Ornithological Monographs

No. 54

Population Dynamics of the California Spotted Owl (*Strix occidentalis occidentalis*): A Meta-Analysis

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, and Susan Britting

POPULATION DYNAMICS OF THE CALIFORNIA SPOTTED OWL (*STRIX OCCIDENTALIS OCCIDENTALIS*): A META-ANALYSIS

ORNITHOLOGICAL MONOGRAPHS

Cover: Spotted Owl (*Strix occidentalis*), ink sketch by Viktor Bakhtin.

POPULATION DYNAMICS OF THE CALIFORNIA SPOTTED OWL (*STRIX OCCIDENTALIS OCCIDENTALIS*): A META-ANALYSIS

By:

ALAN B. FRANKLIN,[1,2] R. J. GUTIÉRREZ,[3] JAMES D. NICHOLS,[4] MARK E. SEAMANS,[3]
GARY C. WHITE,[2] GUTHRIE S. ZIMMERMAN,[3] JAMES E. HINES,[4] THOMAS E. MUNTON,[5]
WILLIAM S. LAHAYE,[3] JENNIFER A. BLAKESLEY,[2] GEORGE N. STEGER,[5]
BARRY R. NOON,[2] DANIEL W. H. SHAW,[5] JOHN J. KEANE,[6] TRENT L. MCDONALD,[7]
AND SUSAN BRITTING[8]

[1]Colorado Cooperative Fish and Wildlife Unit, Colorado State University, Fort Collins, Colorado 80523, USA;
[2]Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523, USA;
[3]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108, USA;
[4]U.S. Geological Survey, Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, Maryland 20708, USA,
[5]U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2081 East Sierra Avenue,
Fresno, California 93710, USA;
[6]U.S. Department of Agriculture, Forest Service, Sierra Nevada Research Center, Pacific Southwest Research Station,
2121 Second Street, Suite A101, Davis, California 95616, USA;
[7]WEST, Inc., 2003 Central Avenue, Cheyenne, Wyoming 82001, USA; and
[8]P.O. Box 377, Coloma, California 95613, USA

TABLE OF CONTENTS

From the Editor

With *Ornithological Monographs #54*, the American Ornithologists' Union implements a new philosophy in the production of its monograph series. Since the series began in 1964, *Ornithological Monographs* have been published sporadically, primarily to present articles that were too large to appear in *The Auk*. Some of those monographs have been enormous (over 1,000 pages), although many were in the 50–100 page range. They were sold as separate issues, with press runs of at most a few thousand copies.

This and subsequent monographs will be provided to all AOU members on a regular basis, packaged with *The Auk*. There are many ornithological research efforts that the AOU and I feel deserve to be published in one setting, without being separated into two or three manuscripts that appear in different journals. If you have a dissertation, major research project, or even a small symposium longer than the 50 pages allowed by *The Auk*, we hope you will consider publishing in *Ornithological Monographs*.

Ornithological Monographs is open to all aspects of ornithology. All that we ask is that the research involve good science, have reasonably broad ornithological interest, and can truly justify the need for monographic treatment. Financial support for publication is not a requirement, although it can certainly help the AOU and may be necessary for larger volumes.

We begin the "new" *Ornithological Monographs* with an analysis of the demography of the California Spotted Owl. Although the Spotted Owl has become the focal species for both sides in arguments about forestry practices in the western United States, most of the national publicity has involved the Northern Spotted Owl of northwestern California, Oregon, and Washington. Similar controversy now surrounds the California Spotted Owl. An attempt to have it listed as an endangered species ended up in the courts, which forced the U.S. Fish and Wildlife Service to conduct a status review. The U.S. Fish and Wildlife Service chose not to list the owl, in part because the U.S Forest Service had developed a management plan (the Sierra Framework) designed to protect the owl and many other resources of the Sierra Nevada. However, on the day that the U.S. Fish and Wildlife Service announced that it would not list the owl, the U.S. Forest Service announced its desire to "modify" the Sierra Framework. The modified framework will be completed in early 2004, and it is unclear at this time whether this will be potentially harmful to the owl. We will undoubtedly hear more about this situation in the future.

As with most threatened or endangered species, we need solid data on demographic patterns across the species' range. This monograph provides such data, combining modern methods such as meta-analysis with sophisticated capture–recapture models across a variety of California sites The topic is critical for conservation purposes, and the approach will introduce readers to the state-of-the-art in the conducting demographic studies. With an interesting and important bird, 16 well-qualified authors, and pioneering methods of analysis, we believe this study sets a high standard for the new *Ornithological Monographs*.

Any scientific editor will admit that outside review is critical to the scientific publishing process Finding reviewers for the long manuscripts that are potential *Ornithological Monographs* will perhaps be a challenge, but we hope readers will be as excited about the concept as we are and will be willing to volunteer time when necessary. For this monograph, Jeffrey R. Walters, Evan Cooch, and Kenneth H. Pollock of the AOU Conservation Committee did an exceptionally detailed review of an early draft. Katie Dugger, Jeffrey R. Walters, and a reviewer who wishes to remain anonymous made comments on what became the final product. We thank these reviewers for the considerable time they contributed toward making this new monograph a high-quality, interesting, and important piece of science. We also want to thank Kimberly Smith, Brad Plummer, Mark Penrose, and Richard Earles of the AOU Publications Office for helping train this new editor in the art of producing scientific publications.

John Faaborg

POPULATION DYNAMICS OF THE CALIFORNIA SPOTTED OWL (*STRIX OCCIDENTALIS OCCIDENTALIS*): A META-ANALYSIS

ALAN B. FRANKLIN,[1,2,9] R. J. GUTIÉRREZ,[3,10] JAMES D. NICHOLS,[4] MARK E. SEAMANS,[3] GARY C. WHITE,[2] GUTHRIE S. ZIMMERMAN,[3] JAMES E. HINES,[4] THOMAS E. MUNTON,[5] WILLIAM S. LAHAYE,[3,11] JENNIFER A. BLAKESLEY,[2] GEORGE N. STEGER,[5] BARRY R. NOON,[2] DANIEL W. H. SHAW,[5] JOHN J. KEANE,[6] TRENT L. MCDONALD,[7] AND SUSAN BRITTING[8]

[1]*Colorado Cooperative Fish and Wildlife Unit, Colorado State University, Fort Collins, Colorado 80523, USA;*
[2]*Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523, USA;*
[3]*Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108, USA,*
[4]*U.S. Geological Survey, Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, Maryland 20708, USA;*
[5]*U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2081 East Sierra Avenue, Fresno, California 93710, USA;*
[6]*U.S. Department of Agriculture, Forest Service, Sierra Nevada Research Center, Pacific Southwest Research Station, 2121 Second Street, Suite A101, Davis, California 95616, USA;*
[7]*WEST, Inc., 2003 Central Avenue, Cheyenne, Wyoming 82001, USA; and*
[8]*P.O. Box 377, Coloma, California 95613, USA*

ABSTRACT.—We conducted a meta-analysis to provide a current assessment of the population characteristics of California Spotted Owls (*Strix occidentalis occidentalis*) resident on four study areas in the Sierra Nevada and one study area in southern California. Our meta-analysis followed rigorous *a priori* analysis protocols, which we derived through extensive discussion during a week-long analysis workshop. Because there is great interest in the owl's population status, we used state-of-the-art analytical methods to obtain results as precise as possible.

Our meta-analysis included data from five California study areas located on the Lassen National Forest (1990–2000), Eldorado National Forest (1986–2000), Sierra National Forest (1990–2000), Sequoia and Kings Canyon national parks (1990–2000), and San Bernardino National Forest (1987–1998). Four of the five study areas spanned the length of the Sierra Nevada, whereas the fifth study area encompassed the San Bernardino Mountains in southern California. Study areas ranged in size from 343 km² (Sequoia and Kings Canyon) to 2,200 km² (Lassen). All studies were designed to use capture–recapture methods and analysis. We used survival in a meta-analysis because field methods were very similar among studies. However, we did not use reproduction in a meta-analysis because it was not clear if variation among individual study-area protocols used to assess reproductive output of owls would confound results. Thus, we analyzed fecundity only by individual study area. We examined population trend using the reparameterized Jolly-Seber capture–recapture estimator (λ_t).

We did not estimate juvenile survival rates because of estimation problems and potential bias because of juvenile emigration from 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 five study areas was 0.833, which was lower than pooled adult survival rates (0.850) from 15 Northern Spotted Owl (*S. o. caurina*) studies. Estimates of survival from the best model on the Lassen ($\hat{\phi}$ = 0.829, 95% confidence intervals [CI] = 0.798 to 0.857), Eldorado ($\hat{\phi}$ = 0.815, 95% CI = 0.772 to 0.851), Sierra ($\hat{\phi}$ = 0.818, 95% CI = 0.781 to 0.850), and San Bernardino ($\hat{\phi}$ = 0.813, 95% CI = 0.782 to 0.841) were not different. However, the Sequoia and Kings Canyon population had a higher survival rate ($\hat{\phi}$ = 0.877, 95% CI = 0.842 to 0.905) than the other study areas. Management history and forest structure (e.g. presence of giant sequoia [*Sequoiadendron giganteum*]) on the Sequoia and Kings Canyon study area differed from all other study areas. There appears to be little or no evidence for temporal variation in adult apparent survival on any of the study areas.

Although we did not directly compare fecundity, estimates were highly variable among years within all study areas (CV of temporal process variation = 0.672–0.817). Estimates for fecundity

[9]E-mail: alanf@cnr.colostate.edu
[10]E-mail: gutie012@tc.umn.edu
[11]Present address: P.O. Box 523, Big Bear City, California 92314, USA.

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 and 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. Because fecundity may be influenced by weather patterns, it was possible that the different weather patterns between southern California and the Sierra Nevada accounted for that difference.

Except for Eldorado, all estimates for λ_t were <1.0, but none was different from λ = 1.0 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 and 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 declined during the study period. Estimated trends in λ_t for the Eldorado and Sierra study areas were negative. Thus, we could not distinguish definitively between alternatives that the populations were stationary or that the estimates of λ_t were not sufficiently precise to detect declines on four of the study areas (Eldorado, Lassen, San Bernardino, and Sequoia and Kings Canyon).

Results of the trend analyses do not allow strong inference about the decline of the populations. Because λ_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 those local populations are imbedded. That is, it is possible that local populations could be producing fewer young but are enhanced by immigration from surrounding areas. It also is possible that the conditions within the study areas may have been better, in terms of habitat loss, than surrounding areas because a Spotted Owl conservation strategy was imposed in the national forest study areas. That may be particularly true where high amounts of private land surrounded study areas (e.g. Lassen, Eldorado). The relatively low survival rates coupled with trend estimates that were either declining or <1.0 suggest a cautious approach to developing 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.

Resumen.—Realizamos un meta-análisis para presentar una evaluación actualizada de las características de las poblaciones de la lechuza *Strix occidentalis occidentalis* residentes en cuatro áreas de estudio ubicadas en la Sierra Nevada y en un área de estudio ubicada en el sur de California. Nuestro meta-análisis siguió unos protocolos *a priori* rigurosos, los cuales desarrollamos a través de discusiones extensivas durante un taller de análisis de una semana de duración. Debido a que existe gran interés en el estatus poblacional de esta lechuza, nos esforzamos para utilizar métodos analíticos modernos que arrojarían resultados científicamente defendibles.

Nuestro meta-análisis incluyó datos de cinco sitios de estudio de California, localizados en el Bosque Nacional Lassen (1990–2000), el Bosque Nacional Eldorado (1986–2000), el Bosque Nacional Sierra (1990–2000), los parques nacionales Sequoia y Kings Canyon (1990–2000), y el Bosque Nacional San Bernardino (1987–1998). Cuatro de estos sitios se extendieron a lo largo de la Sierra Nevada, mientras que el quinto comprendió las montañas de San Bernardino, en el sur de California. Las áreas de estudio variaron en extensión entre 343 km² (Sequoia y Kings Canyon) y 2,200 km² (Lassen). Todos los estudios fueron diseñados para usar métodos y análisis de marcaje y recaptura. Utilizamos datos de supervivencia en un meta-análisis porque los métodos de Weld fueron muy similares entre estudios. Sin embargo, no utilizamos la reproducción en un meta-análisis porque no fue claro si la variación entre los protocolos empleados para determinar el rendimiento reproductivo en las diferentes áreas podría afectar los resultados. Por lo tanto, analizamos la fecundidad de cada área de estudio separadamente. Examinamos las tendencias de la población usando el estimador re-parametrizado de captura–recaptura de Jolly-Seber (λ_t).

No estimamos las tasas de supervivencia de los juveniles debido a problemas de estimación y a sesgos potencialmente causados por la emigración de los juveniles desde las áreas de estudio, pero empleamos estimadores de marcaje-recaptura bajo un marco teórico de información para determinar las tasas aparentes de supervivencia de las lechuzas adultas. El valor estimado de la supervivencia aparente combinado para las cinco áreas fue de 0.833, lo que es menor que 0.850, el valor estimado de supervivencia de adultos combinado para 15 estudios sobre

la subespecie del norte (*S. o. caurina*). Las estimaciones de los mejores modelos para la supervivencia en Lassen ($\hat{\phi}$ = 0.829, intervalo de confianza del 95% [CI] = 0.798 a 0.857), Eldorado ($\hat{\phi}$ = 0.815, CI = 0.772 a 0.851), Sierra ($\hat{\phi}$ = 0.818, CI = 0.781 a 0.850) y San Bernardino ($\hat{\phi}$ = 0.813, CI = 0.782 a 0.841) no fueron diferentes. Sin embargo, la población de Sequoia y Kings Canyon tuvo una tasa de supervivencia mayor ($\hat{\phi}$ = 0.877, CI = 0.842 a 0.905) que las de las otras áreas. La historia de manejo y la estructura del bosque (e.g. presencia de sequoias gigantes [*Sequoiadendron giganteum*]) en Sequioa y Kings Canyon fueron diferentes de las de los otros sitios. En ninguna de las áreas de estudio parece existir evidencia que sugiera la existencia de variación temporal en la supervivencia aparente de los adultos.

Aunque no comparamos la fecundidad directamente, los valores estimados fueron altamente variables entre años en cada uno de los sitios de estudio (coeficiente de variación [CV] del proceso temporal = 0.672–0.817). Los valores estimados de la fecundidad en las distintas poblaciones fueron: Lassen ($\bar{b}$ = 0.336, EE = 0.083), Eldorado ($\bar{b}$ = 0.409, EE = 0.087), Sierra ($\bar{b}$ = 0.284, EE = 0.073), Sequoia y Kings Canyon ($\bar{b}$ = 0.289, EE = 0.074) y San Bernardino ($\bar{b}$ = 0.362, EE = 0.038). Durante la mayor parte de los años, las poblaciones de la Sierra Nevada exhibieron fecundidades bajas o moderadas, mientras que 1992 pareció ser un año excepcional para la reproducción de las lechuzas en esta región. En contraste, la reproducción en la población de San Bernardino fue menos variable (CV del proceso temporal = 0.217), y no presentó la excepcional reproducción de 1992, ni los años extremadamente malos que caracterizaron a todas las áreas ubicadas en la Sierra Nevada. Debido a que la fecundidad puede ser influenciada por los patrones climáticos, es posible que las diferencias encontradas puedan explicarse por las diferentes condiciones de clima del sur de California y la Sierra Nevada.

