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Population Dynamics of Spotted Owls in the Sierra Nevada, California

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ABSTRACT The California spotted owl (*Strix occidentalis occidentalis*) is the only spotted owl subspecies not listed as threatened or endangered under the United States Endangered Species Act despite petitions to list it as threatened. We conducted a meta-analysis of population data for 4 populations in the southern Cascades and Sierra Nevada, California, USA, from 1990 to 2005 to assist a listing evaluation by the United States Fish and Wildlife Service. Our study areas (from N to S) were on the Lassen National Forest (LAS), Eldorado National Forest (ELD), Sierra National Forest (SIE), and Sequoia and Kings Canyon National Parks (SKC). These study areas represented a broad spectrum of habitat and management conditions in these mountain ranges.

We estimated apparent survival probability, reproductive output, and rate of population change for spotted owls on individual study areas and for all study areas combined (meta-analysis) using model selection or model-averaging based on maximum-likelihood estimation. We followed a formal protocol to conduct this analysis that was similar to other spotted owl meta-analyses. Consistency of field and analytical methods among our studies reduced confounding methodological effects when evaluating results. We used 991 marked spotted owls in the analysis of apparent survival. Apparent survival probability was higher for adult than for subadult owls. There was little difference in apparent survival between male and female owls. Model-averaged mean estimates of apparent survival probability of adult owls varied from 0.811 ± 0.021 for females at LAS to 0.890 ± 0.016 for males at SKC. Apparent survival increased over time for owls of all age classes at LAS and SIE, for adults at ELD, and for second-year subadults and adults at SKC. The meta-analysis of apparent survival, which included only adult owls, confirmed an increasing trend in survival over time. Survival rates were higher for owls on SKC than on the other study areas.

We analyzed data from 1,865 observations of reproductive outcomes for female spotted owls. The proportion of subadult females among all territorial females of known age ranged from 0.00 to 0.25 among study areas and years. The proportion of subadults among female spotted owls was negatively related to reproductive output (no. of young fledged/territorial F owl) for ELD and SIE. Eldorado study area and LAS showed an alternate-year trend in reproductive output, with higher output in even-numbered years. Mean annual reproductive output was 0.988 ± 0.154 for ELD, 0.624 ± 0.140 for LAS, 0.478 ± 0.106 for SIE, and 0.555 ± 0.110 for SKC. Eldorado Study Area exhibited a declining trend and the greatest variation in reproductive output over time, whereas SIE and SKC, which had the lowest reproductive output, had the lowest temporal variation. Meta-analysis confirmed that reproductive output varied among study areas. Reproductive output was highest for adults, followed by second-year subadults, and then by first-year subadults.

We used 842 marked subadult and adult owls to estimate population rate of change. Modeling indicated that λ_t (λ_t is the finite rate of population change estimated using the reparameterized Jolly–Seber estimator [Pradel 1996]) was either stationary (LAS and SIE) or increasing after an initial decrease (ELD and SKC). Mean estimated λ_t for the 4 study areas was 1.007 (95% CI = 0.952–1.066) for ELD; 0.973 (95% CI = 0.946–1.001) for LAS; 0.992 (95% CI = 0.966–1.018) for SIE; and 1.006 (95% CI = 0.947–1.068) for SKC. The best meta-analysis model of population trend indicated that λ varied across time but was similar in trend among the study areas. Our estimates of realized population change (Δ_t; Franklin et al. 2004), which we estimated as the product $1 \times \hat{\lambda}_3 \times \hat{\lambda}_4 \times \ldots \times \hat{\lambda}_{k-1}$, were based on estimates of λ_t from individual study areas and did not require estimating annual population size for each study area. Trends represented the proportion of the population size in the first year that remained in each subsequent year. Similar to $\hat{\lambda}_t$ on which they were based, these $\hat{\Delta}_t$ showed evidence of decline over the study period for LAS and SIE. The best model indicated recruitment of male and female adult and subadults varied from 0.10 to 0.31 new territorial individuals at time t/number of territorial individuals at time $t - 1$ and similarly among areas. We also conducted a population viability analysis (PVA) based on results of our meta-analysis. This PVA was of limited utility for ELD and SKC study areas because 95% confidence intervals on the probability of decline or increase spanned the interval [0, 1] within 5–10 years. When we restricted inferences to 7 years,

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estimated probability of a >10% decline for SIE was 0.41 (95% CI = 0.09–0.78); for LAS the probability was 0.64 (95% CI = 0.27–0.94). In contrast, estimated probability of a >10% increase in 7 years for SIE was 0.23 (95% CI = 0.01–0.55) and for LAS was 0.10 (95% CI = 0.00–0.34). For comparisons, we simulated a PVA for a hypothetical population with mean $\lambda = 1.0$ and the same temporal variation as observed in our owl populations. Our PVA suggested that both the SIE and LAS populations had higher probabilities of declining in a 7-year period than increasing but that it would be difficult to determine if a population was in a slight gradual decline. Our analysis and the repository of information on our 4 study populations provide a data-rich template for managers to monitor impacts of future management actions on the owl. Specifically, our data can be used to evaluate the effect of management strategies on spotted owls that are being implemented by the United States Forest Service to reduce the risk of wildfire in the Sierra Nevada ecosystem. Our information also provides baseline information for evaluating the status of the owl for potential listing as a threatened species by the United States Fish and Wildlife Service.

KEY WORDS annual rate of population change, California spotted owl, meta-analysis, population dynamics, reproductive output, Sierra Nevada, *Strix occidentalis occidentalis*, survival rates.

RESUMEN El búho californiano manchado (*Strix occidentalis occidentalis*) es la única subespecie de búhos manchados que no está listada como amenazada o en peligro de extinción en el Acta de E.E.U.U. para las Especies en Peligro de Extinción a pesar de las peticiones para que sea incluida en la lista como una especie amenazada. Nosotros realizamos un meta-análisis de los datos de la población de 4 poblaciones del sur de Cascades y de la Sierra Nevada, California desde 1990 hasta 2005 como ayuda a una evaluación de listado hecha por el U.S Fish and Wildlife Service. Nuestras áreas de estudio (de norte a sur) estuvieron localizadas en el Bosque Nacional Lassen (LAS), en el Bosque Nacional Eldorado (ELD), en el Bosque Nacional Sierra (SIE) y en los Parques Nacionales Sequoia y Kings Canyon (SKC). Estas áreas de estudio representaron un amplio espectro del hábitat y de las condiciones de manejo en estas cadenas de montañas.

Nosotros calculamos la probabilidad de supervivencia aparente, el volumen de reproducción y el cambio en la tasa de población de los búhos manchados en áreas de estudio individuales y para todas las áreas de estudio combinadas (meta-análisis) utilizando selección de modelos o promediando modelos basados en la estimación de máxima probabilidad. Seguimos un protocolo formal para realizar este análisis que fuera similar a otros meta-análisis con búhos manchados. La consistencia del campo y los métodos analíticos en nuestros estudios redujeron la confusión de efectos metodológicos al evaluar los resultados. Utilizamos 991 búhos manchados marcados en el análisis de supervivencia aparente. La probabilidad de supervivencia aparente fue más alta para búhos adultos que para subadultos. Hubo poca diferencia en la supervivencia aparente entre hembras y machos. Para los modelos promediados, los cálculos de la media de la probabilidad de supervivencia aparente para búhos adultos tuvo una variación de 0.811 ± 0.021 para hembras en LAS a 0.890 ± 0.016 para machos en SKA. La supervivencia aparente aumentó con el tiempo para los búhos de todos los grupos de edad en LAS y SIE, para adultos en ELD, y para subadultos del segundo año y para adultos en SKC. El meta-análisis de supervivencia aparente, que incluyó únicamente a búhos adultos, confirmó una tendencia al aumento en la supervivencia con el tiempo. Las tasas de supervivencia fueron más altas para los búhos en SKC que en las otras áreas de estudio.

Analizamos información de 1.865 observaciones de resultados de reproducciones para búhos manchados hembra. La proporción de hembras subadultas entre todas las hembras territoriales de edad conocida fluctuó de 0.00 a 0.25 a través de las áreas de estudio y de los años. La proporción de subadultos entre los búhos manchados hembra estuvo relacionada negativamente con el volumen de reproducción (número de pichones emplumados por búho hembra territorial) para ELD y SIE. ELD y LAS mostraron una tendencia anual alternada en el volumen de reproducción, con un volumen mayor en los años pares. La media del volumen de reproducción anual fue 0.988 ± 0.154 para ELD, 0.624 ± 0.140 para LAS, 0.478 ± 0.106 para SIE y 0.555 ± 0.154 para SKC. ELD exhibió una tendencia a disminuir y la variación más alta en el volumen de reproducción a través del tiempo; mientras que SIE y SKC, que tuvieron el más bajo volumen de reproducción, tuvieron la menor variación temporal. El meta-análisis confirmó que el volumen de reproducción varió entre las áreas de estudio. El volumen de reproducción fue más alto para adultos, seguido por subadultos del segundo año, y luego por subadultos del primer año.

Nosotros utilizamos 842 búhos marcados, adultos y subadultos, para calcular el índice de cambio de la población. La selección de modelos indicó que λ_t era, o relativamente fija (LAS y SIE) o aumentaba después de una disminución inicial (ELD y SKC). La media calculada λ_t para las cuatro áreas de estudio fue: 1.007 (95% CI = 0.952–1.066) para ELD; 0.973 (95% CI = 0.946–1.001) para LAS; 0.992 (95% CI = 0.966–1.018) para SIE; y 1.006 (95% CI = 0.947–1.068) para SKC. El mejor modelo de meta-análisis de la tendencia de población indicó que λ variaba con el tiempo pero que era una tendencia similar entre las áreas de estudio. Nuestros cálculos sobre el cambio de población realizado (Δ_t) se basaron en los cálculos de λ_t de las áreas de estudio individuales y no requirieron calcular el tamaño de la población anual para cada área de estudio. Las tendencias representaron la proporción del tamaño de la población en el primer año que permaneció en cada año subsiguiente. De manera similar a $\hat{\lambda}_t$, en la que se basaron, éstas $\hat{\Delta}_t$ mostraron evidencia de disminución durante el período de estudio para LAS y SIE. El mejor modelo de reclutamiento indicado, el reclutamiento de búhos machos y hembras, adultos y subadultos, varió de 0.10 a 0.31 individuos territoriales nuevos al tiempo t por el número de individuos territoriales al tiempo $t - 1$ y de manera similar entre las otras áreas. También realizamos un análisis de viabilidad de población (PVA) basado en los resultados de nuestro meta-análisis. Este análisis PVA fue de limitada utilidad para las áreas de estudio ELD y SKC porque el 95% de intervalos de confiabilidad en la probabilidad de disminución o aumento extendió el intervalo [0, 1] de 5–10 años. Cuando restringimos las inferencias a 7 años, la probabilidad estimada de a >10% de disminución para SIE fue 0.41 (95% CI = 0.09–0.78); para LAS la probabilidad fue 0.64 (95% CI = 0.27–0.94). En contraste, la probabilidad estimada de un >10% de aumento en 7 años para SIE fue 0.23 (95% CI = 0.01–0.55) y para LAS fue 0.10 (95% CI = 0.00–0.34). Para comparar, simulamos un PVA para una población hipotética con una media $\lambda = 1.0$, y con la misma variación temporal observada en nuestras poblaciones de búhos. Nuestro PVA sugirió que ambas poblaciones SIE y LAS tenían, en un período de 7 años, mayores probabilidades de disminución que de aumento, pero que sería muy difícil determinar si alguna de las poblaciones estaba en una ligera disminución gradual. El depósito de información de nuestras 4 áreas de estudio provee una plantilla rica en información para que los administradores monitoreen los impactos de acciones futuras en el manejo de los búhos (por ejemplo, nuevas estrategias de manejo del Plan de Sierra Nevada Forest). También provee evidencia importante para evaluar el estatus del búho para su potencial inclusión en el listado de especies amenazadas.

RÉSUMÉ Le hibou tacheté californien (*Strix occidentalis occidentalis*) est la seule sous-espèce de hibou tacheté ne figurant pas sur la liste des animaux menacés ou vulnérables sous la Loi des Espèces en Danger des Etats-Unis malgré des pétitions pour l'inscrire sur cette liste en tant que sous-espèce menacée. Nous avons effectué une méta-analyse des données de population pour 4 populations dans le sud des Cascades et dans la Sierra Nevada, en Californie de 1990 à 2005 pour aider une évaluation de leur statut établie par les Services des Eaux et Forêts des Etats-Unis. Nos aires d'étude (du nord au sud) étaient dans la forêt nationale Lassen (LAS), la forêt nationale Eldorado (ELD), la forêt nationale Sierra (SIE), et les parcs nationaux Sequoia et Kings Canyon (SKC). Ces aires d'étude représentaient un large échantillon des conditions de l'habitat et de la gestion dans ces chaînes de montagnes.

Nous avons estimé la probabilité de survie apparente, le succès de reproduction, et le taux de changement de la population pour les hiboux tachetés dans chaque aire d'étude individuelle et dans toutes les aires réunies (méta-analyse) en utilisant la sélection de modèles ou le calcul de la moyenne des modèles basé sur une estimation du maximum de vraisemblance. Pour effectuer cette analyse nous avons suivi un protocole rigoureux similaire à d'autres méta-analyses de hiboux tachetés. La cohérence des observations de terrain et des méthodes analytiques entre ces études a réduit les effets méthodologiques confondants lors des évaluations des résultats. Nous avons utilisé 991 hiboux tachetés marqués dans l'analyse de survie apparente. La probabilité de survie apparente a été plus élevée pour les hiboux adultes que pour les sous-adultes. Il y a eu peu de différence pour ce qui est de la survie apparente entre les hiboux mâles et femelles. La moyenne des estimations de la probabilité de survie apparente des hiboux adultes basée sur la moyenne des modèles a varié entre 0,811 ± 0,021 pour les hiboux femelles à LAS et 0,890 ± 0,016 pour les hiboux mâles à SKC. La survie apparente a augmenté avec le temps pour les hiboux de toutes les classes d'âge à LAS et SIE, pour les adultes à ELD, et pour les sous-adultes de deux ans et les adultes à SKC. La méta-analyse de survie apparente, qui comprenait seulement des hiboux adultes, a confirmé une tendance croissante de survie avec le temps. Les taux de survie étaient plus élevés pour les hiboux de SKC que pour ceux des autres aires d'étude.

Nous avons analysé les données obtenues à partir de 1 865 observations de succès de reproduction de hiboux tachetées femelles. La proportion des hiboux femelles sous-adultes parmi toutes les femelles territoriales d'âge connu a varié de 0,00 à 0,25 selon les aires et les années d'étude. La proportion des sous-adultes parmi les hiboux tachetés femelles a été négativement corrélée avec le succès de reproduction (nombre de jeunes hiboux par femelle territoriale) pour ELD et SIE. La forêt nationale Eldorado et la forêt nationale Lassen ont montré une tendance à alterner selon un cycle biennal pour ce qui est du succès de reproduction, avec un taux plus élevé pendant les années paires. La moyenne du succès de reproduction annuel était de 0,988 ± 0,154 pour ELD, de 0,624 ± 0,140 pour LAS, de 0,478 ± 0,106 pour SIE, et de 0,555 ± 0,110 pour SKD. La forêt nationale Eldorado a montré une tendance décroissante ainsi que la plus grande variation dans le succès de reproduction avec le temps, alors que SIE et SKC, qui ont eu le succès de reproduction le plus bas, ont connu la variation temporelle la plus basse. La méta-analyse a confirmé que le succès de reproduction variait selon les aires d'étude. Le succès de reproduction a été le plus élevé pour les adultes, puis pour les sous-adultes de deux ans, et ensuite pour les sous-adultes d'un an.

Nous avons utilisé 842 hiboux marqués, adultes et sous-adultes, pour estimer le taux de changement de la population. La modélisation a indiqué que λ_t était soit stationnaire (LAS et SIE), soit croissant après une baisse initiale (ELD et SKC). La moyenne estimée λ_t pour les 4 aires d'étude était: 1,007 (95% IC = 0,952–1,066) pour ELD; 0,973 (95% IC = 0,946–1,001) pour LAS; 0,992 (95% IC = 0,966–1,018) pour SIE; et 1,006 (95% IC = 0,947–1,068) pour SKC. Le meilleur modèle de méta-analyse pour la tendance de la population a indiqué que λ variait selon le temps mais suivait la même tendance selon les aires d'étude. Nos estimations du changement de population réalisé (Δ_t) étaient fondées sur les estimations de λ_t des aires d'étude individuelles et n'ont pas nécessité d'estimation de la taille annuelle de la population pour chaque aire d'étude. Les tendances représentaient la proportion de la taille de la population pendant la première année qui s'est maintenue chaque année subséquente. De même que $\hat{\lambda}_t$ sur lesquels ils étaient fondés, ces $\hat{\Delta}_t$ ont apporté des preuves de déclin pendant la période d'étude pour LAS et SIE. Le meilleur modèle a indiqué que le recrutement des hiboux adultes et sous-adultes mâles et femelles variait de 0,10 à 0,31 nouveaux individus territoriaux à un temps t pour un nombre d'individus territoriaux à un temps t-1 et qu'il en était de même dans chaque aire. Nous avons également procédé à une analyse de viabilité de la population (AVP) fondée sur les résultats de notre méta-analyse. Cette AVP a été d'une utilité limitée pour les aires d'étude ELD et SKC parce que les intervalles de confiance de 95% sur la probabilité du déclin ou de la croissance couvraient l'intervalle [0,1] sur une période de 5 à 10 ans. Lorsque nous avons réduit les inférences à 7 ans, la probabilité estimée d'un déclin >10% pour SIE était de 0,41 (95% IC = 0,09–0,78); pour LAS la probabilité était de 0,64 (95% IC = 0,27–0,94). A l'opposé, la probabilité estimée d'une croissance >10% en 7 ans pour SIE était de 0,23 (95% IC = 0,01–0,55) et pour LAS elle était de 0,10 (95% IC = 0,00–0,34). Afin de comparer, nous avons simulé une AVP pour une population hypothétique ayant une moyenne λ = 1,0 et la même variation temporelle que celle observée dans nos populations de hiboux. Notre AVP a suggéré que les populations de SIE et de LAS avaient de plus grandes probabilités de déclin que de croissance sur une période de 7 ans, mais qu'il serait difficile de déterminer si une population présentait un léger déclin graduel. La collecte des informations pour nos 4 aires d'étude fournit aux personnes chargées de la gestion un modèle riche de données permettant de suivre l'impact sur les hiboux des actions de gestion à l'avenir (par exemple, les nouvelles stratégies de gestion du Plan pour la Forêt de Sierra Nevada). Cette collecte fournit également des preuves importantes afin d'évaluer le statut du hibou pour une classification potentielle sur la liste des espèces menacées.

