358
PNF _t	415.76	33	481.76	485.66	68.363	0.000
PNF _T	413.15	3	419.15	419.19	1.890	0.139
PNF _{TT}	413.15	4	421.15	421.22	3.916	0.051
PNF _{lnT}	413.16	3	419.16	419.20	1.900	0.139
PNF _{G vs B}	413.26	3	419.26	419.30	2.000	0.132
PNF _{EO}	413.28	3	419.28	419.32	2.020	0.131
PNF _{EO+T}	413.15	4	421.15	421.22	3.916	0.051

^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.	2082.68	2	2086.68	2086.69	109.672	0.000
PF _t	1947.37	33	2013.37	2014.83	37.818	0.000
PF _T	2081.39	3	2087.39	2087.41	110.390	0.000
PF _{TT}	2078.92	4	2086.92	2086.95	109.930	0.000
PF _{lnT}	2080.37	3	2086.37	2086.39	109.370	0.000
PF_{G vs B}	1971.00	3	1977.00	1977.02	0.000	1.000
PF _{EO}	2063.56	3	2069.56	2069.58	92.560	0.000
PF _{EO+T}	2061.85	4	2069.85	2069.88	92.860	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(Y _r)	4	3854.00	3862.00	3862.03	77.56	0.000
AR(1)	4	3834.70	3842.70	3842.73	59.76	0.000
AR(1) w/ EXP(Y _r)	6	3829.00	3841.00	3841.05	58.18	0.000
CS	3	3854.60	3860.60	3860.62	76.65	0.000
CSH	34	3729.50	3797.50	3799.05	13.82	0.000
ARH(1)	35	3715.60	3785.60	3787.25	3.01	0.130
TOEP	Unable to make hessian positive definite					
TOEPH(3)	36	3709.70	3781.70	3783.44	0.00	0.870
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.	3689.80	37	3763.80	3765.64	39.00	0.00
R _T	3689.70	38	3765.70	3767.64	41.00	0.00
R _{TT}	3688.00	39	3766.00	3768.04	41.40	0.00
R _{lnT}	3689.20	38	3765.20	3767.14	40.50	0.00
R_[G vs B]	3648.70	38	3724.70	3726.64	0.00	1.00
R _{EO}	3686.50	38	3762.50	3764.44	37.80	0.00
R _{EO+T}	3686.20	39	3764.20	3766.24	39.60	0.00

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

Model^a	-2lnL	K	AICc	ΔAICc	Akaike Weight
Rg*f	3471.40	42	3557.86	0.00	0.486
Rg*f'	3475.80	40	3558.03	0.17	0.446
Rg+f	3479.80	40	3562.03	4.17	0.060
Rg+f'	3486.30	39	3566.42	8.56	0.007
Rg*f	3489.20	40	3571.43	13.57	0.001
Rg+f	3494.40	39	3574.52	16.66	0.000
REO*f	3513.00	42	3599.46	41.60	0.000
REO*f'	3517.60	40	3599.83	41.97	0.000
REO*f+T	3512.40	43	3600.97	43.12	0.000
REO*f'+T	3517.00	41	3601.34	43.48	0.000
REO+f	3519.30	40	3601.53	43.67	0.000
Rf	3522.70	39	3602.82	44.96	0.000
REO+T+f	3518.70	41	3603.04	45.18	0.000
RlnT+f	3521.60	40	3603.83	45.97	0.000
RT+f	3522.30	40	3604.53	46.67	0.000
R[T+T2]+f	3520.40	41	3604.74	46.88	0.000
REO+f'	3525.20	39	3605.32	47.46	0.000
Rf'	3528.40	38	3606.41	48.55	0.000
REO+T+f'	3524.60	40	3606.83	48.97	0.000
RlnT+f'	3527.30	39	3607.42	49.56	0.000
RlnT*f	3521.40	42	3607.86	50.00	0.000
RT+f'	3528.00	39	3608.12	50.26	0.000
RT*f	3521.70	42	3608.16	50.30	0.000
R[T+T2]+f'	3526.00	40	3608.23	50.37	0.000
RlnT*f'	3527.20	40	3609.43	51.57	0.000
RT*f'	3527.60	40	3609.83	51.97	0.000
Rg	3532.00	38	3610.01	52.15	0.000
REO*f	3528.50	40	3610.73	52.87	0.000
R[T+T2]*f'	3524.60	42	3611.06	53.20	0.000
R[T+T2]*f	3518.30	45	3611.12	53.26	0.000
REO*f+T	3527.90	41	3612.24	54.38	0.000
REO+f'	3533.30	39	3613.42	55.56	0.000
REO+T+f'	3532.70	40	3614.93	57.07	0.000
Rf	3537.00	38	3615.01	57.15	0.000
RlnT+f'	3536.00	39	3616.12	58.26	0.000
RT+f'	3536.60	39	3616.72	58.86	0.000
R[T+T2]+f'	3534.90	40	3617.13	59.27	0.000
RlnT*f'	3535.90	40	3618.13	60.27	0.000
RT*f'	3536.60	40	3618.83	60.97	0.000
R[T+T2]*f'	3534.00	42	3620.46	62.60	0.000
REO+T	3567.80	38	3645.81	87.95	0.000
REO	3568.30	38	3646.31	88.45	0.000
R.	3571.50	37	3647.41	89.55	0.000
RlnT	3570.60	38	3648.61	90.75	0.000
RT	3571.20	38	3649.21	91.35	0.000
RT+T2	3569.40	39	3649.52	91.66	0.000

