

Annual Progress Report:
Region 5, USDA Forest Service (CS Agreement: 11-CS-11052007-320)

March 1, 2013

**POPULATION ECOLOGY OF THE CALIFORNIA
SPOTTED OWL IN THE CENTRAL SIERRA NEVADA:
ANNUAL RESULTS 2012**

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ABSTRACT

We used data from the 2012 field season to obtain current estimates of California spotted owl (*Strix occidentalis occidentalis*) demographic parameters on the Eldorado Density Study Area (EDSA) and Regional Study Area (RSA). Spotted owl fecundity in 2012 was below the long-term average, continuing the general trend of lower reproduction that we have observed over the last 10 years. Ten of 26 territorial females on the EDSA and RSA successfully nested and produced 13 fledglings. We also observed a continued, long-term decline in the number of occupied territories. We detected owls at 19 of the 45 territories on the EDSA, a historic low and a decline of 45.2% from 1990 in the proportion of surveyed territories where owls were detected. We estimated that the annual finite rate of population change (λ_t) on the EDSA was below 1.0 for the 13th time in the past 16 years ($\lambda_t = 1.0$ for a stationary population). The average λ_t from the random-effects means model suggested that the average λ_t from 1992-2010 was < 1.0 ($\lambda_t = 0.980$, 95% C.I. = 0.946–1.014). The realized population change (Δ) from 1992-2011 was also < 1.0 ($\Delta = 0.763$, 95% C.I. = 0.502–1.161). In both cases, the 95% C.I. overlapped 1.0 because of uncertainty in the parameter estimates. We recently determined that survey coverage of the entire EDSA was not achieved until 1993 because funding constraints precluded hiring sufficient personnel (Tempel and Gutiérrez 2013). Tempel and Gutiérrez (2013) used data from 1993-2010 to obtain two estimates of realized population change (one with mark-recapture data, one with occupancy data). Both the mark-recapture estimate ($\Delta = 0.725$, 95% C.I. = 0.445–1.004) and the occupancy estimate ($\Delta = 0.702$, 95% C.I. = 0.552–0.852) provided additional evidence of a long-term population decline.

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INTRODUCTION

This report provides analyses of the 2012 field results from our long-term monitoring of a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, California. Information from our study can be used by the U.S. Forest Service (USFS) to assess conservation needs and support the goals of the Sierra Nevada Forest Plan Amendment (hereafter the “Forest Plan”; USDA Forest Service 2004). Two main goals of the Forest Plan are: (1) conservation of the spotted owl and its habitat, and (2) limiting the spread of catastrophic wildfire. The compatibility between these 2 goals is a major source of uncertainty in the Forest Plan; hence, our estimates of spotted owl vital rates can be used to assess this compatibility. Additionally, our monitoring provides essential information to the U.S. Fish and Wildlife Service for assessment of the status of the California spotted owl.

In conjunction with the basic demographic monitoring, we have conducted many other spotted owl studies either entirely or partly on the Eldorado Study Area including:

- habitat use (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004, Chatfield 2005, Phillips et al. 2010, Williams et al. 2011).
- population dynamics (Lutz 1992; Seamans et al. 2001; Franklin et al. 2004; Blakesley et al. 2010; Tempel and Gutiérrez 2013).
- life-history strategy and the effect of climate and habitat on population processes (Seamans 2005, Seamans and Gutiérrez 2007a, Seamans and Gutiérrez 2007b).
- development of statistical models to assess site occupancy and statistical power (Nichols et al. 2007, MacKenzie et al. 2009, Popescu et al. 2012).
- genetics and phylogeny (Barrowclough and Gutiérrez 1990, Barrowclough et al. 1999, Barrowclough et al. 2005).
- physiology and assessment of stress (Tempel and Gutiérrez 2003, 2004; Washburn et al. 2004).
- disease (Gutiérrez 1989).
- species distribution patterns and interspecific competition (Crozier et al. 2003, 2005, 2006; Seamans et al. 2004; Gutiérrez and Barrowclough 2005; Seamans and Gutiérrez 2006; Barrowclough and Gutiérrez 2011).
- management applications (Verner et al. 1992, Gutiérrez et al. 1992, Tempel and Gutiérrez 2003, Berigan et al. 2012).
- general ecology (Gutiérrez et al. 1995).

Individuals from our research project have provided data and technical expertise for 2 California spotted owl meta-analyses examining population vital rates throughout its range (Franklin et al. 2004; Blakesley et al. 2010), a California Spotted Owl Technical Assessment (Verner et al. 1992), a California Spotted Owl Federal Advisory Committee (FAC 1997), and the formulation of the Sierra Nevada Forest Plan (i.e., “Sierra Framework,” USDA Forest Service 2001, 2004). In January 2007, we were invited to join scientists from UC-Berkeley, UC-Merced, and UC-Davis as part of the Science Team conducting research for the Sierra Nevada Adaptive Management Project

(SNAMP). The Science Team is assessing the ecological and social impacts of “strategically placed land area treatments” (SPLATs) implemented as part of the Sierra Framework. Our specific role on the Team is to assess the impact of SPLATs on spotted owl survival, reproduction, and territory occupancy on the SNAMP northern study site, which is adjacent to our demography study area. Because the sample of owls on this SNAMP experimental site is too small to support analyses, it was agreed by the SNAMP MOU Partners, which includes the USFS, that we should include data from the Eldorado demography study in the SNAMP assessment. This additional data will increase sample size and will provide a more robust estimate of the effects of SPLATS on spotted owls (Popescu et al. 2012).

In this report, we summarize the results of our field work on the Eldorado Study Area during the April-August 2012 field season and discuss long-term demographic patterns of the study population over the period of 1990-2012. We also present summary statistics, parameter estimates, and temporal trends for the following variables on the Eldorado Study Area as part of our contractual agreement:

- 1) empirical abundance of spotted owls;
- 2) owl fecundity and survival rates;
- 3) population rate of change;

Our long-term dataset and estimation of demographic parameters provide basic information regarding the status of this population and facilitates more complex analyses of factors that affect spotted owl population dynamics (Noon and Franklin 2002). These data also make feasible our participation in SNAMP as noted above.

STUDY AREA

Our study area consisted of a 355-km² Eldorado Density Study Area (EDSA) and a Regional Study Area (RSA) that are located in the central Sierra Nevada, east of Georgetown in El Dorado and Placer Counties, California. We established the EDSA in 1986 to assess population trends and other vital rates of a contiguous owl population; hence, we term this a “density” study area. We initiated the RSA in 1997 to increase our sample of owl territories and to assess emigration from the EDSA. The RSA consisted of individual or clusters of owl territories dispersed over a larger area than the EDSA. The EDSA and RSA together encompassed an area of approximately 925 km². The EDSA was located within the Eldorado National Forest, although 37% of the EDSA consisted of private land. All RSA territory centers (i.e., nesting and roosting locations) except for 1 were located on public land. Fifty-eight percent of the RSA territory centers were located on the Eldorado National Forest and 42% are on the Tahoe National Forest. The location of the EDSA was chosen by the California Department of Fish and Game for study because of its history of spotted owl occupation, previous spotted owl research, and good road access.

The Sierra Nevada was the dominant physical feature of the area. The study area was typical of the mid-elevation Sierra Nevada, with mountainous terrain bisected by steep river canyons. Elevation ranged from 366 m to 2,401 m. From 1962 to 1995,

average annual precipitation was 158 cm at Blodgett Experimental Forest, which was located on the RSA at 1,340 m elevation (Olson and Helms 1996). Thirty-five percent of the precipitation fell as snow; snowfall averaged 254 cm per year. Average minimum temperature in January was 1° C and average maximum temperature in July was 28° C (Olson and Helms 1996).

Vegetation on the study area was influenced by elevation, topography, soil, and natural and anthropogenic disturbance history. Sierran Mixed Conifer Forest was the principal vegetation type (SNEP 1996), dominated by ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*). Other common tree species were sugar pine (*P. lambertiana*), California black oak (*Quercus kelloggii*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Red Fir Forest was less abundant, but common at higher elevations, and was dominated by red fir (*A. magnifica*) and lodgepole pine (*P. contorta*). Montane Manzanita (*Arctostaphylos* spp.), Chaparral, Black Oak Woodland, and barren rock were less common vegetation types or landscape features (SNEP 1996).