A excepción de Eldorado, todos los valores estimados de λ_t fueron menores a 1.0, pero ninguno fue differente de λ = 1.0 dados los intervalos de confianza del 95% (Lassen [$\bar{\lambda}$ = 0.985, EE = 0.026], Eldorado [$\bar{\lambda}$ = 1.042, EE = 0.047], Sierra [$\bar{\lambda}$ = 0.961, EE = 0.024], Sequoia y Kings Canyon [$\bar{\lambda}$ = 0.984, EE = 0.047], San Bernardino [$\bar{\lambda}$ = 0.978, EE = 0.025]). Sin embargo, evidencia adicional en forma de cambio poblacional real basado en λ_t sugirió fuertemente que la población de Sierra declinó durante el período de estudio. Las tendencias estimadas de λ_t para las áreas de estudio de Eldorado y Sierra fueron negativas. Por lo tanto, no pudimos saber de forma definitiva si las poblaciones están estables, o si los valores estimados de λ_t no fueron lo suficientemente precisos como para detectar disminuciones en cuatro de las áreas de estudio (Eldorado, Lassen, San Bernardino, y Sequoia y Kings Canyon).

Los resultados de los análisis de las tendencias no permiten hacer inferencias fuertes sobre el declive de las poblaciones. Debido a que λ_t refleja los cambios en el número de lechuzas en las áreas de estudio (i.e. integra las tasas de inmigración, emigración, natalidad y mortalidad), este parámetro no permite hacer inferencias sobre las poblaciones más grandes en las que están inmersas las poblaciones locales. Esto quiere decir que es posible que las poblaciones locales estén produciendo muy pocas crías, pero que estén siendo suplementadas mediante inmigración desde las áreas circundantes. También es posible que las condiciones dentro de las áreas de estudio hayan sido mejores en términos de pérdida de hábitat que las de las áreas circundantes, debido a que en los bosques nacionales de estudio se implementó una estrategia de conservación para *S. occidentalis*. Esto podría ser particularmente cierto en sitios rodeados por gran cantidad de tierras privadas (e.g. Lassen, Eldorado). Las tasas de supervivencia relativamente bajas, en combinación con las estimaciones de las tendencias que estuvieron en declive o fueron menores a 1.0, sugieren que se debe actuar con cautela al desarrollar estrategias de conservación para S. o. occidentalis hasta que se realicen análisis que acoplen condiciones climáticas y de hábitat con parámetros poblacionales, como la supervivencia y fecundidad de los adultos.

THE CALIFORNIA SPOTTED Owl (*Strix occidentalis occidentalis*) is one of three 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 two subspecies, the Northern (*S. o caurina*) and Mexican (*S. o. lucida*) spotted owls (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 more than a decade (Verner et al. 1992b; U.S. Department of Agriculture [USDA], Forest Service 1998a, b).

Verner et al. (1992a [California Spotted Owl Report, hereafter CASPO]) evaluated the status and trends of, and the state of ecological knowledge about, the California Spotted Owl. Two fundamental findings of CASPO 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 also recommended a set of interim guidelines to the USDA Forest Service (USFS) for the management of Spotted Owl habitat. On the basis of 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 USFS 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 that could justify the changes proposed in the EIS documents, citing in particular the uncertainty regarding potential impact of timber harvest strategies 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 USFS 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 USFS 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 USFS (USDA Forest Service 1998b). Information provided in those documents determined the scope and focus of subsequent land-management planning that was conducted as part of the Sierra Nevada Framework Project. Those 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 USFS 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 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 five 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 Northern 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 (U.S.) President W. J. Clinton. That 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, U.S. Department of the Interior [USDI] 1992). That 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 those analyses, declining trends in owl populations and adult female survival were either 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_t) that was based on capture–recapture data and reflected changes in numbers of territorial owls on study areas. That analysis (discussed below) 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. $\lambda = 1.0$) using that 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 our paper is to present the results of a meta-analysis conducted using data generated from five California Spotted Owl population studies (four within the contiguous owl range of the Sierra Nevada and one from an insular population in southern California) to assess status and trends of some California Spotted Owl populations. In our study, owl researchers from the five demography studies, timber industry consultants, and stakeholders met with experts in analysis of population dynamics from 9 to 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. Participants agreed to adhere to a rigid and formal protocol for analytical sessions proposed by Anderson et al. (1999). That rigorous process was critical to the success of the coordinated analysis and was greatly facilitated by the presence and interaction of that diverse group.

Our intent in analyzing the data 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 whereas 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_t) to estimate annual changes in numbers of owls on the study areas (Pradel 1996). We were then able to re-express those estimates as realized proportional changes in numbers of owls without having to rely on estimation of population abundance.

STUDY AREAS

Demographic data from five study areas were used in the analyses (Table 1, Fig. 1). Specific attributes of each study area are described in the following sections, presented 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 was the dominant physical feature influencing the climate on four of the study areas. That mountain range had cold, wet winters and hot, dry summers. Winter Pacific storm systems were the main source of precipitation for the range. Those storm systems could be either cold or warm depending upon their origin (e.g. Gulf of Alaska or tropical Pacific, respectively). Sierra Nevada vegetation was heavily influenced by climate, elevation, aspect, and edaphic conditions (see below), which resulted in diverse forest types.

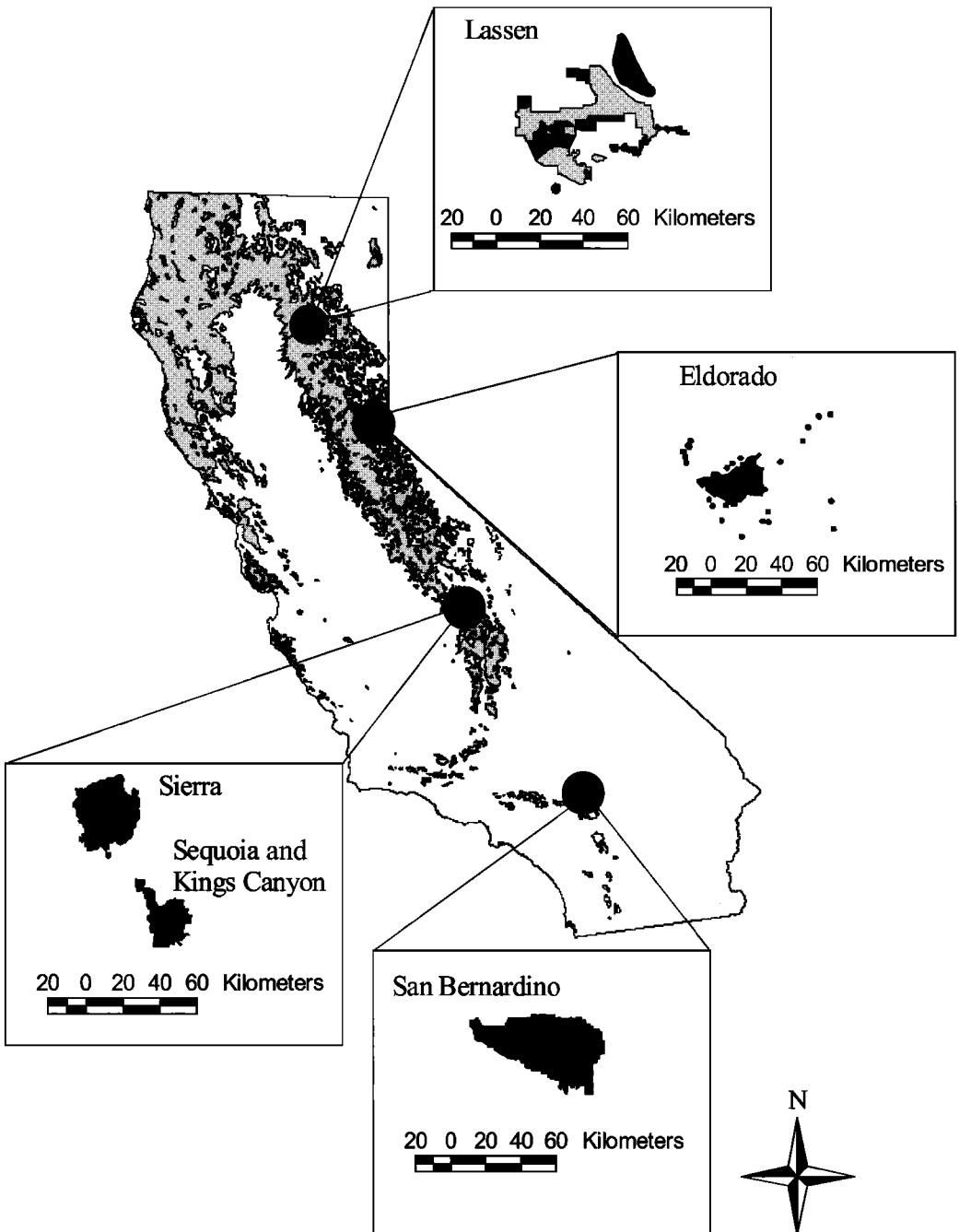Fire has been a primary force shaping the distribution and structure of vegetation in the

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

TABLE 1. Characteristics of five California Spotted Owl demographic study areas in California.

Study area	Acronym	Size (km²)	Organization conducting study	Study period (number 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	2,140	University of Minnesota	1987–1998 (12)	1991–1998
Sierra National Forest	SIE	693	U.S. Department of Agriculture, Forest Service	1990–2000 (11)	1990–2000
Sequoia and Kings Canyon national parks	SKC	343	U.S. Department of Agriculture, Forest Service	1990–2000 (11)	1991–2000

[a] Early years from some 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).

Sierra Nevada 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 that followed 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 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 (Fig. 1). Owls occupying that 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 that 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

The Lassen study area (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 LAS (~1,270 km²) was selected for estimation of λ_t (see 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 National Forest, 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.

Majority of forest types 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 (*P. ponderosa*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*A. magnifica*), and Jeffrey pine (*P. jeffreyi*). California black oak (*Quercus kelloggii*) was present in the understory in some stands.

ELDORADO STUDY AREA

The Eldorado study area (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, accounting for 63% and 37% of the EDSA, respectively.

We began demographic research 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 to 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 year⁻¹. Average minimum temperature in January was 1°C and average maximum temperature in July was 28°C.

The EDSA and RSA were typical of Sierran Montane Forest (SMF; Küchler 1977). From 600 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 (*Q. chrysolepis*), California black oak, Pacific dogwood (*Cornus nuttallii*), and tan oak (*Lithocarpus densiflorus*).

SIERRA STUDY AREA

The Sierra study area (SIE) was located ~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. 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 USFS administrative units and major topographic features such as ridges and drainages.

Annual precipitation from 1961 to 1990 averaged 94 cm at Huntington Lake, ~16 km north of the study area at 2,139 m in elevation (National Oceanic and Atmospheric Administration [NOAA] 1998). Most precipitation occurred during the winter and fell mainly as snow above 1,220 m. Summer temperatures averaged ~16°C at Huntington Lake (NOAA 1998) but could be >38°C at lower elevations.

The SIE had three general vegetation types: oak woodlands, mid-elevation mixed conifer forests, and high-elevation conifer forests. Oak-woodland zone, at the lowest elevation (304–1,220 m), encompassed 26% of the study area and was dominated by blue oak (*Q. douglasii*), interior live oak (*Q. wislizenii*), canyon live oak, and gray pine (*P. sabiniana*). Various foothill chaparral species were abundant. 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, California black oak, Jeffrey pine, red fir, and sugar pine. A small (2 km²) grove of giant sequoia (*Sequoiadendron giganteum*) was within that forest. 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

The Sequoia and Kings Canyon national parks study area (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) that 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 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 winter, precipitation fell primarily as snow above 1,220 m. Average daily temperatures for July at Ash Mountain and Grant Grove were 28 and 17°C, respectively.

Several vegetation types (Verner and Boss 1980) were present on the study area in three distinct 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; 1,220–2,440 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 that zone. Tree species included ponderosa pine, Jeffrey pine, sugar pine, white fir, red fir, incense cedar, and California black oak. Mixed conifer forests included 10 giant sequoia groves. Based on areas estimated from Parsons (1994), those 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 a red fir type and a lodgepole pine type. Trees included red fir, lodgepole pine, and western white pine.

SAN BERNARDINO STUDY AREA

The San Bernardino study area (SAB) was located in the San Bernardino Mountains, ~140 km east of Los Angeles, California (Fig. 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 expanded to encompass all forest habitat within the entire mountain range (2,140 km²). The San Bernardino Mountains were one of a series of mountain ranges that rise above extensive desert (Vasek

and Barbour 1988) and semidesert (Mooney 1988) vegetation types in southern California (Noon and McKelvey 1992, LaHaye et al. 1994). Forests in those mountain ranges were isolates because they occurred at elevations higher 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 to 3,500 m. Climate was Mediterranean with most precipitation falling during the winter months (Fujioka et al. 1998). Annual precipitation ranged from 50 to 100 cm depending on location, elevation, and topography (Minnich 1988). Those 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 ~1,600 m elevation and the dominant tree species were canyon live oak and big-cone Douglas-fir (*Pseudotsuga macrocarpa*). Other tree species associated with those lower elevation sites included Coulter pine (*Pinus coulteri*), white alder (*Alnus rhombifolia*), California sycamore, and big-leaf maple (*Acer macrophyllum*). Montane forests occurred above 1,600 m elevation and were dominated by Jeffrey pine and white fir. Other tree species occurring in montane forests included sugar pine, incense cedar, California 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; that is particularly true of Northern Spotted Owl studies (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, we present here the most consistent methodology used among the studies, but we also present 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 imitating either Spotted Owl territorial vocalizations or playing prerecorded calls from a tape player. We employed three types of survey: point, cruise, and walk-in surveys. We conducted those surveys 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 min (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. We strategically placed survey points to obtain complete survey coverage of individual study areas. Night surveys were generally conducted from dusk to 2400 h. If an owl was detected during a night survey, we conducted a walk-in survey in the same general location to find its roosts and nest (if nesting), locate a possible mate, assess reproductive status, and identify individuals. We attempted to resight all owls located during each walk-in and capture and band all unbanded owls (see below). We conducted additional walk-in surveys to capture and mark unbanded owls if those birds were not captured in the initial survey. We located owls 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. If 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.

We performed multiple complete surveys of each entire study area during the course of a field season. In a study of Northern Spotted Owls, Reid et al. (1999) detected all eight radiomarked nonjuvenile males in their study within three 10-min vocal surveys, which were spaced one 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 any mates. Thus, survey effort should have been sufficient to detect nearly all territorial Spotted Owls on the study areas. Within each study area boundary, we surveyed all areas 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. We surveyed territories on the greater LAS and RSA of the ELD individually. Because those individual territories were not within the bounded density study areas, we did not use them in estimation of λ_t (see below for assumptions of λ_t). 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 λ_t. In SIE and SKC, study areas were divided into sites of the approximate size of owl territories. We included only those sites that were surveyed consistently each year in that analysis. In 1990, survey effort on SKC was less than during the following years and those data were not included in our analysis (Table 1). Finally, in the SAB, we only surveyed forest habitat because owls only occupied forested habitat in that mountain range and there were extensive areas of nonforest habitat (e.g. chaparral) throughout the range.

