

**Demography of the California Spotted Owl in the Sierra Nevada:
Report to the U.S. Fish and Wildlife Service on the January 2006 Meta-Analysis**

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EXECUTIVE SUMMARY

The primary population of the California spotted owl (*Strix occidentalis occidentalis*) occurs in the Sierra Nevada and southern Cascade mountains of California. This subspecies is currently under review for listing under the Endangered Species Act by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2005). Spotted owl researchers and analysts met in Logan, Utah in January 2006 to conduct a meta-analysis of spotted owl demographic data collected from 1990-2005 on four study areas in the Sierra Nevada and southern Cascades. The intended purpose of this report is to provide results of the meta-analysis relevant to the U.S. Fish and Wildlife Service listing decision.

We followed a formal protocol for discussions and analyses at the meta-analysis workshop similar to the protocol followed during the 2001 California spotted owl meta-analysis (Anderson et al. 1999, Franklin et al. 2004). During the first days of the meta-analysis workshop, we agreed on the analyses that we would conduct, and wrote detailed protocols for analyses, including identification and parameterization of *a priori* model sets. There were several analytical and methodological differences between the 2001 meta-analysis (Franklin et al. 2004) and the 2006 meta-analysis (this report). In most cases these changes represented additional analyses which were not previously conducted.

Our four study areas (from north to south) were on the Lassen National Forest (LAS), Eldorado National Forest (ELD), Sierra National Forest (SIE), and Sequoia and Kings Canyon National Parks (SKC). The majority of all study areas was on public land, but the LAS, ELD, and SKC study areas included some private land.

We estimated apparent survival probability, reproductive output, and rate of population change for spotted owls on individual study areas and for all study areas combined (true meta-analysis). We estimated the effect of male and female age-class on reproductive output in a meta-analysis. We also estimated recruitment rate (the number of new individuals in year $t + 1$ per individual in the population in year t) using temporal symmetry models. At the request of the U.S. Fish and Wildlife Service, we conducted an empirically-based population viability analysis (PVA).

We used 991 marked spotted owls in the analysis of apparent survival. Apparent survival probability was higher for adult than for subadult owls. There was little difference in survival between male and female owl except at ELD, where survival was higher for males than for

females. Survival increased over time for owls of all age classes at LAS and SIE, for adults at ELD, and for second-year subadults and adults at SKC. The meta-analysis of survival included only adult owls, and confirmed the increasing trend in survival over time and that survival rates were higher for owls on SKC than the other study areas. Mean estimates of apparent survival probability of adult owls from individual study area analyses were 0.849 for males and 0.803 for females at ELD; 0.844 at LAS; 0.850 at SIE; and 0.888 at SKC (sexes combined for LAS, SIE, and SKC).

Recapture (resighting) probability was a function of “walk-in” survey effort at ELD, and reproductive effort at SKC, with some evidence of an effect of reproductive effort at LAS and SIE. In the meta-analysis of adult survival, the best approximating model indicated recapture probability increased with reproductive output.

We analyzed data from 1,865 observations of reproductive outcomes for female spotted owls. The proportion of subadult females among all territorial females of known age ranged from 0.00 to 0.25 among study areas and years. The proportion of subadults among female spotted owls had a strong negative effect on reproductive output for ELD and SIE. ELD and LAS had showed an even-odd year trend in reproductive output, with higher output in even-numbered years. ELD also exhibited a declining trend in reproductive output over time. Reproductive output estimates varied widely among study areas; the mean point estimate of annual reproductive output for the ELD was more than twice that of the SIE. The ELD also exhibited the greatest temporal variation in reproductive output, while SIE and SKC, which had the lowest reproductive output, had the lowest temporal variation. Mean annual reproductive output was 0.494 for ELD, 0.312 for LAS, 0.239 for SIE, and 0.278 for SKC. Meta-analysis confirmed that reproductive output varied among study areas.

Reproductive output varied by age class for both sexes. Reproductive output was highest for adults, followed by second year subadults, and then by first year subadults.

We used 842 marked subadult and adult owls in the analysis of population change. Modeling indicated λ_t was either relatively stationary, as for LAS and SIE, or increasing after an initial decrease, as for ELD and SKC. Mean estimated λ_t for the four study areas was: 1.007 (95% CI = 0.952 to 1.066) for ELD; 0.973 (95% CI = 0.946 to 1.001) for LAS; 0.992 (95% CI = 0.966 to 1.018) for SIE; and 1.006 (95% CI = 0.947 to 1.068) for SKC. The best meta-analysis

model of population trend indicated that λ varied across time but was similar in trend among the study areas.

Estimates of realized population change were based on the estimates of λ_t from individual study areas and did not require estimating annual population size for each study area. The trends represent the proportion of the population size remaining each year, given the population size in the first year. For example, if there were 100 owls on the LAS study area in 1992 there would be 69 owls in 2004, based on the estimates of λ_t . Similarly, there would be 127 owls on ELD in 2004, 95 on SIE in 2004, and 113 on SKC in 2003 (the last year for which realized change was estimable).

The best model of recruitment indicated recruitment rate varied by time in a similar manner among study areas. Recruitment varied from 0.10 to 0.31 new individuals in year $t + 1$ per individual in the population in year t .

Population viability analyses (PVA) were of limited utility for the ELD and SKC study areas because 95% confidence intervals on the probability of decline or increase spanned the interval [0, 1] within 5-10 years. Restricting inferences to 7 years, the estimated probability of a >10% decline for SIE was 0.41 (95% CI = 0.09 to 0.78); for LAS the probability was 0.64 (95% CI = 0.27 to 0.94). In contrast, the estimated probability of a >10% increase in 7 years for SIE was 0.23 (95% CI = 0.01 to 0.55); for LAS the probability was 0.10 (95% CI = 0.00 to 0.34). For comparisons, we simulated a PVA for a hypothetical population with mean $\lambda = 1.0$, and the same temporal variation observed in our owl populations.

Our analyses represent the most current and comprehensive summary of trends in California spotted owl populations.

INTRODUCTION

The California spotted owl has a very large range; however, its primary population resides within the Sierra Nevada ecosystem (Gutiérrez et al. 1995, Franklin et al. 2004). Spotted owls are distributed as a contiguous population over the length of the Sierra Nevada and into the southern Cascade Mountains (Verner et al. 1992, Gutiérrez and Barrowclough 2005). The geographic range of this subspecies (and three of the study areas reported on herein) is predominantly on the western slope of the Sierra Nevada within a zone dominated by conifer forests (Verner et al. 1992). Although the fourth study area is in the southern Cascade

Mountains, vegetation communities are similar to those of the Sierra Nevada and land management is subject to the same guidelines as the other study areas (U.S. Forest Service 2004). Most land within the geographic range of the California spotted owl in the Sierra Nevada and southern Cascade Mountains is publicly held and managed. Public agencies responsible for managing spotted owl habitat in the Sierra Nevada are the U.S. Forest Service, Bureau of Land Management, National Park Service, and the State of California (listed in decreasing order of owl habitat area; SNEP 1996). There are also large tracts of private industrial timber land within the range of the California spotted owl.

Because its distribution, the California spotted owl is emerging as a central species of concern in the debate over future management of Sierra Nevada forests (U.S. Forest Service 2004). Moreover, this is the only spotted owl subspecies that has not received federal protection under the endangered species act (Gutiérrez et al. 1995). The U.S. Fish and Wildlife Service denied a petition to list the subspecies in 2003 (U.S. Fish and Wildlife Service 2003), but it has undertaken a second status review (U.S. Fish and Wildlife Service 2005). Such status reviews are the legacy of 15 years of owl status evaluations, EIS reports, and population analyses (Verner et al. 1992, U.S. Forest Service 1993, 1996, Federal Advisory Committee 1997, Franklin et al. 2004), which have not resolved the future management strategies for spotted owls and Sierra Nevada Forests to the satisfaction of stakeholders.

The inability to resolve the direction of management for Sierra Nevada forests, at least with respect to the spotted owl, has been partly due the uncertainty surrounding the owl's habitat requirements, its apparent broad use of forests in the Sierra Nevada, the uncertainty of its population trends, and the uncertainty of habitat trends under projected management regimes proposed for the Sierra Nevada (Verner et al. 1992, Federal Advisory Committee 1997, Franklin et al. 2004). Verner et al. (1992) first recognized many of these uncertainties, and proposed an interim management strategy (hereafter called CASPO) for the California spotted owl throughout its United States range. However, the focus for CASPO was primarily the forests of the Sierra Nevada because that is where most of the projected timber harvesting that had the potential to impact the owl would occur in the future. Moreover, CASPO was an interim strategy with the understanding that future research would be conducted that would clarify key areas of uncertainty about the biology of the owl. Many of the recommendations by CASPO for removing uncertainties remain unfulfilled. Yet, substantial progress has been made in some key

areas of habitat selection, population dynamics, and population genetics (Barrowclough et al. 1999, 2005, North et al. 2000, Blakesley et al. 2001, Seamans et al. 2001, Hunsaker et al. 2002, Franklin et al. 2004, Gutiérrez and Barrowclough 2005, Blakesley et al. 2005, 2006, Chatfield 2005, Seamans 2005).

A key analysis of California spotted owl population dynamics was a meta-analysis conducted in 2001 that covered data collected through the 2000 spotted owl field seasons (Franklin et al. 2004). Because of the impending listing decision by the U.S. Fish and Wildlife Service, scientists working with the California spotted owl were asked in 2005 to analyze population data gathered subsequent to the previous meta-analysis, in a second meta-analysis conducted in January 2006. Thus, this report presents results of the 2006 meta-analysis of California spotted owl population data gathered through 2005 in the southern Cascades and Sierra Nevada, California. The intended purpose of this report is to provide relevant information for the U.S. Fish and Wildlife Service listing decision.

We consider this a preliminary report whose primary focus is the analyses and inferences that resulted from the analyses of California spotted owl population data in January, 2006. We accelerated the creation of this report far beyond a normal production schedule. The reader should be aware there was insufficient time to fully develop the discussion and include all relevant literature. However, we affirm the validity of the analytical approach, the results, and the inferences derived from the results. In addition, the authors will continue to work on the refinement of this document and development of explanations and inferences related to the results.

STUDY AREAS

We studied spotted owls on four study areas in the Sierra Nevada and southern Cascade Mountains, California from 1990-2005 (Table 1). Although the Lassen study area was in the southern Cascades, it has been included in the Sierra Nevada province for management purposes (U.S. Forest Service 2004). The majority of the Lassen, Eldorado, and Sierra study areas were located on public land managed by the U.S. Forest Service whereas the Sequoia and Kings Canyon National Parks study area was in two National Parks. The study areas are described in detail in Franklin et al. (2004). A brief summary of each study area follows (ordered from north to south).

LASSEN

The Lassen study area (LAS) was located primarily on the Lassen National Forest between Mineral and Susanville, California. Elevations ranged from 1,200 to 2,100 m. The majority of forest on the study area was mixed conifer. Mixed conifer stands included white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and Jeffrey pine (*Pinus jeffreyi*). Black oak (*Quercus kelloggii*) and pacific dogwood (*Cornus nuttallii*) were present in the under-story of some stands. Red fir (*Abies magnifica*) stands occurred at higher elevations as pure stands or contained occasional white firs.

The entire Lassen study area encompassed 2,200 km². During the 2001 California spotted owl meta-analysis, we selected a subset of the study area (1,270 km²) for estimation of population rate of change, based on portions of the study area surveyed consistently during 1992–2000. Subsequent to the 2001 meta-analysis, we used a geographic information system to delineate a “core” study area similar to the boundaries drawn for the 2001 meta-analysis, based on watershed units and property ownership boundaries. We continued to study and survey for spotted owls both inside and outside the core through the field season of 2005. In the 2006 meta-analysis, data from the entire study area were used for analyses of survival and reproductive output, and data from the core area were used for estimation of population rate of change.

ELDORADO

The Eldorado study area (ELD) was located on the Eldorado National Forest, Tahoe National Forest, and adjacent private land between Georgetown and Lake Tahoe, California. The ELD consisted of a 355 km² “density” study area embedded within a 570 km² regional study area. Elevations ranged from 366 to 2,400 m. Forests were dominated by ponderosa pine on xeric sites and white fir on mesic sites (Chatfield 2005). Above 1,500 m forests were dominated by red fir. Other common tree species included sugar pine, Douglas-fir, incense cedar, canyon live oak (*Q. chrysolepis*), California black oak, pacific dogwood, and tan oak (*Lithocarpus densiflorus*).

SIERRA

The Sierra study area (SIE) was located primarily on the Sierra National Forest, 83 km east of Fresno, California. Elevations ranged from 304 to 2,924 m. The study was initiated in 1990 on a 419 km² area and expanded to 693 km² in 1994. The SIE contained three major vegetation types: low-elevation oak woodlands, mid-elevation mixed conifer forests, and high-elevation conifer forests. The oak woodland zone (304 -1,220 m) encompassed 26% of the study area and was dominated by blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), canyon live oak, and gray pine (*Pinus sabiniana*). Various foothill chaparral species were abundant. Mid-elevation mixed conifer forests (1,220-2,438 m) covered 61% of the study area and were dominated by ponderosa pine, white fir, incense cedar, black oak, Jeffery pine, red fir, and sugar pine. A small (2 km²) grove of giant sequoia (*Sequoiadendron giganteum*) was within this zone. High-elevation conifer forests (2,439-2,924 m) covered 13% of the study area and were dominated by red fir, lodgepole pine (*P. contorta*), and western white pine (*P. monticola*).

SEQUOIA AND KINGS CANYON

The Sequoia and Kings Canyon study area (SKC) encompassed 343 km², and was located in Sequoia and Kings Canyon National Parks, 35 km northeast of Visalia, California. Elevations ranged from 427 to 3,050 m. Vegetation types included low-elevation oak woodlands and dense riparian deciduous forest (24% of SKC; <1,220 m elevation), mid-elevation coniferous forests (67% of SKC; 1220-2440 m elevation), and high-elevation coniferous forests (9% of the SKC; >2,440 m elevation). Tree species within oak woodlands included blue oak, gray pine, interior live oak, canyon live oak, California sycamore (*Platanus racemosa*), California buckeye (*Aesculus californica*) and Fremont cottonwood (*Populus fremontii*). There were large areas of chaparral (primarily chamise [*Adenostoma fasciculatum*]) within the low-elevation oak-woodland. Tree species within mid-elevation conifer forests included ponderosa pine, Jeffrey pine, sugar pine, white fir, red fir, incense-cedar, and black oak. Mixed conifer forests included 10 giant sequoia groves, covering 7% of the study area (Parsons 1994). Sequoia groves were mixed conifer forests that contained giant sequoia trees, although other conifer species (e.g., white fir and sugar pine) were often more numerous (Rundel 1971). High-elevation coniferous forest tree species included red fir, lodgepole pine, and western white pine.

METHODS

FIELD METHODS

Field methods for the study of spotted owl population dynamics are well described (Forsman 1983, Franklin et al. 1996, Franklin et al. 2004). Therefore, we present a brief summary the methods that we used to survey our large study areas to locate, capture, and resight owls, and determine their reproductive status. We conducted surveys from 1 April – 31 August on ELD and LAS, and from 1 March - 30 September on SIE and SKC.

Estimation of spotted owl survival probability by mark-recapture (resight) methods requires a “capture history” for each owl, consisting of 1’s and 0’s, representing occasions (years) in which an owl was identified as alive (=1) or not identified (=0). Identification of an owl is accomplished through capture and banding or by resighting the unique color band of a previously banded owl. We followed rigorous protocols in surveying for and identifying spotted owls to meet the assumptions of mark-recapture analytical methods (Lebreton et al. 1992).

We surveyed spotted owls between dusk and dawn by vocally imitating spotted owls calls or by broadcasting recordings of spotted owl calls. We completely surveyed study areas (core area for LAS, “density” area for ELD) on ≥ 3 occasions throughout each field season. When owls were detected, we conducted walk-in surveys during daylight hours to visually locate owls, identify color bands or capture unbanded owls, determine reproductive status, and locate owl nests and roosts.

We determined spotted owl reproductive status by offering live mice to the owls and observing the fate of the mice and the owls’ behavior. Owls with active nests or fledged young usually take mice to the nest or young, whereas non-reproducing owls usually eat or cache the mice. We followed “mousing” protocols to reduce observer bias in estimation of reproductive status. We concluded that minor differences in mousing protocols among study areas would not hinder comparisons in estimated reproductive rates among study areas (see below).

META-ANALYSIS FORMAT

From 2–7 January, 2006, researchers and analysts met at Utah State University in Logan, Utah, to conduct a formal meta-analysis of all current California spotted owl population data (Appendix A). We followed a formal protocol for discussions and analyses similar to the protocol followed during the 2001 California spotted owl meta-analysis (Anderson et al. 1999,

Franklin et al. 2004). Prior to the workshop, data were checked for errors by independent observers at Utah State University who followed a formal, randomized checking procedure (Appendix B). During the first days of the meta-analysis workshop, we agreed on the analyses that we would conduct, and wrote detailed protocols for analyses, including identification and parameterization of *a priori* model sets (Appendices C-J).

METHODOLOGICAL AND ANALYTICAL DIFFERENCES FROM THE 2001 META-ANALYSIS

There were several analytical and methodological differences between the 2001 meta-analysis (Franklin et al. 2004) and the 2006 meta-analysis (this report). We discussed the advantages and disadvantages of all methodological and analytical changes in detail at the 6-day workshop. In most cases these changes represented additional analyses which were not previously conducted. Such changes allow for additional insight into the population dynamics of the owl in the Sierra Nevada. In other cases we made modifications that allowed for a more rigorous analytical approach.

We conducted a separate analysis for each study area to estimate apparent survival probabilities of subadult and adult spotted owls. We also estimated apparent survival probabilities of adult owls for all study areas combined in a meta-analysis. In contrast, apparent survival probabilities were estimated only for adult owls in a meta-analysis in 2001 (Franklin et al. 2004). Conducting a separate analysis for each study area allowed us more flexibility in modeling trends in survival and allowed additional insight into local trends in survival.

In the 2001 meta-analysis fecundity of adult territorial females was estimated, but not fecundity of subadult females (Franklin et al. 2004). In 2006, we estimated reproductive output of all territorial females, using the annual proportion of subadults in the female owl population as a covariate. We could not use the age of a female owl as a categorical effect in our models because the paucity of subadult females in some years precluded estimation of age-specific time trends. Including data from subadult females more accurately reflected reproductive output of the owl population because subadults accounted for up to 25% of the female owls within a study area in any given year (see below). In addition, for this meta-analysis we evaluated the effect of both male and female age class on reproductive output in a separate meta-analysis. For this latter analysis we used a subset of the reproductive output data for which the age of both the male and

female owls of a pair were known. [Note: Franklin et al. (2004) reported estimates of fecundity, the number of *female* offspring per territorial female owl (=1/2 of reproductive output)].

During the 2001 meta-analysis, Franklin et al. (2004) did not conduct a meta-analysis using the reproductive output data because they were uncertain about the effects of variable field methods among study areas on estimates of reproductive output. Subsequent to the 2001 meta-analysis Seamans (2005) examined some of the issues regarding the effects of using different field methods and determined that the chief difference between methods was the use of a one-visit criterion to determine non-reproduction by the ELD. For the 2006 meta-analysis we applied the two-visit criterion used on the LAS to the ELD data. Although this resulted in removing a few reproductive outcomes from the early years of the ELD dataset, we believed that the ELD reproductive output data was now comparable to the other study areas. Therefore, we used reproductive output from all the study areas in our meta-analysis.

For the 2006 meta-analysis we estimated recruitment rate (the number of new individuals in year $t + 1$ per individual in the population in year t) using a temporal symmetry approach (Pradel 1996). Estimation of study area specific recruitment rates allowed us greater insight into the dynamics of these populations. Further, examining recruitment and apparent survival for individual study areas was a natural complement to our estimation of population rate of change using the temporal symmetry models (Pradel 1996).

The methods we used to estimate survival in 2006 were similar to those we used in 2001. However, further research on estimation of the over-dispersion parameter (\hat{c}) suggested that using a global model and Program RELEASE (Burnham et al. 1987, Franklin et al 2004) likely resulted in overestimation of \hat{c} (G. White, personal communication). It appeared that including just two or three individuals that were not recaptured for more than 4 years before being recaptured in a capture history matrix for a study area greatly inflated the estimate of \hat{c} using the goodness-of-fit test in RELEASE because 1 or more of the component chi-squared tests would contribute large chi-square values. These individuals are typically the result of temporary emigration, which is a violation of the assumptions of the Cormack-Jolly-Seber (CJS) model. However, temporary emigration has little or no effect on estimates of survival because the CJS model is robust to this assumption violation. Removal of these individuals resulted in an estimate of \hat{c} near 1.0 for the RELEASE goodness-of-fit test. Therefore, in 2006 we used a new method to estimate over-dispersion termed “median \hat{c} ” available in Program MARK (White and

Burnham 1999). This method simulates datasets over a range of over-dispersion levels and compares the observed deviance estimate of \hat{c} (deviance divided by degrees of freedom) to that of the deviance \hat{c} from the simulations. This method appeared to result in more reasonable estimates of \hat{c} .

Lastly, at the request of the U.S. Fish and Wildlife Service we conducted an empirically-based population viability analysis (PVA). The PVA used parameter estimates generated from our analyses. We used the PVA developed by White et al. (2002) which generates statistically rigorous estimates based on empirical data, and the conclusions about change are based on the best available data.

DATA ANALYSIS

Survival on individual study areas

We used capture histories of non-juvenile spotted owls to estimate apparent survival (ϕ) and recapture (p) probabilities using open population Cormack-Jolly-Seber models (Lebreton et al. 1992) in Program MARK (White and Burnham 1999). In general we followed methods outlined in Franklin et al. (2004). We used an information-theoretic approach (Burnham and Anderson 2002) to rank competing models (see below and Appendix C). For each study area, we determined goodness-of-fit of the global model $\{\phi(a*s*t), p(a*s*t)\}$ or $\{\phi(s*t), p(s*t)\}$ by estimating median \hat{c} using a simulation procedure in Program MARK. We simulated data sets over a range of overdispersion levels and compared the deviance divided by degrees of freedom from these simulations with the observed deviance divided by degrees of freedom. We simulated 10 data sets at each of 6 levels of overdispersion (c) and estimated via logistic regression the value of c ($= \hat{c}$) where half of the simulated data sets would have deviance divided by degrees of freedom greater than the observed value of deviance divided by degrees of freedom. When median \hat{c} was >1 , we used QAIC_c for model selection and to adjust variances of parameter estimates (Burnham and Anderson 2002).

We developed a set of *a priori* models for estimating apparent survival and recapture probabilities based on results of previous spotted owl meta-analyses (Franklin et al. 2004, Anthony et al. 2004) and established a protocol for model development (Appendix C). Of primary interest were the main effects of age, sex, and time, and interactions between the main effects on spotted owl survival. We also modeled the effects of age, sex, time, survey effort, and

annual reproductive rate on recapture probability. Although estimates of recapture probability were not of primary interest, proper modeling of recapture probability provides more precise estimation of survival probability. To account for model-selection uncertainty we used a model averaging approach to calculate point estimates of survival and their sampling variation (Burnham and Anderson 2002).

In addition to modeling the three non-juvenile age classes of spotted owls separately, we modeled survival of subadults separate from adults ($S1 = S2, A$), and first-year subadults separate from older age classes ($S1, S2 = A$). We modeled time as a categorical effect (t), a linear trend (T), a quadratic trend (TT), and as a log linear (“pseudo threshold”) trend ($\ln T$).

Meta-analysis of survival

We conducted a meta-analysis of survival using the capture histories of adult owls only (including adult portions of capture histories for owls first captured as juveniles or subadults). We followed procedures similar to those described above for estimation of survival on individual study areas (Appendix D). In the meta-analysis, the global model was $\{\phi(g*s*t) p(g*s*t)\}$, where g indicates a study area (or “group”) effect.

In addition to modeling the categorical effect of the four study areas on survival, we also modeled ϕ for the SKC study area separately from the other study areas, based on results of Franklin et al. (2004). We did not include in our *a priori* model set any models of ϕ that had a separate effect for SKC in combination with time effects. We also did not include in our *a priori* model set any models of p that had an interaction between study area and annual reproductive rate (r), despite having included similar but less parsimonious models that had an interaction between study area and year rate ($\{p(g*t)\}$). Upon viewing the ranking of our *a priori* models, we discovered that the top six models included both study area and time effects on ϕ , and study area * year effects on p . We agreed at that juncture to include eight additional post-hoc models incorporating $\{\phi(\text{SKC} + t)\}$, and $\{p(g*r)\}$, and adding sex effects to the top *a priori* models.

Reproductive output on individual study areas

We estimated reproductive output (the number of young fledged per territorial female owl) for all female owls ≥ 1 year-old. The input data used in these analyses consisted of the number of young fledged per female on a particular site (0, 1, 2, and less commonly, 3), the site

(territory) where the young were detected, the year, the age class of the female (S1, S2, adult), and the age class of the male (if present). For each study area in each year, we determined the proportion of subadults among all territorial female owls of known age for which reproductive output was determined. We used the resulting proportion (“*p_{sub}*”) as a covariate in modeling reproductive output for female owls of all ages (including those of unknown age).

We used mixed model analysis of variance (Proc MIXED in Program SAS, Littell et al. 1996, Rao 1997) to estimate spotted owl reproductive output for individual study areas. Site (owl territory) and year (as a categorical variable) were included as random effects. We used mixed models because: (1) individuals and territories were confounded over time because the same females often bred on the same territory for >1 year; this lack of independence would underestimate standard errors if methods assuming independence were used (Franklin et al. 1999); (2) modeling could be conducted in a maximum-likelihood framework; (3) inference was made to years rather than to separate outcomes/year by adjustments of the standard errors; (4) the error covariance matrix could be structured appropriately; and (5) models allowed for unbalanced designs (i.e., missing data).

Analysis of northern spotted owl fecundity data showed that the variation in the number fledged within a year was proportional to the mean, suggesting a Poisson distribution (Evans et al. 1993) although the data were not distributed as Poisson (Franklin et al. 1999, Franklin et al. 2000). In analyzing these data for the California spotted owl using mixed models, we again relied on sample sizes being sufficiently large to justify normal distributional assumptions. Because reliance on this assumption was criticized in the last meta-analysis of California spotted owl data, we used simulations to examine the effect of using estimators based on normal and Poisson distributions on data distributed in the same manner as the reproductive output data from California spotted owls. The results from these simulations indicated that normal-based models were: (1) robust to severe departures from normality similar to results reported by White and Bennetts (1996); and (2) more robust to data from the discrete distributions exhibited by the California spotted owl data than Poisson regression. Therefore, we relied on the robustness of mixed models to non-normally distributed data, rather than relying on Poisson regression to analyze the reproductive output data. The mixed model procedures also allowed us to account for this dependence of sampling variation on the mean (see below). As with previous analyses

(Franklin et al. 1999), we did not separate individual bird effects from territory effects because of the longevity of most individual females on territories.

We first modeled the variance-covariance structure for each study area using the restricted maximum likelihood method (REML), with a linear time trend structure for fixed effects. The variance-covariance structures modeled were: first-order autoregressive (AR[1]); heterogeneous autoregressive (ARH[1]); log-linear variance (LOCAL=EXP[<fixed year effects>]); AR(1) with EXP(YEAR); compound symmetric (CS); compound symmetric heterogeneous (CSH); Toeplitz (TOEP); and a heterogeneous Toeplitz with estimates for the first 2 off-diagonal bands (TOEPH[3]; Littell et al. 1996). We selected the most appropriate variance-covariance structure using AIC_c model selection. We used the top ranked variance-covariance structure for subsequent modeling of fixed effects.

We modeled reproductive output on each study area as a function of time effects: no trend (intercept-only), linear (*T*), quadratic (*TT*), pseudo-threshold or log-linear (*lnT*), Even-Odd year effect (*EO*), and Even-Odd year with a linear time trend (*EO + T*). We considered each time structure on the fixed effects, with and without the subadult covariate, as a competing model (Appendix E); we ranked models using AIC_c.

We estimated temporal process variation ($\sigma_{\text{temporal}}^2$; Franklin et al. 2000) using an intercept only model and the residual variation not explained by the selected fixed-effects model with the best covariance structure ($\hat{\sigma}_{\text{model residual}}$). We estimated the proportion of $\sigma_{\text{temporal}}^2$ in our data explained by our top-ranked model as:

$$1 - \frac{\hat{\sigma}_{\text{model residual}}}{\hat{\sigma}_{\text{temporal}}}$$

Meta-analysis of reproductive output

The meta-analysis of reproductive output followed the procedures described above for individual study areas. The *a priori* model set included the time effects modeled for individual study areas as well as a study area effect and interactions between study area and time effects (Appendix F). We explicitly modeled separate effects for the northern two study areas (LAS and ELD) versus the southern two study areas (SIE and SKC), and a separate effect for the SKC area versus the other study areas.