METHODS

Field Methods

Surveys

We surveyed spotted owls following the methods described by Franklin et al. (1996a). We conducted point, cruise, and walk-in surveys from April 1–August 28, 1986–2012. We generally conducted night surveys from dusk to 0200 hrs. We conducted walk-in and cruise surveys at all times of day, but primarily near dawn and dusk. We surveyed all areas within the EDSA regardless of land ownership or habitats present. We selected RSA territories from among historic owl locations provided by the USFS and from surveys we conducted in 1997.

We considered a territory to be occupied if we observed nesting or roosting owls or an owl(s) was detected within an historic territory on ≥ 2 surveys separated by ≥ 7 days. We surveyed historic territories on ≥ 4 occasions to estimate site occupancy by owls. We surveyed areas within the EDSA boundary and outside of historic owl territories on ≥ 3 occasions. Three surveys should have been sufficient to detect most non-juvenile, territorial males in areas outside historic owl territories (Reid et al. 1999). Once an owl was detected during a night survey we always returned to survey the area, on multiple occasions if necessary, to locate the owl during the day, to locate any possible mate, and to assess its reproductive status.

We estimated owl reproductive characteristics by feeding live mice to owls when we located them during surveys (Franklin et al. 1996a). Reproducing owls usually take offered prey to their nest or young, while non-reproducing owls usually eat or cache the mice. We inferred non-reproduction if: (1) 1 owl took ≥ 2 mice and cached the last mouse without bringing 1 mouse to a nest or young (Franklin et al. 1996a); (2) 1 owl ate or cached ≥ 4 mice without bringing 1 mouse to a nest or young (Franklin et al. 1996a); (3) 1 owl ate 2 mice and ignored a third mouse for > 1 hour; (4) a female owl was captured between April 10 and May 31 and did not have a brood patch; or (5) a female

owl was observed roosting for > 60 minutes between April 10 and May 31 which suggested that the female was not incubating eggs or brooding (Rockweit et al. 2012). We then estimated fecundity (number of female young fledged per territorial female) and productivity (number of female young fledged per reproducing female) assuming a 50:50 sex ratio for fledged young.

Capture

We attempted to capture and band all spotted owls detected following the methods of Franklin et al. (1996a). Once captured, we fitted all owls with a U.S. Geologic Survey (USGS) locking aluminum band on the tarso-metatarsus of 1 leg. On the opposite leg, adult and subadult owls were marked with a unique color band and tab combination while juvenile owls were marked with a color band specific to their cohort (i.e., year of hatching). Juveniles were recaptured and marked with unique color bands and tabs if they became territory holders or were detected elsewhere in later years. However, we believe that sampling issues in the early years of the study may have affected the quality of the mark-recapture data in those years (see below).

Determining sex and age class

Sex of owls was determined by their calls and behavior. Males have a lower-pitched call than females, and females primarily incubate and brood the young (Forsman et al. 1984). We identified 4 age-classes based on plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; 1 year old (first-year subadult); 2 years old (second-year subadult); and ≥ 3 years old (adult).

Sampling issues with mark-recapture data

In last year's report (Peery et al. 2012), we referred to 11 owls captured prior to 1989 that were fitted with a color band that lacked a color tab because of mistakes by inexperienced banders. Although these incorrectly banded owls were not included in the data sets used for our annual reports prior to last year and for prior meta-analyses (Franklin et al. 2004, Blakesley et al. 2010), we determined that it was highly unlikely that 8 of these individuals could have been mistaken for a different owl. Therefore, we conducted 2 separate analyses (with and without these 8 individuals) for population rate of change in last year's report. However, we chose not to include these 8 individuals in this year's analyses based on review comments of Douglas Tempel's dissertation by Alan Franklin and James Nichols. Drs. Franklin and Nichols, who are members of Mr. Tempel's committee, suggested that including the capture histories of individuals that were not uniquely marked was not an ideal solution and that more appropriate analytical solutions may exist.

In addition to the 11 birds which were improperly marked, we had insufficient personnel, due to funding constraints, to survey the EDSA completely in the early years of the study. Full survey coverage of the EDSA was not achieved until 1993 (Tempel and Gutiérrez 2013). Therefore, resident owls at territories not surveyed prior to 1993 were essentially unavailable for capture. Tempel and Gutiérrez (2013) used data from 1993-2010 to obtain two estimates of realized population change (one with mark-recapture data, one with occupancy data). Both the mark-recapture estimate ($\Delta = 0.725$, 95% C.I. = 0.445–1.004) and the occupancy estimate ($\Delta = 0.702$, 95% C.I. = 0.552–0.852)

suggested a long-term population decline. Thus, despite our inclusion of data from 1990-1992 in this year's report, our concerns remain that the data quality in those years may be impacting the results of the Pradel model (see below).

Data Analysis

Reproduction

We used mixed-model analysis of variance (PROC MIXED in program SAS; Littell et al. 1996) to assess variation in fecundity and productivity for the years 1991–2012. We did not use data from 1986–1990 due to small sample sizes and potential sampling biases (Seamans 2005). These potential biases resulted from insufficient funding which led to inadequate survey effort. Beginning with the 2006 annual report (Gutiérrez et al. 2007), we analyzed reproductive data in a manner that was consistent with other researchers studying spotted owls in the Sierra Nevada (Franklin et al. 2004, Blakesley et al. 2010). Thus, we were able to determine reproductive success (i.e., fledging of young) by owls if we met the assessment protocol described above under “Surveys” on at least 2 survey occasions.

When estimating fecundity and productivity, we considered the annual proportion of the female territorial population comprised of subadults (variable “psub”) as a fixed effect in analyses. We considered territory as a random blocking factor. We treated year as a random effect, and we developed linear (T), quadratic (TT), log-linear (ln[T]), and alternating (EO; years with high fecundity preceded by years of low fecundity) time-trend models to assess temporal variation in the reproductive data. Ideally, territories should have been randomly sampled from a larger population of territories. However, treating territory as a random blocking factor allowed us to calculate standard errors of fixed effects based on the number of territories and not the total number of reproductive outcomes. We developed 16 models representing combinations of effects (psub, T, TT, EO, and an intercept-only model [i.e., a null model]). We ranked each model based on its AIC_c value (Akaike's Information Criterion corrected for small sample size; Akaike 1973, Burnham and Anderson 2002).

Linear mixed modeling assumes a normal distribution of errors within years and similar subsample variances across years (Littell et al. 1996:267). Our data probably met the first assumption under the central limit theorem, but may have violated the second because annual variances may have been proportional to their means (e.g., Franklin 1997). We dealt with this assumption by initially using restricted maximum likelihood to identify the appropriate structure of the random error covariance matrix (Littell et al. 1996). We compared the following covariance matrix structures: power of the means, first-order autoregressive, power of the means with first-order autoregressive, heterogeneous autoregressive, compound symmetric, compound symmetric with heterogeneous variances, Toeplitz, and heterogeneous Toeplitz with estimates of the first 3 off-diagonal bands. We used AIC_c to select the best covariance structure. Once we selected an appropriate covariance structure, we used full maximum likelihood estimation to model fecundity and productivity. This approach partitioned the total variance into process and sampling variances which allowed us to directly estimate the temporal process variation ($\hat{\sigma}_{temporal}^2$).

Annual survival

We used open population capture-recapture models to estimate age-, time-, and sex-specific survival and recapture probabilities for territorial spotted owls (Cormack 1964, Jolly 1965, Seber 1965). For time effects, we considered categorical time (t), linear trend (T), quadratic trend (TT), and log-linear trend (ln[T]) models. We also considered the number of walk-in survey hours (wi-effort) and number of young fledged per female (b; Table 7) as annual covariates for modeling recapture rates. We counted an individual as captured in the initial year of its capture and in subsequent years if we resighted its unique color band and tab combination. If an individual lost its color band or tab, we counted it as captured only when we physically recaptured the owl to read its unique USGS band and replace its color band and tab.

We used Program MARK (White and Burnham 1999) to estimate apparent survival ($\hat{\phi}$) and recapture (p) probabilities for each of our hypothesized models. Model notation followed that of Lebreton et al. (1992) and Franklin et al. (1996a). We estimated \hat{c} (variance inflation factor; Anderson et al. 1994) as a measure of overdispersion within the data set by using the median \hat{c} simulation procedure in Program MARK for the $\phi(s^*t)$, $p(s^*t)$ model. We simulated 10 data sets at each of 10 levels of overdispersion and compared the \hat{c} (deviance divided by degrees of freedom) from these simulations with the observed \hat{c} from model $\phi(s^*t)$, $p(s^*t)$. We evaluated our hypothesized survival models using QAIC_c values, which corrected for small sample size and overdispersion in the data (Burnham and Anderson 2002).