Estimation of reproductive effort.—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, whereas nonreproducing owls usually eat or cache the mice. We estimated fecundity (i.e. the number of female young fledged per female; Caughley 1977) from number of females checked for reproductive status and number of young observed. We assumed a 1:1 sex ratio of juveniles for fecundity estimates (Steger 1995, Franklin et al. 1996b).

Criteria for inferring nonreproduction for a pair of owls varied slightly among study areas (Appendix 1). However, we used a data screening process to evaluate the internal consistency of data collected given the methods used by an individual study (see below). In addition, we discussed the efficacy of each study area's criteria 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, we 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 subsample complete data sets of survey data (each study area has conducted thousands of surveys and each study area stores those records·differently), which would have taken more time than allotted for the workshop.

Capture, banding, sex and age identification, and resighting of owls.—We attempted to capture and band all detected Spotted Owls following the methods of Forsman (1983) and Franklin et al. (1996a). We captured most owls with noose poles, snare poles, or mist nets. Once captured, we fitted all owls with a locking federal (U.S. Fish and Wildlife Service) aluminum band on the tarso-metatarsus of one leg. On the opposite leg, we marked adult and subadult owls with a unique combination of color band and color tab (Forsman et al. 1996), whereas we fitted juvenile owls with a plastic band having a color unique to their cohort. We refitted juveniles with unique color bands and tabs when recaptured as territory holders in later years.

We determined sex of nonjuvenile owls 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). We did not sex juveniles, except on the SIE and SKC (Steger 1995). We identified four age-classes on the basis of plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; one year old (first-year subadult); two years old (second-year subadult); and three or more years old (adult).

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

Pre-analysis data screening.—Our 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, the data analyzed represented the extent of current data on population dynamics of California Spotted Owls. The demographic parameters of interest for the 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 by the organizers 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 federal 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), age of the male, and 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 the history was included), its age at first capture, its sex, and its federal band number. The 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, we assumed a 1:1 sex ratio at fledging in each year for the capture-history matrix (Steger 1995, Franklin et al. 1996b). We only used owl reproductive data for each study area that was consistent with the protocols developed for each study (see Appendix 1). However, number of young found in each territory each year had to be based on a minimum of two 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, we did not compare estimates of fecundity across study areas in a meta-analysis because of 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 one-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. data collection was internally consistent within a study). A Spotted Owl researcher not involved in the California Spotted Owl meta-analysis was tasked 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 one male and one 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 analysis after results were viewed (see Anderson et al. 1999). All researchers signed the certification.

Meta-analysis workshop format.—We devoted the first day-and-a-half of the workshop 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, we engaged in considerable discussion and debate about the nature of the analyses to be performed, appropriate inferences to be drawn given a particular analysis, and advantages and disadvantages of different approaches. We reached agreement on the structure and nature of analyses and who would perform a specific analysis. Our discussion also led to a departure from past approaches for Spotted Owl population analyses (see discussion of λ estimation below). Because we knew our effort would be closely followed by many interested parties, we developed and recorded a protocol during the workshop (Appendix 2).

We devoted the remainder of the workshop to selection of relevant *a priori* models for reproduction, recapture, and survival modeling (see Appendix 2); then to executing the *a priori* models. Because researchers were at different stages of their studies, we agreed that covariates (e.g. precipitation, habitat) would not be included in the modeling process. However, we also agreed unanimously that that was a worthwhile endeavor to be pursued in a future meta-analysis (see below). 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, we agreed that the results of our analysis 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 and time periods during which data were collected. Inferences beyond the study populations (e.g. to the California Spotted Owl throughout the Sierra Nevada) are not possible with those data because the study areas represent only a small fraction of the total area of the Sierra Nevada range, and those 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 (Franklin et al.

1996a, Caswell 2000). That 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 banded juvenile owls leave the study area, live, and remain undetected, an estimate of juvenile survival using mark–recapture estimators will be negatively biased. For example, estimates of juvenile survival probabilities on three study areas for the Northern Spotted Owl increased 42–137% when they were adjusted, using radiotelemetry data, for emigration from those study areas (Franklin et al. 1999). Conversely, reproductively active owls are more likely to be detected than nonreproductively 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 λ_{PM} would be biased as well. Thus, an important issue concerns the correct inference to be taken from λ_{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, where juvenile survival was estimated from 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 λ_{PM} because of potential geographic variation in survival rates.

Despite those potential problems, we decided, during the early stages of the workshop, to estimate λ_{PM} because there was sufficient disagreement from some participants in the workshop concerning complete exclusion of λ_{PM} from the analysis. Thus, our initial approach was to estimate rates of population change using both λ_{PM} (see Appendix 2) and a recently developed analytical technique for estimation of λ (referred to here as λ_t; see Pradel 1996). That new method 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 those problems, other issues concerning bias in estimates of juvenile survival became apparent (see also Appendix 3). Eventually, we collectively decided that estimates of λ_{PM} would have some unknown bias because of those problems, and analysts and most researchers agreed the data would not support a projection matrix approach for some of those demographic studies. Thus, we decided to rely on λ_t, which estimates λ directly from the capture–recapture data, to estimate changes in owl numbers within study areas (Pradel 1996, Nichols and Hines 2002). Inferences and assumptions relevant to that technique are explained more fully below and in Appendix 3.

Estimating adult survival.—The meta-analysis of adult apparent survival was based on adult female and adult male capture histories for the five study areas, where captures were either initial captures, recaptures, or resightings of color-banded individuals. We defined apparent survival (ϕ) as the probability that an owl alive in a particular year t survived to the same time next year ($t + 1$) and remained on the study area and, hence, was available for recapture. The reciprocal of apparent survival was a function of both death and emigration. We assumed that permanent emigration of adult Spotted Owls from study areas was very low, on the basis of 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 was 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 ($\phi_{g \ast t \ast s}$, $p_{g \ast t \ast s}$), where ϕ was apparent survival probability, p was recapture probability, g was study area, t was time (year), and s was sex. We assessed goodness-of-fit of this model with program RELEASE (Burnham et al. 1987). Assumptions underlying use of mark–recapture data for Spotted Owls and use of goodness-of-fit to evaluate those assumptions was discussed in greater detail by Franklin et al. (1996a). In general, studies on California Spotted Owls were very similar in design to those for the Northern Spotted Owl. We estimated overdispersion in the data using $\hat{c} = \chi^2/df$ using the combined chi-square (χ^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 Akaike's Information Criterion (AIC_c) values (see below). Twenty-seven models were initially fit to the data from the five study areas with three structures ($\phi_{g \ast t \ast s}$, $\phi_{g \ast t + s}$, and $\phi_{g \ast t}$) on apparent survival, and nine structures ($p_{g + t}$, $p_{g + t + s}$, $p_{[g + t] \ast s}$, $p_{g \ast t}$, $p_{[g \ast t] + s}$, $p_{g \ast t \ast s}$, p_t, $p_{t + s}$, and $p_{t \ast s}$) on recapture, where r was annual reproductive output estimated from the five study areas. Program MARK (White and Burnham 1999) generated the log-likelihood function value, degrees of freedom, and the small-sample bias-corrected quasi-likelihood AIC ($QAIC_c$) (Sakamoto et al. 1986,

Burnham and Anderson 1998) for each model evaluated. That criterion was computed as follows:

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

where K was the number of parameters estimated, $\hat{c}$ was the estimate of overdispersion, and n was the effective sample size (i.e. 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 was 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, we fit the following 10 additional models for ϕ: ϕ_g, ϕ_{g+t}, ϕ_{g+T}, ϕ_{g*T}, ϕ_{g+TT}, ϕ_{g*TT}, ϕ_t, ϕ_T, ϕ_{TT}, and $\phi_.$, where T denoted a linear time trend, TT denoted a quadratic time trend, and "." denoted a means only model. Using the minimum QAIC_c model from those 10 models that included a study area effect, we fit additional models: $\phi_{latitude}$, $\phi_{SAB\ vs.\ rest}$, $\phi_{SKC\ vs.\ rest}$, and $\phi_{SAB, SKC\ vs.\ rest}$, where the term *rest* denoted a single survival parameter estimated for the remaining study areas combined. Thus, we considered a total of 41 models (Table 2).

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

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

where Δ_i was the difference in QAIC_c value for the minimum QAIC_c model and model i, and R was 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). We distinguished between *process variation* ($\sigma^2_{process}$)—the variation in a given parameter, such as ϕ—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 (variation in a parameter over time) and spatial process variation (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.—We analyzed fecundity data for each study area with mixed analysis of variance models (Rao 1997). We analyzed study areas separately because estimates were not comparable across study areas (except for the SIE and SKC study areas) because of differences in the field protocols used to estimate reproductive output (number of fledged young per pair). Raw data used in the analysis for each study area consisted of number of young fledged on a particular site, site (territory) where the young were detected, year, and age of the female (first-year subadult, second-year subadult, or adult), for each female monitored. Prior to analysis, we divided the estimates of reproductive output for each site within each year by 2 to estimate fecundity, assuming a 1:1 sex ratio. We used mixed models because (1) individuals and territories were confounded over time because the same females often bred on the same territory for >1 year; that 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).

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 variation in number fledged within a year was proportional to the mean, which suggests a Poisson distribution (Evans et al. 1993), although data were not distributed as Poisson (Franklin et al. 1999, 2000). When we analyzed the California Spotted Owl data using mixed-model analysis of variance, we relied on sample sizes that were sufficiently large to justify normal distributional assumptions. On the basis of 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 was corrected for overdispersion (White and Bennetts 1996). Therefore, we decided to rely on the robustness of analysis of variance to nonnormally 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 that 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

TABLE 2. Descriptions of mark–recapture models examined in the meta-analysis of adult apparent survival (ϕ) of male and female California Spotted Owls from five study areas in California.

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

TABLE 2. Continued.

Model	Description of ϕ structure	Description of p structure
$\{\phi_{g*t*s}, p_{g*t*s}\}$	Study area, year, and gender effects with all interactions	Study area, year, and gender effects with all interactions
$\{\phi_{g*t*s}, p_{g+t+s}\}$	Study area, year, and gender effects with all interactions	Additive study area, year, and gender effects
$\{\phi_{g*t*s}, p_{g*t+s}\}$	Study area, year, and gender effects with all interactions	Study area and year effects with interactions and an additive gender effect
$\{\phi_{g*TT}, p_{g*t}\}$	Study area and quadratic time effect with interactions	Study area and year effects with interactions
$\{\phi_{Latitude}, p_{g*t}\}$	Latitude effect	Study area and year effects with interactions
$\{\phi_{SAB, Rest}, p_{g*t}\}$	Group effect of SAB study area versus other study areas	Study area and year effects with interactions
$\{\phi_{SAB, SKC, Rest}, p_{g*t}\}$	Group effect of SAB study area versus SKC study area versus other study areas	Study area and year effects with interactions
$\{\phi_{SKC, Rest}, p_{g*t}\}$	Group effect of SKC study area versus other study areas	Study area and year effects with interactions
$\{\phi_t, p_{g*t}\}$	Year effect	Study area and year effects with interactions
$\{\phi_T, p_{g*t}\}$	Linear time effect	Study area and year effects with interactions
$\{\phi_{TT}, p_{g*t}\}$	Quadratic time effect	Study area and year effects with interactions

arose, including (1) mis-specification of the SAS code used to run the models and (2) nonconvergence of some of the models because there were 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 fit models to the data for each study area (see Wolfinger 1993). First, we used restricted maximum likelihood estimation with model {age + T; fecundity = $\beta_0 + \beta_1$ (age) + β_2 (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. That 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). We selected the most appropriate covariance structure 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). We used this step 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 those models; the number of parameters in that 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. That failure to converge was because there were ≤3 subadults (first- and second-year subadult age-classes combined) for six, four, four, and eight 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 five 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.

Again, we did not compute a meta-analysis across the five study areas because of the difference in protocols used to estimate reproductive output in the field.

However, we made comparisons between the SIE and SKC study areas because those two 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 (λ) 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 a stage-structured projection matrix approach (Caswell 2000). The two types of λ differ in their definitions and interpretations, as well as in their methods of computation. Here, we present a brief discussion of those distinctions and differences.

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

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

where N_t is abundance at year *t*. In the case of the California Spotted Owl analysis, abundances and $\hat{\lambda}_t$ apply to subadult and adult territorial owls on the study areas. That 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 those fundamental demographic variables.

Variable $\hat{\lambda}_{PM}$ is computed from projection matrices parameterized with means of time-specific estimates, or constant-parameter model estimates, for stage-specific survival and fecundity for juvenile, subadult, and adult survival. The $\hat{\lambda}_{PM}$ resulting from those computations represents the asymptotic growth rate for a population exposed to the projection matrix vital rates year after year. That 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 efforts are made to adjust apparent survival estimates so that they better

approximate true survival (e.g. previous Spotted Owl analyses in Burnham et al. 1996, Franklin et al. 1999). Those efforts reduce the movement asymmetry and its effect on $\hat{\lambda}_{PM}$. However, those adjustments require additional information on emigration, such as information from radiomarked 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, values of fecundity may be positively biased if nonbreeding 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). That 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 that quantity).

There are several assumptions underlying estimation of λ_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 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 recaptured 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 λ_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

Cormack-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). That same bias also applies to estimates of λ_t. Hines and Nichols (2002) found that bias is positive in the presence of a trap-happy response and negative in the presence of trap-shy response. That bias is 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 λ_t are biased in the presence of heterogeneous capture probabilities among individuals or unidentified classes of individuals. Hines and Nichols (2002) show that heterogeneous capture probabilities do not bias estimates of λ_t when population growth rate is modeled as a single constant over all time periods. Small bias does occur when estimating time-specific λ_t. However, that bias was not as substantial a problem as that resulting from permanent trap response.

