

Population Dynamics of the California Spotted Owl: A Meta-Analysis

Final Report to
U.S. Forest Service
Pacific Southwest Research Station
P.O. Box 245
Berkeley, CA 94701

18 April 2003

by

Alan B. Franklin, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523

R. J. Gutiérrez, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108

James D. Nichols, Patuxent Wildlife Research Center, U.S. Geological Survey, 11510 American Holly Dr. Laurel, Maryland 20708

Mark E. Seamans, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108

Gary C. White, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523

Guthrie S. Zimmerman, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108

James E. Hines, Patuxent Wildlife Research Center, U.S. Geological Survey, 11510 American Holly Dr. Laurel, Maryland 20708

Thomas E. Munton, U. S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2081 E. Sierra Ave., Fresno, California 93710

William S. LaHaye, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108

Jennifer A. Blakesley, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado, 80523

George N. Steger, U. S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2081 E. Sierra Ave., Fresno, California 93710

Barry R. Noon, Department of Fishery and Wildlife Biology, Colorado State University, Ft. Collins, Colorado, 80523

Daniel W. H. Shaw, U. S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2081 E. Sierra Ave., Fresno, California 93710

John J. Keane, Sierra Nevada Research Center, Pacific Southwest Research Station, USDA Forest Service, 2121 Second St, Suite A101, Davis, CA 95616

Trent L. McDonald, WEST, Inc., 2003 Central Avenue, Cheyenne, WY 82001

Susan Britting, P. O. Box 377, Coloma, California 95613

EXECUTIVE SUMMARY

The science supporting conservation strategies developed for the spotted owl (*Strix occidentalis*) has been a focus of discussion among special interest groups, scientists, resource agencies, politicians and the public since the owl was first associated with old growth forests in the United States. One of two scientific issues of high priority is the population status of the species. Two spotted owl subspecies have been listed as threatened because of declining populations and past or potential habitat loss. However, unlike the northern (*S. o. caurina*) and Mexican (*S. o. lucida*) spotted owls, the California spotted owl (*S. o. occidentalis*) has not been listed although it was proposed for listing. One primary reason the California spotted owl was not listed was the implementation by the U.S. Forest Service of an interim California spotted owl conservation strategy developed in 1992 under the auspices of the California Spotted Owl Technical Assessment Team (CASPO). CASPO could not determine with certainty if owl populations were declining in the Sierra Nevada of California because analyses of extant owl population data did not have sufficient statistical power to provide unambiguous assessments of owl population trends on several Sierra Nevada owl study areas. CASPO considered their plan an interim strategy until such time as sufficient scientific information was available to warrant the development of a new conservation strategy. The decade of the 1990s was marked by a series of attempts to derive a comprehensive forest management strategy for the entire Sierra Nevada that considered not only the owl, but other wildlife, forest values, and human safety (i.e., wild fire threats). The most recent of these management efforts was the Sierra Nevada Framework, which was accepted in a USDA Forest Service, Region 5, Record of Decision (ROD) in 2000.

Because of the tenets of the ROD and a petition to list the California spotted owl as threatened, the Sierra Nevada Framework Team of the U. S. Forest Service Pacific Southwest Research Station requested spotted owl researchers and population dynamics experts to convene a workshop in 2001 to analyze all existing spotted owl population data using a meta-analysis framework. The intent of the analyses was to provide a current assessment of the population characteristics of California spotted owls resident on 4 study areas in the Sierra Nevada and 1 study area in southern California. This report is the culmination of that effort. The meta-analysis followed rigorous *a priori* analysis protocols, which were derived through extensive discussion and consensus among the workshop participants about the most scientifically defensible analytical methods to be used in the meta-analysis.

The 5 study areas (with their durations) were located on the Lassen National Forest (1990-2000); Eldorado National Forest (1986-2000); Sierra National Forest (1990-2000); Sequoia-Kings Canyon National Park (1990-2000); and San Bernardino National Forest (1987-1998). Hereafter these study areas are referred to by their place name. Four of the 5 study areas spanned the length of the Sierra Nevada, while the 5th study area encompassed the San Bernardino Mountains in southern California. The study areas ranged in size from 343 km² (Sequoia-Kings Canyon) to 2,200 km² (Lassen). All studies were designed to use capture-recapture methods and analysis. Study methods were very similar in terms of protocols to estimate survival of birds. Thus, survival was used in a meta-analysis. It was not clear during initial discussions if variation in individual study area protocols used to assess reproductive output of owls would confound the results. Since there was insufficient time to simulate the effect of this variation on potential bias in estimates of fecundity using slightly different protocols, fecundity was analyzed only by individual study area. Population trend was examined using the reparameterized Jolly-Seber capture-recapture estimator (\mathfrak{R}_i). This was a significant departure from the method (Leslie projection matrix; \mathfrak{R}_{PM}) biologists used to estimate population trend in spotted owls. This decision was made because we were unable to estimate juvenile survival. In addition, a number of workshop participants felt we needed separate estimates of immigration and/or emigration to properly parameterize a projection model. \mathfrak{R}_i relied on estimation of annual changes in the number of birds on the study area, whereas the \mathfrak{R}_{PM} relied on estimation of the finite rate of population change

based on stage-specific death (survival) and birth (fecundity) rates. Thus, the inference we derived changed from “would the birds replace themselves if the system was geographically closed?” (\mathcal{S}_{PM}) to “are the birds being replaced in this geographically open system?” (\mathcal{S}_t). The new method was not a panacea because a population could still be declining while the numbers of birds on a local study area remained stable. Because methods to locate individuals within study areas were similar, population trend data were combined and used to estimate \mathcal{S}_t in a meta-analysis.

We did not estimate juvenile survival rates because of estimation problems and potential bias due to juvenile emigration from the study areas. We used mark-recapture estimators under an information theoretic framework to assess apparent survival rates of adult owls. The pooled estimate for adult apparent survival for the 5 study areas was 0.833, which was lower than pooled adult survival rates (0.850) from 15 northern spotted owl studies. Best model estimates for survival on the Lassen ($\hat{\phi} = 0.829$, 95% CI = 0.798, 0.857), Eldorado ($\hat{\phi} = 0.815$, 95% CI = 0.772, 0.851), Sierra ($\hat{\phi} = 0.818$, 95% CI = 0.781, 0.850), and San Bernardino ($\hat{\phi} = 0.813$, 95% CI = 0.782, 0.841) were not different. However, the Sequoia-Kings Canyon population had a higher survival rate ($\hat{\phi} = 0.877$, 95% CI = 0.842, 0.905) than the other study areas. Management history and forest structure (e.g., presence of giant sequoia, *Sequoiadendron giganteum*) on the Sequoia-Kings Canyon study area was different from all other study areas. There did not appear to be evidence for temporal variation in adult apparent survival on any of the study areas.

Even though we did not directly compare fecundity, fecundity was highly variable among years within all study areas (CV of temporal process variation = 0.672-0.817). Estimates for fecundity among the study populations were: Lassen ($\bar{b} = 0.336$; SE = 0.083), Eldorado ($\bar{b} = 0.409$; SE = 0.087), Sierra ($\bar{b} = 0.284$; SE = 0.073), Sequoia-Kings Canyon ($\bar{b} = 0.289$; SE = 0.074), and San Bernardino ($\bar{b} = 0.362$; SE = 0.038). During most years the Sierra Nevada populations showed either moderate or poor fecundity. However, 1992 appeared to be an exceptional reproductive year for owls in the Sierra Nevada. In contrast, the San Bernardino population had less variable reproduction (CV of temporal process variation = 0.217), but experienced neither the exceptional reproduction of 1992 nor the extremely poor years that characterized all of the Sierra Nevada study areas. Since fecundity appears to be influenced by weather patterns, it is possible that the different weather patterns of southern California and the Sierra Nevada range account for this difference.

Except for the Eldorado, all estimates for \mathcal{S}_t were less than one, but none was different from $\mathcal{S} = 1$ given the 95% Confidence Intervals (Lassen [$\bar{\lambda} = 0.985$, SE = 0.026]; Eldorado [$\bar{\lambda} = 1.042$, SE = 0.047]; Sierra [$\bar{\lambda} = 0.961$, SE = 0.024]; Sequoia-Kings Canyon [$\bar{\lambda} = 0.984$, SE = 0.047]; San Bernardino [$\bar{\lambda} = 0.978$, SE = 0.025]). However, additional evidence (in the form of realized population change based on $\hat{\lambda}_t$) strongly suggested that the Sierra population had declined during the study period. Estimated trends in \mathcal{S}_t for the Eldorado and Sierra study areas were negative. Thus, we cannot absolutely distinguish between alternatives that the populations were stationary or that the estimates of \mathcal{S}_t were not sufficiently precise to detect declines on 4 of the study areas (Eldorado, Lassen San Bernardino, and Sequoia-Kings Canyon). This result was analogous to the CASPO results a decade earlier when the power of the tests was low.

Results of the trend analyses do not allow strong inference about the decline of the populations. Because \mathcal{S}_t reflects changes in owl numbers on the study areas (i.e., it integrates emigration, immigration, birth and death rates), it does not allow inference about the larger populations in which these local populations are imbedded. That is, it is possible that local

populations could be producing fewer young but are enhanced by emigration from surrounding areas. In addition, the interim CASPO guidelines were designed as a conservation strategy. These CASPO guidelines were in effect during the majority of the studies' duration. Therefore, it is possible that the conditions within the study areas on National Forests may have been better, in terms of habitat loss, than surrounding areas. This may be particularly true where there are high amounts of private land surrounding the study areas (e.g., Lassen, Eldorado). The relatively low survival rates coupled with trend estimates that were either declining or less than 1 suggested that caution is advised in planning conservation strategies for the California spotted owl until further analyses can be conducted that couple climatic and habitat conditions with population parameters, such as adult survival and fecundity.

INTRODUCTION

The California spotted owl (*Strix occidentalis occidentalis*) is 1 of 3 spotted owl subspecies. It occurs as a contiguous population in the Sierra Nevada of California and as insular populations in central coastal California, southern California, and Baja California Norte, Mexico (Gutiérrez et al. 1995). The California spotted owl is genetically differentiated from the other 2 subspecies, the northern (*S. o. caurina*) and Mexican spotted owls (*S. o. lucida*) (Barrowclough et al. 1999). Unlike the northern and Mexican subspecies, the California spotted owl has not been listed as a threatened species under the U.S. Endangered Species Act. Nevertheless, the status, trends, and basic natural history (e.g., habitat selection) of the California spotted owl have been the center of controversy for over a decade (Verner et al. 1992b, USDA Forest Service 1998a,b).

Verner et al. (1992a [CASPO Report]) evaluated the status, trends, and state of the ecological knowledge about the California spotted owl. Two fundamental findings of the CASPO Report were uncertainty in population trends of the owl because of the short duration of extant owl demographic studies, and the probable decline throughout the Sierra Nevada of forest attributes (e.g., very large diameter trees) associated with spotted owls. The CASPO Report also recommended a set of interim guidelines to the U. S. Forest Service for the management of spotted owl habitat. Based on the strategy recommended by CASPO, the Forest Service implemented new guidelines (USDA Forest Service 1993), with the intention of moving beyond the interim guidelines when credible scientific information was gathered from field studies to justify a change from the interim guidelines. The U.S. Forest Service then embarked on a series of Environmental Impact Statements (EIS) (USDA Forest Service 1995, 1996), the last of which was unfavorably reviewed (Federal Advisory Committee 1997). The Federal Advisory Committee (1997) concluded, among other things, that there was little new information on the owl's biology which could justify the changes proposed in the EIS documents, particularly the uncertainty regarding timber harvest strategies and their potential impact on owl habitat and owl population dynamics. Concomitant to the EIS efforts, the Sierra Nevada Ecosystem Project (1996) was established, which attempted to identify multiple concerns relative to conservation and management of the Sierra Nevada ecosystem. The report of the Sierra Nevada Ecosystem Project did not explicitly discuss the ecology or management of the California spotted owl, but it correctly framed issues facing the future of the Sierra Nevada as ecosystem-wide. Thus, the U.S. Forest Service abandoned earlier EIS efforts and initiated a new strategy to evaluate not only the California spotted owl but also other sensitive wildlife species and habitat conditions while considering such issues as the threat of wildfire and timber harvest practices. In 1998, the U.S. Forest Service Pacific Southwest Research Station published a scientific review identifying and synthesizing current knowledge on the highest priority conservation issues across the Sierra Nevada (USDA Forest Service 1998a). An accompanying document that summarized current management direction specific to each of the high priority issues was prepared by the U.S. Forest Service (USDA Forest Service 1998b). The information provided in these documents determined the scope and focus of subsequent land management planning that was conducted as part of the Sierra Nevada Framework Project. These efforts culminated in a final EIS and Record of Decision (ROD) that identified new management direction for California spotted owls and the other high priority issues on U.S. Forest Service lands across the Sierra Nevada (USDA Forest Service 2001a,b). The Sierra Nevada Framework Project team formally requested that a spotted owl population meta-analysis be conducted using the information on owl population dynamics gathered before and after the CASPO Report to address the ongoing controversy regarding the conservation status of California spotted owls. In particular, they requested that the meta-analysis examine trends in California spotted owl populations using data from 5 existing studies that had collected data on demographic characteristics of California spotted owls.

Meta-analysis has been employed as an analytical tool to evaluate the status and trends of northern spotted owls since 1993 (Burnham et al. 1996, Franklin et al. 1999). Meta-analyses allow synthesis of data from independent studies where studies are considered the sampling units

(Wolf 1986, Hunter and Schmidt 1990). They can be performed on statistics collected from published peer-reviewed papers (e.g., Vanderwerf 1992) or from the raw data themselves (Franklin and Shenk 1995). The power of a meta-analysis for California spotted owls is the ability to combine information from several studies to achieve greater sample size and perhaps investigate sources of variation and examine potential correlations in population dynamics, otherwise unavailable from a single study. For example, Burnham et al. (1996) used raw data gathered from 13 spotted owl population studies in the Pacific Northwest to demonstrate an accelerating decline in female survival over the period of study, which supported the inference of a population decline in northern spotted owls.

Coincident with the meta-analysis, a Pacific Northwest Forest Plan was developed for the northern spotted owl and other old forest species (Thomas et al. 1993) at the request of President Clinton. This plan proposed a conservation reserve design to protect spotted owl habitat, which was based on earlier conservation strategies for the northern spotted owl (Thomas et al. 1990, USDI 1992). This reserve design effectively removed large areas from timber harvest consideration, much of which was within existing spotted owl demographic study areas. Essentially the reserve design provided an ad hoc test of the effect of habitat loss on spotted owl population trends. In 1998, a second meta-analysis on the northern spotted owl population data was conducted (Franklin et al. 1999). In these analyses, declining trends in owl populations and adult female survival either were reduced or stabilized. Further, in the 1998 meta-analysis a new analytical method was introduced, direct estimation of λ (the annual finite rate of population change, referred to here as λ) that was based on capture-recapture data and reflected changes in numbers of territorial owls on study areas. This analysis (discussed below in the Methods and Discussion) avoided the effect of potentially biased estimates of juvenile survival that caused uncertainty in estimating λ with the Leslie projection matrix used in previous spotted owl studies. However, a stationary population (i.e., $\lambda = 1$) using this newer analysis still could not demonstrate demographic stability because stationary populations could be maintained solely by immigration from other populations. Nevertheless, it was a clear attempt to incorporate the most modern population analytical methods in the meta-analysis.

The purpose of this report is to present the results of a meta-analysis conducted using data generated from 5 California spotted owl population studies (4 within the contiguous owl range of the Sierra Nevada and 1 from an insular population in southern California) in an effort to assess status and trends of California spotted owl populations. In this study, owl researchers from the 5 demography studies, timber industry consultants, and stakeholders met with experts in analysis of population dynamics from 9 -13 July 2001 at Colorado State University in Fort Collins, Colorado to conduct a formal meta-analysis of all known California spotted owl population data. The participants agreed to adhere to a rigid and formal protocol for analytical sessions proposed by Anderson et al. (1999). This process was rigorous and critical to the success of a coordinated analysis, and was greatly facilitated by the presence and interaction of this diverse group. In addition, an earlier draft of this report underwent 2 separate peer-reviews from outside organizations; these reviews and the responses from the authors of this report are attached as Appendices 4 and 5.

Our intent in analyzing these data under the Forest Service mandate was to examine trends in demographic parameters as well as rates of population change (λ) because changes in demographic parameters (the integral components of λ) can provide better understanding of population dynamics. For example, Franklin et al. (2000) suggested that adult survival defined the magnitude of λ while reproduction and recruitment determined variation in λ over time. Thus, we did not want to rely solely on a single measure of population trend. We did not explicitly evaluate changes in population numbers. Although data were available to estimate numbers of owls on several of the study areas, there were potential biases (see review in Pollock et al. 1990) in estimating numbers of owls using capture-recapture. Rather, we relied on the reverse-time Jolly-Seber estimator (herein referred to as λ) to estimate annual changes in numbers of owls on the study areas (Pradel 1996). We were then able to re-express these estimates as realized

proportional changes in numbers of owls without having to rely on estimation of population abundance.

ACKNOWLEDGMENTS

We thank Peter Carlson for organizing and executing the data verification process. M. Conner, L. McDonald, B. Manly, T. Shenk, and J. Verner participated in the discussion sessions during the workshop and provided many insights to the analysis and its biological/management implications. P. Stine and W. Yung provided logistical support. J. Baldwin provided assistance and very helpful suggestions on the fecundity analysis. Funding for this meta-analysis was provided by the Sierra Nevada Research Center, Pacific Southwest Research Station, and the Pacific Southwest Region, USDA Forest Service. Acknowledgments specific to each study area are listed below.

Lassen. **S**We are grateful for the dedicated work of many field assistants over the years. We appreciate the cooperation of Collins Pine Company, Roseburg Resources Company, Sierra Pacific Industries, and W. M. Beaty and Associates, Inc., for sharing information and permitting us access to their properties. This study was primarily funded by USDA Forest Service Region 5. Additional support was received from the Forest Service Pacific Southwest Research Station, the Lassen National Forest, and Colorado State University.

Eldorado. **S**We thank our many field assistants over the 14 year study period. We also thank the Eldorado National Forest and the personnel of the Georgetown, Pacific, and Foresthill Ranger Districts for their help during the study. M. Bias, M. Bond, D. Lutz, C. Moen, and Z. Peery ably served as project or assistant project leaders at various times during the study. G. Gould, Jr., D. Solis, J. Verner, and J. Robinson provided important support during the study. We thank Blodgett Forest Research Station, University of California - Berkeley, for providing housing for our research staff. The California Department of Fish and Game, California Department of Natural Resources, Pacific Southwest Forest and Range Experiment Station, and Region 5 USDA-Forest Service (contract #FS/53-91S8-00-EC14 to RJG), and the University of Minnesota provided funding for this project.

Sierra. **S**We thank the many field biologists that assisted with the data gathering; it was their untiring effort that made this project possible. We also thank K. Johnson, G. Eberlein, W. Laudenslayer, Jr., and J. Verner who played a substantial role in data collection, analysis, or guidance as this study progressed. In addition, we are grateful for the help from Region 5 and J. Robinson, California Department of Fish and Game and G. Gould, Jr., Sierra National Forest, Kings River Ranger District, and Southern California Edison.

Sequoia/Kings Canyon. **S**We thank the many employees whose efforts in the field, often under difficult conditions, allowed the successful collection of the data. We thank P. Shaklee for supervising field crews, G. Eberlein for managing the data, and W. Laudenslayer, Jr. and J. Verner for their roles in the development and guidance of this study. We thank Sequoia and Kings Canyon National Parks for allowing us to conduct the study and for providing logistical assistance. D. Graber and H. Werner were particularly helpful. We appreciate the support received from G. Gould, Jr. and the California Department of Fish and Game. We thank the University of California, Berkeley, for allowing us access to Whitaker Forest and for providing housing for our field crews.

San Bernardino. **S**We thank the field crews who assisted in collecting these data. We thank San Bernardino National Forest and the personnel of the Big Bear Ranger District for their cooperation and assistance during this study. We also thank G. Gould, Jr., J. Palmer, J. Verner, D. Solis, and J. Robinson for their support. R. Smith, D. Call, M. Engle, M. McLeod ably served as assistant project leaders during the course of this study. The California Department of Fish and Game, California Department of Natural Resources, Southern California Edison, Region 5 USDA-Forest Service (contract #FS/53-91S8-00-EC14 to RJG), Pacific Southwest Forest and

Range Experiment Station, Snow Summit Mountain Resort, Big Bear Mountain Resort, Salad King, Inc., private donors, and the University of Minnesota provided funding for this project.

STUDY AREAS

Demographic data from five study areas were used in the analyses (Table 1, Figure 1). Specific attributes of each study area, described in the following sections, have been presented below in latitudinal order from north to south. Most of the study areas were considered, or included, density study areas, which were geographically defined areas that were surveyed entirely for spotted owls.

The Sierra Nevada is the dominant physical feature influencing the climate on four of the study areas. This mountain range has cold, wet winters and hot, dry summers. Winter Pacific storm systems are the main source of precipitation for the range. These storm systems can be either cold or warm depending upon their origin (e.g., Gulf of Alaska or tropical Pacific, respectively). The Sierra Nevada vegetation is heavily influenced by climate, elevation, aspect, and edaphic conditions (see below) which results in diverse forest types.

Fire has been a primary force shaping the distribution and structure of vegetation in the Sierra because natural fire regimes were characterized by relatively frequent fire return intervals (Skinner and Chang 1996). Fire return intervals and fire behavior have changed as a result of governmental fire suppression policies and other vegetation management activities following European settlement (McKelvey et al. 1996). Sierran vegetation also has been affected by logging and livestock grazing (McKelvey and Johnston 1992). Logging began in the mid to late 1800s and harvest techniques varied from clear felling to individual tree selection. Livestock grazing was intense during the 1800s but has been reduced to relatively low levels today. The net effect of both natural and anthropogenic disturbance has led to a complex mosaic of vegetation types, seral stages, and stand structures. This has resulted in a variety of forest types used by spotted owls in the Sierra Nevada. Each of the Sierra Nevada demography study areas has slightly different histories of land use and vegetation histories, which may have influenced the population dynamics of spotted owls (see Discussion below).

In contrast to the Sierra Nevada study areas, the San Bernardino Mountains study area was located in a relatively isolated mountain range in southern California (Figure 1). The owls occupying this mountain range were the largest population of a presumed owl metapopulation found throughout the disjunct ranges of the region (Noon and McKelvey 1992, LaHaye et al. 1994). The climatic environment in southern California was more benign than the Sierra Nevada because the majority of winter storms pass to the north of the region (Karhl 1979). Logging occurred in the San Bernardino Mountains from the late 1800s through the mid 1980s (Robinson 1989; McKelvey and Johnston 1992). Commercial logging occurred infrequently (McKelvey and Johnston 1992). The historic fire regime in the San Bernardino Mountains included frequent, low intensity fires which played a major role in shaping vegetation mosaics (Minnich 1988). However, modern fire suppression and historic logging have resulted in significant changes in vegetation structure and composition in the wetter portions of the mountain range (Minnich et al. 1995). Mining, urban expansion, and numerous other human activities also have impacted owl habitat to some degree (Verner et al. 1992b).

Lassen Study Area (LAS)

The LAS was located in northeastern California, primarily on the Lassen National Forest (LNF). The greater study area encompassed 2,200 km² and was analogous to the Regional Study Area of the Eldorado study (see below). A subset of this study area (approximately 1,270 km²) was selected for estimation of δ_t (see *Estimating Rates of Population Change*, below) during the meta-analysis, based on portions of the study area surveyed consistently during 1992-2000. Most private land within the study area boundaries was not surveyed, although several owl sites on private timber land adjacent to LNF were included. In addition, a few sites overlapped Lassen

Volcanic National Park, the Plumas NF, and Bureau of Land Management land.

Elevations on the study area ranged from 1,200 to 2,100 m. Annual precipitation at 1,250-1,500 m averaged 141 cm in the west, 86 cm in the center and 36 cm just east of the study area. Most of the precipitation fell as snow from November through April. Average high temperatures at the center of the study area (1,380 m) ranged from 6°C in January to 29°C in July. Average low temperatures ranged from -7°C in January to 7°C in July.

The majority of forested stands on the study area were mixed conifer, with additional stands classified as true fir. Dominant tree species included white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*) and Jeffrey pine (*Pinus jeffreyi*). Black oak (*Quercus kelloggii*) was present in the understory in some stands.

Eldorado Study Area (ELD)

The ELD consisted of a 355 km² Eldorado Density Study Area (EDSA) and a 570 km² Regional Study Area (RSA) located between Georgetown and Lake Tahoe in the central Sierra Nevada, El Dorado and Placer Counties, California. Boundaries for the EDSA were defined by: the Rubicon River, South Fork of the Rubicon River, and Middle Fork of the American River to the south, north, and west; Chipmunk Ridge and Bunker Hill to the north and east; and Forest Road 33 to the east. The ELD was characterized by a “checkerboard” distribution of alternating public (USFS) and private land, comprising 63% and 37% of the EDSA, respectively.

Demographic research began on the EDSA in 1986. We initiated the RSA in 1997 to encompass more owl territories, and to locate owls that may have emigrated from the EDSA. All EDSA owl territories were on the Eldorado National Forest. Thirty-eight percent of the RSA territories were located on the Eldorado National Forest, 38% on the Tahoe National Forest, and 24% on the Tahoe Basin Management Area. All RSA territories were on public land. We did not use owls banded in the Tahoe Basin Management Area for this analysis.

The study area was typical of the mid elevation Sierra Nevada with mountainous terrain bisected by steep river drainages. Elevations ranged from 366 - 2,401 m. From 1962 to 1995 average annual precipitation at the Blodgett Experimental Forest (part of the RSA; 1,340 m elevation) was 158 cm (Olson and Helms 1996). Thirty-five percent of precipitation fell as snow, averaging 254 cm per year. Average minimum temperature in January was 1°C and the average maximum temperature in July was 28°C.

The EDSA and RSA were typical of Sierran Montane Forest (SMF; Küchler 1977). From 600 m to 1,500 m, the SMF was dominated by ponderosa pine on more xeric sites and white fir on more mesic sites. A transition zone above 1,500 m was dominated by red fir (Rundel et al. 1977). Other common tree species that occurred within the study area included: sugar pine, Douglas-fir, incense cedar, canyon live oak (*Quercus chrysolepis*), California black oak, Pacific dogwood (*Cornus nuttallii*), and tan oak (*Lithocarpus densiflorus*).

Sierra Study Area (SIE)

The SIE was located approximately 83 km east of Fresno, California in the southern Sierra Nevada within the watersheds of the San Joaquin River and the North Fork of the Kings River. The study was initiated in 1990 on 419 km² and then expanded in 1994 to 693 km². The Sierra National Forest administered 92% of the lands within the study area.

The SIE was mountainous with steep drainages and elevations ranged from 304 m at the southwestern corner to 2,924 m on the eastern edge. Boundaries of the SIE were defined by U.S. Forest Service administrative units and major topographic features such as ridges and drainages. Annual precipitation from 1961 to 1990 averaged 94 cm at Huntington Lake, approximately 16 km north of the study area at 2,139 m in elevation (NOAA 1998). Most precipitation occurred during the winter and fell mainly as snow above 1,220 m. Summer temperatures averaged about 16°C at Huntington Lake (NOAA 1998), but could be >38°C in the lower elevation on the southwest side of the study area.

The SIE had three general habitat zones: oak woodlands, mid-elevation mixed conifer forests, and high-elevation conifer forests. The oak-woodland zone, at the lowest elevation (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. The mid-elevation mixed conifer forest (1,220-2,438 m) occupied 61% of the study area and was 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 forest (2,439-2,924 m) covered 13% of the study area and was dominated by red fir, lodgepole pine (*P. contorta*), and western white pine (*P. monticola*).

Sequoia and Kings Canyon National Parks Study Area (SKC)

The SKC was 35 km northeast of Visalia and 19 km southeast of the SNF and covered 343 km² in Fresno and Tulare Counties, California. The SKC was managed primarily by Sequoia and Kings Canyon National Parks, but the study area also included the adjacent Whitaker Forest (1.3 km²) which was managed by the University of California. Most of the study area was part of the Kaweah River watershed (primarily the North, Marble, and Middle Forks); however, the northern 14 km² was part of the Kings River watershed. The terrain was mountainous with steep drainages; elevations ranged from 427 m to 3,050 m. Boundaries of the study area were defined by U. S. Park Service administrative boundaries and topography (ridges and elevation). Demographic studies were initiated on SKC in 1990.

From 1961 to 1990, annual precipitation averaged 66 cm on Ash Mountain (521 m) at the southern edge of SKC and 105 cm at Grant Grove (2,013 m) near the northern border of the study area (NOAA 1999). During the winter, precipitation fell primarily as snow above 1,220 m. Average daily temperatures for July at Ash Mountain and Grant Grove were 28°C and 17°C, respectively.

Several forest types (Verner and Boss 1980) were present on the study areas in three distinct vegetation zones. Low-elevation oak-woodlands (24% of SKC below 1,220 m elevation) included low-elevation pine-oak woodlands, blue oak savannas, and dense riparian-deciduous forests. Tree species included blue oak, gray pine, interior live oak, canyon live oak, California sycamore (*Platanus racemosa*), California buckeye (*Aesculus californica*) and Fremont cottonwood (*Populus fremontii*). Large areas adjacent to low-elevation oak-woodland consisted of chaparral (primarily chamise [*Adenostoma fasciculatum*]). Mid-elevation conifer forests (67% of SKC; 1220-2440 m elevation) included a ponderosa pine type at lower elevations, a mid-elevation riparian deciduous type that occurred throughout the zone, and a mixed conifer type that was dominant in this zone. Tree species included ponderosa pine, Jeffrey pine, sugar pine, white fir, red fir, incense-cedar, and black oak. Mixed conifer forests included 10 giant sequoia groves. Based on estimated areas from Parsons (1994), these sequoia groves covered 7% of the study area. Sequoia groves were mixed conifer forests that contained giant sequoia trees and other conifer species (e.g., white fir and sugar pine), which were often more numerous (Rundel 1971). High-elevation coniferous forests (9% of the SKC; above 2,440 m elevation) consisted primarily of the red fir type and the lodgepole pine type. Trees included red fir, lodgepole pine, and western white pine.

San Bernardino Study Area (SAB)

The SAB was located in the San Bernardino Mountains, approximately 140 km east of Los Angeles, California (Figure 1). In 1987, the 535-km² Big Bear Study Area (BBSA) was established, centered on the majority of the spotted owl locations known at that time. In 1989, the size of the study area was increased to encompass the entire mountain range (1,890 km²). The San Bernardino Mountains were 1 of a series of mountain ranges that rise above extensive desert (Vasek and Barbour 1988) and semi-desert (Mooney 1988) vegetation types in Southern California (Noon and McKelvey 1992, LaHaye et al. 1994). The forests in these mountain ranges

occurred as isolates because they occurred at higher elevations than surrounding desert and chaparral vegetation (Noon and McKelvey 1992, LaHaye et al. 1994). They occupied ~2% of the southern California landscape (Scott et al. 1993).

Elevations on the study area ranged from 800 m to 3,500 m. The climate was Mediterranean with most precipitation falling during the winter months (Fujioka et al. 1998). Annual precipitation ranged from 50-100 cm depending on location, elevation, and topography (Minnich 1988). These mountain ranges were mesic compared to the surrounding lowlands, which allowed them to support a diverse assemblage of shrub and forest vegetation types (Minnich 1998). Vegetation types most commonly used by spotted owls in southern California were mixed evergreen (Sawyer et al. 1988) and montane forests (Thorne 1988). Mixed evergreen forests occurred below about 1,600 m elevation and the dominant tree species were canyon live oak and big-cone fir (*Pseudotsuga macrocarpa*). Other tree species associated with these lower elevation sites included Coulter pine (*P. coulteri*) white alder (*Alnus rhombifolia*), California sycamore, and big-leaf maple (*Acer macrophyllum*). Montane forests occurred above 1600 m elevation and were dominated by Jeffrey pine and white fir. Other tree species occurring in montane forests included sugar pine, incense cedar, black oak, ponderosa pine, western juniper (*Juniperus occidentalis*), pinyon pine (*P. monophylla*), and limber pine (*P. flexilis*).

METHODS

FIELD METHODS

Methods among spotted owl population dynamics studies have been similar for some time; this is particularly true in studies of northern spotted owls (Forsman 1983; Franklin et al. 1996a). However, there is some variation among studies of California spotted owls because of local differences in owl behavior, different environmental conditions, and different initial study objectives that required modifications of standard protocols used in northern spotted owl studies. Therefore, in this section the most consistent methodology used among the studies is presented, but is followed by an explicit description of departures from the standard techniques (see also Appendix 1).

Surveys. Spotted owls were surveyed according to the methods of Forsman (1983) and Franklin et al. (1996a). Surveys were performed by either imitating spotted owl territorial vocalizations or by playing pre-recorded calls from a tape player. Surveys consisted of point, cruise, and walk-in surveys and were conducted from 1 April to 31 August, 1986-2000, except in the SIE and SKC study areas where surveys were initiated on 1 March and ended on 30 September and the SAB where surveys ended on 30 September. Night surveys consisted of calling at points (locations) for 10 minutes (15 min on SAB) to determine if spotted owls were present in a new or historically used area. At each survey point, researchers imitated spotted owl vocalizations to elicit a response. Survey points were strategically placed by researchers to obtain complete survey coverage of individual study areas. Night surveys were generally conducted from dusk to 2400 hrs. If an owl was detected during a night survey, a walk-in survey was conducted in the same general location to find its roosts and nest (if nesting), locate any possible mate, assess reproductive status, and identify individuals. Researchers attempted to resight all owls located during each walk-in and capture and band all unbanded owls. Additional walk-in surveys were conducted to capture and mark unbanded owls if these birds were not captured in the initial survey. Owls were located during walk-in surveys by imitating spotted owl vocalizations to elicit a response and by visually searching the area where the owl was detected during the previous night survey. When no spotted owls were detected during a walk-in survey, it was termed a cruise survey. Walk-in or cruise surveys lasted until the objectives were met (i.e., reproductive status and identity of individuals were determined) or the observers deemed that further effort would not help accomplish the objectives (e.g., an owl could not be located within

the first few hours of survey). Therefore, survey effort was a function of the actual time allotted to surveys of various types.

Multiple complete surveys within each study area were conducted during the course of a field season. In a study of northern spotted owls, Reid et al. (1999) detected all 8 radio-marked non-juvenile males in their study within three 10-minute surveys, which were spaced 1 week apart. All studies reported herein conducted ≥ 3 surveys at multiple point locations within owl territories. In addition, if an owl was detected at night, a walk-in survey was conducted to locate potential mates. Thus, survey effort should have been sufficient to detect nearly all spotted owls on the study areas. Within each study area boundary, areas were surveyed regardless of land ownership or habitats present with the exception of the greater LAS where only known spotted owl habitat or previously occupied habitats were surveyed, and the RSA of the ELD where owl territories were selected from historic locations provided by the USFS or from territories that we located during surveys conducted in 1997. Territories on the greater LAS and RSA of the ELD were surveyed individually. Because these individual territories were not within the bounded density study areas they were not used in the estimation of δ_t (see below for assumptions of this procedure). Prior to 1990 on the ELD, funding was not sufficient to adequately survey the density study area, thus, abundance estimates before 1990 were not comparable to estimates from later years and were not used in estimation of δ_t . In SIE and SKC the study areas were divided into sites of the approximate size of owl territories. Only those sites that were surveyed consistently each year were included in this analysis. In 1990, survey effort on SKC was less than during the following years and those data were not included in this analysis (Table 1). Finally, in the SAB only forest habitat was surveyed because owls only occupied forested habitat in this mountain range and there were extensive areas of non-forest habitat (e.g., chaparral).