Our survival estimates represented apparent survival, not true survival, because individuals could have emigrated from the EDSA and RSA and gone undetected. Thus, “apparent survival = true survival – emigration.” We estimated temporal process variation in survival with a random-effects means model in Program MARK.

Population rate of change

We estimated population rate of change (λ_t) following Pradel (1996). We used Program MARK (White and Burnham 1999) to estimate parameters, sampling error, and process variation. Our parameters of interest were apparent survival ($\hat{\phi}$), recapture rate (p), and population rate of change (λ). We used random-effects models in MARK to estimate $\hat{\lambda}_t$ from model $\{\phi_t, p_t, \lambda_t\}$. We eliminated the first 4 years (1986–1989) from this analysis because survey effort in these years was not comparable to subsequent years due to funding constraints. In addition, we did not include the first two and the last estimates of λ_t because they were confounded with estimation of ϕ_t . We only used capture-recapture data from the EDSA to estimate population rate of change to meet the assumption of constant sampling area among years.

We considered 4 random-effects models that differed by temporal constraints on λ_t : linear trend (T), quadratic trend (TT), log linear trend (ln[T]), and no trend (.). We estimated the overdispersion parameter (\hat{c}) using the median \hat{c} procedure in Program MARK as described above for the survival modeling. We used QAIC_c values to evaluate our candidate models. We used the \tilde{S} estimates from the random-effects means (i.e., no time trend) model to obtain annual estimates of λ_t . The \tilde{S} estimates partitioned out the sampling variance from the process variance (Burnham and White 2002). We then used the annual estimates of λ_t to find the realized change in population from 1992–2011. The

realized change represented the proportion of the initial population size remaining each year (Franklin et al. 2004). We calculated standard errors for the point estimates of realized change using the Delta method (Seber 1982).

RESULTS

Surveys

We conducted 1,451 surveys for spotted owls on the EDSA and RSA in 2012, which was similar to the number of surveys conducted in recent years (Table 1). We surveyed each historic owl territory on the EDSA and RSA at least 4 times and the entire EDSA (i.e., random call points) at least 3 times. We detected resident spotted owls at 19 of 48 (39.6%) historic territories on the EDSA and at 15 of 28 (53.6%) historic territories on the RSA (Table 2). The percent of surveyed territories on the EDSA where owls were detected reached an all-time low in 2012 (42.3% in 2012 compared to 87.5% in 1990; Figure 1). Reproduction was assessed successfully (i.e., we either detected fledglings or obtained 2 non-nesting protocols) at 27 of the 34 occupied territories on the EDSA and RSA (Table 2). Ten owl pairs nested successfully on the EDSA and RSA, producing a total of 13 fledglings.

We identified (captured, recaptured, or resighted) 75 individuals in 2012 (Table 3). We captured 9 new adult or subadult birds, and we banded 11 juveniles with cohort bands. We resighted the male barred owl (*Strix varia*) × spotted owl hybrid on the EDSA for the first time in 2012 where he was the lone resident owl at a territory. This individual had been present at the same RSA territory from 2005–2010. We did not detect any barred owls on either the EDSA or RSA. We have made 2,043 individual spotted owl identifications on the EDSA and RSA since 1986, not including multiple recaptures and resightings within the same year.

Sex and Age-class Distribution

Among the territorial owls found in 2012, we classified 5 of 30 (16.7%) females and 3 of 34 (8.8%) males as subadults (Figure 2; Table 4). Thus, the proportion of subadults of both sexes in our study population was nearly unchanged from last year (Figure 2).

Reproduction

Reproductive activity

From 1990–2012, the annual proportion of pairs that nested (Table 5) differed among years ($\chi^2 = 105.23$, 22 df, $p < 0.001$). The annual proportion of pairs fledging young from 1990–2012 (Table 5) also differed among years ($\chi^2 = 161.10$, 22 df, $p < 0.001$). We did not include data from 1986–1989 in the χ^2 analyses due to small sample sizes during this time period, which were the result of inadequate sampling effort due to funding constraints. We did not statistically compare the annual proportions of pairs which nested and subsequently fledged young (i.e., nest success) because of small sample sizes during several years (Table 5).

The overall proportion of successful nests per known nesting attempt (0.796, SE = 0.025) indicated that 20.4% of nesting attempts failed during our study. From 1990–2012, 39.6% of all pairs checked for reproduction fledged young (0.396, SE = 0.018). We observed 4 failed nesting attempts in 2012 (Table 5).

Reproductive output

To estimate variation in fecundity, we assessed reproductive status on 565 occasions at 73 unique territories from 1991–2012. We did not use data from 1986–1990 because of small sample sizes and to be consistent with the 2006 meta-analysis (Blakesley et al. 2010). The best random error covariance matrix structure was first-order autoregressive. We could not distinguish a clearly superior model from our set of competing models, as 2 models were ≤ 2.00 AIC_c units from the top-ranked model (Table 6). The 6 best models included an even-odd year effect (EO), and the 2 best models contained a term for the annual proportion of subadults in the female population (psub; Table 6). The top 2 models differed in the type of time trend that was fit to the data (log-linear vs. quadratic). For the top-ranked model (lnT + EO + psub), the 95% confidence intervals for the lnT effect ($\beta = -0.240$, 95% CI = -0.336 to -0.143) and the EO effect ($\beta = -0.185$, 95% CI = -0.329 to -0.041) did not include zero. However, the 95% confidence interval for the psub effect ($\beta = -1.081$, 95% CI = -2.194 to 0.031) slightly overlapped zero. This model indicated that fecundity declined in a log-linear trend over the study period, varied from year-to-year in an alternating manner, and was negatively related to the proportion of subadults in the female population. Mean annual fecundity was 0.412 female young fledged per territorial female (SE = 0.060). Reproductive output for the 2012 owl population was below the long-term average (Table 6; Figure 3). Total temporal process variation ($\hat{\sigma}_{temporal}^2$) was 0.069 (CV = 0.635), and the top model (EO + lnT + psub) explained 66.8% of the temporal variation in fecundity.

To estimate variation in productivity, we used 268 occasions when young were successfully fledged at 69 unique territories from 1991–2012. The best random error covariance matrix structure was compound symmetric. Again, we could not distinguish a clearly superior model from our set of competing models. The top 2 models [(lnT) and (lnT + EO)] had nearly identical AIC_c values, and 5 models were ≤ 2.0 AIC_c units of the top-ranked model (Table 6). The top 3 models, however, included a log-linear time trend, and models containing the lnT term accounted for 51.1% of the total AIC_c weight for the entire model set. For model (lnT + EO), the 95% confidence interval for the lnT effect ($\beta = -0.064$, 95% CI = -0.112 to -0.016) did not overlap zero, but it slightly overlapped zero for the EO effect ($\beta = -0.056$, 95% CI = -0.129 to 0.017). This model indicated that productivity declined in a log-linear fashion over the study period and varied from year-to-year in an alternating manner. Mean productivity among years was 0.814 female young fledged per reproducing female (SE = 0.022). Temporal process variation in productivity was an order of magnitude less than that of fecundity ($\hat{\sigma}_{temporal}^2 = 0.005$, CV=0.085). Model (lnT) explained 56.5% of the temporal variation in productivity.

Annual Survival

We used the capture histories of 352 individuals to model survival using a data set partitioned by sex and 3 age-classes (first-year subadults [S1], second-year subadults [S2], and adults [A]). We could not model juvenile survival rate because too few of the banded juveniles were subsequently recaptured as territory holders (45 recaptured out of 383 banded prior to 2012). Based on the model $\{\varphi(s \times t), p(s \times t)\}$, we estimated that some overdispersion was present in the data ($\hat{c} = 1.097$). We examined 112 models which included age-class, sex, time, and survey-effort effects on survival and recapture. We modeled recapture rate structure first while using a sex by year ($s \times t$) effect on apparent survival. The model structure $p(A^*s+t)$ best fit the data for recapture rates based on $QAIC_c$ and was used for all subsequent survival modeling.