Violation of the first two assumptions do not produce bias, in that the estimator of λ_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 two conceptually distinct processes. The first process involves expansion of the study area and increase in number of animals exposed to sampling that result from that expansion. The second process involves changes in the number of animals on the sampled area; that is the change of interest and the one to which we would like estimates of λ_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 assumed no tag loss and no tag-induced mortality. Because we had no reason to suspect that those 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, we recaptured owls 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 did 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 did not permit substantial heterogeneity (i.e. 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 expected estimates of λ_t to be unbiased for changes in superpopulation size. However, nonrandom (e.g. Markovian) forms of temporary emigration could lead to biased estimates of λ_t, and we were 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 $\hat{\lambda}_{PM}$ had been phrased as "did the territorial owls on the study area replace themselves?" (Burnham et al. 1996, Franklin et al. 1999). However, that inference provided no information on where replacement owls might go with respect to study area boundaries. In other words, the inference applied 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, we rephrased that inference 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 phrased as "were the territorial owls on the study area being replaced?" (Franklin et al. 1999). That inference was about the owl populations residing within a specific study area. An advantage of λ_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 was avoided. However, a primary limitation of inferences concerning $\hat{\lambda}_t$ was that it was not possible to estimate the relative 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 sink populations), while also supplying recruits to other populations (behavior commonly attributed to source populations). 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 suffice 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 (see

below). 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 λ_t for each study area, we employed random effects models in MARK that used the $\hat{\lambda}_t$ from model $\{\phi_t,\ p_t,\ \lambda_t\}$ as the basis for the analysis. Model $\{\phi_t,\ p_t,\ \lambda_t\}$, which was used as the basis for the random-effects models, allowed ϕ, λ, and p to vary by year; none of the parameters were otherwise constrained. We considered the following random-effects models: linear trend in λ (T), quadratic trend in λ (TT), and mean λ across time (.). Those three models were considered with and without elimination of the first estimable λ_t because of potential biases due to trap response, perhaps exacerbated by a "learning curve" on the part of 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 that parameter. Prior to conducting the analysis on λ_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; 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 $\{\phi_{s*t},\ p_{s*t},\ \lambda_{s*t}\}$ for each study area, with an interaction between sex and year for ϕ, p, and λ.

To make the annual estimates of λ_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. $\Delta_t = N_t/N_x$ where x is the initial year). Therefore, realized change provided the estimated trajectory of the population over the time period for which λ_t was estimated, without requiring estimation of numbers of owls on each of the study areas. Realized change (Δ_t) was estimated as:

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

where x was the first estimated λ_t. For example, if λ_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 three 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 area using model $\phi_t,\ p_t,\ f_t$ in Program MARK. Using those 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 $p_x = \hat{p}_{x+1}$. That latter assumption was needed because we required an initial abundance for demographic simulations but were unable to estimate the initial capture probability. That particular solution (equating the first and second capture probabilities) seemed reasonable to us, although other solutions to that 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 $\phi_t,\ p_t,\ \lambda_t$ to compute estimates of λ_t and, from those, $\hat{\Delta}_t$. We ran 1,000 simulations; from that distribution of simulations, we computed 95% confidence intervals from the ith and jth 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 among those study areas. We considered fixed-effects models λ_t, λ_{g*t}, and λ_{g+t}, where g was study area and with ϕ and p structured as $g * t$ in all three models. We also considered λ_{g+t} without the first and second estimable λ_t; without the first, second, and last λ_t; without the first and last λ_t; and without the first λ_t. In the analysis of the individual study areas and the meta-analyses across the four study areas, we corrected for overdispersion, and we used the same model selection approach that was used to estimate adult survival.

Comparison of Sierra and Sequoia and Kings Canyon national parks study areas.—The SIE and SKC represented paired study areas where SIE had been managed for timber production and SKC had 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 two study areas, which allowed direct comparison of fecundity rates. We used effect sizes to compare the differences between the two study areas in terms of the three 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 goodness-of-fit for the global model was χ^2 = 184.74 with df = 167 (P = 0.165), indicating that the global model fit the capture–recapture data. The results of that

test yielded $\hat{c} = 1.11$. The minimum $QAIC_c$ model for p combined with the three models $\phi_{g^*t^*s}$, ϕ_{g^*t+s}, and ϕ_{g^*t} for apparent survival was p_{g^*t}. Model selection for all 41 models is shown in Table 3. On the basis of minimum $QAIC_c$, the best ϕ model containing separate survival parameters for all five study areas was $\{\phi_g,\ p_{g^*t}\}$, and the best overall model was $\{\phi_{SKC\ vs.\ rest},\ p_{g^*t}\}$ (Table 3). Estimates of apparent survival for the $\{\phi_g,\ p_{g^*t}\}$ model are shown in Table 4. Under model

$\{\phi_{SKC\ vs.\ rest},\ p_{g^*t}\}$, 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 to 0.835), whereas the separate estimate for SKC was $\hat{\phi} = 0.877$ (SE = 0.016, 95% CI = 0.842 to 0.905). Confidence intervals for the estimate from the four study areas combined and the estimate for SKC did not overlap. The two top-ranked models (Table 3) included separate estimates of ϕ for SKC; those two models comprised >86% of

TABLE 3. Model selection results from program MARK for apparent adult survival (ϕ) of male and female California Spotted Owls on five study areas in California.

Model	$QAIC_c$	$\Delta QAIC_c$	Akaike weights	Model likelihood	K	Deviance
$\{\phi_{SKC\ vs.\ rest},\ p_{g^*t}\}$	4034.313	0	0.617	1.000	48	1166.437
$\{\phi_{SAB,\ SKC,\ vs.\ rest},\ p_{g^*t}\}$	4036.144	1.831	0.247	0.400	49	1166.205
$\{\phi_g,\ p_{g^*t}\}$	4039.844	5.531	0.039	0.063	51	1165.775
$\{\phi,\ p_{g^*t}\}$	4041.059	6.746	0.021	0.034	47	1175.246
$\{\phi_{SAB\ vs.\ rest},\ p_{g^*t}\}$	4041.642	7.329	0.016	0.026	48	1173.767
$\{\phi_{g+T},\ p_{g^*t}\}$	4041.737	7.424	0.015	0.024	52	1165.600
$\{\phi_T,\ p_{g^*t}\}$	4042.137	7.824	0.012	0.020	48	1174.262
$\{\phi_{TT},\ p_{g^*t}\}$	4042.896	8.583	0.008	0.014	49	1172.958
$\{\phi_{Latitude},\ p_{g^*t}\}$	4043.038	8.725	0.008	0.013	48	1175.166
$\{\phi_{g+TT},\ p_{g^*t}\}$	4043.103	8.790	0.008	0.012	53	1164.898
$\{\phi_t,\ p_{g^*t}\}$	4044.186	9.873	0.004	0.008	55	1161.839
$\{\phi_{g+t},\ p_{g^*t}\}$	4044.808	10.495	0.003	0.005	59	1154.162
$\{\phi_{g^*T},\ p_{g^*t}\}$	4048.300	13.987	0.001	0.001	56	1163.880
$\{\phi_{g^*TT},\ p_{g^*t}\}$	4052.520	18.207	0.000	0.000	61	1157.717
$\{\phi_{g^*t},\ p_{(g+t)^*s}\}$	4080.515	46.202	0.000	0.000	73	1160.655
$\{\phi_{g^*t},\ p_{g+t}\}$	4081.083	46.770	0.000	0.000	63	1182.118
$\{\phi_{g^*t},\ p_{g^*t}\}$	4082.219	47.906	0.000	0.000	87	1132.878
$\{\phi_{g^*t},\ p_{g+t+s}\}$	4082.346	48.033	0.000	0.000	74	1181.297
$\{\phi_{g^*t+s},\ p_{(g+t)^*s}\}$	4082.397	48.084	0.000	0.000	74	1160.440
$\{\phi_{g^*t+s},\ p_{g+t}\}$	4082.796	48.483	0.000	0.000	64	1181.747
$\{\phi_{g^*t},\ p_{g^*t+s}\}$	4082.903	48.590	0.000	0.000	88	1131.446
$\{\phi_{g^*t+s},\ p_{g^*t}\}$	4083.877	49.564	0.000	0.000	88	1132.420
$\{\phi_{g^*t+s},\ p_{g+t+s}\}$	4083.917	49.604	0.000	0.000	65	1180.783
$\{\phi_{g^*t+s},\ p_{g^*t+s}\}$	4084.757	50.444	0.000	0.000	89	1131.182
$\{\phi_{g^*t},\ p_r\}$	4117.686	83.373	0.000	0.000	48	1249.812
$\{\phi_{g^*t},\ p_{r+s}\}$	4119.096	84.783	0.000	0.000	49	1249.158
$\{\phi_{g^*t^*s},\ p_{g+t}\}$	4119.334	85.021	0.000	0.000	101	1140.243
$\{\phi_{g^*t+s},\ p_r\}$	4119.343	85.030	0.000	0.000	49	1249.404
$\{\phi_{g^*t^*s},\ p_{g^*t}\}$	4119.54	85.227	0.000	0.000	124	1090.980
$\{\phi_{g^*t+s},\ p_{r+s}\}$	4120.62	86.307	0.000	0.000	50	1248.616
$\{\phi_{g^*t^*s},\ p_{g+t+s}\}$	4120.706	86.393	0.000	0.000	102	1139.480
$\{\phi_{g^*t^*s},\ p_{g^*t+s}\}$	4120.898	86.585	0.000	0.000	125	1090.170
$\{\phi_{g^*t},\ p_{r^*s}\}$	4121.059	86.746	0.000	0.000	50	1249.055
$\{\phi_{g^*t+s},\ p_{r^*s}\}$	4122.578	88.265	0.000	0.000	51	1248.509
$\{\phi_{g^*t^*s},\ p_{(g+t)^*s}\}$	4123.396	89.083	0.000	0.000	113	1118.588
$\{\phi_{g^*t},\ p_{g^*t^*s}\}$	4127.375	93.062	0.000	0.000	133	1079.253
$\{\phi_{g^*t+s},\ p_{g^*t^*s}\}$	4129.041	94.728	0.000	0.000	134	1078.739
$\{\phi_{g^*t^*s},\ p_r\}$	4166.548	132.235	0.000	0.000	91	1208.735
$\{\phi_{g^*t^*s},\ p_{r+s}\}$	4168.034	133.721	0.000	0.000	92	1208.100
$\{\phi_{g^*t^*s},\ p_{r^*s}\}$	4170.109	135.796	0.000	0.000	93	1208.051
$\{\phi_{g^*t^*s},\ p_{g^*t^*s}\}$	4177.529	143.216	0.000	0.000	174	1038.802

TABLE 4. Estimates of apparent adult survival from model $\{\phi_g, p_{g*t}\}$ for California Spotted Owls on five study areas in California.

Study area	$\hat{\phi}$	SE ($\hat{\phi}$)	95% CI
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

Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

the Akaike weights. The second-ranked model $\{\phi_{SAB,SKC\ vs.\ rest}, p_{g*t}\}$ suggested that both the SAB and SKC had separate estimates of ϕ from each other as well as from the other three study areas combined. However, that model had a nearly identical deviance to the top-ranked model and the $\Delta QAIC_c \approx 2$ was a result of adding another parameter for the SAB that did not explain any additional variation in the data; the top two models essentially explained the same amount of variation. Thus, we concluded that there was strong evidence for model $\{\phi_{SKC\ vs.\ rest}, p_{g*t}\}$. The annual recapture probabilities from model $\{\phi_{SKC\ vs.\ rest}, p_{g*t}\}$ were generally high, with 87% of the annual estimates >0.8 and 54% of the annual estimates >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 $\{\phi_g, p_{g*t}\}$, mean apparent survival across the study areas was estimated to be $\bar{\phi} =$ 0.831 (SE = 0.012), with a spatial process standard deviation $\hat{\sigma}_{spatial} = 0.0212$ (95% CI = 0.0000 to 0.0752) among the apparent survival estimates. Estimates of temporal variation in apparent survival were computed for each of the five study areas from model $\{\phi_{g*t}, p_{g*t}\}$ (Table 6). On the basis of coefficients of process variation (CV), both spatial process variation (CV = 0.025) and temporal variation (CVs = 0.011 to 0.033; Table 6) were relatively low.

FECUNDITY

We analyzed fecundity data from 1,557 reproductive outcomes for adult female Spotted Owls on all five 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, which suggests that a linear trend may be supported for that 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

TABLE 5. Estimates of annual recapture probabilities (p) for banded California Spotted Owls on five 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 (-------)

Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

TABLE 6. Estimates of mean apparent survival ($\bar{\phi}$) and temporal process standard deviation ($\hat{\sigma}_{temporal}$) in apparent survival for the California Spotted Owl on five study areas in California. Estimates were based on variance components analyses from annual estimates of $\hat{\phi}$ from model $\{\phi_{g*t}, p_{g*t}\}$.

Study area	$\bar{\phi}$	SE ($\bar{\phi}$)	$\hat{\sigma}_{temporal}$	$CV_{temporal}$[a]	95% CI $\hat{\sigma}_{temporal}$
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

[a] Estimated as: $\dfrac{\hat{\sigma}_{temporal}}{\bar{\phi}}$

Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

different from zero in the top-ranked models, based on 95% CI. 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, Fig. 2). The SAB study area had much lower annual variation

TABLE 7. Ranking and weighting of mixed models used to fit trends in adult fecundity for California Spotted Owls from five study areas in California.

Model	$-2\log_e\mathcal{L}$	K [a]	AIC_c	ΔAIC_c	Akaike weight
Eldorado study area (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
Lassen study area (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
San Bernardino study area (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
Sierra study area (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
Sequoia and Kings Canyon study area (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

[a] Number of estimable covariance and fixed-effect parameters.

[b] Number of reproductive outcomes for adult females.

Abbreviations: T = linear time trend, TT = quadratic time trend, EO = even–odd years, $T + EO$ = linear time trend with an additive even–odd year effect.

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 five study areas in California.

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

[a] Estimates 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.

Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

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

Study area	$\bar{b}$ [a]	SE	$\hat{\sigma}_{temporal}$ [b]	CV [c]	Percentage of 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]

[a] Mean estimate across years based on intercepts-only mixed model.
[b] Standard deviation of temporal process variation.

[c] Estimated as $\dfrac{\hat{\sigma}_{temporal}}{\bar{b}}$.

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

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

where $\hat{\sigma}^2_{residual}$ is the variation remaining from that explained by the selected model.
[e] Not applicable because selected model was an intercept-only model. Abbreviations: see Table 8.

TABLE 10. Descriptions of density study area portions of total study areas and time periods used to estimate λ_t for female and male territorial California Spotted Owls in California.

Study area	Study period	Approximate size (km²)
ELD	1990–2000	355
LAS	1992–2000	1,270
SAB	1991–1998	2,140
SIE	1990–2000	419
SKC	1991–2000	343

Abbreviations: see Table 8.