Effect of male and female age-class on reproductive output

Following the meta-analysis of reproductive output, we estimated the effects of both female and male age on reproductive output using a subset of the data for which age class of both the female and male owl were known. We included both male and female age effects in the best model from the meta-analysis (Appendix G). We first used AIC_c to compare the effect of three age-structures of female owl on reproductive output, and three age structures for males: (1) S1, S2, A; (2) S1 = S2, A; and (3) S1, S2 = A. We then combined the top age structure for females with the top age structure for males and compared this model with the age models from the first meta-analysis of reproductive output, using AIC_c .

Population change on individual study areas

We estimated the annual rate of population change in territorial owls (λ_t) directly from spotted owl capture histories using Pradel's temporal symmetry model (Pradel 1996, Nichols and Hines 2002, Franklin et al. 2004) in Program MARK. We estimated median \hat{c} using the simulation procedure in Program MARK under the Cormack-Jolly-Seber global model $\{\phi(s^*t) p(s^*t)\}$. When median \hat{c} was >1 , we used QAIC_c for model selection and to adjust variances of parameter estimates. Our *a priori* model set allowed λ , ϕ , and p to vary as functions of sex and time (Appendix H). Using the best fixed effects model from this set for each study area, we constructed four random effects models, structuring λ as a linear trend, quadratic trend, pseudo-threshold, and constant. We did not include the first and last estimates of λ because these were confounded with estimation of p . We modeled λ for the SIE while allowing for an expansion of the study area in 1994. Appendix H explains in detail how we parameterized the SIE model to include this expansion without loss of estimates for the expansion interval. We estimated $\bar{\lambda}$, $SE(\bar{\lambda})$, and $\hat{\sigma}^2_{\text{temporal}}$ on the log scale, and used the delta method to estimate the variance of the back-transformed $\bar{\lambda}$.

We estimated realized population change (Δ_t ; Franklin et al. 2004) as the product: $1 \times \hat{\lambda}_3 \times \hat{\lambda}_4 \times \dots \times \hat{\lambda}_{k-1}$. We used the delta method to estimate the variance of realized change (on the natural log scale) and the associated back-transformed confidence intervals.

Meta-analysis of population change

We evaluated the similarity in population rate of change across study areas by modeling λ , ϕ , and p as functions of time and study area, including one model that estimated λ for SKC separately from the other study areas (Appendix I). We evaluated the contributions of survival and recruitment (f) to population change for territorial owls across study areas by modeling ϕ , p , and f as functions of time and study area (Appendix I).

Meta-analysis of recruitment

We estimated recruitment (the number of new territorial individuals at time t per number of territorial individuals at time $t - 1$) using the same temporal symmetry models we used to estimate λ (Pradel 1996). We developed a set of *a priori* models that included study area (g) and categorical time effects (t ; Appendix I). We ranked models using AIC_c .

Population Viability Analysis

From the λ_t models for each study area we obtained estimates of the mean $\log(\lambda)$ [$\overline{\log(\lambda)}$] and associated SE along with the estimated temporal process variance of the λ_i across years ($\hat{\sigma}_{\text{temporal}}^2$). We computed the probability of a population decline following White et al. (2002), where the probability of decline is computed as the exponential of the sum of values of $\log(\lambda_i)$, for a given number of years i , $i = 2, 3, \dots, 20$. The $\log(\lambda_i)$ values are selected via a parametric bootstrap based on the estimates of the mean $\log(\lambda)$ [$\overline{\log(\lambda)}$] and its associated $\hat{\sigma}_{\text{temporal}}$. We used the distribution of $\log(\lambda)$ instead of λ because $\log(\lambda)$ is more likely normally distributed than λ . We performed 8,000 simulations for each time interval (e.g., 2 years, 3 years, etc.) and estimated the probability of observing $>10\%$, $>20\%$, and $>30\%$ declines, and $>10\%$, $>20\%$, and $>30\%$ increases in population size for 2–20-year time intervals. For example, the probability of observing a decline $\geq 10\%$ was the number of $\lambda < 0.90$, divided by the number of simulations. For comparison, we also modeled the probability of observing $>10\%$, $>20\%$, and $>30\%$ declines, and $>10\%$, $>20\%$, and $>30\%$ increases in population size for a hypothetical population with mean $\lambda = 1.0$ ($\overline{\log(\lambda)} = 0$), and $\hat{\sigma}_{\text{temporal}}^2$ equivalent to that estimated from our spotted owl studies.

We computed 95% confidence intervals on the probabilities of decline or increase based on White et al. (2002) with a parametric bootstrap approach suggested by James Baldwin (USDA-Forest Service, Pacific Southwest Research Station, personal communication). This approach considered $\overline{\log(\lambda)}$ from each study area modeled with a normal distribution possessing the estimated mean and with standard deviation equal to its associated standard error. The other parameter estimate with sampling variance was $\hat{\sigma}_{\text{temporal}}$. We modeled the sampling uncertainty of the process variance as a multiple of a χ^2 distribution as follows: $\frac{df \cdot \hat{\sigma}_{\text{temporal}}^2}{\sigma_{\text{temporal}}^2} \sim \chi_{df}^2$. We used $df = 7$ to approximate the estimated confidence interval of $\hat{\sigma}_{\text{temporal}}$. To account for this modeled sampling variation, we bootstrapped 1,000 values of the sum of $\overline{\log(\lambda)}$ and $\hat{\sigma}_{\text{temporal}}$ for each of the scenarios $k = 2, 3, \dots, 20$ years. Each of the bootstrapped pairs of $\overline{\log(\lambda)}$ and $\hat{\sigma}_{\text{temporal}}$ in turn were used in the estimation procedure described by White et al. (2002) and given above to obtain 95% confidence intervals on the probability of decline. The 95% confidence intervals were computed as 2.5 and 97.5 percentile values from the 1000 bootstrapped values.

RESULTS

Survival on individual study areas

We used 991 marked spotted owls in the analysis of apparent survival (Table 1). The median \hat{c} ranged from 1.03 to 1.14 (Table 2), suggesting some overdispersion but no serious lack of fit. For each study area we adjusted all estimated standard errors and model selection parameter estimates by study area specific estimates of \hat{c} , and increased the number of parameters in each model by one to account for estimation of \hat{c} . There were some differences in apparent survival by age class; for each study area $\geq 75\%$ of top models within 1 ΔQAIC_c unit of the top model had age effects (Table 2); adult apparent survival was slightly higher than S1 and S2 classes (Table 3). There was little difference in survival between males and females. Only ELD had a sex effect in the top models; males had slightly higher survival rates (0.849) than females (0.803), but the 95% confidence intervals overlapped (Table 3). Appendix K contains complete model selection results for the four study areas.

There was evidence of temporal trends in apparent survival estimates; temporal trends were in the top model for two study areas and in closely competing models ($\Delta\text{QAIC}_c < 0.32$) for the other two study areas (Table 4). The strongest temporal effects for all study areas appeared as linear trends. The direction of the trend was positive (increasing over time) for all age classes at LAS and SIE, for adults at ELD, and for second-year subadults and adults at SKC. The direction of the trend was negative for all subadults at ELD and first year subadults at SKC. However, the 95% confidence intervals overlapped zero for all $\hat{\beta}_T$ except at LAS (Table 4).

There was no consistent pattern to resighting effects among study areas; except that sex was an important effect for three of the four study areas. Survey effort and sex were important at ELD; age, sex, and annual reproductive rate were important at LAS; age and sex were important at SIE; and annual reproductive rate was important at SKC (Table 2).

Meta-analysis of survival

Extra-binomial variation was not severe for these data; $\hat{c} = 1.1$ was used in the analysis of the 38 models in the *a priori* set. Table 5 lists the complete model selection results, including the post-hoc models. The top model included separate estimates of ϕ for SKC versus the other study areas, and a quadratic time trend. The top model had 73% of the model weight, and was 3 QAIC_c units better than the second ranked model (Table 5).

Estimates of apparent survival increased with time, based on the top model (Fig. 1). An increase in survival with time was also suggested by the model averaged estimates from the 38 *a priori* models (Fig. 2). Confidence intervals for one of the coefficient estimates for the quadratic time component in the top model slightly overlapped zero ($\hat{\beta}_T = -0.086$, $\text{SE} = 0.061$, 95% CI = -0.206 to 0.035 ; $\hat{\beta}_{TT} = 0.885$, $\text{SE} = 0.416$, 95% CI = 0.070 to 1.700).

Sex was not an important factor in modeling either survival (ϕ) or resighting probabilities (p). Our conclusion was based on several pieces of evidence. First, none of the top models included sex as a predictor of either ϕ or p . Second, models that did include a sex effect tended to rank lower than corresponding models without a sex effect. Third, in the post-hoc analysis, we built models in which sex was added to the top *a priori* models, and again the improvement was negligible.

None of the 38 *a priori* models included a sex by reproductive output interaction in modeling recapture probability (p). However, when this model was considered post hoc, the much reduced number of parameters in this model compared to the $g*t$ parameterization resulted in the minimum QAIC_c post hoc model. Recapture probability increased with reproductive output on each study area (Fig. 3).

Reproductive output on individual study areas

We analyzed data from 1,865 observations of reproductive outcomes for female spotted owls on all four study areas. The proportion of subadult females among all territorial females of known age ranged from 0.00 to 0.25 among study areas and years (Table 6). The best covariance structure for three of the four study areas was CSH, while TOEPH(3) was the best for LAS (Table 7). These covariance structures were similar and allowed heterogeneity in year to year variance of reproductive output. Subsequent analyses incorporated the best covariance structure for each study area.

The more northern study areas (ELD and LAS) had strong support for an even-odd year effect with *EO* models accounting for >97% of Akaike weights (Table 8, Fig. 4). There was moderate support for the *EO* model for SIE; *EO + psub* was the top model and *EO + T + psub* was the third best model; together they accounted for 38% of the Akaike weights (Table 8, Fig. 4). SKC had the least support for the *EO* effect; the top model was the intercept only model, but *EO* was the second-ranked model, with $\Delta\text{AIC}_c = 0.508$ (Table 8, Fig. 4). The even-odd year effect was similar in magnitude for ELD and LAS and was synchronous among all study areas, with higher reproductive output in even-numbered years (Table 9, Fig. 4). In addition to the even-odd year effect, the ELD also had a negative temporal trend in reproductive output (Table 9).

The proportion of subadults among female spotted owls (*psub*) had a strong negative effect on reproductive output for ELD and SIE, appearing in the top models with 95% CI of coefficients that did not overlap 0 (Table 8). There was weak support for models including *psub* for LAS and SKC.

Reproductive output estimates varied widely among study areas; the mean point estimate of annual reproductive output for the ELD was more than twice that of the SIE (Table 10). The

ELD also exhibited the greatest temporal variation in reproductive output, while SIE and SKC, which had the lowest reproductive output, had the lowest temporal variation.

Meta-analysis of reproduction time trends

The best error covariance structure for the meta-analysis of reproductive output was the TOEPH(3) (Tables 11-12). For both the general reproductive output analysis and the analysis of male and female age effects, this covariance structure was strongly supported, based on Akaike weights. Therefore, we used this covariance structure for all subsequent analyses.

In the meta-analysis of reproductive output, model $\{\text{area} * T + psub\}$ was selected as the best approximating model with an Akaike weight of 0.935 (Table 13) indicating there was very strong support for this model within the set of models examined. However, confidence intervals of parameter estimates from this model tended to include zero (Table 14), except for the ELD study area. Although this model explained only 11.1% of the temporal variation in the data, model $\{\text{area} * T + psub\}$ suggested that the study areas varied differently in reproductive output over time and that the proportion of subadults in the sampled populations affected annual estimates of reproductive output over time (Fig. 5). Ninety-five percent confidence intervals on time trend coefficients in the best model overlapped zero for all study areas except ELD. Because models with additive time trend effects were not well supported, this suggested that: (1) temporal trends in reproductive output were different among the study areas; and (2) reproductive output may have been affected by different factors among the study areas. However, the selected model explained only a small amount of the temporal variation in reproductive output among the study areas.

Effect of male and female age class on reproductive output

To examine the effects of male and female age class on reproductive output, we used model $\{\text{area} * T\}$ as the base model rather than model $\{\text{area} * T + psub\}$, the model selected in the meta-analysis of time trends. The covariate *psub* was removed because it was confounded with the categorical age effects (S1, S2 and A) we wished to examine. Model $\{\text{area} * T + \text{female}(S1, S2, A) + \text{male}(S1, S2, A)\}$ was selected as the best approximating model with an Akaike weight of 0.995 (Table 15). This model suggested that reproductive output varied by age class similarly among males and females, rather than by different combinations of age classes for each sex.

However, this model explained only 6.0% of the temporal variation in the data and confidence intervals for most parameter estimates included zero (Table 16). Estimates of least-square means from this model suggested that adults experienced the highest reproductive output, followed by second-year subadults, then first-year subadults. Support for differences between the two subadult age classes was weak, based on 95% confidence intervals (Table 17).

Population change on individual study areas

We used 842 marked subadult and adult individuals in the analysis of λ_t (180 from ELD, 241 from LAS, 264 from SIE, and 157 from the SKC). The median \hat{c} ranged from 1.03 to 1.21 among study areas (Table 18), suggesting some overdispersion but no serious lack of fit; we adjusted all estimates and model selection factors by site-specific estimates of c , and, to account for this, increased the number of parameters in each model by one.

We did not find strong evidence for decreasing linear trends in λ_t on any of the study areas (Table 18, Fig. 6). In general, λ_t was either relatively stationary, as for LAS and SIE, or increasing after an initial decrease, as for ELD and SKC (Fig. 6). The best approximating model for ELD (1.93 QAIC_c above second model) suggested a quadratic trend in λ_t (Table 18, Fig. 6) with first a decrease (β_1 , Table 19) followed by a very slight increase in λ_t (β_2 , Table 19). The second-ranked model for the ELD was a log-linear trend model. Together, these 2 models accounted for 92% of the Akaike weights. No trend in λ_t was evident for LAS; the best model with any trend was a negative linear, but the Akaike weight was moderate (28%) and similar to the top model (30%), which was a means model (Table 18). The slope parameter for linear trend in λ_t for the LAS was near zero (-0.0005) and the confidence interval was balanced around 0 (95% CI = -0.011 to 0.010). The best two λ_t models for the SIE were the random effects mean and fixed effects categorical time models, which accounted for 70% of the Akaike weights (Table 18). The best approximating λ_t model for the SKC (1.27 QAIC_c above second model) suggested a quadratic trend in λ_t (Table 18, Fig. 6) with first a decrease (β_1 , Table 19) followed by a very slight increase in λ_t (β_2 , Table 19). The second best model for SKC indicated λ_t was constant over time.

The estimates of realized population change (Δ_t) represented the trajectory (or trend in numbers) of each study population (Fig. 7). These estimates were based solely on the estimates of λ_t and did not require estimating annual population size (N_t) for each study area. The trends

represent the proportion of the population size remaining each year, given the population size in the first year. For example, if there were 100 owls on the LAS study area in 1992 there would be 69 owls in 2004, based on the estimates of λ_t and, hence, Δ_t for that study area. [Note: for ELD, LAS, and SIE, estimates covered 1992-2004 for this analysis, whereas estimates for the SKC covered 1993-2003]. Populations on ELD and SKC showed slight increases (100 to 127 and 113 respectively) while SIE showed a slight decrease (100 to 95). However, the 95% confidence interval covered 1.0 at the end of the time period for the SIE, indicating that the ending population size was not statistically different than the initial population. Only the LAS population decreased significantly based on the 95% confidence interval with steady decreases from 1995–1998, and 2002–2004.

Based on a random effects means (intercepts-only) model using annual estimates of λ from model $\{\phi_t, p_t, \lambda_t\}$, 95% confidence intervals of the estimated mean across years ($\bar{\lambda}$) for each of the study areas was not different from that of a stationary population ($\lambda = 1$; Table 20, Fig. 8). However, point estimates were <1 for two of the study areas (LAS and SIE). LAS had the lowest estimate of $\bar{\lambda}$ with a 95% confidence interval that barely overlapped 1 (upper 95% CI = 1.001), suggesting that the owl population on LAS may have been declining (Table 20). Temporal process variation in λ_t was low (CV for ELD = 8.1%, for SKC = 8.3% and 0% for LAS and SIE).

Meta-analysis of population change

The best meta-analysis model of population trend, $\{\phi(g^*t) p(g^*t) \lambda(t)\}$, indicated that λ varied across time but was similar in trend among the study areas (Table 21). However, the model $\{\phi(g^*t) p(g^*t) \lambda(\text{SKC vs. rest})\}$ had $\Delta\text{QAIC}_c = 1.38$ and 30% of the model weight, suggesting λ_t for the SKC may have been different than the other study areas. These two models, which have 89% of the model weights, suggest that λ_t varied in a parallel manner among the study areas.

While recapture rates varied within and among study areas, the recruitment meta-analysis indicated that there were parallel patterns in both apparent survival and recruitment among the four study areas (Table 22). Estimated recruitment rates from the best model appear in Fig. 9.

Population Viability Analysis

Estimates of $\overline{\log(\lambda)}$, $se(\overline{\log(\lambda)})$, and $\hat{\sigma}_{\text{temporal}}^2$ from the λ_t models from each study area appear in Table 23. We used these estimates in the population viability analysis, with the following exceptions: because the value of $\hat{\sigma}_{\text{temporal}}$ was zero for LAS and SIE, and the estimates of ELD and SKC were 0.081 and 0.083, respectively, we used a mean value of 0.082 for $\hat{\sigma}_{\text{temporal}}$ for LAS and SIE (and also used this for the hypothetical population with mean $\lambda = 1.0$).

Ninety-five percent confidence intervals on predictions of >10% decline spanned the interval [0, 1] within 5-10 years into the future for all four of the study areas (Fig. 10). Therefore, we restricted our inferences to 7 years into the future. Spotted owl populations at ELD and SKC were less likely to show declines in populations than LAS and SIE, with the LAS study area showing the greatest probability of decline. For ELD and SKC, the estimated probabilities of observing a population decline >10% in 7 years were 0.23 and 0.25 (95% CI = 0.00 to 0.92, and 0.00 to 0.89, respectively (Fig. 10). For SIE the estimated probability of a >10% decline in 7 years was 0.41 (95% CI = 0.09 to 0.78); for LAS the probability was 0.64 (95% CI = 0.27 to 0.94; Fig. 10).

After about 7 years into the future, 95% confidence intervals on predictions of population increase spanned the interval [0, 1] only for the ELD and SKC (Fig. 11). In contrast, the LAS had only a 0.10 probability of increasing by >10% at the end of 7 years (95% CI = 0.00 to 0.34). The SIE had 0.23 probability of increasing by >10% at the end of 7 years (95% CI = 0.01 to 0.55). Patterns for probabilities of increases of >20 or >30% in population size followed the same pattern as >10% increase, but probabilities were naturally lower and confidence intervals were narrower.

Upper 95% confidence intervals for the hypothetical population with mean $\lambda = 1.0$ and $\hat{\sigma}_{\text{temporal}} = 0.082$ did not exceed 0.43 at the end of the 20 year simulation. At 7 years in the future, the hypothetical population exhibited 0.31, 0.15, and 0.05 probability of declining by >10, >20, and >30%, respectively (Fig. 12). The 95% confidence interval for >10% decline after 7 years was 0.17 to 0.38. At 7 years in the future, the same population exhibited 0.33, 0.20, and 0.11 probability of increasing by >10, >20, and >30%, respectively. The 95% confidence interval for the probability of >10% increase after 7 years was 0.19 to 0.39. The asymmetry of these estimates is due to the asymmetry of the lognormal distribution that results when values of

$\log(\lambda)$ are generated from a symmetric normal distribution and then transformed with the exponential function to produce a lognormal distribution.

DISCUSSION

Noon et al. (1992) were the first to formally evaluate population trends of California spotted owls in the Sierra Nevada. The results of their analysis were ambiguous due to the relatively short length of studies and the small sample size for each study area. Subsequent to Noon et al. (1992) were studies on the population ecology of California spotted owls on several study areas (Bias and Gutiérrez 1992, LaHaye et al. 1992, 1994, 1997, 2001, 2004, Gutiérrez 1994, Smith et al. 1999, Blakesley et al. 2001, Seamans et al. 2001). Franklin et al. (2004) conducted the next comprehensive analysis of California spotted owl population dynamics, a meta-analysis of status and trends of all California spotted owl populations under study (three study populations in the Sierra Nevada, one in the southern Cascade Mountains, and one in the San Bernardino Mountains of southern California). We conducted a meta-analysis that included 5 years of additional data (2001-2005) beyond that used by Franklin et al. (2004). In most respects our current analysis replicates the approach used by Franklin et al. (2004). However, there are two key differences between our study and that of Franklin et al. (2004): (1) the San Bernardino study was not included because its funding was eliminated prior to 2001; and (2) a population viability analysis was included in this study.

We found an increase in apparent survival (ϕ) of adult owls over time. In contrast, in the 2001 meta-analysis no model with a time trend was within 7 QAIC_c units of the top model (Franklin et al. 2004). Most of this increase in survival appears to have occurred since 2000 (Figures 1 and 2). Point estimates of $\bar{\phi}$ for each study area were greater than in the previous analysis by approximately 0.02 on each study area. Apparent survival of spotted owls on the SKC was higher than on the other study areas, consistent with the findings of Franklin et al. (2004).

Estimates of reproductive output on individual study areas were similar to estimates from the 2001 analysis (Franklin et al. 2004). However, there was greater model selection uncertainty in the 2001 analysis. This suggested that patterns in the top models (i.e., the “EO” effect on ELD, LAS, and SIE) have persisted and/or strengthened subsequent to the 2001 meta-analysis,

with 5 years of additional data. The increased percentage of temporal variability explained by the best time-based models also indicates these patterns have strengthened.

Point estimates of population rate of change were slightly lower for the ELD and LAS and slightly higher for the SIE and SKC than reported by Franklin et al. (2004). All point estimates of $\bar{\lambda}$ were within the 95% CI for individual study areas reported by Franklin et al. (2004:Table 20). Results from the 2001 meta-analysis indicated a negative linear trend in λ_t for the ELD and SIE; ELD showing an especially steep decline as evidenced by a significant negative linear trend. Based on the 2006 meta-analysis, λ_t for the ELD exhibited a quadratic trend, the population initially declining through about 1999, and then increasing. This early negative trend was captured in the first meta-analysis by a linear model, while the increasing trend was captured in this meta-analysis by the quadratic model, with 4 years of additional data. The SIE went from a slight decline to a stationary means model because λ_t estimates were slightly >1 for 1998–2004 (except for 2001). LAS and SKC exhibited similar patterns in λ_t , compared to previous analyses.

Franklin et al. (2004) performed no population viability analyses, but our PVA indicated two of the four study areas (LAS and SIE) are likely to experience population declines within 7 years, and very unlikely to experience population increases under current population trends. The probability of decline was greater than that of a hypothetical population with $\lambda = 1$, which under our simulation could decline due to temporal variation in λ . In general, there was great uncertainty in the PVA analyses for time intervals of >10 years; after 10 years, the confidence intervals for most estimated probabilities of decline or increase covered almost 0–1.

Estimated temporal variation in λ ($\hat{\sigma}_{\text{temporal}}$) was zero for LAS and SIE, the two study areas for which mean estimated λ was < 1.0 . However, we conducted the population viability analyses for LAS and SIE using $\hat{\sigma}_{\text{temporal}} = 0.082$. Consequently, estimated probabilities of population decline for LAS and SIE were lower and estimated probabilities of population increase were higher than would have been observed under the PVA had we used a smaller estimate of $\hat{\sigma}_{\text{temporal}}$

Population viability analyses assume that the environmental conditions under which $\bar{\lambda}$ and $\hat{\sigma}_{\text{temporal}}$ were estimated would continue during the projection period (20 years in our PVA).

Another important caveat in interpreting these modeled population increases is that they do not incorporate any assumptions about conditions that may limit spotted owl population growth, e.g., amount of suitable habitat or density dependent mechanisms such as competition for territories.

Patterns in Demographic Rates

Lande (1988) and Noon and Biles (1990) both found that spotted owl population growth rate is most sensitive to changes in adult survival. Other parameters, such as reproductive output and recruitment, have less influence on the magnitude of population growth rate but appear to have a greater impact on the annual variability of population growth; temporal variability in territorial owl survival is much lower than in reproductive output and recruitment (Franklin et al. 2000, Seamans 2005). This inverse relationship between the importance of a demographic parameter to population growth rate and the temporal variability of the parameter appears to be typical for most long-lived vertebrates that produce few young (Pfister 1998, Gaillard et al. 2000, Sæther and Bakke 2000). This life-history strategy, high adult survival with little temporal variability and highly variable reproduction and recruitment, was also estimated for a population of northern spotted owls by Franklin et al. (2000). Therefore, it is imperative for spotted owl management to maintain a high survival rate of territorial owls in order to maintain spotted owl populations. However, because adult survival exhibits such low temporal variability, management directed at increasing reproductive output and subsequent recruitment may be the most successful way to maintain or increase spotted owl populations in the Sierra Nevada, as long as these actions do not decrease adult survival.

We estimated that the survival rate of adult owls (territorial owls ≥ 3 years old) increased through time on all study areas. Annual estimates of survival based on model averaging when all study areas were analyzed jointly indicated a 4-5% increase in annual survival from the first until the last year of study. This phenomenon should have had a large positive influence on population rate of change (see description of life-history above). However, the estimated increase in adult survival over time did not coincide with an increase in annual estimates of population rate change on the study areas. Subsequent to the last meta-analysis (Franklin et al. 2004), point estimates of average annual rate of population change have decreased slightly for two study areas (ELD, LAS) and increased slightly on the other two (SIE and SKC). Analyses of population rate of change for individual study areas suggested models with linear or quadratic

trends were competing models for at least two of the study areas, and the trends suggested an annual decrease in λ for at least part of the study period.

The factors behind the increasing trend in apparent survival probability of adult spotted owls are unknown. California spotted owls in the Sierra Nevada share a common evolutionary history (Barrowclough et al. 1999, 2005) and likely share the same life-history strategy and demographic responses to environmental variation. We put forward three non-mutually exclusive hypotheses that may explain the estimated increase: (1) changes in habitat quality; (2) changes in environmental conditions; or (3) density-dependent mechanisms. All these hypotheses can be formally tested but they require additional sources of information that were beyond the scope of this report. In addition, testing for density-dependent mechanisms will probably require additional years of data (Solow and Steele 1990). Our explanations in the following paragraphs show how these factors may have influenced survival, and these explanations establish the hypotheses for future testing.

Temporal changes in vegetation in the Sierra Nevada are the result of both natural and anthropogenic forces, and occur over varying time scales (SNEP 1996). The standards and guidelines for spotted owl habitat management recommended by CASPO for public lands in the Sierra Nevada were in effect over most of the course of our studies. These guidelines focused on conserving mature conifer forests in and around spotted owl sites. Blakesley et al. (2005) found owl survival probability to be positively associated with the amount of spotted owl habitat used for nesting and roosting within 203 and 814 ha areas surrounding spotted owl site centers on the LAS. Seamans (2005) estimated that adult survival rate was positively related to the amount of mature forest at individual sites on the ELD. However, it is unlikely that mature forest increased over the course of study on the ELD, LAS, or on the other study areas. Thus, it does not seem plausible that the observed increase in adult spotted owl survival was due to improved habitat quality.

Temporal variability in northern and Mexican spotted owl survival appears to be partially related to environmental conditions (Franklin et al. 2000, Seamans et al. 2002). However, Seamans (2005) found no strong relationships between weather and the survival rate of adult California spotted owls on the ELD. Therefore, we suspect that temporal trends in survival were not related to temporal trends in weather.

It is also possible that density-dependent mechanisms (Royama 1977, Hassell et al. 1989) played a role in the estimated increase of adult survival. At lower densities, competition for resources is likely reduced, thus having less of a negative effect on survival. In other words, at low population density there may have been less stress associated with defending a site and obtaining food. A related hypothesis is that there was reduced competition for high quality territories, resulting in only the territories of the highest quality being occupied. Such a mechanism, density-dependent habitat selection, was hypothesized by Fretwell and Lucas (1969) and Fretwell (1972) in their “ideal free” and “ideal despotic” models. Thus, we might expect an increase in survival if: (1) the density of individuals declines on the study areas; (2) individuals are free to select the best sites to occupy; and (3) individuals actively seek the best available sites. Our estimates of realized change (Fig. 6) indicated abundance peaked on the LAS, SIE, and SKC in the first few years of study, and abundance peaked on the ELD in 1997. We did not estimate habitat quality nor investigate whether individuals preferentially sought out high quality sites. Seamans (2005) did estimate that there was a subset of high quality sites on the ELD that were preferentially occupied; sites that had a high probability of occupancy typically had high territorial owl survival rates. Although this line of evidence does lend support to the hypotheses of density dependent mechanisms driving increased survival, it is still unclear if such a mechanism was operating on study areas other than the ELD, or if weather conditions or temporal variability in habitat quality also played a role.