Estimation of reproductive effort. **S**We estimated owl reproductive activity by feeding live mice to owls during walk-in surveys (Forsman 1983, Franklin et al. 1996a). Reproducing owls usually take offered prey to their nest or young, while non-reproducing owls usually eat or cache the mice. We estimated fecundity (i.e., the number of female young fledged per female; Caughley 1977) from the number of females checked for reproductive status and the number of young observed. We assumed a 1:1 sex ratio of juveniles for fecundity estimates (Steger 1995, Franklin et al. 1996b).

The criteria for inferring non-reproduction for a pair of owls varied slightly among study areas (Appendix 1). However, a data screening process was used to evaluate the internal consistency of data collected given the methods used by the individual study (see below). In addition, the efficacy of each study area's criteria was discussed at length during the workshop to assess if the data were sufficiently consistent and rigorous to use in a collective meta-analysis. Researchers generally agreed their data provided unbiased estimates of fecundity within their respective study areas. However, they felt that, because different protocols were used, it was not appropriate to analyze the study areas jointly without further investigation, such as comparing estimated fecundity for each study using protocols employed by the other studies. Such an analysis would have required writing programs to sub-sample complete data-sets of survey data (each study area has conducted 1000s of surveys and each study area stores these records differently), which would have taken more time than allotted for the workshop.

Capture, banding, sex and age identification, and resighting of owls. **S**Researchers attempted to capture and band all spotted owls detected following the methods of Forsman (1983) and Franklin et al. (1996a). Most owls were captured with noose poles, snare poles, or mist nets. Once captured, all owls were fitted with a USFWS locking aluminum band on the tarso-metatarsus of 1 leg. On the opposite leg, adult and subadult owls were marked with a unique color band/colored tab combination (Forsman et al. 1996) while juvenile owls were fitted with a plastic band having a color unique to their cohort. Juveniles were refitted with unique color bands/tabs when recaptured as territory holders in later years.

Sex of non-juvenile owls was determined by their calls and behavior. Males have a lower pitched call than females and only females were known to incubate or brood young (Forsman et al. 1984). Juveniles were not sexed except on the SIE and SKC (Steger 1995). We identified four age-classes based on plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; 1-year old (first-year subadult); 2-year old (second-year subadult); and ≥ 3 -years old (adult).

After initial capture, adult and subadult owls were identified as individuals by resighting their unique color bands and tabs. Resighting of band colors was accomplished using binoculars. When possible, 2 biologists made independent observations of the same bird's color band/tab combination. Birds were recaptured and bands replaced when a colored tab became frayed through wear. When color bands were changed the metal band number was recorded. Band loss was minimal (Forsman et al. 1996).

Pre-analysis Data Screening. The basic philosophy and framework for the meta-analysis workshop followed Anderson et al. (1999). All groups conducting California spotted owl demographic research and experts in demographic analysis and parameter estimation were invited to attend the meta-analysis workshop. Further, representatives from the timber industry and environmental groups were invited to attend. To our knowledge, these data represent the extent of current data on population dynamics for California spotted owls. The demographic parameters of interest for this meta-analysis were sex-specific survival, female fecundity, and population rate of change. Therefore, in the interest of data consistency, researchers from each study area were requested to summarize their data in: 1) a data file with a capture history matrix that described the capture-recapture history of each individual owl, its U.S. Fish and Wildlife Service band number, its age at first capture (juvenile, first-year subadult, second-year subadult, or adult), and its sex; 2) a data file with annual number of young fledged (0, 1, 2, or 3) for individual territorial owls, their territory, social status (paired or single owl), the age of the male, and the age of the female; and 3) a data file with a capture history matrix that documented the capture-recapture history of all individuals encountered as territory holders (i.e., if an individual was first banded as a juvenile only the territorial portion of history was included), its age at first capture, the sex of the individual, and its U.S. Fish and Wildlife Service band number. This latter database was created after the survival database had been checked for errors (see below) and was used to estimate population rate of change.

Although most studies did not use DNA tests to ascertain the sex of juveniles a 1:1 sex ratio was assumed at fledging in each year for the capture-history matrix (Steger 1995, Franklin et al. 1996b). Data on owl reproduction for each study area were based on the protocols developed by the researchers for the respective study (see Appendix 1). However, the number of young found in each territory each year had to be based on a minimum of 2 visits within a year. An exception could be made if statistical justification was provided that indicated single visits had high accuracy (>85%) for counting young. Regardless, estimates of fecundity across study areas were not compared in a meta-analysis because of the differences in protocol used by each study.

Most researchers had to modify their database structure to conform to the meta-analysis' specifications for a compatible database structure (see above). There also was some variation in research protocols among the study areas. Therefore, prior to attending the 1 week workshop and conducting data analysis, all research groups agreed to undergo a formal data screening process to ensure quality control, to ensure that the original field data matched the data in the computer files, and to ensure that the specific criteria used by a study was actually followed by that study (i.e., the data collection was internally consistent within a study). A researcher (Peter Carlson) not involved in the California spotted owl meta-analysis was charged with randomly selecting information from the databases supplied by the respective study area researchers. Ten records were randomly drawn from the capture history database from each study area and 10 from the reproductive database; individual researchers were then required to provide paper copies of the associated original data forms or field notes. At least 1 male and 1 female were drawn from each age-class to check the survival database. The randomly selected information was then

compared with the actual field data recorded on original field notes. If errors were found an additional 10 were randomly selected for checking. If errors were found after the second check, the entire database was checked for errors.

After the first day of the workshop and prior to any data analysis all researchers were required to sign a certification letter stating that their data were correct, had been checked and rechecked, and were ready for final analysis. Failure to sign the certification would have meant exclusion of their data from the final analysis. Further, by signing the certification researchers explicitly agreed that their data could not be withdrawn from the workshop after results were viewed (see Anderson et al. 1999). All researchers signed the certification.

Meta-analysis Workshop Format. The first 1 1/2 days of the workshop were devoted to a discussion of the methods used to infer reproductive output of owls because methods varied somewhat between study areas (Appendix 1, see above). Consensus was reached among researchers that the methods used by the respective studies, despite their differences, were appropriate given the study objectives, location, and behavior of owls within the study area. In addition, considerable discussion and debate transpired among researchers, independent scientists, workshop leaders, U.S. Forest Service personnel, and stakeholders about the nature of the analyses to be performed, the appropriate inferences to be drawn given a particular analysis, and the advantages and disadvantages of different approaches. Agreement was reached on the structure and nature of the analyses and who would perform a specific analysis. This discussion also led to a departure from past approaches for spotted owl population analyses (see discussion of λ estimation below). A written protocol was developed and recorded during the workshop (Appendix 2).

The remainder of the workshop was devoted to selection of relevant *a priori* models for reproduction, recapture, and survival modeling (see Appendix 2); then executing the *a priori* models. Because researchers were at different stages of their studies, it was agreed that covariates (e.g., precipitation, habitat) would not be included in the modeling process. However, there was unanimous agreement that this was a worthwhile endeavor to be pursued in a future meta-analysis. The researchers were convened as a group to discuss particular issues as they arose that might affect the analysis or to maintain consistency in the analytical process. Thus, it was agreed that the results of this workshop would be a first step in setting the basis for subsequent workshops, which would allow more inclusive analyses.

DATA ANALYSIS

Direct inferences from our results are limited to study populations analyzed in the workshop and the time-periods from which data were collected. Inferences beyond the study populations, (e.g., to the California spotted owl throughout the Sierra Nevada) are not possible with these data because the study areas represent only a small fraction of the total area of the Sierra Nevada range, and these study areas were not selected randomly from a sampling frame encompassing the Sierra Nevada.

Changes in Analytical Methodology From Previous Spotted Owl Studies.—There has been considerable debate over the most appropriate measure of the finite rate of population change (λ) in spotted owl populations. Historically, spotted owl researchers have estimated λ using a Leslie projection matrix (λ_{PM}), which was based on estimates of age- or stage-specific survival and fecundity (Caswell 2000; Franklin et al. 1996a). This method was the best available at the time for estimating rates of population change. Nevertheless, the debate on rates of population change in spotted owls using λ_{PM} has centered on the central issue of whether λ_{PM} is biased because the populations are not geographically closed (e.g., there are unknown rates of juvenile emigration from the study areas). If juvenile owls are banded, leave the study area, live, and remain undetected, an estimate of juvenile survival using mark-recapture estimators would be negatively

biased. For example, estimates of juvenile survival probabilities on 3 study areas for the northern spotted owl increased 42-137% when they were adjusted, using radio-telemetry data, for emigration from those study areas (Franklin et al. 1999). Conversely, reproductively active owls are more likely to be detected than non-reproductively active owls, which could result in an overestimate (i.e., positive bias) of reproductive output. If biased survival or reproductive output estimates are used in the projection matrix, estimates of $\mathbf{8}_{PM}$ would be biased as well. Thus, an important issue concerns the correct inference to be taken from $\mathbf{8}_{PM}$ (Raphael et al. 1996). With the exception of the SAB (essentially a geographically closed population for which there was a good estimate of juvenile survival), we could not be certain that we did not have a biased estimate of juvenile survival because of the likelihood of undetected juvenile emigration from the study areas. Previously, studies in the Sierra Nevada (with the exception of the LAS, which estimated juvenile survival from their recapture data) used a projection matrix based on estimates of territorial owl survival and fecundity, and a “surrogate” estimate of juvenile survival which was “borrowed” from the SAB. The use of a surrogate estimate of juvenile survival probably introduced an unknown bias into the estimates of $\mathbf{8}_{PM}$ because of potential geographic variation in survival rates.

Despite these potential problems, we had decided, during the early stages of the workshop, to estimate $\mathbf{8}_{PM}$ because there was sufficient disagreement from some participants in the workshop concerning complete exclusion of $\mathbf{8}_{PM}$ from the workshop results. Thus, our initial approach was to estimate rates of population change using both $\mathbf{8}_{PM}$ (see Appendix 2) and a recently developed analytical technique used to estimate $\mathbf{8}$ (referred to here as $\mathbf{8}_t$, see Pradel 1996) that was employed in a northern spotted owl meta-analysis (Franklin et al. 1999). We spent considerable time attempting to estimate juvenile survival from the capture-recapture data. However, we encountered problems in estimability of parameters for juvenile survival. In attempting to solve these problems, other issues concerning bias in estimates of juvenile survival became apparent (see Appendix 3). In the end, the group collectively decided that estimates of $\mathbf{8}_{PM}$ would have some unknown bias because of these problems and the analysts and most researchers agreed the data would not support a projection matrix approach for some of these demographic studies. Thus, we decided to rely on $\mathbf{8}_t$ to estimate changes in owl numbers within study areas, which estimates $\mathbf{8}$ directly from the capture-recapture data (Pradel 1996, Nichols and Hines 2002). Inferences and assumptions relevant to this technique are explained more fully in the section on *Estimating Rates of Population Change* and in Appendix 3.

Estimating Adult Survival. The meta-analysis of adult apparent survival was based on female and male adult capture histories for the 5 study areas, where captures were either initial captures, recaptures, or resightings of color-band combinations on individuals. Apparent survival (\mathbf{N}) was defined as the probability that an owl alive in a particular year t , survives to the same time next year ($t+1$) and remains on the study area and, hence, is available for recapture. The reciprocal of apparent survival is a function of both death and emigration. For adult spotted owls, we assumed that permanent emigration of adult spotted owls from study areas was very low based on data on northern spotted owls (e.g., Franklin et al. 1996b, Forsman et al. 2002). Hence, we considered apparent survival for California spotted owls to be an approximate estimate of true survival, the reciprocal of which is death only.

From capture histories of individuals first captured as juveniles or subadults, we removed encounters at the younger ages, leaving only captures at the adult age. Estimates of apparent survival and recapture probability (p , probability that an animal alive in year t is captured, recaptured or resighted) were obtained with the Cormack-Jolly-Seber model (Lebreton et al. 1992) using Program MARK. The global model considered was $\{\mathbf{N}_{g^*t^*s}, p_{g^*t^*s}\}$, where \mathbf{N} was apparent survival probability, p was recapture probability, g was study area, t was time (year), and s was sex. Goodness-of-fit of this model was assessed with Program RELEASE (Burnham et al. 1987). Assumptions underlying the use of mark-recapture data for spotted owls and the use of goodness-of-fit to evaluate those assumptions is discussed in greater detail in Franklin et al.

(1996a). In general, the studies on California spotted owls were very similar in design to those for the northern spotted owl. We estimated overdispersion in the data using $\hat{c} = P^2/df$ using the combined P^2 values and degrees of freedom (df) from TEST 2 and TEST 3 from program RELEASE (Lebreton et al. 1992). Estimates of \hat{c} were used to correct estimated standard errors and AIC_c values (see below). Twenty-seven models were initially fit to the data from the five study areas with 3 structures, $N_{g^*t^*s}$, N_{g^*t+s} , and N_{g^*t} , on apparent survival, and 9 structures, P_{g+t} , P_{g+t+s} , $P_{[g+t]^*s}$, P_{g^*t} , $P_{[g^*t]^*s}$, P_{g^*t+s} , P_r , P_{r+s} , and p_{r^*s} , on recapture, where r was annual reproductive output estimated from the 5 study areas. Program MARK (White and Burnham 1999) generated the log-likelihood function value, degrees of freedom (df), and the small sample bias-corrected quasi-likelihood Akaike's Information Criterion ($QAIC_c$) (Sakamoto et al. 1986, Burnham and Anderson 1998) for each model evaluated. This criterion is computed as follows:

$$QAIC_c = \frac{-2\log \text{Likelihood}}{\hat{c}} + 2K + \frac{2K(K+1)}{n-K-1},$$

where K is the number of parameters estimated, \hat{c} is the estimate of overdispersion, and n is the effective sample size, i.e., the number of binomial trials included in the likelihood following Burnham et al. (1987). The smaller the $QAIC_c$ value for a given model, the better an approximation the model is for the information in the observed data, given the set of models examined.

Using the minimum $QAIC_c$ model for p from the initial 27 models, the following 10 additional models for N were fit: N_g , N_{g+t} , N_{g+T} , N_{g^*T} , N_{g+TT} , N_{g^*TT} , N_t , N_T , N_{TT} , and N_{\cdot} , where T denoted a linear time trend, TT denoted as quadratic time trend, “ \cdot ” denoted a means only model. Using the minimum $QAIC_c$ model from these 10 models that included a study area effect, the additional models $N_{latitude}$, $N_{SAB \text{ vs } rest}$, $N_{SKC \text{ vs } rest}$, and $N_{SAB, SKC \text{ vs } rest}$ were fit, where the term “*rest*” denoted a single survival parameter estimated for the remaining study areas combined. Thus, a total of 41 models were considered (Table 2).

The Akaike weights (Burnham and Anderson 1998) were computed as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)},$$

where Δ_i is the difference in $QAIC_c$ value for the minimum $QAIC_c$ model and model i and R is the number of models (41 in our case) in the set. Model likelihood was computed as the $QAIC_c$ weight for the model of interest divided by the $QAIC_c$ weight of the best model. Temporal and spatial process variation of apparent survival were estimated with the variance components module of Program MARK (White et al. 2002, Burnham and White 2002). Here, we

distinguished between *process variation* ($\sigma_{process}^2$), the variation in a given parameter, such as N ,

and *sampling variation* ($\text{var}(\hat{\theta}|\theta)$), the variation attributable to estimating a parameter from sample data (White 2000). Process variation in population parameters can be decomposed into temporal process variation (the variation in a parameter over time) and spatial process variation (the variation in a parameter among different locations), which requires that sampling variation be “removed” from the total variation in the annual or spatial estimates of interest.

Estimating Fecundity. Fecundity data for each study area were analyzed with mixed analysis of variance models (Rao 1997). Study areas were analyzed separately because estimates were not comparable across study areas (except for the SIE and SKC study areas) due to differences in the field protocols used to estimate reproductive output (number of fledged young

per pair). The raw data used in the analysis for each study area consisted of the number of young fledged on a particular site, the site (territory) where the young were detected, the year, and the age of the female (first-year subadult, second-year subadult, or adult) for each female monitored. Prior to analysis, the estimates of reproductive output for each site within each year were divided by 2 to estimate fecundity, assuming a 1:1 sex ratio. Mixed models were used 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 sites 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 (e.g., missing data).

The raw data used in the analysis were integer data (0, 1, 2, and rarely 3 or 4). 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-model analysis of variance, we relied on sample sizes being sufficiently large to justify normal distributional assumptions. Based on simulations, analysis of variance models were robust to severe departures from normality (White and Bennetts 1996). In addition, analysis of variance models were more robust to data from discrete distributions, such as the negative binomial, than was Poisson regression, even when it is corrected for overdispersion (White and Bennetts 1996). Therefore, we decided to rely on the robustness of analysis of variance to non-normally distributed data, rather than relying on Poisson regression to analyze the fecundity data, which have properties similar to a Poisson but are not distributed as Poisson. The mixed model procedures also allowed us to account for this dependence of sampling variation on the mean (see below). As with northern spotted owl 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 used PROC MIXED (SAS Institute 1997) to fit various models to estimate fecundity for each study area. Initially, we followed the protocol developed during the workshop. However, several complications arose including 1) mis-specification of the SAS code used to run the models, and 2) non-convergence of some of the models because of too few individuals in the subadult age classes on most study areas. In both the initial analysis and the subsequent re-analysis, we used a two-stage approach to fitting models to the data for each study area (see Wolfinger 1993). First, we used restricted maximum likelihood estimation with model {age + T; fecundity = $\beta_0 + \beta_1(\text{age}) + \beta_2(\text{year})$ } for each study area, where age of the bird was a categorical variable (either first-year subadult, second-year subadult or adult) and year was a continuous variable. This model was executed with each of four candidate variance structures: log-linear variance (LOCAL=EXP(AGE YEAR), compound symmetric (CS), first-order autoregressive (AR1), and heterogeneous first-order autoregressive (ARH1) (SAS Institute 1997). The most appropriate covariance structure was selected using AIC_c with only the covariance parameters as the number of parameters used in calculating AIC_c because restricted maximum likelihood estimation ignores the fixed effects (Wolfinger 1993). This step was used to select the most appropriate covariance structure for inclusion in the following fixed-effects models with fecundity as the response variable: quadratic time trend (TT), linear time trend (T), even-odd years (EO), linear time trend with an additive even-odd year effect (T+EO), and no time trend (intercept, a means or intercepts-only model). We used full maximum likelihood estimation (rather than restricted maximum likelihood estimation) to analyze these models; the number of parameters in this case were the number of covariance parameters plus the number of fixed effect parameters. The model that best explained the data for each study area was selected using AIC_c . After the workshop, it became apparent that some of the covariance structures had been incorrectly coded. In addition, some models and covariance structures analyzed during the workshop failed to

converge; the log-linear covariance structure for the LAS, SIE and SKC study areas, and fixed-effect models with age and year interactions for the ELD study area. This failure to converge was because there were ≤ 3 subadults (first- and second-year subadult age-classes combined) for 6, 4, 4, and 8 years on the ELD, LAS, SIE, and SKC study areas, respectively. Therefore, we re-analyzed the data with correctly specified covariance structures and we used only adult females for all the time trend models on all 5 study areas. Using data from only ≥ 3 -year old females, the SAS code for each of the covariance structures examined using restricted maximum likelihood estimation was:

```
PROC MIXED METHOD=REML;
RANDOM SITE YR;
REPEATED / LOCAL=EXP(YR) SUB=SITE ;
for log-linear variance,
PROC MIXED METHOD=REML;
RANDOM YR;
REPEATED YR / TYPE=CS SUB=SITE ;
for the compound symmetric,
PROC MIXED METHOD=REML;
RANDOM SITE YR;
REPEATED YR / TYPE=AR(1) SUB=SITE;
for the first-order autoregressive, and
PROC MIXED METHOD=REML;
RANDOM SITE YR;
REPEATED YR / TYPE=ARH(1) SUB=SITE ;
for the heterogeneous first-order autoregressive.
```

We did not compute a meta-analysis across the 5 study areas because of the difference in protocols used to estimate reproductive output in the field. However, comparisons were made between the SIE and SKC study areas because these 2 areas used similar field protocols. In addition, we estimated temporal process variation in fecundity using an intercept only model for each study area.

Estimating Rates of Population Change. We estimated the rate of population increase (8) using the temporal symmetry capture-recapture model of Pradel (1996), which was denoted as $\hat{\lambda}_{RJS}$ where *RJS* was “Reparameterized Jolly-Seber.” For notational ease, we denoted a year-specific *RJS* estimator as $\hat{\lambda}_t$ for year *t*.

Prior analyses of spotted owl data have used a modified Leslie projection matrix (Franklin et al. 1996a) which can be denoted as $\hat{\lambda}_{PM}$ where *PM* denotes “projection matrix” and refers to an age-structured projection matrix approach (Caswell 2000). The 2 types of λ ‘s differ in their definitions and interpretations, as well as in their methods of computation. Here we present a brief discussion of these distinctions and differences.

$\hat{\lambda}_t$ estimates λ_t , the rate of change in population size between years *t* and *t*+1:

$$\lambda_t = \frac{N_{t+1}}{N_t} \quad ,$$

where N_t is abundance at year *t*. In the case of the California spotted owl analysis, the

abundances and $\hat{\lambda}_t$ apply to subadult and adult territorial owls on the study areas. This rate of change in abundance is a function of the four fundamental demographic variables: survival rate, reproductive rate, emigration, and immigration. Thus, demographic explanations for specific values of $\hat{\lambda}_t$ require additional information on these fundamental demographic variables.

$\hat{\lambda}_{PM}$ is computed from projection matrices parameterized with means of time-specific estimates, or constant-parameter model estimates, for age-specific survival and fecundity for juvenile, subadult, and adult survival. The $\hat{\lambda}_{PM}$ resulting from these computations represents the asymptotic growth rate for a population exposed to the projection matrix vital rates year after year. This value can be viewed as a function of the average vital rates but is not necessarily a good estimate of the average rate of change in number of birds on the study area for at least four reasons. First, there is an asymmetry in the way movement is treated in vital rates representing gains and losses. New individuals are added to the projected population only via *in situ* reproduction, as reflected in the fecundity estimates. However, spotted owl survival estimates represent apparent survival in that their complements include both death and permanent emigration from study areas. Thus, losses from the population occur via both death and permanent emigration. Note that sometimes (e.g., previous spotted owl analyses in Burnham et al. 1996, Franklin et al. 1999) efforts are made to adjust apparent survival estimates so that they better approximate true survival. These efforts reduce the movement asymmetry and its effect on $\hat{\lambda}_{PM}$. However, these adjustments require additional information on emigration, such as information from radio-marked birds. Second, the computed $\hat{\lambda}_{PM}$ is an asymptotic value expected to result from the complete absence of temporal variation in the vital rates, whereas there is likely to be evidence of temporal variation in the data. Thus, $\hat{\lambda}_{PM}$ is a constant value over a specified time period whereas $\hat{\lambda}_t$ provides annual estimates that capture the temporal variability in rates of population change. Third, the values of fecundity may be positively biased if non-breeding birds are not detected or if unsuccessful birds are not detected as readily as successful birds. The fourth reason is related to the first and involves the fact that estimates of juvenile survival are probably negatively biased when they are obtained using capture-recapture methods (Franklin et al. 1999). This is of concern with California spotted owls because of the paucity of data for estimating juvenile survival. In summary, the $\hat{\lambda}_t$ should provide reasonable estimates of annual rates of change in abundance of territorial birds on the study area. The $\hat{\lambda}_{PM}$ is perhaps best viewed as an abstraction to the extent that (1) it is an asymptotic quantity that assumes no temporal variation in vital rates, and (2) it includes all losses from, yet not all gains to, the population (no recruitment from outside the study area is included in this quantity).

There are several assumptions underlying estimation of \mathcal{S}_t that need to be considered (see Hines and Nichols 2002 and Franklin 2002 for more complete details). First, interpretation of such estimates is most straightforward when study area size and boundary configurations remain unchanged through time. If study areas expand or contract over time, the resulting $\hat{\lambda}_t$ will reflect the fact that the population to which inferences are being made is also expanding or contracting. Second, all animals within the study area must have some probability of being re-captured throughout the study. If portions of the study area are inaccessible during some years of the study but then become accessible for trapping in subsequent years, individuals captured in the inaccessible portion of the study area will suddenly become “new recruits” to the population even

though they had been present, but not available for sampling, in previous years. Third, permanent trap response in capture probability can bias estimates of δ_t (Hines and Nichols 2002). When animals respond positively or negatively to being captured (Seber 1982), a difference in capture probability occurs between animals that have, and have not, been captured previously and marked. Permanent trap response in the standard Cormack-Jolly-Seber models induces no bias in survival estimates (Pollock et al. 1990) but estimates of population size under the Jolly-Seber model are biased in the face of permanent trap response because the difference in capture probability between marked and unmarked animals causes predictable problems (Nichols and Hines 1984). This same bias also applies to estimates of δ_t . Hines and Nichols (2002) found that bias was positive in the presence of a trap-happy response and negative in the presence of trap-shy responses. This bias was not substantial for small levels of trap responses but could be if levels of trap response are high. If trap response changes over time, then misleading trends in $\hat{\lambda}_t$ could result. Fourth, estimates of δ_t are biased in the presence of heterogeneous capture probabilities among individuals, or unidentified classes of individuals. Hines and Nichols (2002) found that heterogeneous capture probabilities did not bias estimates of δ_t when population growth rate was modeled as a single constant over all time periods. Small bias did occur when estimating time-specific δ_t . However, this bias was not as substantial a problem as that resulting from permanent trap response.

Violation of the first 2 assumptions do not produce bias, in the sense that the estimator of δ_t is not performing as it was intended (Hines and Nichols 2002). When the study area changes, the estimated population change is the result of 2 conceptually distinct processes. The first process involves expansion of the study area and the increase in number of animals exposed to sampling that result from this expansion. The second process involves changes in the number of animals on the sampled area; this is the change of interest and the one to which we would like estimates of δ_t to apply.

Other assumptions underlying open capture-recapture models have not been specifically investigated with respect to effects on $\hat{\lambda}_t$. For example, we assume no tag loss and no tag-induced mortality. Since we had no reason to suspect these were important problems, we did not investigate consequences of their violation. However, loss of the same type of bands used on 3,788 northern spotted owls was only 0.1% (Forsman et al. 1996). In addition, owls were recaptured when color band combinations became difficult to read. Similarly, homogeneity of demographic rate parameters (e.g., survival) among individuals is assumed in open population capture-recapture models. Our focus on territorial birds eliminated the potentially large variation between territorial and “floater” birds, and we do not know the consequences of remaining variation in parameters among individual territorial birds. As with most explorations of heterogeneous rate parameters, we suspected that substantial variation could lead to important bias, whereas relatively minor variation would be less of a problem. The high annual survival estimates for spotted owls do not permit substantial heterogeneity (it would not be possible to have such high mean survival if many individuals exhibited greatly reduced survival). Open model assumptions often include the specification that all emigration is permanent. As noted by Kendall et al. (1997) random temporary emigration led to unbiased estimates of the size of the “superpopulation”, consisting of birds having some chance of being in the sampled area during the sampling period. In the case of random temporary emigration, we expect estimates of δ_t to be unbiased for changes in superpopulation size. However, nonrandom (e.g., Markovian) forms of temporary emigration could lead to biased estimates of δ_t , and we are not aware of investigations on the consequences of such temporary emigration to estimation.

The primary inference from $\hat{\lambda}_{PM}$ regarding population rate of change was to the territorial owls on the study area. Previously, the primary inference from $\hat{\lambda}_{PM}$ has been phrased as “did the

territorial owls on the study area replace themselves?” (Burnham et al. 1996, Franklin et al. 1999). However, this inference provides no information on where replacement owls might go with respect to study area boundaries. In other words, this would apply if all of the young produced on a study area remained on that area and then exhibited similar survival and fecundity rates of adults on that area. Thus, this inference might be properly rephrased as “would the territorial owls on the study area replace themselves if the system was geographically closed?” In contrast, the inference from $\hat{\lambda}_t$ included recognition that the system may not be geographically closed and was “were the territorial owls on the study area being replaced?” (Franklin et al. 1999). This inference was about the owl populations residing within a specific study area. An advantage of \mathcal{B}_t was that estimates of juvenile survival were not required because both immigration and emigration were accounted for by changes in number of owls over time. Thus, the potential bias from imprecise and inaccurate estimates of juvenile survival is avoided. However, a primary limitation about inferences concerning $\hat{\lambda}_t$ is that it is not possible to estimate the relative contributions of the different contributions of the different components to population growth (e.g., reproduction, immigration, death, and emigration) without additional data. For example, immigration could sustain a demographically (based on survival and reproduction) declining population, i.e., the population could be a sink (sensu Pulliam 1988). It should be noted that most spotted owl populations, as defined by the usual scale of study, were likely maintained by immigration (behavior commonly attributed to sinks), while also supplying recruits to other populations (behavior commonly attributed to sources). Thus the source-sink dichotomy may not be as useful with spotted owl populations as with some other animal populations. Thus, $\hat{\lambda}_t$ was an important tool but will not be a panacea as a single assessment of the health of a spotted owl population. Consequently, all relevant information should be used to draw inferences about the stability of California spotted owl populations. For example, estimates and trends in survival and fecundity rates should also be evaluated to assess the health of a spotted owl population.

To estimate \mathcal{B}_t for each study area, we employed random effects models in MARK that used the $\hat{\lambda}_t$ from model $\{N_t, p_t, \mathcal{B}_t\}$ as the basis for the analysis. Model $\{N_t, p_t, \mathcal{B}_t\}$, which was used as the basis for the random-effects models, allowed N , \mathcal{B} , and p to vary by year; none of the parameters were otherwise constrained. We considered the following random effects models: linear trend in \mathcal{B} (T), quadratic trend in \mathcal{B} (TT), and mean \mathcal{B} across time (\cdot). These three models were considered with and without elimination of the first estimable \mathcal{B}_t because of potential biases due to trap response, perhaps exacerbated by a “learning curve” by observers. Because of the possibility of different capture probabilities for marked and unmarked birds, we tended to disregard the first estimable λ_t and to focus on models that did not include this parameter. Prior to conducting the analysis on \mathcal{B}_t for each study area, we adjusted some of the study area definitions to meet the assumption of a geographically consistent area where birds had some probability of being surveyed. For the ELD, only the capture-recapture data from the smaller density study area were used and, for the SIE and LAS study areas, a subset of the capture-recapture data from a smaller geographic area were used. Estimates of overdispersion (\hat{c}) were recomputed for the capture-recapture data using program RELEASE and using a global model of $\{N_{s^*t}, p_{s^*t}, \mathcal{B}_{s^*t}\}$ for each study area, with an interaction between sex and year for N , p , and \mathcal{B} .

To make the annual estimates of \mathcal{B}_t more interpretable, we translated those estimates into estimates of realized change of the populations on each study area. Annual realized changes were estimated as the proportion of the initial population (i.e., in the initial year used for analysis) remaining in year t (i.e., $\lambda_t = N_t/N_x$ where x is the initial year). Therefore, realized change provided the estimated trajectory of the population over the time period for which \mathcal{B}_t was estimated, without requiring estimation of numbers of owls on each of the study areas. Realized

change (λ_t) was estimated as:

$$\hat{\Delta}_t = \prod_{i=x}^{t-1} \hat{\lambda}_i$$

where x was the first estimated $\hat{\lambda}_t$. For example, if $\hat{\lambda}_t$ was 0.9, 1.2, and 0.7 for years 1993, 1994, and 1995, respectively, then $\hat{\Delta}_t$ for $t = 1996$ was $(0.9)(1.2)(0.7) = 0.756$ indicating that 75.6% of the starting population remained after 3 years.

To compute 95% confidence intervals for $\hat{\Delta}_t$, we used a bootstrap algorithm. Specifically, we computed time-specific recruitment rates (f_t) for each study areas using model N_t , p_t , f_t in program MARK. Using these estimates, we simulated data in MARK where the initial population size was computed as $N_x = n_x/p_x$ (where n_x is the number of birds caught in initial year x) and the first recruitment rate as $f_x = \lambda_x - \hat{\phi}_x = n_{x+1}/n_x - \hat{\phi}_x$, assuming $p_x = \hat{p}_{x+1}$. This latter assumption was needed because we required an initial abundance for demographic simulations, but were unable to estimate the initial capture probability. This particular solution (equating the first and second capture probability) seemed reasonable to us although other solutions to this same problem have been used by others (e.g., $N_1 = \hat{N}_2$, Jolly 1965; $p_1 = 1$, Schwarz and Arnason 1996). For each simulation, we used model N_t , p_t , $\hat{\lambda}_t$ to compute estimates of $\hat{\lambda}_t$ and, from these, $\hat{\Delta}_t$. We ran 1000 simulations and, from this distribution of simulations computed 95% confidence intervals from the i th and j th values of $\hat{\Delta}_t$, where $i = (0.05)(1000)$ and $j = (0.95)(1000)$.

We also conducted a meta-analysis using only the study areas in the Sierra Nevada (LAS, ELD, SIE, and SKC) to examine potential correlations in annual variation between these study areas. We considered fixed-effects models $\hat{\lambda}_t$, $\hat{\lambda}_{g^*t}$, and $\hat{\lambda}_{g+t}$, where g was study area and with N and p structured as g^*t in all three models. We also considered $\hat{\lambda}_{g+t}$ models without the first and second estimable $\hat{\lambda}_t$, without the first, second, and last $\hat{\lambda}_t$, without the first and last $\hat{\lambda}_t$, and without the first $\hat{\lambda}_t$. In the analysis of the individual study areas and the meta-analyses across the four study areas, we corrected for overdispersion and used the same model selection approach that we used to estimate adult survival.

Comparison of SIE and SKC Study Areas. – The SIE and SKC represented paired study areas where SIE has been managed for timber production and SKC has been managed as a National Park. They covered similar ranges in elevation and were in close proximity (19 km), minimizing differences in weather patterns. Also, investigators used the same field protocols for reproductive output on the 2 study areas, which allowed direct comparison of fecundity rates. Effect sizes were used to compare the differences between the 2 study areas in terms of the 3 demographic parameters: adult fecundity, adult survival, and mean $\bar{\lambda}$.

RESULTS

ADULT SURVIVAL

We used 975 marked adults in the analysis of apparent survival (171 from the ELD, 223 from the LAS, 307 from the SAB, 168 from the SIE, and 106 from the SKC). From Program RELEASE, the overall χ^2 goodness-of-fit for the global model was 184.74 with 167 degrees of freedom ($P = 0.165$), indicating that the global model fit the capture-recapture data. The results of this test yielded $\hat{c} = 1.11$. The minimum QAIC_c model for p combined with the 3 models

$N_{g^{*t+s}}$, $N_{g^{*t+s}}$, and $N_{g^{*t}}$ for apparent survival was $p_{g^{*t}}$. Model selection for all 41 models is shown in Table 3. Based on minimum QAIC_c, the best N model containing separate survival parameters for all 5 study areas was $\{N_g, p_{g^{*t}}\}$ and the best overall model was $\{N_{SKC \text{ vs } rest}, p_{g^{*t}}\}$ (Table 3). Estimates of apparent survival for the $\{N_g, p_{g^{*t}}\}$ model are shown in Table 4. Under model $\{N_{SKC \text{ vs } rest}, p_{g^{*t}}\}$, the apparent survival estimate for the ELD, LAS, SAB, and SIE study areas combined was $\hat{\phi} = 0.819$ (SE = 0.008, 95% CI = 0.802, 0.835) while the separate estimate for SKC was $\hat{\phi} = 0.877$ (SE = 0.016, 95% CI = 0.842, 0.905). Confidence intervals for the estimate from the 4 study areas combined and the estimate for SKC did not overlap. The 2 top-ranked models (Table 3) included separate estimates of N for SKC; these 2 models comprised > 86% of the Akaike weights. The second-ranked model, $\{N_{SAB,SKC \text{ vs } rest}, p_{g^{*t}}\}$ suggested that both the SAB and SKC had separate estimates of N from each other as well as the other 3 study areas combined. However, this model had a nearly identical deviance to the top-ranked model and the $\Delta QAIC_c = 2$ was a result of adding another parameter for the SAB that did not explain any additional variation in the data; the top 2 models essentially explained the same amount of variation. Thus, we concluded that there was strong evidence for model $\{N_{SKC \text{ vs } rest}, p_{g^{*t}}\}$. The annual recapture probabilities from model $\{N_{SKC \text{ vs } rest}, p_{g^{*t}}\}$ were generally high with 87% of the annual estimates >0.8 and 54% >0.9 (Table 5). The combination of high survival probabilities coupled with high recapture probabilities reduced any bias that may be caused by assumption violations, such as heterogeneous capture probabilities (Pollock et al. 1990).