RATES OF POPULATION CHANGE

We used 1,019 marked subadult and adult individuals in the analysis of λ_t (144 from the ELD, 191 from the LAS, 401 from the SAB, 163 from the SIE, and 120 from the SKC). Those 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.—Study area sizes and time periods used in estimating λ_t are shown in Table 10. Overdispersion was evident in the data for all study areas except SKC (Table 11). We corrected for that in subsequent analyses. Two of the study areas, the ELD and SKC, had strong evidence for trends in λ_t. The lowest $QAIC_c$ model for the ELD suggested a linear trend in λ_t (Table 12, Fig. 3). The second-ranked model was also a linear trend model but with the first estimable λ_t eliminated. Together, those two models accounted for 70% of the Akaike weights. The estimated slope for the linear trend in λ_t on the ELD was negative and different from zero on the basis of 95% CI (Table 13). The best model for the SKC suggested a quadratic trend in λ_t with the first estimable λ_t eliminated (Table 12, Fig. 3). The second-ranked model was also a

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 those models were not very useful for explaining temporal variation in fecundity (Table 9, Fig. 2). Those 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 that trend still only explained 44% of the temporal process variation in fecundity.
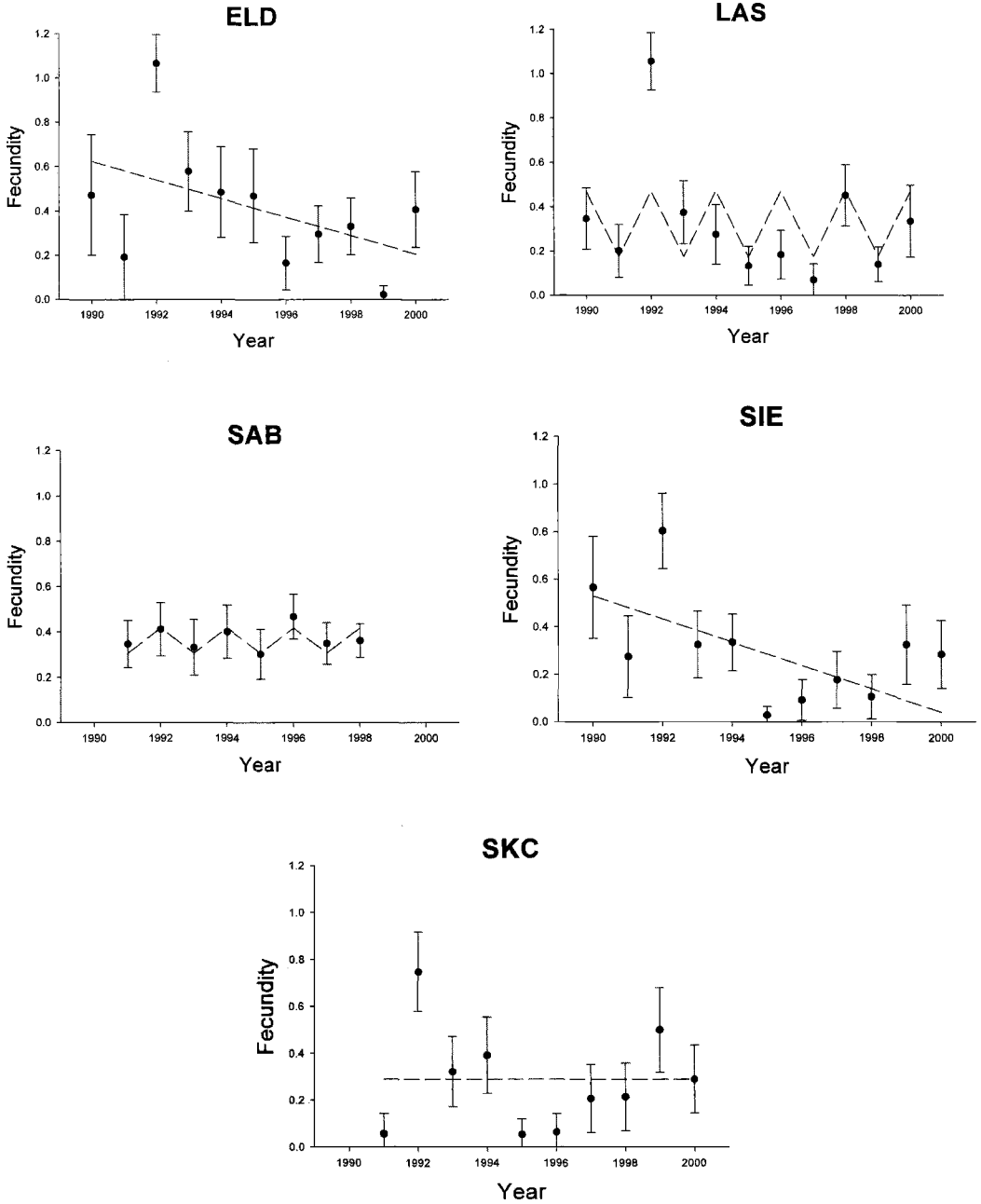
FIG. 2. Annual estimates of fecundity of California Spotted Owls on five study areas in California. Annual estimates (dots) and 95% confidence intervals (bars) are least-squares means from mixed intercept-only model, whereas dashed lines represent estimates from the top-ranked mixed trend model. Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

TABLE 11. Estimates of overdispersion ($\hat{c}$) for capture–recapture data sets used to estimate λ_t from five California Spotted Owl study areas in California. Values for chi-square (χ^2), degrees of freedom (df), and probability (P) are from TEST 2 and TEST 3 in program RELEASE.

Study area	χ^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]

[a] Set SKC to 1.0 for subsequent analyses.

Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

quadratic trend model but included the first estimable λ_t. Those two models accounted for 45.5% of the Akaike weights. Slope parameters for that quadratic trend were different from zero on the basis of 95% CI (Table 13). The best model for the SIE study area also suggested a negative linear trend in λ_t (Table 12, Fig. 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% CI barely overlapped 1.0. There was a weak negative linear trend for the SAB study area (Table 12, Fig. 3). However, there was uncertainty as to whether a linear or means model best explained the data because Akaike weights
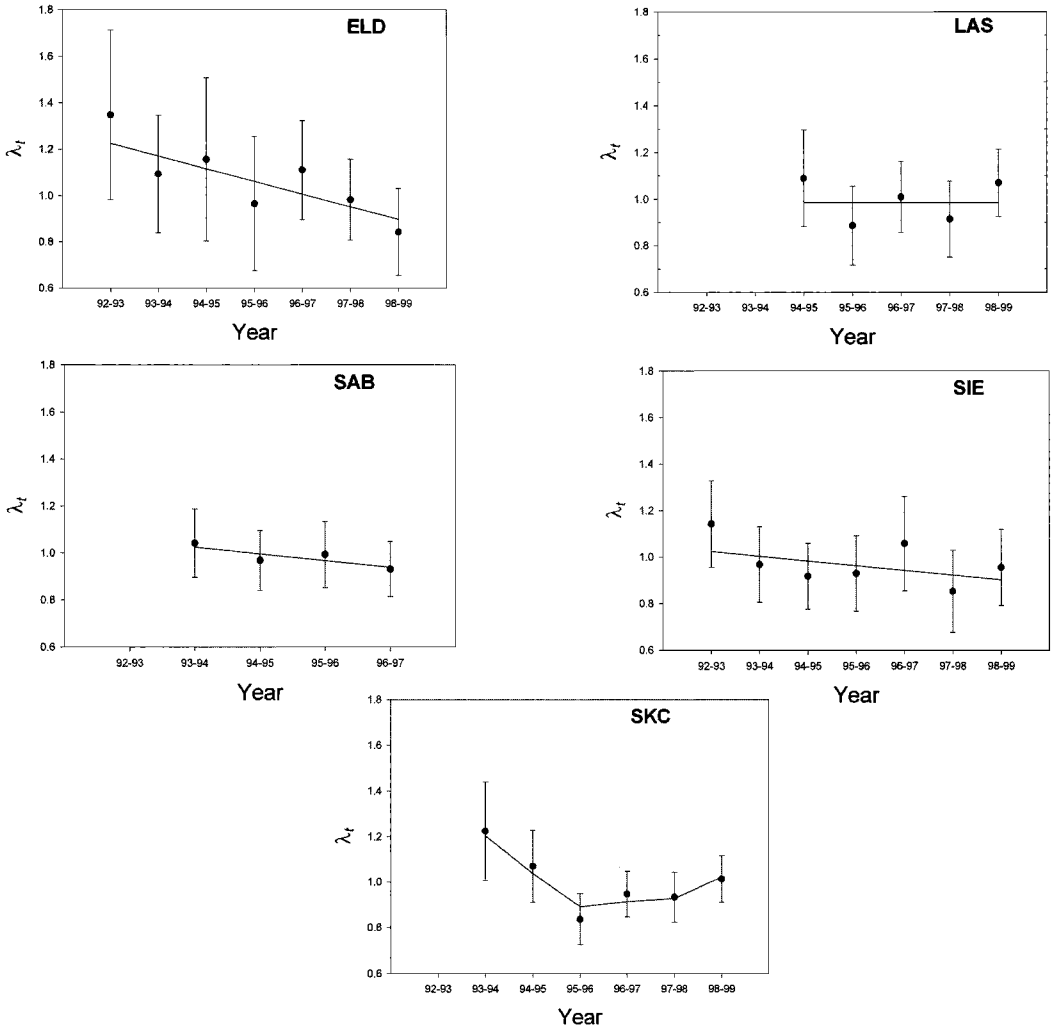
FIG. 3. Trends in λ_t for California Spotted Owls on five study areas in California. Trend lines are from random effects models selected by minimum QAIC$_c$. Dots, with 95% confidence intervals, are annual estimates of λ_t from model {ϕ_t, p_t, λ_t} used to develop the random effects models. Abbreviations: see Table 11.

TABLE 12. Model selection results from λ_t analyses for California Spotted Owls on five study areas in California.

Model	$QAIC_c$	K	Deviance	$\Delta QAIC_c$	Akaike weight
Eldorado study area (ELD)					
Linear random effects	1045.295	23.00	701.409	0.000	0.506
Linear random effects[a]	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[a]	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[a]	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 × sex fixed effects	1106.272	59.00	676.486	60.977	0.000
Lassen study area (LAS)					
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[a]	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[a]	1047.224	21.98	625.082	5.179	0.037
Quadratic random effects[a]	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 × sex fixed effects	1086.595	47.00	608.230	44.550	0.000
San Bernardino study area (SAB)					
Linear random effects	2243.999	16.00	1101.528	0.000	0.395
Mean random effects[a]	2245.078	16.00	1102.606	1.079	0.230
Linear random effects[a]	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[a]	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 × sex fixed effects	2280.433	40.00	1087.362	36.434	0.000
Sierra study area (SIE)					
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[a]	1046.215	24.00	679.230	1.949	0.135
Mean random effects[a]	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[a]	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 × sex fixed effects	1097.288	58.00	651.392	53.022	0.000
Sequoia and Kings Canyon study area (SKC)[b]					
Quadratic random effects[a]	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[a]	1008.258	25.09	619.859	1.725	0.110
Linear random effects[a]	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 × sex fixed effects	1042.473	52.00	591.471	35.940	0.000

[a] First estimable lambda from model $\{\phi_t, p_t, \lambda_t\}$ was omitted from random effects model.

[b] Estimates based on AIC_c rather than $QAIC_c$ because no overdispersion was evident.

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 λ_t for the LAS study area (Table 12, Fig. 3); a means model best supported the data for that area.

Estimates of realized change (Δ_t) represented the trajectory (or trend in numbers) of each study population (Fig. 4). Those estimates were based solely on the estimates of λ_t and did not require estimating annual population size (N_t)

TABLE 13. Parameter estimates for best random effects model of λ_t for California Spotted Owls on five study areas in California. Best models were selected using the lowest QAIC$_c$.

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

Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

for each study area. 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 λ_t and, hence, Δ_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, on the basis of 95% CI. The SIE population decreased steadily from 1993, resulting in a population that was substantially lower and different from the initial population, on the basis of 95% CI. In 1999, 70.9% of the SIE population remained from the initial population in 1993 (Fig. 4).

On the basis of a random effects intercepts-only model, using annual estimates of λ from model $\{\phi_t, p_t, \lambda_t\}$, 95% CI of the estimated mean λ ($\bar{\lambda}$) across years for each of the study areas was not different from a stationary population ($\lambda = 1$; Table 14, Fig. 5), although point estimates

were <1 for four of the study areas (LAS, SAB, SIE, and SKC). The SIE had the lowest estimate of $\bar{\lambda}$ with 95% CI that barely overlapped $\lambda = 1$, which suggests that the owl population on the SIE was declining. Temporal process variation in λ_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 λ_t for the ELD accounted for an estimated 100% of the temporal process variation in λ_t, and the model with the quadratic trend for the SKC accounted for 75.7% of the temporal process variation in λ_t, which suggests that those were useful models for explaining the temporal process variation in λ_t (Franklin et al. 2001).

Meta-analysis across study areas.—There was strong support for an additive study area effect over time (model λ_{g+t}; Table 15); model λ_{g+t} included an additive effect and was weighted much more heavily (99.4% of the Akaike weights) than models with a study area × year interaction, just a year effect, or just a study-area effect. That suggested λ_t changed similarly among the four Sierran study areas, even

TABLE 14. Estimates of mean λ_t ($\bar{\lambda}$) across time and temporal process standard deviation ($\hat{\sigma}_{temporal}$) for California Spotted Owls on five study areas in California. Estimates are based on means (intercept-only) random effects models using time-specific estimates of ϕ, p, and λ.

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

Abbreviations: see Table 13.
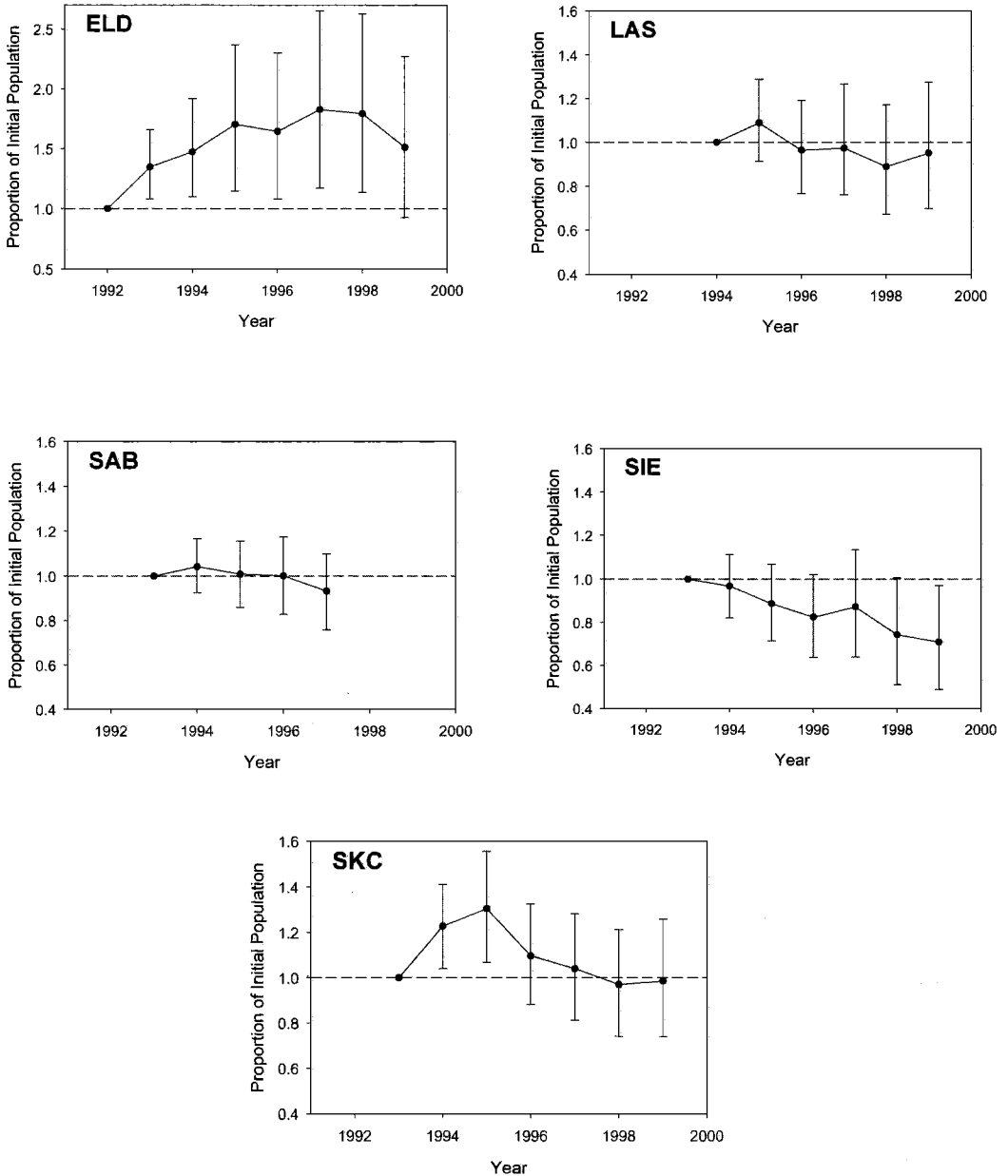
FIG. 4. Trends in populations of California Spotted Owls from five study areas in California. Trends are expressed as realized change (Δ_t) based on estimates of λ_t, which represent the proportion of the initial population remaining for each year. Bars around estimates are 95% confidence intervals. Note that the graph for the ELD study area is scaled differently than the other study areas. Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.
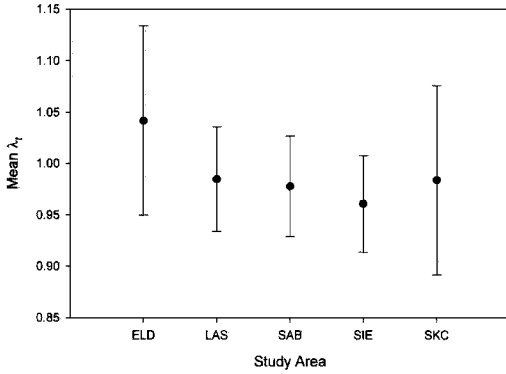
FIG. 5. Estimates of mean λ_t with 95% confidence intervals for California Spotted Owls on five study areas in California. Abbreviations: ELD = Eldorado study area, LAS = Lassen study area, SAB = San Bernardino study area, SIE = Sierra study area, and SKC = Sequoia and Kings Canyon national parks study area.