Our estimate of a higher adult survival rate on the SKC than the other study areas is of interest because of the importance of adult survival to population rate of change. The cause of this difference was unknown but may have been the result of differences in habitat quality resulting from: (1) differences in forest management both before and during the study period; (2) the presence of giant sequoia groves on the SKC; (3) differences in the proportion of oak woodlands; or (4) the interaction between two or more of these factors.

The SKC was within two National Parks and was managed differently than the other study areas; the SKC experienced much less timber harvest than other study areas both during the study period and during the century prior to the start of the demography studies. Territorial owl survival on the ELD was correlated with the amount of mature coniferous forest at individual owl sites (Seamans 2005). If the SKC had larger tracts of mature coniferous forest,

then differences in habitat quality among the study areas may have contributed to the differences in survival.

Alternatively, the higher survival on the SKC than the other study areas may have been influenced by differences in the amounts of forest types. Approximately 7% of the SKC consisted of giant sequoia groves (Parsons 1994) whereas there was only one sequoia grove on the SIE and one on the ELD. Although these groves covered only a small portion of the SKC, almost half of the owl sites on the SKC were in or within 1 km of a sequoia grove. Thus, it is possible that sequoia groves promoted higher survival. In addition, oak woodlands were abundant on the SKC (21% of study area) and the SIE (29% of the study area). Oak woodlands were present on the ELD but intermixed with coniferous forest, and LAS contained no oak woodlands. Although the mechanism was unclear, the abundance of oak woodland was negatively correlated with territorial owl survival at ELD owl sites (Seamans 2005). Thus, higher survival on the SKC versus the SIE could partially be explained by the prevalence of oak woodland, but such a hypothesis would not explain the higher survival at SKC than ELD and LAS. Other explanations, such as differences in topography, or other habitat or population level mechanisms need further exploration but could also explain difference in territorial owl survival. It is unfortunate that insufficient funds were allocated to continue the SKC study after 2004.

We observed an even-odd year pattern (*EO*) in reproductive output for three study areas. We did not know why there was a coincident even-odd year pattern among the study areas. Reproductive output of spotted owls appears to be strongly related to weather in the Sierra Nevada (Seamans 2005) and elsewhere (Franklin et al. 2000, Seamans et al. 2002, Olson et al. 2004). However, weather during the study period did not follow an even-odd year pattern (Seamans personal observation). Temporal trends in the primary prey species of the California spotted owl (northern flying squirrels [*Glaucomys sabrinus*] and woodrats [*Neotoma sp.*]; Williams et al. 1992) are unlikely to follow such patterns. However, Rosenberg et al. (2003) found that northern spotted owl reproductive success in the Oregon Cascade Mountains was positively associated with *Peromyscus* sp. (deer mouse) abundance even though *Peromyscus* sp. accounted for <2% of prey biomass consumed by owls. Rosenberg et al. (2003) observed the same even-odd year pattern in owl reproduction that we observed, and found the pattern to be much stronger for the proportion of owls that attempted to nest than for the number of young per territory. We observed unusually high densities of *Peromyscus* on the LAS during the two years

of highest spotted owl reproduction (1992 and 2002; Blakesley and Shaw personal observations). Therefore, it is possible that prey abundance was responsible for the exceptionally high reproduction in 1992 and 2002, and may in part explain the even-odd year trend in reproductive output.

The negative linear trend in reproductive output on the ELD is of potential concern. However, because reproductive output appears to be largely influenced by weather on the ELD (Seamans 2005) it is likely that the few exceptional years of reproductive output early in the study and the few very poor years towards the end of the study were related to weather and were largely responsible for this trend.

We estimated population trend using the temporal symmetry model (λ_t), which reflects the extent to which spotted owls within a study area were being replaced in a geographically open system. Using this method, one cannot distinguish between study area populations that are self-sustaining, and those that are being sustained through immigration. Note, however, that none of our four study areas should be viewed in a strict meta-population (source-sink) framework (Franklin et al. 2004:Appendix 3).

Population growth rate, λ , can be viewed as the sum of apparent survival probability (ϕ) and the per capita recruitment rate (f) ($\lambda_i = \phi_i + f_i$; Nichols and Hines 2002). Spotted owls recruited into the territorial population are comprised of owls hatched on the study area and establishing territories for the first time, as well as immigrant owls dispersing from outside the study area. Median estimated breeding dispersal distance (distance moved by previously territorial individuals) for spotted owls at LAS was 7 km (Blakesley et al. 2006) whereas median natal dispersal distance (distance moved from the natal site to the first territorial site) was >23 km ($n = 36$; J. Blakesley, unpublished data). Similarly, median breeding distance for northern spotted owls was 3.5 km and median natal dispersal distance was 14 km (Forsman et al. 2002). Therefore, the majority of immigrating owls onto our study areas were likely natal dispersers rather than breeding dispersers, although rates of both types of dispersal would be expected to vary among study areas of different sizes and shapes (Barrowclough 1978).

We observed two peaks in recruitment, one at the beginning of the study period and one at the end of the study period. We suspect that recruitment of new individuals into the areas we sampled was a function of the availability of sites for occupancy and a function of the extant pool of recruits. Site availability should have been partially a function of adult survival; if

territorial owl survival was low there would have been more available sites to occupy. Thus, at the end of the study period, when estimates of realized change indicated abundance on each study area was relatively low, recruitment should have been highest. However, availability of recruits appeared to be related to recent reproductive success of these populations. Recruitment was highest in the first and second annual intervals following peak years in reproductive output (1992 and 2002).

Conclusions and Recommendations

The management of forests in the Sierra Nevada is of concern to many stakeholders. Of particular interest are the potential future impacts of the current management plan for Sierra Nevada National Forests (U.S. Forest Service 2004) on spotted owls throughout the region. It is well known that the owl uses forest types that would be affected by the plan (Gutiérrez et al. 1992, Bias and Gutiérrez 1992, Verner et al. 1992, Moen and Gutiérrez 1997, U.S. Forest Service 2004, Bond et al. 2004, Blakesley et al. 2005, Chatfield 2005). Owls may be especially impacted in the wildland-urban-interface zone, where the plan calls for more aggressive management. Approximately 50% of all known spotted owl sites in the Sierra Nevada are in or near the wildland-urban-interface zone. The potential consequences of the Forest Service management plan to spotted owls are unknown because: (1) the extent of vegetation manipulations is largely under the control of local managers (i.e., Forest and District level) and will likely vary across the Sierra Nevada; and (2) threshold levels of quality habitat necessary to maintain individual pairs of spotted owls on a site are largely unknown.

To address this uncertainty, well designed experimental studies should be coupled with the spotted owl demographic studies. Rigorous experimental studies provide the best avenue for understanding which resources are responsible for the variability in spotted owl demographic parameters (Morrison 2001). An experiment is being conducted within the ELD that incorporates randomly assigned experimental treatment units in an effort to estimate the behavioral response of spotted owls to habitat manipulation. Studies in the LAS and SIE also are aimed at evaluating the effect of forest management on the spotted owl (Plumas-Lassen administrative study, Kings River administrative study). Unfortunately, the administrative studies are quasi-experimental; treatment and control units are not randomly assigned, limiting the scope of inference of the results of the studies.

Our spotted owl demographic data sets are rich in biological information and have been painstakingly collected over many years. However, a major limitation in furthering our understanding of the influence of habitat on spotted owl demographic rates is the lack of an accurate, up to date vegetation cover map of the Sierra Nevada.

We reiterate the recommendations of Franklin et al. (2004:41) that the existing demographic studies continue to be coordinated with forest management activities, that comprehensive, accurate vegetation maps be developed, and that landscape-scale experiments be designed to assess the effects of forest management on spotted owl demographic rates.

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LITERATURE CITED

- Anderson, D. R., K. P. Burnham, A. B. Franklin, R. J. Gutiérrez, E. D. Forsman, R. G. Anthony, and T. M. Shenk. 1999. A protocol for conflict resolution in analyzing empirical data related to natural resource controversies. *Wildlife Society Bulletin* 27:1050-1058.
- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2004. Status and trends in demography of northern spotted owls, 1985-2003. Unpublished Report. Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis.
- Barrowclough, G. F. 1978. Sampling bias in dispersal studies based on finite area. *Bird Banding* 49:333-341.
- Barrowclough, G. F., R. J. Gutiérrez, and J. G. Groth. 1999. Phylogeography of spotted owl (*Strix occidentalis*) populations based on mitochondrial DNA sequences: gene flow, genetic structure, and a novel biogeographic pattern. *Evolution* 53:919-931.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

- Barrowclough, G. F., J. G. Groth, L. A. Mertz, and R. J. Gutiérrez. 2005. Genetic Structure, introgression, and a narrow hybrid zone between northern and California spotted owls (*Strix occidentalis*). *Molecular Ecology* 14:1109-1120.
- Bias, M. A., and R. J. Gutiérrez. 1992. Habitat associations of California spotted owls in the central Sierra Nevada. *Journal of Wildlife Management* 56:584-595.
- Blakesley, J. A., B. R. Noon, and D. W. H. Shaw. 2001. Demography of the California spotted owl in northeastern California. *Condor* 103:667-677.
- Blakesley, J. A., D. R. Anderson, and B. R. Noon. 2006. Breeding dispersal in the California spotted owl. *Condor* 108:71-81.
- Blakesley, J. A., B. R. Noon, and D. R. Anderson. 2005. Site occupancy, apparent survival and reproduction of California spotted owls in relation to forest stand characteristics. *Journal of Wildlife Management* 69:1554-1564.
- Bond, M., M. E. Seamans, and R. J. Gutiérrez. 2004. Modeling nest-site selection of California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada: the value of forest inventory and analysis metrics. *Forest Science* 50:773-780.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5:1-437.
- Chatfield, A. H. 2005. Habitat selection by a California spotted owl population: a landscape scale analysis using resource selection functions. Thesis, University of Minnesota, St. Paul.
- Evans, M., N. Hastings, and B. Peacock. 1993. Statistical distributions. 2nd edition. John Wiley and Sons, New York.
- Federal Advisory Committee. 1997. Final report of the California Spotted Owl federal advisory Committee. U.S. Dept. Agriculture, Washington, D.C.
- Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. U. S. Forest Service. General Technical Report PNW-GTR-162, Portland, Oregon.
- Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, B. L. Biswell, A. Ellingson, E. C. Meslow, G. S. Miller, K. A. Swindle, J. A. Thraikill, F. F. Wagner, D. E. Seaman. 2002. Natal and breeding dispersal of northern spotted owls. *Wildlife Monographs* 149.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12-20.
- Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70:539-590.
- Franklin, A. B., K. P. Burnham, G. C. White, R. G. Anthony, E. D. Forsman, C. J. Schwarz, J. D. Nichols, and J. E. Hines. 1999. Range-wide status and trends in Northern Spotted Owl populations. Unpublished Report. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins.
- Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monograph* 54.
- Fretwell, S. D. 1972. Populations in a seasonal environment. *Monographs in population biology* 5. Princeton University Press, Princeton, New Jersey.
- Fretwell, S. D. and H. L. Lucas. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367-393.
- Gutiérrez, R. J. 1994. Changes in the distribution and abundance of spotted owls during the past century. *Studies in Avian Biology* 15:293-300.
- Gutiérrez, R. J., A. B. Franklin and W. S. LaHaye. 1995. Spotted owl (*Strix occidentalis*). *The birds of North America*, number 179. The American Ornithologists' Union, Washington, D.C., and The Academy of Natural Sciences, Philadelphia, Pennsylvania.
- Gutiérrez, R. J., and G. F. Barrowclough. 2005. Boundaries of the northern and California spotted owls: implications for conservation. *Condor* 107:182-187.
- Gutiérrez, R. J., J. Verner, K. S. McKelvey, B. R. Noon, G. N. Steger, D. R. Call, W. S. LaHaye, B. B. Bingham, and J. S. Senser. 1992. Habitat relations of the California spotted owl. Pages 79–98 in J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould Jr., and T. W. Beck, editors. *The California spotted owl: a technical assessment of its current status*. U. S. Forest Service General Technical Report PSW-113. Pacific Southwest Research Station, Albany, California.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

- Hassell, M. P., J. Latto, and R. M. May. 1989. Seeing the wood for the trees: detecting density dependence from existing life-table studies. *Journal of Animal Ecology* 58:883-892.
- Hunsaker, C. T., B. B. Boroski, and G. N. Steger. 2002. Relations between canopy cover and the occurrence and productivity of California spotted owls. Pages 687-700 in J. M. Scott and P. J. Heglund, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Covolo, California.
- LaHaye, W. S., R. J. Gutiérrez, and H. R. Akçakaya. 1994. Spotted owl metapopulation dynamics in southern California. *Journal of Animal Ecology* 63: 775-785.
- LaHaye, W., R. J. Gutiérrez, and D. R. Call. 1992. Demography of an insular population of spotted owls (*Strix occidentalis occidentalis*). Pages 803-814 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001*. Elsevier Press, New York.
- LaHaye, W. S., R. J. Gutiérrez, and D. R. Call. 1997. Nest-site selection and reproductive success of California spotted owls. *Wilson Bulletin* 109:42-51.
- LaHaye, W. S., R. J. Gutiérrez, and J. R. Dunk. 2001. Natal dispersal of the spotted owl (*Strix occidentalis occidentalis*) in southern California: dispersal profile of an insular population. *Condor* 103:691-700.
- LaHaye, W. S., G. S. Zimmerman, and R. J. Gutiérrez. 2004. Temporal variation in the vital rates of an insular population of spotted owls (*Strix occidentalis occidentalis*): contrasting effects of weather. *Auk* 121:1056-1069.
- Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601-607.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ and demographic contributions to λ , using capture-recapture data. *Journal of Applied Statistics* 29:539-568.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute Inc, Cary, North Carolina.
- Moen, C. A., and R. J. Gutiérrez. 1997. California spotted owl habitat selection in the central Sierra Nevada. *Journal of Wildlife Management* 61:1281-1287.
- Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management* 65:613-623.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

- Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ and demographic contributions to λ , using capture-recapture data. *Journal of Applied Statistics* 29:539-568.
- Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific Northwest. *Journal of Wildlife Management* 54:18-27.
- Noon, B. R., K. S. McKelvey, D. Lutz, W. S. LaHaye, R. J. Gutiérrez, and C. A. Moen. 1992. Estimates of demographic parameters and rates of population change. Pages 175-186. *in* J. Verner et al. (eds). *The California spotted owl: a technical assessment of its current status*. U. S. Forest Service General Technical Report PSW-GTR-133. Pacific Southwest Research Station, Albany, California.
- North, M., G. N. Steger, R. Denton, G. Eberlein, T. Munton and K. Johnson. 2000. Association of weather and nest-site structure with reproductive success in California spotted owls. *Journal of Wildlife Management* 64:797-807.
- Olson, G. S., E. M. Glenn, R. G. Anthony, E. D. Forsman, J. A. Reid, P. J. Loschl, and W. J. Ripple. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. *Journal Wildlife Management* 68:1039-1053.
- Parsons, D. J. 1994. Objects or ecosystems? Giant sequoia management in the National Parks. Pages 109-115 *in* P.S. Aune, technical coordinator. *Proceedings of the symposium on the Giant Sequoias: their place in the ecosystem and society*. June 23-25, 1992, Visalia, CA. U. S. Forest Service General Technical Report PSW-GTR-151. Pacific Southwest Research Station, Berkeley, CA USA.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences* 95:213-218.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703-709.
- Rao, P. S. R. S. 1997. *Variance components estimation: mixed models, methodologies and applications*. Chapman and Hall, London, England.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology* 81:1715-1725.
- Royama, T. 1977. Population persistence and density dependence. *Ecological Monographs* 47:1-35.
- Rundel, P. W. 1971. Community structure and stability in the giant sequoia ecosystem of the Sierra Nevada, California. *American Midland Naturalist* 85:478-492.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

- Sæther, B.-E. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642-653.
- Seamans, M. E., R. J. Gutiérrez, C.A. Moen, and M. Z. Peery. 2001. Spotted owl demography in the central Sierra Nevada. *Journal of Wildlife Management* 65:425-431.
- Seamans, M. E. 2005. Population biology of the California spotted owl in the central Sierra Nevada. Ph.D. dissertation, University of Minnesota, St Paul.
- Seamans, M. E., R. J. Gutiérrez, and C. A. May. 2002. Mexican spotted owl (*Strix occidentalis*) population dynamics: influence of climatic variation on survival and reproduction. *Auk* 119:321-334.
- Smith, R. B., M. Z. Peery, R. J. Gutiérrez, and W. S. LaHaye. 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. *Wilson Bulletin* 111:22-29.
- SNEP. (Sierra Nevada Ecosystem Project). 1996. Sierra Nevada Ecosystem Project: final report to Congress, vol II, Assessments and scientific basis for management options. University of California, Davis, Centers for Water and Wildland Resources.
- Solow, A. R., and J. H. Steele. 1990. On sample size, statistical power, and the detection of density dependence. *Journal Animal Ecology* 59:1073-1076.
- U.S. Fish and Wildlife Service. 2003. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the California spotted owl (*Strix occidentalis occidentalis*). *Federal Register* 68:7580-7608.
- U.S. Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants: 90-day finding on a petition to list the California spotted owl as threatened or endangered. *Federal Register* 70:35607-35614.
- U.S. Forest Service. 1993. California Spotted Owl Sierran Province Interim Guidelines Environmental Assessment, Decision Notice, and Findings of No Significant Impact. USDA Forest Service. Pacific Southwest Region. San Francisco, California.
- U.S. Forest Service. 1996. Revised Draft Environmental Impact Statement: managing California spotted owl habitat in the Sierra Nevada National Forests of California, an ecosystem approach. USDA Forest Service. Pacific Southwest Region. San Francisco, California.
- U.S. Forest Service. 2004. Sierra Nevada Forest Plan Amendment: final supplemental environmental impact statement. Region 5, USDA Forest Service, Vallejo, California.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

- Verner, J., K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, editors. 1992. The California spotted owl: a technical assessment of its current status. U. S. Forest Service General Technical Report PSW-113. Pacific Southwest Research Station, Albany, California.
- White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549-2557.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimates from populations of marked animals. *Bird Study* 46:120–138.
- White, G. C., A. B. Franklin, and T. M. Shenk. 2002. Estimating parameters of PVA models from data on marked animals. Pages 169–190 *in* S. R. Beissinger and D. R. McCullough, editors. *Population Viability Analysis*. University of Chicago Press, Chicago, Illinois.
- Williams, D. F., J. Verner, H. F. Sakai, and J. R. Waters. 1992. General biology of major prey species of the California spotted owl. Pages 207-221 *in* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, editors. The California spotted owl: a technical assessment of its current status. U. S. Forest Service General Technical Report PSW-113. Pacific Southwest Research Station, Albany, California, USA.

DRAFT Demography of the California Spotted Owl: Report from the 2006 Meta-Analysis

Table 1. Description of the four study areas in the southern Cascades and Sierra Nevada, California, used to estimate vital rates of California spotted owls.

Study area	Study area acronym	Years	Area (km ²)	Number of owls banded by age class ^a			Total owls banded	Total captures + recaptures ^b
				S1	S2	Adult		
Eldorado National Forest	ELD	1990–2005	925	47	33	175	255	991
Lassen National Forest	LAS	1990–2005	2200	56	35	213	304	1517
Sierra National Forest	SIE	1990–2005	693	71	53	151	275	1130
Sequoia-Kings Canyon National Park	SKC	1991–2004	343	34	20	103	157	779

^a Age class codes indicate owls that were 1 year old (S1), 2 years old (S2), or ≥ 3 years old (Adults).

^b All captures and recaptures, regardless of age.

Table 2. Top models for estimation of apparent survival probability (ϕ) for California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1990-2005. Models shown are those with $\Delta\text{QAIC}_c < 2.0$, and are ordered by QAIC_c for each study area. The complete model sets appear in Appendix K.

Model ^a	<i>K</i>	QAIC_c	ΔQAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
Eldorado study area (1990-2005; n = 255, $\hat{c} = 1.065$)					
{ $\phi((a2 * T) + s, p(\text{wi-effort} + s))$ }	9	1255.331	0.000	0.077	682.655
{ $\phi(a2 + s), p(\text{wi-effort} + s)$ }	7	1255.417	0.086	0.073	686.816
{ $\phi((a2 * \ln T) + s, p(\text{wi-effort} + s))$ }	9	1256.174	0.843	0.050	683.497
{ $\phi(S1=S2, AD), p(\text{wi-effort} + s)$ }	6	1256.508	1.177	0.043	689.937
{ $\phi(S1=S2, AD)*T, p(\text{wi-effort} + s)$ }	8	1256.593	1.262	0.041	685.956
{ $\phi(s), p(\text{wi-effort} + s)$ }	6	1256.890	1.559	0.035	690.319
Lassen study area (1990-2005; n = 304, $\hat{c} = 1.144$)					
{ $\phi(T) p(a + s)$ }	6	1437.424	0.000	0.058	780.644
{ $\phi((a1) + T) p(a + s)$ }	7	1437.484	0.060	0.056	778.681
{ $\phi(T) p(a + s + r)$ }	7	1437.741	0.317	0.050	778.938
{ $\phi((a1) + T) p(a + s + r)$ }	8	1437.799	0.375	0.048	776.970
{ $\phi((a2) + T) p(a + s + r)$ }	8	1438.031	0.608	0.043	777.202
{ $\phi((a1) + TT) p(a + s + r)$ }	9	1438.264	0.840	0.038	775.405
{ $\phi((a2)*s + T) p(a + s + r)$ }	10	1438.306	0.882	0.037	773.414
{ $\phi((a2) + TT) p(a + s + r)$ }	9	1438.318	0.894	0.037	775.459
{ $\phi(TT) p(a + s + r)$ }	8	1438.399	0.975	0.036	777.570
{ $\phi((a2)*s + TT) p(a + s + r)$ }	11	1438.650	1.226	0.031	771.721
{ $\phi(s*T) p(a + s)$ }	8	1438.882	1.458	0.028	778.053
{ $\phi((a1)*T) p(a + s + r)$ }	9	1438.885	1.461	0.028	776.026
{ $\phi(s*T) p(a + s + r)$ }	9	1439.216	1.792	0.024	776.357
{ $\phi(s + T) p(a + s + r)$ }	8	1439.280	1.856	0.023	778.451
{ $\phi((a1) + s + T) p(a + s + r)$ }	9	1439.326	1.902	0.022	776.467
{ $\phi(\ln(T)) p(a + s + r)$ }	7	1439.413	1.989	0.021	780.610
Sierra study area (1990-2005; n = 275, $\hat{c} = 1.090$)					
{ $\phi(a2), p(a + s)$ }	6	1342.302	0.000	0.053	794.901
{ $\phi(a2 + T), p(a + s + r)$ }	8	1342.405	0.103	0.050	790.945
{ $\phi(a2 + T), p(a + s)$ }	7	1342.434	0.132	0.049	793.005
{ $\phi(a2 + T), p(a + s + T)$ }	8	1342.538	0.235	0.047	791.078
{ $\phi(a2), p(a + s + r)$ }	7	1342.601	0.299	0.046	793.172
{ $\phi(a2 + \ln(T)), p(a + s)$ }	7	1343.023	0.721	0.037	793.594
{ $\phi(a2 + \ln(T)), p(a + s + r)$ }	8	1343.107	0.804	0.035	791.647
{ $\phi(T), p(a + s)$ }	6	1343.189	0.887	0.034	795.788

(continued, next page)

Table 2, continued.

Model ^a	<i>K</i>	QAIC _c	ΔQAIC _c	<i>w_i</i>	-2·log(<i>L</i>)
{φ(a2), p(a + s + T)}	7	1343.200	0.898	0.034	793.772
{φ(a3), p(a + s)}	7	1343.201	0.899	0.034	793.772
{φ(.), p(a + s)}	5	1343.277	0.975	0.032	797.899
{φ(a2 + ln(T)), p(a + s + T)}	8	1343.425	1.123	0.030	791.965
{φ(a1 + T), p(a + s)}	8	1343.451	1.149	0.030	791.991
{φ(a1 * T), p(a + s)}	10	1343.471	1.169	0.029	787.937
{φ(ln(T)), p(a + s)}	6	1343.771	1.469	0.025	796.369
{φ(a3 + ln(T)), p(a + s)}	8	1344.009	1.707	0.023	792.549
{φ(a2 + s), p(a + s)}	7	1344.242	1.939	0.020	794.813
Sequoia-Kings Canyon Study Area (1991-2004; n = 157, $\hat{c} = 1.030$)					
{φ(a1), p(r)}	5	670.165	0.000	0.071	348.426
{φ(a1*T), p(r)}	7	670.479	0.315	0.061	344.666
{φ(a1 + T), p(r)}	6	670.651	0.487	0.056	346.878
{φ(a2 * T), p(r)}	7	671.029	0.864	0.046	345.216
{φ(a1 * ln(T)), p(r)}	7	671.073	0.909	0.045	345.260
{φ(a1), p(r + T)}	6	671.125	0.961	0.044	347.352
{φ(a1 + ln(T)), p(r)}	6	671.285	1.120	0.040	347.512
{φ(a1 * T), p(r + T)}	8	671.578	1.414	0.035	343.719
{φ(a1), p(r + ln(T))}	6	671.705	1.540	0.033	347.932
{φ(a2 * ln(T)), p(r)}	7	671.711	1.547	0.033	345.898
{φ(a1 + TT), p(r)}	7	671.750	1.585	0.032	345.936
{φ(a1 + s), p(r)}	6	671.757	1.593	0.032	347.984
{φ(a1 + T), p(r + T)}	7	671.763	1.599	0.032	345.950
{φ((a1 * T) + s), p(r)}	8	672.093	1.929	0.027	344.234
{φ(a1 * T), p(r + ln(T))}	8	672.101	1.936	0.027	344.242

^aKey to model notation:

a1: age effect, with S2 = adults; S1 different;

a2: age effect, with S1 = S2; adults different;

a3: age effect, with different estimates for S1, S2, and adults;

a: age effect in recapture probability (only 2 age classes possible);

s: sex;

T: linear time trend;

ln(T): pseudo-threshold time trend;

TT: quadratic time trend;

r: annual reproductive rate;

wi-effort: “walk-in” survey effort.

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Table 3. Estimates of apparent survival probability (ϕ) by age and sex classes from top model for California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1990-2005. “ p ” indicates probability of recapture.

Study area	Best Model ^a		Sex	1-year-old		2-year-old		≥ 3 -year-old	
	ϕ structure	p structure		$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\phi}$	SE($\hat{\phi}$)
ELD	(a2*T) + s	wi-effort + s	M	0.817	0.049	0.817	0.049	0.849	0.017
			F	0.765	0.055	0.765	0.055	0.803	0.020
LAS	T	a + s + r		0.844	0.011	0.844	0.011	0.844	0.011
SIE	a2	a + s		0.785	0.038	0.785	0.038	0.850	0.012
SKC	a1	r		0.675	0.088	0.888	0.012	0.888	0.012

^aKey to model notation:

a1: age effect, with S2 = adults; S1 different;

a2: age effect, with S1 =S2; adults different;

a: age effect in recapture probability (only 2 age classes possible);

s: sex;

T: linear time trend;

r: annual reproductive rate;

wi-effort: “walk-in” survey effort.

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Table 4. Logit-link function parameter estimates from the best model with a temporal effect for apparent survival (ϕ) of California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1990-2005. Best models were defined by the lowest QAIC_c.

Study area	Model ^a	Δ QAIC _c	Temporal effect	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$)	
							Lower	Upper
ELD	$\phi \{(a2 * T) + s\}$	0.000	T (S1 and S2)	-0.122	0.070	0.58	-0.015	0.259
			T (Adult)	0.022	0.025	1.10	-0.071	0.026
LAS	$\phi \{T\}$	0.000	T	0.045	0.020	0.45	0.006	0.085
SIE	$\phi \{a2 + T\}$	0.103	T	0.033	0.023	0.68	-0.011	0.078
SKC	$\phi \{a1 * T\}$	0.315	T (S1)	-0.112	0.111	0.99	-0.330	0.106
			T (S2 and Adult)	0.057	0.035	0.61	-0.012	0.126

^aKey to model notation:

a1: age effect, with S2 = adults; S1 different;

a2: age effect, with S1 = S2; adults different;

s: sex;

T: linear time trend.

Table 5. Model selection results from a meta-analysis of apparent survival probability (ϕ) for adult California spotted owls in the southern Cascades and Sierra Nevada, California, 1990-2005. Models are ordered by QAIC_c.