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INTRODUCTION

The California spotted owl (*Strix occidentalis occidentalis*; hereafter, CASPO) has a large range, extending from the southern Cascade Mountains south to Baja California Norte in North America (Verner et al. 1992*b*, Gutiérrez et al. 1995). However, its primary population resides within the southern Cascade and Sierra Nevada ecosystems (Gutiérrez et al. 1995, Franklin et al. 2004). The geographic range of this subspecies within the Sierra Nevada is predominantly on its western slope within a zone dominated by conifer forests (Verner et al. 1992*b*). The CASPO has emerged as a central species of concern in the debate over future management of Sierra Nevada forests because distribution of the subspecies is contiguous with valuable timber resources in this range (U.S. Forest Service [USFS] 2004). Moreover, this is the only spotted owl subspecies that has not received federal protection under the Endangered Species Act (Gutiérrez et al. 1995). The United States Fish and Wildlife Service (USFWS) denied petitions to list the CASPO subspecies following reviews of its status (USFWS 2003, 2006). These status reviews were the legacy of 15 years of owl status evaluations, environmental impact statement reports (EIS), and population analyses (Verner et al. 1992*b*; USFS 1993, 1996; Federal Advisory Committee 1997; Franklin et al. 2004) but have not resolved the future of management strategies for spotted owls and Sierra Nevada Forests to the satisfaction of stakeholders.

The inability to resolve the future management of Sierra Nevada forests, at least with respect to the spotted owl, has been partly due to uncertainty surrounding the owl's habitat requirements, its apparent broad use of forests in the Sierra Nevada, uncertainty of its population trends, and uncertainty of habitat trends under projected management regimes proposed for the Sierra Nevada (Verner et al. 1992*b*; USFS 1996, 2004; Federal Advisory Committee 1997; Franklin et al. 2004). Verner et al. (1992*b*) first recognized many of these uncertainties and proposed an interim management strategy for the CASPO throughout its range in the United States. However, the focus for CASPO was primarily the forests of the Sierra Nevada because that is where most of the projected timber harvest having the potential to impact the owl would occur in the future. Moreover, CASPO was proposed as an interim conservation strategy with the understanding that future research would clarify key areas of uncertainty about biology of the owl. Many recommendations by CASPO for removing uncertainties remained unfulfilled. Yet, substantial progress has been made in our understanding of CASPO habitat selection, population dynamics, and population genetics (Barrowclough et al. 1999, 2005; North et al. 2000; Blakesley et al. 2001, 2005, 2006; Seamans et al. 2001; Hunsaker et al. 2002; Franklin et al. 2004; Chatfield 2005; Gutiérrez and Barrowclough 2005; Seamans 2005).

Franklin et al. (2004) conducted the first meta-analysis of CASPO population data in 2001 using all extant data collected through the year 2000. We were asked by the USFWS to conduct a second meta-analysis because they were conducting a status review of the owl for potential listing as threatened or endangered under the United States Endangered Species Act (USFWS 2006). Thus, our general objective was to assess population dynamics of this subspecies using all available population data from the southern Cascades and Sierra Nevada, California. Our specific objectives were to estimate key vital rates on each of our 4 study areas and to examine temporal trends and trends among study areas, with the ultimate goal of evaluation of status of the population from multiple perspectives provided by the demographic analyses. We then attempted to provide the best estimate of the collective status and trends of study populations in these mountain ranges.

STUDY AREA

We studied spotted owls on 4 study areas in the Sierra Nevada and southern Cascade Mountains, California, USA, from 1990 to 2005 (Fig. 1; Table 1). This area contained the largest contiguous population of CASPOs. Although our study areas were not randomly selected, they spanned the length of these ranges and encompassed all habitat types known to be used by most of the owl population in this area. The Lassen study area was in the southern Cascades, but it was included in the Sierra Nevada province by the USFS for management purposes (USFS 2004). Most of the Lassen, Eldorado, and Sierra study areas were located on public land managed by the USFS, whereas the Sequoia and Kings Canyon study area was in 2 National Parks. However, the proportion of area under public ownership varied among study areas, as described by Franklin et al. (2004).

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

The LAS encompassed 2,200 km^2. During a previous meta-analysis Franklin et al. (2004) selected a subset (core area) of this study area (1,270 km^2) and surveyed consistently for estimation of population rate of change. Subsequently, we delineated a new core area of 1,471 km^2 whose boundaries were similar to those delineated for the Franklin et al. (2004) 2001 meta-analysis but based on watershed units and property ownership boundaries. We

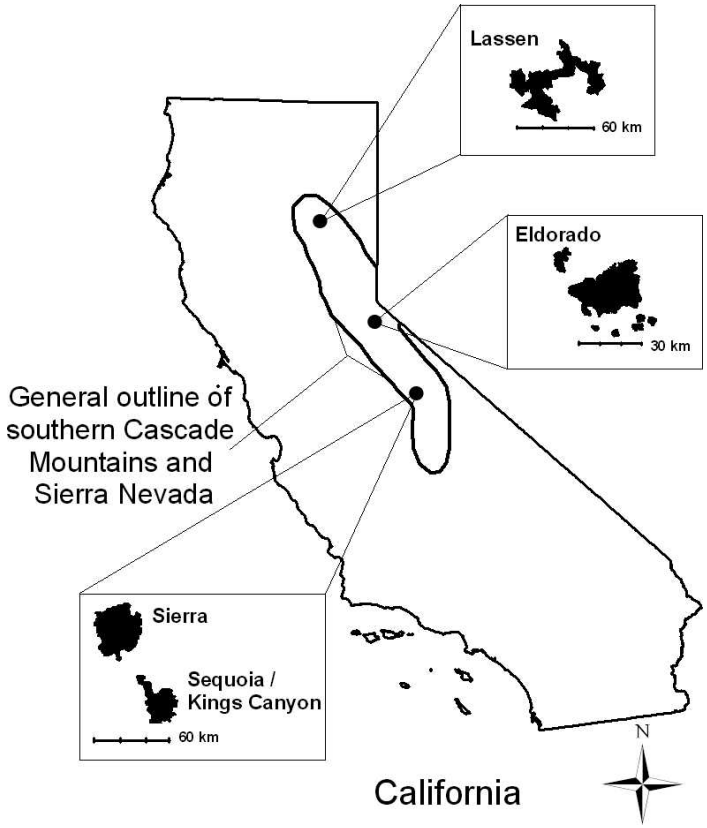

Figure 1. Outline of southern Cascade Mountains and Sierra Nevada, California, USA, showing location of 4 study areas for California spotted owls, 1990–2005.

continued to study and survey for spotted owls both inside and outside this core area through the field season of 2005. We used data from the entire study area to analyze survival and reproductive output, whereas we used data from only the core area for estimation of population rate of change to meet the assumptions of the analytical technique (see below).

The Eldorado study area (ELD) was located on the Eldorado National Forest, Tahoe National Forest, and adjacent private land between Georgetown and Lake Tahoe, California. The ELD consisted of a 355-km^2 density study area (entire study area surveyed for owls) embedded within a 570-km^2 regional study area (only selected territories within this area surveyed for owls). We used data from the entire study area to estimate survival and reproductive output and data only from the density study area to estimate population rate of change and recruitment. Neither the size nor shape of the study area changed between the 2001 meta-analysis (Franklin et al. 2004) and our meta-analysis. Elevations ranged from 366 m to 2,400 m. Forests were dominated by ponderosa pine on xeric sites and white fir on mesic sites (Chatfield 2005). Above 1,500 m, forests were dominated by red fir. Other common tree species included sugar pine, Douglas-fir, incense cedar, canyon live oak (*Q. chrysolepis*), black oak, pacific dogwood, and tan oak (*Lithocarpus densiflorus*).

The Sierra study area (SIE) was located primarily on the Sierra National Forest, 83 km east of Fresno, California. The overall study area was initially 419 km^2 and we later expanded it to 693 km^2 on the fifth year of the study (1994). Within the overall study area was the 477-km^2 core study area, consisting of 339 km^2 from the original study area and 158 km^2 from the expansion in 1994. The core study area represented the area consistently surveyed during the study, whereas the overall study area size reported in Franklin et al. (2004) represents a larger area that encompassed the core area and a few disjunct, surrounding owl sites with consistent survey coverage and areas without consistent survey coverage across years. We used the total core area of 477 km^2 for estimation of population rate of change, which differed from the 2001 meta-analysis where only the 339-km^2 original core study area was used for estimation of population rate of change. We used marked owls within the 477-km^2 core study area along with marked owls from 6 sites located outside the core area but within the overall study area in analyses of survival and reproductive output. Elevations ranged from 304 m to 2,924 m. The SIE contained 3 major vegetation types: low-elevation oak woodlands, mid-elevation mixed conifer forests, and high-elevation conifer forests. Oak woodlands (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 (*Pinus sabiniana*). Various foothill chaparral species were abundant in a chaparral vegetation type that occurred at lower elevations. Mixed-conifer forests (1,220–2,438 m) covered 61% of the study area and were dominated by ponderosa pine, white fir, incense cedar, black oak, Jeffery pine, red fir, and sugar pine. A 2-km^2 grove of giant sequoia (*Sequoiadendron giganteum*) was within this zone. Conifer forests (2,439–2,924 m) covered 13% of the study area and were dominated by red fir, lodgepole pine (*P. contorta*), and western white pine (*P. monticola*).

The Sequoia and Kings Canyon overall study area (SKC) encompassed 343 km^2 and was located in Sequoia and Kings Canyon National Parks, 35 km northeast of Visalia, California. Similar to SIE, SKC contained a 283-km^2 core study area that was consistently surveyed during the study, whereas the overall study area reported in Franklin et al. (2004) represented a larger area that encompassed both the core area and surrounding areas

Table 1. Description of the 4 study areas in the southern Cascades and Sierra Nevada, California, USA, that we used to estimate vital rates of California spotted owls, 1990–2005.

Study area	Yr	Area (km^2)	No. of owls banded by age class[a]			Total owls banded	Total captures + recaptures[b]
			S1	S2	Ad		
Eldorado	1990–2005	925	47	33	175	255	991
Lassen	1990–2005	2,200	56	35	213	304	1,517
Sierra	1990–2005	693	71	53	151	275	1,130
Sequoia and Kings Canyon	1991–2004	343	34	20	103	157	779

[a] Age-class codes indicate owls that were 1 yr old (S1), 2 yr old (S2), or ≥3 yr old (Ad).
[b] All captures and recaptures, regardless of age.

with inconsistent survey coverage across years. We used marked owls within the core study area for estimation of population rate of change, survival, and reproductive output in both the 2001 and 2006 meta-analyses. Elevations ranged from 427 m to 3,050 m. Vegetation types included 24% low-elevation (<1,200 m) oak woodlands and dense riparian deciduous forest, 67% mid-elevation (1,220–2,440 m) mixed-conifer forests, and 9% high-elevation (>2,400 m) conifer forests. Tree species within oak woodlands included blue oak, gray pine, interior live oak, canyon live oak, California sycamore (*Platanus racemosa*), California buckeye (*Aesculus californica*), and Fremont cottonwood (*Populus fremontii*). There were large areas of chaparral (primarily chamise [*Adenostoma fasciculatum*]) within the low-elevation zone. Tree species within mid-elevation mixed conifer forests included ponderosa pine, Jeffrey pine, sugar pine, white fir, red fir, incense cedar, and black oak. Included within these mid-elevation conifer forests were 10 giant sequoia groves covering 7% of the study area (Parsons 1994). Sequoia groves were mixed-conifer forests that contained giant sequoia trees, although other conifer species (e.g., white fir and sugar pine) were often more numerous (Rundel 1971). High-elevation coniferous forest tree species included red fir, lodgepole pine, and western white pine.

METHODS

Field Methods

Field methods for the study of spotted owl population dynamics are well described (Forsman 1983; Franklin et al. 1996, 2004; Anthony et al. 2006). Therefore, we present only a brief summary of the methods we used to survey our study areas to locate, capture, and resight banded owls and to determine their reproductive status. We conducted surveys from 1 April to 31 August on ELD and LAS and from 1 March to 30 September on SIE and SKC.

Estimation of apparent survival probability using mark–recapture (resight) methods required a capture history for each owl representing occasions (i.e., yr) in which an owl was identified as alive and on the study area (= 1) or not identified (= 0). We identified owls by capturing and banding or by resighting of owls previously banded with unique color band combinations. We classified owls to sex (M, F) by vocalization and behavior and age by plumage characters (Franklin et al. 1996). Owls can be identified to 4 age classes (juv [young of the yr], 2 subad ages [1–2 yr old = Subadult1 or S1; 2–3 yr old = Subadult2 or S2], and ad [≥3 yr old = Ad]; see Moen et al. 1991). We captured adults as ≥3-year-old birds or aged to that class. We use the term nonjuvenile owl to refer to S1, S2, and Ad age classes. We followed rigorous protocols when surveying for and identifying spotted owls to meet assumptions of mark–recapture analytical methods (Lebreton et al. 1992). We surveyed spotted owls between dusk and dawn by vocally imitating spotted owl calls or by broadcasting recordings of spotted owl calls. We completely surveyed study areas (core area for LAS, density area for ELD) on ≥3 occasions throughout each field season. When we detected owls, we conducted walk-in surveys during daylight hours to visually locate owls, identify color bands or capture unbanded owls, determine reproductive status, and locate owl nests and roosts.

We assessed spotted owl reproductive status by offering live mice to owls and observing the fate of the mice and the owls' behavior by following owls once they captured offered mice. Owls with active nests or fledged young usually take mice to the nest or young, whereas nonreproducing owls usually eat or cache the mice. We followed mousing protocols to reduce observer bias in estimation of reproductive status (Franklin et al. 1996). We primarily determined nonreproduction (we use this term to denote that we detected no evidence of reproduction for pair after following our protocol to evaluate the likelihood of reproduction of that pair) of owls on each study area if on 2 occasions, one member of a pair ate or cached ≥4 mice without bringing a mouse to a female on a nest or to young birds (Seamans 2005). We concluded that after adjusting for substantive differences in mousing protocols (see Methodological and Analytical Differences from the 2001 meta-analysis below), the remaining minor differences in protocols among study areas would not hinder comparisons of estimated reproductive outputs among study areas (see also Seamans [2005] for a discussion of these differences).

Meta-Analysis Design

We conducted a meta-analysis of all population data from extant CASPOs at a workshop held at Utah State University in Logan, Utah, USA, during 2–7 January 2006 (Appendices A–I). We followed a formal protocol that included a priori discussions to structure and agree upon analyses to be subsequently conducted (see Anderson et al. 1999). Our process and analyses were similar to those of Franklin et al. (2004). During development of our protocol, we vetted as many models as deemed reasonable by group consensus but chose only those for which we had both the data and the time to incorporate into our analysis framework. Our basic philosophy was to consider those models that were informative in our previous meta-analysis, those that were biologically plausible, and those that would be informative for evaluating the status of the owl with respect to the parameters of interest. We chose population parameters that we felt would provide the most relevant population information we could provide for the USFWS team that was reviewing the status of the owl for possible listing. Our process was facilitated by the rich literature and history of population analyses and listing processes conducted on all 3 subspecies of spotted owl. As is often the case, the structure of potential models becomes apparent only after the analysis and we, thus, considered subsequent models as post hoc models for consideration in a posteriori analyses. Before the workshop, the data from all studies were checked for errors by independent observers who followed a formal, randomized checking procedure (Appendix A).

There were several analytical and methodological differences between the 2001 meta-analysis (Franklin et al. 2004) and our present meta-analysis. We discussed the advantages and disadvantages of all methodological and analytical changes in detail at the 6-day workshop. In most cases, these changes represented additional analyses that were not previously conducted on spotted owls. These new analyses expanded our understanding of the population dynamics of spotted owl in the Sierra Nevada. In other cases, we modified the approach to enhance rigor of the analysis.

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

We estimated apparent survival as in Franklin et al. (2004). However, recent research (G. C. White, Colorado State University, unpublished data) on estimation of the overdispersion parameter ($\hat{c}$) suggested that using a global model and Program RELEASE (Burnham et al. 1987, Franklin et al. 2004) likely resulted in overestimation of $\hat{c}$. It appeared that including just 2 or 3 individuals in a study area that were not recaptured for >4 years before being recaptured and reentered into a capture history matrix greatly inflated the estimate of $\hat{c}$ using the goodness-of-fit test in RELEASE because ≥1 of the component chi-squared tests contributed large chi-square values. Such individuals are typically the result of temporary emigration, which was a violation of the assumptions of the Cormack–Jolly–Seber (CJS) model. Although temporary emigration has negligible effects on estimates of survival, it does increase individual heterogeneity of detection probabilities, which results in lack-of-fit based on the RELEASE goodness-of-fit test. When we removed these individuals, our estimate of $\hat{c}$ was near 1.0 for the RELEASE goodness-of-fit test. Therefore, we used a new method to estimate overdispersion termed median $\hat{c}$ available in Program MARK (White and Burnham 1999). This method simulates data sets over a range of overdispersion and compares the observed deviance estimate of $\hat{c}$ (deviance divided by df) to that of the deviance $\hat{c}$ derived from simulations. This method appeared to result in more reasonable estimates of $\hat{c}$. We included the temporary emigrants to estimate median $\hat{c}$ and in subsequent analyses of apparent survival.