though there were differences in magnitude of the λ_t (Fig. 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 to 0.101) for the SKC, 0.083 (95% CI = –0.070 to 0.173) for the ELD, and 0.050 (95% CI = –0.031 to 0.132) for the LAS, which suggests that 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. On the basis of the results for the individual study areas, three 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 λ_t over time.
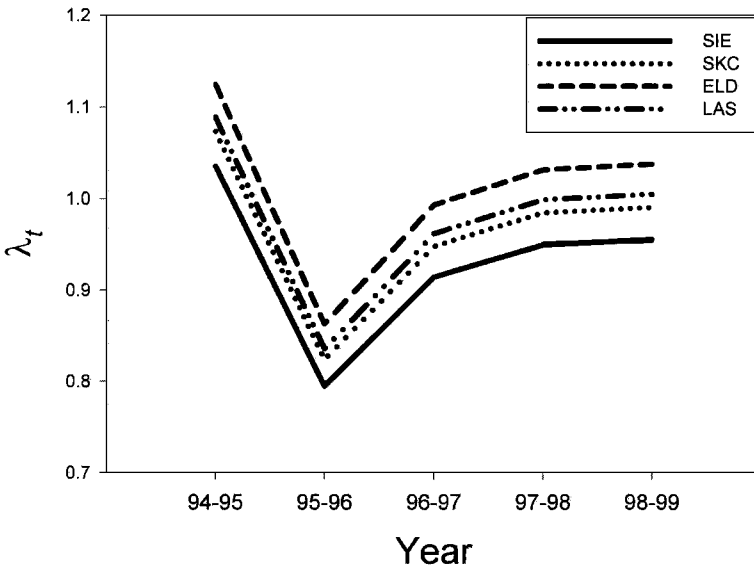
FIG. 6. Trends in λ_t based on model $\{\lambda_{g+t}\}$ from meta-analysis on California Spotted Owls from four study areas (ELD, LAS, SIE, and SKC) in the Sierra Nevada, California. Abbreviations: see Fig. 5.

TABLE 15. Model selection results (adjusted with $\hat{c}$ = 1.2739) for meta-analysis of λ_t for California Spotted Owls on four study areas (ELD, LAS, SIE, and SKC) in California.

Model	K	Deviance	AIC_c	ΔAIC_c	Akaike weight
$\phi_{g*t},\ p_{g*t},\ \lambda_{g+t}$	73	3660.86	6446.29	0.00	0.994
$\phi_{g*t},\ p_{g*t},\ \lambda_t$	75	3666.81	6456.39	10.10	0.006
$\phi_{g*t},\ p_{g*t},\ \lambda_{g*t}$	92	3641.71	6466.67	20.38	0.000
$\phi_{g*t},\ p_{g*t},\ \lambda_g$	72	3707.72	6491.08	44.79	0.000
$\phi_g,\ p_g,\ \lambda_g$	12	4087.45	6748.38	302.09	0.000

Abbreviations: see Fig. 5.

Using the estimates from model $\{\phi_{g*t}, p_{g*t}, \lambda_{g*t}\}$, 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 to 1.005) for the SIE, 0.958 (95% CI = 0.866 to 1.049) for the SKC, 1.001 (95% CI = 0.913 to 1.090) for the ELD, and 0.985 (95% CI = 0.927 to 1.042) for the LAS.

COMPARISON OF SIERRA AND SEQUOIA AND KINGS CANYON NATIONAL PARKS STUDY AREAS

On the basis of the 95% CI for the effect sizes, only adult survival was different between the two study areas (95% CI for the difference did not overlap zero) with SKC having higher adult survival than SIE (Table 16). However, point estimates for adult fecundity and $\bar{\lambda}$ were also higher for the SKC than for the SIE study area. In addition, population trends in the two 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. That resulted in a decline in the population on the SIE but not on the SKC (Fig. 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 two decades (Gutiérrez et al. 1995).

In general, population studies of California Spotted Owls began later than those of 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 began in 1986 in the central Sierra Nevada 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 and 1992 on Mount San Jacinto, southern California (Gutiérrez and Pritchard 1990). That latter study was terminated because of 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 and Kings Canyon national parks, SKC).

Our studies were well suited to a meta-analysis because the techniques were very similar among studies. Our ability to detect the owls with vocal lures and color band them facilitated a strong mark–recapture study design. However, Milligan et al. (2003) suggested that observers misread band combinations, with 5% and 16% error rates for trained and untrained observers, respectively. We did not believe such high error rates pertained to our studies for several reasons. First, part of the high error rate observed by Milligan et al. (2003) was from switching color combinations between left and right legs. In our study, birds carried color bands on only one leg; the other leg was

TABLE 16. Comparison of effects in demographic parameters for California Spotted Owls between the Sierra study area (SIE) and Sequoia and Kings Canyon national parks study area (SKC) 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 to 0.209
Adult survival[d]	0.877	0.016	0.818	0.017	0.059	0.023	0.013 to 0.105
$\bar{\lambda}$ [e]	0.984	0.047	0.961	0.024	0.023	0.053	−0.080 to 0.126

[a] (Estimate for SKC) – (estimate for SIE).

[b] $\sqrt{\widehat{SE}^2_{SKC} + \widehat{SE}^2_{SIE}}$

[c] Estimates from Table 9.

[d] Estimates from Table 4.

[e] Estimates from Table 14.

banded with an aluminum federal band. Color combinations were unique to each bird. Second, nonexistent color combinations that might have erroneously been observed could be corrected to the appropriate combination, or else discarded and the bird re-observed to obtain the correct combination. Finally, the geographic location of an observation often uniquely identified the band combination, in contrast to the Milligan et al. (2003) protocol, where multiple birds were observed at the same location. For example, if observers, upon returning from the field in our study, noted that a bird with an unexpected band combination was recorded in a territory, other observers would return to confirm that observation. Although it was possible that mistaken band identifications occurred in our studies, we do not believe that the error rate was nearly as high as that reported by Milligan et al. (2003). Further, the high resighting probabilities and survival rates estimated in our study suggested that the effect of an erroneous identification was not of major consequence in the Cormack-Jolly-Seber models. That is, mistakenly labelling bird A as bird B means that bird B will get a 1 in its encounter history, and bird A will be recorded as not being observed. With the high resighting probability, bird B will likely be observed anyway, given that it is alive, which is also likely because of the high survival rate. However, frequent occurrences of that scenario would have lowered the estimated resighting probability. The high resighting probabilities we reported here suggest that the hypothesized scenario of mistaken band identifications occurred infrequently.

Although the study areas covered a large latitudinal gradient, results of our meta-analysis cannot be considered representative of owl demographic trends throughout the Sierra Nevada. If, at the inception of those 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 that question. If initial placement of the demography studies was based on a history of owl occupancy (i.e. they were not randomly located), then the

conditions on the study areas may have been different from those on the surrounding areas (i.e. study areas were of higher quality 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, those population studies did 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, Mexico (Gutiérrez et al. 1995) Nevertheless, the extant population studies spanned a major latitudinal gradient over the range of that subspecies. Each of the five study areas had unique characteristics that capture much of the inherent environmental variation within the California Spotted Owl range.

Therefore, in the following discussion, we first present a set of general inferences regarding population characteristics and trends for the California Spotted Owl populations represented in our meta-analysis. Those 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 ϕ 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 for Northern and Mexican spotted owls. Average adult apparent survival estimates across all three subspecies of Spotted Owl ranged from 0.8 to 0.9 (Gutiérrez et al. 1995).

In our meta-analysis, temporal variation in adult apparent survival on all study areas was very low (CV = 0–3%). That inference was expected for an animal 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 have accounted for most of the temporal variability in Spotted Owl survival. However, because our data did not support time-based apparent survival models and because temporal process variation in apparent survival was very low, we suspected 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 other study areas. The four study areas with similar apparent survival were on national forests (i.e. managed for multiple use) whereas the SKC was in national parks (i.e. managed as a preserve). Therefore, differences in forest management were 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 one sequoia grove on the SIE and one on the RSA of the ELD. It was possible that those groves promoted higher survival of Spotted Owls compared to other conifer forest types. If those

groves promoted higher survival, the causative mechanism was unknown.

An important biological issue with open capture–recapture models is that mortality and emigration are confounded (Schwarz and Seber 1999). Therefore, those 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 those 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 believed we could safely 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 owls (Seamans et al. 2002), it was 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, whereas all other years were either moderately successful or poor reproductive years. That 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 those trends (e.g. correlation of fecundity and weather patterns).

San Bernardino study area 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%) than the Sierra Nevada study areas. Weather patterns appeared to have a strong link to owl fecundity in the SAB (W. S. LaHaye et al. unpubl. data). 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 <1.0 except for the ELD. However, 95% CI 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. That latter point was important because point estimates for four of the five study areas indicated annual population declines of 2–4%, but the estimates were not sufficiently precise to differentiate those estimates from stationary populations. That inference was similar to one

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 That 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 four Sierra Nevada studies may have been responsible for driving those 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 number of new recruits entering the territorial population in 1993. If juvenile survival was ~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, high estimates of λ_t in the interval 1992–1993 (and subsequent years) may have resulted from the increased recruitment from that cohort. If density increased because owls occupied lower-quality habitats, a decline would be expected because of lower vital rates of owls in the less productive habitats subsequent to that breeding pulse. That 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. That 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% CI 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 Nevada 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 those time frames are not appropriate. Estimates of λ_t also should not be interpreted as numbers of birds; those are annual estimates of rates of change in the number of birds. For example, periodic estimates of λ_t that are <1.0 in the SIE and LAS study areas represent a decrease in the number of birds. Intervening values >1.0 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 numbers in the preceding year. Thus, a cyclic pattern in λ_t can exist that ultimately results in losses of birds over time. However, that 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, on the basis of estimates of λ_t. On the basis of those 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 that 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 that bias by using estimates of emigration rates derived from studies of radiomarked juvenile Spotted Owls (Forsman et al. 1996). Following Northern Spotted Owl meta-analysis (Burnham et al. 1996), researchers on the ELD proposed a study of juvenile survival using radiotelemetry. 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). That approach was unsatisfactory because the conditions on the SAB were not similar to those on the ELD, SIE, and SKC. Consequently, an alternative approach was to examine the juvenile survival rate needed to achieve an estimate of $\lambda = 1.0$, 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 of 153) was substantially less than in other studies, which suggests that either the dispersal pattern for that 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 did not use λ_{PM} for the meta-analysis of owl trends.

Summary of general results.—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 suggested that variation in λ_t will likely result from variation in recruitment (e.g. the boom reproductive year and the hypothesized subsequent lag effect in λ_t, described above).

All of the study areas in our analyses demonstrated similar patterns in vital rates, with two main exceptions: (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 those 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 demographic differences among the SAB, SKC, and other study areas was unknown.

We attempted to address three possible scenarios with our 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 λ_t, and no evidence of a trend in fecundity. At the opposite end of that spectrum was the SIE study, which had the lowest estimate of $\bar{\lambda}$, low adult apparent survival, and declining trends in both λ_t and fecundity. The ELD and LAS studies were between those 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. Those analyses indicated that four of the study populations (ELD, LAS, SAB, and SKC) appeared to be stationary or slightly declining The SIE owl population probably experienced a decline during the period of study. Evidence that the SIE population declined included (1) a linear decline in fecundity, (2) a 95% CI on $\hat{\lambda}_t$ that barely encompassed 1, and (3) a linear decline in $\hat{\lambda}_t$ that suggests an accelerated decline in the owl population, which was best illustrated with the realized change estimates. Our results supported the third scenario, that Spotted Owls declined within a portion of the studies and appeared stationary in some of the studies. Thus, there was uncertainty across all studies whether California Spotted Owls were declining or were stationary. For example, point estimates of $\hat{\lambda}_t$ for four out of five study areas were <1.0 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 will be needed to resolve those uncertainties.

STUDY-AREA-SPECIFIC INFERENCES

Lassen study area.—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).

TABLE 17. Summary of estimates and trends in population parameters for California Spotted Owls from five 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

[a] Not different than $\lambda = 1.0$ (see Fig. 5).
[b] Considered different than $\lambda = 1.0$ (see Fig. 5).
Abbreviations: SKC = Sequoia and Kings Canyon national parks study area, LAS = Lassen study area, ELD = Eldorado study area, SIE = Sierra study area, SAB = San Bernardino study area.

Our estimate of 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). Our higher fecundity estimate resulted from 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 diameter at breast height (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 that 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. Forces driving that 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 (J. A. Blakesley pers. obs.). 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. That weak downward trend may have been an artifact of the extremely high reproductive year occurring in year 3 of the 11-year study.

Our estimated population trend for LAS 1994–1999 using λ_t was higher than that estimated for 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, that implied that the population of owls in the LAS was being sustained by immigration or that the population declined more steeply from 1990 to 1994 than from 1994 to 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 methods used to estimate rates of population change, and in the inferences to be drawn from the two methods (discussed above), the discrepancy in λ estimates may have resulted from the following factor. Because the

smaller LAS study area was designated *post hoc* during this analysis (i.e. to be comparable to the other studies in the meta-analysis, contiguous segments of LAS were chosen that 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 that 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 λ_t.