Model ^a	<i>K</i>	QAIC _c	ΔQAIC _c	<i>w_i</i>	-2·log(<i>L</i>)
{ ϕ (SKC vs. Rest + TT), p(g * r)} Post-hoc	12	3868.898	0.000	0.727	1691.565
{ ϕ (SKC vs. Rest + t), p(g * r)} Post-hoc	23	3871.945	3.047	0.158	1672.378
{ ϕ (g + t), p(g * r)} Post-hoc	25	3874.951	6.053	0.035	1671.326
{ ϕ (SKC vs. Rest + t), p(g * t)} Post-hoc	69	3875.401	6.503	0.028	1581.274
{ ϕ (SKC vs. Rest + TT), p(g * t)} Post-hoc	59	3876.119	7.221	0.020	1602.769
{ ϕ (SKC vs. Rest + T), p(g * t)} Post-hoc	58	3877.595	8.697	0.009	1606.316
{ ϕ (g + t [coded as mean]), p(g * t)}	71	3878.448	9.550	0.006	1580.151
{ ϕ (g + TT), p(g * t)}	61	3879.338	10.440	0.004	1601.842
{ ϕ (g + t + s), p(g * t + s)} Post-hoc	73	3879.688	10.790	0.003	1577.215
{ ϕ (g + TT + s), p(g * t + s)} Post-hoc	63	3880.618	11.720	0.002	1598.972
{ ϕ (g + T), p(g * t)}	60	3880.630	11.732	0.002	1605.208
{ ϕ (g + t), p(g + r)} Post-hoc	22	3881.010	12.112	0.002	1683.471
{ ϕ (t), p(g * t)}	68	3882.867	13.969	0.001	1590.824
{ ϕ (SKC, Rest), p(g * t)}	57	3883.156	14.258	0.001	1613.946
{ ϕ (TT), p(g * t)}	58	3883.356	14.458	0.001	1612.077
{ ϕ (T), p(g * t)}	57	3884.560	15.662	0.000	1615.351
{ ϕ (g * T), p(g * t)}	63	3884.739	15.841	0.000	1603.093
{ ϕ (g + ln(T)), p(g * t)}	60	3884.785	15.887	0.000	1609.363
{ ϕ (g), p(g * t)}	59	3886.561	17.663	0.000	1613.211
{ ϕ (g * TT), p(g * t)}	66	3886.919	18.021	0.000	1599.038
{ ϕ (g * ln(T)), p(g * t)}	63	3888.922	20.024	0.000	1607.275
{ ϕ (.), p(g * t)}	56	3889.557	20.659	0.000	1622.416
{ ϕ (g * t), p(g * t)}	106	3928.948	60.050	0.000	1556.855
{ ϕ (g * t + s), p(g * t + s)}	108	3929.794	60.896	0.000	1553.437
{ ϕ (g * t + s), p(g * t)}	107	3930.948	62.050	0.000	1556.724
{ ϕ (g * t), p((g + t) * s)}	89	3936.634	67.736	0.000	1600.579
{ ϕ (g * t), p(g + t + s)}	73	3938.089	69.191	0.000	1635.616
{ ϕ (g * t), p(g + t)}	72	3938.889	69.991	0.000	1638.505
{ ϕ (g * t + s), p((g + t) * s)}	90	3938.907	70.009	0.000	1600.742
{ ϕ (g * t), p(r * s)}	59	3939.250	70.352	0.000	1665.900
{ ϕ (g * t + s) p(g + t + s)}	74	3940.144	71.246	0.000	1635.582
{ ϕ (g * t + s), p(g + t)}	73	3940.927	72.029	0.000	1638.454
{ ϕ (g * t + s), p(r * s)}	60	3941.299	72.401	0.000	1665.877
{ ϕ (g * t) p(r + s)}	58	3941.945	73.047	0.000	1670.665

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Table 5, continued

Model ^a	K	QAIC _c	Δ QAIC _c	w_i	$-2 \cdot \log(\mathcal{L})$
{ ϕ (g * t), p(r)}	57	3942.785	73.887	0.000	1673.575
{ ϕ (g * t + s), p(r + s)}	60	3946.079	77.181	0.000	1670.656
{ ϕ (g * t + s), p(r)}	59	3946.889	77.991	0.000	1673.538
{ ϕ (g * t * s), p(g * t + s)}	162	3986.390	117.492	0.000	1492.923
{ ϕ (g * t * s), p(g * t)}	161	3987.463	118.565	0.000	1496.201
{ ϕ (g * t * s), p((g + t) * s)}	144	3992.543	123.645	0.000	1538.542
{ ϕ (g * t + s), p(g * t * s)}	162	3992.689	123.791	0.000	1499.222
{ ϕ (g * t * s), p(g + t + s)}	130	3998.240	129.342	0.000	1574.636
{ ϕ (g * t * s), p(g + t)}	129	3999.477	130.579	0.000	1578.035
{ ϕ (g * t * s), p(r * s)}	114	4011.929	143.031	0.000	1622.749
{ ϕ (g * t * s), p(r + s)}	113	4014.214	145.316	0.000	1627.175
{ ϕ (g * t * s), p(r)}	112	4015.242	146.344	0.000	1630.341
{ ϕ (g * t * s), p(g * t * s)}	212	4040.300	171.402	0.000	1434.880

^aKey to model notation:

g: study area effect;

t: year effect;

s: sex effect;

T: linear time trend;

Ln(T): pseudo-threshold time trend;

TT: quadratic time trend;

r: annual reproductive rate.

Table 6. Proportion of subadults among all female California spotted owls of known age for which reproductive output was determined on each of four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005.

Year	Study Area			
	ELD	LAS	SIE	SKC
1991	0.20	0.05	0.00	0.14
1992	0.00	0.06	0.03	0.04
1993	0.00	0.21	0.06	0.08
1994	0.25	0.12	0.15	0.07
1995	0.00	0.02	0.10	0.03
1996	0.09	0.02	0.13	0.04
1997	0.03	0.08	0.11	0.00
1998	0.10	0.08	0.13	0.04
1999	0.20	0.10	0.22	0.11
2000	0.04	0.08	0.20	0.14
2001	0.08	0.12	0.11	0.21
2002	0.09	0.18	0.03	0.04
2003	0.13	0.18	0.11	0.04
2004	0.06	0.03	0.10	0.09
2005	0.07	0.00	0.13	--

Table 7. Model selection results for covariance structures used in mixed models analyses of time trends and age effects in reproductive output of California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005.

Covariance structure	K	AIC_c	ΔAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
<i>El Dorado study area (n = 349)</i>					
CSH	17	806.249	0.000	0.637	770.4
ARH(1)	18	808.073	1.824	0.256	770.0
TOEPH(3)	19	809.810	3.561	0.107	769.5
CS	3	837.870	31.621	0.000	831.8
AR(1)	4	838.616	32.367	0.000	830.5
Exp(Yr)	4	839.916	33.667	0.000	831.8
AR(1) w/ EXP(Yr)	6	842.746	36.497	0.000	830.5
TOEP	18	857.373	51.124	0.000	819.3
<i>Lassen study area (n = 623)</i>					
TOEPH(3)	19	1436.560	0.000	0.763	1397.3
ARH(1)	18	1439.432	2.872	0.182	1402.3
CSH	17	1441.812	5.251	0.055	1406.8
Exp(Yr)	4	1496.865	60.304	0.000	1488.8
CS	3	1496.239	59.678	0.000	1490.2
AR(1)	4	1496.265	59.704	0.000	1488.2
AR(1) w/ EXP(Yr)	6	1497.036	60.476	0.000	1484.9
TOEP	18	1509.132	72.572	0.000	1472.0
<i>Sierra study area (n = 519)</i>					
CSH	17	1043.522	0.000	0.435	1008.3
ARH(1)	18	1043.668	0.146	0.405	1006.3
TOEPH(3)	19	1045.523	2.001	0.160	1006.0
AR(1)	4	1191.678	148.156	0.000	1183.6
CS	3	1193.047	149.525	0.000	1187.0
Exp(Yr)	4	1194.978	151.456	0.000	1186.9
AR(1) w/ EXP(Yr)	6	1195.564	152.043	0.000	1183.4
TOEP	18	1213.768	170.246	0.000	1176.4
<i>Sequoia-Kings Canyon study area (n = 374)</i>					
CSH	16	870.624	0.000	0.676	837.1
ARH(1)	17	873.119	2.495	0.194	837.4
TOEPH(3)	18	873.927	3.303	0.130	836.0
Exp(Yr)	4	923.108	52.485	0.000	915.0
CS	3	925.165	54.541	0.000	919.1
AR(1) w/ EXP(Yr)	6	926.029	55.405	0.000	913.8
AR(1)	4	927.508	56.885	0.000	919.4
TOEP	17	940.919	70.295	0.000	905.2

Table 8. Model selection results for mixed models analyses of time trends and age effects in reproductive output of California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005.

Model	K	AIC_c	ΔAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
El Dorado study area (CSH covariance structure; $n = 349$)					
EO + T + psub	21	793.726	0.000	0.792	748.9
EO + T	20	796.761	3.035	0.174	754.2
T	19	802.910	9.184	0.008	762.6
T + psub	20	803.261	9.535	0.007	760.7
ln(T)	19	803.510	9.784	0.006	763.2
ln(T) + psub	20	803.861	10.135	0.005	761.3
TT	20	804.661	10.935	0.003	762.1
TT + psub	21	805.126	11.400	0.003	760.3
EO	19	806.810	13.084	0.001	766.5
EO + psub	20	807.061	13.335	0.001	764.5
Intercept	18	808.973	15.247	0.000	770.9
psub	19	810.110	16.384	0.000	769.8
Lassen study area (TOEPH(3) covariance structure; $n = 623$)					
EO	21	1423.837	0.000	0.507	1380.3
EO + psub	22	1425.687	1.849	0.201	1380.0
EO + T	22	1425.787	1.949	0.191	1380.1
EO + T + psub	23	1427.643	3.806	0.076	1379.8
Intercept	20	1431.795	7.958	0.009	1390.4
ln(T)	21	1433.637	9.800	0.004	1390.1
T	21	1433.837	10.000	0.003	1390.3
psub	21	1433.937	10.100	0.003	1390.4
TT	22	1435.187	11.349	0.002	1389.5
ln(T) + psub	22	1435.687	11.849	0.001	1390.0
T + psub	22	1435.887	12.049	0.001	1390.2
TT + psub ^b					

(continued, next page)

Table 8, continued.

Model	K	AIC_c	ΔAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
Sierra study area (CSH covariance structure; $n = 519$)					
EO + psub	20	1035.787	0.000	0.285	994.1
psub	19	1036.523	0.736	0.197	997.0
EO + T + psub	21	1037.859	2.072	0.101	994.0
Intercept	18	1038.368	2.581	0.078	1001.0
ln(T) + psub	20	1038.387	2.600	0.078	996.7
T + psub	20	1038.587	2.800	0.070	996.9
EO	19	1038.823	3.036	0.062	999.3
T	19	1039.623	3.836	0.042	1000.1
TT + psub	21	1039.859	4.072	0.037	996.0
EO + T	20	1039.987	4.200	0.035	998.3
TT	20	1041.787	6.000	0.014	1000.1
ln(T) ^b					
Sequoia-Kings Canyon Study Area (CSH covariance structure; $n = 374$)					
Intercept	17	865.119	0.000	0.232	829.4
EO	18	865.627	0.508	0.180	827.7
psub	18	866.427	1.308	0.121	828.5
EO + psub	19	867.247	2.128	0.080	827.1
T	18	867.327	2.208	0.077	829.4
ln(T)	18	867.327	2.208	0.077	829.4
EO + T	19	867.847	2.728	0.059	827.7
T + psub	19	868.447	3.328	0.044	828.3
ln(T) + psub	19	868.547	3.428	0.042	828.4
TT	19	868.947	3.828	0.034	828.8
TT + psub	20	869.480	4.361	0.026	827.1
EO + T + psub	20	869.480	4.361	0.026	827.1

^a Key to parameter codes:

EO = even-odd year effect;

T = linear time trend;

PSub = proportion of subadult females in among female owls sampled.

^b Model would not converge because of infinite likelihood.

Table 9. Parameter estimates from mixed models analyses of time trends in reproductive output of California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005.

Study Area	Model	Parameter ^a	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$)	
						Lower	Upper
ELD	EO + T + psub	Intercept	2.279	0.175	0.077	1.937	2.622
		EO	-0.631	0.133	0.210	-0.891	-0.371
		T	-0.089	0.016	0.176	-0.120	-0.058
		psub	-2.323	0.881	0.379	-4.050	-0.596
LAS	EO	Intercept	1.033	0.150	0.145	0.739	1.327
		EO	-0.757	0.201	0.266	-1.151	-0.363
SIE	EO + psub	Intercept	1.038	0.211	0.203	0.625	1.452
		EO	-0.301	0.168	0.560	-0.631	0.029
		psub	-3.736	1.499	0.401	-6.673	-0.798
SKC	Intercept	Intercept	0.555	0.110	0.199	0.339	0.771

^a Key to parameter codes:

EO: even-odd year effect;

T: linear time trend;

Psub: proportion of subadult females in among female owls sampled.

Table 10. Estimate of mean reproductive output (\bar{b}) across years, temporal process standard deviation ($\hat{\sigma}_{\text{temporal}}$), and amount of process variation explained by the mixed model analyses of trends in reproductive output of California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005.

Study area	\bar{b} ^a	SE (\bar{b})	$\hat{\sigma}_{\text{temporal}}$ ^b	CV ^c	% of variation explained ^d
ELD	0.988	0.154	0.317	0.321	87.2
LAS	0.624	0.140	0.275	0.441	51.6
SIE	0.478	0.106	0.153	0.320	41.1
SKC	0.555	0.110	0.152	0.275	- ^e

^a Mean estimate across years based on intercepts-only mixed model.

^b Standard deviation of temporal process variation.

^c Estimated as $\frac{\hat{\sigma}_{\text{temporal}}}{\bar{b}}$.

^d Percentage of the temporal variation explained by the fixed-effect trend model selected using minimum AIC_c calculated as:

$$\frac{\hat{\sigma}_{\text{temporal}}^2 - \hat{\sigma}_{\text{residual}}^2}{\hat{\sigma}_{\text{temporal}}^2}$$

where $\hat{\sigma}_{\text{residual}}$ is the variation remaining from that explained by the selected model.

^e Not applicable because selected model was an intercept-only model.

Table 11. Model selection results for covariance structures used in mixed models meta-analysis of time trends and age effects in reproductive output of California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2005.

Covariance structure	K	AIC_c	ΔAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
TOEPH(3)	19	4301.912	0.000	0.612	4263.5
ARH(1)	18	4303.071	1.159	0.343	4266.7
CSH	17	4307.131	5.219	0.045	4272.8
AR(1) w/ EXP(Yr)	10	4385.519	83.607	0.000	4365.4
Exp(Yr)	8	4388.278	86.366	0.000	4372.2
AR(1)	4	4434.822	132.910	0.000	4426.8
CS	3	4437.013	135.101	0.000	4431.0
TOEP	17	4441.831	139.919	0.000	4407.5

Table 12. Model selection results for covariance structures used in mixed models meta-analysis examining effects of both male and female age on reproductive output of California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2005.

Covariance structure	K	AIC_c	ΔAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
TOEPH(3)	19	3952.048	0.000	0.848	3913.6
ARH(1)	18	3955.503	3.455	0.151	3919.1
CSH	17	3964.861	12.812	0.001	3930.5
AR(1) w/ EXP(Yr)	9	4059.506	107.457	0.000	4041.4
AR(1)	4	4061.823	109.775	0.000	4053.8
TOEP	17	4064.861	112.812	0.000	4030.5
CS	3	4071.314	119.266	0.000	4065.3
Exp(area)	7	4073.266	121.217	0.000	4059.2

Table 13. Model selection results for a mixed models meta-analysis of time trends in reproductive output of California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2005.

Model	K	AIC_c	ΔAIC_c	w	$-2 \cdot \log(\mathcal{L})$
Area * T + psub	28	4275.785	0.000	0.935	4218.9
Area * TT + psub	32	4281.253	5.468	0.061	4216.1
Area * T	27	4288.223	12.439	0.002	4233.4
Area * ln(T) + psub	28	4288.685	12.900	0.001	4231.8
Area * TT	31	4290.582	14.798	0.001	4227.5
Area * ln(T)	27	4301.823	26.039	0.000	4247.0
Area * EO + psub	28	4308.285	32.500	0.000	4251.4
Area + EO + psub	25	4320.107	44.322	0.000	4269.4
Area + EO + T + psub	26	4320.964	45.179	0.000	4268.2
Area * EO	27	4321.823	46.039	0.000	4267.0
Area + psub	24	4324.452	48.668	0.000	4275.8
Area + ln(T) + psub	25	4325.507	49.722	0.000	4274.8
Area + T + psub	25	4325.707	49.922	0.000	4275.0
Area + TT + psub	26	4327.364	51.579	0.000	4274.6
Area + EO	24	4332.252	56.468	0.000	4283.6
Area + EO + T	25	4332.907	57.122	0.000	4282.2
Area	23	4336.700	60.915	0.000	4290.1
Area + ln(T)	24	4337.552	61.768	0.000	4288.9
Area + T	24	4337.852	62.068	0.000	4289.2
Area + TT	25	4339.207	63.422	0.000	4288.5
ELD&LAS * T + psub	24	4344.052	68.268	0.000	4295.4
SKC * T + psub	24	4362.752	86.968	0.000	4314.1
ELD & LAS vs SIE & SKC	21	4362.801	87.017	0.000	4320.3
TT + psub	23	4366.200	90.415	0.000	4319.6
EO + T + psub	23	4366.900	91.115	0.000	4320.3
psub	21	4369.201	93.417	0.000	4326.7
ln(T) + psub	22	4370.349	94.565	0.000	4325.8
EO + psub	22	4370.649	94.865	0.000	4326.1
T + psub	22	4370.749	94.965	0.000	4326.2
EO	21	4390.401	114.617	0.000	4347.9
EO + T	22	4391.449	115.665	0.000	4346.9
SKC vs Other	21	4392.301	116.517	0.000	4349.8
Intercept	20	4394.856	119.071	0.000	4354.4
ln(T)	21	4396.001	120.217	0.000	4353.5
T	21	4396.201	120.417	0.000	4353.7
TT	22	4397.549	121.765	0.000	4353.0

^a Key to parameter codes: EO = even-odd year effect; T = linear time trend; Psub = proportion of subadult females in among female owls sampled.

Table 14. Parameter estimates for the best model from a mixed-models meta-analysis of time trends in reproductive output of California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2005.

Model	Parameter	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$)	
					Lower	Upper
Area * T + psub	Intercept	0.628	0.236	0.376	0.165	1.092
	AREA (ELD)	1.222	0.132	0.108	0.963	1.481
	AREA (LAS)	0.201	0.104	0.514	-0.002	0.404
	AREA (SIE)	0.122	0.109	0.888	-0.091	0.335
	T	0.004	0.026	6.137	-0.047	0.056
	T * AREA (ELD)	-0.093	0.014	0.153	-0.121	-0.065
	T * AREA (LAS)	-0.016	0.012	0.762	-0.040	0.008
	T * AREA (SIE)	-0.017	0.013	0.742	-0.042	0.008
	psub	-1.366	0.348	.255	-2.048	-0.684

Table 15. Model selection results for a mixed models meta-analysis of the effects of male and female age on reproductive output of California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2005.

Model	K	AIC_c	ΔAIC_c	w_i	$-2 \cdot \log(\mathcal{L})$
Area *T + female[S1, S2, A] + male[S1, S2, A]	31	3922.079	0.000	0.995	3858.9
Area *T + female[S1, S2, A]	29	3933.733	11.654	0.003	3874.7
Area *T + female[a2]	28	3934.763	12.684	0.002	3877.8
Area *T + female[a1]	28	3942.063	19.984	0.000	3885.1
Area *T + male[S1, S2, A]	29	3951.733	29.654	0.000	3892.7
Area *T + male[a1]	28	3953.163	31.084	0.000	3896.2
Area *T + male[a2]	28	3953.363	31.284	0.000	3896.4
Area *T (psub removed)	27	3966.096	44.017	0.000	3911.2
Intercept	20	4394.896	472.817	0.000	4354.4

Table 16. Parameter estimates for the best model from a mixed-models meta-analysis examining effects of male and female age on reproductive output of California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2005.

Model	Parameter	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$)	
					Lower	Upper
Area * T + female[S1, S2, A] + male[S1, S2, A]	Intercept	0.210	0.265	1.263	-0.310	0.730
	Area (ELD)	1.162	0.140	0.120	0.888	1.435
	Area (LAS)	0.175	0.106	0.603	-0.032	0.382
	Area (SIE)	0.088	0.110	1.254	-0.128	0.304
	T	0.001	0.027	27.224	-0.052	0.054
	T*Area (ELD)	-0.091	0.015	0.162	-0.120	-0.062
	T*Area (LAS)	-0.012	0.013	1.087	-0.036	0.013
	T*Area(SIE)	-0.018	0.013	0.731	-0.043	0.008
	Male (A)	0.132	0.080	0.605	-0.024	0.288
	Male (S1)	-0.239	0.128	0.537	-0.490	0.013
	Female (A)	0.269	0.082	0.304	0.109	0.429
	Female (S1)	-0.182	0.122	0.671	-0.422	0.057

Table 17. Least-squared means estimates of reproductive output (\hat{b}) for male and female California spotted owls of three age-classes in the southern Cascades and Sierra Nevada, California, 1991-2005. Estimates are from the mixed model {Area*T + female(S1, S2, A) + male(S1, S2, A)}.

Sex and age-class	\hat{b}	SE (\hat{b})	95% CI (\hat{b})	
			Lower	Upper
Male A	0.978	0.232	0.492	1.466
Male S2	0.714	0.276	0.156	1.274
Male S1	0.238	0.302	0.000	0.844
Female A	1.124	0.234	0.634	1.614
Female S2	0.586	0.280	0.018	1.152
Female S1	0.222	0.290	0.000	0.804

Table 18. Model selection results from analyses of population change for California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004. Random effects were run on $\phi(t)$ $p(t)$ $l(t)$ models, the best fixed effects model for each study area. Models are ordered by QAIC_c.

Model	QAIC _c	Δ QAIC _c	w_i	K	$-2 \cdot \log(\mathcal{L})$
El Dorado study area (1990-2005; n = 180, $\hat{c} = 1.051$)					
TT random effects	1902.799	0.000	0.664	36	461.706
ln(T) random effects	1904.728	1.928	0.253	36.31	462.946
T random effects	1907.546	4.747	0.062	39.21	459.287
constant random effects	1909.788	6.989	0.020	40.57	458.473
$\lambda(t)$, $\phi(t)$, $p(t)$ fixed effects	1916.610	13.811	0.001	45	455.271
$\lambda(s^*t)$, $\phi(t)$, $p(t)$ fixed effects	1929.354	26.555	0.000	60	433.042
$\lambda(t)$, $\phi(s^*t)$, $p(t)$ fixed effects	1936.082	33.282	0.000	62	434.986
$\lambda(s^*t)$, $\phi(s^*t)$, $p(s^*t)$ fixed effects	1982.214	79.415	0.000	89	413.558
Lassen study area (1990-2005; n = 241, $\hat{c} = 1.129$)					
constant random effects	2146.256	0.000	0.553	34	454.345
ln(T) random effects	2148.428	2.172	0.187	35	454.367
T random effects	2148.430	2.174	0.187	35	454.369
TT random effects	2150.289	4.032	0.074	36	454.073
$\lambda(t)$, $\phi(t)$, $p(t)$ fixed effects	2161.260	15.004	0.000	45	445.444
$\lambda(t)$, $\phi(s^*t)$, $p(t)$ fixed effects	2183.981	37.725	0.000	62	430.096
$\lambda(s^*t)$, $\phi(t)$, $p(t)$ fixed effects	2187.363	41.107	0.000	60	438.030
$\lambda(s^*t)$, $\phi(s^*t)$, $p(s^*t)$ fixed effects	2227.680	81.424	0.000	89	410.357
Sierra study area (1990-2005; n = 264, $\hat{c} = 1.210$)					
constant random effects	2364.711	0.000	0.512	36	657.285
T random effects	2366.700	1.990	0.190	37	657.133
ln(T) random effects	2366.860	2.149	0.175	37	657.293
TT random effects	2367.568	2.857	0.123	38	655.855
$\lambda(t)$, $\phi(t)$, $p(t)$ fixed effects	2381.068	16.357	0.000	47	649.869
$\lambda(t)$, $\phi(s^*t)$, $p(t)$ fixed effects	2392.796	28.085	0.000	64	623.869
$\lambda(s^*t)$, $\phi(t)$, $p(t)$ fixed effects	2406.546	41.835	0.000	62	642.122
$\lambda(s^*t)$, $\phi(s^*t)$, $p(s^*t)$ fixed effects	2429.490	64.779	0.000	91	598.043
Sequoia-Kings Canyon Study Area (1991-2004; n = 157, $\hat{c} = 1.030$)					
TT random effects	1492.866	0.000	0.426	36.07	268.755
constant random effects	1494.133	1.267	0.226	36.75	268.529
ln(T) random effects	1494.911	2.045	0.153	37.30	268.090
T random effects	1494.933	2.067	0.152	37.23	268.271
$\lambda(t)$, $\phi(t)$, $p(t)$ fixed effects	1497.432	4.566	0.043	39	266.850
$\lambda(s^*t)$, $\phi(t)$, $p(t)$ fixed effects	1515.676	22.810	0.000	52	255.724
$\lambda(t)$, $\phi(s^*t)$, $p(t)$ fixed effects	1520.534	27.669	0.000	54	255.970
$\lambda(s^*t)$, $\phi(s^*t)$, $p(s^*t)$ fixed effects	1547.716	54.850	0.000	77	228.221

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Table 19. Parameter estimates for the best random effects models (β parameters) of population change of California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004. Best models were defined by the lowest QAIC_c.

Study area	Best model	Parameter	$\hat{\beta}_i$	SE($\hat{\beta}_i$)	95% CI ($\hat{\beta}_i$)	
					Lower	Upper
ELD	Quadratic	β_0	0.344	0.098	0.152	0.536
		β_1	-1.027	0.336	-1.686	-0.368
		β_2	0.635	0.250	0.145	1.125
LAS	Mean	β_0	-0.027	0.014	-0.054	0.000
SIE	Mean	β_0	-0.008	0.014	-0.035	0.019
SKC	Quadratic	β_0	0.204	0.109	-0.010	0.418
		β_1	-1.029	0.433	-1.878	-0.180
		β_2	0.965	0.372	0.236	1.694

Table 20. Estimates of mean rate of population change ($\bar{\lambda}$) across time, and temporal process standard deviation ($\hat{\sigma}_{temporal}$) for California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004. Estimates are based on means (intercept-only) random effects models using time-specific estimates of ϕ , p , and λ .

Study area	$\bar{\lambda}$	SE($\bar{\lambda}$)	95% CI($\bar{\lambda}$)		$\hat{\sigma}_{temporal}$	95% CI($\hat{\sigma}_{temporal}$)	
			Lower	Upper		Lower	Upper
ELD	1.007	0.029	0.952	1.066	0.081	0.000	0.188
LAS	0.973	0.014	0.946	1.001	0.000	0.000	0.094
SIE	0.992	0.013	0.966	1.018	0.000	0.000	0.085
SKC	1.006	0.031	0.947	1.068	0.083	0.018	0.195

Table 21. Model selection results from a meta-analyses of population change of California spotted owls in the southern Cascades and Sierra Nevada, California, 1992-2004.

Model ^a	K	QAIC _c	Δ QAIC _c	w_i	$-2 \cdot \log(\mathcal{L})$
$\{\phi(g * t), p(g * t), \lambda(t)\}$	127	6940.351	0.000	0.594	1204.284
$\{\phi(g * t), p(g * t), \lambda(\text{SKC vs. rest})\}$	117	6941.730	1.380	0.298	1227.151
$\{\phi(g * t), p(g * t), \lambda(g)\}$	119	6944.727	4.380	0.067	1225.860
$\{\phi(g * t), p(g * t), \lambda(g + t)\}$	132	6945.690	5.340	0.041	1198.831
$\{\phi(g * t), p(g * t), \lambda(g * t)\}$	163	6980.524	40.170	0.000	1166.030

^a \hat{p} estimated separately for the year immediately following the expansion of the SIE study area and is fixed to zero on the expansion area for years prior to the expansion.. λ estimated separately for the intervals immediately preceding and following the expansion of the Sierra study area.

Table 22. Model selection results from a meta-analysis of recruitment of California spotted owls in the southern Cascades and Sierra Nevada, California, 1992-2004.