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, [T+T2] = quadratic trend, lnT = log-linear trend, g = good versus bad years [GvsB], EO = even-odd years, EO+T = even-odd year plus linear trend, f = female S1 vs female S2 vs female adult ages [fS1vsfS2vsfA], f' = female S1 vs combined female S2 and adult ages [fS1vsfS2+fA], f'' = female subadult vs female adult ages [fS1+fS2vsfA].

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	916.70	924.70	924.77	0.83	0.211
AR(1)	4	916.60	924.60	924.67	0.73	0.222
AR(1) w/ EXP(Yr)	6	912.30	924.30	924.44	0.50	0.248
CS	3	917.90	923.90	923.94	0.00	0.319
CSH	34	Unable to make hessian positive definite				
ARH(1)	34	Unable to make hessian positive definite				
TOEP	33	Unable to make hessian positive definite				
TOEPH(3)	35	Unable to make hessian positive definite				
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	-2logL	K	AICc	ΔAICc	Akaike Weight
P.	854.00	5	864.10	0.00	0.0915
Pf ^o	852.00	6	864.15	0.04	0.0896
Pg+f ^o	851.00	7	865.20	1.09	0.0530
Pg	853.10	6	865.25	1.14	0.0517
Pf	851.60	7	865.80	1.69	0.0393
PlnT+f ^o	851.80	7	866.00	1.89	0.0355
PT	853.90	6	866.05	1.94	0.0347
PlnT	853.90	6	866.05	1.94	0.0347
PT+T2	851.90	7	866.10	1.99	0.0338
PEO	854.00	6	866.15	2.04	0.0330
Pf ^o	854.00	6	866.15	2.04	0.0330
PEO*f ^o	849.90	8	866.15	2.05	0.0329
P[T+T2]+f ^o	849.90	8	866.15	2.05	0.0329
PT+f ^o	852.00	7	866.20	2.09	0.0322
PEO+f ^o	852.00	7	866.20	2.09	0.0322
Pg*f ^o	850.40	8	866.65	2.55	0.0256
Pg+f	850.60	8	866.85	2.75	0.0232
Pg+f ^o	853.10	7	867.30	3.19	0.0186
PlnT*f ^o	851.20	8	867.45	3.35	0.0172
PT*f ^o	851.40	8	867.65	3.55	0.0155
PlnT+f	851.50	8	867.75	3.65	0.0148
P[T+T2]+f	849.50	9	867.82	3.71	0.0143
PT+f	851.60	8	867.85	3.75	0.0140
PEO+f	851.60	8	867.85	3.75	0.0140
PEO*f ^o	851.60	8	867.85	3.75	0.0140
PEO*f	847.50	10	867.89	3.78	0.0138
PEO+T	853.90	7	868.10	3.99	0.0124
PT+f	853.90	7	868.10	3.99	0.0124
PlnT+f ^o	853.90	7	868.10	3.99	0.0124
PEO*f+T	849.80	9	868.12	4.01	0.0123
P[T+T2]+f ^o	851.90	8	868.15	4.05	0.0121
PEO+f ^o	854.00	7	868.20	4.09	0.0118
PEO+T+f ^o	852.00	8	868.25	4.15	0.0115
Pg*f	850.00	9	868.32	4.21	0.0111
PT*f	852.70	8	868.95	4.85	0.0081
P[T+T2]*f ^o	848.60	10	868.99	4.88	0.0080
PlnT*f	853.00	8	869.25	5.15	0.0070
Pg*f ^o	853.10	8	869.35	5.25	0.0066
PEO+T+f	851.60	9	869.92	5.81	0.0050
PEO*f ^o +T	851.60	9	869.92	5.81	0.0050
PEO*f+T	847.50	11	869.97	5.86	0.0049
PEO+T+f ^o	853.90	8	870.15	6.05	0.0044
PT*f	850.30	10	870.69	6.58	0.0034
PlnT*f	850.50	10	870.89	6.78	0.0031
P[T+T2]*f	850.60	10	870.99	6.88	0.0029
P[T+T2]*f ^o	847.70	13	874.35	10.24	0.0005