Eldorado study area.—Seamans et al. (2001b) reported that from 1990 to 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 of both sexes followed a log-linear pattern over time. Here, 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 those 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. That 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.

Our current estimate of mean fecundity was similar to that from a previous published estimate for the ELD ($\hat{b}$ = 0.400, SE = 0.010; Seamans et al. 2001b). Although a negative linear decline best fit the data, this model explained only 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 λ_t ($\bar{\lambda}$ = 1.042, SE = 0.047; this study) was higher than that estimated for 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 those two estimates of λ, they indicated different population trajectories; λ_t a stable or increasing population, and λ_{PM} a declining population. It was unlikely that 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 λ_{PM} assumes constant vital rates over the study period), or, that one or both were biased (see above).

We do not know if the negative linear trend in λ_t, and the point estimates of λ_t < 1.0 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 λ_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. 2002). Thus, factors that exhibited temporal variability, such as weather and prey availability, may have been responsible for the observed variation in λ_t.

Changes in habitat quality on the ELD may also have affected λ_t and were of greater concern because they may have long-term effects on vital rates. Two apparent 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 six owl territories. Although the Cleveland Fire was adjacent to the ELD in what would later become part of the Regional Study Area, that 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). That pattern was a relic of land allocation to the Central Pacific Railroad in the late 1800s (Beesley 1996). Most of that 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 because of 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; that is, 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.

Sierra and Sequoia and Kings Canyon national parks study areas. — Adult apparent survival may have been different between the SIE and SKC because of natural or management-induced differences in vegetation. We propose three hypotheses that could relate differences in vegetation to differences in apparent survival between the study areas: (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 woodlands, whereas 21% (8 of 39) on the SKC were in that 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 above). 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 ≥50% canopy cover on the SIE.

Changes in vegetation resulting from timber management may have lowered adult survival in the SIE. Timber harvest on the SIE began in the late 1800s (Johnston 1968) 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 our study, there were at least 11 timber sales within SIE, several of them 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, ~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 ~80% of SKC from commercial logging activities. By the end of 1940, only two small areas totaling <8 km² were not under National 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 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; ~3,724 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); actual burn dates are 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 ~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), had different objectives, and have been used as a management tool for a 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. Those 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. That may have resulted from variation in prey abundance, weather conditions, habitat quality, or all three during that 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, 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.

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, 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, 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.

San Bernardino study area.—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, those owl populations were relatively isolated from one another, and intermountain movements (i.e. inter-population movements) were rare (LaHaye et al. 2001). That 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 was 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 because of 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. 2002) spotted owl populations. Southern California was at the southern margin of the polar front jet stream (Minnich 1986). Therefore, winter storms, which provided most of the annual precipitation in the San Bernardino Mountains (Minnich 1986), occurred less frequently and tended to be of shorter duration than storms 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 (W. S. LaHaye and R. J. Gutiérrez pers. obs.) Thus, our fecundity estimates may have been biased high. That 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 have expected to see more unbanded recruits to the territorial population).

Although estimates of population change based on λ_{PM} contained an unknown amount of bias in many Spotted Owl studies, λ_{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 λ_{PM} from the SAB study area, using all 12 years of data, was significantly less than 1.0 ($\bar{\lambda} = 0.91$, SE = 0.01, LaHaye et al. 1999). The different population trajectories indicated by λ_{PM} from LaHaye et al. (1999) and λ_t in this meta-analysis may have been due to (1) a decline in the SAB population between 1988 and 1992 that was not captured by estimation of λ_t in our meta-analysis; (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 λ_{PM}; or (4) a violation of the assumption of constant vital

rates during the study period when estimating λ_{PM}. Regardless, concern may still be warranted for that 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 λ_t was <1.0, and (3) the model for λ_t indicated a negative linear trend.

CONCLUSION 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 is most likely attributable to weather or prey availability. That 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 did all the Sierra studies. The role habitat played in the above is unclear. Therefore, we were unable to ascribe a causative effect on estimates of apparent survival or fecundity to land management without incorporating habitat, management, or both covariates in the anaysis.

Although four of the five study areas had point estimates of $\lambda_t < 1.0$, there was uncertainty regarding the trajectory of those 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. That was of concern because survival of territorial owls may establish the baseline for λ; whereas other population parameters, such as fecundity and recruitment, may be responsible for most of the temporal variability in λ (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 that event. If California Spotted Owl population dynamics were largely driven by such events, then continued monitoring of those populations will be necessary to capture those 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 those reasons, we believed that the currently ongoing studies should be continued and the SAB study should be reinstated. The SAB was unique among those 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.

Our 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, those 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 five study areas work closely together to develop more consistent protocols for conducting surveys and estimating reproductive output in the field. In that way, more meaningful comparisons could be made in future analyses. In general, we feel that the following short-term recommendations would clarify the results from our initial meta-analysis of the data:

- Analyze those 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 that 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.

- Encourage the refinement of estimation models using λ_t that have particular application to those 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 outlined an interim plan for the 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 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:

- Develop comprehensive, accurate vegetation maps on the demographic study areas 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 those activities on demographic parameters.

- Design landscape-scale experiments to assess the effects of silvicultural treatments designed to reduce fire risks and the owl's response to controlled logging and silvicultural treatments.

Thus, we recommend that those study populations continue to be monitored because (1) uncertainties exist in interpreting λ_t with respect to source and sink population dynamics, (2) most of the point estimates of λ_t were <1.0, (3) apparent survival rates on four study areas were relatively low compared to those for 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 λ_t, such as local recruitment from outside immigration (Nichols and Hines 2002), and those should be used in conjunction with continued data collection on all of the study areas.

In summary, analyses we present in this meta-analysis represent the best available data on demography of the California Spotted Owl. Therefore, they will be essential for conservation planning. Indeed, the California Spotted Owl was petitioned to be listed as an endangered species under the ESA. The USFWS issued a 12-month finding on 14 February 2003, not to list the owl (USDI 2003). We believe it is important that such conservation assessments on the status of the owl be based on all the relevant data. We also believe that all the demographic evidence available—such as estimated vital rates, rates of population change, and differences between paired studies —suggest substantial caution in owl conservation and management efforts.

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, vol. II, Assessments and Scientific Basis for Management Options. Centers for Water and Wildland Resources, University of California, Davis.

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. Ph.D. dissertation, Colorado State University, Fort Collins.

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 Acta XIX Congressus Internationalis Ornithologici (H. O. Ouellet, Ed.). National Museum of Natural Science, Ottawa, Ontario.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model Selection and Inference: A Practical Information Theoretic Approach. Springer, New York.

BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph, no. 5.

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, 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

CAUGHLEY, G. 1977. Analysis of Vertebrate Populations. John 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., AND W. C. TWEED. 1990. Challenge of the Big Trees: A Resource History of Sequoia and Kings Canyon National Parks. Sequoia Natural History Association, Three Rivers, California.

EVANS, M., N. HASTINGS, AND B. PEACOCK. 1993. Statistical Distributions, 2nd ed. J. Wiley and Sons, New York.

FEDERAL ADVISORY COMMITTEE. 1997. Final Report of the California Spotted Owl Federal Advisory Committee. U.S. Department of 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. Department of Agriculture, Forest Service General Technical Report PNW-GTR-162.

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, no. 149.

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, no. 87.

FRANKLIN, A. B. 2002. Exploring ecological relationships in survival and estimating rates of population change using program MARK. Pages 290–296 in Wildlife, Land, and People: Priorities for the 21st Century (R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, Eds.). Wildlife Society, Bethesda, Maryland.

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., 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. U.S. Fish and Wildlife Service unpublished report, Portland, Oregon.

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.

FRANKLIN, A. B., AND T. M. SHENK. 1995. Meta-analysis as a tool for monitoring wildlife populations. Pages 484–487 in Integrating People and Wildlife for a Sustainable Future (J. A. Bissonette and P. R. Krausman, Eds.). 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 Modeling in Natural Resource Management: Development, Interpretation, and Application (T. M. Shenk and A. B. Franklin, Eds.). Island Press, Washington, D.C.

FUJIOKA, F. M., J. O. ROADS, AND S.-C. CHEN. 1998. Climatology. Pages 28–43 in Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains (P. R. Miller and J. R. McBride, Eds.). Springer, New York.

GAILLARD, J.-M., M. F.-B. BIANCHET, AND N. G. YOCCOZ. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

GAILLARD, J.-M., M. F.-B. BIANCHET, N. G. YOCCOZ, A. LOISON, AND C. TOÏGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

GUTIÉRREZ, R. J., 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.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

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.

HINES, J. E., AND J. D. NICHOLS. 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture–recapture data. Journal of Applied Statistics 29:573–588.

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 Predicting Species Occurrences: Issues of Accuracy and Scale (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, Eds.). Island Press, Washington, D.C.

HUNTER, J. E., AND F. L. SCHMIDT. 1990. Methods of Meta-analysis: Correcting Error and Bias in Research Findings. Sage Publications, Beverly Hills, California.

JOHNSTON, H. 1968. Thunder in the Mountains. Trans-Anglo Books, Los Angeles.

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, 2nd ed. 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. Pages 909–938 in Terrestrial Vegetation of California (M. G. Barbour and J. Major, Eds.). John Wiley and Sons, New York.

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 J. R. DUNK. 2001. Natal dispersal of the Spotted Owl in southern California: Dispersal profile of an insular population. Condor 103:691–700.

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. Department of Agriculture, Forest Service, Vallejo, California.

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 The California Spotted Owl: A Technical Assessment of Its Current Status (J. Verner, K. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-133.

McKELVEY, K. S., C. N. SKINNER, C. CHANG, D. C. ERMAN, S. J. HUSARI, D. J. PARSONS, J. W. VAN WAGTENDONK, AND C. P. WEATHERSPOON. 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.

MILLER, P. R., M. J. ARBAUGH, AND P. J. TEMPLE. 1997. Ozone and its known and potential ef-

fects on forests in the western United States. Pages 39–68 *in* Forest Decline and Ozone: A Comparison of Controlled Chamber and Field Experiments (H. Sandermann, A. R. Wellburn, and R. L. Heath, Eds.). Ecological Studies, vol. 134, Springer, Berlin.

MILLIGAN, J. L., A. K. DAVIS, AND S. M. ALTIZER. 2003. Errors associated with using colored leg bands to identify wild birds. Journal of Field Ornithology 74:111–118.

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 Press, Berkeley.

MINNICH, R. A. 1998. Vegetation, fire regimes, and forest dynamics. Pages 44–80 *in* Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains (P. R. Miller and J. R. McBride, Eds.). 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 61:1281–1287.

MOONEY, H. A. 1988. Southern coastal scrub. Pages 471–490 *in* Terrestrial Vegetation of California, 2nd ed. (M. G. Barbour and J. Major, Eds.). California Native Plant Society, Sacramento.

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 λ and demographic contributions to λ, 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.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 1998. Climatological Data Annual Summary California, vol. 102, no. 13. U.S. National Oceanic and Atmospheric Administration, Asheville, North Carolina.

NATIONAL   OCEANIC   AND   ATMOSPHERIC

ADMINISTRATION (NOAA). 1999. Climatological Data Annual Summary California, vol. 103, no. 13. U.S. National Oceanic and Atmospheric Administration, Asheville, North Carolina.

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* The California Spotted Owl: A Technical Assessment of Its Current Status (J. Verner, K. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-133.

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* The California Spotted Owl: A Technical Assessment of Its Current Status (J. Verner, K. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-133.

NORTH, M., G. N. STEGER, R. DENTON, G. EBERLEIN, T. MUNTON, AND K. JOHNSON. 2000. Association of weather and nest-site structure with reproductive success in California Spotted Owls. Journal of Wildlife Management 64:797–807.

OLSON, 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. Centers for Water and Wildland Resources, University of California, Davis.

PARSONS, D. J. 1994. Objects or ecosystems? Giant sequoia management in the national parks. Pages 109–115 *in* Proceedings of the Symposium on the Giant Sequoias: Their Place in the Ecosystem and Society (P. S. Aune, Ed.). U.S. Department of Agriculture, Forest Service, General Technical Report PSW-GTR-151.

PFISTER, C. A. 1998. Patterns of variation in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Science USA 95:213–218.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs, no. 107.

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.

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 Bernardinos: The Mountain Country from Cajon Pass to Oak Glen, Two Centuries of Changing Use. Big Santa Anita Historical Society, Arcadia, California.

ROMBOUT, P. J. A., J. A. M. A. DORMANS, L. VAN BREE, AND M. MARRA. 1991. Structural and biochemical effects 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 Terrestrial Vegetation of California (M. G. Barbour and J. Major, Eds.). John Wiley and Sons, New York.

SAKAMOTO, Y., M. ISHIGURO, AND G. KITAGAWA. 1986. Akaike Information Criterion Statistics. KTK Scientific Publishers, Dordrecht, The Netherlands.

SAS INSTITUTE. 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 Terrestrial Vegetation of California, 2nd ed. (M. G. Barbour and J. Major, Eds.). California Native Plant Society, Sacramento.

SCHOEN, R. 1988. Modeling Multigroup Populations. Plenum Press, New York.

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. Estimating animal abundance: Review III. Statistical Science 14:427–456.

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, no. 123.

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. U.S. Department of Agriculture, Forest Service, unpublished report, Region 5, Contract No. #53-91S8-6, Vallejo, California.

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.

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.

SEBER, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters. Charles Griffin, London.

SIERRA NEVADA ECOSYSTEM PROJECT (SNEP). 1996. Status of the Sierra Nevada: Assessment Summaries and Management Strategies, vol. 1. University of California, Davis.

SIMMONS, R. E. 1996. Population declines, viable breeding areas, and management options for flamingos in southern 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 re-captured 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. U.S. Department of Agriculture, Forest Service,

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. U.S. Department of Agriculture, Forest Service, U.S. Department of Interior, Bureau of Land Management, Fish and Wildlife Service, and National Park Service. U. S. Government Printing Office 791-171/20026, Washington, D.C.

THOMAS, J. W., M. G. RAPHAEL, R. G. ANTHONY, E. D. FORSMAN, A. G. GUNDERSON, R. S. HOLTHAUSEN, B. G. MARCOT, G. H. REEVES, J. R SEDELL, AND D. M. SOLIS. 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, Portland, Oregon.