Model ^a	K	QAIC _c	Δ QAIC _c	w_i	$-2 \cdot \log(\mathcal{L})$
$\{\phi(g), p(g * t), f(g + t)\}$	81	6899.559	0.000	0.919	1261.288
$\{\phi(g + t), p(g * t), f(g + t)\}$	96	6904.616	5.060	0.073	1234.747
$\{\phi(g + t), p(g * t), f(g)\}$	81	6910.027	10.470	0.005	1271.756
$\{\phi(g), p(g * t), f(g)\}$	68	6911.373	11.810	0.003	1300.262
$\{\phi(\cdot), p(g * t), f(\cdot)\}^a$	64	6915.604	16.050	0.000	1312.809
$\{\phi(g), p(g * t), f(g * t)\}$	115	6924.926	25.370	0.000	1214.629
$\{\phi(g * t), p(g * t), f(g)\}$	119	6957.921	58.360	0.000	1239.054
$\{\phi(g * t), p(g * t), f(g * t)\}$	162	6978.322	78.760	0.000	1166.030

^a \hat{p} set equal to zero for years prior to the expansion of the Sierra study area, and estimated separately for the year immediately following the expansion. \hat{f} estimated separately for the intervals immediately preceding and following the expansion of the Sierra study area.

Table 23. Estimated $\log(\lambda)$ (mean and SE), and temporal variation in λ ($\hat{\sigma}_{\text{temporal}}$, estimate and 95% CI) for California spotted owls on each of four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004.

Study Area	$\overline{\log(\lambda)}$	$se(\overline{\log(\lambda)})$	$\hat{\sigma}_{\text{temporal}}$	95% CI (σ_{temporal})	
				Lower	Upper
ELD	0.007	0.029	0.081	0.000	0.188
LAS	-0.027	0.014	0.000	0.000	0.094
SIE	-0.008	0.014	0.000	0.000	0.085
SKC	0.006	0.031	0.083	0.018	0.195

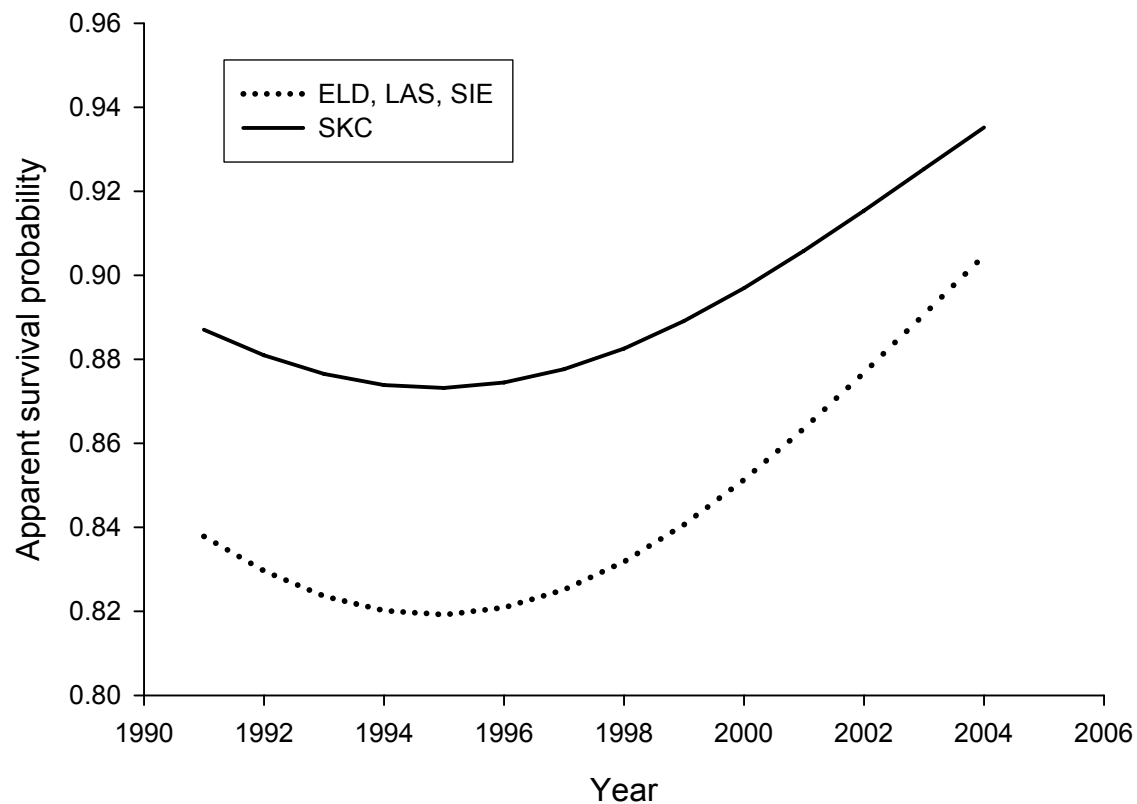


Figure 1. Apparent survival probability of adult California spotted owls in the southern Cascades and Sierra Nevada, California, 1991-2004, based on the model $\{\phi(\text{SKC vs. Rest} + \text{TT}), p(g * r)\}$.

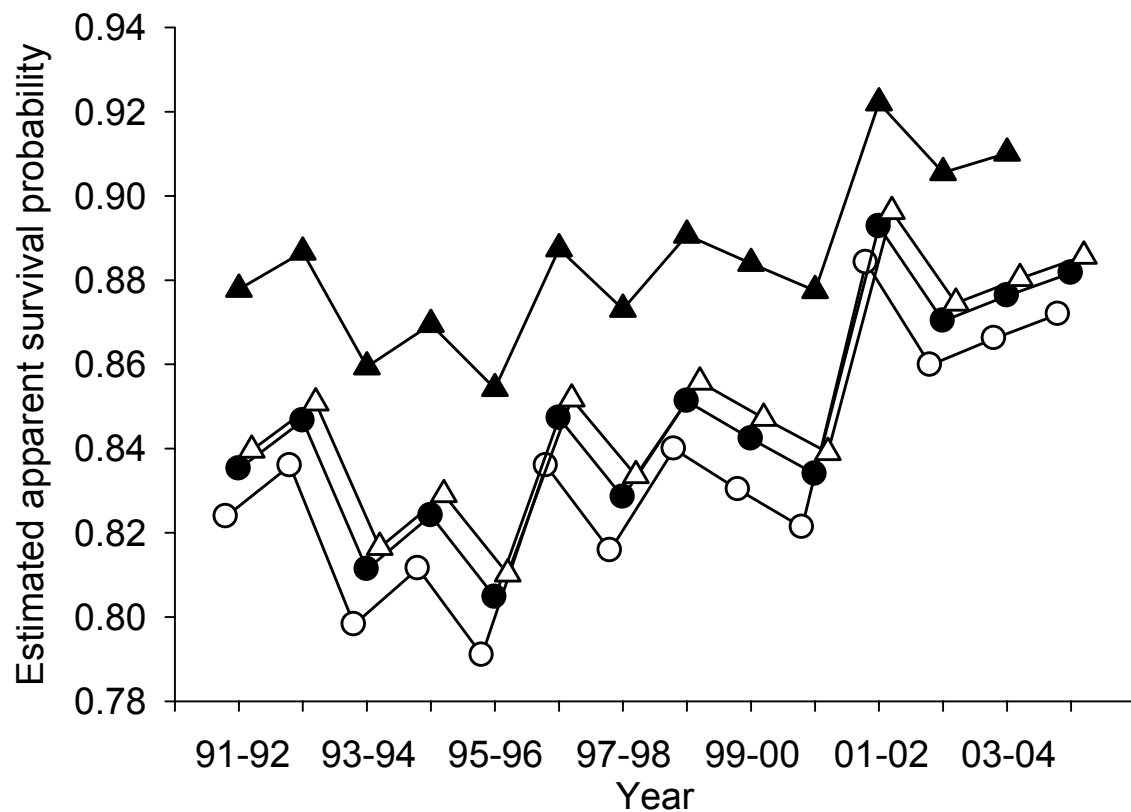


Figure 2. Apparent survival probability of adult California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005, based on model averaged estimates from the meta-analysis *a priori* set of models.

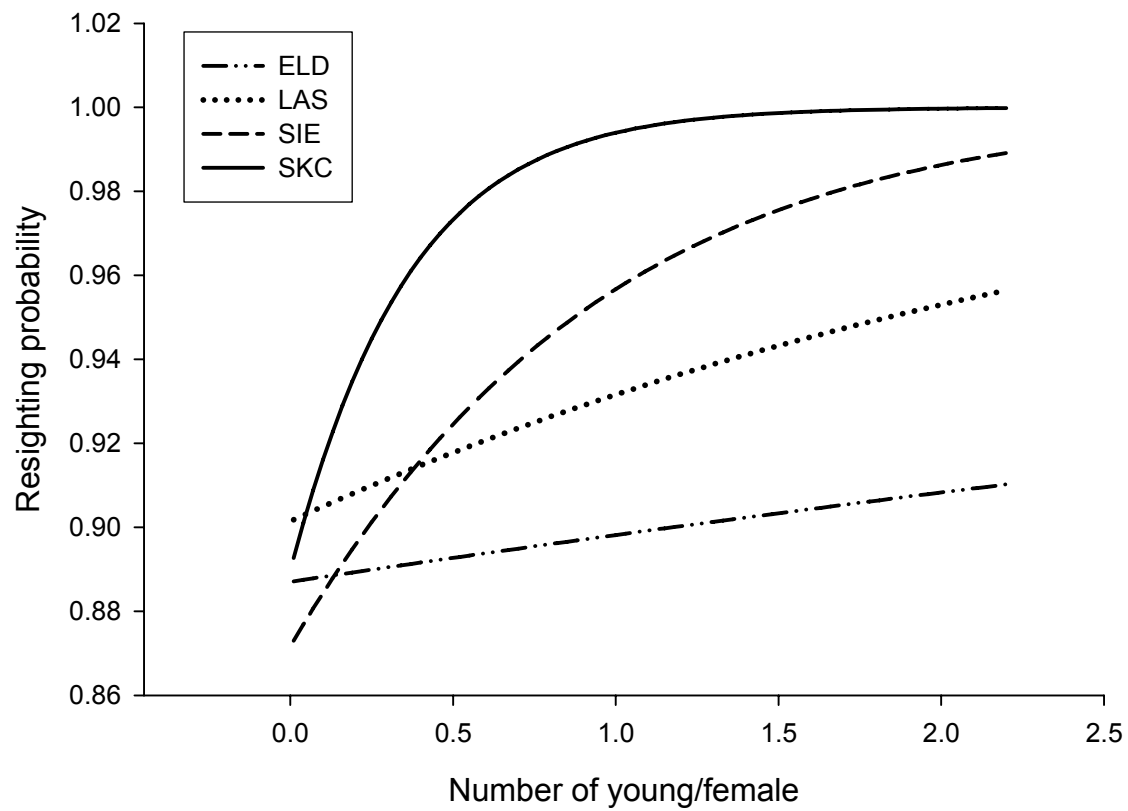


Figure 3. Resighting probability for California spotted owls as a function of reproductive output for four study areas in the southern Cascades and Sierra Nevada, California, 1991-2004, based on the model $\{\phi(\text{SKC vs. Rest} + \text{TT}), p(g * r)\}$.

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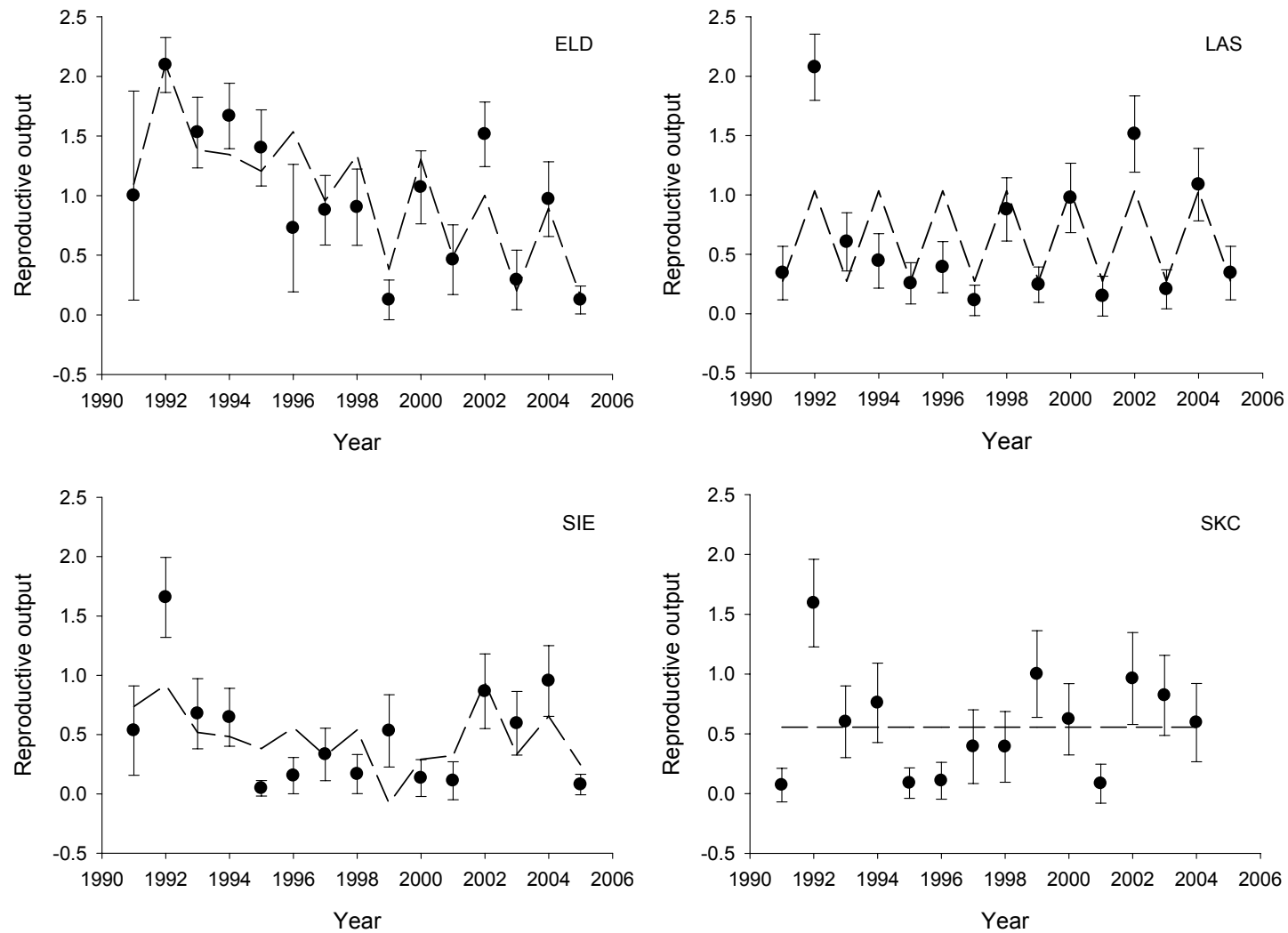


Figure 4. Annual reproductive output of California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005 (point estimates and 95% confidence intervals). Dashed lines indicate the best approximating models from mixed models analyses.

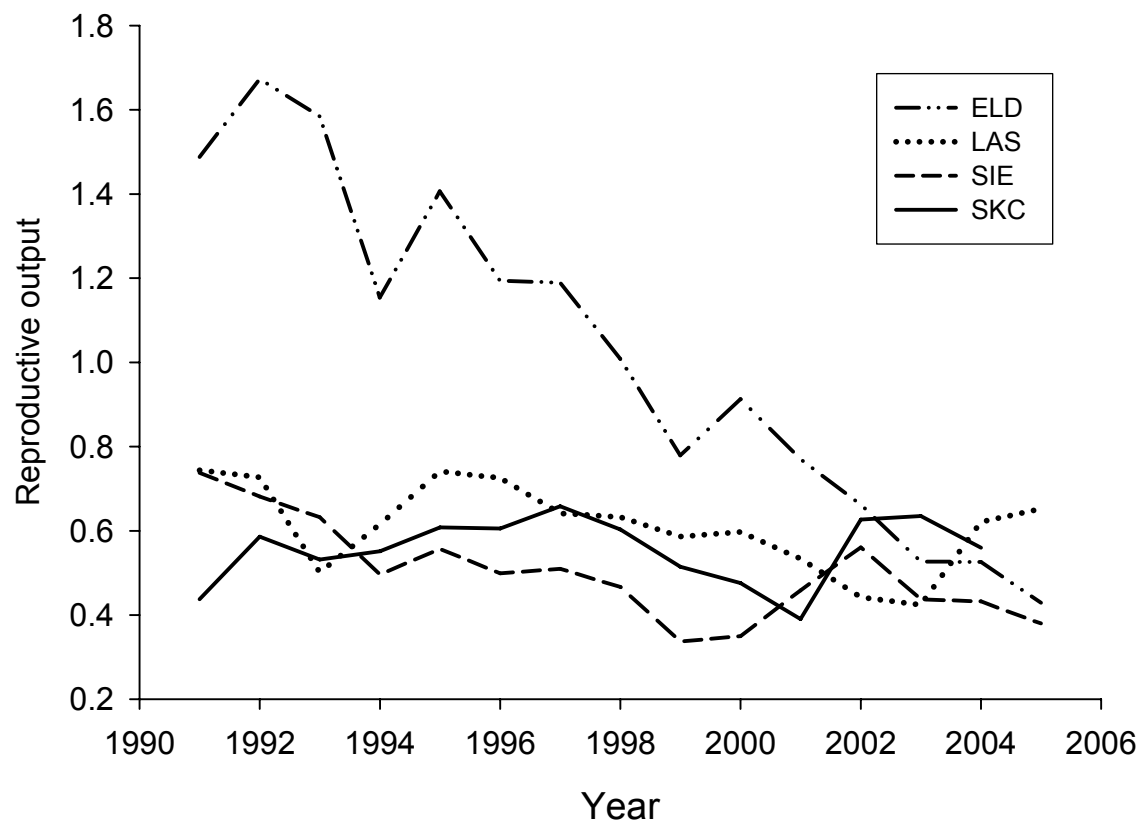


Figure 5. Time trends in reproductive output for California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1991-2005, based on the mixed model {area*T+psub}.

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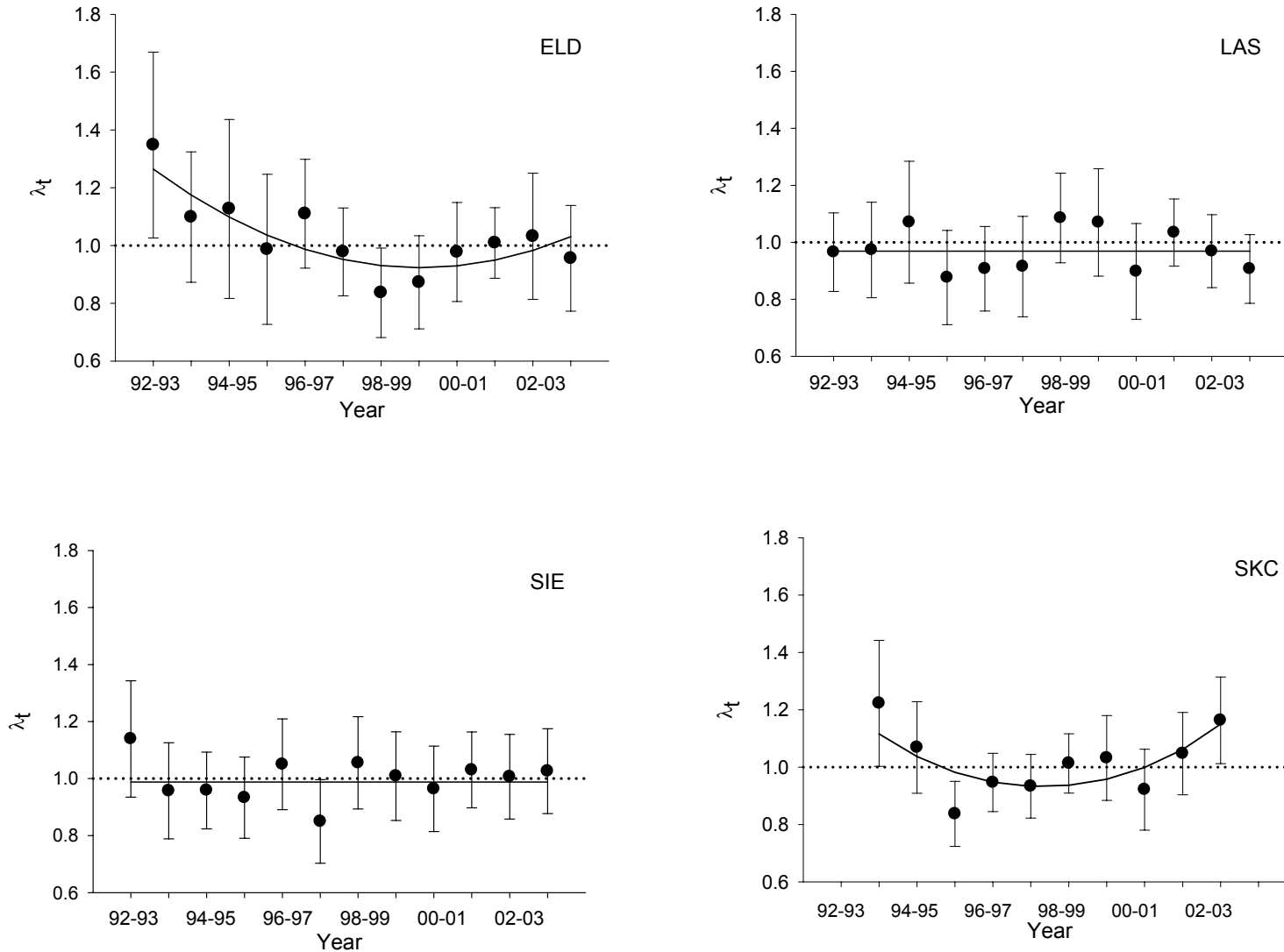


Figure 6. Annual estimates of population trend (λ_t) for California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004 (point estimates and 95% confidence intervals). Solid lines indicate the best random effects model for each study area.

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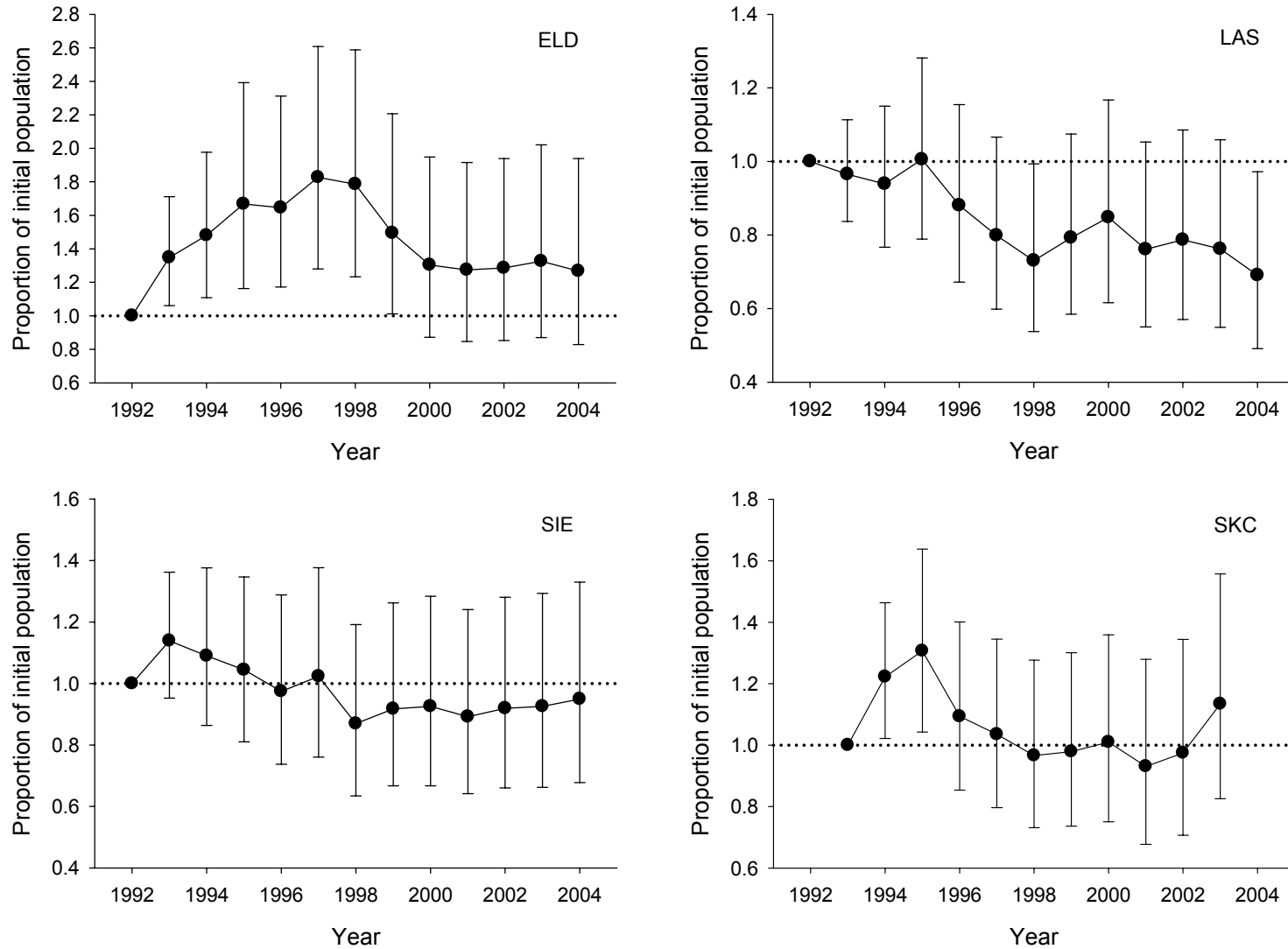


Figure 7. Trends in population size expressed as realized change (Δ_t), based on estimates of λ_t , for California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004 (point estimates and 95% confidence intervals). Realized change is the proportion of the initial population size remaining each year. Note that the graphs area scaled differently.

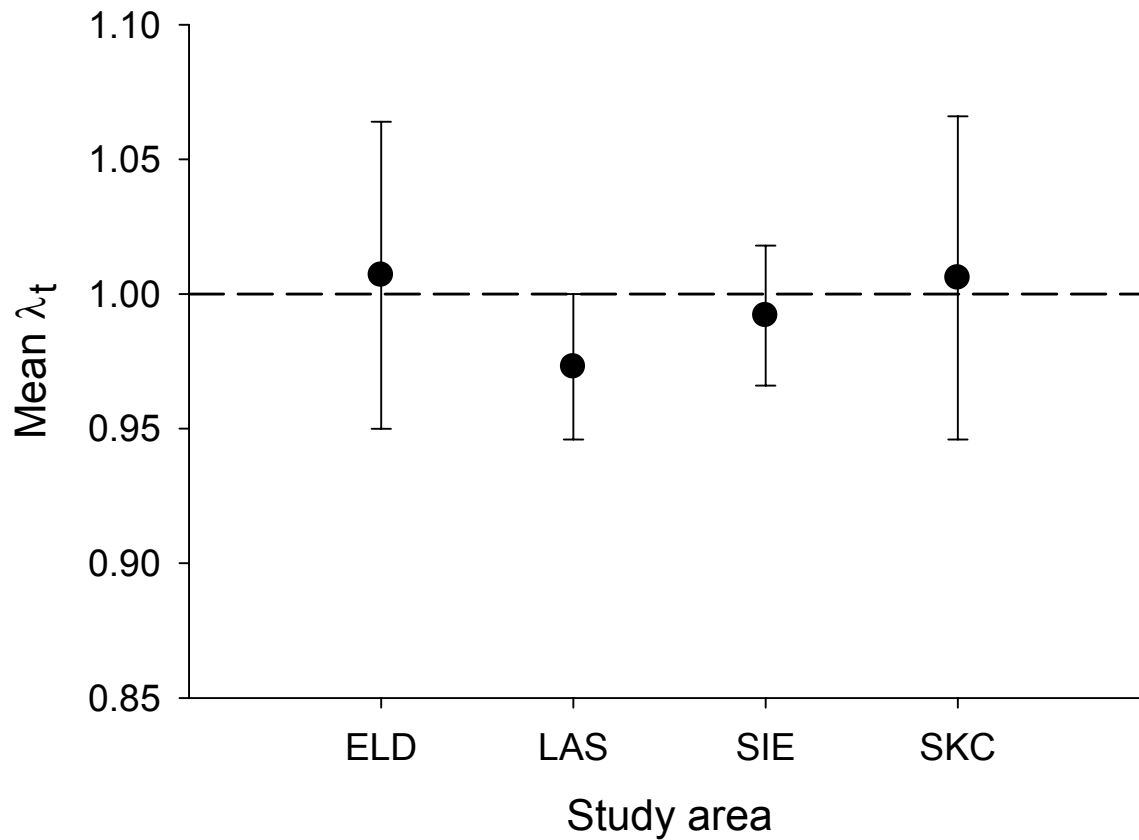


Figure 8. Mean estimated population change (λ_t) for California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004 (point estimates and 95% confidence intervals).