We estimated reproductive output (no. of young fledged/territorial F) of all territorial females, using the annual proportion of subadults in the female population as a covariate because subadult females composed as much as 25% of all territorial females. We could not use the age of a female owl as a categorical effect in our models because the low number of subadult females in some years precluded estimation of age-specific time trends. In addition, we evaluated the effect of both male and female age class on reproductive output in a separate meta-analysis. For this latter analysis, we used a subset of the reproductive output data for which we knew the age of both members of a pair. Our approach differed from the previous CASPO meta-analysis, in which Franklin et al. (2004) estimated fecundity (no. of F offspring/territorial F owl, assuming a 50:50 sex ratio of offspring) for adult females only and did not consider age of the male owl.

Franklin et al. (2004) did not conduct a meta-analysis on reproductive output because they were uncertain about effects of variable field methods among study areas on estimates of reproductive output. Subsequent to their meta-analysis, Seamans (2005) examined some effects of using different field methods and determined that the chief difference between methods was that the ELD area used a 1-visit criterion to determine nonreproduction by owls. We defined nonreproduction as simply the failure to detect evidence that owls fledged young given application of a consistent protocol to assess reproduction (i.e., feeding of mice to owls or behavioral responses of owls given the opportunity to take such mice). Therefore, we applied the 2-visit criterion used on LAS to the ELD data. Although this resulted in removing a few reproductive outcomes from the early years of the ELD data set, we believed that ELD reproductive output data were now comparable to those of the other study areas, which enabled us to use reproductive output from all the study areas in our meta-analysis.

We estimated recruitment rate (no. of new territorial individuals at time t/no. of territorial individuals at time $t - 1$) using a temporal symmetry approach (Pradel 1996). Recruitment rate differs from reproductive output by 1) focusing on recruits to the breeding population, and 2) including immigration of new recruits from other locations. Estimation of study-area–specific recruitment rates allowed us greater insight into the dynamics of these populations. Further, examining recruitment and apparent survival for individual study areas was a natural complement to our estimation of population rate of change using the temporal symmetry models (Pradel 1996, see also below).

We used temporal symmetry models of Pradel (1996) to estimate population rate of change (λ), where λ is rate of change of the population of territorial owls in a specific study area, directly from mark–recapture data because of bias in juvenile survival rates caused by undetected emigration (Zimmerman et al. 2007) and assumptions of asymptotic population demographics required for the Leslie projection method (Franklin at al. 2004). Currently, it is not possible to estimate relative contributions of different components to population growth (e.g., reproduction, immigration, death, and emigration) without additional data (Franklin et al. 2004). However, estimates of juvenile survival are not required because both immigration and emigration are accounted for by changes in number of territorial owls over time (Pradel 1996, Nichols and Hines 2002). Using the Pradel method, one cannot distinguish between populations that are self-sustaining and those sustained through immigration (see Franklin et al. 2004, appendix A for a discussion of source–sink inference and CASPOs).

Lastly, we conducted a population viability analysis (PVA) using parameter estimates generated from our analyses. We then used the PVA developed by White (2000), which predicts population viability in the future based on empirical data and its temporal variation. Thus, our conclusions about hypothetical population viability were based on the best available field data.

Data Analysis

Survival on individual study areas.—We used capture histories of nonjuvenile spotted owls to estimate apparent survival (φ) and recapture (p) probabilities using open-population CJS models (Lebreton et al. 1992) in Program MARK (White and Burnham 1999). In general, we followed methods outlined in Franklin et al. (2004). We used an information–theoretic approach (Burnham and Anderson 2002) to rank candidate models (see below and Appendix B). For each study area, we determined goodness-of-fit of the global model $\varphi(a \times s \times t)$, $p(a \times s \times t)$ or $\varphi(s \times t)$, $p(s \times t)$, where a = age, s = sex, and t = time (yr), by estimating median overdispersion parameter ($\hat{c}$) using a simulation procedure in Program MARK. We first estimated

observed $\hat{c}$ as the deviance divided by degrees of freedom for the global model. We then simulated data sets over a range of overdispersion levels (e.g., 1.0–2.0) and compared the deviance divided by degrees of freedom from these simulations with the observed deviance divided by degrees of freedom (see above). Specifically, we simulated 10 data sets for $\geq$6 levels of overdispersion (e.g., 1.0, 1.1, 1.2, 1.3, 1.4, 1.5) and calculated the proportion of the 10 data sets, at each level, having a $\hat{c}$ less than the observed $\hat{c}$. Then, using logistic regression, median $\hat{c}$ was the value where 50% of the 10 simulated data sets had a $\hat{c}$ greater than the observed $\hat{c}$. When median $\hat{c}$ was >1, we used $QAIC_c$ (quasi-Akaike's Information Criterion with a second-order correction for small sample sizes) for model selection and to adjust variances of parameter estimates (Burnham and Anderson 2002).

We developed a protocol for model development and a set of a priori models for estimating apparent survival and recapture probabilities based on results of previous spotted owl meta-analyses (Franklin et al. 2004, Anthony et al. 2006; Appendix B). Of primary interest were the main effects of age, sex, and time, as well as interactions among main effects on owl survival. In addition to modeling the 3 nonjuvenile age classes of owls separately, we modeled survival of the subadult age classes combined separate from adults (i.e., S1 = S2 vs. Ad), and first-year subadults separate from older age classes (i.e., S1 vs. S2 = Ad). We modeled time as a categorical effect (t), a linear trend (T), a quadratic trend (TT), and as a log-linear (pseudo threshold) trend [ln(T)].

We also modeled effects of age, sex, time, and survey effort on recapture probability. We included models with annual reproductive output (r; no. of young fledged/F, see *Reproductive output on individual study areas* below) for recapture probability because spotted owls are easier to locate and, therefore, resight, when they have an active nest than when they are not nesting. Although estimates of recapture probability were not of primary interest, proper modeling of recapture probability provided less biased estimates of survival probability. To account for model-selection uncertainty, we used a model-averaging approach to calculate point estimates of survival and their sampling variation (Burnham and Anderson 2002).

Meta-analysis of survival.—We conducted a meta-analysis of survival using capture histories of adults only (including ad portions of capture histories for owls first captured as either juv or subad). We chose to not include juvenile encounters in the meta-analysis because of potential bias in estimating juvenile apparent survival as a result of unknown rates of emigration. We followed procedures similar to those described above for estimation of survival on individual study areas (Appendix C). In the meta-analysis, the global model was $\varphi(g \times s \times t)$, $p(g \times s \times t)$, where g indicated a study area (or group) effect.

The first meta-analysis of CASPO population dynamics found that spotted owls at SKC had higher survival rates than other study areas (Franklin et al. 2004). Therefore, we also modeled φ for SKC separately from the other study areas. Our a priori model set did not include any models of φ that had a separate effect for SKC in combination with time effects. We also did not include in our a priori models any models of p that had an interaction between study area and annual reproductive output despite having included similar but less parsimonious models that had an interaction between study area and year, $p(g \times t)$. To capture observed difference between SKC and other study areas, as well as to evaluate whether reproductive output influenced p, we included 6 additional post hoc models that replaced g with SKC versus the rest of the study areas for φ and replaced $p(g \times t)$ with $p(g \times r)$. Finally, we added 2 post hoc models that included a sex effect for φ and p. We used the structure from the top 2 models to run these additional post hoc models.

Reproductive output on individual study areas.—We estimated reproductive output for all nonjuvenile females. Data we used in these analyses consisted of the number of young fledged/female on a particular site (0, 1, 2, 3), the site (territory) where we detected the young, year, age class of the female (S1, S2, Ad), and age class of the male (if present). For each study area in each year, we determined the proportion of subadults among all territorial females of known age for which we assessed reproductive output. We used the resulting proportion (*psub*) as a covariate in modeling reproductive output for females of all ages (including those of unknown age).

We used mixed-model analysis of variance (Proc MIXED in Program SAS [Version 9.13; SAS Institute Inc., Cary, NC]; Littell et al. 1996, Rao 1997) to estimate reproductive output for individual study areas. We included site (owl territory) and year (as a categorical variable) as random effects. We used mixed models because 1) individuals and territories were confounded over time because the same females often bred on the same territory for >1 year; any lack of independence associated with such repeat breeding would lead to an underestimation of standard errors if we used methods assuming independence (Franklin et al. 1999); 2) we could conduct modeling in a maximum-likelihood framework; 3) we made inference to years rather than to the time period of the study; 4) we could appropriately structure the error covariance matrix; and 5) models allowed for unbalanced designs (i.e., missing data).

Analysis of fecundity data from northern spotted owls (*S. o. caurina*) showed that variation in the number fledged within a year was proportional to the mean, suggesting a Poisson distribution (Evans et al. 1993), although data were not distributed as Poisson (Franklin et al. 2000, McDonald and White 2010). In analyzing our data using mixed models, we again relied on sample sizes being sufficiently large to justify normal distributional assumptions. Franklin et al. (2004) were criticized for relying on this assumption in an earlier study of CASPOs. Because our reproductive data were distributed similarly to data from Franklin et al. (2004), we used simulations to examine the effect of using estimators based on normal and Poisson distributions (McDonald and White 2010). Results from these simulations indicated that normal-based models were 1) robust to severe departures from normality, similar to results reported by White and Bennetts (1996), and 2) more robust to data from the discrete distributions exhibited by our CASPO data than Poisson regression (McDonald and White 2010). Therefore, we relied on the robustness of mixed models to nonnormally distributed data, rather than relying on Poisson regression, to analyze the reproductive output data. The mixed-model procedures also allowed us to account for the dependence of sampling variation on the mean (see below). We did not separate individual bird effects

from territory effects because many females remained on territories for a long time.

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

We modeled reproductive output on each study area as a function of time effects: no trend (intercept-only), linear (T), quadratic (TT), pseudo-threshold or log-linear [ln(T)], even–odd year effect (EO), and even–odd year with a linear time trend ($EO + T$). We considered each time structure on the fixed effects, with and without the subadult covariate, as a candidate model (Appendix D). We ranked models using AIC_c.

We estimated temporal process variation ($\sigma^2_{\text{temporal}}$; Franklin et al. 2000) using an intercept-only model. This approach can be viewed as estimation of a variance component, with the overall variance of a weighted average of point estimates written as the sum of true process variance and average sampling variance (Burnham et al. 1987). We then used the estimate of temporal process variation with the residual variation not explained by the selected fixed-effects model with the best covariance structure ($\hat{\sigma}_{\text{model residual}}$) to estimate the proportion of $\sigma^2_{\text{temporal}}$ in our data explained by the top-ranked model as

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

Meta-analysis of reproductive output.—The meta-analysis of reproductive output followed procedures described above for individual study areas. The a priori model set included time effects modeled for individual study areas as well as a study-area effect and interactions between study-area and time effects (Appendix E). We explicitly modeled separate effects for the northern 2 study areas (LAS and ELD) versus the southern 2 study areas (SIE and SKC) and a separate effect for SKC versus the other study areas.

We also estimated effects of both female and male age on reproductive output using a subset of the data for which age class of both the female and male owl were known. We began with best model(s) from the reproductive output meta-analysis (we used a max. of 3 models $\leq 2\ \Delta AIC_c$ of the top model; Appendix F). We then included 3 age structures for males: 1) S1 versus S2 versus Ad; 2) S1 = S2 versus Ad; and 3) S1 versus S2 = Ad, in the best model(s). We used AIC_c to compare models with male age structure with the best model(s) from the first meta-analysis of reproductive output.

Estimation of population change and recruitment.—We estimated the annual rate of population change in territorial owls (λ_t) directly from capture histories using Pradel's temporal symmetry model (Pradel 1996, Nichols and Hines 2002, Franklin et al. 2004) in Program MARK. We estimated median $\hat{c}$ using the simulation procedure in Program MARK under the CJS global model $\varphi(s \times t)$, $p(s \times t)$. When median $\hat{c}$ was >1, we used $QAIC_c$ for model selection and to adjust variances of parameter estimates. Our a priori model set allowed λ, φ, and p to vary as functions of sex and time (Appendix G). Using the best fixed-effects model from this set for each study area, we constructed 4 random-effects models, structuring λ as a linear trend, quadratic trend, pseudo-threshold, and constant. We did not include the first 2 estimates and last estimate of λ because these were confounded with estimation of p. We modeled λ for SIE while allowing for an expansion of the study area in 1994. We parameterized the SIE model to include this expansion without loss of estimates for the expansion interval (see Appendix G for details). We estimated $\bar{\lambda}$, SE($\bar{\lambda}$), and $\hat{\sigma}^2_{\text{temporal}}$ on the log scale and used the delta method to estimate variance of the back-transformed $\bar{\lambda}$. We chose to work with estimates on the log scale to provide an estimate of the geometric mean of λ. The geometric mean provided an unbiased estimate of overall change in the population over a finite interval, whereas the arithmetic mean generated a biased estimate of population change (Morris and Doak 2002).

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

We evaluated the similarity in population rate of change across study areas by modeling λ, φ, and p as functions of time and study area, including one model that estimated λ for SKC separately from the other study areas (Appendix H). We evaluated the contributions of survival and recruitment (f) to population change for territorial owls across study areas by modeling φ, p, and f as functions of time and study area (Appendix H). We estimated recruitment (no. of new territorial individuals at time t/no. of territorial individuals at time $t - 1$) using the same temporal symmetry models we used to estimate λ (Pradel 1996). We developed a set of a priori models that included study area (g) and categorical time effects (t; Appendix H). We ranked models using AIC_c or $QAIC_c$.

Population viability analysis.—From the λ_t models for each study area, we estimated means of the natural log of λ estimates [ln($\bar{\lambda}$)] and their associated standard errors along with the estimated temporal process variance of the λ_t across years ($\hat{\sigma}^2_{\text{temporal}}$). We computed the probability of a population decline following White (2000; Appendix I), where we computed probability of decline as the exponential of the sum of values of ln(λ_i) for a given number of years i, i = 2, 3, …, 20. We selected ln(λ_i) values via a parametric bootstrap based on (ln($\bar{\lambda}$)) and its associated $\hat{\sigma}_{\text{temporal}}$. We used distribution of ln(λ) instead of λ because ln(λ) tends to be more normally distributed than λ. We performed 8,000 simulations for each time interval (e.g., 2 yr, 3 yr, etc.) and estimated probability of observing >10%, >20%, and >30% declines, and >10%, >20%, and >30% increases in population size for 2–20-year time intervals. For example, the probability of observing a decline ≥10% was the number of simulated populations <0.90 of the initial

population size divided by the number of simulations. For comparison, we also modeled the probability of observing >10%, >20%, and >30% declines and >10%, >20%, and >30% increases in population size for a hypothetical population with mean $\lambda = 1.0$ [$\ln(\bar{\lambda}) = 0$] and $\hat{\sigma}^2_{\text{temporal}}$ equivalent to that estimated from our spotted owl studies.

We computed 95% confidence intervals on probabilities of decline or increase based on White (2000) with a parametric bootstrap approach suggested by J. Baldwin (USFS, Pacific Southwest Research Station, personal communication). This approach considered $\ln(\bar{\lambda})$ from each study area modeled with a normal distribution possessing the estimated mean and with standard deviation equal to its associated standard error. Because $\hat{\sigma}_{\text{temporal}}$ also has sampling variance, we modeled sampling uncertainty of the process variance as a multiple of a chi-square distribution as follows:

$$\frac{\text{df} \times \hat{\sigma}^2_{\text{temporal}}}{\sigma^2_{\text{temporal}}} \sim \chi^2_{\text{df}}.$$

We used df = 7 to approximate (i.e., fit) the estimated confidence interval of $\hat{\sigma}_{\text{temporal}}$. To account for this modeled sampling variation, we bootstrapped 1,000 values of the sum of $\ln(\bar{\lambda})$ and $\hat{\sigma}_{\text{temporal}}$ for each of the scenarios $k = 2, 3, \ldots, 20$ years. We in turn used each of the bootstrapped pairs of $\ln(\bar{\lambda})$ and $\hat{\sigma}_{\text{temporal}}$ in the estimation procedure above (White 2000) to obtain 95% confidence intervals on probability of decline. We computed 95% confidence intervals as 2.5 and 97.5 percentile values from the 1,000 bootstrapped values.

RESULTS

Survival on Individual Study Areas

We used 991 banded owls in our analysis of apparent survival (Table 1). Median $\hat{c}$ ranged from 1.03 to 1.14 (Table 2; see Table S1, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model-averaged results), suggesting some overdispersion but no serious lack of fit; plus, these results demonstrated agreement across the 4 study areas. We adjusted estimated standard errors and model-selection parameter estimates for each study area using study area–specific estimates of $\hat{c}$ and increased the number of parameters (K) in each model by 1 to account for estimation of $\hat{c}$. There were some differences in apparent survival by age class; for each study area, all top models included age effects and ≥75% of models within 1 ΔQAIC$_c$ unit of top models had age effects (Table 2). However, there was little consistency in the sets of top models and resulting survival patterns across the 4 study areas. Moreover, there was little delineation among models, because 6–17 models were within 2 ΔAIC$_c$ units of the top model for the study areas (in fact, all but ELD had 15–17 models within 2 ΔAIC$_c$ units of the top model). Consequently, we presented only model-averaged results. Model-averaged estimates of adult apparent survival for the median year ranged from 0.811 to 0.890 among study areas and within study areas was ≥S1 (0.679–0.848) and ≥S2 (0.771–0.869) age classes (Table 3; see Table S2, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model-averaged results). However, the pattern of apparent survival by age class varied among areas (Fig. 2); for ELD and SKC, adult survival was higher than for S1 and S2; for SKC adult and S2 survival was greater than S1; for LAS and SIE there was little difference among age classes (Fig. 2; Table 3).

Apparent survival varied little between sexes. Only ELD had a sex effect in top models (Table 2); males had slightly higher survival rates (0.843) than females (0.811), but 95% confidence intervals overlapped (Table 3). There were some nonsignificant coefficients in some top models because top AIC$_c$ models can include coefficients for which ≥85% confidence intervals overlap zero. (Note: a decrease of 2 units on the −2log-likelihood scale for one df is a chi-square test with the statistic = 2 and df = 1, which results in $\alpha = 0.15$. However, as one adds more parameters and changes the df, α becomes increasingly smaller.)

There was no consistent pattern in resighting effects among study areas, except that sex was an effect in all top models (<2 ΔQAIC$_c$ models from top model) for 3 of the 4 study areas. Survey effort and sex were in the top models for ELD resighting probabilities; age, sex, and annual reproductive output were in the top models for LAS; age and sex were important for SIE; and annual reproductive output was in the top models for SKC (Table 2).