THORNE, R. F. 1988. Montane and subalpine forests of the transverse and peninsular ranges. Pages 537–558 in Terrestrial Vegetation of California, 2nd ed. (M. G. Barbour and J. Major, Eds.). California Native Plant Society, Sacramento, California.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 1993. California Spotted Owl Sierran Province interim guidelines environmental assessment, decision notice, and findings of no significant impact. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, San Francisco, California.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 1995. Draft environmental impact statement: Managing California Spotted Owl habitat in the Sierra Nevada national forests of California, an ecosystem approach. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, San Francisco, California.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 1996. Revised draft environmental impact statement: Managing California Spotted Owl habitat in the Sierra Nevada national forests of California, an ecosystem approach. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, San Francisco, California.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 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. U.S. Department of Agriculture,

Forest Service, Pacific Southwest Region, Sacramento, California

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 1998b. Sierra Nevada framework for conservation and collaboration: Summary of existing management direction, report of the Forest Service Interdisciplinary Analysis Team. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Sacramento, California.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 2001a. Sierra Nevada Forest Plan Amendment Final Environmental Impact Statement, vols. 1–6. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Sacramento, California.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE (USDA). 2001b. Sierra Nevada Forest Plan Amendment Final Environmental Impact Statement: Record of Decision. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Sacramento, California.

U.S. DEPARTMENT OF INTERIOR (USDI). 1992. Final draft recovery plan for the Northern Spotted Owl. U.S. Department of Interior, Washington, D.C.

U.S. DEPARTMENT OF INTERIOR (USDI). 2003. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the California Spotted Owl (Strix occidentalis occidentalis). Federal Register 68:7580–7608.

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 Terrestrial Vegetation of California, 2nd ed. (M. G. Barbour and J. Major, Eds.). California Native Plant Society, Sacramento, California.

VERNER, J., AND A. S. BOSS. 1980. California wildlife and their habitats: Western Sierra Nevada. U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-37.

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. Department of Agriculture, Forest Service General Technical Report PSW-GTR-133.

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 The California Spotted Owl: A Technical Assessment of its Current Status (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-133.

WAGNER, F. F., E. C. MESLOW, G. M. BENNET, C. J. LARSON, S. M. SMALL, AND S. 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? American Midland Naturalist 128:150–154.

WHITE, G. C. 2000. Population viability analysis: Data requirements and essential analyses. Pages 288–331 in Research Techniques in Animal Ecology: Controversies and Consequences (L. Boitani and T. K. Fuller, Eds.). Columbia University Press, 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 Integrating People and Wildlife for a Sustainable Future (R. Fields, Ed.). Wildlife Society, Bethesda, Maryland.

Wolf, F. M. 1986. Meta-analysis: Quantitative Methods for Research Synthesis. Sage Publications, Beverly Hills, California.

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.

APPENDIX 1. Variation in survey methods among California Spotted Owl studies.

	LAS	ELD	SIE & SKC	SAB
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 less than one-quarter mile apart on ≥2 occasions separated by ≥7 days or same owls from the previous year observed at the site.	Owl(s) heard in locations less than one-quarter mile apart on ≥2 occasions.
Criteria for reproductive determination	Nonreproduction inferred if any of the following observed on two occasions ≥1 week apart: (1) female owl roosted for ≥60 min before 1 May; (2) owl ate or cached (or both) four mice; (3) owl ate or cached (or both) ≥2 mice and refused another; (4) female observed in hand without brood patch from 15 April to 30 June (only one observation required).	Nonreproduction inferred if: (1) owl took ≥2 mice and cached one without taking to young; (2) one owl ate ≥3 mice; or (3) one owl ate two mice and ignored third.	Nonreproduction inferred if: (1) female roosted for ≥30 min on at least two visits before 01 June; (2) one 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) female determined to be single social status (six complete surveys of site, no mate detected).	Nonreproduction inferred if: (1) female roosted for ≥45 min on at least one 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).

Abbreviations: LAS = Lassen study area, ELD = Eldorado study area, SIE = Sierra study area, SKC = Sequoia and Kings Canyon national parks study area, and SAB = San Bernardino study area.

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 A1):
   a. San Bernardino Mountains (SAB)
   b. Sierra (SIE) National Forest
   c. Sequoia and 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. Those 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 case for SKC) and frequency was converted from –1 to 1.
   c. One capture history for Barred Owl (*Strix varia*) × Spotted Owl hybrid on LAS was deleted.
   d. Expansion of study area on ELD—Birds that emigrated into regional before expansion area was surveyed and then were found. Solution was to keep those records and, hence, ignore that source of individual heterogeneity in p values 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 frequency = 1 was split into 1010000 with frequency = –1 and 0011101 with frequency = 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 do not meet the protocol for each study area. Ignore July 15 cutoff on SIE and SKC because that was not used on other study areas.
   d. Records of resident birds with unknown social status were not included in the SIE and 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 five 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 values separate from S1, S2, or A age-classes.
         2. Using $\{\phi(a * s * t)\}$, find best p value from the following set:
            a. For juveniles, consider the four models J., J3, JA, or JAA, and pick the best juvenile model, holding the non-juveniles as a dot model—total of four models.
            b. For nonjuveniles, consider the four models dot, sex (s), reproductive rate covariate (= r), or $r * s$, plus a model of choice based on previous experience,

TABLE A1. Summary of data collection for the five study areas.

Characteristic	SAB	SIE	SKC	ELD	LAS
Time period total[a]	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	89D↑	94↑97↓D	97↓D	97↑T	–
Unusual circumstances	91	Migration	–	97	–
Method consistency	91–98	90–00	91–00	90–00	90–00
Density area (km²)	2140	419	343	355	1450
Study area (km²)	2140	686	343	925	2200
Survey period (month)	April–August	March–September	March–September	April–August	April–August

[a] Time period total = Total time period when demography study was conducted.

Abbreviations: SAB = San Bernardino study area, SIE = Sierra study area, SKC = Sequoia and Kings Canyon national parks study area, ELD = Eldorado study area, and LAS = Lassen study area.

using the best juvenile model from step (a) above—total of four 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 three $QAIC_c$ units of the best model from step (3) and run them with no time effect on juvenile ϕ.

5. Run the best 2–3 ϕ models from steps (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 on the basis of male and female groups (with S1, S2, and A pooled across each sex with the juvenile portion of CHs removed). Implication is that $\hat{c}$ may be high.

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

1. $\{\phi(g * t * s) \, p(g * t * s)\}$ global model.

2. The following ϕ models are to be estimated against the nine p models in step (4) below:

    $\phi(g * t * s)$
    $\phi(g * t + s)$
    $\phi(g * t)$
    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 ϕ:

    $\phi(g)$
    $\phi(g + t)$
    $\phi(g * T)$
    $\phi(g + T)$
    $\phi(g * TT)$

    $\phi(g + TT)$
    $\phi(t)$
    $\phi(TT)$
    $\phi(T)$
    $\phi(.)$
    ϕ(Latitude) with best group effect model from above 6
    ϕ(SAB, Rest) with best group effect model from above 6
    ϕ(SKC, Rest) with best group effect model from above 6
    ϕ(SAB, SKC, Rest) with best group effect model from above 6
    ϕ(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 those two models will be made using AIC model selection with REML in an 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. Ten models to run for each study area.

iv. λ from Pradel model.
   1. Truncate data sets to first year when "density" study area adequately surveyed.
   2. Select either $\{\lambda(t)\ \phi(t)\ p(t)\}$ or $\{\lambda(s * t)\ \phi(s * t)\ p(s * t)\}$ based on AIC_c.
   3. Eliminate λ_1 (confounded), λ_2 (may be biased), and λ_{k-1} (confounded) from analysis.
   4. Do variance components on best model above with the following structures, and select the best of those three with AIC_c:
      a. T
      b. TT
      c. dot
   5. Total of five models run for each study area.
   6. Goodness of fit determined with RELEASE.

v. λ from Leslie matrix.
   1. Use 4-age class projection matrices for all study areas.
   2. Estimate age-specific ϕ 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 ($E_{J|\lambda=1}$) and adult ($E_{A|\lambda=1}$) emigration rates necessary to achieve a stationary population ($\lambda = 1.0$).
   4. Calculate juvenile ($\phi_{J|\lambda=1}$) and adult ($\phi_{A|\lambda=1}$) survival rates necessary to achieve a stationary population ($\lambda = 1.0$).
   5. Estimate SE(λ) using delta method.
   6. If unable to estimate juvenile survival for a given study area, then won't attempt to estimate λ.

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 λ_{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 five 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 ($\hat{\sigma}^2_{temporal}$).
   i. Within each study area.
      1. Estimate $\hat{\sigma}^2_{temporal}$ for adult apparent survival (ϕ_A) from random effects means model in MARK using estimates from model $\{\phi(a * s * t)\ p(a * s * t)\}$ if there is a sex effect and $\{\phi(a * t)\ p(a * t)\}$ if there is no sex effect.
      2. Estimate $\hat{\sigma}^2_{temporal}$ for juvenile apparent survival (ϕ_J) from random effects means model in MARK using estimates from model $\{\phi(a * s * t)\ p(a * s * t)\}$ if there is a sex effect and $\{\phi(a * t)\ p(a * t)\}$ if there is no sex effect.
      3. Estimate $\hat{\sigma}^2_{temporal}$ for λ_{RJS} from random effects means model in MARK using estimates from model $\{\lambda(t), \phi(t),\ p(t)\}$.
      4. Estimate $\hat{\sigma}^2_{temporal}$ for adult fecundity (b_A) from intercepts-only model in PROC MIXED in SAS.
      5. Do not estimate $\hat{\sigma}^2_{temporal}$ for ϕ_{S1}, ϕ_{S2}, b_{S1}, or b_{S2} because of known sample size limitations.

c. Spatial process variation ($\hat{\sigma}^2_{spatial}$).
   1. Within each study area.
      a. Estimate $\hat{\sigma}^2_{spatial}$ for b_A based on territories (owl sites).
   2. Among study areas.
      a. Estimate $\hat{\sigma}^2_{spatial}$ for adult apparent survival (ϕ_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 $\hat{\sigma}^2_{spatial}$ for juvenile apparent survival (ϕ_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 $\hat{\sigma}^2_{spatial}$ for λ_{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 $\hat{\sigma}^2_{spatial}$ for ϕ_{S1}, ϕ_{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 ϕ over time represent 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 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. λ_{RJS} represents change in number of territorial owls.

        i. $\hat{\sigma}$ provides information on probability of change over a specified time period, given $\hat{\sigma}$ under conditions of study.

        ii. Change based on λ_{RJS} can be due to local birth, immigration, death, emigration, or both.

    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 compiling 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 U.S. Forest Service).

                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.

FURTHER DISCUSSION OF PROJECTION MATRIX
POPULATION MODELS

During the workshop, the group debated the utility of developing projection matrices and computing asymptotic λ_{PM}. Subsequent reviews of the draft workshop report also raised that issue, so we present here our reasoning for not estimating λ_{PM} more completely. A central theme of our internal discussions and the reviews was that λ_t 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_t 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, because 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 those open systems.

During both internal workshop discussion and external reviews, it was noted that computation of λ_t 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 those 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 those relaxed definitions reflect a conceptual framework that may not be especially useful when considering open systems such as those of Spotted Owls at the spatial scale of study. Indeed, we believe that at least four of the five 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 those four study areas represent sinks in the sense that many if not most birds recruited to the breeding population come from elsewhere and are not produced on the study areas. Thus, the source–sink dichotomy does not seem to be especially useful for describing that 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 are not produced on the study area. In that 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 that metric may provide insights about the relevance of movement to population dynamics that cannot be obtained using λ_t. We do not believe that that 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, that work was not completed at the workshop, so we have no such estimates at this time.

Thus, 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 here and in other Spotted Owl reports, that 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 on the basis of 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 were based on closed-population modeling, assuming that all surviving individuals produced in the population exhibited 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. see 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 those 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 those systems. However, we disagree with reviewers that that 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 those open systems. More importantly, we view that 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.

ORNITHOLOGICAL MONOGRAPHS

(Continued from back cover)

No. 35. *Ecogeographical Variation in Size and Proportions of Song Sparrows (Melospiza melodia).* J. W. Aldrich. x + 134 pp. 1984. $15.00 ($12.00).

No. 37. *Avian Monogamy.* P. A. Gowaty and D. W. Mock, Eds. vi + 121 pp. 1985. $15.00 ($12.00).

No. 38. *An Analysis of Physical, Physiological, and Optical Aspects of Avian Coloration with Emphasis on Wood-Warblers.* E. H. Burtt, Jr. x + 122 pp. 1986. $15.00 ($12.50).

No. 39. *The Lingual Apparatus of the African Grey Parrot, Psittacus erithacus Linne (Aves: Psittacidae): Description and Theoretical Mechanical Analysis.* D. G. Homberger. xii + 236 pp. 1986. $30.00.

No. 40. *Patterns and Evolutionary Significance of Geographic Variation in the Schistacea Group of the Fox Sparrow (Passerella iliaca).* R. M. Zink. viii + 119 pp. 1986. $15.00.

No. 41. *Hindlimb Myology and Evolution of Old World Suboscine Passerine Birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae).* R. J. Raikow. viii + 81 pp. 1987. $15.00.

No. 42. *Speciation and Geographic Variation in Black-tailed Gnatcatchers.* J. L. Atwood. vii + 74 pp. 1988. $10.00.

No. 43. *A Distributional Survey of the Birds of the Mexican State of Oaxaca.* L. C. Binford. viii + 418 pp. 1989. $20.00.

No. 44. *Recent Advances in the Study of Neogene Fossil Birds: I. The Birds of the Late Miocene-Early Pliocene Big Sandy Formation, Mohave County, Arizona* (K. J. Bichart); *II. Fossil Birds of the San Diego Formation, Late Pliocene, Blancan, San Diego County, California* (R. M. Chandler). vi + 161 pp. 1990. $20.00.

Nos. 45 & 46. *Descriptions of Thirty-two New Species of Birds from the Hawaiian Islands: Part I. Non-Passeriformes* (S. L. Olson and H. F. James), 88 pp.; *Part II. Passeriformes* (H. F. James and S.. L. Olson), 88 pp. 1991. Bound together (not available separately). $25.00 ($22.50).

No. 47. *Parent-Offspring Conflict and Its Resolution in the European Starling.* E. Litovich and H. W. Power. 71 pp. 1992. $15.00 ($12.00).

No. 48. *Studies in Neotropical Ornithology Honoring Ted Parker.* J. V. Remsen Jr., Ed. xiv + 918 pp. 1997. $49.95 ($39.95).

No. 49. *Avian Reproductive Tactics: Female and Male Perspectives.* P. G. Parker and N. T. Burley, Eds. v + 195 pp. 1998. $20.00 ($16.00).

No. 50. *Avian Community, Climate, and Sea-Level Changes in the Plio-Pleistocene of the Florida Peninsula.* S. D. Emslie. iii + 113 pp. 1998. $20.00 ($16.00).

No. 51. *A Descriptive and Phylogenetic Analysis of Plumulaceous Feather Characters in Charadriiformes.* C. J. Dove. iii + 163 pp. 2000. $19.95 ($15.96).

No. 52. *Ornithology of Sabah: History, Gazetteer, Annotated Checklist, and Bibliography.* F. H. Sheldon, R. G. Moyle, and J. Kennard. vi + 285 pp. 2001. $25.00 ($22.50).

No. 53 *Evolution of Flightlessness in Rails (Gruiformes: Rallidae): Phylogenetic, Ecomorphological, and Ontogenetic Perspectives.* B. C. Livezey. x + 654 pp. 2003. $10.00 ($9.00).

ORNITHOLOGICAL MONOGRAPHS