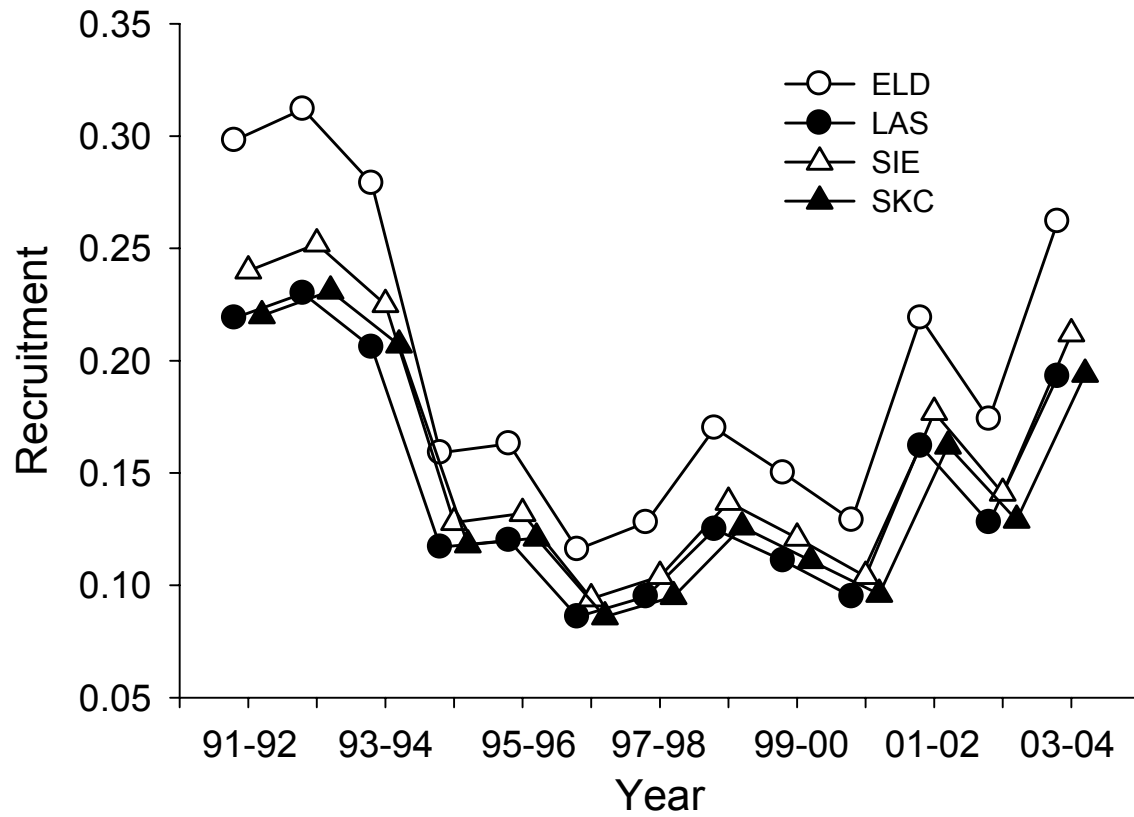


Figure 9. Annual estimates of recruitment rates (f) for California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 1992-2004, based on the model $\{\phi(g), p(g * t), f(g + t)\}$.

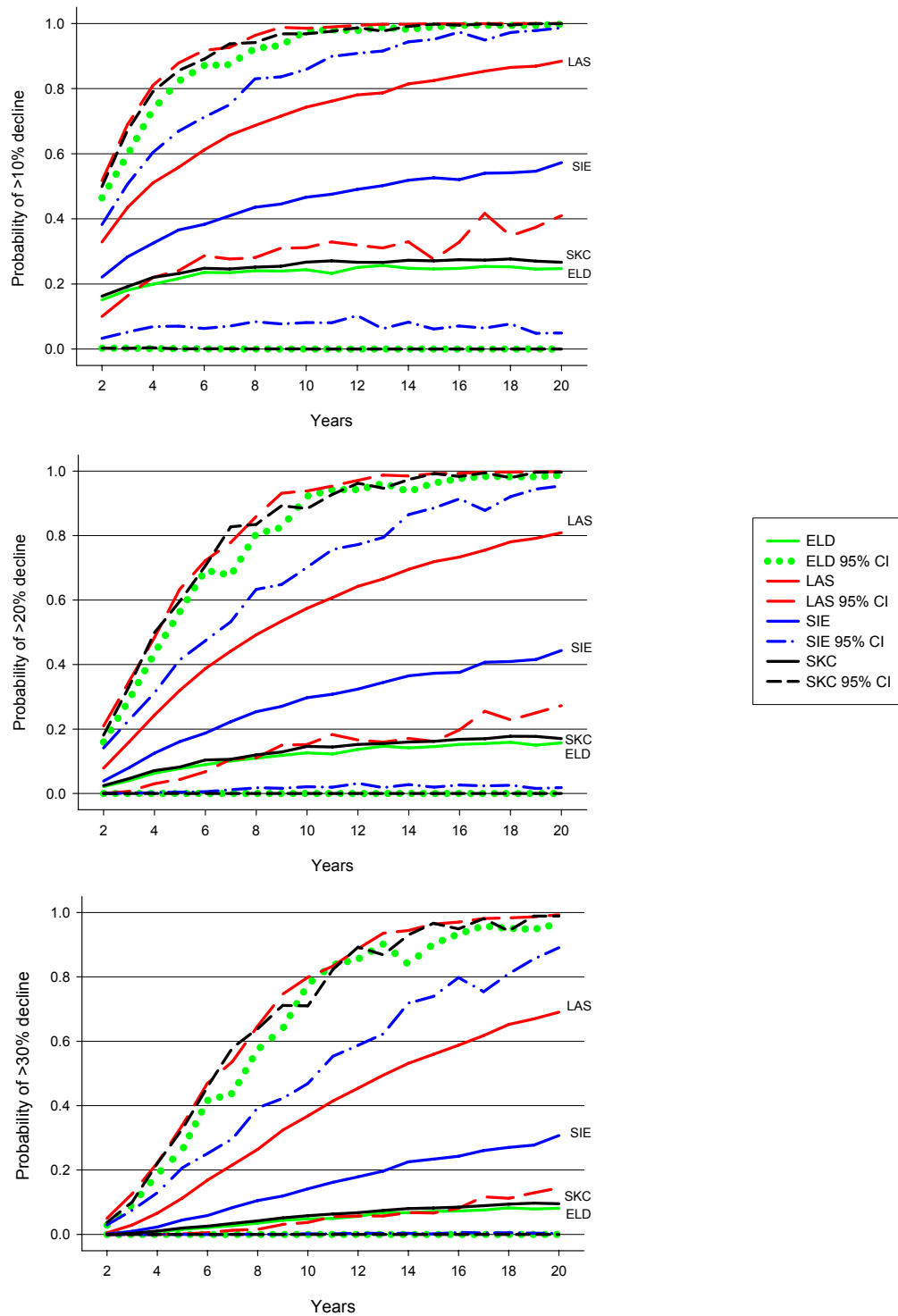


Figure 10. Probability of detecting >10%, >20% and >30% declines in populations of California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 2-20 years into the future, given current estimates of population trend and associated estimated temporal process variance.

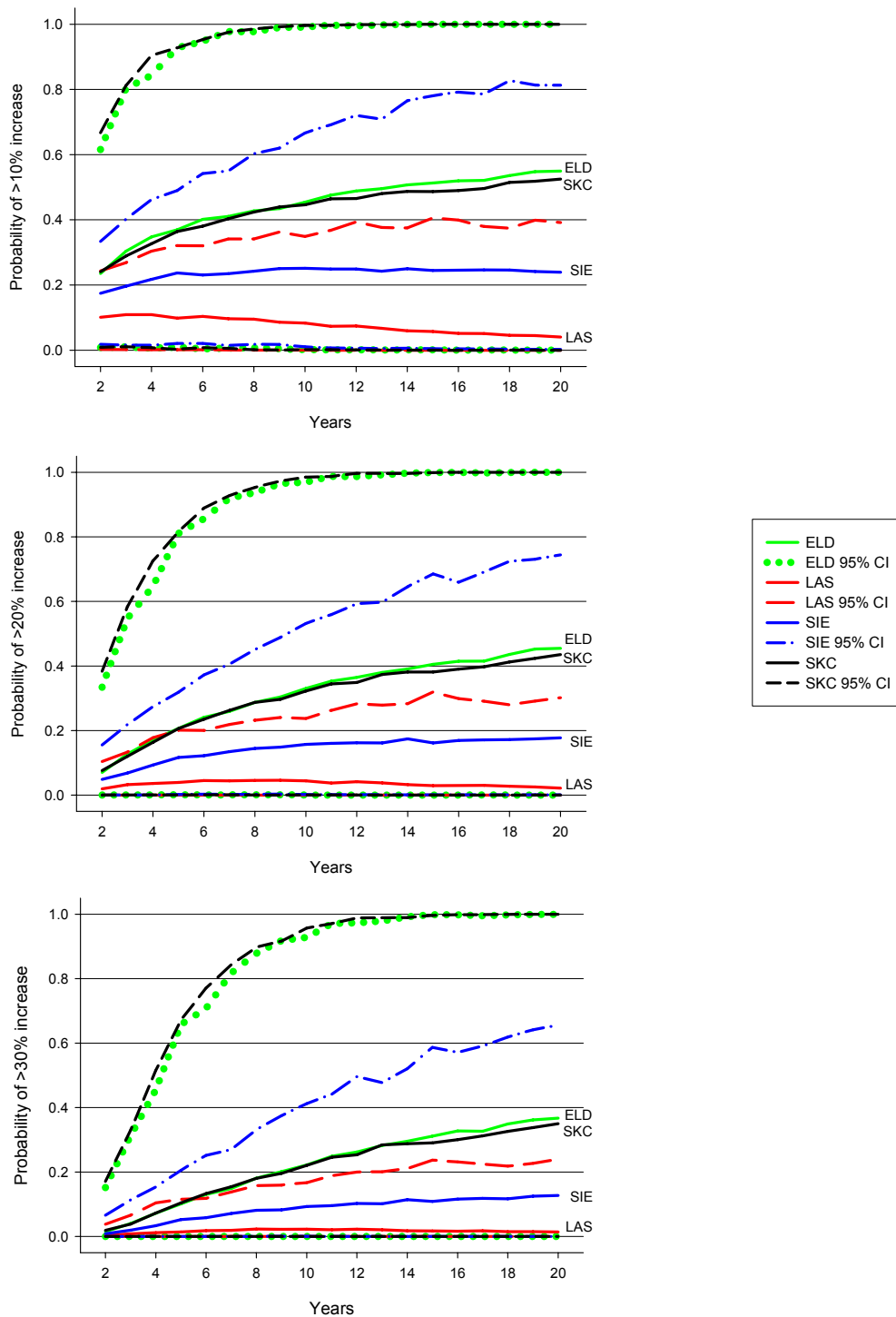


Figure 11. Probability of detecting >10%, >20% and >30% increases in populations of California spotted owls on four study areas in the southern Cascades and Sierra Nevada, California, 2-20 years into the future, given current estimates of population trend and associated estimated temporal process variance, and assuming habitat is not limiting.

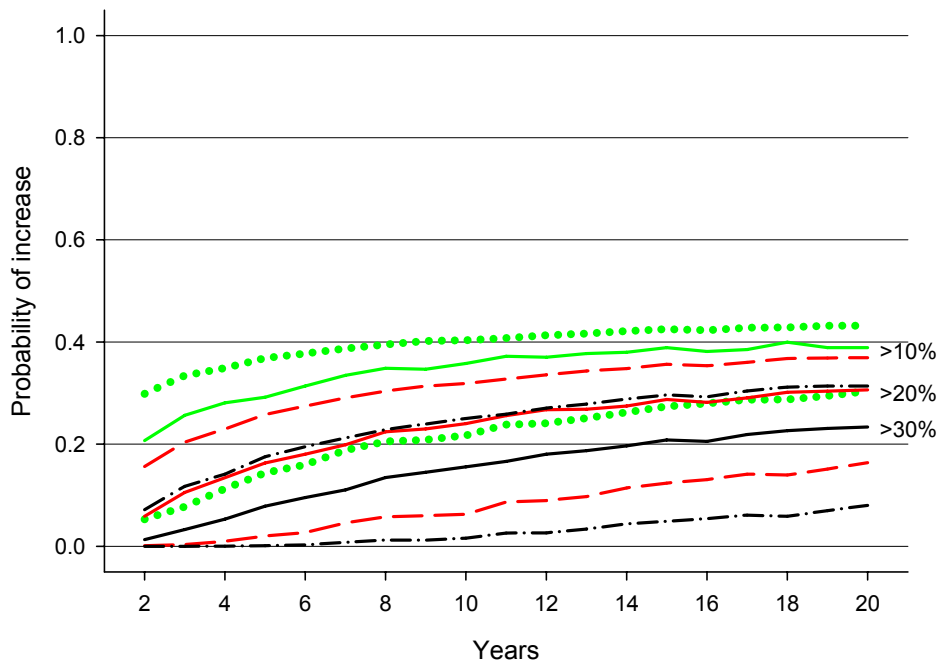
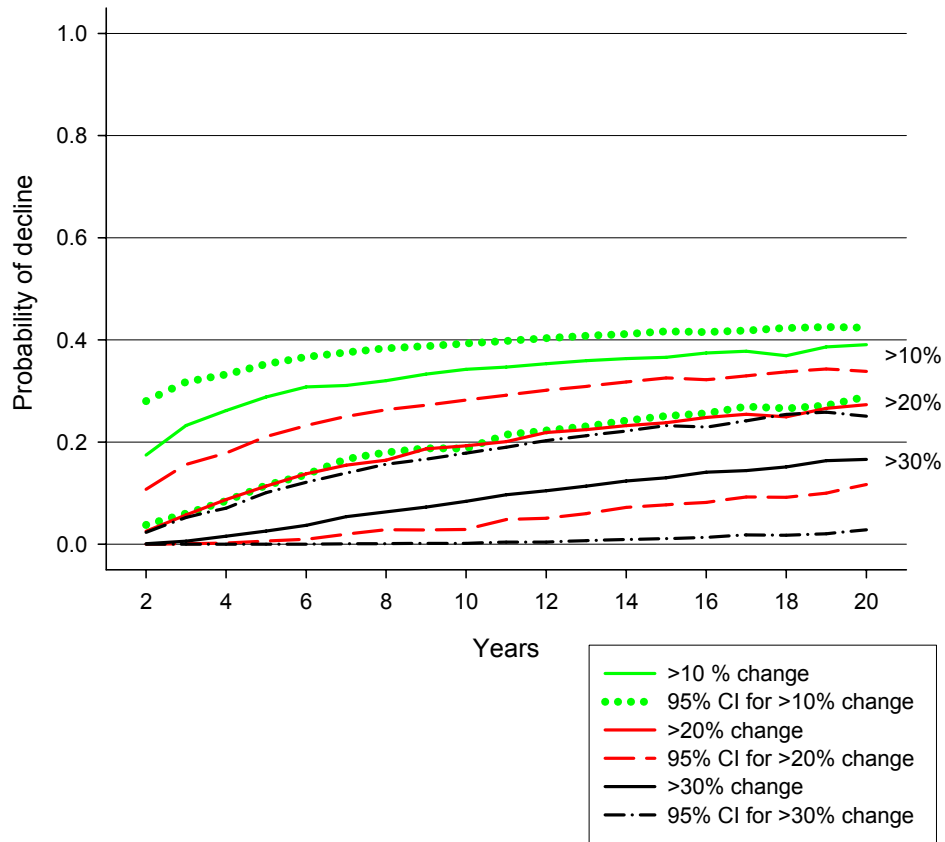


Figure 12. Probability of decrease and increase in a hypothetical population 2-20 years into the future, given $\lambda = 1.0$ and estimated temporal process variance equal to that observed for California spotted owls in the southern Cascades and Sierra Nevada from 1991-2005.

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Appendix B. Protocol for error-checking data sets.

The data files for survival analysis (capture history file) and reproductive output analysis were error checked by a hired independent observer. The third data file for rates of population change was condensed from the survival analysis data file after it was fully cleaned and verified.

To error check the survival files, 10 capture histories were drawn for each study area, and then study area biologists were asked to provide paper copies of the data forms that supported each capture history. One male and one female record from each age class (S1, S2, A) was randomly drawn, 2 records were drawn at random, and 2 “unusual” records (records that had a -1 frequency code, etc.) were drawn. The draw of the “unusual” records was done, if needed, to ensure that at least 2 of the records selected included capture histories with gaps (e.g. 11001110). To error check reproductive output files, 10 records were drawn at random for each study area, and then study area biologists were asked to provide paper copies of the data forms that supported each record.

All survival (capture histories) and reproductive output records were sent as field data sheets that were scanned PDF files attached to e-mails or as paper copies through overnight mail.

When the verifier found any suspicious or unclear details in a record, the verifier contacted the biologist for clarification. If it was an issue of clarity (each biologist had unique methods to record their data and it took some experience to understand) a note was made and kept with the record. When errors were found in the first round of error checking, another sample of 10 records was selected as described above, and the error checking process was repeated. If there had been are errors in the second sample, the entire file may have been checked (as specified in the verification protocol), however there were no errors in the second round of files we checked (2 files did not pass on the first round).

Paper copies of the records that were error-checked were kept. Study area biologists signed a statement at the workshop certifying that their data were accurate, up to-date, and ready for analysis (see form below).

Certification of Data

Name of Study Area _____

Location of Study Area _____

Number of Years of Banding _____

I (we) have checked and rechecked both the capture-recapture data and fecundity data and certify that these data sets are ready for analysis and interpretation.

I (we) also certify that these data have undergone the data verification procedures for the workshop.

(print and sign name)

Date: _____

I (we) have participated in, and/or agree to, the selection of models and analyses to be used for the January 2006 meta-analysis of California spotted owl data, and agree to allow my (our) data to be used in that analysis.

print and sign name

Date: _____

An ASCII data file for input to Program MARK was generated from each study area's survival and population change database files after the survival file was verified as free from errors. The reproductive output files were imported into SAS as Excel files after being verified as free from errors.

Appendix C. Protocol for modeling apparent survival probability on individual study areas using QAICc model selection criteria in program MARK.

1. $\{\phi(a*s*t) p(a*s*t)\}$ is the global model using the CJS model. Structure 6 sets of PIMs with time-specific values separate for each sex and age class (S1, S2, A).

2. Determine goodness of fit using median \hat{c} on global model. Use median \hat{c} for QAICc and model selection.

Note: the global model would not converge in program MARK for some study areas; in such cases, $\{\phi(s*t) p(s*t)\}$ was the global model.

3. Using $\{\phi(a*s*t)\}$, model p as follows:

- a. $p(.)$
- b. $p(a)$
- c. $p(s)$
- d. $p(a+s)$
- e. $p(c)$, where c = choice of one covariate selected based on biologist's experience (e.g., survey effort, TT, etc., where TT is a quadratic time trend).
- f. $p(r)$, where r = reproductive rate covariate
- g. $p(t)$, where t = categorical time effect
- h. $p(T)$, where T = linear time trend
- i. $p(\ln[T])$, log-linear, or "pseudo-threshold" time trend

Add the following temporal structures on p to the best model(s) among a-d (and e, if appropriate):

- j. $p(r)$, where r = reproductive rate covariate
- k. $p(t)$ unless it crashes
- l. $p(T)$
- m. $p(\ln(T))$

4. Using the best p structure from the models in step 3, model ϕ with the following age and sex structure models:

Structure	Coding
(S1, S2, A) + s	$\{\phi (a3 + s)\}$
(S1, S2, A)	$\{\phi (a3)\}$
(S1, S2 = A) + s	$\{\phi (a1 + s)\}$
(S1, S2 = A)	$\{\phi (a1)\}$
(S1= S2, A) + s	$\{\phi (a2 + s)\}$
(S1= S2, A)	$\{\phi (a2)\}$
(S1= S2 = A) + s	$\{\phi (s)\}$
(S1= S2 = A)	$\{\phi (.)\}$
(S1, S2 = A) * s	$\{\phi (a1 * s)\}$
(S1= S2, A) * s	$\{\phi (a2 * s)\}$

by the following time models:

+ t
+ T
* T
+ TT
*TT
+ ln(T)
*ln(T)
no time effect

giving a total of 80 additional models.

Note: in models with a sex effect and a multiplicative time effect, we modeled $\{\phi (\text{age}*\text{time}) + \text{sex}\}$.

5. Run the best 2-3 ϕ models from step 4 with the best 2-3 p models from step 4.
6. Construct table of model selection results.
7. Graph age, sex, and time-specific model averaged survival estimates and SE of survival.
8. Report estimates, SE, and CI for important ϕ beta variables (e.g., sex effects, trend effects, age effects).

Note: Profile likelihood CI will be used for estimates of ϕ at parameter boundaries, as needed.

Note: The “best” model(s) is/are defined as a maximum of the 3 lowest AICc models with $\Delta\text{AICc} \leq 2$.

Appendix D. Protocol for meta-analysis modeling of apparent survival probability using QAICc model selection criteria in program MARK.

1. $\{\phi(g*s*t) p(g*s*t)\}$ is the global model for CJS model.
2. Determine goodness of fit using median \hat{c} on global model. Use median \hat{c} for QAICc and model selection.
3. Run the following models.

Model		Description of ϕ structure	Description of p structure
1	$\{\phi_{\cdot}, p_{g*t}\}$	No effects	Study area and year effects with interactions
2	$\{\phi_g, p_{g*t}\}$	Study area effect	Study area and year effects with interactions
3	$\{\phi_{g+t}, p_{g*t}\}$	Study area effect with additive year effects	Study area and year effects with interactions
4	$\{\phi_{g+T}, p_{g*t}\}$	Study area effect with additive linear time effect	Study area and year effects with interactions
5	$\{\phi_{g+TT}, p_{g*t}\}$	Study area effect with additive quadratic time effect	Study area and year effects with interactions
6	$\{\phi_{g+\ln(T)}, p_{g*t}\}$	Study area effect with additive log time effect	Study area, year, and gender effects with all interactions
7	$\{\phi_{g*t}, p_{g+t+s}\}$	Study area and year effects with interactions	Additive study area, year and gender effects
8	$\{\phi_{g*t}, p_{g*t}\}$	Study area and year effects with interactions	Study area and year effects with interactions
9	$\{\phi_{g*t}, p_r\}$	Study area and year effects with interactions	Annual reproductive rate effect
10	$\{\phi_{g*t}, p_{r*s}\}$	Study area and year effects with interactions	Annual reproductive rate and gender effects with interactions
11	$\{\phi_{g*t}, p_{g+t}\}$	Study area and year effects with interactions	Additive study area and year effects
12	$\{\phi_{g*t}, p_{r+s}\}$	Study area and year effects with interactions	Additive annual reproductive rate and gender effects
13	$\{\phi_{g*t}, p_{(g+t)*s}\}$	Study area and year effects with interactions	Additive study area and year effects interacting with gender
14	$\{\phi_{g*T}, p_{g*t}\}$	Study area and linear time effects with interactions	Study area and year effects with interactions
15	$\{\phi_{g*t+s}, p_r\}$	Study area and year effects with interactions and an additive gender effect	Annual reproductive output
16	$\{\phi_{g*t+s}, p_{r+s}\}$	Study area and year effects with interactions and an additive gender effect	Annual reproductive output with an additive gender effect
17	$\{\phi_{g*t+s}, p_{g*t*s}\}$	Study area and year effects with interactions and an additive gender effect	Study area, year, and gender effects with all interactions
18	$\{\phi_{g*t+s}, p_{g*t+s}\}$	Study area and year effects with	Study area and year effects with

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		interactions and an additive gender effect	interactions and an additive gender effect
19	$\{\phi_{g^*t+s}, p_{(g+t)^*s}\}$	Study area and year effects with interactions and an additive gender effect	Additive study area and year effects interacting with gender
20	$\{\phi_{g^*t+s}, p_{g^*t}\}$	Study area and year effects with interactions and an additive gender effect	Additive study area and year effects
21	$\{\phi_{g^*t+s}, p_{g+t+s}\}$	Study area and year effects with interactions and an additive gender effect	Additive study area, year, and gender effects
22	$\{\phi_{g^*t+s}, p_{g^*t}\}$	Study area and year effects with interactions and an additive gender effect	Study area and year effects with interactions
23	$\{\phi_{g^*t+s}, p_{r^*s}\}$	Study area and year effects with interactions and an additive gender effect	Annual reproductive rate and gender effects with interactions
24	$\{\phi_{g^*t^*s}, p_{r+s}\}$	Study area, year, and gender effects with all interactions	Additive annual reproductive rate and gender effects
25	$\{\phi_{g^*t^*s}, p_{r^*s}\}$	Study area, year, and gender effects with all interactions	Annual reproductive rate and gender effects with interactions
26	$\{\phi_{g^*t^*s}, p_{(g+t)^*s}\}$	Study area, year, and gender effects with all interactions	Additive study area and year effects interacting with gender
27	$\{\phi_{g^*t^*s}, p_{g+t}\}$	Study area, year, and gender effects with all interactions	Additive study area and year effects
28	$\{\phi_{g^*t^*s}, p_r\}$	Study area, year, and gender effects with all interactions	Annual reproductive rate effects
29	$\{\phi_{g^*t^*s}, p_{g^*t}\}$	Study area, year, and gender effects with all interactions	Study area and year effects with interactions
30	$\{\phi_{g^*t^*s}, p_{g^*t^*s}\}$	Study area, year, and gender effects with all interactions	Study area, year, and gender effects with all interactions
31	$\{\phi_{g^*t^*s}, p_{g+t+s}\}$	Study area, year, and gender effects with all interactions	Additive study area, year, and gender effects
32	$\{\phi_{g^*t^*s}, p_{g^*t+s}\}$	Study area, year, and gender effects with all interactions	Study area and year effects with interactions and an additive gender effect
33	$\{\phi_{g^*TT}, p_{g^*t}\}$	Study area and quadratic time effect with interactions	Study area and year effects with interactions
34	$\{\phi_{g^*\ln(T)}, p_{g^*t}\}$	Study area and log-linear time effect with interactions	Study area and year effects with interactions
35	$\{\phi_{SKC, Rest}, p_{g^*t}\}$	Group effect of SKC study area vs. other study areas	Study area and year effects with interactions
36	$\{\phi_t, p_{g^*t}\}$	Year effect	Study area and year effects with interactions
37	$\{\phi_T, p_{g^*t}\}$	Linear time effect	Study area and year effects with interactions
38	$\{\phi_{TT}, p_{g^*t}\}$	Quadratic time effect	Study area and year effects with interactions

4. Report table of model selection results.
5. Graph study area, sex, and time-specific model averaged survival estimates and SE of survival.
6. Report estimates, SE, and CI for important ϕ beta variables (e.g., area effects, trend effects, sex effects).

Note: Profile likelihood CI will be used for estimates of ϕ at parameter boundaries, as needed.

Note: The “best” model(s) is/are defined as a maximum of the 3 lowest AICc models with $\Delta\text{AICc} \leq 2$.

Appendix E. Protocol for modeling California spotted owl reproductive output on individual study areas.

1. For known age class females, calculate the proportion of subadults for each study area each year. Use this proportion as a covariate in reproductive output estimation (covariate_{p_{sub}}). Analysis will include all females, regardless of whether or not age class was determined.

2. Estimate reproductive output using the following models with and without covariate_{p_{sub}}:

Intercept-only

T (linear time trend)

TT (quadratic time trend)

ln(T) (log-linear or “pseudo-threshold” time trend)

EO (Even/Odd year effect)

EO + T (Even/Odd year effect with a linear time trend)

3. Site and year will each be modeled as a random effect.

4. Proc MIXED will be used to model reproductive output. The variance-covariance structures modeled include: AR(1), AR(1) with EXP(Yr), ARH(1), CS, CSH, LOCAL EXP(fixed effect time), TOEPLITZ, and TOEPH(3). Choice between variance-covariance structures will be made using AIC_c model selection based on REML in the T model without covariate_{p_{sub}}.

5. Estimate $\hat{\sigma}^2_{\text{temporal}}$ for reproductive output from the intercept-only model.

Appendix F. Protocol for meta-analysis of California spotted owl reproductive output to evaluate time effects.

1. For known age class females, calculate the proportion of subadults for each study area each year. Use this proportion as a covariate in reproductive output estimation (covariate_{psub}). Analysis will include all females, regardless of whether or not age class was determined. Years for reproductive output meta-analysis will be 1991-2005.