Meta-Analysis of Survival

We did not detect severe extra-binomial variation for these data; we used $\hat{c} = 1.1$ in the analysis of our 38 a priori models. The top model included separate estimates of φ for SKC versus the other study areas and a quadratic time trend. The top model had 73% of model weight and was 3 QAIC$_c$ units better than the second-ranked model (Table 4; see Table S3, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set).

Estimates of apparent survival showed a quadratic trend, with an increase in apparent survival in recent years, based on the top model (Fig. 3). An increase in survival over the last years of study was also suggested by the model-averaged estimates from the 38 a priori models (Fig. 4). Confidence intervals for one of the coefficient estimates for the quadratic time component in the top model slightly overlapped zero ($\hat{\beta}_T = -0.086$, SE = 0.061, 95% CI = −0.206–0.035; $\hat{\beta}_{TT} = 0.885$, SE = 0.416, 95% CI = 0.070–1.700).

Sex was not an important factor in modeling either survival (φ) or resighting probabilities (p). None of the top models included sex as a predictor of either φ or p. Models that included a sex effect tended to rank lower than corresponding models without a sex effect. In the post hoc analysis, we built models in which we added sex to the top a priori models, which resulted in negligible improvement.

When we modeled recapture probability (p), none of the 38 a priori models included a study area (g) by reproductive output (r) interaction. However, when we considered this model in our post hoc analysis, the reduced number of parameters in this model, compared to the $g \times t$ parameterization, resulted in the minimum QAIC$_c$ post hoc model. Recapture probability also increased with higher reproductive output on each study area (Fig. 5).

Reproductive Output on Individual Study Areas

We analyzed data derived from 1,865 observations of reproductive outcomes for females on all study areas. The best covariance structure for 3 of the 4 study areas was CSH, whereas TOEPH(3) was the best for LAS (see Table S1, <http://dx.doi.org/10.2193/

Table 2. Top models for estimation of apparent survival (φ) of California spotted owls on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1990–2005. Models shown are those with $\Delta QAIC_c < 2.0$ ordered by $QAIC_c$ for each study area. See Table S1, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a]	K	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Eldorado (1990–2005; $n = 255$, $\hat{c} = 1.065$)					
φ[(a2 × T) + s], p(wi-effort + s)	9	1,255.331	0.000	0.077	682.655
φ(a2 + s), p(wi-effort + s)	7	1,255.417	0.086	0.073	686.816
φ[(a2 × ln(T)] + s, p(wi-effort + s)	9	1,256.174	0.843	0.050	683.497
φ(a2), p(wi-effort + s)	6	1,256.508	1.177	0.043	689.937
φ(a2 × T), p(wi-effort + s)	8	1,256.593	1.262	0.041	685.956
φ(s), p(wi-effort + s)	6	1,256.890	1.559	0.035	690.319
Lassen (1990–2005; $n = 304$, $\hat{c} = 1.144$)					
φ(T), p(a + s)	6	1,437.424	0.000	0.058	780.644
φ(a1 + T), p(a + s)	7	1,437.484	0.060	0.056	778.681
φ(T), p(a + s + r)	7	1,437.741	0.317	0.050	778.938
φ(a1 + T), p(a + s + r)	8	1,437.799	0.375	0.048	776.970
φ(a2 + T), p(a + s + r)	8	1,438.031	0.608	0.043	777.202
φ(a1 + TT), p(a + s + r)	9	1,438.264	0.840	0.038	775.405
φ(a2 × s + T), p(a + s + r)	10	1,438.306	0.882	0.037	773.414
φ(a2 + TT), p(a + s + r)	9	1,438.318	0.894	0.037	775.459
φ(TT), p(a + s + r)	8	1,438.399	0.975	0.036	777.570
φ(a2 × s + TT), p(a + s + r)	11	1,438.650	1.226	0.031	771.721
φ(s × T), p(a + s)	8	1,438.882	1.458	0.028	778.053
φ(a1 × T), p(a + s + r)	9	1,438.885	1.461	0.028	776.026
φ(s × T), p(a + s + r)	9	1,439.216	1.792	0.024	776.357
φ(s + T), p(a + s + r)	8	1,439.280	1.856	0.023	778.451
φ(a1 + s + T), p(a + s + r)	9	1,439.326	1.902	0.022	776.467
φ[ln(T)], p(a + s + r)	7	1,439.413	1.989	0.021	780.610
Sierra (1990–2005; $n = 275$, $\hat{c} = 1.090$)					
φ(a2), p(a + s)	6	1,342.302	0.000	0.053	794.901
φ(a2 + T), p(a + s + r)	8	1,342.405	0.103	0.050	790.945
φ(a2 + T), p(a + s)	7	1,342.434	0.132	0.049	793.005
φ(a2 + T), p(a + s + T)	8	1,342.538	0.235	0.047	791.078
φ(a2), p(a + s + r)	7	1,342.601	0.299	0.046	793.172
φ[a2 + ln(T)], p(a + s)	7	1,343.023	0.721	0.037	793.594
φ[a2 + ln(T)], p(a + s + r)	8	1,343.107	0.804	0.035	791.647
φ(T), p(a + s)	6	1,343.189	0.887	0.034	795.788
φ(a2), p(a + s + T)	7	1,343.200	0.898	0.034	793.772
φ(a3), p(a + s)	7	1,343.201	0.899	0.034	793.772
φ(.), p(a + s)	5	1,343.277	0.975	0.032	797.899
φ[a2 + ln(T)], p(a + s + T)	8	1,343.425	1.123	0.030	791.965
φ(a1 + T), p(a + s)	8	1,343.451	1.149	0.030	791.991
φ(a1 × T), p(a + s)	10	1,343.471	1.169	0.029	787.937
φ[ln(T)], p(a + s)	6	1,343.771	1.469	0.025	796.369
φ[a3 + ln(T)], p(a + s)	8	1,344.009	1.707	0.023	792.549
φ(a2 + s), p(a + s)	7	1,344.242	1.939	0.020	794.813
Sequoia and Kings Canyon (1991–2004; $n = 157$, $\hat{c} = 1.030$)					
φ(a1), p(r)	5	670.165	0.000	0.071	348.426
φ(a1 × T), p(r)	7	670.479	0.315	0.061	344.666
φ(a1 + T), p(r)	6	670.651	0.487	0.056	346.878
φ(a2 × T), p(r)	7	671.029	0.864	0.046	345.216
φ[a1 × ln(T)], p(r)	7	671.073	0.909	0.045	345.260
φ(a1), p(r + T)	6	671.125	0.961	0.044	347.352
φ[a1 + ln(T)], p(r)	6	671.285	1.120	0.040	347.512
φ(a1 × T), p(r + T)	8	671.578	1.414	0.035	343.719
φ(a1), p[r + ln(T)]	6	671.705	1.540	0.033	347.932
φ[a2 × ln(T)], p(r)	7	671.711	1.547	0.033	345.898
φ(a1 + TT), p(r)	7	671.750	1.585	0.032	345.936
φ(a1 + s), p(r)	6	671.757	1.593	0.032	347.984
φ(a1 + T), p(r + T)	7	671.763	1.599	0.032	345.950
φ[(a1 × T) + s], p(r)	8	672.093	1.929	0.027	344.234
φ(a1 × T), p[r + ln(T)]	8	672.101	1.936	0.027	344.242

[a] Key to model notation: K = no. of parameters; $QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model; w_i = model wt based on model $QAIC_c$ compared to all other model $QAIC_c$ values; S1 = owls that were 1 yr old; S2 = owls that were 2 yr old; Ad = owls that were ≥3 yr old; a1: age effect, with S2 = Ad, S1 different; a2 = age effect, with S1 = S2, Ad different; a3 = age effect, with different estimates for S1, S2, and Ad; a = age effect in recapture probability (only 2 age classes possible); s = sex; T = linear time trend; ln(T) = pseudo-threshold time trend; TT = quadratic time trend; r = annual reproductive output; wi-effort = walk-in survey effort.

Table 3. Model-averaged estimates of apparent survival (φ) for the median year of the study period by age and sex classes for California spotted owls on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1990–2005. See Table S2, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

		1 yr old		2 yr old		≥3 yr old	
Study area[a]	Sex	$\hat{\varphi}$[b]	SE($\hat{\varphi}$)	$\hat{\varphi}$	SE($\hat{\varphi}$)	$\hat{\varphi}$	SE($\hat{\varphi}$)
Eldorado	M	0.775	0.073	0.802	0.060	0.843	0.020
	F	0.740	0.073	0.771	0.059	0.811	0.021
Lassen	M	0.795	0.067	0.829	0.036	0.840	0.017
	F	0.787	0.069	0.823	0.044	0.848	0.016
Sierra	M	0.813	0.062	0.797	0.050	0.848	0.015
	F	0.818	0.061	0.800	0.048	0.848	0.015
Sequoia and	M	0.707	0.105	0.869	0.048	0.890	0.016
Kings Canyon	F	0.679	0.106	0.864	0.050	0.885	0.016

[a] Median yr was 1997 for Eldorado, Lassen, and Sierra, and 1996 for Sequoia and Kings Canyon.

2008-475.s1>, for complete model set). These covariance structures were similar and allowed heterogeneity in annual variance of reproductive output. Subsequent analyses incorporated the best covariance structure for each study area.

We detected strong support for an even–odd year (*EO*) effect on the northern study areas (ELD and LAS), with *EO* models accounting for >97% of Akaike weights (Table 5; Fig. 6; see Table S4, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set). We also detected moderate support for the *EO* model for SIE because *EO* + *psub* was the top model, where *psub* = proportion of subadults among female spotted owls; *EO* + *T* + *psub* was the third-best model, and together they accounted for 38% of Akaike weights (Table 5; Fig. 6). Sequoia and Kings Canyon study area had the least support among the 4 study areas for an *EO* effect with <35% of all model weight. In addition, the top model was an intercept-only model; however, *EO* was the second-ranked and competing model with ΔAIC_c = 0.508 (Table 5; Fig. 6), but the model weight was 0.180. The *EO* effect had similar model weight for ELD and LAS (0.97 for both) and was synchronous among all study areas, with reproductive output 1.4–3.7× higher (respectively) in even-numbered years (Table 6; Fig. 6). In addition to the *EO* effect, ELD had a negative temporal trend in reproductive output (Table 6).

The proportion of subadult females among all territorial females of known age ranged from 0.00 to 0.25 among areas and years

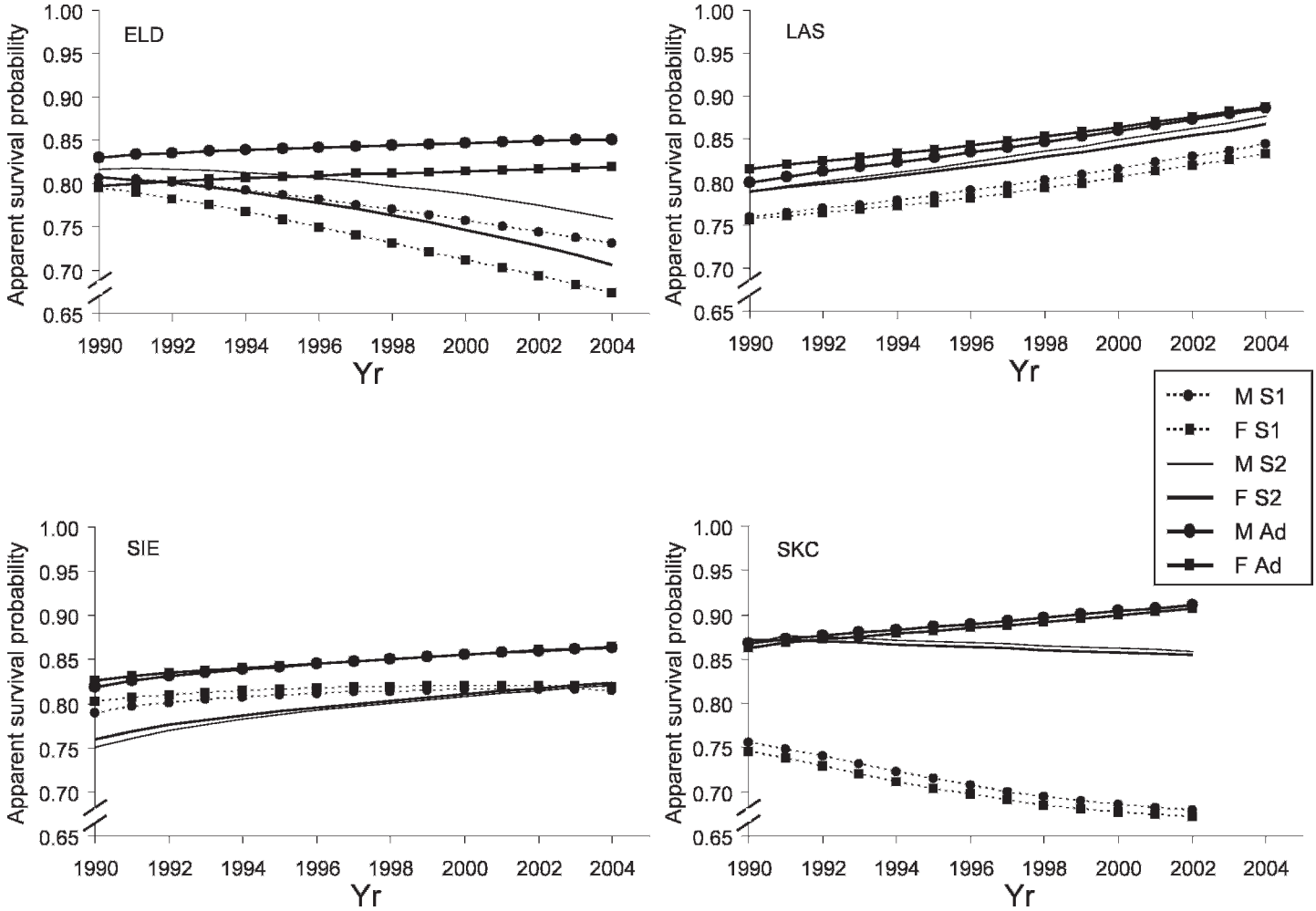

Figure 2. Apparent survival of California spotted owls by age and sex on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1990–2004, based on model-averaged estimates from an a priori set of models for each study area. S1 = owls that were 1 year old; S2 = owls that were 2 years old; Ad = owls that were ≥3 years old.

Table 4. Model-selection results from a meta-analysis of apparent survival (φ) for adult California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1990–2005. Models shown are those with $w_i > 0.001$ ordered by $QAIC_c$ for each study area. See Table S3, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a]	K	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
φ(SKC vs. Rest + *TT*), *p*(*g* × *r*) post hoc	12	3,868.898	0.000	0.727	1,691.565
φ(SKC vs. Rest + *t*), *p*(*g* × *r*) post hoc	23	3,871.945	3.047	0.158	1,672.378
φ(*g* + *t*), *p*(*g* × *r*) post hoc	25	3,874.951	6.053	0.035	1,671.326
φ(SKC vs. Rest + *t*), *p*(*g* × *t*) post hoc	69	3,875.401	6.503	0.028	1,581.274
φ(SKC vs. Rest + *TT*), *p*(*g* × *t*) post hoc	59	3,876.119	7.221	0.020	1,602.769
φ(SKC vs. Rest + *T*), *p*(*g* × *t*) post hoc	58	3,877.595	8.697	0.009	1,606.316
φ[*g* + *t* (coded as mean)], *p*(*g* × *t*)	71	3,878.448	9.550	0.006	1,580.151
φ(*g* + *TT*), *p*(*g* × *t*)	61	3,879.338	10.440	0.004	1,601.842
φ(*g* + *t* + *s*), *p*(*g* × *t* + *s*) post hoc	73	3,879.688	10.790	0.003	1,577.215
φ(*g* + *TT* + *s*), *p*(*g* × *t* + *s*) post hoc	63	3,880.618	11.720	0.002	1,598.972
φ(*g* + *T*), *p*(*g* × *t*)	60	3,880.630	11.732	0.002	1,605.208
φ(*g* + *t*), *p*(*g* + *r*) post hoc	22	3,881.010	12.112	0.002	1,683.471
φ(*t*), *p*(*g* × *t*)	68	3,882.867	13.969	0.001	1,590.824
φ(SKC, Rest), *p*(*g* × *t*)	57	3,883.156	14.258	0.001	1,613.946
φ(*TT*), *p*(*g* × *t*)	58	3,883.356	14.458	0.001	1,612.077

[a] Key to model notation: K = no. of parameters; $QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model; w_i = model wt based on model $QAIC_c$ compared to all other models; g = study-area effect; t = yr effect; s = sex effect; Rest = all other study areas (a comparison of all study areas to Sequoia and Kings Canyon Study Area [SKC]); T = linear time trend; TT = quadratic time trend; r = annual reproductive output.

(Table 7). The proportion of subadults among females (*psub*) had a strong negative correlation with reproductive output for ELD and SIE, appearing in the top models with 95% confidence intervals of coefficients that did not overlap zero (Table 6). Model weights indicated there was weak support for models including *psub* for LAS and SKC, <28% and <34%, respectively.

Reproductive output estimates varied among study areas; the mean-point estimate of annual reproductive output for ELD was more than twice that of SIE (0.48 vs. 0.99 young fledged/territorial F; Table 8). The ELD also exhibited the greatest temporal variation in reproductive output, whereas SIE and SKC, which had the lowest reproductive output, had the lowest temporal variation; theirs was less than half that of Eldorado (Table 8). However, all temporal variance confidence intervals overlapped (Table 8). In general, the pattern of reproductive variables of ELD being highest and SIE lowest held for all estimates and variances.