We found that no survival model was clearly superior to the other models in the candidate set, as 7 models were ≤ 2.0 $QAIC_c$ units from the top-ranked model (Table 8). Examination of parameter estimates from all of the models showed that: 1) adults always had a higher survival rate than first-year subadults with some models suggesting that adults survived better than both first- and second-year subadults; and 2) males had a higher survival rate than females. In the top-ranked model, $\varphi(S1+s)$, the parameter estimate for S1 indicated that first-year subadults had lower survival than second-year subadults and adults ($\beta_{S1} = -0.515$, 95% C.I. = -1.122 to 0.092). The parameter estimate for sex indicated that males survived better than females ($\beta_{\text{male}} = 0.248$, 95% C.I. = -0.023 to 0.520). However, the 95% confidence intervals overlapped zero in both cases.

Survival models that contained either a linear (T) or log-linear (lnT) time trend received some support, as 3 such models were < 2.0 $QAIC_c$ units from the top-ranked model. However, the parameter estimates indicated that the trends in survival were weak for either the highest-ranked model with a linear term ($\beta_T = -0.105$, 95% C.I. = -0.345 to 0.136) or a log-linear term ($\beta_{\ln T} = -0.052$, 95% C.I. = -0.311 to 0.206). The random-effects means model for $\{\varphi(t), p(A^*s+t)\}$ suggested that annual survival has been slightly greater than 80% ($\hat{\varphi} = 0.823$, SE = 0.015; see Figure 4), while exhibiting low temporal variability ($\hat{\sigma}_{\text{temporal}}^2 = 0.0045$, 95% C.I. = 0.0020 to 0.0114). The best structure for p included a year effect (t). Thus, we did not include the first two and the last estimates of φ_t because they were confounded with estimation of p_t .

Population Rate of Change

We used the capture histories of 229 individuals partitioned by sex to model the population rate of change. We examined 8 models that included time effects for the estimation of φ , p , and λ . The data exhibited some overdispersion ($\hat{c} = 1.065$), so we used $QAIC_c$ units to rank the models. The top-ranked model was the random-effects model with a log-linear trend in λ_t (Table 9). The second-ranked model, the random-effects model with a quadratic trend in λ_t , was 2.83 $QAIC_c$ units behind the top model.

The random-effects log-linear trend model suggested that λ_t declined during the study ($\beta_{\ln T} = -0.082$, SE = 0.028), similar to our observed trends in territory occupancy (see Figure 1). The random-effects means model (Figure 5) suggested that the population was declining by 2% per year, but the 95% confidence interval for the average of λ_t overlapped 1.0 ($\bar{\lambda}_t = 0.980$, 95% C.I. = 0.946 to 1.014). Annual population rate of change

exhibited relatively low temporal variability ($\hat{\sigma}_{temporal}^2 = 0.004$, 95% C.I. = 0.000 to 0.020). The estimate of realized population change, which shows the proportion of the initial population size remaining each year, suggested an approximately 34% decline in owl abundance ($\Delta = 0.763$, 95% C.I. = 0.502 to 1.161; Figure 6), but again the 95% confidence interval overlapped 1.0.

DISCUSSION

Spotted owl reproductive output on our study area in 2012 was below the long-term average, continuing the general trend of lower reproductive output that we have observed over the last 10 years (Figure 3). We have yet to observe another “boom” year in reproduction comparable to the breeding seasons of 1992–1995 and 2002. As a result, we found considerable support for a negative, log-linear trend in fecundity and productivity over the course of our study (Table 6). Although population rate of change (λ) on our study area is most sensitive to adult survival, the greater temporal variation that occurs with spotted owl reproductive output relative to survival makes reproduction an important component of λ (Seamans and Gutiérrez 2007b). Thus, many of the vacant owl territories (60.4% of known historic territories on the EDSA) may not be reoccupied until recruitment within the population is boosted by at least 1 year of high reproductive output. Juvenile survival also influences recruitment into the population, but we have no reliable information on variation in juvenile survival rates because so few (11.7%) of our banded fledglings disperse within our monitoring areas and, hence, are “unavailable” for recapture.

The age and sex of individual birds continue to be the best predictors of annual survival rates (Table 8). The apparent survival of males is greater than that of females, and the apparent survival of adults is higher than that of younger birds. We found weak support for a negative time trend in survival. Three models with either a linear or log-linear time covariate were among our competing models (< 2.0 QAIC_c units from the top-ranked model), but in all cases the parameter estimates extensively overlapped zero (see Results—*Annual survival*).

We continued to observe a long-term decline in owl abundance on the EDSA. The annual λ estimate has been < 1.0 in 13 of the past 16 years (Figure 5), and the realized population change is lower than at any previous point during the study (Figure 6). In conjunction with this decline in λ and realized population change, we have observed a 45.2% decline from 1990–2012 in the proportion of surveyed territories on the EDSA where owls were detected (Figure 1). Finally, when we used data from 1993–2010 in Tempel and Gutiérrez (2013), we observed large, concurrent declines in realized population change estimated using either mark-recapture or occupancy data (see Methods—*Sampling issues with mark-recapture data*). Thus, we believe there is strong evidence that the EDSA owl population has declined over the study period.

We believe that continued monitoring is needed in case the population continues to decline in future years because we do not know the cause of the past decline. Our future effort will focus on identifying factors (e.g., changes in landscape habitat features, habitat modification, and climate) that could be related to the decline of owls. It is possible that spotted owls may show natural long-term fluctuations. For example, owls

may reoccupy vacant sites after 1-2 years of extremely favorable conditions such as those in the early 1990s, which resulted in very high reproductive output in the population. Alternatively, some other factor such as land-use management or weather patterns may be resulting in negative impacts on owls.

Monitoring of this population will also become increasingly important as the USFS implements landscape-wide fuel treatments (i.e., SPLATs) under the direction of the 2004 Sierra Nevada Forest Plan Amendment. Due to the uncertain effects of SPLATs on wildlife populations and other resources, the Forest Plan identified an adaptive management program as an important component of forest management in the Sierra Nevada (USDA Forest Service 2004). Our monitoring contributes to the adaptive management process by providing information on spotted owl vital rates and how those might be affected by specific management actions. In particular, this monitoring provides essential data for our continued participation in the Sierra Nevada Adaptive Management Project (SNAMP) because without the EDSA and RSA owl territories there would be an insufficient number of occupied owl territories on the SNAMP study site for us to effectively assess the effects of SPLAT treatments on owls. However, the inclusion of owl territories from the EDSA and RSA should provide the needed sample size to evaluate potential effects of SPLATs on California spotted owls in the central Sierra Nevada.

ACKNOWLEDGMENTS

We thank former project leaders Mike Bias (1986–87), Daryl Lutz (1988–89), Christine Moen (1991–95), and Mark Seamans (1996–2006), and former assistant project leaders Monica Bond (1999–2001) and Michelle Crozier (2002–04) for their contributions in previous years. Sheila Whitmore, Casey Phillips, Laura Erickson, Lorelle Berkleley, David Grandmaison, Don Mitchell, Jennifer Fox, Alan Franklin, Bill LaHaye, Jim Nichols, Gary White, and Guthrie Zimmerman provided valuable assistance and consultation at various times during this project. We thank the many field technicians for their assistance in data collection during this study. We thank Nancy Rothman, Christina Clarkson, Jenni Snyder, and the Sponsored Project Administration at the University of Minnesota for managing the finances. Rob York, Frieder Schurr, and Amy Mason of the University of California’s Blodgett Forest Research Station provided field accommodations and assisted with field logistics. For logistical support, we thank Claudia Funari and others on the Georgetown Ranger District (Eldorado NF), Chris Fischer and others on the American River Ranger District (Tahoe NF), Susan Yasuda of the Pacific Ranger District, and Dawn Lipton at the Eldorado National Forest Supervisor’s Office. In past years this study has been funded by the California Department of Fish and Game, the California Environmental License Plate Fund, the USDA Forest Service Pacific Southwest Forest and Range Experiment Station, and private donations. Funding from 1994–2012 was provided by Region 5, USDA Forest Service (contracts 53-9158-6-FW12, FS/53-9158-00-EC14, and 06-CR-11052007-174 to RJG, and contract 11-CS-11052007-320 to MZP), the University of Minnesota, and the University of Wisconsin.

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Table 1. Annual number of California spotted owl surveys conducted in the Eldorado Density Study Area (EDSA) and Regional Study Area (RSA), 1986–2012, in the central Sierra Nevada, California.