Using a random effects model with estimates from model $\{N_g, p_{g^{*t}}\}$, mean apparent survival across the study areas was estimated to be $\bar{\phi} = 0.831$ (SE = 0.012), with a spatial process standard deviation $\hat{\sigma}_{\text{spatial}} = 0.0212$ (95% CI = 0.0000, 0.0752) among the apparent survival estimates. Estimates of temporal variation in apparent survival were computed for each of the 5 study areas from model $\{N_{g^{*t}}, p_{g^{*t}}\}$ (Table 6). Based on coefficients of process variation (CV), both spatial process variation (CV = 0.025) and temporal variation (CVs = 0.011 - 0.033; Table 6) were relatively low.

FECUNDITY

We analyzed fecundity data from 1,557 reproductive outcomes for adult female spotted owls on all 5 study areas (see Table 7 for study area sample sizes). There was uncertainty in selecting a smooth trend model for fecundity in all of the study areas (Table 7). In all study areas, multiple, highly-ranked models had similar Akaike weights, especially for the ELD, SAB and SIE study areas. In the case of four of the study areas (ELD, LAS, SAB, and SKC), the uncertainty in selecting an appropriate model for fecundity suggested different trends. For example, an intercept-only model was almost as likely as a model suggesting a linear trend and an intercept-only model was almost as likely as a model with even-odd year variation for the SAB. However, models that were similarly likely for the SIE study area all included a linear trend, suggesting that a linear trend may be supported for this study area.

The issue of model uncertainty was further illustrated by the parameter estimates for the effects of interest (Table 8). Two of the study areas (ELD and SAB) had estimates that were not different from zero in the top-ranked models, based on 95% confidence intervals. The parameter estimates for the fixed effects were different from zero for the LAS, SIE, and SKC study areas, and there was evidence of a negative linear trend in fecundity on the SIE study area.

Although fecundity estimates were not comparable across study areas (except for SIE and SKC), we felt that estimates of temporal process standard deviations and their coefficients of variation were comparable; assuming that biases within study areas were constant among years. Except for the SAB study area, there was considerable temporal variation in fecundity in four study areas with coefficients of process variation ranging from 67.2 to 81.7% (Table 9, Figure 2).

The SAB study area had much lower annual variation in fecundity than the other study areas. Except for the SIE, the percent variation explained by the top-ranked trend models for the study areas was low, indicating that these models were not very useful for explaining temporal variation in fecundity (Table 9, Figure 2). These three indicators (model selection uncertainty, imprecise parameter estimation, and low amounts of process variation explained) suggested that there was little support for a smooth trend in fecundity in four of the five study areas. The single exception was the SIE study area, where there was some evidence for a negative linear trend in fecundity. However, the top-ranked model that suggested this trend still only explained 44% of the temporal process variation in fecundity.

RATES OF POPULATION CHANGE

We used 1,019 marked subadult and adult individuals in the analysis of δ_t (144 from the ELD, 191 from the LAS, 401 from the SAB, 163 from the SIE, and 120 from the SKC). These numbers differed from those used to estimate adult apparent survival because of inclusion of the subadult age-classes, changes in study area sizes and time periods examined.

Individual Study Areas. The study area sizes and time periods used in estimating δ_t are shown in Table 10. Overdispersion was evident in the data for all of the study areas except SKC (Table 11). We corrected for this in the subsequent analyses. Two of the study areas, the ELD and SKC, had strong evidence for trends in δ_t . The lowest QAIC_c model for the ELD suggested a linear trend in δ_t (Table 12, Figure 3). The second-ranked model was also a linear trend model but with the first estimable δ_t eliminated. Together, these 2 models accounted for 70% of the Akaike weights. The estimated slope for the linear trend in δ_t on the ELD was negative and different from zero based on 95% confidence intervals (Table 13). The best model for the SKC suggested a quadratic trend in δ_t with the first estimable δ_t eliminated (Table 12, Figure 3). The second-ranked model was also a quadratic trend model but included the first estimable δ_t . These 2 models accounted for 45.5% of the Akaike weights. The slope parameters for this quadratic trend were different from zero based on 95% confidence intervals (Table 13). The best model for the SIE study area also suggested a negative linear trend in δ_t (Table 12, Figure 3) but the second-ranked model suggested a quadratic trend. In addition, the estimated slope for the linear trend was not different from zero (Table 13) although 95% confidence intervals barely overlapped 1. There was a weak negative linear trend for the SAB study area (Table 12, Figure 3). However, there was uncertainty as to whether a linear or means model best explained the data because Akaike weights were similar (Table 12) and the estimated slope for the linear model was not different from zero (Table 13). There was no evidence of a trend in δ_t for the LAS study area (Table 12, Figure 3); a means model best supported the data for this area.

The estimates of realized change (λ_t) represented the trajectory (or trend in numbers) of each study population (Figure 4). These estimates were based solely on the estimates of δ_t and did not require estimating annual population size (N_t) for each study area. The trends in Figure 4 represent the proportion of the population remaining each year, given the initial population in the first year. For example, if there were 100 owls on the SIE study area in 1993, there were 71 owls in 1999, based on the estimates of δ_t and, hence, λ_t for that study area. Populations on the LAS, SAB, and SKC study areas remained fairly stationary over the course of the study. The ELD population increased and then decreased to a level that was higher, but not different than the initial population, based on 95% confidence intervals. The SIE population decreased steadily from 1993 resulting in a population that was substantially lower and different from the initial population, based on 95% confidence intervals. In 1999, 70.9% of the SIE population remained of the initial population in 1993 (Figure 4).

Based on a random effects intercepts-only model using annual estimates of δ from model $\{N_t, p_t, \delta_t\}$, 95% confidence intervals of the estimated mean δ ($\bar{\lambda}$) across years for each of the

study areas was not different from a stationary population ($\mathcal{R} = 1$; Table 14, Figure 5) although point estimates were <1 for four of the study areas (LAS, SAB, SIE, and SKC). The SIE study area had the lowest estimate of $\bar{\lambda}$ with 95% confidence intervals that barely overlapped $\mathcal{R} = 1$, suggesting that the owl population on the SIE was declining. Temporal process variation in \mathcal{R}_t was low (CV for ELD = 8.4%, for SIE = 1.5%, for SKC = 10.1% and 0% for LAS and SAB). The model with the negative linear trend in \mathcal{R}_t for the ELD accounted for an estimated 100% of the temporal process variation in \mathcal{R}_t , and the model with the quadratic trend for the SKC accounted for 75.7% of the temporal process variation in \mathcal{R}_t . This suggested that these were useful models for explaining the temporal process variation in \mathcal{R}_t (Franklin et al. 2001).

Meta-analysis Across Study Areas. There was strong support for an additive study area effect over time (model \mathcal{R}_{g+t} ; Table 15); model \mathcal{R}_{g+t} included an additive effect, and was weighted much more heavily (99.4% of the Akaike weights) than models with a study area by year interaction, just a year effect or just a study area effect. This suggested \mathcal{R}_t changed similarly among the four Sierran study areas even though there were differences in magnitude of the \mathcal{R}_t (Figure 6). In the best model, study area effects (expressed as the difference from SIE on a logit scale) were 0.036 (95% CI = -0.030, 0.101) for the SKC, 0.083 (95% CI = -0.07, 0.173) for the ELD, and 0.050 (95% CI = -0.031, 0.132) for the LAS, suggesting the ELD was slightly higher than the other study areas in terms of magnitude of $\hat{\lambda}_t$ during the time period (1994-1999) examined. Because we were interested in temporal covariation, we did not consider any smooth time trend models as we did with the individual study areas. Based on the results for the individual study areas, 3 of the studies had negative linear trends. However, the additive effect of time suggests that the study areas tracked each other in terms of changes in \mathcal{R}_t over time.

Using the estimates from model $N_{g^*t}, p_{g^*t}, \mathcal{R}_{g^*t}$, we used random effects intercepts-only models to estimate $\bar{\lambda}$ for each Sierran study area for the common time period, 1994-1999. In general, estimates were lower than those computed in Table 14: 0.942 (95% CI = 0.878, 1.005) for the SIE, 0.958 (95% CI = 0.866, 1.049) for the SKC, 1.001 (95% CI = 0.913, 1.090) for the ELD, and 0.985 (95% CI = 0.927, 1.042) for the LAS.

COMPARISON OF SIE AND SKC STUDY AREAS

Based on the 95% confidence intervals for the effect sizes, only adult survival was different between the 2 study areas (95% confidence intervals for the difference did not overlap zero) with SKC having higher adult survival than SIE (Table 16). However, the point estimates for adult fecundity and $\bar{\lambda}$ were also higher for the SKC study area than for the SIE study area. In addition, the population trends in the 2 companion studies (SIE representing lands managed for timber production and SKC representing National Park Service lands) had different trajectories in $\hat{\lambda}_t$; the SIE had a negative linear trend in $\hat{\lambda}_t$ whereas the SKC had a quadratic trend over the same time period; $\hat{\lambda}_t$ initially declined and then increased on the SKC. This resulted in a decline in the population on the SIE but not on the SKC (Figure 4). However, there was less strength of evidence for the linear trend in $\hat{\lambda}_t$ on the SIE than for the quadratic trend in $\hat{\lambda}_t$ on the SKC.

DISCUSSION

The spotted owl has been the focus of both extensive and intensive population studies for nearly 2 decades (Gutiérrez et al. 1995). In general, population studies of California spotted

owls began later than those for northern spotted owls because there was a perceived difference in habitat use patterns and prior anthropogenic disturbance of habitat (Verner et al. 1992b). The first study to estimate population characteristics and assess spotted owl population trends in the central Sierra Nevada began in 1986 on the Eldorado National Forest (Noon et al. 1992, Seamans et al. 2001a). The ELD study was followed in 1987 by a study (SAB) in the San Bernardino Mountains of southern California. The SAB study area contained the largest population of spotted owls in southern California (LaHaye et al. 1994). A third study on a small population occurred between 1988-1992 on Mount San Jacinto, southern California (Gutiérrez and Pritchard 1990). This latter study was terminated due to lack of funding. Finally, three studies were begun in 1990 in the northern (Lassen National Forest, LAS) and southern Sierra Nevada (Sierra National Forest, SIE: and Sequoia-Kings Canyon National Parks, SKC).

Although the study areas covered a large latitudinal gradient, the results of this meta-analysis cannot be considered representative of owl demographic trends throughout the Sierra Nevada. If, at the inception of these studies, habitat management on the study areas was either different than that of the surrounding areas or changed as a result of the study location (i.e., study areas were preferentially protected from management activities), then general inference beyond the study areas cannot be made. A study comparing habitat quality within the study areas to habitat quality off the study areas in the Sierra Nevada could elucidate this question. If initial placement of the demography studies was due to a history of owl occupancy (i.e., they were not randomly located), then the conditions on the study areas may have been different than those on the surrounding areas (i.e., study areas were higher quality areas because there were more owls). Therefore, our inferences applied to the populations of owls within the study areas that participated in the meta-analysis. Further, these population studies do not encompass the range of the California subspecies because a significant population exists in central Coastal California and other populations exist in southern California, and northern Baja California (Gutiérrez et al. 1995). Nevertheless, the extant population studies span a major latitudinal gradient over the range of this subspecies. Each of the 5 study areas had unique characteristics that capture much of the inherent environmental variation within the California spotted owl range. Therefore, in this discussion, we first present a set of general inferences regarding population characteristics and trends for the California spotted owl populations represented in this meta-analysis. These general inferences are followed by study area specific inferences, which capture some of the unique environmental characteristics or owl population dynamics for the individual areas. In this latter section, we include a discussion on the comparisons between the SIE and SKC, which represent paired studies using the same field techniques, but having different management regimes. Lastly, we synthesize the information from the general and area-specific inferences and present recommendations for managers and for future meta-analyses of the California spotted owl.

General Inferences

Apparent Survival. Noon and Biles (1990) and Blakesley et al. (2001) demonstrated that survival rate of breeding adults was a key demographic parameter of spotted owl population dynamics. Our best model for apparent survival of adults indicated that rates were similar among the ELD, LAS, SAB, and SIE study areas (0.819), but higher for the SKC study area (0.877). The pooled estimate of \hat{N} for ELD, LAS, SAB, and SIE was comparable to estimates of two Mexican spotted owl populations (Seamans et al. 1999), but slightly lower than the mean estimate for adult northern spotted owls among 15 study areas (0.850; Franklin et al. 1999), whereas apparent survival on the SKC was higher than average rates of northern and Mexican spotted owl. Average adult apparent survival estimates across all three subspecies of spotted owl ranged from 0.8-0.9 (Gutiérrez et al. 1995).

In this meta-analysis, temporal variation in adult apparent survival on all study areas was very low (CV = 0 - 3%). This inference is expected for animals with high adult survival rates (e.g., Gaillard et al. 1998, Pfister 1998). Estimates of temporal variation in adult survival for

Mexican spotted owl populations were slightly higher (Seamans et al. 2002; CV = 7 - 13%), but estimates from a study of northern spotted owls were comparable (Franklin et al. 2000; CV = 4%). Weather explained >50% of the temporal process variation in apparent survival in Mexican spotted owls (Seamans et al. 2002) and all of the temporal process variation in a northern spotted owl population (Franklin et al. 2000). Thus, weather may account for most of the temporal variability in spotted owl survival. However, because our data did not support time-based apparent survival models and temporal process variation in apparent survival was very low, we suspect weather did not have a large effect on survival.

Spatial process variation in adult survival from this meta-analysis (CV = 3%) was similar to estimates from a meta-analysis on northern spotted owls (Franklin et al. 1999; CV = 2%). The small amount of spatial process variation in our meta-analysis was largely due to differences between SKC and the rest of the study areas. The four study areas with similar apparent survival were on National Forests (i.e., were managed for multiple use) whereas the SKC was in a National Park (i.e., managed as a preserve). Therefore, differences in forest management was one possible cause of the differences in adult apparent survival between SKC and the other Sierra Nevada study areas (see individual study area discussions for local habitat and management details). Another major difference between SKC and the other study areas was the presence of giant sequoia groves on the SKC. Almost half of the historic roost sites of pairs using mixed-conifer forests in SKC were in or within 1 km of sequoia groves. In contrast, there was only 1 sequoia grove on the SIE and 1 on the RSA of the ELD. It was possible that these groves promoted higher survival of spotted owls compared to other conifer forest types. If these groves promote higher survival, the causative mechanism is unknown.

An important biological issue with open capture-recapture models is that mortality and emigration are confounded (Schwarz and Seber 1999). Therefore, these models provide estimates of apparent survival, which is defined as the probability of surviving and staying within the sampled population (Franklin et al. 2000). However, territorial spotted owls infrequently switch territories, which indicates that permanent emigration is low (Raphael et al. 1996). For example, within the insular SAB, territorial male and female owls dispersed an average of 2.95 and 4.28 km, respectively, from their initial location. Breeding dispersal was detected in 7% of between-year observations (territory change; $n = 54$ of 743 observations) in the LAS. The median breeding dispersal distance within the LAS was 7 km (range 1-33, $n = 54$; Blakesley 2003). Because dispersal distances were short relative to the size of the LAS, most dispersing owls probably remained in the study area. Further, we estimated emigration from the ELD density study area using observations of banded owls on the regional study area and documented that 1.4% (5/354) of territorial owls moved from the density to the regional study area over a six-year period. Thus, adult emigration was probably low in these studies.

Fecundity. Except for the SKC and SIE, we did not directly compare fecundity estimates among study areas because we were not sure if differences in protocol were confounded with other differences among study areas. However, because protocol was consistent within study areas, we believe that we could compare temporal process variation and general patterns.

Although our point estimates of mean fecundity for the California spotted owl were within the range of those for the northern (Franklin et al. 1999) and Mexican spotted owl (Seamans et al. 2002), it is possible that differences were the result of unique protocols among studies. Except for the SIE, there was little support for a smooth trend in fecundity for any of the other study areas. For Sierra Nevada studies, fecundity varied substantially among years within all study areas (range in CV of temporal process variation = 67.2% - 81.7%); 1992 appeared to be an exceptional year for reproduction, and all other years were either moderately successful or poor reproductive years. This large temporal variation in fecundity was consistent with results of a northern spotted owl meta-analysis (Franklin et al. 1999) as well as with general predictions for long-lived animals (Gaillard et al. 1998, 2000; Pfister 1998).

Climate models explained all of the estimable temporal process variation in fecundity in a population of northern spotted owls (Franklin et al. 2000). Other studies also have linked climatic

factors with reproductive output in northern (Wagner et al. 1996, Zabel et al. 1996), California (North et al. 2000), and Mexican spotted owls (Seamans et al. 2002). In addition, weather patterns were highly variable throughout the range of the California spotted owl (Kahrl 1979), and may have accounted for the large temporal variation in fecundity. Factors that may have contributed to the occurrence of exceptional years in spotted owl reproduction included mild spring weather (Franklin et al. 2000) and high prey abundance. Prey abundance has been positively associated with reproduction in other owl species (Verner et al. 1992a). The exceptionally high fecundity in 1992, which occurred near the beginning of the Sierra Nevada studies, may have driven the negative linear trend seen on the SIE. Additional study and analyses using weather covariates will be needed to elucidate these trends (e.g., correlation of fecundity and weather patterns).

SAB exhibited neither the extremely successful reproduction in 1992 nor any of the very poor reproductive years seen in all of the Sierra Nevada studies and thus was less variable (CV of temporal process variation = 21.7%) the Sierra Nevada study areas. Weather patterns appeared to have a strong link to owl fecundity in the SAB (LaHaye et al. in review). Therefore, different weather patterns were one possible explanation for the differences in temporal variability.

Population Trend. Mean estimates of λ_t from all study areas were < 1 except for the ELD. However, the 95% confidence intervals for all estimates included 1, indicating that all of the populations were stationary or the estimates of λ_t were not sufficiently precise to detect declines if they occurred. This latter point was important because point estimates for 4 of the 5 study areas indicated annual population declines of 2-4%, but the estimates were not sufficiently precise to differentiate those estimates from stationary populations. This inference was similar to that drawn by Noon et al. (1992) when they estimated California spotted owl trends using a Leslie projection matrix (see below). Three of the study areas (LAS, SKC, SAB) had little evidence supporting a declining trend in λ_t . A negative trend in λ_t was observed on both the ELD and SIE. This was cause for concern on the SIE because it suggested an accelerated rate of decline in the owl population on the SIE during most of the study period. However, the high reproduction in 1992 on the 4 Sierra Nevada studies may have been responsible for driving these trends under the following hypothetical scenario. The estimate of λ_t for 1992-1993 was a function of both numbers of adults surviving from 1992 and the number of new recruits entering the territorial population in 1993. If juvenile survival was approximately 30%, then a relatively large number of new recruits would have been available to enter the territorial population in 1993 (and later years) from the large cohort produced in 1992. Thus, the high estimates of λ_t in the interval 1992-1993, and subsequent years, may have resulted from the increased recruitment from this cohort. If density increased because owls occupied lower quality habitats, a decline would be expected due to lower vital rates of owls in the less productive habitats subsequent to this breeding pulse. This prediction could be tested on some study areas by examining territory occupancy patterns to determine if territories originally occupied after 1992 were the first to become vacant. Alternatively, populations prior to 1993 could have been at relatively high or low densities, thus confounding subsequent territory occupancy patterns. This breeding/recruitment pulse could have affected estimates of mean λ_t ; earlier high estimates would have increased the mean estimate and also contributed to a larger standard error.

Although estimates of temporal process variation appeared higher for the ELD and SKC, 95% confidence intervals for all study areas overlapped considerably, and four of the five confidence intervals included zero. Therefore, rate of population change varied only slightly among years on the individual study areas. However, the best model from the meta-analysis of the Sierra Nevada study areas indicated that λ_t was different for each of the study areas, that the estimates varied among years, and that differences among study areas were additive across years. The added power of the meta-analysis may have allowed us to detect time effects in the Sierra study areas.

Our estimates of λ_t apply only to the years when the studies occurred (Raphael et al. 1996). Thus, predictions regarding the trajectory of California spotted owl populations beyond

these time frames are not appropriate. Estimates of λ_t also should not be interpreted as numbers of birds; these are annual estimates of rates of change in the number of birds. For example, the periodic estimates of λ_t that are <1 in the SIE and LAS study areas represent a decrease in the number of birds. The intervening values >1 do not indicate that the population was restored to the original numbers at the beginning of the study; they only indicate that numbers increased relative to the number in the preceding year. Thus, a cyclic pattern in λ_t can exist that ultimately results in losses of birds over time. However, this should be somewhat balanced in the estimates of mean λ_t over time. We attempted to understand how λ_t relates to changes in abundance by estimating realized changes in populations on each study area, based on estimates of λ_t . Based on these population trajectories, the SIE was the only study area exhibiting evidence of a significant reduction of the original population over the course of the study.

Historically, stage-based Leslie projection matrices were used to estimate λ_{PM} in spotted owl populations (e.g., Forsman et al. 1996, Noon et al. 1992, Blakesley et al. 2001). Initially, we did not use the Leslie projection matrix approach because of problems in estimability of parameters for juvenile survival. However, a number of workshop participants felt that the larger problem was that we could not calculate an unbiased estimate of juvenile survival or juvenile emigration, parameters necessary for an unbiased estimate of λ_{PM} . The possible exception to this problem was the SAB study area. Using the alternative estimator for population rates of change (λ_t), the demographic components of λ_t (apparent survival and recruitment) in our analyses were confounded; apparent survival was a function of death and emigration, whereas recruitment was a function of owls born on the study area and recruited into the study population plus immigration and subsequent recruitment of owls from outside the study area. Consequently, λ_t did not separate population growth within the study area (i.e., recruitment of young born on the study area) from immigration from outside the study area (i.e., recruitment of immigrants born outside the study area).

Burnham et al. (1996) recognized the potential for underestimating juvenile survival from mark-recapture methods using study areas with finite size (see also Barrowclough 1978). They corrected this bias by using estimates of emigration rates derived from studies of radio-marked juvenile spotted owls (Forsman et al. 1996). Following northern spotted owl meta-analysis (Burnham et al. 1996), researchers on the ELD proposed to effect a study of juvenile survival using radio telemetry. Unfortunately, funding constraints did not allow for such a study. California spotted owl researchers on the ELD, SIE, and SKC recognized the limitations of their juvenile survival estimates and how those limitations potentially biased analyses using a Leslie projection matrix. Therefore, they used a “surrogate” estimate of juvenile survival derived from studies of the SAB population, which was believed to accurately reflect juvenile survival in that population (Steger et al. 2000, Seamans et al. 2001b). This approach was unsatisfactory because the conditions on the SAB were not similar to the ELD, SIE, and SKC. Consequently, an alternative approach was to examine the juvenile survival rate needed to achieve an estimate of $\lambda = 1$, given the other vital rates (Seamans et al. 2001b). The LAS study was designed to use a Leslie projection matrix approach, thus, they used an estimate of juvenile survival derived from their data (Blakesley et al. 2001). The percentage of juveniles born on the ELD and subsequently recruited into the ELD population (9%; 13/153) was substantially less than other studies, suggesting that either the dispersal pattern for this population was very different from other owl populations (i.e., more juveniles disperse further) or that juvenile survival was much lower. Thus, because we were uncertain if juvenile survival rates from all studies were biased by emigration, we agreed not to use λ_{PM} for the meta-analysis of owl trends.

Summary of General Results – The metrics estimated in this meta-analysis were linked because λ_t is the sum of apparent survival (survival and emigration) and recruitment (births plus immigration). For example, survival of territorial owls probably established the baseline for λ and fecundity and recruitment affected temporal variability in λ for a northern spotted owl population (Franklin et al. 2000). Similarly, low process variation in our apparent survival estimates suggest

that variation in \mathcal{R}_t will likely result from variation in recruitment (e.g., the boom reproductive year and, hypothesized, subsequent lag effect in \mathcal{R}_t described above).

All of the study areas in our analyses demonstrated similar patterns in vital rates. The two main exceptions were: (1) apparent survival was higher for SKC than the other study areas, and (2) SAB did not experience the boom and bust years in fecundity observed in the Sierra Nevada. Two differences between these study areas and the other three were that the SKC was in a national park and the SAB was an insular population disjunct from the Sierra Nevada. However, the cause of the demographic differences between the SAB, SKC, and the other study areas was unknown.

We attempted to address three possible scenarios with this meta-analysis; (1) California spotted owls declined across the studies; (2) California spotted owls were stationary across the studies, and (3) California spotted owls declined within a portion of the studies. When the estimates and trends in the population parameters were examined as a whole, there appeared to be two ends of a spectrum (Table 17). In the Sierran province, the SKC population on National Park lands seemed to be the most viable population with the highest adult apparent survival, a positive trend in $\hat{\lambda}_t$ and no evidence of a trend in fecundity. At the opposite end of this spectrum was the SIE study, which had the lowest estimate of $\bar{\lambda}$, low adult apparent survival, and declining trends in both $\hat{\lambda}_t$ and fecundity. The ELD and LAS studies were between these two endpoints and were difficult to classify in terms of their status. The SAB study area was also difficult to classify, although it had both low estimates of $\bar{\lambda}$ and low adult apparent survival. These analyses indicated that 4 of the study populations (ELD, LAS, SAB, and SKC) appeared to be stationary or slightly declining. The SIE population probably experienced a decline during the period of study. Evidence that this owl population declined included 1) a linear decline in fecundity, 2) a 95% confidence interval on $\hat{\lambda}_t$ that barely encompassed 1, and 3) a linear decline in $\hat{\lambda}_t$, suggesting an accelerated decline in the owl population, which was best illustrated with the realized change estimates. Our results support the third scenario that spotted owls declined within a portion of the studies and appear stationary in some of the studies. Thus, there was uncertainty whether California spotted owls were declining or were stationary across all the studies. For example, point estimates of $\hat{\lambda}_t$ for 4 out of 5 study areas were less than 1, but were not sufficiently precise to differentiate them as slight declines or as stationary populations. Further, estimates of apparent survival were less than those reported in a meta-analysis of the declining northern spotted owl (Franklin et al. 1999). Thus, additional data may be needed to resolve these uncertainties.

Study Area Specific Inferences

LAS. – Estimated apparent survival probability of adult spotted owls was nearly identical to a previously published estimate for the LAS, 1990-1999 ($\hat{\phi} = 0.827$, SE = 0.015; Blakesley et al. 2001). Additional research indicated that apparent survival was positively correlated with the amount of specific cover types selected by the owl at the landscape scale for nesting, roosting and foraging within owl core and nest areas (814 and 203 ha areas around nest areas; Blakesley 2003).

Estimated mean fecundity was slightly higher than a previously published estimate for the LAS, 1990-1999 ($\hat{b} = 0.291$, SE = 0.065; Blakesley et al. 2001). The higher fecundity estimate in this study was due to the additional year of data (2000), during which the owls had relatively high fecundity. Blakesley (2003) found that reproductive output in the LAS was negatively

correlated with elevation and amount of non-forested habitat or habitat dominated by trees < 30 cm dbh within 203 ha of the nest area.

The even/odd year (high/low) effect on fecundity in the LAS may be a general trait of spotted owls in the Cascade geographic province. For example, all of the study areas in the Oregon and Washington Cascades showed this same effect in a meta-analysis of northern spotted owls (Franklin et al. 1999). However, the even/odd year relationship was more regular in many of the northern spotted owl Cascade study areas than in the LAS. The forces driving this phenomenon were unknown, but the pattern may have been influenced by a combination of variable prey densities and weather. The very high owl reproductive output in 1992 coincided with a mild winter, and a peak in *Peromyscus* density which immediately followed an unusually large sugar pine cone crop (JAB personal observation). The second best model of fecundity for LAS included a weak negative time trend in addition to the even/odd year effect of the best model. This weak downward trend may have been an artifact of the extremely high reproductive year occurring in year 3 of the 11 year study.

The estimated population trend at LAS 1994-1999 using \mathcal{S}_t was higher than that estimated at LAS 1990-1999 using the Leslie projection matrix ($\hat{\lambda}_{PM} = 0.910$, SE = 0.025; Blakesley et al. 2001). If both estimates were correct, this implied that the population of owls in the LAS was being sustained by immigration or that the population declined more steeply from 1990-1994 than from 1994-1999. Immigrants to the LAS would most likely come from the Plumas National Forest, to the south, because there was little suitable spotted owl habitat to the west, north and east of the LAS. In addition to the differences in the methods and the inferences to be drawn from the 2 methods discussed above (*Estimating Rates of Population Change*), the discrepancy in \mathcal{S} estimates may have been due to the following factor. Because the smaller LAS study area was designated *post hoc* during this analysis (i.e., in order to be comparable to the other studies in the meta-analysis, contiguous segments of LAS were chosen which would serve as a *de facto* density study area by virtue of their complete survey each year), the assumption of equal capture probability of banded and unbanded birds may not have been met. In addition to the behavioral response of animals to being trapped, discussed above, “trap response” may have been present in the data if field personnel learned where to find individual owls over time, increasing the probability that banded owls were recaptured. Although this may have occurred to a small extent in all of the spotted owl demography studies, it may have been more pronounced in the LAS study area because the study was originally designed to follow the fates of individual owls through time, rather than to locate and capture every owl within a predefined area. If trap response was present, it would have positively biased estimates of \mathcal{S}_t .

ELD. – Previously published results from the ELD (Seamans et al. 2001b) indicated that, from 1990-1999, the apparent survival rate of males ($\hat{\phi} = 0.844$, SE = 0.015) was higher than that of females ($\hat{\phi} = 0.819$, SE = 0.018), and that the apparent survival rate for both sexes followed a log-linear pattern over time. For this study, the meta-analysis of apparent survival examined the study areas jointly, which precluded modeling sex effects or time trends separately for the ELD. Thus, it was unclear if these patterns would still be supported with the additional year of data. Regardless, estimates of temporal process variation indicated that apparent survival varied little over time. This suggested that annual changes in biotic and abiotic factors, such as prey availability, habitat, and weather, had only a small effect on annual apparent survival.

The estimate of mean fecundity from this study was similar to that from a previous published estimate for the ELD ($\hat{b} = 0.400$, SE = 0.010; Seamans et al. 2001). Although a negative linear decline best fit the data, this model only explained 24% of the inter-annual variation in fecundity estimates. Selection of the linear model may have been a consequence of the relatively high estimate of fecundity in 1992, which was early in the study. Further, the large

amount of process variation left unexplained by the linear time trend suggested that annual variation in biotic and abiotic factors probably affected owl reproduction.

The estimated population trend in the ELD, 1992-1999, using δ_t ($\bar{\lambda} = 1.042$, SE = 0.047; this study) was higher than that estimated in the ELD, 1990-1999, using the Leslie projection matrix ($\hat{\lambda}_{PM} = 0.948$, SE = 0.026; Seamans et al. 2001b). Although the confidence intervals overlapped for these two estimates of δ , they indicated different population trajectories; δ_t a stable or increasing population, and δ_{PM} a declining population. It was unlikely this was due to the different time periods because abundance of territorial owls increased from 1990 to 1992 (Seamans et al. 2001b). Therefore, the difference occurred because either the two methods did not share the same inferences (particularly because δ_{PM} assumes constant vital rates over the study period), or, that one or both were biased (see *Estimating Rates of Population Change* in methods).

It was unclear if the negative linear trend in δ_t , and the point estimates of $\delta_t < 1$ in the latter part of the study were reason for concern. Further, understanding the mechanisms behind the increase and subsequent decline in the population will be of ultimate interest. Vital rates responsible for changes in abundance exhibit varying degrees of temporal variability. During our study, inter-annual variation in δ_t was probably most closely related to vital rates with large temporal variability, such as fecundity and recruitment (Franklin et al. 2000, Seamans et al. 2002b). Thus, factors that exhibit temporal variability, such as weather and prey availability, may have been responsible for the observed variation in δ_t .

Changes in habitat quality on the ELD may also have affected δ_t , and were of greater concern because they may have long-term effects on vital rates. Two apparent potential causes of habitat loss during the study were logging and wildfire. There were two catastrophic wildfires that occurred during our study, the 1992 Cleveland Fire (99 km²) and the 2001 Star Fire (65 km²), which burned all or part of 6 owl territories. Although the Cleveland Fire was adjacent to the ELD in what would later become part of the Regional Study Area, this large wildfire may have displaced individual owls that subsequently immigrated to the ELD. It was too early to determine the effect of the Star Fire on the population.

The ELD was unique among the study areas because it was a mosaic (“checkerboard”) of public and private land ownership (Bias and Gutiérrez 1992). This pattern was a relic of land allocation to the Central Pacific Railroad in the late 1800s (Beesley 1996). Most of this land has since passed to individuals or corporations and has been managed primarily for timber production. Although both public and private land were harvested on the ELD, private land harvest rates were probably higher than on adjacent public land during the study due to application of CASPO guidelines (Verner et al. 1992a). Timber harvest on the ELD may have affected territorial owls by reducing suitable habitat for roosting, foraging, or nesting (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). Conversely, forest succession may have increased the amount of mature forests during the study; forests with characteristics that were associated with spotted owls on the ELD (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). Although we did not know the net effect of the above factors on habitat quality, they likely will influence the long-term population trajectory of spotted owls on the ELD.

SIE and SKC. **S** Adult apparent survival may have been different between the SIE and SKC because of natural or management induced differences in vegetation. Three hypotheses that could relate differences in vegetation to differences in apparent survival were: 1) natural differences in amount of oak-woodland and sequoia groves; 2) differences in timber management; and 3) differences in the application of prescribed burning. Twenty nine percent (13 of 45) of owl sites on the SIE were in the low elevation oak-woodland, whereas 21% (8 of 39) on the SKC were in this vegetation type. Owl sites in oak-woodland had less live tree basal area and canopy cover than sites in conifer forests (Verner et al. 1992a). If sites in oak-woodland were of lower quality, then owls in those sites may have had lower survival rates. Another difference in

vegetation was that there were substantially more giant sequoia groves on the SKC (see General Discussion). Giant sequoia groves may have provided high quality spotted owl habitat because they represented large blocks of old growth forest, which were positively correlated to northern spotted owl survival (Bart 1995, Franklin et al. 2000). Hunsaker et al. (2002) also found that owl productivity scores, based on presence of owls and their reproduction, were positively correlated with the proportion of the area having $\geq 50\%$ canopy-cover on the SIE.