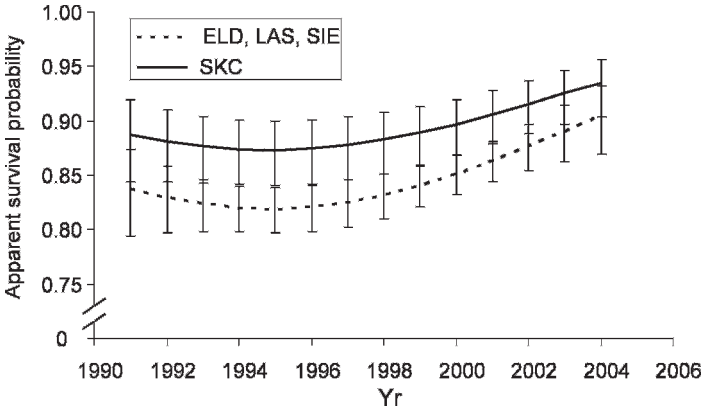

Figure 3. Apparent survival of adult California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1991–2004 (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon), based on the top (by 3.1 $\Delta QAIC_c$ units [$QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model]) meta-analysis model φ(SKC vs. Rest + *TT*), *p*(*g* × *r*) where Rest = all other study areas not including SKC; *TT* = quadratic time trend; *g* = study-area effect; *r* = annual reproductive output.

Meta-Analysis of Reproduction Time Trends

The best error covariance structure for the meta-analysis of reproductive output was the TOEPH(3) (see Tables S2, S3, <http://dx.doi.org/10.2193/2008-475.s1>). For both the general analysis of reproductive output and the analysis of male and female age effects, this covariance structure was strongly supported based on Akaike weights. Therefore, we used this covariance structure for all subsequent analyses.

In the meta-analysis of reproductive output, model (area × *T* + *psub*) was the best approximating model with an Akaike weight of 0.935 (Table 9; see Table S5, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set), which indicated strong support for this model among the models examined. Models with additive time-trend effects were not well-supported; the best model with additive time trend was >45 $\Delta QAIC_c$ from top model. Model (area × *T* + *psub*) suggested that temporal trends in reproductive output varied among areas (Fig. 7) and that, as the annual proportion of subadults in the sampled populations increased, annual reproductive output decreased (Table 10). However, confidence intervals of parameter estimates from this model tended to include zero (Table 10), except for the ELD study area. In addition, the top model explained only 11.1% of temporal variation in the data.

We used model (area × *T*) as the base model rather than model (area × *T* + *psub*), which was the model selected in the meta-analysis of time trends, to examine effects of male and female age class on reproductive output. We removed the covariate *psub* because it was confounded with categorical age effects (S1, S2, and Ad). The best approximating model had an Akaike weight of 0.995 and suggested that reproductive output varied by age class similarly among males and females, rather than by different combinations of age classes for each sex (Table 11; see Table S6, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model

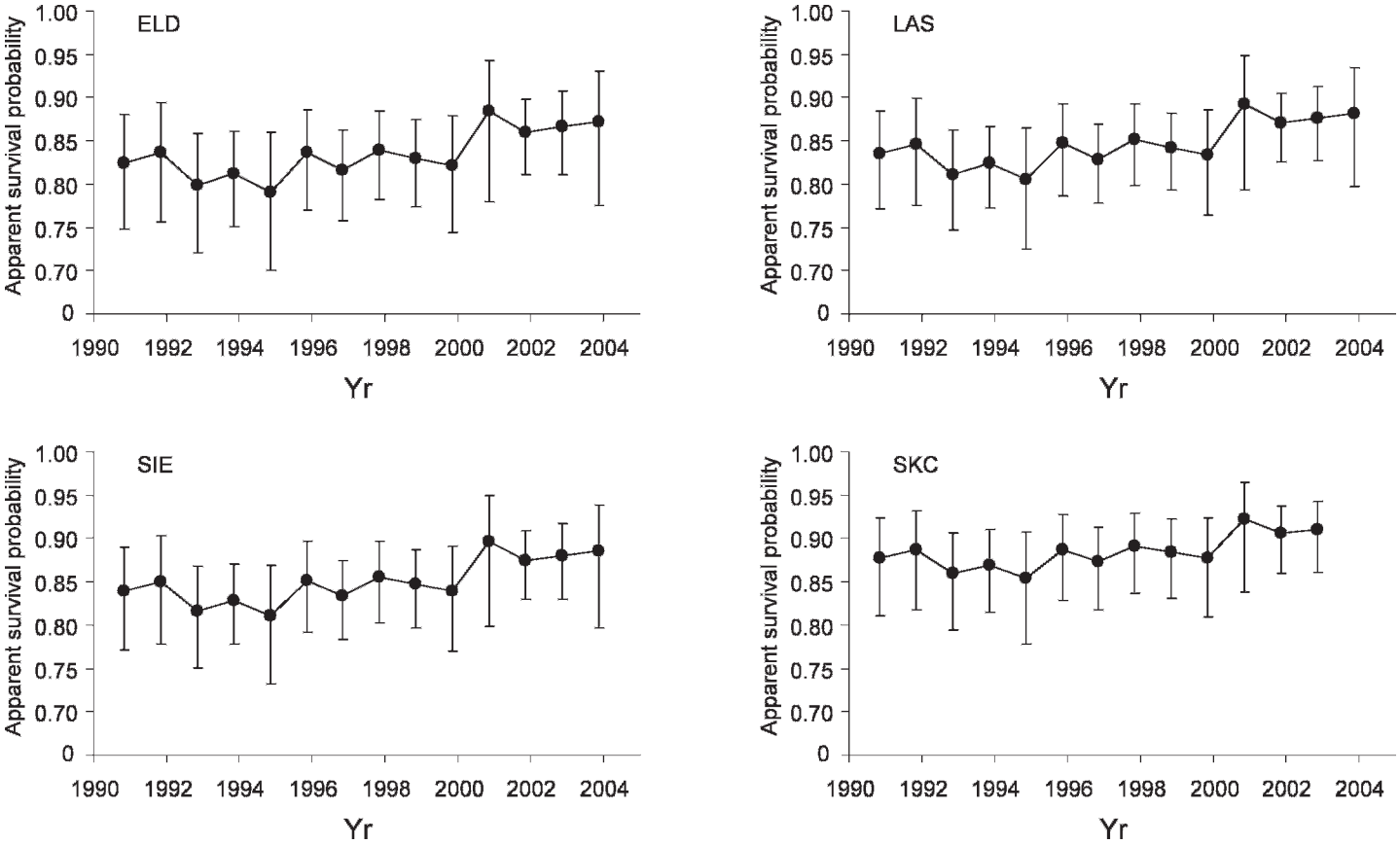

Figure 4. Apparent survival of adult California spotted owls on 4 studies areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon), in the southern Cascades and Sierra Nevada, California, USA, 1991–2005, based on model-averaged estimates from the meta-analysis a priori set of models.

set). However, this model explained only 6.0% of temporal variation in the data and confidence intervals for most parameter estimates included zero (Table 12). Estimates of least-square means from this model suggested that adults had 1.4–1.9× greater reproductive output than second-year subadults, and that second-year subadults had 2.6–3.0× greater output than first-year subadults. However, support for differences was weak, because 95% confidence intervals for all age-class estimates overlapped (Table 13).

Population Change: Individual Study Areas and Meta-Analysis

We used 842 (180 from ELD, 241 from LAS, 264 from SIE, and 157 from SKC) marked subadult and adult individuals to estimate λ_t. Median $\hat{c}$ ranged from 1.03 to 1.21 among areas (Table 14; see Table S6, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set), suggesting some overdispersion but no lack of fit. We adjusted all estimates and model-selection factors by site-specific estimates of c; to account for the inclusion of an overdispersion factor we increased the number of parameters in each model by one.

We did not find evidence for decreasing linear trends in λ_t on any of the study areas (Table 15; Fig. 8). In general, λ_t was either stationary, as for LAS and SIE, or increasing after an initial decrease, as for ELD and SKC (Fig. 8). The best approximating model for ELD (1.93 $QAIC_c$ above second model) suggested a quadratic trend in λ_t (Table 14; Fig. 8) with an initial decrease (β_1; Table 15) followed by a slight increase in λ_t (β_2; Table 15). The second-ranked model for ELD was a log-linear trend model. Together, these 2 models accounted for 92% of Akaike weights. No trend in λ_t was evident for LAS; the best model with any trend was a negative log-linear, but the Akaike weight was low (19%) and less than half the weight of the top model (55%), which was a means model (Table 14). The slope parameter for the linear trend in λ_t for LAS was near zero ($-<0.001$) and the confidence interval was balanced around zero (95% CI = −0.011–0.010). The best 2 models of λ_t for SIE were the random-effects mean and fixed-effects categorical time models, which accounted for 70% of Akaike weights (Table 14). The best approximating λ_t model for SKC (1.27 $QAIC_c$ above the second model) suggested a quadratic trend in λ_t (Table 14; Fig. 8) with an initial decrease (β_1; Table 15) followed by a slight increase in λ_t (β_2; Table 15). The second-best model for SKC indicated λ_t was constant over time.

Estimates of realized population change (Δ_t; Franklin et al. 2004), represented the trajectory (or trend in numbers) of each study population (Fig. 9). We based these estimates solely on estimates of λ_t and, thus, did not need to estimate annual population size (N_t) for each study area. Trends represented the proportion of the population size in the first year that remained in each subsequent year. For example, if there were 100 owls on the LAS study area in 1992 there would be an estimated 69 owls in 2004 (95% CI = 49–97) based on estimates of λ_t and, hence, Δ_t

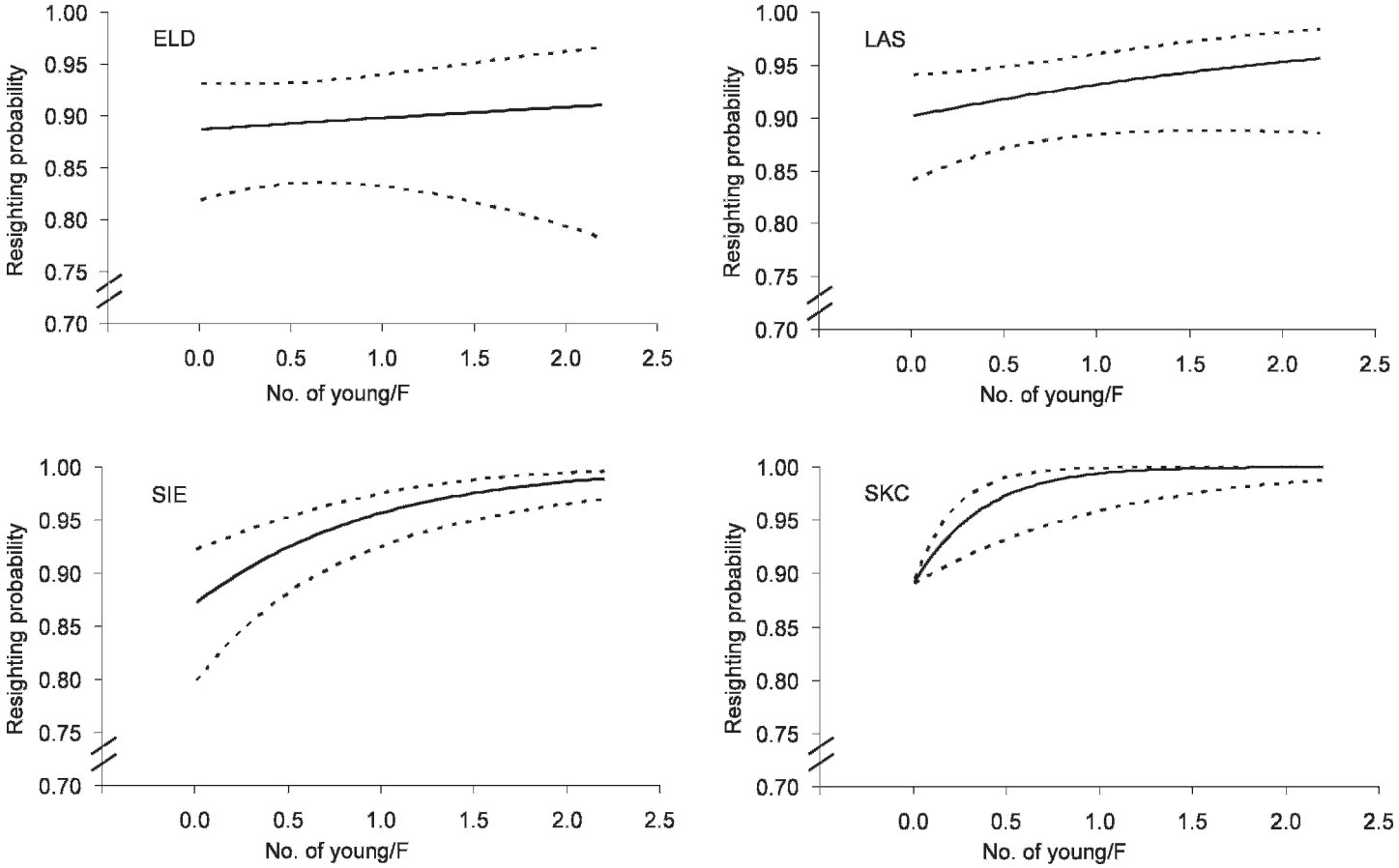

Figure 5. Resighting probability for California spotted owls as a function of reproductive output (no. of young fledged/F) for 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon), in the southern Cascades and Sierra Nevada, California, USA, 1991–2004, based on the top (by 3.1 $\Delta QAIC_c$ units [$QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model]) model φ(SKC vs. Rest + *TT*), $p(g \times r)$ where Rest = all other study areas not including SKC; *TT* = quadratic time trend; *g* = study-area effect; *r* = annual reproductive output.

for that study area. (Note: for ELD, LAS, and SIE, estimates covered 1992–2004 for our analysis, whereas estimates for SKC covered 1993–2003). Populations on ELD and SKC showed small estimated increases, whereas SIE showed a slight estimated decrease. However, the 95% confidence intervals for $\hat{\Delta}_t$ for the final year of each series covered 1.0, indicating no strong evidence of population change for these 3 areas. Based on realized change, only the LAS population had an ending population size that was lower than the starting population (95% CI for proportion remaining = 0.49–0.97).

Based on a random-effects-means (intercepts-only) model using annual estimates of λ from model (φ_t, p_t, λ_t), 95% confidence intervals of the estimated mean across years ($\hat{\bar{\lambda}}$) for each area except LAS provided little evidence of differences from a stationary population (λ = 1; Table 16). Point estimates were <1 for LAS and SIE. The Lassen study area had the lowest estimate of $\hat{\bar{\lambda}}$ with a 95% confidence interval that barely overlapped 1 (upper 95% CI = 1.001), suggesting that the owl population on LAS may have been declining (Table 16). Estimates of temporal process variation in λ_t were low (CV for ELD = 8.1%, for SKC = 8.3%, and 0% for LAS and SIE).

The best meta-analysis model of population trend, $\varphi(g \times t)$, $p(g \times t)$, $\lambda(t)$, indicated that λ varied across time but was similar among areas (Table 17; Fig. 10; see Table S7, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set). However, the second-best model $\varphi(g \times t)$, $p(g \times t)$, λ(SKC vs. rest) had $\Delta QAIC_c$ = 1.38 and 30% of model weight, providing evidence that λ_t for SKC may have been different than those of the other study areas. These 2 models, which had 89% of model weights, suggested that λ_t varied in a parallel manner among study areas. Although recapture rates varied within and among areas, the recruitment meta-analysis indicated there were parallel patterns in both apparent survival and recruitment among areas (Table 18; Table S7, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set). Meta-analysis patterns in annual recruitment (Fig. 11) did not mirror those of reproductive output (Fig. 7). Although recruitment showed peaks near the beginning and end of the study period (Fig. 11), reproductive output was either stable (on 3 of 4 areas) or declined (Fig. 7).

Population Viability Analysis

We estimated $\ln(\hat{\bar{\lambda}})$, which was the mean annual population growth rate, $SE[\ln(\hat{\bar{\lambda}})]$, and $\hat{\sigma}^2_{temporal}$ from the λ_t models for each study area (Table 19). We used these estimates in the population viability analysis, with the following exceptions: when the value of $\hat{\sigma}_{temporal}$ was zero for LAS and SIE, and estimates for ELD and

Table 5. Model-selection results for mixed-models analyses of time trends and age effects in reproductive output (no. of young fledged/F) of California spotted owls on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1991–2005. Models shown are those with $w_i > 0.001$ ordered by AIC_c for each study area. See Table S4, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a]	K	AIC_c	ΔAIC_c	w_i	$-2\ln(L)$
Eldorado study area (CSH covariance structure; n = 349)					
EO + *T* + *psub*	21	793.726	0.000	0.792	748.9
EO + *T*	20	796.761	3.035	0.174	754.2
T	19	802.910	9.184	0.008	762.6
T + *psub*	20	803.261	9.535	0.007	760.7
ln(*T*)	19	803.510	9.784	0.006	763.2
ln(*T*) + *psub*	20	803.861	10.135	0.005	761.3
TT	20	804.661	10.935	0.003	762.1
TT + *psub*	21	805.126	11.400	0.003	760.3
EO	19	806.810	13.084	0.001	766.5
EO + *psub*	20	807.061	13.335	0.001	764.5
Lassen study area (TOEPH(3) covariance structure; n = 623)					
EO	21	1,423.837	0.000	0.507	1,380.3
EO + *psub*	22	1,425.687	1.849	0.201	1,380.0
EO + *T*	22	1,425.787	1.949	0.191	1,380.1
EO + *T* + *psub*	23	1,427.643	3.806	0.076	1,379.8
Intercept	20	1,431.795	7.958	0.009	1,390.4
ln(*T*)	21	1,433.637	9.800	0.004	1,390.1
T	21	1,433.837	10.000	0.003	1,390.3
Psub	21	1,433.937	10.100	0.003	1,390.4
TT	22	1,435.187	11.349	0.002	1,389.5
ln(*T*) + *psub*	22	1,435.687	11.849	0.001	1,390.0
T + *psub*	22	1,435.887	12.049	0.001	1,390.2
TT + *psub*[b]					
Sierra study area (CSH covariance structure; n = 519)					
EO + *psub*	20	1,035.787	0.000	0.285	994.1
Psub	19	1,036.523	0.736	0.197	997.0
EO + *T* + *psub*	21	1,037.859	2.072	0.101	994.0
Intercept	18	1,038.368	2.581	0.078	1001.0
ln(*T*) + *psub*	20	1,038.387	2.600	0.078	996.7
T + *psub*	20	1,038.587	2.800	0.070	996.9
EO	19	1,038.823	3.036	0.062	999.3
T	19	1,039.623	3.836	0.042	1,000.1
TT + *psub*	21	1,039.859	4.072	0.037	996.0
EO + *T*	20	1,039.987	4.200	0.035	998.3
TT	20	1,041.787	6.000	0.014	1,000.1
ln(*T*)[b]					
Sequoia and Kings Canyon study area (CSH covariance structure; n = 374)					
Intercept	17	865.119	0.000	0.232	829.4
EO	18	865.627	0.508	0.180	827.7
Psub	18	866.427	1.308	0.121	828.5
EO + *psub*	19	867.247	2.128	0.080	827.1
T	18	867.327	2.208	0.077	829.4
ln(*T*)	18	867.327	2.208	0.077	829.4
EO + *T*	19	867.847	2.728	0.059	827.7
T + *psub*	19	868.447	3.328	0.044	828.3
ln(*T*) + *psub*	19	868.547	3.428	0.042	828.4
TT	19	868.947	3.828	0.034	828.8
TT + *psub*	20	869.480	4.361	0.026	827.1
EO + *T* + *psub*	20	869.480	4.361	0.026	827.1

[a] Key to model notation: K = no. of parameters; AIC_c = Akaike's Information Criterion corrected for small sample size and lack of model fit; ΔAIC_c = difference between the model listed and the AIC_c of the best model; w_i = model wt based on model AIC_c compared to all other model AIC_c values; *EO* = even–odd yr effect; *T* = linear time trend; *TT* = quadratic time trend; ln(*T*) = log-linear time trend; *psub* = proportion of subad F among all F owls we sampled; CSH = compound symmetric with heterogeneous variance; TOEPH[3] = Toeplitz with heterogeneous variance estimates for the first 2 off-diagonal bands. −2ln(L) = natural log of the likelihood function.