	Survey Type						
	Point		Walk-in		Cruise		
<u>Year</u>	<u>EDSA</u>	<u>RSA</u>	<u>EDSA</u>	<u>RSA</u>	<u>EDSA</u>	<u>RSA</u>	<u>Total</u>
1986	306	0	53	0	8	0	367
1987	157	0	54	0	27	0	238
1988	333	0	74	0	45	0	452
1989	287	0	52	0	42	0	381
1990	462	0	98	0	64	0	624
1991	365	0	81	0	46	0	492
1992	499	0	107	0	31	0	637
1993	656	0	122	0	49	0	827
1994	583	0	120	0	40	0	743
1995	562	0	81	0	53	0	696
1996	427	0	179	8	28	1	643
1997	419	79	201	71	44	22	836
1998	477	116	161	173	54	29	1010
1999	568	78	102	86	49	20	903
2000	611	82	154	100	26	20	993
2001	593	77	134	126	48	25	1003
2002	709	104	166	140	57	9	1179
2003	699	67	142	109	55	24	1096
2004	643	121	212	152	77	43	1248
2005	674	82	122	135	72	53	1138
2006	774	111	105	64	112	44	1210
2007	873	273	165	84	166	49	1610
2008	600	249	156	139	328	101	1573
2009	580	201	122	125	235	82	1345
2010	600	228	133	104	234	108	1407
2011	496	194	105	102	386	146	1429
2012	582	279	123	98	244	125	1451

Table 2. Number of historic California spotted owl territories surveyed, occupied, and successfully checked for reproduction (2 non-nesting protocols required to infer non-reproduction) in 2012 in the Eldorado Density and Regional Study Areas in the central Sierra Nevada, California.

	Study Area		<u>Combined</u>
	<u>EDSA</u>	<u>RSA</u>	
<u>No. Territories</u>			
Surveyed	48	28	76
With Unknown Status	0	0	0
Assumed Unoccupied	29	13	42
Found Occupied By:			
Pairs	17	14	31
Single Males	2	1	3
Single Females	<u>0</u>	<u>0</u>	<u>0</u>
Total	19	15	34
Checked For Reproduction			
Where Occupied By:			
Pairs	15	11	26
Single Males	1	0	1
Single Females	<u>0</u>	<u>0</u>	<u>0</u>
Total	16	11	27

Table 3. Number of California spotted owls identified in the Eldorado Density and Regional Study Areas, 1986–2012, in the central Sierra Nevada, California.

Year	Birds newly captured ^a			Birds recaptured or resighted ^b			Grand Total
	Adult & Subadult	Juvenile	Total	Recaptured	Resighted	Total	
1986	19	6	25	0	0	0	25
1987	11	0	11	0	13	13	24
1988	12	4	16	0	17	17	33
1989	5	1	6	0	25	25	31
1990	8	8	16	0	26	26	42
1991	12	2	14	0	24	24	38
1992	11	26	37	0	32	32	69
1993	16	14	30	2	37	39	69
1994	9	16	25	1	45	46	71
1995	10	13	23	2	42	44	67
1996	18	8	26	11	40	51	77
1997	33	23	56	5	55	60	116
1998	15	25	40	6	75	81	121
1999	11	2	13	2	64	66	79
2000	13	27	40	4	62	66	106
2001	17	11	28	4	63	67	95
2002	6	51	57	9	70	79	136
2003	12	7	19	7	60	67	86
2004	7	30	37	15	56	71	108
2005	5	3	8	9	55	64	72
2006	15	0	15	6	35	41	56
2007	14	27	41	5	49	54	95
2008	16	20	36	10	58	68	104
2009	10	22	32	5	56	61	93
2010	7	16	23	5	56	61	84
2011	9	7	16	4	51	55	71
2012	9	11	20	6	49	55	75
Total	330	380	710	118	1215	1333	2043

^aBoth territorial adults/subadults and young of the year (i.e., juveniles) are listed.

^bRecaptured birds were physically recaptured to replace a missing tab or band, or to replace a juvenile cohort band.

Table 4. Age-class distribution, by sex, of territorial California spotted owls in 2012 on the Eldorado Density and Regional Study Areas in the central Sierra Nevada, California.

	Male		Female		Both Sexes	
	\underline{n}^a	$\underline{\%}^b$	\underline{n}^a	\underline{p}^b	\underline{n}^a	\underline{p}^b
<u>Age-Class</u>						
Adult	31	91.2	25	83.3	56	87.5
2nd-year Subadult	3	8.8	4	13.3	7	10.9
1st-year Subadult	0	0.0	1	3.3	1	1.6

^aTotal number of territorial owls detected by age-class.

^bPercentage of all territorial owls in each age-class.

Table 5. Reproductive success of California spotted owl pairs that were successfully checked for reproduction (2 non-nesting protocols required to infer non-reproduction) on the Eldorado Density and Regional Study Areas, 1986–2012, in the central Sierra Nevada, California.

Year	Proportion of pairs that fledged young ^a	Proportion of nesting attempts that were successful ^b
1986	0.83 (10/12)	1.00 (5/5)
1987	0.25 (2/8)	1.00 (2/2)
1988	0.73 (8/11)	1.00 (5/5)
1989	0.60 (6/10)	0.60 (3/5)
1990	0.73 (11/15)	1.00 (2/2)
1991	0.25 (3/12)	0.50 (2/4)
1992	1.00 (21/21)	1.00 (10/10)
1993	0.62 (16/26)	0.83 (5/6)
1994	0.63 (17/27)	1.00 (9/9)
1995	0.71 (10/14)	1.00 (2/2)
1996	0.16 (5/31)	0.80 (4/5)
1997	0.39 (19/49)	0.86 (12/14)
1998	0.37 (17/46)	0.65 (11/17)
1999	0.06 (2/31)	— (0/0)
2000	0.51 (20/39)	0.88 (14/16)
2001	0.21 (8/39)	0.78 (7/9)
2002	0.69 (29/42)	0.95 (19/20)
2003	0.16 (5/32)	0.67 (4/6)
2004	0.48 (19/40)	0.90 (18/20)
2005	0.11 (4/36)	0.14 (1/7)
2006	0.00 (0/31)	— (0/0)
2007	0.56 (20/36)	0.85 (17/20)
2008	0.38 (13/34)	0.87 (13/15)
2009	0.37 (13/35)	0.71 (12/17)
2010	0.39 (12/31)	0.56 (9/16)
2011	0.10 (3/31)	0.75 (3/4)
2012	0.37 (10/27)	0.71 (10/14)
Total	0.40 (303/766)	0.80 (199/250)

^a Numbers in parentheses indicate the total number of pairs that fledged young divided by the total number of pairs that were checked for reproduction.

^b Numbers in parentheses indicate the number of pairs that were known to be nesting before May 31 and subsequently fledged young divided by the number of pairs that were known to be nesting before May 31.

Table 6. Ranking of mixed models used to fit temporal trends in fecundity (number of female young per territorial female) and productivity (number of female young per reproductive female) for California spotted owls in the Eldorado Density and Regional Study Areas, 1991–2012, in the central Sierra Nevada, California. We list the models that provide $\geq 90\%$ of the Akaike weight for the candidate model sets.

<u>Model</u>	<u>$-2\log_e \mathcal{L}$</u>	<u>K^a</u>	<u>AIC_c</u>	<u>ΔAIC_c</u>	<u>Akaike weight</u>
<i>Fecundity:</i>					
lnT + EO + psub	527.8	8	544.06	0.00	0.262
TT + EO + psub	526.3	9	544.62	0.57	0.197
lnT + EO	531.3	7	545.50	1.44	0.127
TT + EO	530.0	8	546.26	2.20	0.087
T + EO + psub	530.5	8	546.76	2.70	0.068
T + EO	532.6	7	546.80	2.74	0.066
lnT + psub	533.5	7	547.70	3.64	0.042
lnT	535.7	6	547.85	3.79	0.039
TT + psub	531.8	8	548.06	4.00	0.035
<i>Productivity:</i>					
lnT	26.4	6	38.72	0.00	0.166
lnT + EO	24.3	7	38.73	0.01	0.165
lnT + EO + psub	23.0	8	39.56	0.83	0.109
T	27.8	6	40.12	1.40	0.082
T + EO	25.7	7	40.13	1.41	0.082
lnT + psub	26.0	7	40.43	1.71	0.071
T + EO + psub	24.7	8	41.26	2.53	0.047
TT	27.1	7	41.53	2.81	0.041
intercept	31.4	5	41.63	2.91	0.039
TT + EO	25.1	8	41.66	2.93	0.038
T + psub	27.4	7	41.83	3.11	0.035
EO	29.8	6	42.12	3.40	0.030

^anumber of estimated covariance and fixed-effect parameters.