Changes in vegetation due to timber management may have lowered adult survival in the SIE. Timber harvest on the SIE began in the late 1800s (Johnston 1989) and has continued until the present, although at a much reduced rate since 1930. Nearly all logging was in the form of selective cutting with only scattered small (<8 ha) clearcuts. Selective cutting removed the largest, most valuable trees and in some areas reduced large-diameter stands to small remnant populations of large trees (Verner et al. 1992a). During the course of this study there were at least 11 timber sales within SIE, with several sales occurring within owl roost or nest areas. In 1993 CASPO guidelines (Verner et al. 1992a) resulted in restricted timber harvest on National Forest land within the study area. However, in 1997 and 1998 about 600 ha in the Kings River Administration Study were given an exemption from the CASPO guidelines to facilitate an experiment using more intensive forest management strategies. Other timber harvest activities within SIE included “hazard” tree removal along roads and salvage of insect infested trees. In contrast, relatively little timber harvesting occurred on the SKC. Some SKC areas were harvested in the late 1800s and early 1900s. In 1890, the Sequoia National Park and General Grant National Park (which became part of Kings Canyon National Park) were established (Dilsaver and Tweed 1990). Park designation protected about 80% of SKC from commercial logging activities. By the end of 1940, only 2 small areas totaling less than 8 km² were not under Park Service administration. Management activities, such as hazard tree removal and the construction of new visitor facilities, have removed relatively few trees. Thus, there was probably more mature or old-growth coniferous forest in the SKC than the SIE.

The history of fire management was different between the SKC and SIE. Prescribed fire appeared to have little immediate effect on apparent survival of adult owls on the SIE, or in other studies (Bond et al. 2002). However, long-term effects of prescribed fire (e.g., changes in vegetation structure and community composition, and the reduction of the risk of catastrophic wildfire) on spotted owl survival were unknown. Prescribed burning on the SKC occurred prior to and throughout the study period; approximately 3724 ha (10.9% of study area) in SKC were burned during the study period. Burns typically occurred in summer or fall, and were of moderate intensity with smaller areas of high intensity. In contrast, the Sierra National Forest did not begin a prescribed burning program in the SIE until 1995. Prescribed fire in the SIE was designed to be multi-entry, with the first entry in the cool season (November to May) with actual burn dates dictated by weather conditions. The emphasis of the first burn was the removal of fine fuels, shrubs, and small diameter (1 to 5 cm) conifers. There were 16 cool season burns in the SIE that covered approximately 4,850 ha (7% of study area). Thus, prescribed fires in the SKC were of higher intensity based on season of burn, observations of resulting tree mortality and reduction of large diameter logs, and had different objectives, and have been used as a management tool for longer time than in the SIE.

Mean fecundity was not statistically different between the SIE and SKC. However, fecundity appeared to decline linearly on the SIE, but remained relatively constant on the SKC. These different patterns in fecundity may have been real or may have been an artifact of having an additional year of data (1990) for the SIE. Annual fecundity rates from 1995 through 1998 were the lowest estimates for the SIE and were among the lowest for the SKC. This may have resulted from variation in prey abundance, weather conditions, and/or habitat quality during this portion of the study. We did not monitor prey populations in the study area so their effect on fecundity rates was unknown. North et al. (2000) found that fledgling production was negatively correlated with precipitation during the nesting period and positively correlated with minimum temperatures in April on the SIE and SKC. From 1990 to 1993, the minimum temperatures in April on the SIE

were higher than for the period 1994 to 1998, and precipitation was higher in years 1991, 1995, 1996, and 1998 (North et al. 2000). Thus, weather may have reduced mean annual fecundity from 1995 to 1998.

The selection of different time trend models for $\hat{\lambda}_t$ for the SIE and SKC suggested that population dynamics may have been different between the two study areas. Even though linear and quadratic models were similarly weighted for each of the study areas, the realized changes based on the annual estimates (without model constraints) suggested the two populations were following different trajectories. Although the SIE and SKC were designed to provide insight into the effect of different land management practices on spotted owl demographics (e.g., SIE = management included commercial timber harvesting and SKC = preserved national park), the application of CASPO guidelines (Verner et al. 1992a) may have reduced the effect of the differences in management. Nonetheless, point estimates of apparent survival, fecundity, and $\hat{\lambda}_t$ were higher on the SKC. However, only apparent survival was significantly different between the study areas.

SAB. – Estimates of apparent survival were likely unbiased estimates of true survival for the SAB. Insular populations of spotted owls in southern California were restricted to the higher elevations of the larger mountain ranges because desert and shrub environments dominated lower elevations in the region (Noon and McKelvey 1992, LaHaye et al. 1994). Consequently, these owl populations were relatively isolated from one another, and inter-mountain movements (i.e., inter-population movements) were rare (LaHaye et al. 2001). This isolation may have been exacerbated by urban expansion and associated vegetation changes that have occurred during the last century (Noon and McKelvey 1992, LaHaye et al. 2001).

Although research has not demonstrated a causative influence of habitat on apparent survival, landscape structure (Franklin et al. 2000) and forest management (Franklin et al. 1999) have been correlated with apparent survival in previous studies. Logging operations were limited in the San Bernardino Mountains during the study, so timber harvest probably did not influence apparent survival estimates in the SAB. However, other factors that could have influenced spotted owl habitat and apparent survival in the SAB included long-term drought (LaHaye et al. 1994), habitat fragmentation and loss due to urbanization (LaHaye et al. 2001), and air pollution (e.g., ozone levels were particularly high in some forested areas of the San Bernardino Mountains; Miller et al. 1997). Ozone could have affected owls directly through potential damage to lung tissue (Rombout et al. 1991), or indirectly by reducing forest productivity (Miller et al. 1997).

Fecundity was more variable than survival in the SAB. Temporal variability in fecundity correlated with weather in northern (Franklin et al. 2000), California (North et al. 2000), and Mexican (Seamans et al. 2001b) spotted owl populations. Southern California was at the southern margin of the polar front jet stream (Minnich 1986). Therefore, winter storms, which provide most of the annual precipitation in the San Bernardino Mountains (Minnich 1986), occurred less frequently and tend to be of shorter duration than in northern and central California. Thus, milder winter weather may have been one explanation for lower temporal variability in fecundity for the SAB. Alternatively, low temporal variability in SAB fecundity could have been influenced by less variable prey dynamics or intrinsically low variability in fecundity with infrequent pulses in reproduction (e.g., Simmons 1996). However, rare events have been difficult to document in studies of short duration (Weatherhead 1986).

Some data from the SAB study area were not included in the fecundity analysis because protocols for assessing reproduction differed from the other study areas. Most deviations from standard protocols occurred when owls failed to fledge young because owls without young were less aggressive and less likely to take mice when assessing reproduction on the SAB (W. S. LaHaye, R. J. Gutiérrez personal observation). Thus, our fecundity estimates may have been biased high. This conjecture was supported by the low number of unbanded owls detected on the

study area each year (i.e., if we were failing to detect and band fledglings, we would expect to see more unbanded recruits into the territorial population).

Although estimates of population change based on δ_{PM} contained an unknown amount of bias in many spotted owl studies, δ_{PM} may have been appropriate for the SAB because of the insular nature of the study area (LaHaye et al. 2001). A previous estimate of δ_{PM} from the SAB study area, using all 12 years of the data, was significantly less than 1.0 ($\bar{\lambda} = 0.91$, SE = 0.01; LaHaye et al. 1999). The different population trajectories indicated by δ_{PM} from LaHaye et al. (1999) and δ_t in this meta-analysis may have been due to: (1) a decline in the SAB population between 1988 and 1992 which was not captured in estimation of δ_t in the meta-analysis (LaHaye et al. 2001); (2) recruitment of floaters that were present prior to the study's initiation (i.e., individuals fledged prior to the beginning of the study), such that territorial birds were being replaced, but females were not replacing themselves; (3) bias in one or more of the components of δ_{PM} ; or (4) the assumption of constant vital rates during the study period when estimating δ_{PM} . Regardless, concern may still be warranted for this population because: 1) the estimate of apparent survival was lower than reported for declining northern spotted owl populations (Franklin et al. 1999), 2) the point estimate of δ_t was <1.0, and 3) the model for δ_t indicated a negative linear trend.

CONCLUSIONS AND RECOMMENDATIONS.

Although sequoia groves may have provided a positive influence on apparent survival rates, we suspected that the disparity in apparent survival rates between SKC and the other study areas in the Sierra Nevada was also influenced by different rates of timber harvesting. Apparent survival varied little among years for any of the study areas. Conversely, fecundity exhibited relatively large temporal variation, which was most likely attributed to weather or prey availability. This relationship was suggested by estimates from the SAB, which experienced different weather patterns and exhibited much lower temporal variability in fecundity. In addition, the SAB did not experience the peak year in fecundity, 1992, as all the Sierra studies did. The role habitat played in the above was unclear. Therefore, we were unable to ascribe a causative effect of land management on estimates of apparent survival or fecundity with the data used in this analysis.

Although 4 of the 5 study areas had point estimates of $\delta_t < 1$, there was uncertainty regarding the trajectory of these populations because, if there were small declines, we could not have statistically detected them given the precision of our estimates. With the exception of SKC, estimates of apparent survival for the study areas were lower than those reported by Franklin et al. (1999) for the northern spotted owl, whose numbers were probably declining. This was of concern because survival of territorial owls may establish the baseline for δ while other population parameters, such as fecundity and recruitment, may be responsible for most of the temporal variability in δ (Franklin et al. 2000). The populations we studied may have exhibited slightly different dynamics than the northern subspecies, but still followed a similar "bet-hedging" life history strategy (Boyce 1988, Franklin et al. 2000). Further, different habitat structures and configurations may have affected individual vital rates differently (Franklin et al. 2000). Thus, understanding how different landscape characteristics and management strategies affect vital rates, especially survival, will be essential for conservation of the spotted owl in the Sierra Nevada.

Although the data in our analyses spanned 7-10 years, the study periods were still relatively short for capturing some of the dynamics of California spotted owl populations. For example, the high reproductive output observed in 1992 may have affected rates of population change for several years following this event. If California spotted owl population dynamics were largely driven by such events, then continued monitoring of these populations will be necessary to capture relatively rare events. In addition, comparisons between the SAB and the Sierran studies and between the SIE and SKC will yield further understanding on the effects of weather patterns

and habitat conditions on demographic parameters and rates of population change. For these reasons, we believed that the currently ongoing studies should be continued and the SAB study should be reinstated. The SAB was unique among these studies because of its different dynamics, its closed population characteristic, and its representation as the only segment of the southern California spotted owl metapopulation under study.

These studies are observational in their design, and not experimental. However, they will be the only means by which we can understand the effects of environmental variation on spotted owl population dynamics (and the interactions with habitat) and will assist in defining specific treatments for large-scale experiments (Noon and Franklin 2002). Thus, these long-term observational studies should form the backbone for a larger research program that also includes experiments examining current and alternative silvicultural treatments. We also recommend that researchers from the 5 study areas work more closely together to develop more consistent protocols for conducting surveys and estimating reproductive output in the field. In this way, more meaningful comparisons could be made in future analyses. In general, we feel the following short-term recommendations would clarify the results from this initial meta-analysis of these data:

- Analyze these data with covariates, such as climate, rates of timber harvest, presence of sequoia groves, and territory-specific habitat configurations, combined with appropriate biologically-based hypotheses that include both positive and negative influences of the covariates. In this manner, some of the processes influencing the initial patterns observed during this meta-analysis can be better understood;
- Continue the existing studies to capture the “infrequent” reproductive pulses (and subsequent recruitment) observed in 1992 that may have important influences on population dynamics of the owls; and
- Encourage the refinement of estimation models using \mathcal{R}_t models that have particular application to these studies on California spotted owls. Such refinements should include the separate estimation of local births from immigration to better understand the role and spatial scale of recruitment in population dynamics of California spotted owls.

In 1992, the CASPO report outlined an interim plan for conservation of the California spotted owl and its habitat in the Sierra Nevada (Verner et al. 1992a). One recommendation of that report was to expand the basic demographic studies in order to answer questions of critical management concern regarding the California spotted owl. A decade later, we are still asking many of the same questions because a comprehensive research program, beyond the demographic studies, was never implemented. Therefore, we reiterate the following recommendations based on those in the CASPO report:

- Develop comprehensive, accurate vegetation maps on the demographic study areas in order to evaluate the influence of landscape habitat characteristics on variation and trends in demographic parameters of California spotted owls;
- Coordinate the existing demographic studies with forest management activities to develop quasi-experiments on the effects of these activities on demographic parameters; and
- Design landscape-scale experiments to assess the effects of silvicultural treatments designed to reduce fire risks and the owls response to controlled logging and silvicultural treatments.

Thus, we recommend that these study areas continue to be monitored because (1) of uncertainties in interpreting \mathcal{R}_t with respect to source and sink population dynamics; (2) most of the point estimates of \mathcal{R}_t were < 1 ; (3) the relatively low apparent survival rates on 4 study areas compared to northern spotted owls; and (4) they provide the best opportunity for long-term monitoring and future testing of hypotheses regarding the effect climate and habitat have on

spotted owl population dynamics. Advances continue to be developed in partitioning the components of δ_p , such as local recruitment from outside immigration (Nichols and Hines 2002) and these should be used in conjunction with continued data collection on all of the study areas.

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.
- ARMSWORTH, P.R. 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology* 83:1092-1104.
- 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.
- BART, J. 1995. Amount of suitable habitat and viability of northern spotted owls. *Conservation Biology* 9:913-916.
- BEESLEY, D. 1996. Reconstructing the landscape: an environmental history, 1820-1960. Pages 3-24 in *Sierra Nevada Ecosystem Project: Final report to Congress, volume II, Assessments and scientific basis for management options*. University of California, Centers for Water and Wildland Resources.
- 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. 2003. Ecology of the California spotted owl: breeding dispersal and associations with forest stand characteristics in northeastern California. PhD Dissertation. Colorado State University, Fort Collins, CO.
- 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.
- BOND, M.L., R.J. GUTIÉRREZ, A.B. FRANKLIN, W.S. LAHAYE, C.A. MAY, and M.E. SEAMANS. 2002. Short-term effects of wildfires on spotted owl survival, site fidelity, mate fidelity, and reproductive success. *Wildlife Society Bulletin* 30:1022-1028.
- BOYCE, M. S. 1988. Bet hedging in avian life histories. Pages 3-18 in H. Ouellet editor. *Acta International Ornithological Congress XIX. Volume 2*. University of Ottawa Press, Ottawa, Canada.
- 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.
- BURNHAM, K. P., and D. R. ANDERSON. 1998. *Model selection and inference: A practical information theoretic approach*. Springer. New York., New York, USA.
- BURNHAM, K. P., D. R. ANDERSON, AND G. C. WHITE. 1996. Meta-analysis of vital rates of the northern spotted owl. *Studies In Avian Biology* 17:92-101.
- BURNHAM, K. P., and G. C. WHITE. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245-264.
- CASWELL, H. 2000. *Matrix population models: construction, analysis, and interpretation*, second edition. Sinauer Associates, Inc. Sunderland, Massachusetts.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. J. Wiley and Sons, New York.
- CONNOR, E.F., S.H. FAETH, AND D. SIMBERLOFF. 1983. Leafminers on oak: the role of immigration and *in situ* reproductive recruitment. *Ecology* 64:191-204.

- COOCH, E., R.F. ROCKWELL, AND S. BRAULT. 2001. Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs*. 71:377-400.
- DESANTE, D.F. 1995. Suggestions for future directions for studies of marked migratory landbirds from the perspective of a practitioner in population management and conservation. *Journal of Applied Statistics*. 22:949-965.
- DILSAVER, L. M., W. C. TWEED. 1990. Challenge of the big trees: a resource history of Sequoia and Kings Canyon national parks. Sequoia Natural History Association, Inc. Three Rivers, California.
- EVANS, M., N. HASTINGS, AND B. PEACOCK. 1993. Statistical distributions, second edition. John Wiley and Sons, New York, 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. 1981. Molt of the spotted owl. *Auk* 98:735-742.
- FORSMAN, E. D. 1983. Methods and materials for locating and studying spotted owls. U. S. Forest Service. General Technical Report PNW-GTR-162, Portland, Oregon.
- FORSMAN, E. D., A. B. FRANKLIN, F. M. OLIVER, AND J. P. WARD. 1996. A color band for spotted owls. *Journal of Field Ornithology* 67:507-510.
- FORSMAN, E. D., E. C. MESLOW, and H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* 87. 64 pp.
- 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. THRAILKILL, F. F. WAGNER, and D. E. SEAMAN. 2002. Natal and breeding dispersal of northern spotted owls. *Wildlife Monographs* 149:1-35.
- FRANKLIN, A. B. 2002. Exploring ecological relationships in survival and estimating rates of population change using program MARK. Pages 290-296 *In* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land, and people: priorities for the 21st century*. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland.
- 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 US Fish and Wildlife Service, Portland, OR.
- FRANKLIN, A. B. AND T. M. SHENK. 1995. Meta-analysis as a tool for monitoring wildlife populations. Pages 484-487 *In* J. A. Bissonette and P. R. Krausman, editors. *Integrating people and wildlife for a sustainable future*. Proceedings of the International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland.
- FRANKLIN, A. B., T. M. SHENK, D. R. ANDERSON, AND K. P. BURNHAM. 2001. Statistical model selection: the alternative to null hypothesis testing. Pages 75-90 *In*: T. M. Shenk and A. B. Franklin, editors. *Modeling in natural resource management: development, interpretation, and application*. Island Press, Washington, D.C.
- FRANKLIN, A. B., D. R. ANDERSON, E. D. FORSMAN, K. P. BURNHAM, and F. F. WAGNER. 1996a. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12-20.
- FRANKLIN, A. B., R. J. GUTIÉRREZ, B. R. NOON, and J. P. WARD, Jr. 1996b. Demography of the northern spotted owl: northwestern California. *Studies in Avian Biology* 17:83-91.
- FUJIOKA, F. M., J. O. ROADS, and S.-C. CHEN. 1998. Climatology, p. 28-43. *In* P. R. Miller and J. R. McBride, eds. *Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains*. Springer, New York.

- GUTIÉRREZ, R. J., AND J. PRITCHARD. 1990. Distribution, density, and age structure of spotted owls on two southern California habitat islands. *Condor* 92:491-495.
- GUTIÉRREZ, R. J., A. B. FRANKLIN, AND W. S. LAHAYE. 1995. Spotted owl (*Strix occidentalis*). In *The Birds of North America*, No. 179 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D. C.
- GAILLARD, J.-M., M. F.-B. BIANCHET, and N.G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *TREE* 13:58-63.
- GAILLARD, J.-M., M. F.-B. BIANCHET, N.G. YOCCOZ, A. LOISON, and C. TOIGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Ann. Rev. Ecol. Syst.* 31:367-393.
- HINES, J. E., AND J. D. NICHOLS. 2002. Investigations of potential bias in the estimation of θ using Pradel's (1996) model for capture-recapture data. *Journal of Applied Statistics* 29:573-588.
- HUNTER, J. E., AND F. L. SCHMIDT. 1990. *Methods of meta-analysis: correcting error and bias in research findings*. Sage Publications, Beverly Hills, California.
- 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 697-700 *In*: J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D.C.
- JOHNSTON, H. 1989. *Thunder in the mountains*. Interurban Press, Glendale, California.
- JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247.
- KAHRL, W. L. 1979. *The California Water Atlas*, Second Edition. California Department of Water Resources, Sacramento, California.
- KENDALL, W. L., J. D. NICHOLS, and J. E. HINES. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563-578.
- KÜCHLER, A. W. 1977. The map of natural vegetation of California. *In* M.G. Barbour, and J. Major, eds. *Terrestrial vegetation of California*. J. Wiley and Sons, New York. 1002 pp.
- 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. S., R. J. GUTIÉRREZ, and G. S. ZIMMERMAN. 1999. Demography of the California spotted owl in the San Bernardino Mountains. Final Report to Region 5, U. S. D. A. Forest Service, San Bernardino, California.
- LAHAYE, W. S., R. J. GUTIÉRREZ, and J. R. DUNK. 2001. Natal dispersal of the spotted owl in southern California: dispersal profile of an insular population. *Condor* 103:691-700.
- LEBRETON, J.-D. 1996. Demographic models for subdivided populations: the renewal equation approach. *Theoretical Population Biology* 49:291-313.
- 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.
- McKELVEY, K. S., AND J. D. JOHNSTON. 1992. Historical perspectives on forests of the Sierra Nevada and the transverse ranges of southern California: forest conditions at the turn of the century. Pages 225-246. *in* J. Verner, K. McKelvey, B. R. Noon, R. J. Gutierrez, G. I. Jr. Gould, and T. W. Beck [Tech. Eds.]. *The California spotted owl: a technical assessment of its current status*. U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station. Gen Tech. Rept. PSW-GTR-133, Berkeley, California.

- MCKELVEY, K. S., C. N. SKINNER, C. CHANG, D. C. ERMAN, S.J. HUSARI, D. J. PARSONS, J. W. VAN WAGTENDONK, C. P. WEATHERSPONN. 1996. An overview of Fire in the Sierra Nevada. Pages 1033-1040 *In* Sierra Nevada Ecosystem Project, Final Report to Congress, vol II, Assessments and Scientific Basis for Management Options. Centers for Water and Wildland Resources, University of California, Davis, CA.
- MILLER, P. R., M. J. ARBAUGH, and P. J. TEMPLE. 1997. Ozone and its known and potential effects on forests in the western United States. Pages 39-68 *in* H. Sandermann, A. R. Wellburn, and R. L. Heath, eds. Forest decline and ozone. A comparison of controlled chamber and field experiments. Ecological Studies 127. Springer, Berlin, Germany.
- MINNICH, R. A. 1986. Snow levels and amounts in the mountains of southern California. *Journal of Hydrology* 89:37-58.
- MINNICH, R. A. 1988. The biogeography of fire in the San Bernardino Mountains of California: a historical study. University of California Publications in Geography, Volume 28. University of California Press, Los Angeles.
- MINNICH, R. A. 1998. Vegetation, fire regimes, and forest dynamics. Pages 44-80. *In* P. R. Miller and J. R. McBride, eds. Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains. Ecological Studies, Volume 134. Springer. New York.
- MINNICH, R. A., M. G. BARBOUR, J. H. BURK, and R. F. RENAU. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conservation Biology* 9:902-914.
- MOEN, C. A., A. B. FRANKLIN, and R. J. GUTIÉRREZ. 1991. Age determination of subadult northern spotted owls in northwest California. *Wildlife Society Bulletin* 19:489-493.
- MOEN, C.A., and R.J. GUTIÉRREZ. 1997. California spotted owl habitat selection in the central Sierra Nevada. *Journal of Wildlife Management* 61:1287-1287.
- MOONEY, H. A. 1988. Southern coastal scrub. Pages 471-490. *In* M. G. Barbour and J. Major, eds. Terrestrial vegetation of California, Second edition. California Native Plant Society, Sacramento, CA.
- NICHOLS, J. D., and J. E. HINES. 1984. Effects of permanent trap responses in capture probability on Jolly-Seber capture-recapture model estimates. *Journal of Wildlife Management* 48:289-294.
- NICHOLS, J. D., and J. E. HINES. 2002. Approaches for the direct estimation of θ and demographic contributions to θ , using capture-recapture data. *Journal of Applied Statistics* 29:539-568.
- NICHOLS, J.D., and K.H. POLLOCK. 1990. Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. *Ecology* 71:21-26.
- NOAA. 1998. Climatological data annual summary California. Volume 102, Number 13. U.S. National Oceanic and Atmospheric Administration, Asheville, NC.
- NOAA 1999. Climatological data annual summary California. Volume 103 Number 13. U.S. National Oceanic and Atmospheric Administration, Asheville, NC.
- 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. and A. B. FRANKLIN. 2002. Scientific research and the spotted owl: opportunities for major contributions to avian population ecology. *Auk* 199:311-320.
- NOON, B. R., and K. MCKELVEY. 1992. Stability properties of the Spotted Owl metapopulation in southern California. Pages 187-206. *In* J. Verner, K. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Jr. Gould, and T. W. Beck, 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, Berkeley, California.

- NOON, B. R., K. MCKELVEY, D. W. 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, K. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Jr. Gould, and T. W. Beck (Tech. 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, Forest Service, Berkeley, California.
- NORTH, M., G. N. STEGER, R. DENTON, E. G., 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, C. and J. A. HELMS. 1996. Forest growth and stand structure at Blodgett Forest Research Station 1933-1995. Pages 681-732 *in* Sierra Nevada Ecosystem Project: Final report to Congress, vol. III, chap 16. University of California, Centers for Water and Wildland Resources.
- PARSONS, D. J. 1994. Objects or ecosystems? Giant sequoia management in the National Parks. Pages 109-115 *in* Philip 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, California.
- PFISTER, C.A. 1998. Patterns of variation in stage-structured populations: evolutionary predictions and ecological implications. *Proc. Nat. Acad. Sci.* 95:213-218.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, and J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1-97.
- PRADEL, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703-709.
- PULLIAM, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- RAO, P. S. R. S. 1997. Variance components estimation: mixed models, methodologies and applications. Chapman and Hall, London, England.
- RAPHAEL, M. G., R. G. ANTHONY, S. DESTEFANO, E. G. FORSMAN, A. B. FRANKLIN, R. HOLTHAUSEN, E. C. MESLOW, AND B. R. NOON. 1996. Use, interpretation, and implications of demographic analyses of northern spotted owl populations. *Studies In Avian Biology* 17:102-112.
- REID, J. A., R. B. HORN, and E. D. FORSMAN. 1999. Detection rates of spotted owls based on acoustic-lure and live-lure surveys. *Wildlife Society Bulletin* 27:986-990.
- ROBINSON, J. W. 1989. The San Bernardino: the mountain country from Cajon Pass to Oak Glen, two centuries of changing use. Big Santa Anita Historical Society, Arcadia, CA.
- ROMBOUT, P. G. A., J. A. M. A. DORMANS, L. VAN BREE, and M. MARRA. 1991. Structural and biochemical in lungs of Japanese quail following a 1-week exposure to ozone. *Environmental Research* 54:39-51.
- ROUGHGARDEN, J., Y. IWASA, AND C. BAXTER. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66:54-67.
- RUNDEL, P. W. 1971. Community structure and stability in the giant sequoia ecosystem of the Sierra Nevada, California. *American Midland Naturalist* 85:478-492.
- RUNDEL, P. W., D. J. PARSONS, and D. T. GORDON. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Pages 559-599 *In* Barbour, M. G., and J. Major, eds. Terrestrial vegetation of California. J. Wiley and Sons. New York.
- SAKAMOTO, Y., M. ISHIGURO, and G. KITAGAWA. 1986. Akaike information criterion statistics. KTK Scientific Publ., Dordrecht, Boston, Massachusetts, USA.
- SAS INSTITUTE, INC. 1997. SAS/STAT Software: changes and enhancements through Release 6.12. SAS Institute, Inc., Cary, North Carolina.

- SAWYER, J. O., D. A. THORNBURGH, and J. R. GRIFFIN. 1988. Mixed evergreen forest. Pages 359-382 in M. G. Barbour and J. Major, eds. *Terrestrial vegetation of California*, Second edition. California Native Plant Society, Sacramento, CA.
- SCHWARZ, C. J., and A. N. ARNASON. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52:860-873.
- SCHWARZ, C. J., and G. A. F. SEBER. 1999. A review of estimating animal abundance III. *Statistical Science* 14:427-456.
- SCHOEN, R. 1988. *Modeling multigroup populations*. Plenum Press, New York.
- SCOTT, J. M., F. DAVIS, B. CSUTI, R. NOSS, B. BUTTERFIELD, C. GROVES, H. ANDERSON, S. CAICCO, F. D'ERCHIA, T. C. EDWARDS Jr., J. ULLIMAN, and R. G. WRIGHT. 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs* 123:1-41.
- SEBER, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Charles Griffin, London.
- SEAMANS, M.E., R.J. GUTIÉRREZ, and M. BOND. 2001a. Population ecology of the California spotted owl in the central Sierra Nevada; annual results, 2000. Unpublished Report, USDA Forest Service, Region 5. Contract No. #53-91S8-6.
- SEAMANS, M. E., R. J. GUTIÉRREZ, C. A. MAY, and M. Z. PEERY. 1999. Demography of two Mexican spotted owl populations. *Conservation Biology* 13:744-754.
- SEAMANS, M. E., R. J. GUTIÉRREZ, C.A. MOEN, and M.. Z. PEERY. 2001b. Spotted owl demography in the central Sierra Nevada. *Journal of Wildlife Management* 65:425-431.
- SEAMANS, M. E., R. J. GUTIÉRREZ, and C.A. MAY. 2002. Mexican spotted owl population dynamics: influence of climatic variation on survival and reproduction. *Auk* 110:321-334.
- SIERRA NEVADA ECOSYSTEM PROJECT (SNEP). 1996. Status of the Sierra Nevada: assessment summaries and management strategies. Volume 1. Wildland Resources Center Report No. 36, University of California, Davis.
- SIMMONS, R. E. 1996. Population declines, viable breeding areas and management options for flamingos in south Africa. *Conservation Biology* 10:504-514.
- SKINNER, C. N. AND C. CHANG. 1996. Fire Regimes, Past and Present. Pages 1041-1069 In *Sierra Nevada Ecosystem Project, Final Report to Congress, vol II, Assessments and Scientific Basis for Management Options*. Centers for Water and Wildland Resources, University of California, Davis.
- STEGER, G. N. 1995. Sex ratios of fledgling and recaptured subadult spotted owls in the southern Sierra Nevada. *Transactions of the Western Section of The Wildlife Society* 31:36-39.
- STEGER, G. N., T. E. MUNTON, G. P. EBERLEIN, K. D. JOHNSON, AND P. A. SHAKLEE. 2000. A study of spotted owl demographics in the Sierra National Forest and Sequoia and Kings Canyon National Parks. Annual Progress Report 2000, Pacific Southwest Research Station, Fresno, California.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. Report of the Interagency Scientific Committee to address the conservation of the northern spotted owl. USDA For. Serv., USDI Bur. Land Manage., Fish and Wildlife Serv., and Natl. Park Serv. U. S. Government Printing Office 791-171/20026, Washington, D. C.
- THOMAS, J. W., RAPHAEL, M. G., ANTHONY, R. G. [and others]. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest: the report of the Scientific Analysis Team. U.S. Department of Agriculture, Forest Service, National Forest System, Forest Service Research.
- THORNE, R. F. 1988. Montane and subalpine forests of the Transverse and Peninsular Ranges. Pages 537-558 in M. G. Barbour and J. Major, eds. *Terrestrial vegetation of California*. Second edition. California Native Plant Society, Sacramento, CA.

- USDA 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, CA.
- USDA FOREST SERVICE. 1995. 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, CA.
- USDA 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, CA.
- USDA FOREST SERVICE. 1998a. Sierra Nevada Science Review: Report of the Science Review Team charged to synthesize new information of rangewide urgency to the National Forests of the Sierra Nevada. USDA Forest Service. Pacific Southwest Region. Sacramento, CA.
- USDA FOREST SERVICE. 1998b. Sierra Nevada Framework for Conservation and Collaboration: summary of existing management direction, report of the Forest Service Interdisciplinary Analysis Team. USDA Forest Service. Pacific Southwest Region. Sacramento, CA.
- USDA FOREST SERVICE. 2001a. Sierra Nevada Forest Plan Amendment Final Environmental Impact Statement. Volumes 1-6. USDA Forest Service. Pacific Southwest Region. Sacramento, CA.
- USDA FOREST SERVICE. 2001b. Sierra Nevada Forest Plan Amendment Final Environmental Impact Statement: Record of Decision. USDA Forest Service. Pacific Southwest Region. Sacramento, CA.
- USDI (UNITED STATES DEPARTMENT OF INTERIOR). 1992. Final draft recovery plan for the northern spotted owl, 2 Vols. U. S. Dept. Interior, Washington, D.C.
- VANDERWERF, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* 73:1699-1705.
- VASEK, F. C., and M. G. BARBOUR. 1988. Mojave desert scrub vegetation. Pages 835-868 in M. G. Barbour and J. Major, eds. *Terrestrial vegetation of California*, Second edition. California Native Plant Society, Sacramento, CA.
- VERNER, J. and A. S. BOSS. 1980. California wildlife and their habitats: western Sierra Nevada. U. S. Forest Service, General Technical Report PSW-GTR-37. Pacific Southwest Research Station, Berkeley, California.
- VERNER, J., K. E. McKELVEY, B. R. NOON, R. J. GUTIÉRREZ, G. I. GOULD, Jr., AND T. W. BECK. 1992a. The California Spotted Owl: A technical assessment of its current status. U. S. Forest Service, Gen. Tech. Rept. PSW-GTR-133. Pacific Southwest Research Station. Berkeley, California.
- VERNER, J., K. S. McKELVEY, B. R. NOON, R. J. GUTIÉRREZ, G. I. GOULD, Jr., and T. W. BECK. 1992b. Assessment of the current status of the California spotted owl, with recommendations for management. Pages 3-26. In Verner, J. et al. [eds]. *The California spotted owl: a technical assessment of its current status*. U.S. Forest Service, Gen. Tech. Rept. PSW-GTR-133. Pacific Southwest Research Station. Berkeley, California.
- WAGNER, F. F., E. C. MESLOW, G. M. BENNET, C. J. LARSON, S. M. SMALL, AND STEPHEN DESTEFANO. 1996. Demography of northern spotted owls in the southern Cascades and Siskiyou Mountains, Oregon. *Studies in Avian Biology* 17:67-76.
- WEATHERHEAD, P. J. 1986. How unusual are unusual events? *The American Midland Naturalist* 128:150-154.
- WHITE, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288-331 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, New York.

- 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 estimation from populations of marked animals. *Bird Study* 46 Supplement:120-138.
- WHITE, G. C., K. P. BURNHAM, and D. R. ANDERSON. 2002. Advanced features of Program MARK. Pages 368-377 *In* R. Fields, ed. Integrating people and wildlife for a sustainable future. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.
- WOLF, F. M. 1986. Meta-analysis: quantitative methods for research synthesis. Sage Publications, Beverly Hills, Calif.
- WOLFINGER, R. 1993. Covariance structure selection in general mixed models. *Communications in statistics - Simulation and computation* 22:1079-1106.
- ZABEL, C. J., S. E. SALMONS, AND M. BROWN. 1996. Demography of northern spotted owls in southwestern Oregon. *Studies in Avian Biology* 17:77-82.