^aModel notation: . = means (intercept-only) model, t = varies by year, T= linear trend, [T+T2] = quadratic trend, lnT = log-linear trend, g = good versus bad years [GvsB], EO = even-odd years, EO+T = even-odd year plus linear trend, f = female S1 vs female S2 vs female adult ages [fS1vsfS2vsfA], f^o = female S1 vs combined female S2 and adult ages [fS1vsfS2+fA], f^o = female subadult vs female adult ages [fS1+fS2vsfA].

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+BO	42.89	4550.33	0	0.466
ϕ_t, p_t : RE GvsB*BO	44.12	4551.64	1.31	0.242
ϕ_t, p_t : RE GvsB	44.76	4551.91	1.58	0.211
ϕ_t, p_t : RE BO	48.72	4556.74	6.41	0.019
ϕ_t, p_t : RE lnT	48.63	4556.75	6.43	0.019
ϕ_t, p_t : RE T	49.24	4557.45	7.12	0.013
ϕ_t, p_t : RE lnBO	49.38	4557.52	7.19	0.013
ϕ_t, p_t : RE Mean	49.99	4558.21	7.88	0.009
ϕ_t, p_t : RE TT	50.14	4558.60	8.27	0.007
ϕ_t, p_t	61	4573.27	22.94	0
ϕ_t, p_{s^*t}	92	4610.24	59.91	0
ϕ_{s^*t}, p_t	92	4615.48	65.15	0
ϕ_{s^*t}, p_{s^*t}	122	4650.46	100.13	0

^aModel notation: “*” indicates full additive effects and interactions; RE = random effects model, 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, BO = annual number of northern spotted owl sites with barred owl detections on the WCSA, lnBO = natural log of annual number of northern spotted owl sites with barred owl detections on the WCSA.

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

Model ^a	K	QAICc	Δ QAICc	Akaike Weight
ϕ_t, p_t, λ_t RE GvsB+BO	67	3544.77	0	0.346
ϕ_t, p_t, λ_t RE GvsB*BO	68	3546.1	1.32	0.178
ϕ_t, p_t, λ_t RE GvsB	66	3546.13	1.35	0.176
ϕ_t, p_t, λ_t RE BO	66	3547.23	2.46	0.101
ϕ_t, p_t, λ_t RE T	66	3548.17	3.39	0.063
ϕ_t, p_t, λ_t RE lnBO	66	3548.62	3.85	0.051
ϕ_t, p_t, λ_t RE lnT	66	3548.8	4.03	0.046
ϕ_t, p_t, λ_t RE TT	67	3550.18	5.41	0.023
ϕ_t, p_t, λ_t RE Means	70.6	3550.98	6.21	0.016
ϕ_t, p_t, λ_t	92	3579.95	35.18	0.000

^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, BO = annual number of northern spotted owl sites with barred owl detections on the WCSA, lnBO = natural log of annual number of northern spotted owl sites with barred owl detections on the WCSA.