Table 7. Mean productivity (number of female young per reproductive female) and fecundity (number of female young per territorial female) for California spotted owls in the Eldorado Density and Regional Study Areas, 1991–2012, in the central Sierra Nevada, California.

<u>Year</u>	<u>Productivity</u>			<u>Fecundity</u>		
	<u>n^a</u>	<u>Mean</u>	<u>SE</u>	<u>n^b</u>	<u>Mean</u>	<u>SE</u>
1991	3	0.83	0.06	5	0.50	0.14
1992	21	1.05	0.04	21	1.05	0.08
1993	16	0.81	0.05	17	0.76	0.09
1994	17	0.88	0.05	18	0.83	0.08
1995	10	0.70	0.05	10	0.70	0.11
1996	5	0.80	0.06	11	0.36	0.10
1997	20	0.90	0.04	41	0.44	0.06
1998	17	0.82	0.05	31	0.45	0.07
1999	2	0.50	0.07	16	0.06	0.09
2000	20	0.78	0.04	29	0.53	0.07
2001	8	0.75	0.06	26	0.23	0.07
2002	30	0.88	0.04	35	0.76	0.06
2003	5	0.70	0.06	24	0.15	0.07
2004	19	0.84	0.04	33	0.48	0.06
2005	4	0.50	0.06	32	0.06	0.06
2006	0	— ^c	— ^c	30	0.00	0.00
2007	21	0.83	0.05	37	0.47	0.06
2008	12	0.79	0.05	32	0.30	0.06
2009	13	0.85	0.05	34	0.32	0.06
2010	12	0.79	0.06	30	0.32	0.07
2011	3	0.83	0.05	30	0.08	0.07
2012	10	0.65	0.02	30	0.22	0.07
Total	268	0.81	0.02	572	0.41	0.06

^aTotal number of reproductive females.

^bTotal number of territorial females checked for fledging status.

^cNo females reproduced in 2006.

Table 8. Top-ranked models (within 3.0 QAIC_c units of top model) for estimation of apparent survival (ϕ) of territorial male and female California spotted owls in the Eldorado Density and Regional Study Areas, 1990–2011, in the central Sierra Nevada, California. We used age (adult or subadult), sex, the interaction between age and sex, and a categorical time effect as covariates to model the recapture rate.

<u>Model^a</u>	<u>K^b</u>	<u>QAIC_c</u>	<u>ΔQAIC_c</u>	<u>Akaike Weight</u>	<u>Deviance</u>
ϕ (S1 + sex)	28	1942.97	0.00	0.076	1121.94
ϕ (sex)	27	1943.36	0.39	0.063	1124.41
ϕ (A + sex)	28	1944.05	1.08	0.044	1123.02
ϕ (S1)	27	1944.11	1.14	0.043	1125.16
ϕ (S1 + sex + T)	29	1944.32	1.35	0.039	1121.21
ϕ (sex + T)	28	1944.65	1.68	0.033	1123.62
ϕ (.)	26	1944.82	1.86	0.030	1127.95
ϕ (S1 + sex + lnT)	29	1944.90	1.93	0.029	1121.78
ϕ (age + sex)	29	1945.04	2.07	0.027	1121.92
ϕ (S1*sex)	29	1945.05	2.08	0.027	1121.93
ϕ (S1 + sex + TT)	30	1945.08	2.11	0.027	1119.88
ϕ (A)	27	1945.24	2.28	0.024	1126.29
ϕ (sex + lnT)	28	1945.26	2.29	0.024	1124.23
ϕ (sex + TT)	28	1945.37	2.40	0.023	1122.25
ϕ (A + sex + T)	29	1945.39	2.42	0.023	1122.27
ϕ (S1 + T)	28	1945.45	2.48	0.022	1124.42
ϕ (S1*T + sex)	30	1945.81	2.84	0.018	1120.60
ϕ (S1*lnT + sex)	30	1945.87	2.90	0.018	1120.66
ϕ (A + sex + lnT)	29	1945.97	3.00	0.017	1122.85

^aExplanation of model abbreviations:

S1 = 2 age classes (1st-year subadults, other).

A = 2 age classes (adults, other).

age = 3 age classes (1st-year subadults, 2nd-year subadults, adults).

t = categorical time effect (i.e., different parameter for each year).

T = linear time trend.

lnT = log-linear time trend.

TT = quadratic time trend.

^bNumber of estimable parameters.

Table 9. Model selection results from analysis of population rate of change using a modified data set for California spotted owls on the Eldorado Density Study Area, 1992–2010, in the central Sierra Nevada, California. Survival (ϕ) and recapture rate (p) were estimated using a fixed, categorical time effect. $\lambda(t)$ was modeled as a random factor under different temporal trends.

<u>Model</u>	<u>K^a</u>	<u>QAIC_c</u>	<u>ΔQAIC_c</u>	<u>Akaike Weight</u>	<u>Deviance</u>
{ $\phi_t, p_t, \lambda_{\text{log-linear random effects}}$ }	48.0	3005.00	0.00	0.68	841.85
{ $\phi_t, p_t, \lambda_{\text{quadratic random effects}}$ }	52.7	3007.83	2.83	0.17	834.27
{ $\phi_t, p_t, \lambda_{\text{linear random effects}}$ }	53.6	3008.50	3.50	0.12	833.02
{ $\phi_t, p_t, \lambda_{\text{mean random effects}}$ }	56.3	3011.21	6.21	0.03	829.74

^aNumber of estimable parameters.

Figure 1. Percent of surveyed territories that were occupied by California spotted owls on the Eldorado Density Study Area, 1990–2012, in the central Sierra Nevada, California.