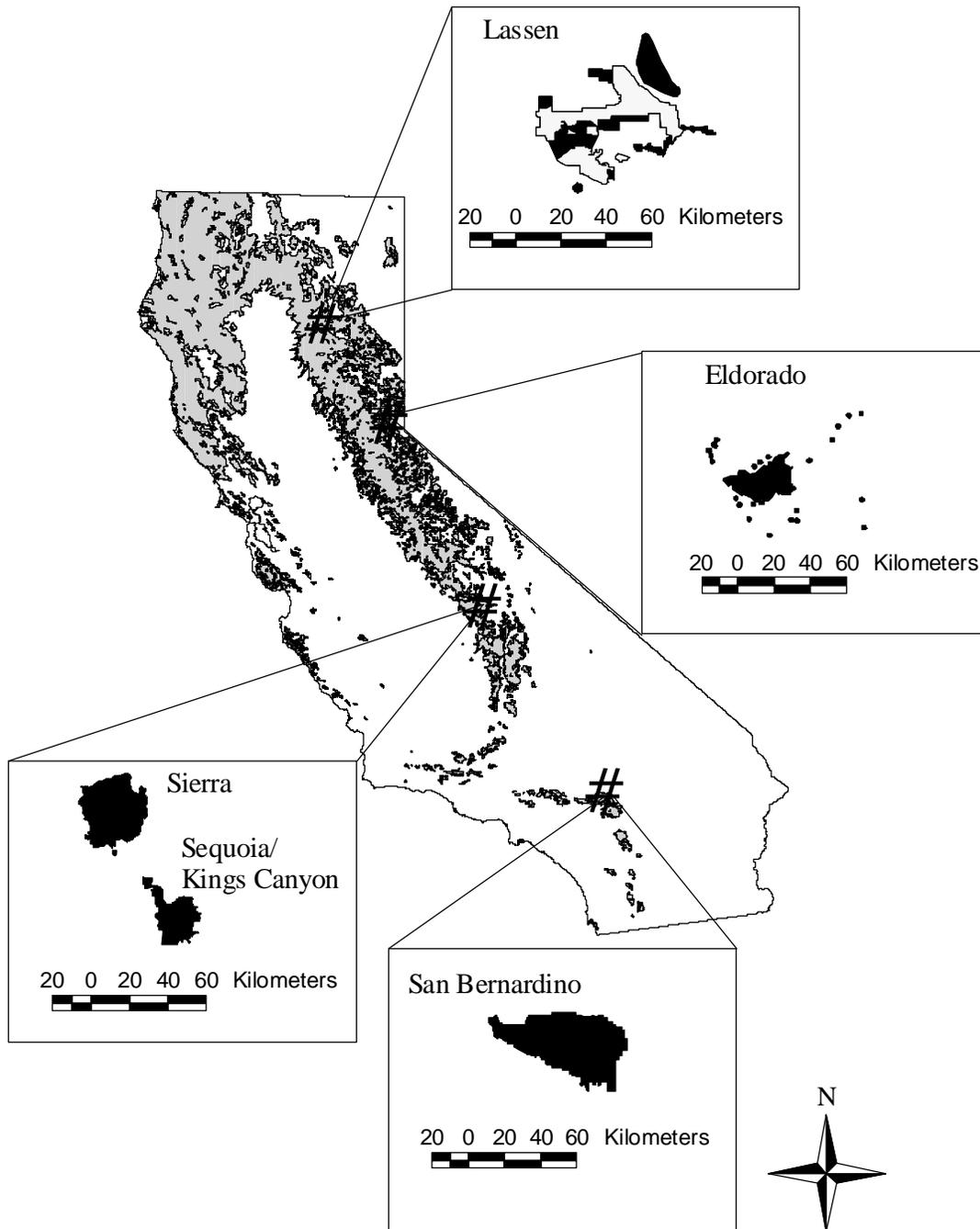


FIGURE 1. Relative locations of California spotted owl demography studies in relation to forested habitat (shaded gray) throughout California, USA. Cross-hatched area within the Lassen inset was used to estimate δ_r . Dark-colored circles within the Eldorado are owl sites external to the density study area (dark shaded area within inset).

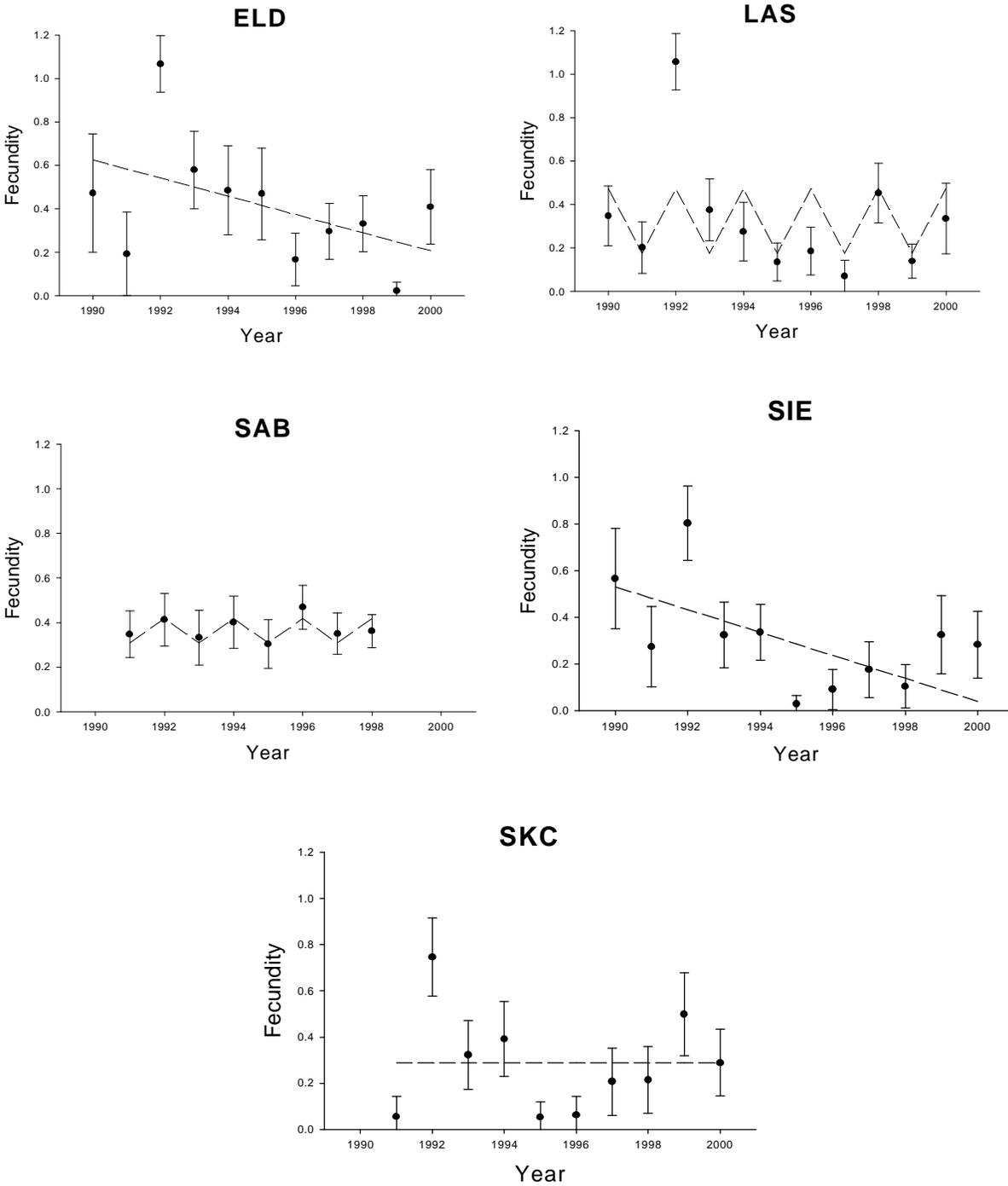


FIGURE 2. Annual estimates of fecundity for California spotted owls on 5 study areas in California. Annual estimates (dots) and 95% confidence intervals (bars) are least-squares means from mixed intercept-only model while dashed lines represent estimates from the top-ranked mixed trend model.

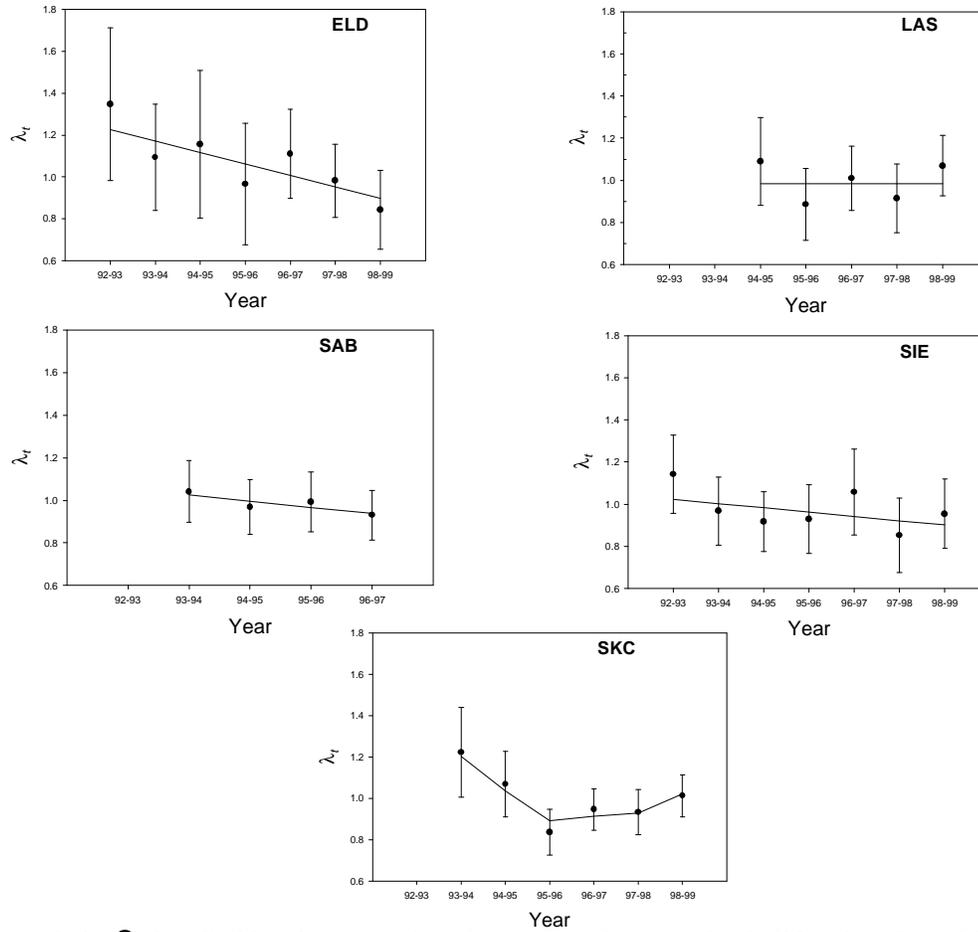


FIGURE 3. Trends in λ_t for California spotted owls on 5 study areas in California. Trend lines are from random effects models selected by minimum QAIC_c. Dots, with 95% confidence intervals, are annual estimates of λ_t from model $\{N_t, p_t, \lambda_t\}$ used to develop the random effects models.

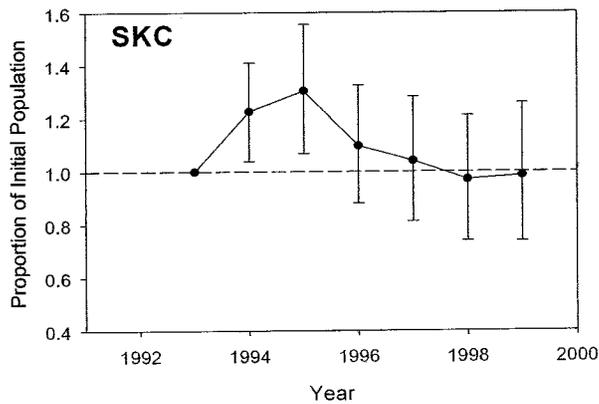
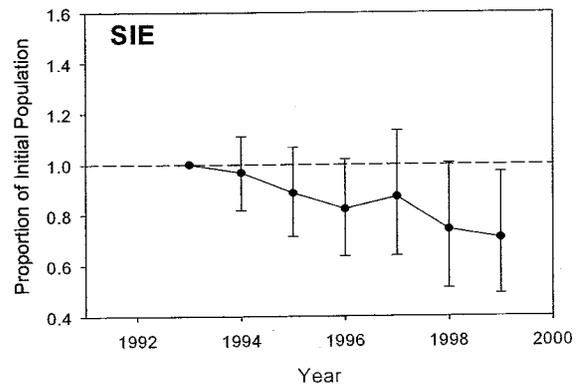
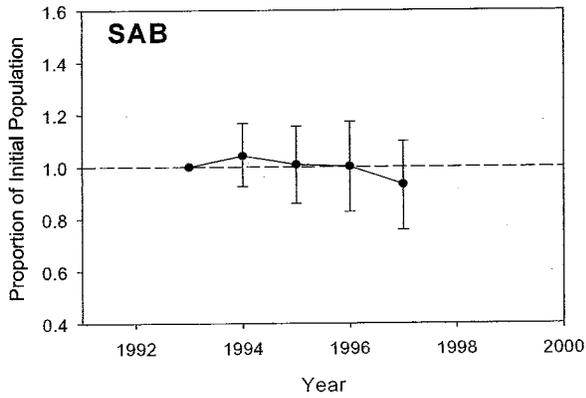
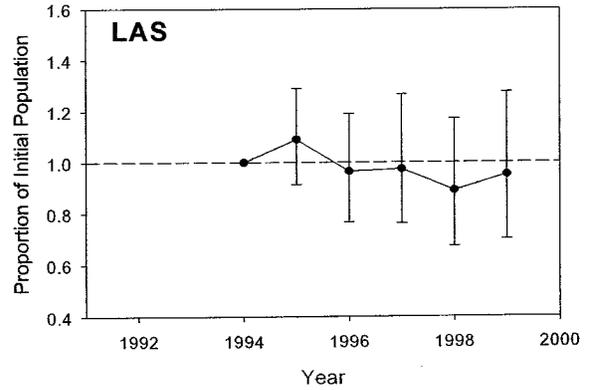
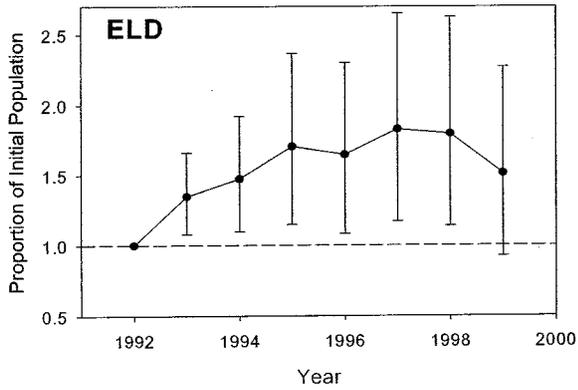


FIGURE 4. Trends in populations of California spotted owls from 5 study areas in California. Trends are expressed as realized change (Δ) based on estimates of λ_t , which represent the proportion of the initial population remaining for each year. Bars around estimates are 95% confidence intervals. Note that the graph for the ELD study area is scaled differently than the other study areas.

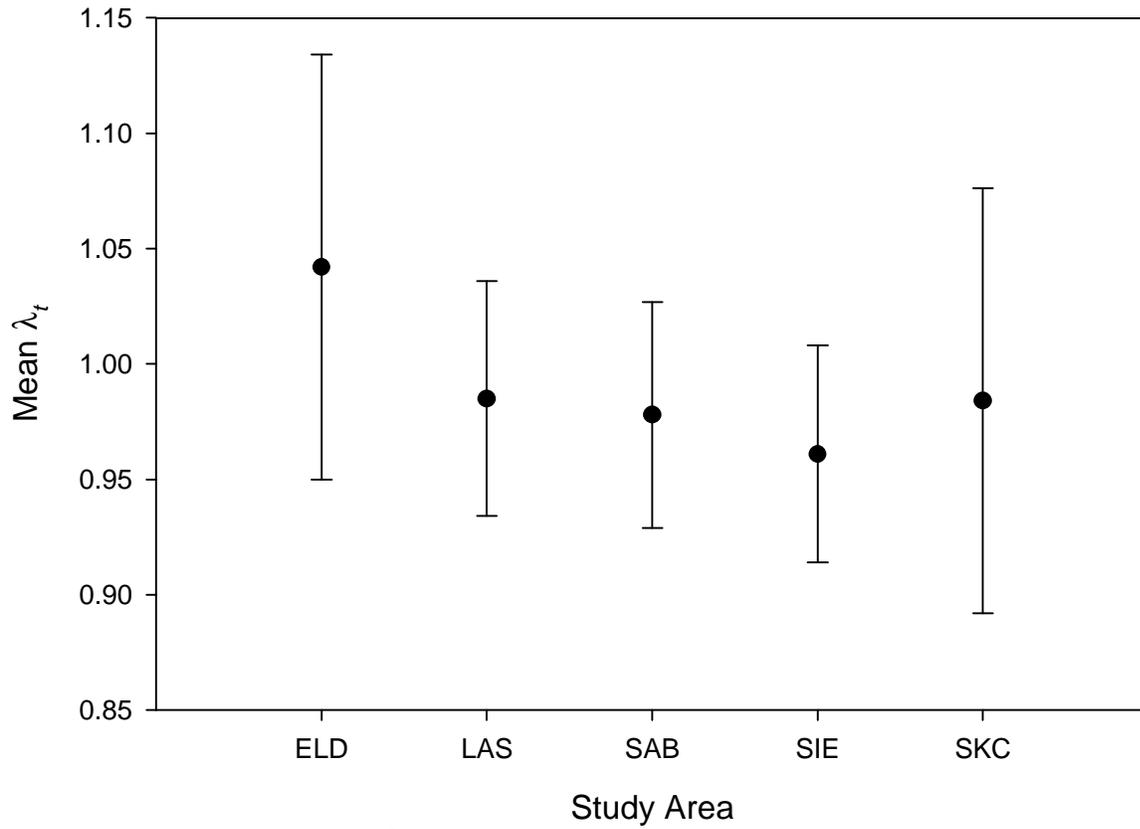


FIGURE 5. Estimates of mean λ_t with 95% confidence intervals for California spotted owls on 5 study areas in California.

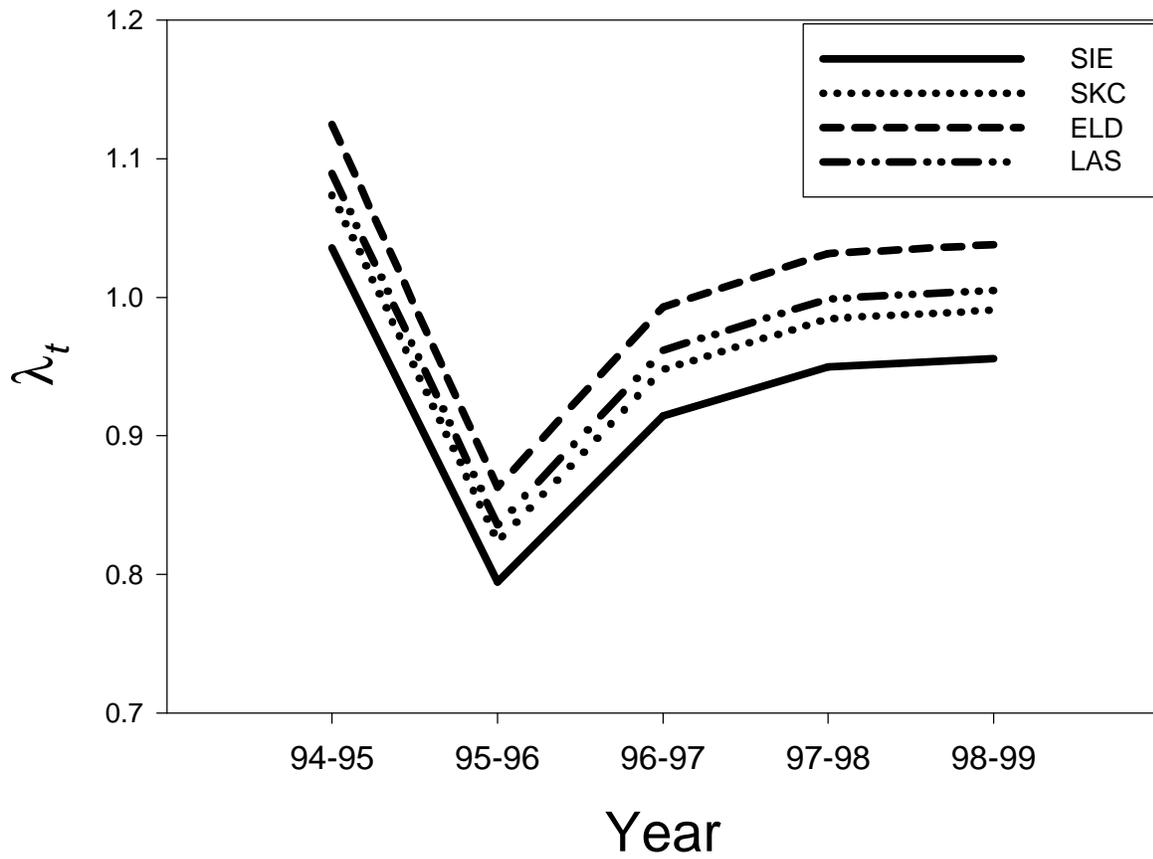


FIGURE 6. Trends in λ_t based on model ($\lambda_{g,t}$) from meta-analysis on California spotted owls from 4 study areas (ELD, LAS, SIE, and SKC) in the Sierra Nevada mountains, California.

TABLE 1. Characteristics of 5 California spotted owl demographic study areas in California.

Study Area	Acronym	Size (km ²)	Organization conducting study	Study period (No. of years)	Years used in demographic analyses ^a
Eldorado National Forest	ELD	925	University of Minnesota	1986 - 2000 (15)	1990-2000
Lassen National Forest	LAS	2,200	Colorado State University	1990 - 2000 (11)	1990-2000
San Bernardino National Forest	SAB	1,890	University of Minnesota	1987 - 1998 (12)	1991-1998
Sierra National Forest	SIE	693	USDA Forest Service	1990 - 2000 (11)	1990-2000
Sequoia-Kings Canyon National Park	SKC	343	USDA Forest Service	1990 - 2000 (11)	1991-2000

^aEarly years from select study areas were not included in survival, fecundity, and population growth analyses because focus of studies was on telemetry (SAB) or differences in protocols and survey effort with latter years (ELD, SKC).

TABLE 2. Descriptions of mark-recapture models examined in the meta-analysis of adult apparent survival (N) of male and female California spotted owls from 5 study areas in California.

Model	Description of N structure	Description of p structure
$\{N_{\cdot}, p_{g^*t}\}$	No effects	Study area and year effects with interactions
$\{N_g, p_{g^*t}\}$	Study area effect	Study area and year effects with interactions
$\{N_{g+t}, p_{g^*t}\}$	Study area effect with additive year effects	Study area and year effects with interactions
$\{N_{g+T}, p_{g^*t}\}$	Study area effect with additive linear time effect	Study area and year effects with interactions
$\{N_{g+TT}, p_{g^*t}\}$	Study area effect with additive quadratic time effect	Study area and year effects with interactions
$\{N_{g^*t}, p_{g^*t*s}\}$	Study area and year effects with interactions	Study area, year, and gender effects with all interactions
$\{N_{g^*t}, p_{g^*t+s}\}$	Study area and year effects with interactions	Study area and year effects with interactions and an additive gender effect
$\{N_{g^*t}, p_{g+t+s}\}$	Study area and year effects with interactions	Additive study area, year and gender effects
$\{N_{g^*t}, p_{g^*t}\}$	Study area and year effects with interactions	Study area and year effects with interactions
$\{N_{g^*t}, p_r\}$	Study area and year effects with interactions	Annual reproductive rate effect
$\{N_{g^*t}, p_{r^*s}\}$	Study area and year effects with interactions	Annual reproductive rate and gender effects with interactions
$\{N_{g^*t}, p_{g+t}\}$	Study area and year effects with interactions	Additive study area and year effects
$\{N_{g^*t}, p_{r+s}\}$	Study area and year effects with interactions	Additive annual reproductive rate and gender effects
$\{N_{g^*t}, p_{(g+t)^*s}\}$	Study area and year effects with interactions	Additive study area and year effects interacting with gender
$\{N_{g^*T}, p_{g^*t}\}$	Study area and linear time effects with interactions	Study area and year effects with interactions
$\{N_{g^*t+s}, p_r\}$	Study area and year effects with interactions and an additive gender effect	Annual reproductive output
$\{N_{g^*t+s}, p_{r+s}\}$	Study area and year effects with interactions and an additive gender effect	Annual reproductive output with an additive gender effect
$\{N_{g^*t+s}, p_{g^*t*s}\}$	Study area and year effects with interactions and an additive gender effect	Study area, year, and gender effects with all interactions
$\{N_{g^*t+s}, p_{g^*t+s}\}$	Study area and year effects with interactions and an additive gender effect	Study area and year effects with interactions and an additive gender effect
$\{N_{g^*t+s}, p_{(g+t)^*s}\}$	Study area and year effects with interactions and an additive gender effect	Additive study area and year effects interacting with gender
$\{N_{g^*t+s}, p_{g+t}\}$	Study area and year effects with interactions and an additive gender effect	Additive study area and year effects
$\{N_{g^*t+s}, p_{g+t+s}\}$	Study area and year effects with interactions and an additive gender effect	Additive study area, year, and gender effects
$\{N_{g^*t+s}, p_{g^*t}\}$	Study area and year effects with interactions and an additive gender effect	Study area and year effects with interactions
$\{N_{g^*t+s}, p_{r^*s}\}$	Study area and year effects with interactions and an additive gender effect	Annual reproductive rate and gender effects with interactions
$\{N_{g^*t*s}, p_{r+s}\}$	Study area, year, and gender effects with all interactions	Additive annual reproductive rate and gender effects
$\{N_{g^*t*s}, p_{r^*s}\}$	Study area, year, and gender effects with all interactions	Annual reproductive rate and gender effects with interactions
$\{N_{g^*t*s}, p_{(g+t)^*s}\}$	Study area, year, and gender effects with all interactions	Additive study area and year effects interacting with gender
$\{N_{g^*t*s}, p_{g+t}\}$	Study area, year, and gender effects with all interactions	Additive study area and year effects
$\{N_{g^*t*s}, p_r\}$	Study area, year, and gender effects with all interactions	Annual reproductive rate effects

$\{N_{g^*t^*s}, p_{g^*t}\}$	interactions Study area, year, and gender effects with all interactions	Study area and year effects with interactions
$\{N_{g^*t^*s}, p_{g^*t^*s}\}$	Study area, year, and gender effects with all interactions	Study area, year, and gender effects with all interactions
$\{N_{g^*t^*s}, p_{g^{+t+s}}\}$	Study area, year, and gender effects with all interactions	Additive study area, year, and gender effects
$\{N_{g^*t^*s}, p_{g^*t+s}\}$	Study area, year, and gender effects with all interactions	Study area and year effects with interactions and an additive gender effect
$\{N_{g^*TT}, p_{g^*t}\}$	Study area and quadratic time effect with interactions	Study area and year effects with interactions
$\{N_{Latitude}, p_{g^*t}\}$	Latitude effect	Study area and year effects with interactions
$\{N_{SAB, Rest}, p_{g^*t}\}$	Group effect of SAB study area vs other study areas	Study area and year effects with interactions
$\{N_{SAB, SKC, Rest}, p_{g^*t}\}$	Group effect of SAB study area vs SKC study area vs other study areas	Study area and year effects with interactions
$\{N_{SKC, Rest}, p_{g^*t}\}$	Group effect of SKC study area vs other study areas	Study area and year effects with interactions
$\{N_t, p_{g^*t}\}$	Year effect	Study area and year effects with interactions
$\{N_T, p_{g^*t}\}$	Linear time effect	Study area and year effects with interactions
$\{N_{TT}, p_{g^*t}\}$	Quadratic time effect	Study area and year effects with interactions

TABLE 3. Model selection results from Program MARK for apparent adult survival (\hat{N}) of male and female California spotted owls on 5 study areas in California.

Model	QAIC _c	Δ QAIC _c	Akaike Weights	Model Likelihood	K	Deviance
$\{N_{SKC \text{ vs } rest}, P_{g^*t}\}$	4034.313	0	0.617	1.000	48	1166.437
$\{N_{SAB, SKC, \text{ vs } rest}, P_{g^*t}\}$	4036.144	1.831	0.247	0.400	49	1166.205
$\{N_{g^*}, P_{g^*t}\}$	4039.844	5.531	0.039	0.063	51	1165.775
$\{N_{\cdot}, P_{g^*t}\}$	4041.059	6.746	0.021	0.034	47	1175.246
$\{N_{SAB \text{ vs } rest}, P_{g^*t}\}$	4041.642	7.329	0.016	0.026	48	1173.767
$\{N_{g+T}, P_{g^*t}\}$	4041.737	7.424	0.015	0.024	52	1165.600
$\{N_T, P_{g^*t}\}$	4042.137	7.824	0.012	0.020	48	1174.262
$\{N_{TT}, P_{g^*t}\}$	4042.896	8.583	0.008	0.014	49	1172.958
$\{N_{Latitude}, P_{g^*t}\}$	4043.038	8.725	0.008	0.013	48	1175.166
$\{N_{g+TT}, P_{g^*t}\}$	4043.103	8.79	0.008	0.012	53	1164.898
$\{N_{\cdot}, P_{g^*t}\}$	4044.186	9.873	0.004	0.008	55	1161.839
$\{N_{g+t}, P_{g^*t}\}$	4044.808	10.495	0.003	0.005	59	1154.162
$\{N_{g^*T}, P_{g^*t}\}$	4048.300	13.987	0.001	0.001	56	1163.880
$\{N_{g^*TT}, P_{g^*t}\}$	4052.520	18.207	0.000	0.000	61	1157.717
$\{N_{g^*t}, P_{(g+t)*s}\}$	4080.515	46.202	0.000	0.000	73	1160.655
$\{N_{g^*t}, P_{g+t}\}$	4081.083	46.77	0.000	0.000	63	1182.118
$\{N_{g^*t}, P_{g^*t}\}$	4082.219	47.906	0.000	0.000	87	1132.878
$\{N_{g^*t}, P_{g+t+s}\}$	4082.346	48.033	0.000	0.000	64	1181.297
$\{N_{g^*t+s}, P_{(g+t)*s}\}$	4082.397	48.084	0.000	0.000	74	1160.440
$\{N_{g^*t+s}, P_{g+t}\}$	4082.796	48.483	0.000	0.000	64	1181.747
$\{N_{g^*t}, P_{g^*t+s}\}$	4082.903	48.59	0.000	0.000	88	1131.446
$\{N_{g^*t+s}, P_{g^*t}\}$	4083.877	49.564	0.000	0.000	88	1132.420
$\{N_{g^*t+s}, P_{g+t+s}\}$	4083.917	49.604	0.000	0.000	65	1180.783
$\{N_{g^*t+s}, P_{g^*t+s}\}$	4084.757	50.444	0.000	0.000	89	1131.182
$\{N_{g^*t}, P_r\}$	4117.686	83.373	0.000	0.000	48	1249.812
$\{N_{g^*t}, P_{r+s}\}$	4119.096	84.783	0.000	0.000	49	1249.158
$\{N_{g^*t*s}, P_{g+t}\}$	4119.334	85.021	0.000	0.000	101	1140.243
$\{N_{g^*t+s}, P_r\}$	4119.343	85.03	0.000	0.000	49	1249.404
$\{N_{g^*t*s}, P_{g^*t}\}$	4119.54	85.227	0.000	0.000	124	1090.980
$\{N_{g^*t+s}, P_{r+s}\}$	4120.62	86.307	0.000	0.000	50	1248.616
$\{N_{g^*t*s}, P_{g+t+s}\}$	4120.706	86.393	0.000	0.000	102	1139.48
$\{N_{g^*t*s}, P_{g^*t+s}\}$	4120.898	86.585	0.000	0.000	125	1090.170
$\{N_{g^*t}, P_{r*s}\}$	4121.059	86.746	0.000	0.000	50	1249.055
$\{N_{g^*t+s}, P_{r*s}\}$	4122.578	88.265	0.000	0.000	51	1248.509
$\{N_{g^*t*s}, P_{(g+t)*s}\}$	4123.396	89.083	0.000	0.000	113	1118.588
$\{N_{g^*t}, P_{g^*t*s}\}$	4127.375	93.062	0.000	0.000	133	1079.253
$\{N_{g^*t+s}, P_{g^*t*s}\}$	4129.041	94.728	0.000	0.000	134	1078.739
$\{N_{g^*t*s}, P_r\}$	4166.548	132.235	0.000	0.000	91	1208.735
$\{N_{g^*t*s}, P_{r+s}\}$	4168.034	133.721	0.000	0.000	92	1208.100
$\{N_{g^*t*s}, P_{r*s}\}$	4170.109	135.796	0.000	0.000	93	1208.051
$\{N_{g^*t*s}, P_{g^*t*s}\}$	4177.529	143.216	0.000	0.000	174	1038.802

TABLE 4. Estimates of apparent adult survival from model $\{N_g, p_{g^*t}\}$ for California spotted owls on 5 study areas in California.

Study Area	$\hat{\phi}$	SE($\hat{\phi}$)	95% confidence intervals
ELD	0.815	0.020	0.772, 0.851
LAS	0.829	0.015	0.798, 0.857
SAB	0.813	0.015	0.782, 0.841
SIE	0.818	0.017	0.781, 0.850
SKC	0.877	0.016	0.842, 0.905

TABLE 5. Estimates of annual recapture probabilities (p) for banded California spotted owls on 5 study areas in California. Standard errors for estimates are in parentheses.

Year	ELD	LAS	SAB	SIE	SKC
1991	0.892 (0.101)	1.000 (-----)	--	0.833 (0.078)	--
1992	0.911 (0.062)	0.963 (0.027)	0.782 (0.048)	1.000 (-----)	1.000 (-----)
1993	0.919 (0.057)	0.933 (0.034)	0.863 (0.038)	0.975 (0.025)	0.976 (0.025)
1994	0.866 (0.064)	0.895 (0.045)	0.857 (0.039)	0.971 (0.030)	1.000 (-----)
1995	0.643 (0.086)	0.876 (0.049)	0.822 (0.041)	1.000 (-----)	0.922 (0.045)
1996	0.922 (0.055)	0.832 (0.054)	0.762 (0.046)	1.000 (-----)	0.909 (0.045)
1997	0.899 (0.049)	0.865 (0.046)	0.829 (0.043)	0.924 (0.038)	0.957 (0.031)
1998	0.868 (0.045)	0.793 (0.054)	0.763 (0.058)	0.862 (0.053)	0.912 (0.044)
1999	0.798 (0.061)	0.925 (0.034)	--	0.976 (0.025)	0.978 (0.023)
2000	0.908 (0.082)	0.899 (0.063)	--	0.933 (0.074)	1.000 (-----)

Table 6. Estimates of mean apparent survival ($\bar{\phi}$) and temporal process standard deviation ($\hat{\sigma}_{\text{temporal}}$) in apparent survival for the California spotted owl on 5 study areas in California.

Estimates were based on variance components analyses from annual estimates of $\hat{\phi}$ from model $\{N_{e^*t}, p_{e^*t}\}$.

Study Area	$\bar{\phi}$	SE($\bar{\phi}$)	$\hat{\sigma}_{\text{temporal}}$	CV _{temporal} ¹	95% confidence intervals for
					$\hat{\sigma}_{\text{temporal}}$
ELD	0.823	0.019	0.0091	0.011	0.0000, 0.1325
LAS	0.837	0.017	0.0271	0.032	0.0000, 0.0943
SAB	0.814	0.015	0.0000	0.000	0.0000, 0.0455
SIE	0.824	0.017	0.0000	0.000	0.0000, 0.0577
SKC	0.891	0.019	0.0293	0.033	0.0000, 0.1005

¹estimated as $\frac{\hat{\sigma}_{\text{temporal}}}{\bar{\phi}}$

TABLE 7. Ranking and weighting of mixed models used to fit trends in adult fecundity for California spotted owls from 5 study areas in California.

Model	$-2\log_e\langle$	K^a	AIC_c	$) AIC_c$	Akaike Weight
<i>Eldorado Study Area</i> (ARH1 covariance structure; $n = 252^b$)					
T	219.3	16	253.6	0.00	0.28
Intercept	221.9	15	253.9	0.32	0.24
T+EO	217.4	17	254.0	0.40	0.23
EO	220.5	16	254.8	1.20	0.16
TT	219.3	17	255.9	2.30	0.09
<i>Lassen Study Area</i> ((ARH1 covariance structure; $n = 418$)					
EO	379.7	16	413.0	0.00	0.44
T+EO	378.8	17	414.3	1.27	0.23
Intercept	383.4	15	414.5	1.54	0.20
T	382.8	16	416.1	3.10	0.09
TT	382.4	17	417.9	4.87	0.04
<i>San Bernardino Study Area</i> (AR1 covariance structure; $n = 323$)					
EO	389.4	6	401.6	0.00	0.31
Intercept	391.6	5	401.8	0.12	0.29
T+EO	388.2	7	402.6	0.89	0.20
T	391.2	6	403.5	1.80	0.13
TT	390.0	7	404.4	2.69	0.08
<i>Sierra Study Area</i> (ARH1 covariance structure; $n = 312$)					
T	178.3	16	212.1	0.00	0.39
TT	176.7	17	212.8	0.64	0.28
T+EO	177.1	17	213.2	1.04	0.23
Intercept	183.9	15	215.5	3.38	0.07
EO	183.3	16	217.1	5.00	0.03
<i>Sequoia Kings Canyon Study Area</i> (EXP(YR) covariance structure; $n = 252$)					
Intercept	190.7	13	218.3	0.00	0.47
EO	189.8	14	219.6	1.35	0.24
T	190.7	14	220.5	2.25	0.15
T+EO	189.7	15	221.8	3.53	0.08
TT	190.0	15	222.1	3.83	0.07

^anumber of estimable covariance and fixed-effect parameters.