2. Estimate reproductive output using the following models with and without covariate_{psub}:

Intercept-only

T (linear time trend)

TT (quadratic time trend)

ln(T) (log-linear or “pseudo-threshold” time trend)

EO (Even/Odd year effect)

EO + T (Even/Odd year effect with a linear time trend)

Study Area

Study Area + T

Study Area * T

Study Area + TT

Study Area * TT

Study Area + ln(T)

Study Area * ln(T)

Study Area + EO

Study Area * EO

Study Area + T + EO

SKC vs. other 3 study areas

LAS and ELD vs. SIE and SKC

QUASI POST HOC ANALYSIS to evaluate similarity in trends:

SKC vs. other 3 study areas + best time structure from above

LAS and ELD vs. SIE and SKC + best time structure from above

3. Site and year will be modeled as in analyses of individual study areas.

4. Methods for modeling and structuring variance will be the same as those used in analyses of individual study areas.

Appendix G. Protocol for meta-analysis of California spotted owl reproductive output to evaluate effects of male and female age.

1. Begin with data sets used in individual study area and meta-analyses of reproductive output. Eliminate all records in which age class of any owl is unknown. Eliminate all records of unpaired owls.
2. Define the “top models” from results of meta-analyses of reproductive output with any covariate structure removed by the following criterion: maximum of top 3 models within $\Delta AIC=2$. Estimate reproductive output using the following models:
 - 2a. Top models
 - 2b. Top models + male age class [S1, S2, A]
 - 2c. Top models + male age class [S1, (S2 + A)]
 - 2d. Top models + male age class [(S1 + S2), A]
 - 2e. Top models + female age class [S1, S2, A]
 - 2f. Top models + female age class [S1, (S2 + A)]
 - 2g. Top models + female age class [(S1 + S2), A]
 - 2h. Top model + best structure of male age class from models 2b-2d, and best structure of female age class among models 2e-2g (“best” based on ΔAIC).
3. Territory and year will be modeled as in analyses of individual study areas.
4. Methods for modeling and structuring variance will be the same as those used in analyses of individual study areas.

Appendix H. Protocol for modeling population change on individual study areas using the Pradel model and QAICc model selection criteria in program MARK.

1. Truncate data sets to the first year when “core” or “density” study areas were adequately surveyed. Input files for studies without expansion areas will have two groups, males and females (labeled Mcore and Fcore). Input files for studies with expansion areas will have four groups: males from the core study area, females from the core study area, males from the expansion area, and females from the expansion area (Mcore, Fcore, Mexp, and Fexp, respectively). This differs from the instructions for coding data sent to participants prior to the workshop, and allows for estimation of population change in the interval between pre- and post-study area expansion. See below for parameterization of data sets from studies with expansion areas.
2. Estimate median \hat{c} under CJS for territorial owls using model $\{\phi(s^*t) p(s^*t)\}$. For studies with expansion areas (only SIE in 2006), estimate \hat{c} with core and expansion sites combined. Use median \hat{c} for model selection and calculation of QAICc.
3. Run the following 4 fixed effects models, adjusting the number of parameters in MARK using the associated formulae, where K = number of encounter occasions:

Model	No. Parameters	No. Parameters with adjustment for \hat{c}
$\{\lambda(t) \phi(t) p(t)\}$	3K - 4	[3K - 4] + 1
$\{\lambda(s^*t) \phi(s^*t) p(s^*t)\}$	2(3K - 4)	[2(3K - 4)] + 1
$\{\lambda(s^*t) \phi(t) p(t)\}$	4(K - 2) + 3	[4(K-2) + 3] + 1
$\{\lambda(t) \phi(t) p(s^*t)\}$	4(K-2) + 5	[4(K-2) + 5] + 1

Note: we had originally proposed to construct the following three additional models, but upon further consideration, they were deemed biologically nonsensical, because they constrained phi less than they constrained lambda. This required that recruitment for each of the sexes must exactly compensate for the differences in phi to give the same lambda value. (Furthermore, these models did not converge properly).

Nonsensical Model	No. Parameters	No. Parameters with adjustment for \hat{c}
$\{\lambda(t) \phi(s^*t) p(t)\}$	4(K-2) + 3	[4(K-2) + 3] + 1
$\{\lambda(t) \phi(s^*t) p(s^*t)\}$	5(K-2) + 5	[5(K-2) + 5] + 1
$\{\lambda(s+t) \phi(s^*t) p(s^*t)\}$	5(K-2) + 6	[5(K-2) + 6] + 1

4. Select the best fixed effects model from step 3 based on QAICc. If there is a sex effect in top models of any individual study, then incorporate the sex effect in the meta-analysis of population change.

5. Estimate variance components of the best model for $\ln(\lambda)$ using the following random effects model structures. If the best fixed effects model did not contain sex effects, constrain the PIMs so that males = females for all parameters. Save the results (real parameter estimates) from each model. Do not include λ_1 (confounded, non-identifiable), λ_2 (may be biased), and λ_{k-1} (confounded, non-identifiable) from analysis. For studies with expansion areas, use the λ_i from the core area for the first year prior to and following the expansion.

- T (linear time trend)
- TT (quadratic time trend)
- ln(T) (log-linear or “pseudo-threshold” time trend)
- dot (constant across time)

6. Select the best random effects model from Step 5 based on $QAIC_c$, and graph the predicted λ estimates.

7. Estimate $\bar{\lambda}$, $SE(\bar{\lambda})$, and $\hat{\sigma}^2_{\text{temporal}}$ on the log scale (beta parameter estimates) from the intercept (mean) random effects model. (This will provide a geometric mean rather than the arithmetic mean that comes from real estimates.) Back transform $\bar{\lambda}$ and the CI; use the Delta method to estimate the variance of the back-transformed $\bar{\lambda}$.

8. Estimate realized population change as the product: $1 * \lambda_3 * \lambda_4 * \dots * \lambda_{k-1}$. Use the Delta method to estimate variance of realized change (on log scale) and associated back-transformed CI.

Parameterization of data from a study with an expansion area – see following page for example. These instructions pertain to a “t” model.

Purpose: to ensure that lambda estimates for the core area for intervals immediately prior to and the p and lambda estimates immediately following an expansion are not confounded with data from the expansion area.

Steps:

1. The design matrix for the core area is unchanged.
2. Add two new columns to the design matrix to calculate lambda estimates for the expansion area for the intervals immediately before and after the expansion.
3. For the expansion group, insert zeros in the cells corresponding to the lambda estimate for the interval prior to the expansion and the lambda estimate for the interval immediately following the expansion. This removes the expansion area data from the lambda calculations for the core area.
4. Insert a 1 in the corresponding cells in the new columns added in step 2 (above) to calculate lambda estimates for the expansion area for the intervals immediately prior to and following the expansion.
5. Follow steps 2-4 for the p estimate for the interval immediately following the expansion, except add only one new column rather than 2. Also, set p for the year of and years prior to the expansion equal to 0 (the fix parameters option in Program MARK).
6. See example on next page.

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Hypothetical study with 8 years data and an expansion in year 4.

Parameter Index Matrix constrained for this example as -- {phi(t) p(t) lambda(t)}

core = original ("core") study area; exp = expansion study area

Design Matrix shown is for model {phi(T) p(T) lambda(t)}. Blank cells below would contain zeros in Mark.

	β_1	β_2	β_3	β_4	β_5	β_6	β_7	β_8	β_9	β_{10}	β_{11}
	Phi T	p T	λ_1	λ_2	λ_3	λ_4	λ_5	λ_6	λ_7	λ_4 exp	λ_5 exp
phi M & F core year 1	1										
phi M & F core year 2	2										
phi M & F core year 3	3										
phi M & F core year 4	4										
phi M & F core year 5	5										
phi M & F core year 6	6										
phi M & F core year 7	7										
phi M & F exp year 1	1										
phi M & F exp year 2	2										
phi M & F exp year 3	3										
phi M & F exp year 4	4										
phi M & F exp year 5	5										
phi M & F exp year 6	6										
phi M & F exp year 7	7										
p M & F core year 2		1									
p M & F core year 3		2									
p M & F core year 4		3									
p M & F core year 5		4									
p M & F core year 6		5									
p M & F core year 7		6									
p M & F core year 8		7									
p M & F exp year 2		1									
p M & F exp year 3		2									
p M & F exp year 4		3									
p M & F exp year 5		4									
p M & F exp year 6		5									
p M & F exp year 7		6									
p M & F exp year 8		7									
lambda M & F core year 1			1								
lambda M & F core year 2				1							
lambda M & F core year 3					1						
lambda M & F core year 4						1					
lambda M & F core year 5							1				
lambda M & F core year 6								1			
lambda M & F core year 7									1		
lambda M & F exp year 1			1								
lambda M & F exp year 2				1							
lambda M & F exp year 3										1	
lambda M & F exp year 4											1
lambda M & F exp year 5							1				
lambda M & F exp year 6								1			
lambda M & F exp year 7									1		

Appendix I. Protocol for meta-analysis of population change using the Pradel model and QAICc model selection criteria in program MARK.

Meta-analyses will be done for the years 1991-2005. A decision on whether or not to include sex effects in the meta-analysis will be made after determining whether individual study area analyses showed sex effects [they did not]. To evaluate the contributions of survival and recruitment to population growth rate (λ) for male and female subadult and adult territorial owls across study areas, a meta-analysis will be done with the following models:

Model #	Model	Model Structure
1	$\{\phi_{(g^{*t})} p_{(g^{*t})} f_{(g)}\}$	All variation is in ϕ
2	$\{\phi_{(g)} p_{(g^{*t})} f_{(g^{*t})}\}$	All variation is in f
3	$\{\phi_{(g^{*t})} p_{(g^{*t})} f_{(g^{*t})}\}$	Variation is in ϕ and f
4	$\{\phi_{(g)} p_{(g^{*t})} f_{(g)}\}$	No variation in ϕ or f
5	$\{\phi_{(g^{+t})} p_{(g^{*t})} f_{(g)}\}$	Variation in ϕ is parallel across study areas
6	$\{\phi_{(g)} p_{(g^{*t})} f_{(g^{+t})}\}$	Variation in f is parallel across study areas
7	$\{\phi_{(g^{+t})} p_{(g^{*t})} f_{(g^{+t})}\}$	Variation in f and ϕ are parallel across study areas
8	$\{\phi_{(-)} p_{(g^{*t})} f_{(-)}\}$	No study area effect

To evaluate whether population growth rate (λ) for male and female subadult and adult territorial owls are correlated across study areas, use the $\{\phi_{(g^{*t})} p_{(g^{*t})} \lambda_{(g^{*t})}\}$ for variance components (random effects) models with the following structures:

Model #	Model	Model Structure
1	$\{\phi_{(g^{*t})} p_{(g^{*t})} \lambda_{(t)}\}$	Time only
2	$\{\phi_{(g^{*t})} p_{(g^{*t})} \lambda_{(g^{*t})}\}$	Study area and time interaction
3	$\{\phi_{(g^{*t})} p_{(g^{*t})} \lambda_{(g^{+t})}\}$	Study area and time additive
4	$\{\phi_{(g^{*t})} p_{(g^{*t})} \lambda_{(g)}\}$	Study area only
5	$\{\phi_{(g^{*t})} p_{(g^{*t})} \lambda_{(SKC-vs-Others)}\}$	Is SKC different than other study areas?

We will not report a single λ for all 4 study areas. Rather, we will report a λ for each study area from the analysis of individual study areas from the best random effects model (see protocol for individual study areas). If the model λ SKC-vs-Others is a top model, we will also report a single λ for (LAS, ELD, SIE).

Notes:

1. Do not include λ_1 (confounded, non-identifiable), λ_2 (may be biased), and $\lambda_{(k-1)}$ (confounded, non-identifiable) in results. When there is an expansion, use the λ from the non-expanded area for the first year following expansion of density study areas. There will be 4 groups for study areas with an expansion; male core, female core, male expansion, female expansion.
2. These are fixed effects models.
3. Determine goodness of fit with program RELEASE with ages pooled for territorial owls, model $\{\phi_{(s^{*t})} p_{(s^{*t})} \lambda_{(s^{*t})}\}$ and median \hat{c} . Use median \hat{c} for model selection and calculation of QAICc, use RELEASE to evaluate lack of fit.

Appendix J. Protocol for population viability analysis (PVA).

Replicate Franklin's 2005 PVA for USFWS with the following changes:

1. Include λ estimates from 2006 (this week's results).
2. Use log-transformed estimates of λ and SE.
3. Eliminate probability of "any decline". Estimate probability of >30%, >20%, and >10%, declines over 20 years.
4. Estimate probability of >30%, >20%, and >10% increases over 20 years.
5. Compare results to hypothetical study area with $\lambda = 1.0$ and process variation from each of: LAS, ELD, SIE, SKC. Overlay hypothetical study population projections with results from 3 above. (Note: cite Lewontin and Cohen, 1969, PNAS)
6. Further expand PVA philosophy and applicability in discussion.

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Appendix K. Full list of model results for individual study area analyses of apparent survival probability.

Model selection results from apparent survival analyses for California Spotted Owls on Eldorado study area.

Model	K	QAICc	Δ QAICc	Akaike Weights	Deviance
{ $\phi((S1=S2,AD)*T)+s$, p(wi-effort+s)}	9	1255.331	0.000	0.077	682.655
{ $\phi(S1=S2,AD)+s$, p(wi-effort+s)}	7	1255.417	0.086	0.073	686.816
{ $\phi((S1=S2,AD)*\ln T)+s$, p(wi-effort+s)}	9	1256.174	0.843	0.050	683.497
{ $\phi(S1=S2,AD)$, p(wi-effort+s)}	6	1256.508	1.177	0.043	689.937
{ $\phi(S1=S2,AD)*T$, p(wi-effort+s)}	8	1256.593	1.262	0.041	685.956
{ $\phi(s)$, p(wi-effort+s)}	6	1256.890	1.559	0.035	690.319
{ $\phi(S1=S2,AD)+s+\ln T$, p(wi-effort+s)}	8	1257.336	2.004	0.028	686.699
{ $\phi((S1=S2,AD)*T)+s$, p(wi-effort*s)}	10	1257.354	2.023	0.028	682.634
{ $\phi(S1=S2,AD)*s$, p(wi-effort+s)}	8	1257.369	2.037	0.028	686.732
{ $\phi(S1=S2,AD)+s+T$, p(wi-effort+s)}	8	1257.428	2.096	0.027	686.791
{ $\phi(S1=S2,AD)*\ln T$, p(wi-effort+s)}	8	1257.480	2.148	0.026	686.843
{ $\phi(S1=S2,AD)*s*\ln T$, p(wi-effort+s)}	12	1257.481	2.150	0.026	678.659
{ $\phi(S1,S2=AD)$, p(wi-effort+s)}	6	1257.502	2.171	0.026	690.931
{ $\phi(S1=S2,AD)*s*T$, p(wi-effort+s)}	12	1257.752	2.421	0.023	678.930
{ $\phi((S1=S2,AD)+s)*T$, p(wi-effort)}	8	1258.124	2.792	0.019	687.487
{ $\phi(S1,S2=AD)+s+\ln T$, p(wi-effort+s)}	8	1258.187	2.856	0.018	687.550
{ $\phi(S1,S2,AD)$, p(wi-effort+s)}	7	1258.240	2.909	0.018	689.638
{ $\phi(S1,S2=AD)*s$, p(wi-effort+s)}	8	1258.277	2.946	0.018	687.640
{ $\phi(S1,S2=AD)+s+T$, p(wi-effort+s)}	8	1258.290	2.958	0.017	687.653
{ $\phi((S1,S2=AD)+s)*\ln T$, p(wi-effort+s)}	9	1258.351	3.020	0.017	685.675
{ $\phi(S1=S2,AD)+\ln T$, p(wi-effort+s)}	7	1258.448	3.117	0.016	689.846
{ $\phi(S1=S2,AD)+T$, p(wi-effort+s)}	7	1258.519	3.188	0.016	689.917
{ $\phi(S1,S2=AD)+s$, p(wi-effort+s)}	7	1258.539	3.207	0.015	687.693
{ $\phi(S1=S2,AD)+s$, p(wi-effort)}	6	1258.575	3.244	0.015	692.004
{ $\phi(\cdot)$, p(wi-effort+s)}	5	1258.641	3.310	0.015	694.096
{ $\phi(s+\ln T)$, p(wi-effort+s)}	7	1258.825	3.493	0.013	690.223
{ $\phi((S1=S2,AD)+s)*TT$, p(wi-effort+s)}	11	1258.850	3.519	0.013	682.081
{ $\phi(s+T)$, p(wi-effort+s)}	7	1258.903	3.571	0.013	690.301
{ $\phi((S1,S2=AD)+s)*T$, p(wi-effort+s)}	9	1259.069	3.738	0.012	686.393
{ $\phi([S1,S2,AD]+s+\ln T)$, p(wi-effort+s)}	9	1259.119	3.788	0.012	686.443
{ $\phi([[S1,S2,AD]+s]*T)$, p(wi-effort+s)}	11	1259.184	3.852	0.011	682.415
{ $\phi([S1,S2,AD]+s+T)$, p(wi-effort+s)}	9	1259.219	3.888	0.011	686.542
{ $\phi(S1=S2,AD)*s+\ln T$, p(wi-effort+s)}	9	1259.287	3.956	0.011	686.611
{ $\phi(S1=S2,AD)+s+TT$, p(wi-effort+s)}	9	1259.380	4.049	0.010	686.703
{ $\phi(S1=S2,AD)*s+T$, p(wi-effort+s)}	9	1259.381	4.050	0.010	686.705
{ $\phi(S1,S2=AD)+\ln T$, p(wi-effort+s)}	7	1259.415	4.083	0.010	690.813

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$\{\phi(S1,S2=AD)+T, p(wi\text{-}effort+s)\}$	7	1259.496	4.165	0.010	690.895
$\{\phi(S1,S2=AD)*\ln T, p(wi\text{-}effort+s)\}$	8	1259.553	4.222	0.009	688.916
$\{\phi(s*T), p(wi\text{-}effort+s)\}$	8	1259.895	4.563	0.008	689.258
$\{\phi([S1,S2,AD]+s)*TT, p(wi\text{-}effort+s)\}$	14	1259.953	4.622	0.008	677.012
$\{\phi(s*\ln T), p(wi\text{-}effort+s)\}$	8	1260.021	4.690	0.007	689.385
$\{\phi(S1=S2,AD)*TT, p(wi\text{-}effort+s)\}$	10	1260.051	4.720	0.007	685.331
$\{\phi([S1,S2,AD]+s)*\ln T, p(wi\text{-}effort+s)\}$	11	1260.061	4.730	0.007	683.292
$\{\phi(S1,S2,AD)+\ln T, p(wi\text{-}effort+s)\}$	8	1260.170	4.839	0.007	689.533
$\{\phi(S1,S2=AD)*s+\ln T, p(wi\text{-}effort+s)\}$	9	1260.174	4.842	0.007	687.497
$\{\phi(S1,S2=AD)*T, p(wi\text{-}effort+s)\}$	8	1260.216	4.885	0.007	689.579
$\{\phi(S1,S2=AD)+s+TT, p(wi\text{-}effort+s)\}$	9	1260.243	4.912	0.007	687.567
$\{\phi(S1,S2,AD)+T, p(wi\text{-}effort+s)\}$	8	1260.249	4.918	0.007	689.612
$\{\phi(S1,S2=AD)*s+T, p(wi\text{-}effort+s)\}$	9	1260.275	4.944	0.006	687.599
$\{\phi(S1,S2,AD)*T, p(wi\text{-}effort+s)\}$	10	1260.434	5.103	0.006	685.713
$\{\phi(S1=S2,AD)+TT, p(wi\text{-}effort+s)\}$	8	1260.502	5.171	0.006	689.866
$\{\phi(\ln T), p(wi\text{-}effort+s)\}$	6	1260.596	5.264	0.006	694.025
$\{\phi(T), p(wi\text{-}effort+s)\}$	6	1260.653	5.322	0.005	694.082
$\{\phi(s+TT), p(wi\text{-}effort+s)\}$	8	1260.851	5.520	0.005	690.214
$\{\phi([S1,S2,AD]+s)+TT, p(wi\text{-}effort+s)\}$	10	1261.173	5.842	0.004	686.453
$\{\phi(S1,S2,AD)*\ln T, p(wi\text{-}effort+s)\}$	10	1261.247	5.916	0.004	686.527
$\{\phi((S1,S2=AD)+s)*TT, p(wi\text{-}effort+s)\}$	11	1261.338	6.007	0.004	684.569
$\{\phi(S1=S2,AD)*s+TT, p(wi\text{-}effort+s)\}$	10	1261.339	6.007	0.004	686.618
$\{\phi(S1,S2,AD)*TT, p(wi\text{-}effort+s)\}$	13	1261.392	6.061	0.004	680.512
$\{\phi(S1,S2=AD)+TT, p(wi\text{-}effort+s)\}$	8	1261.483	6.152	0.004	690.847
$\{\phi(S1,S2,AD)+TT, p(wi\text{-}effort+s)\}$	9	1262.235	6.903	0.002	689.558
$\{\phi(S1,S2=AD)*s+TT, p(wi\text{-}effort+s)\}$	10	1262.239	6.907	0.002	687.518
$\{\phi(TT), p(wi\text{-}effort+s)\}$	7	1262.641	7.309	0.002	694.039
$\{\phi(S1,S2=AD)*TT, p(wi\text{-}effort+s)\}$	10	1262.665	7.334	0.002	687.944
$\{\phi(S1,S2=AD)*s*\ln T, p(wi\text{-}effort+s)\}$	12	1263.639	8.308	0.001	684.817
$\{\phi(s*TT), p(wi\text{-}effort+s)\}$	10	1263.888	8.556	0.001	689.167
$\{\phi(S1,S2=AD)*s*T, p(wi\text{-}effort+s)\}$	12	1263.930	8.599	0.001	685.108
$\{\phi(S1=S2,AD)*s*TT, p(wi\text{-}effort+s)\}$	16	1265.386	10.055	0.001	678.306
$\{\phi(S1=S2,AD)+s, p(wi\text{-}effort*s)\}$	8	1268.599	13.267	0.000	697.962
$\{\phi(S1=S2,AD)+s+t, p(wi\text{-}effort+s)\}$	21	1268.799	13.468	0.000	671.295
$\{\phi(S1,S2=AD)*s*TT, p(wi\text{-}effort+s)\}$	16	1269.742	14.411	0.000	682.663
$\{\phi(s+t), p(wi\text{-}effort+s)\}$	20	1269.858	14.527	0.000	674.447
$\{\phi(S1=S2,AD)+t, p(wi\text{-}effort+s)\}$	20	1270.135	14.804	0.000	674.725
$\{\phi([S1,S2,AD]+s+t), p(wi\text{-}effort+s)\}$	22	1270.322	14.990	0.000	670.718
$\{\phi(S1,S2=AD)+t, p(wi\text{-}effort+s)\}$	20	1270.325	14.994	0.000	674.915
$\{\phi(S1=S2,AD)*s+t, p(wi\text{-}effort+s)\}$	22	1270.753	15.422	0.000	671.149
$\{\phi(S1,S2,AD)+t, p(wi\text{-}effort+s)\}$	21	1271.567	16.236	0.000	674.062

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$\{\phi(t), p(\text{wi-effort}+s)\}$	19	1271.914	16.583	0.000	678.593
$\{\phi(S1, S2=AD)+s+t, p(\text{wi-effort}+s)\}$	21	1272.085	16.754	0.000	674.581
$\{\phi(\cdot), p(\cdot)\}$	3	1285.790	30.459	0.000	725.285
$\{\phi(s*t), p(\text{wi-effort}+s)\}$	34	1286.938	31.606	0.000	661.778
$\{\phi(s*t), p(\text{wi-effort}*s)\}$	35	1289.094	33.763	0.000	661.774
$\{\phi(s*t), p(\text{wi-effort})\}$	33	1289.714	34.382	0.000	666.710
$\{\phi(s*t), p(\text{wi-effort}+r)\}$	34	1290.582	35.251	0.000	665.423
$\{\phi(s*t), p(t)\}$	45	1299.925	44.594	0.000	650.725
$\{\phi(s*t), p(T)\}$	33	1304.704	49.373	0.000	681.700
$\{\phi(s*t), p(\ln T)\}$	33	1309.395	54.063	0.000	686.391
$\{\phi(s*t), p(s)\}$	33	1309.687	54.356	0.000	686.684
$\{\phi(s*t), p(a+s)\}$	34	1311.276	55.945	0.000	686.117
$\{\phi(s*t), p(\cdot)\}$	32	1312.419	57.087	0.000	691.566
$\{\phi(s*t), p(r)\}$	33	1313.704	58.373	0.000	690.701
$\{\phi(s*t), p(a)\}$	33	1313.814	58.482	0.000	690.810
$\{\phi(s*t), p(s*t)\}$	59	1315.174	59.843	0.000	634.491
$\{\phi(a*s*t), p(a*s*t)\}$	114	1376.869	121.538	0.000	561.940

^a "wi-effort" = walk-in effort.

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Model selection results from apparent survival analyses for California Spotted Owls on Lassen study area.