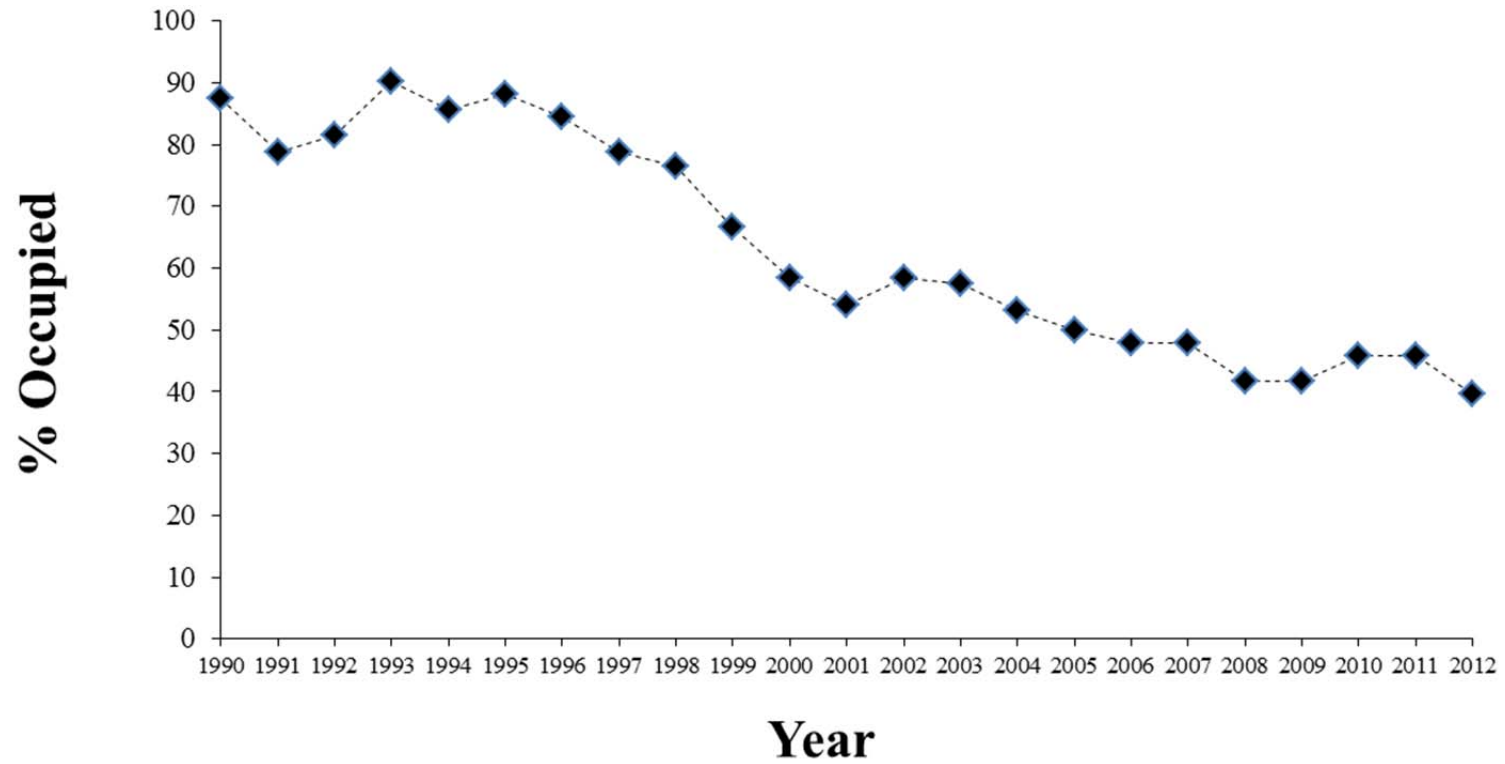


Figure 2. Proportion of subadult California spotted owls within the population of territorial birds on the Eldorado Density and Regional Study Areas, 1990–2012, in the central Sierra Nevada, California.

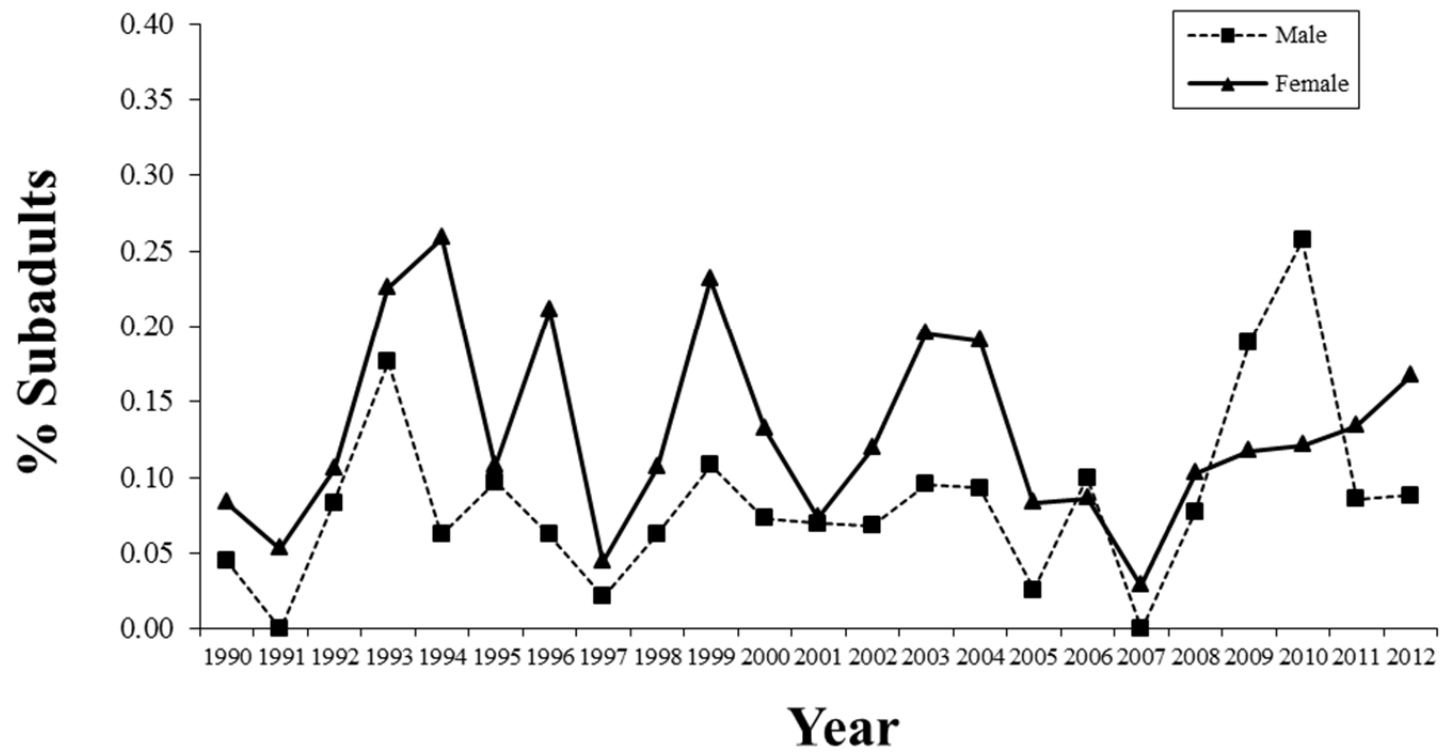


Figure 3. Annual fecundity (# female young per territorial female) of California spotted owls on the Eldorado Density and Regional Study Areas, 1991–2012, in the central Sierra Nevada, California. Error bars represent ± 1 standard error. The solid line indicates the best-fit quadratic time trend.

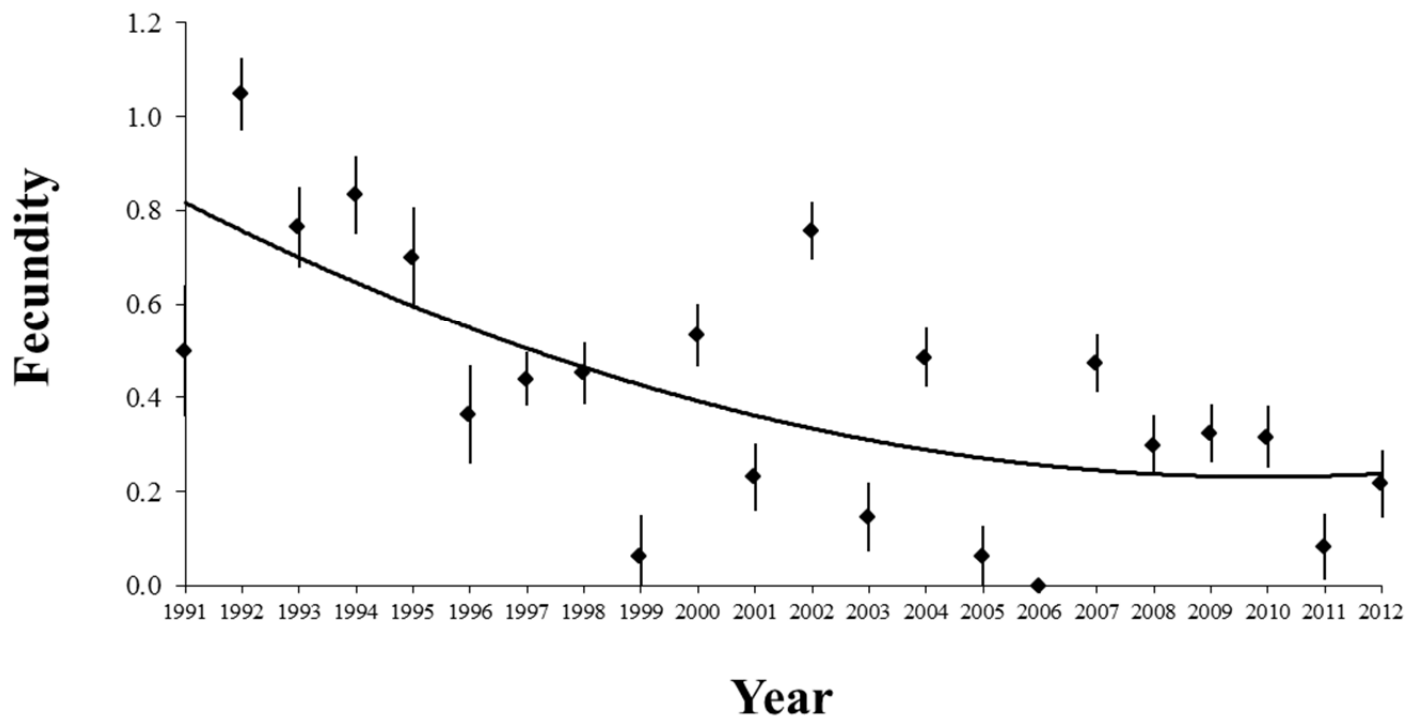


Figure 4. Annual estimates of California spotted owl survival (ϕ_t) on the combined Eldorado Density and Regional Study Areas in the central Sierra Nevada, 1992–2010, using a random-effects means model for $\{\phi(t), p(A*s+t)\}$. Juvenile owls were not included in the analysis. Error bars represent ± 1 standard error. Average survival over the study period ($\phi = 0.823$) is indicated by the horizontal line. The first two and the last estimates of ϕ_t are not included because they were confounded with estimation of p_t .