^bnumber of reproductive outcomes for adult females.

TABLE 8. Estimates of fixed effect parameters for the top-ranked mixed model used in estimating trends for adult fecundity of California spotted owls on 5 study areas in California.

Study area	Effect	$\hat{\beta}_{effect}^a$	SE	CV	95% Confidence intervals
ELD	T	-0.042	0.024	0.585	-0.090, 0.006
LAS	EO	0.296	0.141	0.475	0.020, 0.571
SAB	EO	0.111	0.071	0.647	-0.030, 0.251
SIE	T	-0.049	0.018	0.370	-0.085, -0.013
SKC	Intercept	0.289	0.074	0.256	0.144, 0.434

^aEstimates of intercepts were 0.667 (SE = 0.170) for the ELD, 0.176 (SE = 0.103) for the LAS, 0.308 (SE = 0.049) for the SAB, and 0.581 (SE = 0.126) for the SIE.

TABLE 9. Estimates of mean fecundity (\bar{b}) across years, temporal process standard deviation ($\hat{\sigma}_{temporal}$) and the amount of process variation explained by the mixed model for trends in fecundity selected based on minimum AIC_c for adult California spotted owls on 5 study areas in California.

Study area	\bar{b}^a	SE	$\hat{\sigma}_{temporal}^b$	CV ^c	% Variation explained ^d
ELD	0.409	0.087	0.275	0.672	24.2
LAS	0.336	0.083	0.267	0.795	30.5
SAB	0.362	0.038	0.078	0.217	29.9
SIE	0.284	0.073	0.232	0.817	44.4
SKC	0.289	0.074	0.222	0.767	— ^e

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

^bstandard deviation of temporal process variation.

^cestimated as $\frac{\hat{\sigma}_{temporal}}{\bar{b}}$.

^dPercent of the temporal variation explained by the fixed-effect trend

model selected using minimum AIC_c , calculated as $\frac{\hat{\sigma}_{temporal}^2 - \hat{\sigma}_{residual}^2}{\hat{\sigma}_{temporal}^2}$

where $\hat{\sigma}_{residual}^2$ is the variation remaining from that explained by the selected model.

^enot applicable because selected model was an intercept-only model.

TABLE 10. Descriptions of the density study area portions of total study areas and the time periods used to estimate $\hat{\theta}_t$ for female and male territorial California spotted owls in California.

Study Area	Study period	Approx. size (km ²)
ELD	1990 – 2000	355
LAS	1992 – 2000	1,270
SAB	1991 - 1998	1,890
SIE	1990 – 2000	355
SKC	1991 - 2000	343

TABLE 11. Estimates of overdispersion (\hat{c}) for capture-recapture data sets used to estimate $\hat{\theta}_t$ from 5 California spotted owl study areas in California. Values for P^2 , df, and P are from TEST 2 and TEST 3 in program RELEASE.

Study Area	P^2	df	P	\hat{c}
ELD	51.34	38	0.0720	1.3526
LAS	55.08	35	0.0167	1.5736
SAB	41.58	32	0.1196	1.2994
SIE	47.19	32	0.0408	1.4746
SKC	14.55	27	0.9753	0.5388 ^a

^aset to 1.0 for subsequent analyses.

TABLE 12. Model selection results from $\mathbf{8}_i$ analyses for California spotted owls on 5 study areas in California.

Model	QAIC _c	K	Deviance	ΔQAIC _c	Akaike Weight
<i>El Dorado Study Area (ELD)</i>					
Linear random effects	1045.295	23.00	701.409	0.000	0.506
Linear* random effects	1047.211	24.00	701.116	1.916	0.194
Quadratic random effects	1047.264	24.00	701.170	1.969	0.189
Quadratic* random effects	1049.402	25.00	701.089	4.107	0.065
Mean random effects	1051.461	26.53	699.743	6.166	0.023
Mean* random effects	1051.776	26.33	700.508	6.481	0.020
Time-specific fixed effects	1055.940	29.00	698.659	10.645	0.002
Time X Sex fixed effects	1106.272	59.00	676.486	60.977	0.000
<i>Lassen Study Area (LAS)</i>					
Mean random effects	1042.045	19.00	626.289	0.000	0.494
Linear random effects	1044.169	20.00	626.277	2.124	0.171
Mean* random effects	1044.171	20.00	626.279	2.126	0.171
Quadratic random effects	1045.595	21.00	625.561	3.550	0.084
Linear* random effects	1047.224	21.98	625.082	5.179	0.037
Quadratic* random effects	1047.243	22.00	625.059	5.198	0.037
Time-specific fixed effects	1050.544	24.00	624.039	8.499	0.007
Time X Sex fixed effects	1086.595	47.00	608.230	44.550	0.000
<i>San Bernardino Study Area (SAB)</i>					
Linear random effects	2243.999	16.00	1101.528	0.000	0.395
Mean* random effects	2245.078	16.00	1102.606	1.079	0.230
Linear* random effects	2246.058	17.00	1101.523	2.059	0.141
Mean random effects	2246.504	16.00	1104.033	2.505	0.113
Quadratic* random effects	2248.118	18.00	1101.516	4.119	0.050
Quadratic random effects	2248.119	18.00	1101.517	4.120	0.050
Time-specific fixed effects	2249.926	19.00	1101.253	5.927	0.020
Time X Sex fixed effects	2280.433	40.00	1087.362	36.434	0.000
<i>Sierra Study Area (SIE)</i>					
Linear random effects	1044.266	23.00	679.456	0.000	0.358
Quadratic random effects	1045.361	24.00	678.376	1.095	0.207
Linear* random effects	1046.215	24.00	679.230	1.949	0.135
Mean* random effects	1046.268	23.98	679.332	2.002	0.132
Mean random effects	1046.928	24.75	678.302	2.662	0.095
Quadratic* random effects	1047.501	25.00	678.332	3.235	0.071
Time-specific fixed effects	1054.071	29.00	676.090	9.805	0.003
Time X Sex fixed effects	1097.288	58.00	651.392	53.022	0.000
<i>Sequoia King Canyon Study Area (SKC)^a</i>					
Quadratic* random effects	1006.533	24.03	620.471	0.000	0.262
Quadratic random effects	1007.141	24.36	620.362	0.608	0.193
Linear random effects	1007.678	24.91	619.684	1.145	0.148
Mean random effects	1008.004	25.03	619.754	1.471	0.125
Mean* random effects	1008.258	25.09	619.859	1.725	0.110
Linear* random effects	1008.412	25.31	619.530	1.879	0.102
Time-specific fixed effects	1009.499	26.00	619.096	2.966	0.059
Time X Sex fixed effects	1042.473	52.00	591.471	35.940	0.000

*indicates that first estimable lambda from model $\{\mathbf{N}_i, p_i, \mathbf{8}_i\}$ was omitted from the random effects model

^aEstimates based on AIC_c rather than QAIC_c because no overdispersion was evident.

TABLE 13. Parameter estimates for best random effects model of β_t for California spotted owls on 5 study areas in California. Best models were selected using the lowest QAIC_c.

Study Area	Best Model	Model Parameters			
		Parameter	Estimate	SE	95% C. I
ELD	Linear	β_0	1.280	0.098	1.089, 1.472
		β_1	-0.055	0.021	-0.094, -0.015
LAS	Mean	β_0	0.985	0.026	0.934, 1.036
SAB	Linear	β_0	1.054	0.078	0.901, 1.207
		β_1	-0.029	0.028	-0.084, 0.026
SIE	Linear	β_0	1.044	0.066	0.915, 1.174
		β_1	-0.020	0.015	-0.050, 0.009
SKC	Quadratic	β_0	1.439	0.167	1.112, 1.765
		β_1	-0.275	0.094	-0.459, -0.091
		β_2	0.034	0.012	0.011, 0.058

TABLE 14. Estimates of mean \mathfrak{B}_t ($\bar{\lambda}$) across time and temporal process standard deviation ($\hat{\sigma}_{\text{temporal}}$) for California spotted owl on 5 study areas in California. Estimates are based on means (intercepts-only) random effects models using time-specific estimates of \mathbf{N} , p , and \mathfrak{B} .

Study Area	$\bar{\lambda}$	SE($\bar{\lambda}$)	95% C. I. for $\bar{\lambda}$	$\hat{\sigma}_{\text{temporal}}$	95% C. I. for $\hat{\sigma}_{\text{temporal}}$
ELD	1.042	0.047	0.950, 1.133	0.088	0.000, 0.323
LAS	0.985	0.026	0.934, 1.036	0.000	0.000, 0.241
SAB	0.978	0.025	0.929, 1.026	0.000	0.000, 0.157
SIE	0.961	0.024	0.915, 1.008	0.015	0.000, 0.189
SKC	0.984	0.047	0.892, 1.076	0.100	0.001, 0.313

TABLE 15. Model selection results (adjusted with $\hat{c} = 1.2739$) for meta-analysis of \mathfrak{B}_t for California spotted owls on 4 study areas (ELD, LAS, SIE, and SKC) in California.

Model	K	Deviance	AIC_c	ΔAIC_c	Akaike Weight
$\mathbf{N}_{g^*t}, P_{g^*t}, \mathfrak{B}_{g^*t}$	73	3660.86	6446.29	0.00	0.994
$\mathbf{N}_{g^*t}, P_{g^*t}, \mathfrak{B}_t$	75	3666.81	6456.39	10.10	0.006
$\mathbf{N}_{g^*t}, P_{g^*t}, \mathfrak{B}_{g^*t}$	92	3641.71	6466.67	20.38	0.000
$\mathbf{N}_{g^*t}, P_{g^*t}, \mathfrak{B}_g$	72	3707.72	6491.08	44.79	0.000
$\mathbf{N}_{g^*}, P_{g^*}, \mathfrak{B}_g$	12	4087.45	6748.38	302.09	0.000

TABLE 16. Comparison of effects in demographic parameters for California spotted owls between the SIE and SKC study areas in California.

Parameter	SKC study area		SIE study area		Effect size		
	Estimate	SE	Estimate	SE	Estimate ^a	SE ^b	95% CI
Adult fecundity ^c	0.289	0.074	0.284	0.073	0.005	0.104	-0.199, 0.209
Adult survival ^d	0.877	0.016	0.818	0.017	0.059	0.023	0.013, 0.105
$\bar{\lambda}$ ^e	0.984	0.047	0.961	0.024	0.023	0.053	-0.080, 0.126

^a(Estimate for SKC) - (Estimate for SIE)

$$^b\sqrt{\hat{SE}_{SKC}^2 + \hat{SE}_{SIE}^2}$$

^cestimates from Table 9.

^destimates from Table 4.

^eestimates from Table 14.

Table 17. Summary of estimates and trends in population parameters for California spotted owls from 5 demographic study areas in California.

Study Area	Land Owner	Province	$\bar{\lambda}$	Trend in $\hat{\lambda}_t$	$\bar{\phi}$	Trend in Fecundity
SKC	National Park	Sierran	0.984 ^a	Declining then increasing	0.89	No trend
LAS	National Forest	Sierran	0.985 ^a	Stable	0.84	Even-odd year
ELD	National Forest	Sierran	1.042 ^a	Declining	0.82	No trend
SIE	National Forest	Sierran	0.961 ^b	Declining	0.82	Declining
SAB	National Forest	S. Californian	0.978 ^a	Stable?	0.81	No trend

^anot different than $\lambda = 1$ (see Figure 5).

^bconsidered different than $\lambda = 1$ (see Figure 5).

APPENDIX 1. Variation in survey methods among California spotted owl studies.

	LAS	ELD	SIE & SKC	SBM
Criteria to estimate occupancy	Owl(s) heard at same location on \$2 occasions separated by \$7 days, OR same owls from the previous year observed at the site	Owl(s) heard at same location on \$2 occasions separated by \$7 days	Owl(s) heard in locations <1/4 mi apart on \$2 occasions separated by \$7 days or same owls from the previous year observed at the site	Owl(s) heard in locations <1/4 mi apart on \$2 occasions
Criteria for reproductive determination	Non-reproduction inferred if any of the following observed on 2 occasions \$1 week apart: 1)female owl roosted for \$60 min. before 1 May. 2)owl ate and/or cached 4 mice. 3)owl ate and/or cached \$2 mice and refused another 4)female observed in hand w/o brood patch from 15 April - 30 June (only 1 observation required)	Non-reproduction inferred if: 1) owl took \$2 mice and cached one without taking to young 2) 1 owl ate \$3 mice -or- 3) 1 owl ate 2 mice and ignored 3rd	Non-reproduction inferred if: 1) & roosted for \$30 min on at least 2 visits before 01 June 2) 1 owl took \$2 mice of 4 but did not deliver to nest or young during \$ 2 surveys -Once pair known to nest, visited site to visually observe and count fledglings 3) & determined to be single social status (6 complete surveys of site, no mate detected)	Non-reproduction inferred if: 1) & roosted for \$45 min on at least 1 visit, prior to 15 May 2) 1 owl took \$4 mice but did not deliver to nest during \$ 1 survey -Once pair known to nest, visited site to visually observe and count fledglings

APPENDIX 2. Final written protocol developed during the workshop on status and trends in California spotted owl populations held 9 -13 July 2001 at Colorado State University, Fort Collins, Colorado.

1. Study Area Characteristics (Table 1)
 - a. San Bernardino Mountains (SAB)
 - b. Sierra (SIE)
 - c. Sequoia/Kings Canyon (SKC)
 - d. Eldorado National Forest (ELD)
 - e. Lassen National Forest (LAS)
2. Data handling issues for apparent survival (ϕ)
 - a. Bird identified by juvenile cohort band, but not captured to give adult individual identification bands. These birds were not recorded as being resighted until the bird was actually recaptured and banded as a uniquely identifiable individual.
 - b. Birds recaptured off study areas that were located by someone else were treated as not recaptured (0 cases for SAB, 2 cases for LAS, 2 cases for SIE, 0 cases for ELD, 1 cases for SKC) and frequency was converted from -1 to 1.
 - c. 1 capture history for barred owl-spotted owl hybrid on LAS was deleted.
 - d. Expansion of study area on ELD – birds that emigrated into expansion before expansion area was surveyed, and then were found. Solution was to keep these records and, hence, ignore this source of individual heterogeneity in p 's because of the small number of cases.
 - e. Juvenile capture histories were split at first recapture to separate juvenile recapture probabilities from S1, S2 and A age classes, e.g. a juvenile CH of 1011101 with freq = 1 was split into 1010000 with freq = -1 and 0011101 with freq = 1.
3. Data handling issues for fecundity (b)
 - a. Unknown age birds should be coded as unknown. Using unbanded birds in fecundity file is acceptable.
 - b. Delete radioed birds to be consistent with survival analysis
 - c. Delete records that don't meet the protocol for each study area. Ignore July 15 cutoff on SIE and SKC because was not used on other study areas.
 - d. Records of resident birds with unknown social status were not included in the SIE & SKC.
 - e. Recognize that b is biased high because establishing no reproduction is more difficult than demonstrating reproduction.
 - f. Estimates are based on females of known age only (unknown age females not included in estimates).
4. Estimate demographic parameters for California Spotted Owls across 5 study areas:
 - a. To be estimated:
 - i. Age-specific apparent survival (ϕ) using QAIC_c model selection criteria in program MARK
 - (1) $\{\phi(a*s*t) p(a*s*t)\}$ is the global model where juvenile PIMs are structured with time-specific p 's separate from S1, S2, or A age-classes.
 - (2) Using $\{\phi(a*s*t)\}$, find best p from the following set:
 - (a) For Juveniles, consider the 4 models J., J3, JA, or JAA, and pick the best Juvenile model, holding the non-juveniles as a dot model – total of 4 models.
 - (b) For non-juveniles, consider the 4 models dot, sex (s), reproductive rate covariate (= r), or $r*s$, plus a model of

choice based on previous experience, using the best Juvenile model from step (a) above – total of 4 models.

- (3) Using best p model from the models in step (2) above, run the following age and sex structure models on ϕ :

(J, [S1, S2+A])*s
 (J, [S1, S2+A])+s
 (J, [S1, S2+A])
 (J, [S1+ S2, A])*s
 (J, [S1+ S2, A])+s
 (J, [S1+ S2, A])
 (J, [S1+ S2+A])+s
 (J, [S1+ S2+A])

against the following time models (all age-classes):

+t
 +T
 *T
 +TT
 *TT
 dot

giving a total of 48 additional models.

- (4) Take top models from within 3 QAIC_c units of the best model from step 3 and run them with no time effect on juvenile N.
 (5) Run the best 2-3 N models from (3) and (4) above with the best 2-3 p models for 4-9 more additional models. Maximum number of models to be run is 70 for each study area.
 (6) Goodness of fit determined with RELEASE based on male and female groups (with S1, S2, and A pooled across each sex with the juvenile portion of CHs removed). Implication is that \hat{e} may be high.

- ii. Conduct a meta-analysis of adult females and males (>S2, but truncate J, S1, and S2 histories) across 5 study areas using QAIC_c model selection criteria in program MARK

- (1) {N(g^*t*s) $p(g^*t*s$)} global model

- (2) The following N models are to be estimated against the 9 p models in (4) below:

N(g^*t*s)
 N(g^*t+s)
 N(g^*t)
 27 Models

- (3) Include a sex effect, if necessary, from the above 27 models with the best p model of the 27 and run the following additional models on N

N(g)
 N($g+t$)
 N(g^*T)
 N($g+T$)
 N(g^*TT)
 N($g+TT$)
 N(t)
 N(TT)

- N(*T*)
 - N(.)
 - N(Latitude) with best group effect model from above 6
 - N(SAB, Rest) with best group effect model from above 6
 - N(SKC, Rest) with best group effect model from above 6
 - N(SAB, SKC, Rest) with best group effect model from above 6
 - N(SKC vs. SIE) with best group effect model from above 6
 - (4) *p* models to be estimated (with and without sex effect, both * and +):
 - $p(g^*t)$
 - $p(g+t)$
 - $p(r)$
 - (5) Total models = 43
 - (6) Goodness of fit determined with RELEASE.
- iii. Age-specific fecundity (*b*) by study area analyzed in PROC MIXED in SAS
 - (1) Fixed effects
 - (a) Female age (S1, S2, A) as a fixed effect
 - (b) Fixed TT model
 - (c) Fixed T model
 - (d) Fixed intercept only model (dot)
 - (e) Fixed Even/Odd model (denoted EO)
 - (f) Fixed Even/Odd model with a linear trend (T)
 - (2) Random effects with ALL of the above fixed effects
 - (a) Territories as a random effect
 - (b) Year as a random effect
 - (3) Structure variance as proportional error distribution, LOCAL=EXP(Female Age, Year or Even/Odd) for the on-diagonal elements. Candidate variance structures for off-diagonal elements are Compound Symmetric (CS) or Autoregressive with lag of 1 (AR1). Choice between these two will be made using AIC model selection with REML in a AGE+T model.
 - (4) Models run will be:
 - Age + TT
 - Age*TT
 - Age+T
 - Age*T
 - Age
 - Age+EO
 - Age*EO
 - Age+EO+T
 - Age*T+EO
 - Intercept only
 - (5) Model selection using AIC.
 - (6) 10 models to run for each study area.
- iv. $\mathbf{8}$ from Pradel model
 - (1) Truncate data sets to first year when “density” study area adequately surveyed
 - (2) Select either $\{\mathbf{8}(t) \mathbf{N}(t) p(t)\}$ or $\{\mathbf{8}(s^*t) \mathbf{N}(s^*t) p(s^*t)\}$ based on AIC_c
 - (3) Eliminate $\mathbf{8}_1$ (confounded), $\mathbf{8}_2$ (may be biased), and $\mathbf{8}_{k-1}$

- (confounded) from analysis
- (4) Do variance components on best model above with the following structures, and select the best of these 3 with AIC_c :
 - (a) T
 - (b) TT
 - (c) dot
 - (5) Total of 5 models run for each study area.
 - (6) Goodness of fit determined with RELEASE.
- v. δ from Leslie matrix
- (1) Use 4-age class projection matrices for all study areas.
 - (2) Estimate age-specific \mathbf{N} and b (and their standard errors) from best model resulting from age-specific survival modeling in MARK and from best model in fecundity analysis from PROC MIXED, respectively, as inputs for the matrix
 - (3) Calculate juvenile ($E_{J\delta=1}$) and adult ($E_{A\delta=1}$) emigration rates necessary to achieve a stationary population ($\delta = 1$).
 - (4) Calculate juvenile ($N_{J\delta=1}$) and adult ($N_{A\delta=1}$) survival rates necessary to achieve a stationary population ($\delta = 1$).
 - (5) Estimate $se(\delta)$ using delta method.
 - (6) If unable to estimate juvenile survival for a given study area, then won't attempt to estimate δ .
- b. Not to be estimated:
- i. Percent territory occupancy
 - ii. Number of owls detected per unit effort (assuming N works above)
 - iii. Juvenile emigration
 - iv. Year-specific N , from Jolly-Seber model. Would have used same data used to estimate δ_{RJS} .
 - v. Change in age of new recruits through time to evaluate change in age structure of floater population
5. Estimate temporal and spatial variation in demographic parameters for California Spotted Owls across 5 study areas
- a. Predictions
- i. Sierra study areas should have higher temporal variation in survival and reproduction than SAB because of weather patterns
 - ii. Two northern Sierra study areas (LAS and ELD) should have different temporal variation in survival and reproduction than the two southern Sierra study areas (SIE and SKC). Not sure about the SAB.
- b. Temporal process variation ($\hat{\sigma}_{temporal}^2$)
- i. Within each study area
 - (1) Estimate $\hat{\sigma}_{temporal}^2$ for adult apparent survival (N_A) from random effects means model in MARK using estimates from model $\{N(a*s*t) p(a*s*t)\}$ if there is a sex effect and $\{N(a*t) p(a*t)\}$ if there is no sex effect.
 - (2) Estimate $\hat{\sigma}_{temporal}^2$ for juvenile apparent survival (N_J) from random effects means model in MARK using estimates from model $\{N(a*s*t) p(a*s*t)\}$ if there is a sex effect and $\{N(a*t) p(a*t)\}$ if there is no sex effect.
 - (3) Estimate $\hat{\sigma}_{temporal}^2$ for δ_{RJS} from random effects means model in

MARK using estimates from model $\{\mathbf{g}(t), \mathbf{N}(t), p(t)\}$.

- (4) Estimate $\hat{\sigma}_{temporal}^2$ for adult fecundity (b_A) from intercepts-only model in PROC MIXED in SAS.
- (5) Do not estimate $\hat{\sigma}_{temporal}^2$ for N_{S1} , N_{S2} , b_{S1} , or b_{S2} because of known sample size limitations.

c. Spatial process variation ($\hat{\sigma}_{spatial}^2$)

- (1) Within each study area
 - (a) Estimate $\hat{\sigma}_{spatial}^2$ for b_A based on territories (owl sites).
- (2) Among study areas
 - (a) Estimate $\hat{\sigma}_{spatial}^2$ for adult apparent survival (N_A) from mean adult apparent survival ($\bar{\phi}_A$) computed from each study area (see 4.a.v.(2)) and using method-of-moments variance components outlined in Burnham et al. 1987.
 - (i) Estimate temporal covariance from model g+t in meta-analysis of apparent survival
 - (b) Estimate $\hat{\sigma}_{spatial}^2$ for juvenile apparent survival (N_J) from mean juvenile apparent survival ($\bar{\phi}_J$) computed from each study area (see 4.a.v.2) and using method-of-moments variance components outlined in Burnham et al. 1987.
 - (c) Estimate $\hat{\sigma}_{spatial}^2$ for \mathbf{g}_{RJS} from $\bar{\lambda}_{RJS}$ computed from each study area (see 4.a.iv) and using method-of-moments variance components outlined in Burnham et al. 1987.
 - (i) Estimate temporal covariance from model g+t in meta-analysis of apparent survival
 - (d) Do not estimate $\hat{\sigma}_{spatial}^2$ for N_{S1} , N_{S2} , b_{S1} , or b_{S2} because of known sample size limitations and do not estimate for b_A because of differences in protocols among study areas. However, compare trends in b_A across study areas.

6. Interpretation and reporting of results

- a. Apparent survival estimates
 - i. Changes in \mathbf{N} over time represents changes in emigration, death or both.
 - ii. The emigration component in juvenile apparent survival is greater than for other age-classes.
 - iii. Bias from resighting heterogeneity in estimates of apparent survival for S1, S2, and A will be small.
 - iv. Inferences about apparent survival estimates apply only to the marked population.
- b. Fecundity estimates
 - i. May be positively biased because of methodology used to determine reproductive output (number of fledged young).
 - ii. Point estimates are not comparable among study areas because of differences in protocol used on different study areas. An exception is

- iii. comparisons between the SIE and SKC study areas.
 - iii. Differences in fecundity estimates within each study area are comparable because bias due to protocol should be similar among years within a particular study area. Thus, trends in fecundity will be examined within study areas.
 - c. $\lambda_{R/S}$ represents change in number of territorial owls
 - i. δ provides information on probability of change over specified a specified time period, given δ under conditions of study.
 - ii. Change based on $\lambda_{R/S}$ can be due to local birth, immigration, death and/or emigration.
 - d. λ_{PM} represents the asymptotic change in the female population size given a specific set of apparent survival and fecundity rates.
 - i. Does not include immigration
 - ii. Represents asymptotic conditions for fixed values of apparent survival and fecundity – i.e., emigration (part of apparent survival) is a function of study area size and edge to area ratio, so that λ_{PM} is a function of study area characteristics
 - iii. Assume 50:50 sex ratio of juveniles
 - e. General Inferences
 - i. Inferences are confined to
 - (1) Within the study areas
 - (2) Within the study period
 - (3) The territorial population of owls? This interpretation needs to be reconsidered carefully.
 - (4) Among study areas for meta-analyses.
 - f. Reporting results
 - i. Lead responsibility for final report will be R. J. Gutiérrez
 - ii. Draft report will be written (not submitted) by end of October 2001
 - (1) All participants will be authors
 - (2) All participants will review final report before submission
 - (a) Deadline for participant reviews; report will be submitted regardless if participant reviews not received within deadline to be established by R. J. Gutiérrez
 - (3) Final report will be reviewed (prior to submission) by two outside reviewers familiar with analytical methods used in report (may be vetoed by USFS)
 - (a) Outside reviewers will be paid to ensure timely review.
 - (4) Internal editor will arbitrate reviews and content of final report
 - (a) Gary White selected
 - iii. Final report will eventually be published in a peer-reviewed outlet
 - (1) Wildlife Monographs suggested outlet
 - (2) Order of authorship and inclusion of authors will be determined by group

Table 1. Summary of data collection for the 5 study areas.

Characteristic	SAB	SIE	SKC	ELD	LAS
Time Period Total	87-98	90-00	90-00	86-00	90-00
Time Period ϕ	91-98	90-00	91-00	90-00	90-00
Time Period b	91-98	90-00	91-00	90-00	90-00
Pradel λ Time Period	91-98	90-00	91-00	90-00	92-00
Leslie Matrix Lambda	91-98	90-00	91-00	90-00	90-00
Study Area Changes	89D8	948979D	979D	978T	---
Unusual Circumstances	91	Migr.		97	
Method Consistency	91-98	90-00	91-00	90-00	90-00
Density Area (km ²)	1890	419	343	355	1450
Study Area (km ²)	1890	686	343	925	2200
Survey Period (mo)	Apr-Aug	Mar-Sep	Mar-Sep	Apr-Aug	Apr-Aug
Time Period Total = Total time period when demography study was conducted					

APPENDIX 3. Further discussion of projection matrix population models.

During the workshop itself, the group debated the utility of developing projection matrices and computing asymptotic λ_{PM} . Subsequent reviews of the draft workshop report also raised this issue (Appendices 4 and 5), so we will try to present our reasoning more completely here. A central theme of our internal discussions and the reviews was that λ_i , estimated using capture-recapture data reflects changes in numbers of birds resulting from all sources of loss from and gain to the study areas. Although we believe that λ_i is relevant to population change at the scale of the individual study areas, we recognize that for some questions, it would be valuable to separate losses from death and emigration and gains from *in situ* recruitment and immigration, as spotted owl populations at the scale of study appear to be geographically open. Thus, dynamics at the scale of study areas are determined at least in part by contributions from other areas. Here we discuss geographic openness and the related source-sink dichotomy and ask whether development of projection matrix models might be useful in increasing our understanding of these open systems.

During both internal workshop discussion and external reviews, it was noted that computation of λ_i was inadequate to determine whether an area was a “source” or a “sink”. It is fairly clear that the studied spotted owl populations do not correspond to the strict source-sink model system of Pulliam (1988). However, we understand that most ecologists no longer view these terms in a strict manner, and that the term “source” has come to mean an area that supplies recruits to other locations. Similarly, we believe that many ecologists view a “sink” as an area in which population size is not maintained strictly by recruitment of locally produced young. We believe that even these relaxed definitions reflect a conceptual framework that may not be especially useful in considering open systems such as those of spotted owls at the spatial scale of study. Indeed, we believe that at least 4 of the 5 spotted owl study areas are sources in the sense that many juvenile owls emigrate and likely recruit to the breeding population elsewhere. We also recognize that these 4 study areas represent sinks in the sense that many if not most birds recruited to the breeding population come from elsewhere and were not produced on the study areas. Thus, the source-sink dichotomy does not seem to be especially useful for describing this system. We suggest that spotted owl populations, as defined by the scale of study, are better viewed as open-recruitment systems in which a substantial fraction of the recruitment to the breeding population is by birds that were not produced on the study area. In this sense of geographic openness, we believe that spotted owl populations are similar to many populations of passerine birds (DeSante 1995), insects (Connor et al. 1983), small mammals (Nichols and Pollock 1990), and marine fish (Roughgarden et al. 1985, Armsworth 2002).

Some of the recommendations to use λ_{PM} suggest that this metric may provide insights about the relevance of movement to population dynamics that can not be obtained using λ_i . We do not believe that this is true. Instead, we believe that the key issue is not one of which λ to use, but of how to estimate relevant quantities. Inferences about movement require the ability to separate gains and losses in the estimation process. Indeed, at the workshop we worked on expressions for decomposing recruitment into *in situ* reproduction and immigration components using a multi-age version of the approach suggested by Nichols and Pollock (1990). But although the appropriate estimators were developed, this work was not completed at the workshop, so we have no such estimates at this time.

Thus, the parameters that were well-estimated and that were suited to incorporation into projection matrix models were age-specific reproductive rates and rates of loss that include both death and emigration. As noted in this and other spotted owl reports, this asymmetry in the treatment of movement would lead to projection matrix results that were of little use. Thus, previous efforts have adjusted or corrected estimates of juvenile survival to remove permanent emigration as a source of loss based on poor estimates of juvenile dispersal. The rationale was that removal of movement from projection matrix entries would yield inferences about λ that were based on only reproduction and mortality, thus providing inferences about whether the populations would decline or increase *if they were geographically closed*. Projection matrices

used previously for spotted owl work are based on closed-population modeling, assuming that all surviving individuals produced in the population exhibit the stage-specific survival and reproductive rates of the area. So even when we “correct” estimates of apparent juvenile survival to remove the movement component, the projection matrix is assigning survival rates and reproductive rates of the study area to the surviving juveniles in subsequent years. However, the reality of the modeled system is that juveniles are thought to move elsewhere and to experience the vital rates of the populations into which they recruit. Thus, we believe that closed-population projection matrix results are much more of an abstraction of the dynamics of open systems than is generally realized.

The above discussion is not intended as a criticism of the use of traditional projection matrices in general, but simply argues that we do not expect them to yield useful inferences for geographically open systems. One of the report reviewers thus suggested that we modify the projection matrices to incorporate immigration, e.g., as in Cooch et al. (2001). As noted, we did not have reliable estimates for such incorporation, and matrix asymptotics (e.g., projected λ) would depend heavily on the magnitude of the immigration. A more satisfying approach would be to use multi-site projection matrices (e.g., Schoen 1988, Lebreton 1996) to include not only the dynamics of the study populations but also of the population(s) with which they are connected via movement. Still another alternative is to use open-recruitment models similar to those developed for marine systems (e.g., Roughgarden et al. 1985). The central point here is that we have considered alternative modeling approaches and have some ideas about how to proceed, but we believe that it makes little sense to implement these approaches now in the absence of estimates of the relevant movement parameters and possibly vital rates of connected populations.

In summary, we agree with reviewers that more detailed inferences about movement would be valuable. In particular, the ability to decompose gains and losses to study populations has potential to yield increased understanding of these systems. However, we disagree with reviewers that this problem can be dealt with via modeling with existing estimates, in particular via computation of λ_{PM} as in previous spotted owl reports. If we did choose to model the study systems, we would select different model structures that were more appropriate for these open systems. More importantly, we view this problem of insights about movement as fundamentally a problem in estimation rather than modeling. We see no reason to expect model-based asymptotics from projection matrices of poorly estimated (even guessed) vital rates to yield reliable insights. Our focus should thus be on estimation of movement-related parameters.

APPENDIX 4. Statistical review of first draft of report by James A. Baldwin, Rudy M. King, and Timothy A. Max, and response to this review by the authors of this report.



United States
Department of
Agriculture

Forest
Service

Pacific Northwest
Research Station
P.O. Box 3890
Portland, OR 97208

Pacific Southwest
Research Station
P.O. Box 245
Berkeley, CA 94701

Rocky Mountain
Research Station
240 W. Prospect Rd.
Ft. Collins, CO 80526

File Code: 1470

Date: October 8, 2002

Alan B. Franklin, Ph. D.
Research Associate
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523

Dear Alan,

We, the Western Research Statisticians of Forest Service Research, were asked by Dr. Peter Stine (Pacific Southwest Research Station, USDA Forest Service) to perform a statistical review of your report "Population Dynamics of the California Spotted Owl: A Meta-Analysis." We have done so and offer the following comments below:

• **Meta-analysis**

1. **Framework of meta-analysis.** On page 4 you quote the statement "Meta-analyses allow synthesis of data from independent studies where studies are considered the sampling unit (Wolf 1986, Hunter and Schmidt 1990)." This quote seems more applicable to a simple, classical meta-analysis rather than to the situation described in this paper. *The Handbook of Research Synthesis* (Cooper and Hedges, 1994) states: "Research synthesis directly addresses the issue of generalization during the problem formulation stage as well as during the analysis and interpretation stage of research". We are concerned whether such research syntheses occurred in your analyses.

For all three characteristics of primary interest (*i.e.*, fecundity, survival, and population rate of change) there is no clear synthesis across studies and no generalized inference about these individual characteristics with associated measures of variability to a clearly identified larger population. A variety of composite analyses is performed but those analyses compare separate locations rather than perform a synthesis. No overall generalizations about California spotted owls are made from the analyses and summary statistics remain separate for each study location. So we are concerned in what sense meta-analyses were performed.