[b] Model would not converge because of infinite likelihood.

SKC were 0.081 and 0.083, respectively, we used a mean value of 0.082 for $\hat{\sigma}_{temporal}$ for LAS and SIE (and also for the hypothetical population with mean λ = 1.0).

For all 4 of the study areas 95% confidence intervals on predictions of >10% decline spanned the interval [0, 1] within 8–10 years into the future (Fig. 12). Therefore, we restricted our inferences to 7 years into the future. For all declines, spotted owl populations at ELD and SKC were less likely to show declines in populations than were LAS and SIE, with LAS showing the greatest probability of decline. For ELD and SKC, estimated probabilities of observing a population decline >10% in 7 years were 0.23 and 0.25, respectively (95% CI = 0.00–0.87 and 0.00–0.94, respectively; Fig. 12). For SIE estimated probability of a >10% decline in 7 years was 0.41 (95% CI = 0.09–0.75); for LAS probability was 0.66 (95% CI = 0.28–0.93; Fig. 12).

Patterns were similar for >20% and >30% declines, although probabilities for higher declines were lower compared to >10% declines. At year 7, estimated probabilities of observing a population decline >20% for ELD and SKC were 0.10 and 0.11, respectively (95% CI = 0.00–0.68, and 0.00–0.83, respectively; Fig. 12). For SIE estimated probability of a >20% decline was 0.22 (95% CI = 0.01–0.53); for LAS probability was 0.44 (95% CI = 0.11–0.78; Fig. 12). Only LAS had a >10% probability of a decline >30% (0.22; 95% CI = 0.01–0.54); ELD, SKC, and SIE had probabilities of >30% decline of 0.03, 0.04, and 0.08, respectively (95% CI = 0.00–0.44, 0.00–0.58, and 0.00–0.30, respectively; Fig. 12).

After about 7 years into the future, 95% confidence intervals on predictions of population increase spanned the interval [0, 1] only for ELD and SKC (Fig. 13). In contrast, LAS had only a 0.10 probability of increasing by >10% after 7 years (95% CI = 0.00–0.34). The SIE had 0.23 probability of increasing by >10% after 7 years (95% CI = 0.01–0.55). Similar to patterns for probabilities of decline, patterns for probabilities of increases of >20% or >30% in population size followed the same pattern as >10% increase, but probabilities were naturally lower and confidence intervals were narrower in a manner similar to declines (Fig. 13).

For the hypothetical population with mean λ = 1.0 and $\hat{\sigma}_{temporal}$ = 0.082, the upper 95% confidence interval on probability of declining >10% did not exceed 0.43 at the end of the 20-year simulation (Fig. 14). At 7 years in the future, the hypothetical population exhibited 0.31, 0.15, and 0.05 probability of declining by >10%, >20%, and >30%, respectively (Fig. 14). The 95% confidence interval for >10% decline after 7 years was 0.17–0.38. At 7 years in the future, the same population exhibited 0.33, 0.20, and 0.11 probability of increasing by >10%, >20%, and >30%, respectively. The 95% confidence interval for the probability of >10% increase after 7 years was 0.19–0.39. Asymmetry of these estimates is due to asymmetry of the log-normal distribution that results when values of ln(λ) are generated from a symmetric normal distribution and then transformed with the exponential function to produce a log-normal distribution.

DISCUSSION

An important step in responding to listing petitions under the Endangered Species Act is to assess the best available information

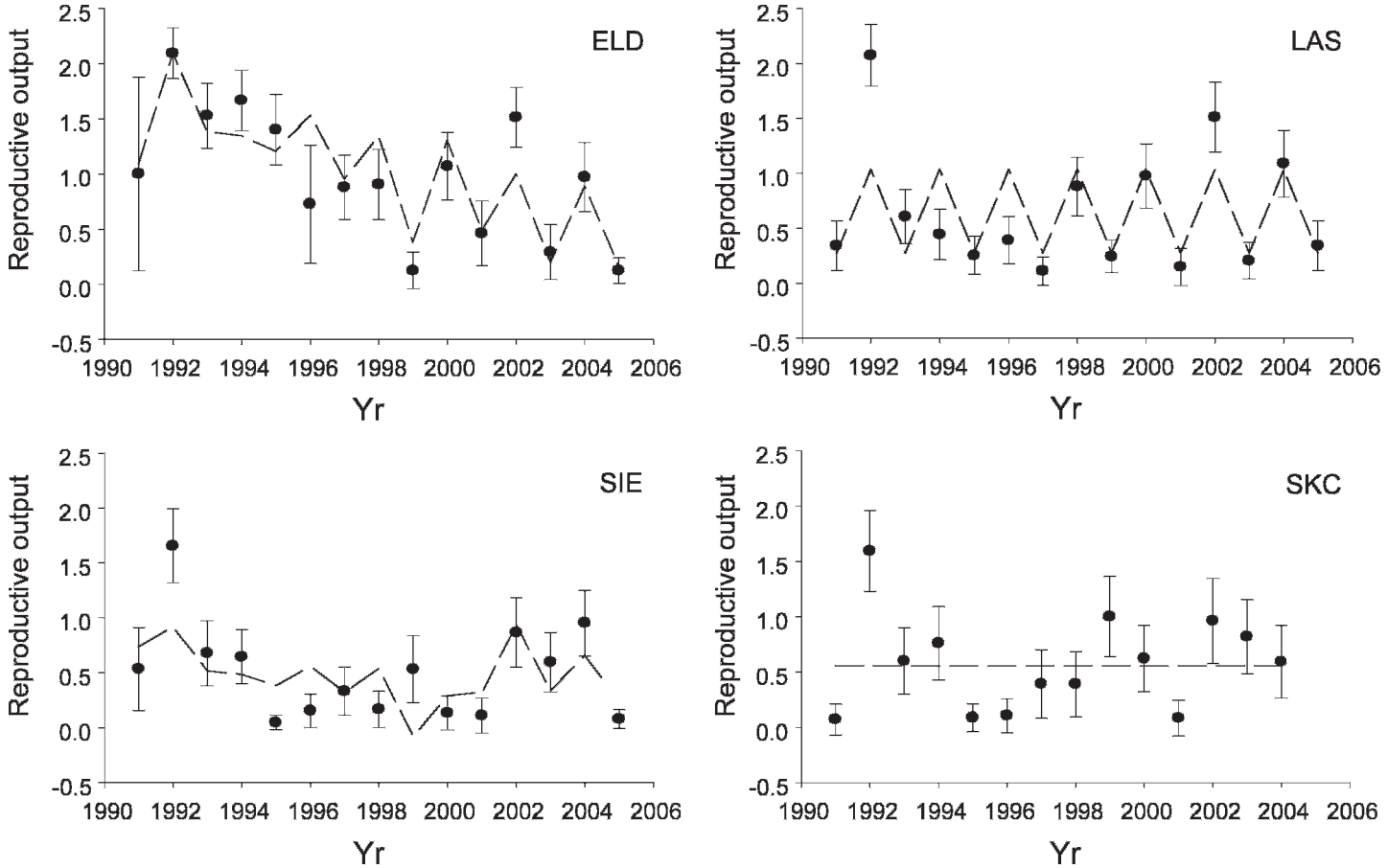

Figure 6. Annual reproductive output (no. of young fledged/F) of California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1991–2005 (point estimates and 95% CIs). Dashed lines indicate the best approximating models from mixed-models analyses.

about the species' status. Our meta-analysis of owl study populations in the Sierra Nevada is an important contribution to that step. In general, owl population growth rates in the Sierra Nevada were stationary, but there was evidence that vital rates of owl populations fluctuated over time. Reproduction did not increase or decrease over time, but showed a pattern of alternating high and low reproduction among years. Populations in protected areas (National Parks) appeared to have higher vital rates than populations inhabiting managed forests. Although our population analysis is necessary to understand population dynamics of owls over the time periods we studied them, it does not answer the key uncertainty about the effect of proposed management changes on owl habitat in the Sierra Nevada because our studies preceded implementation of the Sierra Framework (USFS 2004).

To address the uncertainty of the plan's effect on spotted owls, well-designed experimental studies should be coupled with studies of spotted owl demographics such as ours. Rigorous experimental studies provide the best avenue for understanding which resources are responsible for the variability in demographic parameters (Morrison 2001). Such an experiment is ongoing within ELD that incorporates randomly assigned experimental treatment units to estimate the behavioral response of spotted owls to habitat manipulation. Other studies in LAS, SIE, and ELD also propose to evaluate the effect of forest management on the spotted owl (Plumas-Lassen administrative study, Kings River Project, Sierra Nevada Adaptive Management Project, respectively). Unfortunately, these latter studies are quasi-experimental and lack random assignment of treatment and control units, which limits the scope of inference. Still, these latter studies are a step toward more rigorous study design because they typically yield stronger inferences than observational studies (e.g., Williams et al. 2002) such as our meta-analysis.

Comparison of Meta-Analyses for the California Spotted Owl

Noon et al. (1992) conducted the first analysis of owl population trends in the Sierra Nevada. Results of that analysis were ambiguous because of the short length of population studies and the small sample size for each study area. Subsequent to Noon et al. (1992), there have been many studies of the population ecology of the CASPO throughout its California range (LaHaye et al. 1992, 1994, 1997, 2001, 2004; Smith et al. 1999; Blakesley et al. 2001; Seamans et al. 2001). Using data from these studies, Franklin et al. (2004) conducted a comprehensive meta-analysis of status and trends of CASPO populations under study at the time (3 study populations in the Sierra Nevada, one in the southern Cascade Mountains, and one in the San Bernardino Mountains of southern California). Our study included the same populations as those in Franklin et al. (2004) except the San Bernardino study.

Table 6. Parameter estimates for best approximating models from mixed-models analyses of time trends in reproductive output (no. of young fledged/F) of California spotted owls on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1991–2005.

Study area	Model[a]	Parameter	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$) Lower	95% CI ($\hat{\beta}$) Upper
Eldorado	*EO* + *T* + *psub*	Intercept	2.279	0.175	0.077	1.937	2.622
		EO	−0.631	0.133	0.210	−0.891	−0.371
		T	−0.089	0.016	0.176	−0.120	−0.058
		Psub	−2.323	0.881	0.379	−4.050	−0.596
Lassen	*EO*	Intercept	1.033	0.150	0.145	0.739	1.327
		EO	−0.757	0.201	0.266	−1.151	−0.363
Sierra	*EO* + *psub*	Intercept	1.038	0.211	0.203	0.625	1.452
		EO	−0.301	0.168	0.560	−0.631	0.029
		Psub	−3.736	1.499	0.401	−6.673	−0.798
Sequoia and Kings Canyon	Intercept	Intercept	0.555	0.110	0.199	0.339	0.771

[a] *EO* = even–odd yr effect; *T* = linear time trend; *psub* = proportion of subad F among F owls we sampled.

Table 7. Proportion of subadults among all female California spotted owls of known age for which we determined reproductive output (no. of young fledged/F) on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1991–2005.

	Study area			
Yr	Eldorado	Lassen	Sierra	Sequoia and Kings Canyon
1991	0.20	0.05	0.00	0.14
1992	0.00	0.06	0.03	0.04
1993	0.00	0.21	0.06	0.08
1994	0.25	0.12	0.15	0.07
1995	0.00	0.02	0.10	0.03
1996	0.09	0.02	0.13	0.04
1997	0.03	0.08	0.11	0.00
1998	0.10	0.08	0.13	0.04
1999	0.20	0.10	0.22	0.11
2000	0.04	0.08	0.20	0.14
2001	0.08	0.12	0.11	0.21
2002	0.09	0.18	0.03	0.04
2003	0.13	0.18	0.11	0.04
2004	0.06	0.03	0.10	0.09
2005	0.07	0.00	0.13	

Our analysis included 5 years of additional data (2001–2005) beyond Franklin et al. (2004). In most respects, we replicated the approach used by Franklin et al. (2004) except that we conducted a PVA.

We found an increase in apparent survival (φ) of adult owls over time. In contrast, Franklin et al. (2004) found no survival model with a time trend within 7 $QAIC_c$ units of the top model. Most of the increase in survival appeared to have occurred since 2000 (Figs. 2, 3). Point estimates of $\bar{\varphi}$ for each study area were greater, by approximately 0.02 on each study area, than those reported by Franklin et al. (2004). Apparent survival of spotted owls on SKC was higher than on the other study areas, which was consistent with findings of Franklin et al. (2004).

Estimates of reproductive output on individual study areas were similar to estimates reported by Franklin et al. (2004). However, there was greater model-selection uncertainty in the earlier analysis by Franklin et al. (2004), which suggests that patterns in the top models (i.e., the *EO* effect on ELD, LAS, and SIE) persisted or strengthened with the addition of 5 years of data since Franklin et al. (2004). The increased amount of temporal variability explained by the best models (with *EO* effect) also indicated these patterns strengthened.

Our point estimates of population rate of change were lower for ELD and LAS and higher for SIE and SKC than those reported by Franklin et al. (2004). All point estimates of $\hat{\bar{\lambda}}$ were within the 95% confidence interval for individual study areas reported by Franklin et al. (2004; Table 16). Meta-analysis by Franklin et al. (2004) indicated a negative linear trend in λ_t for ELD and SIE; ELD showed an especially steep decline as evidenced by a significant negative linear trend. In our analysis, λ_t for ELD

Table 8. Estimate of mean reproductive output ($\bar{b}$; no. of young fledged/F) across years, temporal process standard deviation ($\hat{\sigma}_{temporal}$), and amount of process variation explained by mixed-model analyses of trends in reproductive output of California spotted owls on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1991–2005.

Study area	$\bar{b}$[a]	SE ($\bar{b}$)	$\hat{\sigma}_{temporal}$[b]	95% CI	CV[c]	% of variation explained[d]
Eldorado	0.988	0.154	0.317	0.079–0.555	0.321	87.2
Lassen	0.624	0.140	0.275	0.065–0.486	0.441	51.6
Sierra	0.478	0.106	0.153	0.029–0.277	0.320	41.1
Sequoia and Kings Canyon	0.555	0.110	0.152	0.022–0.283	0.275	[e]

[a] Mean estimate across yr based on intercept-only mixed model.
[b] SD of temporal process variation and its 95% CI.
[c] Estimated as $\hat{\sigma}_{temporal}/\bar{b}$.
[d] % of temporal variation explained by the fixed-effect trend model selected using min. Akaike's Information Criterion corrected for small sample size and lack of model fit (AIC_c) calculated as $\frac{\hat{\sigma}^2_{temporal} - \hat{\sigma}^2_{residual}}{\hat{\sigma}^2_{temporal}}$ where $\hat{\sigma}_{residual}$ is the variation remaining from that explained by the selected model.
[e] Not applicable because selected model was an intercept-only model.

Table 9. Model-selection results for a mixed-models meta-analysis of time trends in reproductive output (no. of young fledged/F) of California spotted owls for 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1991–2005. Models shown are those with $w_i > 0.001$ ordered by Akaike's Information Criterion with a second-order correction for small sample sizes (AIC_c) for each study area. See Table S5, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a]	K	AIC_c	ΔAIC_c	w_i	$-2\ln(L)$
Area × T + *psub*	28	4,275.785	0.000	0.935	4,218.9
Area × TT + *psub*	32	4,281.253	5.468	0.061	4,216.1
Area × T	27	4,288.223	12.439	0.002	4,233.4
Area × ln(T) + *psub*	28	4,288.685	12.900	0.001	4,231.8
Area × TT	31	4,290.582	14.798	0.001	4,227.5

[a] Key to model notation: K = no. of parameters; AIC_c = Akaike's Information Criterion corrected for small sample size and lack of model fit; ΔAIC_c = difference between the model listed and the AIC_c of the best model; w_i = model wt based on model AIC_c compared to all other model AIC_c values; Area = study areas (Eldorado, Lassen, Sierra, and Sequoia and Kings Canyon); T = linear time trend; TT= quadratic time trend; ln(T) = logarithmic time trend; *psub* = proportion of subad F among F owls we sampled. −2ln(L) = natural log of the likelihood function.

exhibited a quadratic trend, which suggested that the population initially declined through about 1999 and then increased. This early negative trend was captured in the Franklin et al. (2004) meta-analysis by a linear model, whereas the increasing trend was captured in our meta-analysis by a quadratic model incorporating 5 years of additional data. The SIE changed from a slight decline to a stationary means model because λ_t estimates were >1 for 1998–2004 (except for 2001). The LAS and SKC exhibited similar patterns in λ_t compared to previous analyses (Franklin et al. 2004).