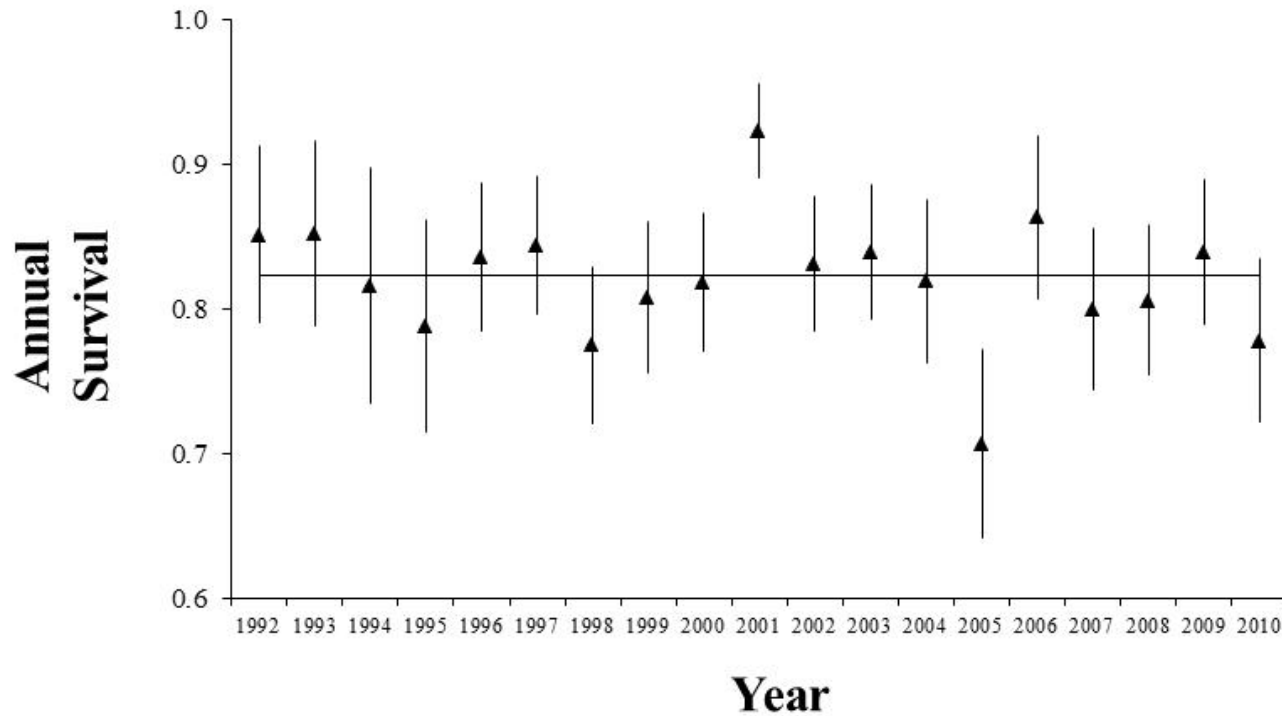


Figure 5. Annual estimates of California spotted owl population rate of change (λ_t) on the Eldorado Density Study Area in the central Sierra Nevada, 1992–2010, using the random-effects means model. Error bars represent ± 1 standard error. Population rate of change for a hypothetical stable population ($\lambda = 1.00$) is indicated by the horizontal line. The most recent annual value (λ_{2011}) could not be estimated because it was confounded with p_t .

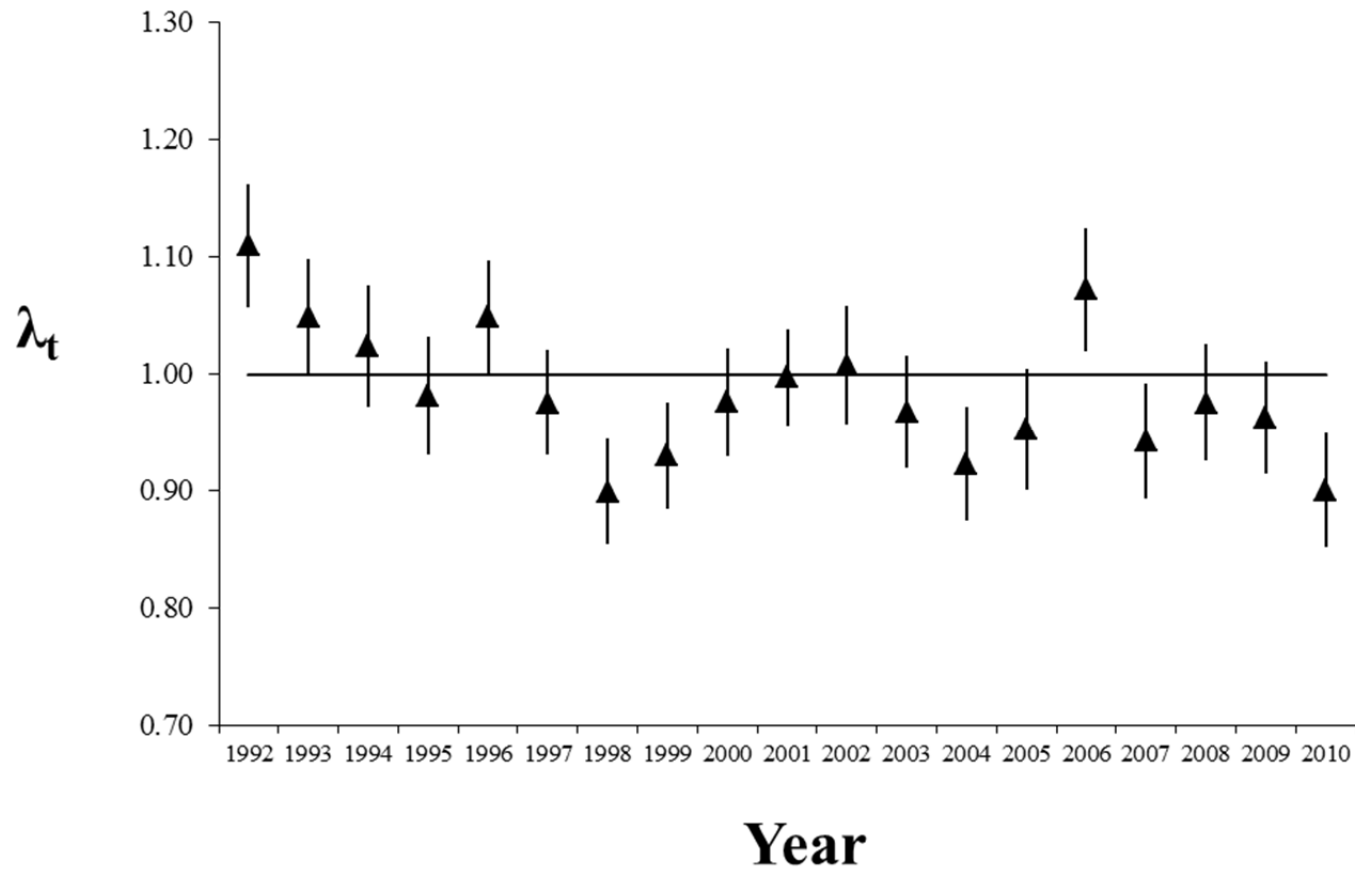


Figure 6. Realized population change on the Eldorado Density Study Area in the central Sierra Nevada, 1992-2011, using the random-effects means model. Realized change is the proportion of the initial population size remaining each year. Error bars represent the 95% confidence intervals. Population rate of change for a hypothetical stable population ($\lambda = 1.00$) is indicated by the horizontal line.