Model	K	QAICc	Δ QAICc	Akaike Weights	Deviance
$\{\phi(T) p(a+s)\}$ model cross	6	1437.424	0.000	0.058	780.644
$\{\phi((S1, S2=A)+T) p(a+s)\}$ model cross	7	1437.484	0.060	0.056	778.681
$\{\phi(T) p(a+s+r)\}$	7	1437.741	0.317	0.050	778.938
$\{\phi((S1, S2=A)+T) p(a+s+r)\}$	8	1437.799	0.375	0.048	776.970
$\{\phi((S1=S2, A)+T) p(a+s+r)\}$	8	1438.031	0.608	0.043	777.202
$\{\phi((S1, S2=A)+TT) p(a+s+r)\}$	9	1438.264	0.840	0.038	775.405
$\{\phi((S1=S2, A)*s+T) p(a+s+r)\}$	10	1438.306	0.882	0.037	773.414
$\{\phi((S1=S2, A)+TT) p(a+s+r)\}$	9	1438.318	0.894	0.037	775.459
$\{\phi(TT) p(a+s+r)\}$	8	1438.399	0.975	0.036	777.570
$\{\phi((S1=S2, A)*s+TT) p(a+s+r)\}$	11	1438.650	1.226	0.031	771.721
$\{\phi(s*T) p(a+s)\}$ model cross	8	1438.882	1.458	0.028	778.053
$\{\phi((S1, S2=A)*T) p(a+s+r)\}$	9	1438.885	1.461	0.028	776.026
$\{\phi(s*T) p(a+s+r)\}$	9	1439.216	1.792	0.024	776.357
$\{\phi(s+T) p(a+s+r)\}$	8	1439.280	1.856	0.023	778.451
$\{\phi((S1, S2=A)+s+T) p(a+s+r)\}$	9	1439.326	1.902	0.022	776.467
$\{\phi(\ln(T)) p(a+s+r)\}$	7	1439.413	1.989	0.021	780.610
$\{\phi((S1, S2, A)+T) p(a+s+r)\}$	9	1439.592	2.168	0.020	776.733
$\{\phi((S1=S2, A)+s+T) p(a+s+r)\}$	9	1439.593	2.169	0.020	776.734
$\{\phi((S1, S2=A)+\ln(T)) p(a+s+r)\}$	8	1439.594	2.170	0.020	778.765
$\{\phi((S1, S2=A)+s+TT) p(a+s+r)\}$	10	1439.720	2.296	0.018	774.828
$\{\phi((S1=S2, A)*T) p(a+s+r)\}$	9	1439.737	2.313	0.018	776.878
$\{\phi((S1=S2, A)+s+TT) p(a+s+r)\}$	10	1439.810	2.386	0.018	774.917
$\{\phi((S1=S2, A)+\ln(T)) p(a+s+r)\}$	8	1439.837	2.413	0.017	779.007
$\{\phi((s+TT) p(a+s+r)\}$	9	1439.874	2.450	0.017	777.015
$\{\phi((S1, S2, A)+TT) p(a+s+r)\}$	10	1439.926	2.503	0.017	775.034
$\{\phi((S1=S2, A)*s+\ln(T)) p(a+s+r)\}$	10	1440.184	2.761	0.015	775.292
$\{\phi(((S1, S2= A)*T)+s) p(a+s+r)\}$	10	1440.421	2.997	0.013	775.529
$\{\phi((s*T) p(a+s+T))\}$ model cross	9	1440.714	3.290	0.011	777.855
$\{\phi((S1, S2=A)*s+T) p(a+s+r)\}$	10	1440.717	3.293	0.011	775.825
$\{\phi(.) p(a+s+r)\}$	6	1440.851	3.427	0.010	784.071
$\{\phi((S1, S2=A)*\ln(T)) p(a+s+r)\}$	9	1440.915	3.492	0.010	778.056
$\{\phi(s+\ln(T) p(a+s+r)\}$	8	1441.008	3.584	0.010	780.179
$\{\phi((S1, S2, A)+s*T) p(a+s+r)\}$	11	1441.127	3.703	0.009	774.198
$\{\phi((S1, S2, A)+s+T) p(a+s+r)\}$	10	1441.138	3.714	0.009	776.246
$\{\phi((S1, S2=A)*s+TT) p(a+s+r)\}$	11	1441.153	3.730	0.009	774.225
$\{\phi((S1, S2=A)+s+\ln(T)) p(a+s+r)\}$	9	1441.180	3.757	0.009	778.321

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$\{\phi((S1=S2, A)) p(a+s+r)\}$	7	1441.256	3.832	0.009	782.453
$\{\phi(((S1=S2, A)*(T))+s) p(a+s+r)\}$	10	1441.280	3.856	0.008	776.388
$\{\phi((S1, S2=A)) p(a+s+r)\}$	7	1441.317	3.893	0.008	782.514
$\{\phi(s*\ln(T) p(a+s+r))\}$	9	1441.400	3.976	0.008	778.541
$\{\phi((S1, S2, A)+s+TT) p(a+s+r)\}$	11	1441.402	3.978	0.008	774.473
$\{\phi((S1, S2, A)+\ln(T)) p(a+s+r)\}$	9	1441.417	3.993	0.008	778.558
$\{\phi(((S1=S2, A)*TT)) p(a+s+r)\}$	11	1441.661	4.237	0.007	774.732
$\{\phi((S1=S2, A)*\ln(T)) p(a+s+r)\}$	9	1441.775	4.351	0.007	778.916
$\{\phi(s*TT) p(a+s+r)\}$	11	1441.940	4.516	0.006	775.011
$\{\phi((S1=S2, A)*s) p(a+s+r)\}$	9	1441.944	4.521	0.006	779.085
$\{\phi((S1=S2, A)*s*T) p(a+s+r)\}$	13	1442.231	4.807	0.005	771.219
$\{\phi(((S1, S2= A)*\ln T)+s) p(a+s+r)\}$	10	1442.508	5.085	0.005	777.616
$\{\phi(s) p(a+s+r)\}$	7	1442.550	5.126	0.004	783.747
$\{\phi((S1, S2=A)*s+\ln(T)) p(a+s+r)\}$	10	1442.559	5.135	0.004	777.667
$\{\phi((S1, S2, A)+s*T) p(a+s+T)\}$ model cross}	11	1442.596	5.172	0.004	775.668
$\{\phi((S1, S2, A)*T) p(a+s+r)\}$	11	1442.649	5.225	0.004	775.721
$\{\phi((S1=S2, A)+s) p(a+s+r)\}$	8	1442.966	5.543	0.004	782.137
$\{\phi((S1, S2=A)+s) p(a+s+r)\}$	8	1443.012	5.589	0.004	782.183
$\{\phi((S1, S2, A)+s+\ln(T)) p(a+s+r)\}$	10	1443.019	5.595	0.004	778.127
$\{\phi((S1, S2, A)) p(a+s+r)\}$	8	1443.025	5.601	0.004	782.196
$\{\phi(((S1=S2, A)*TT)+s) p(a+s+r)\}$	12	1443.151	5.727	0.003	774.182
$\{\phi(((S1=S2, A)*\ln(T))+s) p(a+s+r)\}$	10	1443.382	5.958	0.003	778.489
$\{\phi((S1, S2, A)+s*\ln(T)) p(a+s+r)\}$	11	1443.471	6.048	0.003	776.543
$\{\phi((S1, S2=A)*s*T) p(a+s+r)\}$	13	1443.963	6.539	0.002	772.951
$\{\phi(((S1, S2, A)*T)+s) p(a+s)\}$ model cross}	11	1443.966	6.542	0.002	777.038
$\{\phi((S1, S2=A)*s) p(a+s+r)\}$	9	1444.404	6.980	0.002	781.545
$\{\phi((S1, S2, A)*\ln(T)) p(a+s+r)\}$	11	1444.617	7.193	0.002	777.689
$\{\phi((S1, S2, A)+s) p(a+s+r)\}$	9	1444.732	7.308	0.002	781.873
$\{\phi(((S1, S2, A)*(\ln T))+s) p(a+s+r)\}$	12	1446.246	8.823	0.001	777.278
$\{\phi((S1, S2=A)*s*\ln T) p(a+s+r)\}$	13	1446.477	9.053	0.001	775.465
$\{\phi((S1, S2=A)+t) p(a+s+r)\}$	21	1446.826	9.402	0.001	759.347
$\{\phi(((S1=S2=A)+t) p(a+s+r)\}$	20	1446.914	9.490	0.001	761.505
$\{\phi((S1=S2, A)+t) p(a+s+r)\}$	21	1447.236	9.813	0.000	759.757
$\{\phi((S1=S2, A)*s+t) p(a+s+r)\}$	23	1447.968	10.544	0.000	756.337
$\{\phi((S1, S2=A)+s+t) p(a+s+r)\}$	22	1448.123	10.699	0.000	758.570
$\{\phi(s+t) p(a+s+r)\}$	21	1448.257	10.833	0.000	760.778
$\{\phi((S1=S2, A)+s+t) p(a+s+r)\}$	22	1448.571	11.147	0.000	759.018
$\{\phi((S1, S2, A)+t) p(a+s+r)\}$	22	1448.707	11.283	0.000	759.154
$\{\phi((S1, S2=A)*s+t) p(a+s+r)\}$	23	1449.612	12.188	0.000	757.981

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$\{\phi((S1, S2, A)+s+t) p(a+s+r)\}$	23	1450.015	12.591	0.000	758.385
$\{\phi(((S1, S2, A)*TT)) p(a+s+r)\}$	14	1454.967	17.543	0.000	781.909
$\{\phi((S1,S2= A)*s*TT) p(a+s+r)\} a\}$	15	1456.379	18.955	0.000	781.271
$\{\phi((S1,S2= A)*s*TT) p(a+s+r)\} a\}$	15	1456.379	18.955	0.000	781.271
$\{\phi(((S1, S2, A)*TT)+s) p(a+s+r)\}$	15	1462.210	24.786	0.000	787.102
$\{\phi(((S1, S2= A)*TT)) p(a+s+r)\}$	11	1463.331	25.907	0.000	796.403
$\{\phi(((S1,S2= A)*TT)+s) p(a+s+r)\}$	12	1464.814	27.390	0.000	795.846
$\{\phi(s*t) p(a+s)\}$	34	1464.907	27.483	0.000	750.196
$\{\phi(s*t) p(a+s+r)\}$	35	1465.134	27.710	0.000	748.304
$\{\phi(s*t) p(a+s+\ln(T))\}$	35	1466.581	29.158	0.000	749.751
$\{\phi(s*t) p(s)\}$	33	1466.601	29.177	0.000	754.006
$\{\phi(s*t) p(a+s+T)\}$	35	1466.984	29.560	0.000	750.153
$\{\phi(s*t) p(a)\}$	33	1471.760	34.336	0.000	759.165
$\{\phi(s*t) p(.)\}$	32	1473.154	35.731	0.000	762.672
$\{\phi(s*t) p(r)\}$	33	1473.545	36.121	0.000	760.950
$\{\phi(a*s*t) p(a*s*t) PIM\}$	76	1475.035	37.612	0.000	668.129
$\{\phi(s*t) p(\ln(T))\}$	33	1475.051	37.627	0.000	762.456
$\{\phi(s*t) p(T)\}$	33	1475.123	37.699	0.000	762.528
$\{\phi(s*t) p(t)\}$	46	1484.028	46.604	0.000	743.646
$\{\phi(s*t) p(s*t)\}$	61	1499.091	61.667	0.000	725.876

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Model selection results from apparent survival analyses for California Spotted Owls on Sierra study area.

Model	K	QAICc	Δ QAICc	Akaike Weights	Deviance
{ $\phi((S1=S2, A)) p(a+s)$ }	6	1342.302	0.000	0.053	794.901
{ $\phi(((S1=S2, A)+T)) p(a+s+r)$ }	8	1342.405	0.103	0.050	790.945
{ $\phi(((S1=S2, A)+T)) p(a+s)$ }	7	1342.434	0.132	0.049	793.005
{ $\phi(((S1=S2, A)+T)) p(a+s+T)$ }	8	1342.538	0.235	0.047	791.078
{ $\phi((S1=S2, A)) p(a+s+r)$ }	7	1342.601	0.299	0.046	793.172
{ $\phi(((S1=S2, A)+\ln(T))) p(a+s)$ }	7	1343.023	0.721	0.037	793.594
{ $\phi(((S1=S2, A)+\ln(T))) p(a+s+r)$ }	8	1343.107	0.804	0.035	791.647
{ $\phi(T) p(a+s)$ }	6	1343.189	0.887	0.034	795.788
{ $\phi((S1=S2, A)) p(a+s+T)$ }	7	1343.200	0.898	0.034	793.772
{ $\phi((S1, S2, A)) p(a+s)$ }	7	1343.201	0.899	0.034	793.772
{ $\phi(.) p(a+s)$ }	5	1343.277	0.975	0.032	797.899
{ $\phi(((S1=S2, A)+\ln(T))) p(a+s+T)$ }	8	1343.425	1.123	0.030	791.965
{ $\phi(((S1, S2, A)+T)) p(a+s)$ }	8	1343.451	1.149	0.030	791.991
{ $\phi(((S1, S2, A)*T)) p(a+s)$ }	10	1343.471	1.169	0.029	787.937
{ $\phi(\ln(T)) p(a+s)$ }	6	1343.771	1.469	0.025	796.369
{ $\phi(((S1, S2, A)+\ln(T))) p(a+s)$ }	8	1344.009	1.707	0.023	792.549
{ $\phi((S1=S2, A)+s) p(a+s)$ }	7	1344.242	1.939	0.020	794.813
{ $\phi(((S1=S2, A)+s+T)) p(a+s)$ }	8	1344.398	2.096	0.019	792.939
{ $\phi(((S1=S2, A)+TT)) p(a+s)$ }	8	1344.418	2.115	0.018	792.958
{ $\phi(((S1=S2, A)*T)) p(a+s)$ }	8	1344.453	2.150	0.018	792.993
{ $\phi(((S1, S2, A)*\ln(T))) p(a+s)$ }	10	1344.470	2.167	0.018	788.936
{ $\phi(((S1, S2= A)*T)) p(a+s)$ }	8	1344.772	2.469	0.015	793.312
{ $\phi((s*TT)) p(a+s)$ }	10	1344.779	2.477	0.015	789.245
{ $\phi(((S1=S2, A)*\ln(T))) p(a+s)$ }	8	1344.815	2.513	0.015	793.355
{ $\phi(((S1=S2, A)+\ln(T))+s) p(a+s)$ }	8	1344.981	2.679	0.014	793.522
{ $\phi((s*\ln(T))) p(a+s)$ }	8	1345.093	2.790	0.013	793.633
{ $\phi(s+T) p(a+s)$ }	7	1345.141	2.838	0.013	795.712
{ $\phi(((S1, S2= A)+T)) p(a+s)$ }	7	1345.143	2.841	0.013	795.714
{ $\phi((S1, S2, A)+s) p(a+s)$ }	8	1345.156	2.854	0.013	793.696
{ $\phi(TT) p(a+s)$ }	7	1345.195	2.892	0.012	795.766
{ $\phi(s) p(a+s)$ }	6	1345.207	2.904	0.012	797.805
{ $\phi((S1, S2=A)) p(a+s)$ }	6	1345.223	2.921	0.012	797.821
{ $\phi((S1, S2, A)+s+T) p(a+s)$ }	9	1345.428	3.126	0.011	791.933
{ $\phi((S1=S2, A)*s) p(a+s)$ }	8	1345.434	3.132	0.011	793.974
{ $\phi((s+\ln(T))) p(a+s)$ }	7	1345.716	3.414	0.010	796.287
{ $\phi(((S1, S2= A)+\ln(T))) p(a+s)$ }	7	1345.730	3.428	0.010	796.302
{ $\phi(s*T) p(a+s)$ }	8	1345.828	3.526	0.009	794.368
{ $\phi((S1=S2, A)*s)+T p(a+s)$ }	9	1345.832	3.530	0.009	792.337

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$\{\phi(((S1, S2, A)+\ln(T))+s) p(a+s)\}$	9	1345.980	3.678	0.008	792.485
$\{\phi(((S1, S2= A)*\ln(T))) p(a+s)\}$	8	1346.243	3.941	0.007	794.784
$\{\phi((S1=S2, A)*s+\ln(T)) p(a+s)\}$	9	1346.382	4.080	0.007	792.887
$\{\phi(((S1=S2, A)+TT)+s) p(a+s)\}$	9	1346.388	4.085	0.007	792.893
$\{\phi(((S1=S2, A)*T)+s) p(a+s)\}$	9	1346.426	4.124	0.007	792.931
$\{\phi(((S1, S2, A)*\ln(T))+s) p(a+s)\}$	11	1346.482	4.179	0.007	788.905
$\{\phi(((S1, S2= A)*T)+s) p(a+s)\}$	9	1346.694	4.392	0.006	793.199
$\{\phi(((S1=S2, A)*\ln(T))+s) p(a+s)\}$	9	1346.802	4.500	0.006	793.307
$\{\phi(((S1, S2= A)+T)+s) p(a+s)\}$	8	1347.098	4.796	0.005	795.638
$\{\phi(((S1, S2= A)+TT)) p(a+s)\}$	8	1347.148	4.846	0.005	795.688
$\{\phi((s+TT)) p(a+s)\}$	8	1347.152	4.849	0.005	795.692
$\{\phi((S1, S2=A)+s) p(a+s)\}$	7	1347.156	4.853	0.005	797.727
$\{\phi(((S1=S2, A)*TT)) p(a+s)\}$	10	1347.462	5.160	0.004	791.928
$\{\phi(((S1, S2= A)+\ln(T))+s) p(a+s)\}$	8	1347.679	5.377	0.004	796.219
$\{\phi((S1=S2, A)*s+TT) p(a+s)\}$	10	1347.798	5.496	0.003	792.264
$\{\phi((S1, S2= A)*s*\ln(T)) p(a+s)\}$	11	1347.832	5.529	0.003	790.255
$\{\phi((S1, S2= A)*s*T) p(a+s)\}$	12	1347.852	5.550	0.003	788.228
$\{\phi((S1, S2=A)*s) p(a+s)\}$	8	1347.930	5.628	0.003	796.470
$\{\phi((S1, S2= A)*s+T) p(a+s)\}$	9	1348.011	5.709	0.003	794.516
$\{\phi(((S1, S2= A)*\ln(T))+s) p(a+s)\}$	9	1348.149	5.846	0.003	794.654
$\{\phi(((S1=S2, A)*\ln(T))*s) p(a+s)\}$	11	1348.505	6.203	0.002	790.928
$\{\phi((S1, S2= A)*s+\ln(T)) p(a+s)\}$	9	1348.609	6.307	0.002	795.114
$\{\phi(((S1, S2= A)+TT)+s) p(a+s)\}$	9	1349.109	6.807	0.002	795.614
$\{\phi(((S1=S2, A)*TT)+s) p(a+s)\}$	11	1349.474	7.172	0.001	791.897
$\{\phi(((S1, S2, A)+TT)) p(a+s)\}$	9	1349.946	7.644	0.001	796.451
$\{\phi((S1, S2= A)*s+TT) p(a+s)\}$	10	1349.990	7.688	0.001	794.456
$\{\phi((S1=S2, A)*s)*T p(a+s)\}$	12	1351.030	8.728	0.001	791.406
$\{\phi(((S1, S2, A)+TT)+s) p(a+s)\}$	10	1351.958	9.655	0.000	796.424
$\{\phi(((S1=S2, A)*TT)*s) p(a+s)\}$	15	1352.191	9.889	0.000	786.402
$\{\phi(((S1, S2, A)*TT)) p(a+s)\}$	13	1356.799	14.497	0.000	795.125
$\{\phi(((S1, S2= A)*TT)) p(a+s)\}$	10	1357.492	15.190	0.000	801.958
$\{\phi((S1=S2, A))+t p(a+s)\}$	20	1358.147	15.845	0.000	782.003
$\{\phi((S1, S2, A))+t p(a+s)\}$	21	1358.655	16.353	0.000	780.427
$\{\phi(t) p(a+s)\}$	19	1358.736	16.434	0.000	784.671
$\{\phi(((S1, S2, A)*TT)+s) p(a+s)\}$	14	1358.842	16.540	0.000	795.112
$\{\phi(((S1, S2= A)*TT)+s) p(a+s)\}$	11	1359.469	17.166	0.000	801.892
$\{\phi((S1=S2, A)+s)+t p(a+s)\}$	21	1360.154	17.851	0.000	781.926
$\{\phi((S1, S2= A)*s*TT) p(a+s)\}$	14	1360.613	18.311	0.000	796.883
$\{\phi((S1, S2, A)+s)+t p(a+s)\}$	22	1360.680	18.378	0.000	780.365
$\{\phi(s+t) p(a+s)\}$	20	1360.719	18.417	0.000	784.575
$\{\phi((S1, S2=A))+t p(a+s)\}$	20	1360.810	18.508	0.000	784.665
$\{\phi((S1=S2, A)*s)+t p(a+s)\}$	22	1361.753	19.450	0.000	781.437
$\{\phi((S1, S2=A)+s)+t p(a+s)\}$	21	1362.797	20.495	0.000	784.570

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$\{\phi((S1, S2=A)*s)+t p(a+s)\}$	22	1363.939	21.637	0.000	783.624
$\{\phi(s*t) p(a+s)\}$	34	1375.305	33.003	0.000	769.617
$\{\phi(s*t) p(a+s+T)\}$	35	1376.408	34.106	0.000	768.578
$\{\phi(s*t) p(a+s+r)\}$	35	1376.474	34.172	0.000	768.644
$\{\phi(s*t) p(a+s+\ln(T))\}$	35	1376.941	34.639	0.000	769.111
$\{\phi(s*t) p(s*r)\}$	35	1377.420	35.118	0.000	769.590
$\{\phi(s*t) p(a)\}$	33	1378.728	36.426	0.000	775.177
$\{\phi(s*t) p(s)\}$	33	1380.050	37.747	0.000	776.499
$\{\phi(s*t) p(s+r)\}$	34	1380.949	38.646	0.000	775.260
$\{\phi(s*t) p(a+s+t)\}$	47	1383.070	40.768	0.000	749.202
$\{\phi(s*t) p(\cdot)\}$	32	1383.132	40.830	0.000	781.715
$\{\phi(s*t) p(r)\}$	33	1383.784	41.482	0.000	780.234
$\{\phi(s*t) p(T)\}$	33	1384.471	42.168	0.000	780.920
$\{\phi(s*t) p(\ln(T))\}$	33	1384.910	42.608	0.000	781.359
$\{\phi(s*t) p(t)\}$	45	1392.052	49.750	0.000	762.567
$\{\phi(s*t) p(s*t)\}$	59	1396.061	53.758	0.000	735.516
$\{\phi(a*s*t) p(a*s*t)\}$	145	1539.627	197.325	0.000	666.947

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Model selection results from apparent survival analyses for California Spotted Owls on Sequoia and Kings Canyon study area.

Model	K	QAICc	Δ QAICc	Akaike Weights	Deviance
$\{\phi(a1), p(r)\}$	5	670.165	0.000	0.071	348.426
$\{\phi(a1*T), p(r)\}$	7	670.479	0.315	0.061	344.666
$\{\phi(a1 + T), p(r)\}$	6	670.651	0.487	0.056	346.878
$\{\phi(a2*T), p(r)\}$	7	671.029	0.864	0.046	345.216
$\{\phi(a1*\ln(T)), p(r)\}$	7	671.073	0.909	0.045	345.260
$\{\phi(a1), p(r + T)\}$	6	671.125	0.961	0.044	347.352
$\{\phi(a1 + \ln(T)), p(r)\}$	6	671.285	1.120	0.040	347.512
$\{\phi(a1*T), p(r + T)\}$	8	671.578	1.414	0.035	343.719
$\{\phi(a1), p(r + \ln(T))\}$	6	671.705	1.540	0.033	347.932
$\{\phi(a2*\ln(T)), p(r)\}$	7	671.711	1.547	0.033	345.898
$\{\phi(a1 + TT), p(r)\}$	7	671.750	1.585	0.032	345.936
$\{\phi(a1 + s), p(r)\}$	6	671.757	1.593	0.032	347.984
$\{\phi(a1 + T), p(r + T)\}$	7	671.763	1.599	0.032	345.950
$\{\phi((a1*T) + s), p(r)\}$	8	672.093	1.929	0.027	344.234
$\{\phi(a1*T), p(r + \ln(T))\}$	8	672.101	1.936	0.027	344.242
$\{\phi(a3), p(r)\}$	6	672.193	2.028	0.026	348.420
$\{\phi(a1 + s + T), p(r)\}$	7	672.206	2.042	0.026	346.393
$\{\phi(a1 + T), p(r + \ln(T))\}$	7	672.279	2.114	0.025	346.466
$\{\phi(a1*TT), p(r)\}$	9	672.639	2.474	0.021	342.728
$\{\phi(a3 + T), p(r)\}$	7	672.691	2.527	0.020	346.878
$\{\phi(a1*\ln(T) + s), p(r)\}$	8	672.705	2.541	0.020	344.846
$\{\phi(a3 + \ln(T)), p(r)\}$	7	673.324	3.159	0.015	347.511
$\{\phi(a3*\ln(T)), p(r)\}$	9	673.398	3.234	0.014	343.488
$\{\phi(a2*\ln(T) + s), p(r)\}$	8	673.492	3.327	0.013	345.633
$\{\phi(a2*TT), p(r)\}$	9	673.507	3.342	0.013	343.596
$\{\phi(a2), p(r)\}$	5	673.775	3.611	0.012	352.036
$\{\phi(a1*s), p(r)\}$	7	673.790	3.626	0.012	347.977
$\{\phi(a3 + s), p(r)\}$	7	673.790	3.626	0.012	347.977
$\{\phi(a2*T + s), p(r)\}$	8	674.082	3.917	0.010	346.223
$\{\phi(a1*s + T), p(r)\}$	8	674.235	4.070	0.009	346.376
$\{\phi(a1 + s + \ln(T)), p(r)\}$	7	674.239	4.074	0.009	347.031
$\{\phi(a3 + s + T), p(r)\}$	8	674.252	4.087	0.009	346.393
$\{\phi(a3*T + s), p(r)\}$	10	674.382	4.218	0.009	342.414
$\{\phi(a1*TT + s), p(r)\}$	10	674.384	4.219	0.009	342.416
$\{\phi(a2 + T), p(r)\}$	6	674.685	4.520	0.007	350.911
$\{\phi(a1*s + \ln(T)), p(r)\}$	8	674.877	4.713	0.007	347.018

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$\{\phi(a3 + s + \ln(T)), p(r)\}$	8	674.889	4.724	0.007	347.030
$\{\phi(a3*\ln(T)) + s), p(r)\}$	10	675.160	4.995	0.006	343.192
$\{\phi(a2 + \ln(T)), p(r)\}$	6	675.196	5.031	0.006	351.422
$\{\phi(a1*s*T), p(r)\}$	11	675.304	5.140	0.005	341.273
$\{\phi(a2 + s), p(r)\}$	6	675.309	5.145	0.005	351.536
$\{\phi(a2*TT) + s), p(r)\}$	10	675.376	5.211	0.005	343.408
$\{\phi(a1*s) + TT), p(r)\}$	9	675.390	5.226	0.005	345.479
$\{\phi(a3 + s + TT), p(r)\}$	9	675.401	5.237	0.005	345.491
$\{\phi(a2 + TT), p(r)\}$	7	675.903	5.739	0.004	350.090
$\{\phi(a2 + s + T), p(r)\}$	7	676.160	5.995	0.004	350.347
$\{\phi(a1 + s + TT), p(r)\}$	8	676.285	6.120	0.003	345.491
$\{\phi(a3 + TT), p(r)\}$	8	676.285	6.120	0.003	345.936
$\{\phi(\text{dot}), p(r)\}$	4	676.410	6.245	0.003	356.699
$\{\phi(a3*TT), p(r)\}$	12	676.441	6.276	0.003	340.340
$\{\phi(a1*s*\ln(T)), p(r)\}$	11	676.505	6.340	0.003	342.473
$\{\phi(a2 + s + \ln(T)), p(r)\}$	7	676.690	6.526	0.003	350.877
$\{\phi(T), p(r)\}$	5	677.270	7.105	0.002	355.531
$\{\phi(a2*s), p(r)\}$	7	677.348	7.184	0.002	351.535
$\{\phi(a2 + s + TT), p(r)\}$	8	677.401	7.236	0.002	349.542
$\{\phi(a2*s*T), p(r)\}$	11	677.711	7.546	0.002	343.679
$\{\phi(\ln(T)), p(r)\}$	5	677.804	7.639	0.002	356.065
$\{\phi(s), p(r)\}$	5	677.902	7.738	0.001	356.163
$\{\phi(a2*s*\ln(T)), p(r)\}$	11	678.076	7.911	0.001	344.044
$\{\phi(a3*T), p(r)\}$	9	678.336	8.172	0.001	342.683
$\{\phi(a3*TT) + s), p(r)\}$	13	678.368	8.203	0.001	340.192
$\{\phi(TT), p(r)\}$	6	678.510	8.345	0.001	354.737
$\{\phi(a2*s) + \ln(T)), p(r)\}$	8	678.727	8.562	0.001	350.868
$\{\phi(s + T), p(r)\}$	6	678.728	8.563	0.001	354.955
$\{\phi(s + \ln(T)), p(r)\}$	6	679.268	9.103	0.001	355.495
$\{\phi(a2*s) + TT), p(r)\}$	9	679.405	9.240	0.001	349.494
$\{\phi(s*T), p(r)\}$	7	679.818	9.654	0.001	354.005
$\{\phi(s + TT), p(r)\}$	7	679.998	9.833	0.001	354.184
$\{\phi(s*\ln(T)), p(r)\}$	7	680.354	10.189	0.000	354.540
$\{\phi(a1 + t), p(r)\}$	17	680.576	10.411	0.000	334.038
$\{\phi(a1 + s + t), p(r)\}$	18	682.164	11.999	0.000	333.521
$\{\phi(s*TT), p(r)\}$	9	682.506	12.342	0.000	352.596
$\{\phi(a3 + t), p(r)\}$	18	682.588	12.423	0.000	333.945
$\{\phi(a2*s*TT), p(r)\}$	15	683.409	13.245	0.000	341.065
$\{\phi(a1*s) + t), p(r)\}$	19	684.187	14.023	0.000	333.434
$\{\phi(a3 + s + t), p(r)\}$	19	684.193	14.029	0.000	333.440
$\{\phi(a2 + s)*TT), p(r)\}$	12	684.303	14.138	0.000	348.202

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$\{\phi(a2 + t), p(r)\}$	17	684.644	14.479	0.000	338.107
$\{\phi(t), p(r)\}$	16	685.500	15.335	0.000	341.062
$\{\phi(a2 + s + t), p(r)\}$	18	686.162	15.997	0.000	337.519
$\{\phi(s + t), p(r)\}$	17	687.025	16.860	0.000	340.488
$\{\phi(a2*s) + t), p(r)\}$	19	688.184	18.020	0.000	337.430
$\{\phi(a1*s*TT), p(r)\}$ - estimation problems	15	688.783	18.618	0.000	346.438
$\{\phi(s*t) p(r)\}$ - estimation problems (2 yr)					
from here on	29	695.744	25.580	0.000	323.535
$\{\phi(s*t), p(r + T)\}$	30	697.109	26.945	0.000	322.720
$\{\phi(s*t), p(r + \ln(T))\}$	30	697.562	27.397	0.000	323.173
$\{\phi(s*t), p(r*s)\}$	31	698.772	28.608	0.000	322.196
$\{\phi(s*t), p(t)\}$ - major estimation problems	37	705.127	34.962	0.000	315.295
$\{\phi(s*t), p(a)\}$	29	706.292	36.127	0.000	334.083
$\{\phi(s*t), p(r + t)\}$ - major est problems	38	707.360	37.195	0.000	315.295
$\{\phi(s*t), p(.)\}$	28	707.854	37.690	0.000	337.819
$\{\phi(s*t), p(a + s)\}$	30	708.270	38.106	0.000	333.881
$\{\phi(s*t), p(T)\}$	29	708.549	38.385	0.000	336.340
$\{\phi(s*t), p(\ln(T))\}$	29	709.936	39.771	0.000	337.727
$\{\phi(s*t), p(s)\}$	29	709.947	39.783	0.000	337.738
$\{\phi(s*t), p(s*t)\}$ major estimation problems	49	722.919	52.755	0.000	305.852
$\{\phi(a*s*t)p(a*s*t)\}$ - major est problems	121	880.753	210.589	0.000	276.974