Franklin et al. (2004) did not conduct a PVA. Our PVA indicated that 2 of the 4 study areas (LAS and SIE) were likely to experience population declines within 7 years and were very unlikely to experience population increases under current population trends. Probability of decline was greater than that of a hypothetical population with $\lambda = 1$, which would occur based on our simulation and that of theoretical predictions due to temporal variation in λ (Lewontin and Cohen 1969). In general, there was great uncertainty in PVA analyses for time intervals of >10 years; after 10 years, confidence intervals for most estimated probabilities of decline or increase spanned almost the entire interval [0, 1].

Our estimated temporal variation in λ ($\hat{\sigma}_{temporal}$) was zero for LAS and SIE, the 2 study areas for which mean estimated λ was <1.0. We viewed this estimate as a consequence of small sample size and large sampling variation and took it as evidence of small year-to-year variation in growth rate. We conducted the PVA for LAS and SIE using $\hat{\sigma}_{temporal} = 0.082$, which was the average estimate for the other 2 study areas. If the temporal variance of LAS and SIE was truly lower than this value then estimated probabilities of population decline for LAS and SIE were biased high and estimated probabilities of population increase were biased low. That is, positively biased estimates of temporal variance will result in more dire predictions than what would be observed.

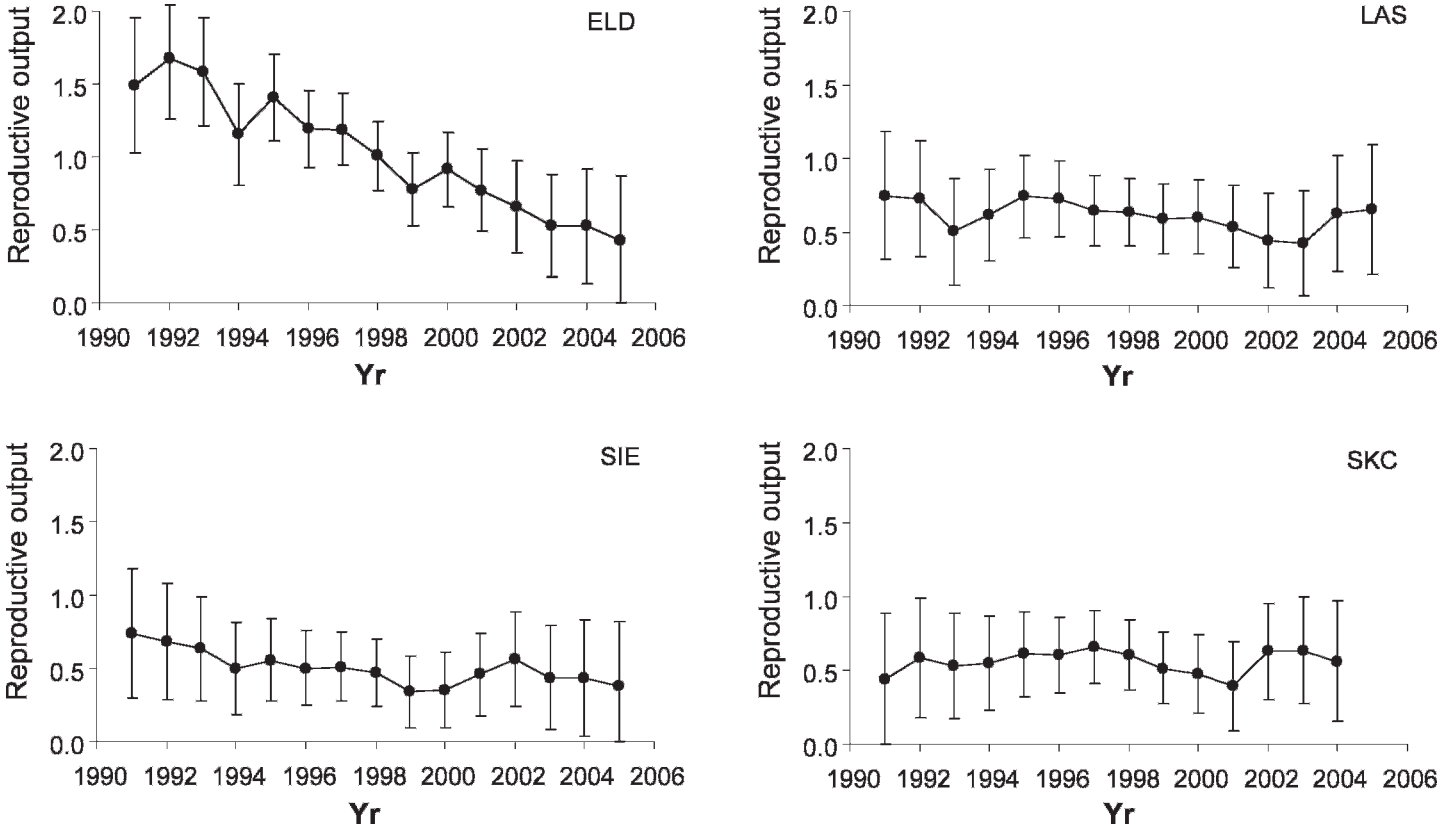

Figure 7. Time trends in reproductive output (no. of young fledged/F) for California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1991–2005, based on the mixed model ($g \times T$ + *psub*) where g = study-area effect; T = linear time trend; *psub* = proportion of subadult females among all female owls we sampled.

Table 10. Parameter estimates for the best model from a mixed-models meta-analysis of time trends in reproductive output (no. of young fledged/F) of California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1991–2005.

Model[a]	Parameter	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$) Lower	Upper
Area × *T* + *psub*	Intercept (Sequoia and Kings Canyon)	0.628	0.236	0.376	0.165	1.092
	Area (Eldorado)	1.222	0.132	0.108	0.963	1.481
	Area (Lassen)	0.201	0.104	0.514	−0.002	0.404
	Area (Sierra)	0.122	0.109	0.888	−0.091	0.335
	T (Sequoia and Kings Canyon)	0.004	0.026	6.137	−0.047	0.056
	T × area (Eldorado)	−0.093	0.014	0.153	−0.121	−0.065
	T × area (Lassen)	−0.016	0.012	0.762	−0.040	0.008
	T × area (Sierra)	−0.017	0.013	0.742	−0.042	0.008
	psub	−1.366	0.348	0.255	−2.048	−0.684

[a] *T* = linear time trend; *psub* = proportion of subad F among F owls we sampled.

Table 11. Model-selection results for a mixed models meta-analysis of effects of male and female age on reproductive output (no. of young fledged/F) of California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1991–2005. Models shown are those with $w_i > 0.001$ ordered by AIC_c for each study area. See Table S6, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a]	*K*	AIC_c	ΔAIC_c	w_i	Deviance
Area × *T* + female(S1, S2, Ad) + male(S1, S2, Ad)	31	3,922.079	0.000	0.995	3,858.9
Area × *T* + female(S1, S2, Ad)	29	3,933.733	11.654	0.003	3,874.7
Area × *T* + female(a2)	28	3,934.763	12.684	0.002	3,877.8

[a] Key to model notation: *K* = no. of parameters; AIC_c = Akaike's Information Criterion corrected for small sample size and lack of model fit; ΔAIC_c = difference between the model listed and the AIC_c of the best model; w_i = model wt based on model AIC_c compared to all other model AIC_c values; Area = study area (Eldorado, Lassen, Sierra, and Sequoia and Kings Canyon), *T* = linear time trend; S1 = owls that were 1 yr old; S2 = owls that were 2 yr old; Ad = owls that were ≥3 yr old; a2 = age effect, with S1 = S2, Ad different.

Population viability analyses assume that environmental conditions under which we estimated $\bar{\lambda}$ and $\hat{\sigma}_{temporal}$ will continue during the projection period (20 yr in our PVA; White 2000). Another important caveat in interpreting these modeled population increases is that they do not incorporate any assumptions about conditions that may limit spotted owl population growth (e.g., amount of suitable habitat or density-dependent mechanisms such as inter- and intra-specific competition for territories).

Table 12. Parameter estimates for the best model (Area × *T* + F[S1, S2, Ad] + M[S1, S2, Ad]) from a mixed-models meta-analysis examining effects of male and female age on reproductive output (no. of young fledged/F) of California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1991–2005.

Parameter[a]	$\hat{\beta}$	SE($\hat{\beta}$)	CV	95% CI ($\hat{\beta}$) Lower	Upper
Intercept (Sequoia and Kings Canyon, S2)	0.210	0.265	1.263	−0.310	0.730
Area (Eldorado)	1.162	0.140	0.120	0.888	1.435
Area (Lassen)	0.175	0.106	0.603	−0.032	0.382
Area (Sierra)	0.088	0.110	1.254	−0.128	0.304
T (Sequoia and Kings Canyon)	0.001	0.027	27.224	−0.052	0.054
T × Area (Eldorado)	−0.091	0.015	0.162	−0.120	−0.062
T × Area (Lassen)	−0.012	0.013	1.087	−0.036	0.013
T × Area (Sierra)	−0.018	0.013	0.731	−0.043	0.008
M (Ad)	0.132	0.080	0.605	−0.024	0.288
M (S1)	−0.239	0.128	0.537	−0.490	0.013
F (Ad)	0.269	0.082	0.304	0.109	0.429
F (S1)	−0.182	0.122	0.671	−0.422	0.057

[a] Key to model notation: *T* = linear time trend; S1 = owls that were 1 yr old; S2 = owls that were 2 yr old; Ad = owls that were ≥3 yr old.

Patterns in Demographic Rates

Survival.—Population growth rate for spotted owls is most sensitive to small changes in adult survival (Lande 1988, Noon and Biles 1990). Small changes in other parameters, such as reproductive output and recruitment, have less influence on the magnitude of population growth rate. However, temporal variability in territorial owl survival is substantially lower than in reproductive output and recruitment, and these latter parameters thus appear to have a greater impact on annual variability of population growth (Franklin et al. 2000, Seamans and Gutiérrez 2007*a*). This inverse relationship between the importance of a demographic parameter to population growth rate and the temporal variability of the parameter appears to be typical for most long-lived vertebrates that produce few young (Pfister 1998, Gaillard et al. 2000, Sæther and Bakke 2000). Franklin et al.

Table 13. Least-squared means estimates of reproductive output ($\dot{b}$; no. of young fledged/F) for male and female California spotted owls of 3 age classes in the southern Cascades and Sierra Nevada, California, USA, 1991–2005. Estimates are from the mixed model [Area × *T* + female(S1, S2, Ad) + male(S1, S2, Ad)].

Sex and age class[a]	$\dot{b}$	SE ($\dot{b}$)	95% CI ($\dot{b}$) Lower	Upper
M Ad	0.978	0.232	0.492	1.466
M S2	0.714	0.276	0.156	1.274
M S1	0.238	0.302	0.000	0.844
F Ad	1.124	0.234	0.634	1.614
F S2	0.586	0.280	0.018	1.152
F S1	0.222	0.290	0.000	0.804

[a] Key: S1 = owls that were 1 yr old; S2 = owls that were 2 yr old; Ad = owls that were ≥3 yr old.

Table 14. Model-selection results from analyses of population change (λ) for California spotted owls on 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1992–2004. We used model $\lambda(t)$, $\varphi(t)$, $p(t)$, parameterized with apparent survival (φ), to develop the random-effects models for each study area; we only modeled random effects for $\lambda(t)$. Models are ordered by $QAIC_c$. Models shown are those with $w_i > 0.001$. See Table S7, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a]	$QAIC_c$	$\Delta QAIC_c$	w_i	K	Deviance
Eldorado (1990–2005; n = 180, $\hat{c}$ = 1.051)					
$\lambda(TT)$ random effects	1,902.799	0.000	0.664	36	461.706
$\lambda[\ln(T)]$ random effects	1,904.728	1.928	0.253	36.31	462.946
$\lambda(T)$ random effects	1,907.546	4.747	0.062	39.21	459.287
λ(.) random effects	1,909.788	6.989	0.020	40.57	458.473
$\lambda(t)$, $\varphi(t)$, $p(t)$ fixed effects	1,916.610	13.811	0.001	45	455.271
Lassen (1990–2005; n = 241, $\hat{c}$ = 1.129)					
λ(.) random effects	2,146.256	0.000	0.553	34	454.345
$\lambda[\ln(T)]$ random effects	2,148.428	2.172	0.187	35	454.367
$\lambda(T)$ random effects	2,148.430	2.174	0.187	35	454.369
$\lambda(TT)$ random effects	2,150.289	4.032	0.074	36	454.073
Sierra (1990–2005; n = 264, $\hat{c}$ = 1.210)					
λ(.) random effects	2,364.711	0.000	0.512	36	657.285
$\lambda(T)$ random effects	2,366.700	1.990	0.190	37	657.133
$\lambda[\ln(T)]$ random effects	2,366.860	2.149	0.175	37	657.293
$\lambda(TT)$ random effects	2,367.568	2.857	0.123	38	655.855
Sequoia and Kings Canyon (1991–2004; n = 157, $\hat{c}$ = 1.030)					
$\lambda(TT)$ random effects	1,492.866	0.000	0.426	36.07	268.755
λ(.) random effects	1,494.133	1.267	0.226	36.75	268.529
$\lambda[\ln(T)]$ random effects	1,494.911	2.045	0.153	37.30	268.090
$\lambda(T)$ random effects	1,494.933	2.067	0.152	37.23	268.271
$\lambda(t)$, $\varphi(t)$, $p(t)$ fixed effects	1,497.432	4.566	0.043	39	266.850

[a] Key to model notation: K = no. of parameters; $QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model; w_i = model wt based on model $QAIC_c$ compared to all other model $QAIC_c$ values; s = sex; t = yr effect; T = linear time trend; $\ln(T)$ = log-linear time trend; TT = quadratic time trend.

(2000) and Anthony et al. (2006) report the same life-history pattern for northern spotted owls: high adult survival with little temporal variability but highly variable reproduction and recruitment.

Survival estimates we reported reflect apparent survival (φ) from capture–recapture estimators and are defined as probability that an owl alive in year t survives until year $t + 1$, remains alive within the study area, and is exposed to sampling efforts at $t + 1$. Apparent survival differs from true survival (S; probability that an owl alive in yr t survives to yr $t + 1$) in that $1 - \varphi$ includes mortality and permanent emigration whereas $1 - S$ includes only mortality (see Franklin et al. 2006). When permanent emigration is negligible, $\hat{\varphi}$ approximates S and can be used as an estimate of true survival. When comparing estimates of φ among study areas and across years, it is assumed that permanent emigration is either negligible or constant across study areas and years.

Several lines of evidence support the assumption that permanent emigration of adult spotted owls is probably negligible. First, Forsman et al. (2002) report that only 5% of adult northern spotted owls dispersed each year from their territories, and that there was no evidence of temporal variation. When adults disperse, they move only short distances ($\bar{x}$ = 6.0 km; Forsman et al. 2002), usually to adjacent territories, which suggests a low likelihood of crossing study area boundaries. Second, Blakesley et al. (2006) found only 7% of adult CASPOs dispersed each year from their territories, and their movements were generally short-distance (median = 7 km). Third, Paton et al. (1991) report no difference between survival rates (0.82–0.92) of radiomarked northern spotted owls (a closer approximation to true survival) and apparent survival estimates (0.82–0.94) of owls banded on a nearby area, with the exception of one year when a catastrophic wildfire occurred in that telemetry study area. Finally, Zimmerman et al. (2007) show that estimates of apparent survival for nonjuvenile CASPOs did not vary with study-area size (range = 81–1,400 km^2) in a demographically closed population in the San Bernardino mountains, suggesting that permanent emigration of adult owls from a range of study areas of different sizes has minimal effects on apparent survival estimates. Thus, we believe there is evidence that comparisons and trends in our apparent survival rates are reflective of changes in true survival rather than being confounded by emigration from study areas.

Results from our meta-analysis using either a priori models (Fig. 4) or the best model, a post hoc model (Fig. 3), indicated that survival rates of adult owls (territorial owls ≥3 yr old) increased from 1994 to 2004 on all study areas. Annual estimates of survival based on model-averaging of a priori models when we jointly analyzed all study areas indicated a 4–5% increase in annual survival from the first until the last year of study. Post hoc models suggested a quadratic pattern in survival with declines in middle years of the study and increases in later years. Increases in survival should have had a large positive influence on population growth rate (see description of life history above). Similarly, recruitment exhibited a quadratic pattern across study areas based on the meta-analysis (Fig. 11), and increased recruitment also would be expected to have a positive influence on population change. However, our meta-analysis of estimates of population change suggested it varied across time without a quadratic pattern for the 4 study areas (Fig. 10). Although we documented the highest annual estimates of λ based on the top model at the beginning and end of the study period, the pattern in population change did not follow patterns of apparent survival and recruitment as expected.

Relationships among demographic parameters estimated for individual study areas exhibited less consistent patterns within study areas than those estimated from the meta-analysis. Of the 4 study areas, the best models for survival were either linear with an increasing trend over time (ELD, LAS) or constant random-effects (stationary) models (SIE, SKC). Low AIC_c models for population change indicated either quadratic patterns (ELD and SKC) or random-effects means (stationary) patterns (SIE, LAS). Based on top models and model-averaged values, each study area exhibited a subtly unique combination of the 4 possible survival and population-change patterns. Similarly, the best model for reproduction varied across the 4 study areas, although 3 study areas included an even–odd year effect, and 2 of those 3 study areas also shared an effect from the proportion of subadults in the population (Table 7). We did estimate recruitment separately for each study area. Different patterns among demographic rates at both the meta-analysis and individual study-area scales suggest that additional factors influence how survival, recruitment, and reproduction interact to yield a given population growth rate.