We realize that a meta-analysis performed on these data would be more difficult than a typical meta-analysis since:

- The number of studies is very small;
- Primary interest is in inference about trends of parameters over time, which is more difficult than typical meta-analyses; And
- It is not clear how well the populations in this collection of studies represent the larger geographical population of interest;



Caring for the Land and Serving People

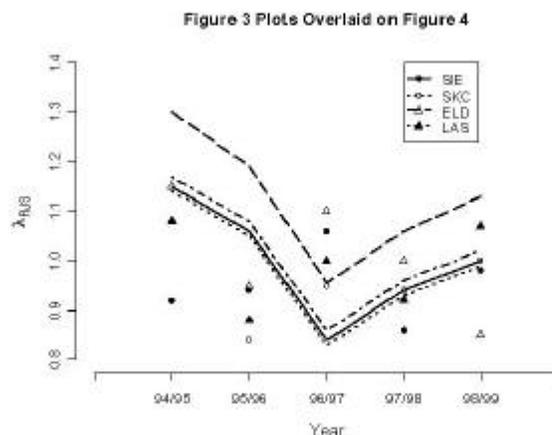
Printed on Recycled Paper



2. **Need for synthesis.** With just five study locations in a meta-analysis it is not reasonable to expect a large increase in understanding of the processes involved. However, for the analyses performed, the explanatory variables consisted almost entirely of “study” and “year” (as categorical variables) both of which have no explanatory power. With “study” as the sampling unit in a meta-analysis, “study” cannot be considered explanatory. To determine that one study location has different values from the other four studies is interesting but provides no synthesis. The same is true for determining that a particular year has larger values than all of the other years.

The report suggests that the next step is to perform a meta-analysis with environmental variables. We agree with that statement and recommend labeling that as a meta-analysis rather than the current report (along with appropriately addressing the other issues mentioned in this review).

3. **Concurrent presentation of individual analyses and the composite analyses.** The report has the individual analyses and the composite analyses presented concurrently. A presentation of all of the individual analyses and individual conclusions followed by the introduction, objectives, analysis, and conclusions from the composite analysis would make it easier to discern the nature and the impact of an overall analysis. As currently written we cannot even determine the relationship between the stated meta-analysis objectives and the analyses performed. In short, the individual analyses and the combined analyses need to be completely separated.
4. **Statistical populations associated with meta-analytic approaches.** On page 4 is the statement “The purpose of this paper is to ... assess status and trends of California spotted owl populations.” However, on page 38 is the statement “We did not know if the results of this meta-analysis were representative of owl demographic trends throughout the Sierra Nevada.” It is critical for a meta-analysis to identify the populations of interest at the beginning of the report, whether those populations are spotted owls in the Sierra or just the spotted owls at the five study sites. The selection of the population does not depend on the observed values of the summary statistics, and is critical for defining the scope of a meta-analysis and the applicability of its results.
5. **The model selection process of the individual analyses and the composite analyses results in inconsistencies.** These inconsistencies are illustrated by the following figure that overlays Figures 3 and 4. The model predictions simply do not fit the data. The composite model predictions do not resemble any of the individual site models and do not fit the estimated λ_t values.



In addition, consider that the SKC composite prediction (in Figure 4) is lower than all of the other sites for every single year. However, the SKC site has λ_t estimates that exceed several of the other sites for several years, and Figure 5 shows the SKC site with a mean λ numerically higher than two of the four other sites.

The cause of the inconsistency stems from (1) over-reliance on automatic model selection procedures rather than examining model fit to the data, and (2) AICc weights providing a relative measure of goodness-of-fit rather than an absolute measure. While the composite model $\{\lambda_{q,t}\}$ has the lowest AICc value, this “best” model still does not fit the data.

- **Avoidance of population sizes**

With the choice of λ_t over λ_{TM} and with λ_t being defined by the estimates of abundance ($\lambda_t = N_{t+1} / N_t$), it seems curious that direct analysis of abundance estimates is completely avoided. We wonder how much the annual patterns observed are related to the use of λ_t without explicit consideration of N_t . Further, we suggest that assessment of status and trends of California spotted owl populations requires attention be given to estimated population sizes.

- **Discussion section**

We have concerns about the numerous speculations interspersed with the analysis results throughout this section.

- **General Conclusions and Recommendations section**

None of the recommendations appears to be associated with the results of the composite analysis. For example, the recommendation to “Encourage the refinement of estimation

models using λ_t models...” does not state how much effect might be expected on any bias or variability of estimates or why the analysis performed justifies or influences the recommendation. In effect, none of the recommendations would change even if the analysis results differed. The conclusions do not appear to be based on any of the analyses.

- **Tables and Figures**

1. Table 16 and Figure 3. The table gives very definite predictions of trend from the “best” models even when some of the critical coefficients are not significantly different than zero and even when examination of the plots in Figure 3 show great variability (which would appear even greater if the measure of variability was changed from “ ± 1 SD” to effectively “ ± 2 SD” which the other figures display).

For example, the manuscript states on page 22: “The best model for the SIE study area also suggested a negative linear trend in λ_t (Table 11, Figure 3) but the second ranked model suggested a quadratic trend. In addition, the estimated slope for the linear trend was not different from zero (Table 12)...” The manuscript cannot state the lack of significance in the text and then declare a “Declining” trend in Table 16. Such statements are not statistically defensible as apparent trends are generally contained within the envelope of variability of each site.

Also on page 22 is the statement “The SIE study area had the lowest estimate of with 95% confidence intervals that barely overlapped $\lambda = 1$, suggesting that the owl population on the SIE was declining.” This, too, is not statistically defensible.

2. Table 16 and Figure 5. To be able to compare λ values among study sites, it is critical to use a common set of years to average over and yet the manuscript does not clearly state whether this is the case in Table 16 or Figure 5. In any event, in Figure 5 none of the λ values are significantly different than zero (even without any adjustments for multiple comparisons). But in Table 16, the mean λ value is declared significantly different for SIE and is therefore inconsistent with Figure 5.

We did develop a list of additional and very specific comments but in light of our major concerns given above, we did not feel it would be useful to include those comments. We hope that our review can be of use, and please contact us if you have any questions or need more details about our comments.

Sincerely,

James A. Baldwin
Station Statistician
Pacific Southwest
Research Station

Rudy M. King
Station Statistician
Rocky Mountain
Research Station

Timothy A. Max
Station Statistician
Pacific Northwest
Research Station

cc: Hilda Diaz-Soltero, Peter A Stine, R. J. Gutierrez

Colorado Cooperative Fish & Wildlife Research Unit

201 Wagar Building
Colorado State University
Fort Collins, Colorado 80523-1484

Phone: 970-491-4870
FAX: 970-491-1413
alanf@cnr.colostate.edu

28 October 2002

James A. Baldwin
Rudy M. King
Timothy A. Max
Pacific Southwest Research Station
P.O. Box 245
Berkeley, CA 94701

Dear Jim, Rudy, and Tim,

Thank you very much for your review of the report "Population Dynamics of the California Spotted Owl: A Meta-Analysis". As a subset of the authors on the report, we discussed your comments and had the following responses:

1. **Framework of meta-analysis.** In the first paragraph of your comment, you suggested that our use of the term meta-analysis was inappropriate. We decided to retain the term "meta-analysis" in the document because it has been used in a generally broad sense and the strict classical definition has been relaxed considerably (see Wachter and Straf 1990. The future of meta-analysis. Sage Publications, New York). For example, Wolf (1986) acknowledges situations where meta-analyses are non-review applications used in multi-regional data sets (a situation similar to the one in our report). However, because of your suggestion, we will try to clarify the section on what we mean by a meta-analysis in the next draft of the report.

In the second paragraph of your comment, you stated that there was no clear synthesis across studies. We were confused by this comment because we had done substantial syntheses of survival probabilities and rates of population change. We conducted a synthetic analysis of adult survival (see Table 3 in the report) that examined differences among study areas and also estimated spatial variation in survival and examined differences in temporal variation among studies (see page 21). We also examined rates of population change for temporal correlations among study areas (see page 22). Although we had intended to synthesize more of the information on fecundity across studies, we were unable to do this because of differences in methodologies (explained in the Methods section). This decision was the consensus opinion of the lead biologists for each of the demographic studies. Thus, we disagree that no synthesis was done. However, we will examine the report more carefully before the next draft to see if there are areas where we could make this clearer.

2. **Need for synthesis.** We believe a meta-analysis can apply to an examination of spatial and temporal variation just as well as if explanatory variables are included. We did not understand why you felt that this was not a meta-analysis because environmental variables were not included. While the inclusion of environmental variables would have been more useful in identifying processes, rather than just patterns, that is not what we were asked to do by the Forest Service. For the most part, information on environmental covariates was generally lacking at the time of the workshop. However, such analyses are now being

conducted by individual researchers. For example, Mark Seamans (University of Minnesota) and Jennifer Blakesley (Colorado State University) are exploring these issue as part of their doctoral research. Your comment here did point out the need for us to explicitly state at the beginning what our mandate for the workshop was. However, we did explicitly state in the report that exploration of variation associated with environmental covariates was something that should be pursued in a future meta-analysis of these data.

3. **Concurrent presentation of individual analyses and the composite analyses.** This seemed to be a minor organizational consideration. We felt we could go either way but that the current organization allowed readers to examine both the individual analyses and the meta-analyses for each parameter. We felt it was less confusing and would require much less flipping back and forth among different sections of the report. We patterned this report after past meta-analyses conducted for the northern spotted owl, which also included information on individual study sites as requested by the Forest Service and the U.S. Fish and Wildlife Service.
4. **Statistical populations associated with meta-analytic approaches.** You were correct in that we failed to clearly and adequately define the population of interest at the beginning. We were not attempting to define this population after the fact but simply failed to clearly define it in the report. We will add a section to the Introduction.
5. **The model selection process of the individual analyses and the composite analyses results in inconsistencies.** The problem with the inconsistencies in Figures 3 and 4 were not a result of the model selection process but a mistake that was made in transfer of data during the workshop. The data from some of the study areas was accidentally lagged by one year. We really appreciate that you found and pointed out this error to us. We have corrected this error in the revised draft of the report; the general results and inferences did not change with the correction of the error. Thus, the problem arose from a data error and not from use of model selection and AIC_c weights. There is a large body of statistical theory that supports the use of model selection and our use of model selection was not the cause of the problem.
6. **Avoidance of population sizes.** An initial minor point to note is that we defined \mathcal{S}_i as a ratio of abundances, not of abundance estimates. More to the point, we do not understand why it is “curious” to conduct analyses on \mathcal{S}_i rather than on the abundances themselves. If we did not have to estimate either abundances or \mathcal{S}_i (if we knew the true values), then we would probably still prefer to draw inferences based on \mathcal{S}_i simply because of the relationship of these parameters to the concept of “trend”, and the importance of this concept in current conservation thinking. However, we do have to estimate parameters, and this need provides an additional rationale for our selection of \mathcal{S}_i , rather than abundance, as the appropriate quantity to model and estimate. As we noted in the report, potential problems such as heterogeneity of capture probabilities among individuals, lead to relatively small biases in capture-recapture estimates of \mathcal{S}_i . However, heterogeneous capture probabilities lead to substantial negative bias in capture-recapture estimates of abundance. We do little covariate modeling in this report, but we note that \mathcal{S}_i is a much more natural quantity to use in such modeling. In general, it makes little sense to predict that a certain management action or environmental effect will produce a specific number of owls, whereas it does make sense to think of such an effect producing a specific proportional increase or decrease in abundance. In summary, because of the definition of \mathcal{S}_i as a ratio of abundances, properly interpreted analyses based on these 2 metrics are equivalent and do not lead to a strong natural preference for one or the other. However, capture-recapture estimates of \mathcal{S}_i tend to be relatively robust to many common kinds of assumption violations, whereas estimates of abundance are not. In addition, \mathcal{S}_i is a much

more natural quantity to use in many modeling efforts, especially those involving covariates. Thus, we believe it is more reasonable to base analyses on $\mathbf{8}_t$.

7. **Discussion section.** It would have been useful if you could have provided some examples of the speculations. We let the researchers conducting each of the individual studies have free rein in writing their own discussion sections. What exactly were your concerns here? Are you suggesting that the individual discussion sections be eliminated or condensed?
8. **General Conclusions and Recommendations section.** We agreed that we could have done a better job here. However, we did not understand your point about the refinement of estimation models for $\mathbf{8}_t$. We stated that we would like to be able to estimate local births and immigration to better understand the process of recruitment. This had nothing to do with bias or variability of estimates. This was a mechanistic refinement to enhance our understanding of biological processes and not to refine the statistical aspects (i.e., bias and precision) of the models.
9. **Tables and Figures.** We agreed with your point that the trend in $\mathbf{8}_t$ for the SIE in Table 16 should be changed from “Declining” to “Stable?”. However, this and the estimate of $\bar{\lambda}$ for the SIE were the only cases in Table 16 where this occurred (we assumed you meant “SE” rather than “SD” in your comments). Concerning the estimate of $\bar{\lambda}$ in Table 16, we argue our conclusion is correct as follows. In the most technical sense of hypothesis testing and making a dichotomous decision based on an *a priori* setting of $\alpha = 0.05$, we should not conclude that the estimate of $\mathbf{8}$ is not 1 because the confidence interval overlaps zero. However, in the real world of data analysis, our conclusion is quite defensible. The choice of $\alpha = 0.05$ for construction of the confidence interval is arbitrary, and an $\alpha = 0.10$ would have resulted in significance as a dichotomous decision. The evidence from the data argues that the population is declining. An estimate of $\mathbf{8} = 1$ is not the most plausible value considering the strength of the evidence presented. Thus, we agree that your point is technically valid, but irrelevant given the strength of the evidence that is presented.

Your point of making estimates more comparable by using a common set of years is a good one; we will include this in the next draft of the report. However, we stick with our conclusion concerning the SIE based on our arguments in the previous paragraph.

We felt that the last paragraph implied that your additional specific comments would not be useful because the analysis and subsequent report was so severely flawed due to your major concerns. We did not feel that the concerns outlined in your letter were all that major (as we have outlined above) and would appreciate any additional comments that you had on our report.

Again, we appreciate the time you took to review the report and for your thoughtful comments.

Sincerely,

Alan B. Franklin R. J. Gutiérrez James D. Nichols Barry R. Noon Gary C. White

cc: Dr. Hilda Diaz-Soltero
 Dr. Peter A. Stine

APPENDIX 5. Statistical review of first draft of report by the American Ornithologists' Union Conservation Committee, and the response to this review by the authors of this report.

December 2002

The AOU Conservation Committee Review of

Franklin et al., Population dynamics of the California Spotted Owl: a meta-analysis

Jeffrey R. Walters, Evan Cooch and Kenneth H. Pollock

In August 2002, the U. S. Forest Service, Pacific Southwest Research Station, submitted a request to John Fitzpatrick, then President of the American Ornithologists' Union, to provide a review of a draft report describing a meta-analysis of the demography and population dynamics of California Spotted Owls (*Strix occidentalis occidentalis*). The report, entitled "Population dynamics of the California Spotted Owl: a meta-analysis" and authored by Alan B. Franklin and 15 others, is based on a workshop held in July 2001. President Fitzpatrick allocated responsibility for conducting the review to the AOU Conservation Committee. Three individuals, Jeffrey R. Walters, Evan Cooch and Kenneth H. Pollock, were selected to produce the review. The review consists of this summary statement, and the three individual reviews attached.

The three individual reviews are highly consistent, although they were produced independently. The primary purpose of this brief summary is to articulate major points, especially those common to the three reviews. Details and additional comments are found in the individual reviews.

The report is based on a meta-analysis of data on fecundity, survival and population trend from five long-term studies. The reviewers were uniformly impressed by the quality of the methodology, commending attention paid to data quality control and use of state-of-the-art analyses, among other things. One reviewer (Pollock) provides a detailed, thorough assessment of methods and assumptions, and another (Cooch) provides suggestions about the modeling used. More description of some analysis methods would be useful. Also, the reviewers felt that the objectives of the analyses were not sufficiently clear, particularly for the fecundity analysis, and analyses of spatial and temporal variation. The reviewers were surprised that the individual analyses of fecundity and survival were not adequately integrated into the analysis of overall population change. Nevertheless the meta-analysis was viewed as successful in synthesizing existing information.

The organization of the report requires further attention. In particular, the individual study area sections are not well integrated with the general sections. Some critical information of general significance appears only in a section about a particular study area, and what is said in the study area sections is not always consistent with conclusions drawn in the general sections. As a result, it is often difficult to determine what messages the report is intended to convey.

The primary, substantive criticism of the report has to do with \mathcal{R}_t , the metric of population change employed. None of the reviewers felt that \mathcal{R}_t was entirely sufficient to characterize population change, and all indicated the report could be substantially improved by addition of data on two alternative metrics, a matrix-based measure of \mathcal{R} (\mathcal{R}_{pm}) and population counts. Recommendations had to do with both limitations of \mathcal{R}_t and advantages of the other metrics. The authors acknowledge that no single metric is entirely satisfactory, and thus presenting results from several metrics might collectively provide a stronger basis for some of the conclusions drawn. Limitations of \mathcal{R}_t include possible impacts of temporary emigration and immigration and lack of sensitivity to small but biologically significant changes in population. \mathcal{R}_{pm} could be employed in an exploratory fashion, for example through sensitivity analysis. Rejection of \mathcal{R}_{pm} begs the question of

availability of data on movements. In summary, the reviewers felt that the depiction of population dynamics provided by 8, although extremely useful, was insufficient by itself.

The understanding between the AOU and the Forest Service is that the authors of the report will consider the AOU review as they revise the report in order to submit it to a scientific journal for publication. Once the paper is accepted for publication, the AOU will examine it again and issue a final report. The final report will constitute a revised, summary review based on the response of the authors to these first comments from the AOU, and will be published in *The Auk*.

Review of **'Population Dynamics of the California Spotted Owl: A Meta-Analysis'** –
*Franklin, Gutiérrez, Blakesley, Keane, Munton, Steger, Seamans,
Zimmerman, LaHaye, White, Hines, Nichols, Noon, Britting, McDonald &
Shaw*

There are few species as characteristic of the often rancorous debate concerning the relative impacts of anthropogenic activities on natural systems as the spotted owl: it is a virtual 'poster child' for the seemingly endless conflicts between parties interested in fair use of natural resources, and those concerned that such use is perhaps anything but fair, at least to the constituents of the affected ecosystem. This report is intended to present the current state of understanding concerning the demography of this species.

The report has 3 primary structural elements: the first consists of a fairly detailed description of the various study populations, as well as the variety of field methods used for estimation of the various demographic parameters. The second consists of a discussion of various approaches to assessing the 'status' of populations, using estimates of population growth as a proxy for relative 'health' of a population. Finally, results are discussed, within the larger context of the challenges of estimation, as well as implications and suggestions for future work.

My comments (below) roughly parallel the structure of the report. Since it was not clear to me who the intended audience is for the report (ultimately), I treated it as a regular paper as submitted to a peer-reviewed scientific journal, concerning a species and a subject that might be of interest to a diverse readership who might read the paper because of some degree of interest in the topic. As such, some of my comments may reflect a difference between how I perceive the paper and the intents of the authors.

FIELD METHODS AND DATA SELECTION

Without direct knowledge of the system, it is not reasonable to critically review the description of methods, and I won't do so here. However, there are 2 points that I do think worth mentioning. First, the detailed description of the field approaches indicates clearly the efforts that individuals have made to try to provide the most appropriate data needed to characterize the population biology of this species. It is perhaps sobering for the reader to consider how much time and effort has been directed in the study of this species, only to accept that there still remains a considerable level of uncertainty, despite these efforts. Of course, if the species in question were 'better suited' to data collection (colonial, large breeding colonies, ground-nesting), then the level of uncertainty (which to some degree is a problem of the size of the sample from which inference is made) would likely be reduced. However, the 'Catch 22' of many 'threatened' species is that because of their low population numbers (in many cases), there will always be limits to the precision of various parameter estimates, made all the more difficult in the present case because of the 'challenges' posed by the basic biology of spotted owls. Second, it is of some importance to acknowledge the efforts of the authors to fairly and objectively evaluate the data, collected over multiple studies, within a formal, meta-analytical framework, as described by Anderson et al. (1999). All too often, discussions of contentious 'management' or 'conservation' issues have dissolved into squabbles concerning the nature of the data collected (in fact, the scientific literature at large is replete with examples where 'competing' research groups working on a common taxon often claim 'superiority' of results by finding some supposed fault in the data collected by other researchers, or how those data were analyzed). In this report, consensus standards were established, both in terms of the collation and abstraction of the data, but also in terms of basic decisions on analytical approaches. This is not only a critical step for good management, but good science in general. The authors are to be congratulated for taking this step, which is all too rare. Beyond acknowledging their efforts, the reader has some comfort that any differences resulting from comparisons among populations (studies) are unlikely to be artifacts of differences in field techniques. As the authors fully acknowledge, the analytical methods are still subject to potential error, but such errors will not impact comparisons among populations, which is very much part of the intent of the analyses presented in the report.

POPULATION ASSESSMENT AND ANALYSIS: METHODS

The basic question at the heart of the debate concerning spotted owls can be stated fairly simply: are the populations in jeopardy (i.e., are they declining), and if so, is this decline due to anthropogenic activities? For the most part, this report focuses on the first question, and defers the second question to future work. To establish the 'status' of various spotted owl populations, the authors use measures of population growth rate (hereafter, λ). If population growth $\lambda < 1$, then there is some indication that, given a stated set of conditions (see below) the population is in decline. As such, the report is very much focused on how best to characterize the growth rate of the various spotted owl populations. In so doing, the authors distinguish between *realized* λ (which they refer to as λ_t), and *asymptotic* λ , derived from a stage-based population projection matrix (which they refer to as λ_{PM}). This distinction is critical, and is in fact the point at which methods presented in this paper depart from those used in previous studies. As the authors note, λ_{PM} (which had been used previously) is derived from a projection matrix, and is given as the dominant eigenvalue of the matrix. λ_{PM} is the expected growth rate if the assumptions underlying the matrix projection model are met (e.g., time-invariance of vital rates). This measure of population growth is contrasted with the realized rate λ_t , which is an estimate of the realized change in population abundance between successive time steps. The authors' basic contention is that realized λ_t may be a more robust indicator of the growth trajectory of the population than is λ_{PM} . They base this contention on a series of arguments addressing one or more assumptions implicit in the projection matrix approach.

One clear challenge common to both approaches to characterizing population growth is that any measure of growth will be influenced by uncertainties in the parameters used to estimate growth. Since growth is essentially the outcome of the net balance equation of 'additions' to the population (births and/or immigrants) and 'subtractions' from the population (deaths and/or emigration), then the precise estimation of sources of 'addition' and 'subtraction' is critical. The authors make considerable use of modern, robust approaches for estimation of various parameters, and have provided sufficient detail to allow the reader to evaluate what they've done.

I have some questions/comments on the various methods used, both in terms of the estimation of various parameters, as well as the use and interpretation of the parameters in various analyses. I also have some questions concerning the structuring of this section.

1. *growth rate vs individual vital rates* - The 'estimation' section focuses on 3 pieces: survival, fecundity, and 'growth rate'. While there is little doubt as to the technical veracity of the methods, and results, I think better motivation of the analysis of the individual vital rates (survival and fecundity) is needed. One of the rationales for assessing variation in λ is that it is an omnibus measure of the integrated effects of variation in both survival and fertility on the dynamics of the population. If your intent is primarily to establish differences among populations in growth rate only, then it seems to me that analysis of survival and fertility are superfluous. However, if part of the intent is to assess the underlying cause of any differences in growth among populations, then clearly assessment of the relative contributions of the vital rates may be needed. Is this the intent? If so (and this seems highly likely), then I think this should be stated clearly – what do you hope to gain from the separate survival and fecundity analyses that adds to the implicit results of the growth rate analyses? Since fertility and survival integrate in complex ways, then it can be difficult to interpret vital rates alone – this is why considering growth rate is perhaps a more robust assessment of the state of the population.
2. *estimating fecundity* – The authors' state (pp. 15-16) that the raw data used in the analysis were integer data (essentially all 0, 1 or 2). They suggested that positive covariation of the mean and the variance was consistent with a Poisson distribution, although not formally demonstrated as such (citation of Franklin et al. 1999 and 2000). However, the authors then invoke 'sample size sufficiency' to justify normal distributional assumptions, in fitting a series of mixed models which differed in the covariance structure to their data. They made use of PROC MIXED in SAS, and used an information theoretic criterion to select models. I'm curious about 2 things. First, at the minimum, rather than rely on the 'normality' assumption, why not consider analysis of the transformed data (square-root being the standard transformation for Poisson data), or (since not strictly Poisson) a Box-Cox transformation? This would still allow the use of PROC MIXED, and the flexibility that procedure offers for specifying different covariance structures. In fact, this could also be done directly using a newer procedure, PROC NLMIXED, which allows explicit modeling of Poisson response

data, in a fully mixed models framework (in fact, PROC MIXED is just a special case of the more general procedure NLMIXED; R. Wolfinger, *pers. comm.*). While the authors may be entirely correct that their sample is sufficiently large to justify reliance on ‘normal’ assumptions, I think that to guard against the potential criticism that their result might be influenced by this assumption it would be worth at least some degree of re-analysis using an explicit Poisson distribution to confirm this (the good news is that virtually no modification of the SAS code is needed). In fact, the mere fact that the authors felt compelled to include the SAS code means that they may have had some concerns over whether or not a reader would ‘accept’ their results as published. The more technical the analysis, the more prone to criticism the methodology might be if the reader finds the results don’t meet his/her expectations, if they don’t have full information on how the analysis was done. Publishing the SAS code used makes this point moot, since the structure of the mixed model, and the corresponding assumptions, are explicit. Given that an effort to do this has already been made, then perhaps it is worth addressing the normality assumption as well.

3. The authors take some issue with what they see as limitations in the utility of δ_{PM} . This comment (and several following) concerns the arguments they make (beginning on p. 17). First, two technical questions, concerning estimation of δ_t . First, is δ_t robust to temporary emigration/immigration (we’ll assume for the moment that such movements are random)? I ask, because δ_t is estimated based on the ratio of the relative proportions of individuals currently in the population that were in the population the year before. I may have missed something in the literature, but I’ve wondered whether or not variation in δ_t can be partitioned easily between *in situ* recruitment and immigration, or emigration, in situations where these movements aren’t permanent (i.e., are temporary). What does δ_t reveal if, for example, in some years there is a temporary influx of birds that are resident for (say) only a single year, and then disappear? I’m thinking this is probably related to the issue of capture rate heterogeneity, and the assumption in the temporal symmetry approach that capture rate of individuals in the population before and those not in the population before at some time (i) is the same. This may be unlikely to be true in the presence of temporary movements, but I could be wrong here.

Second, I am concerned about the derivation of a mean value for δ_t . How was this mean calculated? Since random effects models were used to derive the estimates of δ_t , then would

I be correct in assuming that the mean was estimated as in the variance components module in MARK? If so, then my question relates to how such values are interpreted given structural uncertainty in the candidate model set? This is something I’ve done a bit of work on, but only enough to allow me to articulate the question: suppose we have 3 models in the model set, each with time-dependence in some parameter β , but with variation in the parameterization of other parameters in the model. We can, using the variance components approach, come up with an estimate of mean survival, for each of the 3 models. But, the models may differ in terms of relative support. Most people seem to follow the strategy of selecting the most parsimonious model with time-variation in survival, and deriving an estimate of the mean from that one single model (I’m guessing that was done here). However, borrowing from the philosophy of model averaging, it strikes me that this is ignoring uncertainty in model selection among models in the candidate model set. One approach that might be reasonable is to derive the estimate of mean survival for each of the models with time-dependent survival, and then use the normalized AIC weights to weight these model-specific estimates, to derive an overall mean. I actually tried this, and it can, in some cases, make a rather large difference. I was wondering if the authors might comment on this.

4. I have a basic conceptual issue concerning the idea that δ_{PM} is ‘biased’. The authors contend that δ_{PM} is likely to be biased because of asymmetry in how emigration is handled. First, emigration and immigration can, in fact, be readily incorporated in matrix models, provided estimates are available. Explicit accounting for emigration and immigration in matrix models has been used in a number of studies (Hitchcock & Gratto-Trevor 1995; Wootton & Bell 1992; Cooch et al. 2001; Sandercock & Beissinger 2002); in fact, this has been previously noted by one of the authors (Nichols et al. 2000; Nichols & Hines 2002). The ‘bias’ in δ_{PM} is not characteristic of projection models per se, but rather reflects inadequate parameterization of the model. Second, the authors seem to suggest that because realized survival is a product of true survival and fidelity rate, that use of realized survival can negatively bias estimates of growth from projection models. I think the authors should note that this bias reflects not so much a problem with using apparent survival per se, but rather,

that by using apparent survival (which includes both mortality and emigration as contributing processes), it creates an asymmetry in modeling the dynamics of the population, since the fertility elements are still derived from *in situ* production only (and typically do not account for immigration). However, if estimates of immigration rate were available, then (in theory) it should be possible to construct a matrix model that would mitigate the potential for bias (see for example Cooch et al. 2001). Would it be possible to derive estimates of immigration rate for this system? Nichols and Pollock (1990) describe methods that might be tractable. If not, why not? If it were possible, then this would potentially allow a comparative retrospective study between estimates of δ_{PM} and δ_t (in fact, it was just this sort of study recently described by Sandercock & Beissinger, 2002).

5. There is a natural concern over uncertainty in modeling a population given that one or more parameters are difficult to estimate with any precision. However, one of the singular advantages of analytical approaches using the projection matrix is that it allows you to assess the relative consequences of variation in a particular parameter, even if only poor estimates are available. Using simple, representative values from an earlier study of this species (Lande 1988), it is easily shown that projected δ (given the parameter values specified in that study) was most sensitive (in the prospective sense) to variation in adult survival: in fact, the sensitivity of growth to adult survival is many orders of magnitude greater than that for offspring survival. Moreover, because of the extreme sensitivity of growth to adult survival, a large proportion of the estimated variance of δ reflects variation in adult survival. However, this does not necessarily indicate that any differences among populations are due to differences in adult survival; it merely indicates that a unit change in the value, or variance, of adult survival will have a very large impact relative to an equivalent change in offspring survival. Determining whether differences between populations are due to adult survival requires a formal, retrospective analysis. And, all other things being equal, given the strength of selection against variation in adult survival, the pattern of variation among populations is perhaps most likely due to differences in fertility or offspring survival: there is little canalizing selection minimizing variation in vital rates with low sensitivity values (*sensu* Pfister 1998; Gaillard et al. 2000). However, and this is the point made clearly in Caswell (2001), identifying what may have led to a declining growth rate in a particular population (if it exists) may not inform the most appropriate ‘management’ solution.

Which leads to a basic question I kept coming back to: the report focuses on growth rate. The analyses of survival and fecundity imply (to me, at least) that there is interest in explaining any detected differences in realized growth among the various populations. And yet, despite the careful efforts at characterizing variation in survival, and fertility, the ‘retrospective’ analysis that seems like the logical next step is only addressed in a post-hoc manner. Differences in growth are ‘assessed’ in terms of possible differences in survival or fertility, but based (as far as I can tell) on verbal arguments only. Why no formal retrospective analysis? In the context of δ_{PM} , why not an LTRE (*sensu* Caswell 2001)? The authors note that they do not calculate δ_{PM} (and thus cannot execute the LTRE analysis I mention) because they do not have estimates of emigration rate. I don’t think this justification is entirely fair: the LTRE works to partition variation in δ derived from any set of structurally consistent matrices; the lack of an estimate for emigration rate does not preclude the LTRE for any mechanical reason. It merely influences the interpretation. Regardless, the authors have chose to consider δ_t instead. I wonder if it would be worth discussing why sources of variation in contributions to δ_t (*sensu* Nichols et al. 2000, Nichols & Hines 2002) were not presented. If there are technical reasons for not doing so, it might be worth mentioning to the reader. Without such an analysis, it seems to me that no real, formal retrospective analysis is done here. Also, in the interests of a fair discussion of the relative merits of the 2 approaches, it strikes me that one current advantage of δ_{PM} is that it allows for a more thorough partitioning of sources of variation in δ than does the methods for partitioning δ_t described by Nichols & Hines (2002). This was noted recently by Sandercock & Beissinger (2002). There does not appear to be an obvious analogue to lower-level elasticity analysis for δ_t as exists for δ_{PM} , although I can imagine some scenarios for simple models where it might be possible. It is perhaps also worth noting that Nichols & Hines (2002) suggested (p. 560) that ‘the asymptotic nature of elasticity analysis leads to uncertainty about their relevance to situations involving transient dynamics...or simple temporal variation in vital rates and population growth’. In fact, as discussed at some length in Caswell (2001), deterministic elasticity analysis does ‘remarkably well’, even given significant variation (see also Benton & Grant etc.). I think that if you’re going to draw a contrast between δ_{PM} and δ_t based on a utility

argument, it is fair to consider more fully both sides of it. In fact, the absence of any estimate of emigration rate is, arguably, justification alone for using the λ_t approach. Having said that, I'm not sure how much further along our understanding is of the retrospective dynamics of this system, since we don't seem to have a formal way to assess relative contributions of different vital rates to variation on λ_t .

6. It is suggested that one disadvantage of λ_{PM} is that it is valid (potentially) only over the long term (since it is an asymptotic measure), whereas λ_t captures 'annual variation'. While this is true, it seems to me that an assessment of trajectory for a given population still relies on a time series of λ_t terms, and as such, the 'time-scale' advantage may not be particularly relevant. Moreover, the problem of transients has a fair bit to do with damping ratio, which I suspect is pretty big for this population. Further, in the presence of a trend in vital rates, there are methods that might be applied to deal with short-term forecasts (Lee & Tuljapurkar 1994).

In summary, this is an extremely thorough analysis of 'difficult data'. My only 'criticisms' involve 'packaging' – I think the reader may want a more formal assessment of the degree to which 'population growth' (by whatever criterion it is assessed) represents an integration of the underlying 'processes' contributing to growth rate differences.

LITERATURE CITED

- Anderson, D.R., Burnham, K.P., Franklin, A.B., Gutierrez, R.J., Forsman, E., Anthony, R.G., & Shenk, T. (1999). A protocol for conflict resolution in analyzing empirical data related to natural resource controversies. *Wildlife Society Bulletin*, 27:1050-1058.
- Caswell, H. (2000) Prospective and retrospective analyses: their roles in conservation biology. *Ecology*, 81: 619-627.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis and Interpretation* (2nd Edition). Sunderland, MA., Sinauer Associates.
- Cooch, E.G., Rockwell, R.F., & Brault, S. (2001) Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs*, 71: 377-400.
- Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. and Toïgo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.*, 31:367-393.
- Hitchcock, C.L., & Gratto-Trevor, C. (1996) Diagnosing a shorebird local population decline with a stage-structured model. *Ecology*, 78: 522-534.
- Lande, R. (1988) Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia*, 75: 601-607.
- Lee, R.D., & Tuljapurkar, S. (1994) Stochastic population forecasts for the United States: beyond high, medium, and low. *Journal of the American Statistical Association*, 89: 1175-1189.
- Nichols, J.D., Hines, J.E., Lebreton, J.-D., & Pradel, R. (2000) Estimation of contributions to population growth: a reverse-time recapture approach. *Ecology*, 81: 3361-3376.
- Nichols, J.D., & Hines, J.E. (2002) Approaches for the direct estimation of λ , and demographic contributions to λ , using capture-recapture data. *Journal of Applied Statistics*, 29: 539-568
- Pfister, A.C., 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proc. Nat. Acad. Sci.*, 95: 213-218.
- Sandercock, B.K., & Beissinger, S.R. (2002) Estimating rates of population change for a

neotropical parrot with ratio, mark-recapture and matrix methods. *Journal of Applied Statistics*, 29: 589-607.

Wooton, J.T., & Bell, D.A. (1992) A metapopulation model of the Peregrine falcon in California: viability and management strategies. *Ecological Applications*, 2: 307-321.

I welcome the opportunity to discuss further any of the comments I've made in my review.

Evan Cooch
Department of Natural Resources
Cornell University
evan.cooch@cornell.edu

Population Dynamics of the California Spotted Owl: A Meta-Analysis Franklin et al. (2002) Manuscript

Reviewer

Kenneth H. Pollock, Statistics, Biomathematics, and Zoology, North Carolina State University, Raleigh, NC 27695-8203, U.S.A.

Disclaimer

I reserve the right to change details of my review after discussions with my co-reviewers Evan Cooch and Hal Caswell and also after feedback from the authors of the report.

1. Introduction

The authors are to be commended for writing a very comprehensive, stimulating and interesting report. The report is based on five detailed individual studies on widely spaced and diverse study areas. Also the report uses state-of-the-art capture-recapture analysis methodology. Therefore my review should be viewed as suggestions for relatively minor improvements in how the material is presented. I think that this is an important document for the conservation and management of the California Spotted Owl.

2. Structural Issues

I realize that this is a draft manuscript, however, inclusion of an abstract would have been very helpful. I was not totally clear, from reading to the end of the manuscript, what major points would have been emphasized in such an abstract. There is the need for a clear concise statement of what was found, what was lacking and then finally clear recommendations for the future in terms of research and management. The current conclusion section has some of this but it is mixed in with more general discussion of the complexities of such studies.

The individual site reports are not written in consistent style and sometimes contain important more general information that should have also been presented elsewhere. For example, on page 28, when discussing the Lassen study area, the authors mention that the assumption of equal capture probabilities of banded and unbanded birds may not have been met. I had already wondered a lot about this assumption when reading the General methods and Results sections and it should have been given much more prominence related to all the studies not just the one on Lassen. Another example is reference to population numbers on say page 34, whereas population numbers are not referred to at all in the general parts of the report. Perhaps a table of population numbers of territory holders for each study area could be included? Perhaps this is not practical due to lack of consistency of definition? Yet another example is reference to capture probabilities on say page 29, whereas in the general part of the report I did not see any capture probabilities reported and I think they should have been. The authors should decide on a consistent style for the individual site reports and even more importantly make sure that important general information does not appear there for the first time.

3. Methods and Results

(a). Quality Control of Data

I was impressed by the importance that the authors placed on quality control of the data going into the meta-analysis (pages 11-12). This is crucial to good, sound data analysis, but is often only implicitly addressed.

(b). Methods Description

I think that this report should provide a much more detailed description of the methodology used in the field component of the capture-recapture process. While some of this may be in other owl study reports, not all of these have been published, and not all readers will be familiar with this literature.

One could consider this to be a resighting study where marked animals are followed to estimate apparent survival. However, in this study the unmarked animals are handled differently from those in other resighting studies (Jim Nichols, personal communication). Normally marked to unmarked ratios of resighted birds are used in combination with the resighting of marked birds to estimate population sizes and population changes (The unmarked resighted individuals are added to the capture history information and then treated as losses on capture (Nichols and Hines 2002)). In this study, it is my understanding that, during the same resighting visits to all sections of the study area, all unmarked territorial subadult and adult owls are noted and then captured. This makes the analysis like a regular capture-recapture study, rather than a resighting study. This may be obvious to the researchers involved and perhaps also to the other reviewers, but it was not obvious to me because I have not done a detailed study of the owl capture-recapture methodology literature.

As I discuss later, this special capture-recapture methodology gives rise to a set of crucial assumptions which are that marked and unmarked owls have the same capture probability, all marked owls are captured, and that new and marginal territories are sampled with equal probability to long established stable territories. I am not saying that these issues will cause problems with the estimates but they might and should be presented more thoroughly.

(c). Properties of Estimates

Considering the importance of the population estimates to the management of the California Spotted Owl, I think that a more detailed and systematic discussion of the properties of each set of estimates in terms of potential bias as well as precision would be useful. As the focus of the report is on the population change estimates (8) and survival estimates that are both based on capture-recapture models, I shall focus primarily on those estimates in my comments on this section. I would have liked to have seen an explicit list of all assumptions (most were given in the report but not always explicitly and not in totality) and have attempted such a list below but it still may be incomplete.

Assumptions

1. Capture Probability

There are two related assumptions related to the capture probability process for this sampling scheme.

- a. All animals are assumed to have homogeneous capture probabilities on each sampling occasion. (No Heterogeneity)
- b. Marked and unmarked animals are assumed to have equal capture probability on each sampling occasion. (No Trap Response)

2. There is no tag loss.

3. There is no tag-induced mortality.

4. The study area does not change in size during the temporal duration of the study.

5. All owls have equal apparent survival probability.

6. The length of the sampling interval in each year is short (instantaneous).

7. All emigration of marked animals is permanent.

Potential Bias Due to Assumption Violations

1. Capture Probability

- a. All animals are assumed to have homogeneous capture probabilities on each sampling occasion.

Is there any age dependence of capture probabilities between subadults and adults and might this interact with age-dependence of apparent survival probabilities (See 5 below)? The simulations by Hines and Nichols (2002) suggest that any bias here in population change is likely to be quite small. Also earlier simulations suggest that apparent survival estimates are little affected by heterogeneity.

- b. Marked and unmarked animals are assumed to have equal capture probability on each sampling occasion.

The special capture-resighting methodology used in these owl studies gives rise to a set of crucial questions all related to this assumption that marked and unmarked owls have the same capture probability. I think it implies that every unmarked owl is captured, and is this true?

I also think that it implies that new and marginal territories within each core study area are sampled equally as well as the long established stable territories. (This was discussed briefly in the report only under the LAS Study area inferences on P 28). Hines and Nichols (2002) show that a trap happy response (i.e., unmarked have lower capture rates than marked) causes a positive bias in population change estimates and that the bias can be substantial. I suspect that the authors believe that this is not a serious problem because while there is a difference in capture probabilities between marked and unmarked owls both capture probabilities are high and so it doesn't cause much bias. If so then this should be stated explicitly. In addition presentation of average capture probabilities for all study areas would offer some reassurance on this point. This issue will not cause bias in the apparent survival estimates.

There is also the related question as to whether owls that have been called in and marked are then harder or easier to be called in for resighting. This could be another form of trap response? I suspect it doesn't occur but I did wonder about it as another complication.

2. There is no tag loss.

The authors stated that little or none has occurred based on a study some time ago (P11). I also wonder about metal band loss vs colour band loss used for resighting the marked birds? I also wondered about how much problem there was in reading frayed or worn colour bands?

3. There is no tag induced mortality

This was not discussed and I assume earlier work has shown that it is not a problem? A statement to that effect would be helpful.

4. The study area does not change in size during the temporal duration of the study.

The authors discuss this at length and made special efforts to avoid it.

5. All owls have equal apparent survival probability.

There could be some age dependence of apparent survival probabilities between subadults and adults but this heterogeneity is unlikely to cause much bias unless it interacts with age-dependence of capture probabilities.

6. The length of the sampling interval in each year is short (instantaneous).

This is violated I suspect as the sampling interval each year is several months? It is not clear what bias this might cause. I do not know of simulation studies of this violation of the Jolly-Seber model but they may exist? If not someone ought to look at this in general as so many studies violate this assumption and then ignore the violation.

7. All emigration of marked animals is permanent.

I saw no discussion of temporary emigration issues here and so assume that the authors believe it is unimportant? If so I would prefer to see this stated explicitly. There has been a lot of interest in temporary emigration using the robust design recently by Jim Nichols and Bill Kendall as well as others. Nonrandom temporary emigration can cause bias in estimates from Jolly-Seber analyses. I wonder if scientists working on spotted owls have considered use of the robust design to look at temporary emigration issues? It seems a natural for the robust design because during each year territories are visited on multiple occasions reasonably close together.

Precision of the Estimates

The precision of the apparent survival estimates (Table 5) is very good (SEs of 2-3%). However the precision of the fecundity estimates (Table 8) is worse (SEs up to 25%). The precision of the population change estimates (Table 13) is also good (SEs of about 5%). While this is a well-designed study and this is not meant as a criticism of the authors of the report, the confidence intervals for the population change parameters are wide (plus or minus 0.1). Considering the importance of detecting significant declines, there is still much uncertainty engendered when using estimates with this level of precision. For example, from Table 13 the 95% confidence interval for the average population change for the El Dorado study area is 0.95 up to 1.13. This range goes from a decline of up to 5% per year to an increase of up to 13% per year. For managers this is an enormous amount of uncertainty. Of course there is also the additional uncertainty of potential unknown biases in the estimates.

(d). Other Points

1. Temporal variation calculation makes sense to me but I wonder about the value of the spatial variation calculation?
2. The trends in δ_t are based on different years for different study areas. I wonder if it would not be better to have them based on exactly the same set of years? This is especially so seeing as the authors emphasize the unusual nature of 1992?
3. I am glad that covariates will be examined in future meta-analyses.
4. Do owls ever call in response without being territorial?
5. That apparent survival from a capture-recapture study is equivalent to true survival for adult owls appears to be the implicit assumption made in this report. Is it known to be true absolutely? This assumption will affect the interpretation of the apparent survival estimates but whether it is true or not does not affect the population change estimates.
6. Why is there not more emphasis on the study of movement (immigration and emigration processes)? For example, is radio-telemetry not practical? Perhaps territorial subadult or adult owls are the only owls catchable and they are not the ones doing much moving?
7. I wonder about the inclusion of some measure of the population size of the territory holders for each study area. I noticed this in at least one of the individual site reports.

4. Relationship Between Metrics

There is not a clear relationship or linkage between the three metrics analyzed in this paper. The primary focus seems to be on population change. It is not totally clear to me what is gained by including the fecundity estimates at all considering that the authors state that they cannot be compared between areas? I also wonder if it would be feasible to have a brief presentation of population size by study area as well?

5. Alternative Population Change Metrics

While I would probably have used the same approach as the authors and focused on the λ_t approach the end result is still somewhat unsatisfactory. A population with a $\lambda_t = 1$ could still be a sink population being maintained by immigration. The population changes over time due to four processes of recruitment and immigration for gains and mortality and emigration for losses. These processes vary by age. It seems that the biologists have assumed that adult owls have no emigration or immigration component and have estimates for survival and fecundity (recruitment). It also seems that biologists have great concern about the degree of movement of younger owls and also have little knowledge of their true survival rate. I wonder if there would not be some value in calculating λ_{PM} values based on guesses for some of the parameters? Sensitivity analyses could be carried out as well? I am very unclear on this point and realize the authors debated this topic at the workshop and decided on their current course.

I cannot help but think though that at the end of this long process the conclusions of this report are fairly weak and that managers might benefit by some projection modeling as well as the statistical approach used here. Of course both approaches have large uncertainties and different potential biases.

6. Concluding Remarks

The authors are to be commended on a fine coordinated effort. This is a very good report and represents an enormous field effort as well as very detailed analysis and synthesis

The three metrics used in the report (apparent survival, fecundity and population change) are not very well integrated and perhaps a little on population size could also be included? The nuisance parameter of capture probability should also be included.

Describe methods in much more detail

List all assumptions and discuss their potential bias effects in more detail.

Standardize individual reports and do not leave any general information until this point to discuss.

Discuss why it is not practical to get more information on emigration and immigration processes. Lack of knowledge of these metrics seems a major problem. A naïve observer like myself obviously wonders why telemetry studies are not being included in some combined approach for field sampling?

Reconsider some usage of the population projection matrix approach as well as the capture-recapture approach to estimating population change.

Kenneth H. Pollock
December 3, 2002.

Review of Franklin et al.,

Population Dynamics of the California Spotted Owl: A Meta-Analysis

This report is based largely on a meta-analysis of results from long-term studies of 5 populations of California Spotted Owls, conducted during a workshop held in July 2001. The report also includes pertinent supporting information, and thus with respect to the population biology of the subspecies serves somewhat as both a review of previous knowledge and a synthesis resulting in new understanding. A meta-analysis is only as good as the underlying data, and in this case the data are quite good and do not overly constrain the analyses. Field methods are well established for this species, and similar methods are employed in all the study areas. Sample sizes are large, and well-conceived data screening procedures were employed to achieve data quality control. Some excellent biostatisticians were involved in the effort, and this shows in the rigor of the methods. Techniques used to estimate apparent survival are particularly good. In sum, the procedures followed in conducting the meta-analysis are first rate, and important conclusions result.

Although the procedures used are flawless, I am concerned about some of the decisions made about which procedures to employ. The most important of these concerns has to do with analysis of population growth rate. Certainly it is true that \mathcal{R}_{pm} has significant problems, as the authors point out. (Initial references to these problems are too vague, however, i.e., “we encountered problems in estimability of parameters for juvenile survival”, “other issues concerning bias”, p14. Be more specific.) Thus I concur that it would be a mistake to rely on \mathcal{R}_{pm} as others have done, and applaud the use of \mathcal{R}_t . What I question is the total commitment to \mathcal{R}_t to the total exclusion of \mathcal{R}_{pm} . \mathcal{R}_t is not without its problems. This measure cannot detect source-sink dynamics, an issue the authors explore on p19. (There is ample discussion of how sinks could bias estimates, but why is there no comparable discussion of bias produced by sources?). Also, the behavior of \mathcal{R}_t can be strongly influenced by the presence of a large non-breeding class (i.e., floaters, discussed on p37). Just as inaccessible areas are a problem for \mathcal{R}_{pm} , inaccessible individuals (floaters) are a problem for \mathcal{R}_t , but the authors evidently are not as troubled by the latter as they are by the former. Further, \mathcal{R}_t does not really measure the same thing as \mathcal{R}_{pm} . \mathcal{R}_{pm} is well established through theory and tradition as a measure of population change. \mathcal{R}_t seems to me a hybrid between traditional \mathcal{R} and a sophisticated breeding population count. \mathcal{R}_t certainly indicates breeding population trend, but its meaning is site specific, and it can be quite difficult to interpret. For instance, it can be influenced by habitat change as well as demography. I will illustrate this effect, and that of floaters, using the species I know best, the Red-cockaded Woodpecker (*Picoides borealis*). In this species, \mathcal{R}_t reflects changes in habitat condition rather than demography. Two substantial classes of non-breeders (floaters and helpers) from which replacement breeders are readily available exist in Red-cockaded Woodpeckers. Variation in survival and fecundity are reflected in changes in the size of these non-breeding classes rather than in \mathcal{R}_t . However, the birds are highly sensitive to certain habitat components, and will abandon territories as habitat deteriorates. \mathcal{R}_t reflects changes in the number of suitable territories, and where habitat degrades population size (measured in number of breeding pairs) declines precipitously in the absence of any change in fecundity or survival. I doubt that anything so dramatic occurs in California Spotted Owls, but certainly it is possible that \mathcal{R}_t is influenced by changes in habitat suitability, and by the dynamics of the floater class. Indeed, it is precisely these potential influences that cause problems in interpreting patterns in \mathcal{R}_t (e.g., p26). A further problem is that \mathcal{R}_t may not be sufficiently sensitive to be a reliable indicator of slow population decline.

I recommend that the authors, although continuing to treat \mathcal{R}_t as primary, also make use of \mathcal{R}_{pm} . On p19 the authors state that \mathcal{R}_t “will not be a panacea as a single assessment of the health of a spotted owl population”. Yet it seems to me that in the end they do treat it as a panacea, at least in making general inferences. I think a report that relies heavily on \mathcal{R}_t but also makes limited use of \mathcal{R}_{pm} would be more compelling. Even if juvenile survival cannot be reliably estimated, there is still insight to be gained from exploring a range of possible values and their implications for source-sink dynamics and other aspects not captured by \mathcal{R}_t . In fact procedures for doing just that are described in **Appendix 2** (item

4.a.v.), but apparently either were not carried out or were not included in the report. The authors feel they have a reliable estimate of juvenile survival from one study area (SAB), and could make use of this in setting bounds on likely values. Some features of population dynamics will remain unclear without information on juvenile survival, so it seems prudent to address it to the extent possible, rather than ignore it because current information is less than perfect.

It would also be useful to provide population count data, that is, counts of numbers of active territories in long-term study areas. Where count data are provided (p28 for LAS) they are quite revealing, and aid interpretation of \mathcal{R}_t . Again, I suspect that assessments based on not only \mathcal{R}_t , but also supporting information from \mathcal{R}_{pm} and population counts, would allow even stronger conclusions than those contained in the current version of the report. Indeed, in the case of LAS the discrepancies between the three measures reveal much about population dynamics, and might potentially enable insights about such things as habitat change, immigration and source-sink dynamics.

It seems from reading the **Inferences and assessment by study area** section (pp 27-37) that the authors of some portions of this section are more comfortable basing their interpretations on all three measures of population behavior than relying on \mathcal{R}_t . Inconsistency between what is said here and in the **General Inferences** section is a problem, one which in my view should be solved by bringing the approach used in the individual study area discussions to the more general discussion. This would of course involve not only revision of the discussion in the **General Inferences** section, but also adding some appropriate data and analysis. The utility of this approach is evident in not just the LAS section discussed in the preceding paragraph, but in others as well. The usefulness of considering count data when interpreting \mathcal{R}_t is again apparent in the section on SIE and SKC (p34). In fact, \mathcal{R}_t appears to be misleading in this case, suggesting more positive population dynamics than actually exist. The U-shaped pattern in annual variation in \mathcal{R}_t (**Figure 3**) indicates a return to stability after a period of instability in the SKC population. Mean \mathcal{R}_t also suggests SKC is a stable population. What the counts, but not \mathcal{R}_t , reveal is that the recent stable population is smaller than the former stable population, that is, that the losses during the period of instability were never regained. Perhaps the most revealing section, though, is that on SAB. Here a good case is made that the estimate of \mathcal{R}_{pm} for this isolated population is reliable. There is however a sizeable discrepancy between \mathcal{R}_{pm} and \mathcal{R}_t (p37), which is explained by invoking many of the problems with \mathcal{R}_t discussed above. As with SKC, \mathcal{R}_t indicates more positive population dynamics than does \mathcal{R}_{pm} . The authors' initial statement that \mathcal{R}_t "will not be a panacea as a single assessment of the health of a spotted owl population" is certainly germane here.

I would not change anything about the analysis of apparent survival. It is exceptional. Neither would I question the decisions made about how to conduct the analysis of fecundity. Here the authors do a marvelous job of extracting information from studies that differ in methodology. They are careful to avoid direct comparisons of parameters that are not measured identically in all areas, but still manage to answer many important questions about reproduction. This is accomplished by focusing on annual variation, and frankly I was impressed that the authors were able to achieve as many insights as they did despite the limitations they placed on the analyses. Although I do not question the analysis of fecundity, I do think presentation could be improved. It would be useful to have a little more justification of reproductive methods. The authors make a convincing case for the quality of the data used to estimate survival and \mathcal{R} , but do not do the same for fecundity. The conclusion that the methods are too different to be directly compared implies that at least some of them are inaccurate. The reader needs more reason to believe that the fecundity data have validity. Also, the objectives of the analysis of fecundity are not explained well. What is the purpose of modeling fecundity rather than just estimating it, for example? I also have one criticism of how the results of the fecundity analysis are used (see below).

The authors are to be commended on the care they take in interpreting the results of their analyses, and the insight they apply. Generally I found their conclusions to be well justified and insightful. Of particular interest were the generally lower survival rates of California Spotted Owls compared to Northern Spotted Owls, and with respect to the

former, the higher survival rate in the National Park population compared to the other four. These patterns are well supported by the data, and both the presence of sequoia groves and different management (i.e., retention of old growth) are reasonable explanations of higher survival in the Park. These explanations should be viewed as hypotheses to be tested. Comparison to the Northern Spotted Owl is one respect in which the constraints placed on the fecundity analyses are limiting. It would be useful to know whether lower survival of California Spotted Owls in comparison to Northern Spotted Owls was balanced by higher fecundity, that is, whether there might be some basic difference in life history. The authors of the ELD section are willing to draw such a conclusion (p30), but it seems that this should appear in the **General Inferences** section rather than in one of the study area sections. That estimates from different study areas cannot be analyzed together does not preclude drawing conclusions from patterns in the data from the two subspecies, particularly given that the possible biases in the individual estimates are well known. That is, the constraints put on the analysis do not necessarily apply to discussion. A discussion of life history might help in putting bounds on juvenile survival (see above).

I do take exception to one rather pervasive interpretation of the population trend data. This point relates to the problems with over-reliance on \mathcal{R}_t discussed at length above. Repeatedly the authors offer a more optimistic interpretation of population dynamics than the data suggest based on the assumption that the populations were at some sort of peak at the outset of the study. The data clearly indicate that there was an exceptional year of reproduction at the outset of the study, but interpreting subsequent values of \mathcal{R}_t that were less than 1 as something other than population decline depends on other, untested assumptions, such as fecundity driving population dynamics, and that populations were not exceptionally low prior to the reproductive event. An extreme instance of this interpretation, involving assumptions about use of marginal habitat and behavior of floaters, is found on p35. Standard procedure is to treat year 0 as baseline, and doing otherwise requires more evidence than is offered. Historic population counts, especially those immediately pre-peak (1990-1994), would constitute especially relevant evidence. SAB at least declined during 1988-1992, which makes me wonder whether the post-1992 “peak” could possibly represent anything close to carrying capacity. It is especially important to avoid interpreting trends in \mathcal{R}_t in an overly optimistic way given that \mathcal{R}_t depicts population dynamics more optimistically than other measures in some circumstances (see above).

If habitat effects are an issue (e.g., sequoia may be favorable, oak habitat unfavorable), why is there no analysis of apparent survival by habitat? Analyses of habitat effects are recommended (p39), and perhaps the lack of “accurate vegetation maps” mentioned in the recommendation has precluded looking at effects of habitat on apparent survival. Yet, habitat effects on fecundity have been examined (p33).

Finally, I have a few minor comments. (1) There is too much repetition in the **Methods**, that is, discussion of the same topic in different sections. (2) From the outset, indicate clearly (and in plain English) what “temporal and spatial process variation” mean biologically (e.g., annual variation in fecundity). Perhaps the most important place to do this is when this is first mentioned in the **Methods** (p15), but there are others (e.g., caption of **Table 5**). (3) Generally the results are heavy on statistical description and light on biological significance. The **Fecundity** section (p21) is a prime example. In some instances biological significance is more apparent from **Appendix 2** than from the **Results** section. Perhaps the authors could incorporate more of the biological framework evident in **Appendix 2** into the **Results** section. (4) There are several typographical errors in **Appendix 2**. (5) On p25, “different weather patterns” is not a satisfying explanation of reduced annual variation in fecundity on SAB compared to the other study areas. The various, specific differences between SAB and the other areas (including milder weather) discussed on p36 should be mentioned here. (6) Whether these sample populations are representative of the region (p29) is a key question. The issue should be discussed more extensively and prominently in the **General Inferences** section rather than being buried in a discussion of an individual study area. (7) The detailed speculation about what drives fecundity within an individual study area (e.g., p33, paragraph 3) is not very useful. The

overall summary, based on the meta-analysis, in the **General Inferences** section suffices. Perhaps the overall summary could be expanded slightly in order to cut the material from the individual study area sections. (8) The discussion of reasons for lower survival on SAB (p36) is excessively speculative, given that this pattern is not statistically significant. (9) Given the call for long-term studies in order to draw conclusions, it is difficult to envision how the silvicultural treatment experiments recommended (p39) could provide definitive answers.

Jeffrey R. Walters, Bailey Professor of Biology, Virginia Tech, Blacksburg, VA 24061-0406 (540-231-3847) (jrwalt@vt.edu)

Colorado Cooperative Fish & Wildlife Research Unit

201 Wagar Building
Colorado State University
Fort Collins, Colorado 80523-1484

Phone: 970-491-4870
FAX: 970-491-1413
alanf@cnr.colostate.edu

April 16, 2003

Dr. Jeffrey R. Walters
Bailey Professor of Biology
Virginia Tech University
Blacksburg, VA 24061-0406

Dear Dr. Walters:

We received the review of our report entitled *Population dynamics of the California spotted owl: a meta-analysis*, which was conducted by you, Dr. Evan Cooch, and Dr. Kenneth Pollock as members of the American Ornithologists' Union Conservation Committee. First, we thank you, Dr. Cooch, and Dr. Pollock for your excellent and exhaustive review. While we did not agree with all the points made, we attempted to incorporate many of the comments into the final draft of the report. We have responded to each reviewer's comments below. In response to the general summary comments, we had the following responses:

- We attempted to clarify the objectives of the analyses throughout the report and tried to integrate them better in the Discussion.
- We completely revised the Discussion section and tried to better integrate the general and study-specific inferences.
- We included an estimate of trend in population numbers (realized proportional change) based on the estimates of \mathcal{R}_t for each study area, which did not require estimation of numbers or inclusion of raw counts. This helped in interpreting the estimates of \mathcal{R}_t . We still argue that estimates of \mathcal{R}_{PM} are inappropriate for these data because of the estimation problems with juvenile survival. In addition, there are no studies on juvenile survival of California spotted owls using radio-telemetry upon which we can rely. We felt that no amount of simulations or guesswork would overcome this limitation. We also added an additional Appendix that clarified the differences between \mathcal{R}_t and \mathcal{R}_{PM} . Hopefully, this clarified the perceived limitations in \mathcal{R}_t relative to \mathcal{R}_{PM} . Exploratory analyses concerning \mathcal{R}_{PM} have been done extensively with northern and Mexican spotted owl data and we did not feel another exploratory analysis would add anything to our analyses.

The following sections constitute our specific responses to the reviews provided by each of the Conservation Committee members:

RESPONSE TO REVIEWER - EVAN COOCH

Our numbered comments below correspond to numbered comments in his review:

1. We felt that examination of the components of \mathcal{R} (survival and fecundity) were critical because reliance on a single number (i.e., \mathcal{R}) does not provide a complete overview of trends in populations and the dynamics of populations. We added a paragraph in the Introduction to make this point more clear.

2. We decided not to use the Poisson regression approach suggested by the reviewer because of problems with this approach when data are not distributed as Poisson (see the White and Bennetts 1996 reference in the report); ANOVA approaches perform better with non-normal data that is not distributed as Poisson than does Poisson regression or even over-dispersed Poisson regression. We were not as concerned with departures from normality because of the robustness of ANOVA to violations of this assumption. Rather, we were more concerned with heteroscedasticity which we could control for with specification of covariance structures. Given the evidence, we did not think re-analysis with Poisson regression would add much.
3. We addressed the reviewer's question concerning the robustness of \mathbf{g}_t to temporary emigration/immigration by incorporating further discussion on the assumptions in using \mathbf{g}_t (see Methods section). The reviewer's point about partitioning \mathbf{g}_t into *in situ* recruitment and immigration is an excellent one and should be done in future workshops. However, the methodology to estimate this is still incomplete and would require further work beyond the scope of our report. The mean value for \mathbf{g}_t was estimated using an intercepts-only random effects model (as we stated in the manuscript). The reviewer's concerns regarding structural uncertainty do not apply to our analysis because annual variation was the only structure we used on \mathbf{g} , p or \mathbf{N} in the model $\{\mathbf{N}_t, p_t, \mathbf{g}_t\}$ from which we derived the annual estimates of \mathbf{g}_t in the random-effects models. We added a sentence in the Methods to clarify this issue.
4. Notwithstanding our other arguments concerning use of the projection matrix estimates of \mathbf{g} , our primary problem in using \mathbf{g}_{PM} for the California spotted owl data was 1) estimation of juvenile survival and 2) potential bias in the estimates of juvenile survival because of unknown emigration. The first problem was encountered during the workshop and had no immediate solution. The second problem cannot be corrected without some measure of emigration of juveniles from the study areas. This probably cannot be done without a concurrent radio-telemetry study. We don't think we could estimate immigration rates with the data used during the workshop and we are not sure it would be possible without additional ancillary data. The robust design advocated by Nichols and Pollock (1990) require a closed-capture component that is not possible with the current spotted owl data.
5. We did not pursue the analyses suggested by the reviewer for the simple reason that we could not reliably estimate juvenile survival. Thus, as the reviewer points out, this would not preclude us deriving some numbers, but it would influence our interpretation. The entire point of the analyses was to examine trends in California spotted owl populations on the study areas and do so in as rigorous manner as possible using the available empirical data. For this reason, we ruled out speculative analyses based on estimates that were known to be unreliable (i.e., juvenile survival). We agree that relative contributions of the various components of \mathbf{g} to population change are important but this was beyond the scope of the workshop. It should be an important component of future meta-analyses.
6. We did not really understand the point being made here or whether this was an observation or a criticism. Regardless, our previous assertions regarding the use of \mathbf{g}_{PM} still apply here.

RESPONSE TO REVIEWER - KENNETH H. POLLOCK

Our comments below correspond to the specific sections in his review:

Structural Issues

- We included an Executive Summary as a summary (rather than an abstract) of the report because this report will be read by both scientists and non-scientists.
- We completely re-wrote the Discussion to clarify the points, reduce the redundancy and improve the consistency
- We decided not to include population numbers because the emphasis was on direct and appropriate analysis of the empirical data. We could not justify doing the extensive capture-recapture analyses and then present just raw counts (numbers). As we pointed out in the manuscript, there are problems and biases in estimating numbers using capture-recapture data in open population models; our estimation of \mathcal{S}_t eliminated some of these problems and biases. However, we attempted to characterize \mathcal{S}_t in terms of trends in numbers by using realized proportional changes based on the \mathcal{S}_t estimates. We added new sections to the Methods, Results, and Discussion, as well as an additional figure. We felt this was a good compromise in lieu of raw counts.
- As suggested, we included a table of recapture probabilities.

Methods and Results

- We attempted to add more detail about the field components of the survey and capture-recapture processes for clarification.
- We included more detail concerning the properties of the estimators, but also relegated some of the details to published sources. The level of detail requested by the reviewer has been outlined well in other published sources on spotted owl data (see references cited in the manuscript); we tried to reduce the redundancy in this report with those of previously published sources by citing those sources.

Precision of the Estimates

- We agree with the reviewer that the precision of some of the estimates is poor. To improve the precision would require increased sampling effort which would require increased funding.

Other Points

Our numbered comments below correspond to those of the reviewer under this section:

1. We decided to retain the spatial variation estimates because they have some value in understanding the extent that parameters varied among the study areas.
2. We dealt with this in two ways. First, we computed a mean estimate of \mathcal{S}_t for a set of common years and added this to the Results section. Second, we computed realized proportional change and added these results to the report.
3. No comment required.
4. Floaters occasionally call and are located and banded.
5. The emigration component of the reciprocal of apparent survival is very low. We addressed this further in the Methods and included some additional references for northern spotted owls that supported our assumption that apparent survival for adults was close to true survival, i.e., that emigration in this class of birds is negligible.
6. This is an area for further study. Radio-telemetry is practical but no studies have been funded at a scale to address the immigration and emigration component. This is an area that needs to be addressed in the future.
7. We addressed the issue of population size indirectly by translating our estimates of \mathcal{S}_t into realized proportional change to examine trends in numbers.

Relationship Between Metrics

We attempted to address this more clearly in the Discussion.

Alternative Population Change Metrics

In a contentious issue, such as management of California spotted owl populations, we felt strongly that analyses based on guesses, rather than empirical data, would add little to our understanding of the status of the owl or its population dynamics. Sensitivity analyses of matrix projection models have been done extensively with northern spotted owls, which have very similar life history characteristics to California spotted owls. In addition, these sensitivity analyses really only represent sensitivity to the model, rather than to actual population dynamics, because they do not include empirical estimates of temporal process variation in the life-history traits. We did not believe that modeling based on guesses would offer any clarification of the situation and, in fact, would strongly detract from our understanding. Rather, we believe that the empirical data are the source of information that will resolve current conflicts bearing on this species.

RESPONSE TO REVIEWER - JEFFREY R. WALTERS

Our responses to the reviewer's comments are below and correspond to the specific points in his review:

Decision not to use \mathcal{R}_{PM}

We agree that estimating \mathcal{R}_{PM} may have provided some insights in conjunction with estimates of \mathcal{R}_t . However, the central issue remains that we were unable to reliably estimate \mathcal{R}_{PM} based on empirical data because of unknown bias in juvenile survival probabilities; the central focus of the workshop was reliable estimation of key parameters based on empirical data. We disagree (as we did with the other reviews) that using a range of values to estimate \mathcal{R}_{PM} is very useful in the context and mission of the workshop. Thus, we decided not to include analyses on \mathcal{R}_{PM} . However, we did reference additional published works that have examined \mathcal{R}_{PM} in spotted owl populations. This seems to be overly speculative. We agree that floaters can be an additional source of recruitment for the territorial population but we have no way to measure the floating population with surveys. Thus, recruitment into the territorial population can come from the floater population, but ultimately these immigrants either were born outside the study area or were born within the study area and their entry into the territorial population was delayed by their entry into the unknown floating population before their entry into the territorial population. Although we agree that habitat conditions can affect the demography, this was beyond the scope of the workshop (as we pointed out in the manuscript).

Population Count Data

As we explained in the manuscript, estimation of numbers can be problematic and our estimates of \mathcal{R}_t essentially accounts for changes in numbers. We also avoided inclusion of just raw counts (e.g., number of territories, number of owls counted, etc.) because detectability is not accounted for in these counts, i.e., detection probabilities are not 1. However, we did transform the estimates of \mathcal{R}_t for each study area into realized proportional changes, which represented trends in numbers over time.

Discussion Section

We re-wrote the entire Discussion section to make it more clear, more integrated, and less speculative. Hopefully, the inclusion of realized proportional change estimates clarified

the changes in δ_t . We also added an additional Appendix that attempted to clarify the differences between δ_t and δ_{PM} .

Reproductive Data

We added some additional material to the Methods section to try and clarify the reproductive methods. There seems to be some confusion about the term “model” here. We were referring to a statistical model (e.g., one that models empirical data). Thus, we were estimating fecundity using a statistical model. In re-writing the Discussion, we attempted to further address the comments concerning whether there are differences in life-history strategies between northern and California spotted owls. In addition, we removed some of the overly speculative statements in the individual study area sections and edited them for content. Some of the authors of these sections represented speculations as facts and we attempted to correct the misleading statements and overt speculations.

Interpretation of Population Trend

In re-writing the Discussion, we still included the possibility of the peak 1992 year driving the observed dynamics of the situation but presented it in terms of a hypothesis. This hypothesis is a plausible alternative and needs further examination. We felt the need to include this alternative explanation of trends that we estimated because it was plausible; we were not trying to be optimistic but we were trying to be objective and complete.

Habitat Effects on Survival

We did not analyze survival by habitat because 1) the necessary habitat covariates were unavailable, and 2) such analyses were beyond the scope of the initial workshop. Habitat effects on fecundity were not examined during the workshop but were examined separately on some of the study areas.

Minor Comments

The following numbered responses correspond to those in the review:

1. We attempted to remove some of the redundancy in the Methods.
2. We added a section explaining the term “process variation”.
3. We attempted to incorporate more “biological significance” in the Results and Discussion. However, our primary focus was estimation of trends and we generally lacked data to examine the biological processes behind those trends.
4. We corrected the typographical errors in Appendix 2.
5. We clarified this statement in the Discussion.
6. We added a paragraph in the Data Analysis section of the Methods and added further clarifications in the Discussion concerning the representativeness of the study areas.
7. We re-wrote the Discussion to deal with the issues mentioned here.
8. We reduced this and other speculations throughout the document.
9. We were hoping that we could encourage closer examination of cause-and-effect through experimentation rather than solely relying on long-term observational studies. These two types of studies should complement each other rather than supplant each other.

In closing, we would like to again thank you, Dr. Cooch, and Dr. Pollock for your thorough and insightful reviews. We hope we have adequately incorporated them in our revisions and in our responses to your comments.

Sincerely,

Alan B. Franklin

R. J. Gutiérrez

James D. Nichols

Mark E. Seamans

Gary C. White

Guthrie S. Zimmerman

James E. Hines

Thomas E. Munton

William S. LaHaye

Jennifer A. Blakesley

George N. Steger

Barry R. Noon

Daniel W. H. Shaw

John J. Keane

Trent L. McDonald

Susan Britting

cc: Dr. Hilda Diaz-Soltero
Dr. Peter Stine