The factors behind the increasing trend in apparent survival probability of adult spotted owls are unknown. CASPOs in the

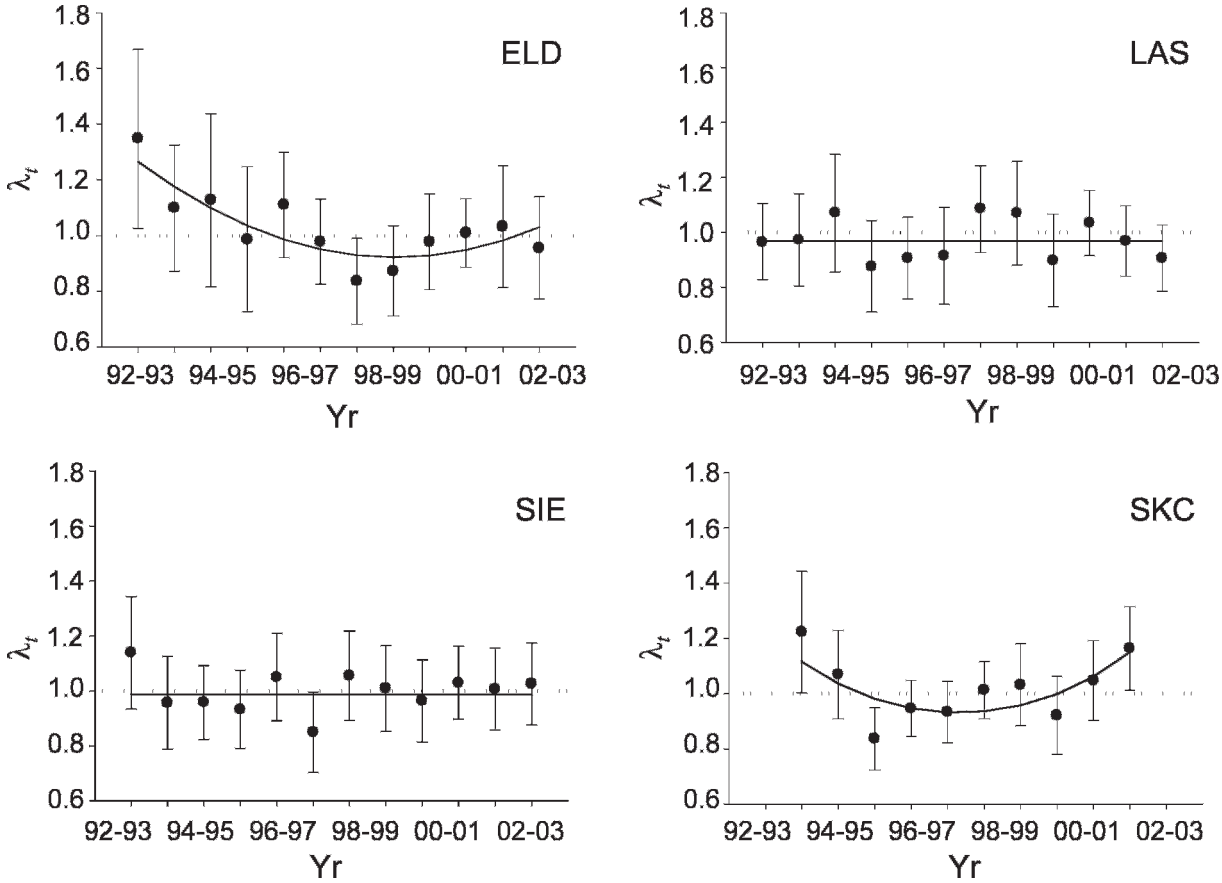

Figure 8. Annual estimates of population growth rate (λ_t) for California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1992–2003 (point estimates and 95% CIs). Solid lines indicate the best random-effects model for each study area.

Sierra Nevada share a common evolutionary history (Barrowclough et al. 1999, 2005); likely they share the same life-history strategy and demographic responses to environmental variation. We put forward 3 nonmutually exclusive, a posteriori hypotheses that may explain the estimated increase: 1) changes in habitat quality, 2) changes in environmental conditions, or 3) density-dependent mechanisms. All these hypotheses can be formally tested but require additional sources of information beyond the scope of our research. In addition, testing for density-dependent mechanisms will probably require additional years of data (Solow and Steele 1990). The following explanations show how these factors may have influenced survival, and these explanations establish hypotheses for future testing.

Temporal changes in vegetation in the Sierra Nevada have resulted from natural and anthropogenic forces and have occurred over various time scales (Sierra Nevada Ecosystem Project 1996). Standards and guidelines for spotted owl habitat management recommended by CASPO for public lands in the Sierra Nevada were in effect during most of our studies (see Verner et al. 1992*b*). These guidelines centered on conserving mature-conifer forests in and around spotted owl sites as well as maintaining forest structure and larger trees, which were known to be associated with spotted owl habitat (Verner et al. 1992*b*). Blakesley et al. (2005) found owl survival probability to be positively associated with the amount of spotted owl habitat used for nesting and roosting within 203-ha and 814-ha areas surrounding spotted owl site centers on LAS. Seamans (2005) estimated that adult survival rate was positively related to the amount of mature forest at individual sites on ELD. However, it was unlikely that mature forest increased during our study on ELD, LAS, or on the other study areas because there were modest levels of logging on public land and sometimes extensive logging on private land (R. J. Gutiérrez,

Table 15. Parameter estimates for the best random-effects models (β parameters) of population change of California spotted owls on 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1992–2004. We used model $\lambda(t)$, $\varphi(t)$, $p(t)$, parameterized with apparent survival (φ), to develop the random-effects models for each study area; we only modeled random effects for $\lambda(t)$. We defined best models by the lowest quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit ($QAIC_c$).

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

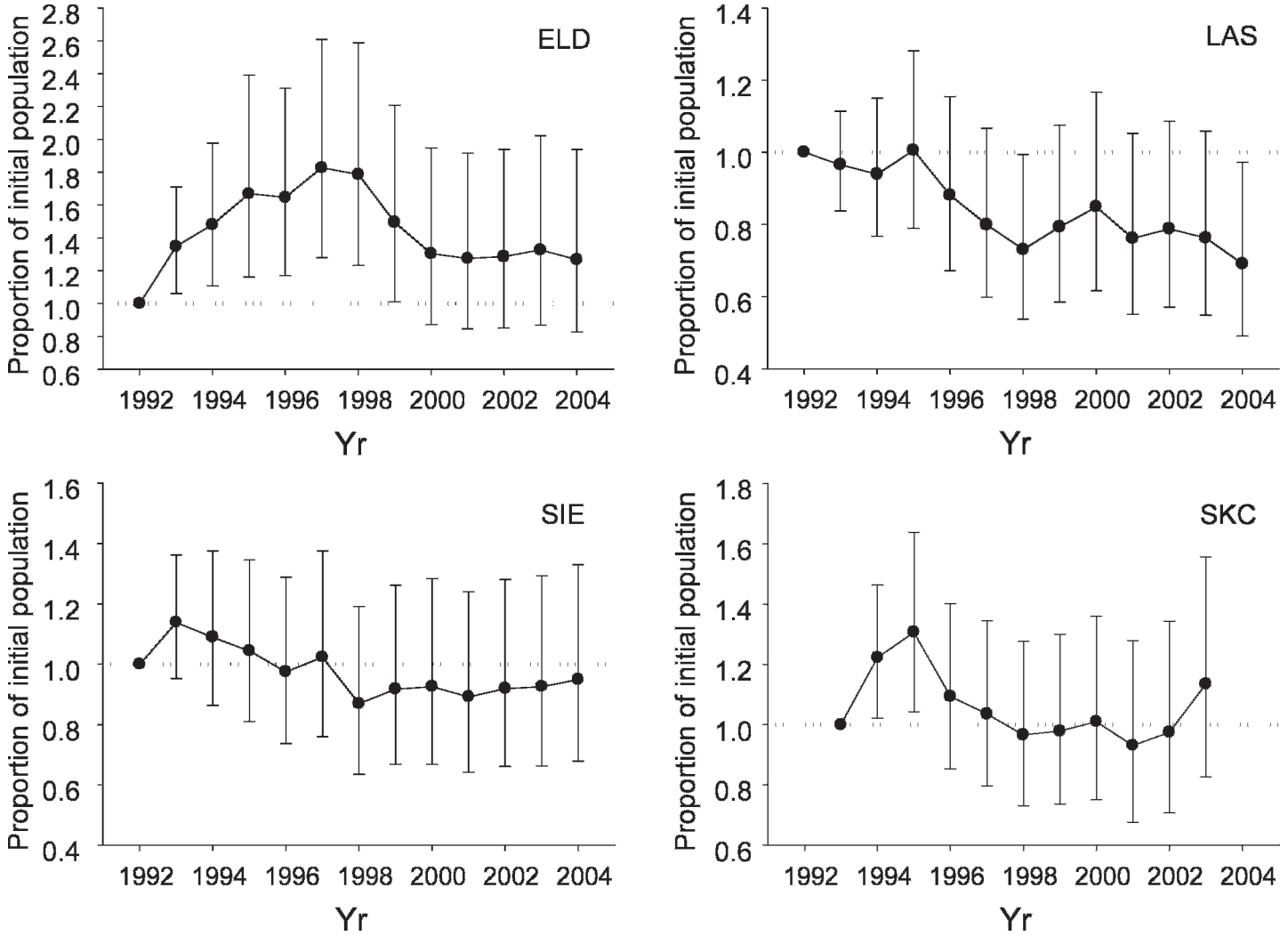

Figure 9. Trends in population size expressed as realized change in population growth rate (Δ_t), based on estimates of λ_t, for California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1992–2004 (point estimates and 95% CIs). Realized change is the proportion of the initial population size remaining each year. Note that graphs area-scaled differently.

University of Minnesota, personal observation). Thus, it did not seem plausible that the observed increase in adult spotted owl survival was due to improved habitat quality.

Temporal variability in northern and Mexican spotted owl survival appeared to be partially related to environmental conditions, particularly weather conditions (Franklin et al. 2000, Seamans et al. 2002). Weather (e.g., precipitation) also was variable among years in the Sierra Nevada during our study but it was correlated among study areas (Franklin et al. 2004). However, Seamans and Gutiérrez (2007*a*) found no strong relationships between weather and survival rate of adult CASPOs on ELD. In addition, regional climate data for the Sierra Nevada did not show any obvious patterns in seasonal temperatures or precipitation that would explain patterns we observed in apparent survival probability. Water years (Oct–Sep) ending in 1995 and 1998 had high precipitation, whereas 1990–1992, 1994, 2001, and 2004 were drier, compared to 1994–2005 averages as well as the duration of our study (Western Regional Climate Center 2009). Warmer years and seasons were interspersed with colder years and seasons during 1990–2005 (Western Regional Climate Center 2009). Neither of these general weather patterns appears related to apparent survival (Fig. 4). Therefore, it was possible that temporal trends in survival were not strongly related to weather in the Sierra Nevada during our study.

It was also possible that density-dependent mechanisms played a role in the estimated increase of adult survival (Royama 1977, Hassell et al. 1989). At lower densities, competition for resources was likely reduced, thus decreasing negative impacts on survival. A related hypothesis was reduced competition for high-quality territories, resulting in only the territories of the highest quality being occupied. Such a mechanism, density-dependent habitat selection, has been formalized as hypotheses by Fretwell and Lucas (1969) and Fretwell (1972) by their ideal-free and ideal-despotic models. Zimmerman et al. (2003) presented evidence for such a mechanism in a population of CASPOs. Thus, we expected an increase in survival if density of individuals declined on the study areas, individuals were free to select the best sites to occupy, and individuals actively sought the best available sites. Our estimates of realized change (Fig. 8) suggested that abundance peaked on LAS, SIE, and SKC in the first few years of study and

Table 16. Estimates of mean rate of population change ($\bar{\lambda}$) across time and temporal process standard deviation ($\hat{\sigma}_{temporal}$) for California spotted owls on 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1992–2004. We used model $\lambda(t)$, $\varphi(t)$, $p(t)$, parameterized with apparent survival (φ), to develop the random-effects models for each study area; we only modeled random effects for $\lambda(t)$. We based estimates on means (intercept-only) from the random-effects models.

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

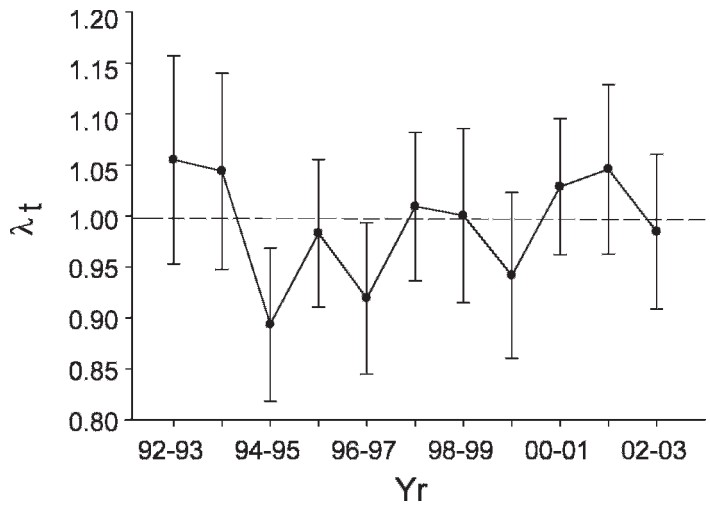

Figure 10. Annual estimates of population growth rate (λ_t) for California spotted owls on 4 study areas (Lassen, Eldorado, Sierra, Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1992–2002 (point estimates and 95% CIs), based on the model $\varphi(g \times t)$, $p(g \times t)$, $\lambda(t)$ where g = study-area effect; t = year effect.

on ELD in 1997. We did not estimate either habitat quality or investigate whether individuals preferentially sought high-quality sites. However, Seamans (2005) and Seamans and Gutiérrez (2007*b*) found a subset of high-quality sites on ELD that were preferentially occupied; sites with high probability of occupancy typically had high survival rates of territorial owls. Furthermore, Blakesley et al. (2006) found that territorial spotted owls at LAS were more likely to disperse from low-quality sites (as measured by mean reproductive output of a territory) and that breeding dispersal, although rare, resulted in improved territory quality in 72% of cases. Although this line of evidence lends support to the hypotheses of density-dependent mechanisms driving increased survival, it was still unclear if such a mechanism was operating on study areas other than ELD and LAS or if weather conditions or temporal variability in habitat quality also played a role.

Our estimate of a higher adult survival rate on SKC compared to the other study areas was of interest because of the importance of adult survival to population rate of change. We do not know why adult survival rate was higher on SKC, but it may have been related to differences in habitat quality resulting from differences in forest management both before and during the study period, presence of giant sequoia groves on SKC, differences in the proportion of oak woodlands, lower rates of breeding dispersal from SKC, or the interaction between ≥2 of these factors. In addition, Seamans and Gutiérrez (2007*b*) estimated that probability of breeding dispersal on ELD increased when habitat at a site was altered. Thus, because SKC is a National Park, it may have experienced less habitat alteration and lower rates of breeding dispersal, which may have resulted in higher estimates of apparent survival for adults relative to other study areas.

The SKC was within 2 National Parks and was managed differently than the other study areas; that is, SKC experienced less timber harvest than other study areas both during the study and during the century before the demographic studies. Territorial owl survival on ELD was correlated with the amount of mature coniferous forest at individual owl sites (Seamans 2005). The protected conservation status of SKC resulted in larger tracts of mature coniferous forest, which may have been correlated with differences in survival relative to managed forests.

Alternatively, higher survival on SKC than the other study areas may have been influenced by differences in amounts of different forest types. Such variability of forest types could be viewed as increased heterogeneity of habitats, which is correlated with higher fitness in northern spotted owls (Franklin et al. 2000). In addition, oak woodlands were abundant on SKC (21% of study area) and SIE (29% of the study area). Oak woodlands were present on ELD but intermixed with coniferous forest, and LAS contained no oak woodlands. Although the mechanism was unclear, abundance of oak woodland was negatively correlated with territorial owl survival at ELD owl sites (Seamans 2005). Thus, higher survival on SKC versus SIE could partially be explained by the lower prevalence of oak woodland, but this relationship would not hold relative for LAS. Therefore, it remains unclear how owls are responding both to variation in

Table 17. Model-selection results from a meta-analysis of rate of population change (λ), using models parameterized with apparent survival (φ) structure, of California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1992–2004. Models shown are those with $w_i > 0.001$ ordered by $QAIC_c$ for each study area. See Table S8, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a,b]	K	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
$\lambda(t)$, $\varphi(g \times t)$, $p(g \times t)$	127	6,940.351	0.000	0.594	1,204.284
λ(SKC vs. Rest), $\varphi(g \times t)$, $p(g \times t)$	117	6,941.730	1.380	0.298	1,227.151
$\lambda(g)$, $\varphi(g \times t)$, $p(g \times t)$	119	6,944.727	4.380	0.067	1,225.860
$\lambda(g + t)$, $\varphi(g \times t)$, $p(g \times t)$	132	6,945.690	5.340	0.041	1,198.831

[a] We estimated $\hat{p}$ separately for the yr immediately following the expansion of the Sierra study area and fixed it to zero on the expansion area for yr prior to the expansion. We estimated λ separately for intervals immediately preceding and following the expansion of the Sierra study area.

[b] Key to model notation: K = no. of parameters; $QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model; w_i = model wt based on model $QAIC_c$ compared to all other model $QAIC_c$ values; g = study-area effect (Eldorado, Lassen, Sierra, and Sequoia and Kings Canyon); t = yr effect; Rest = all other study areas not including SKC; SKC = Sequoia and Kings Canyon study area.

Table 18. Model-selection results from a meta-analysis of recruitment (no. of new territorial individuals at time t/no. of territorial individuals at time $t - 1$) of California spotted owls in the southern Cascades and Sierra Nevada, California, USA, 1992–2004. Models shown are those with $w_i > 0.001$ ordered by $QAIC_c$ for each study area. See Table S9, <http://dx.doi.org/10.2193/2008-475.s1>, for complete model set.

Model[a,b]	K	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
$f(g + t)$, $\varphi(g)$, $p(g \times t)$	81	6,899.559	0.000	0.919	1,261.288
$f(g + t)$, $\varphi(g + t)$, $p(g \times t)$	96	6,904.616	5.060	0.073	1,234.747
$f(g)$, $\varphi(g + t)$, $p(g \times t)$	81	6,910.027	10.470	0.005	1,271.756
$f(g)$, $\varphi(g)$, $p(g \times t)$	68	6,911.373	11.810	0.003	1,300.262

[a] We set $\hat{p}$ (probability of detection) equal to zero for yr prior to expansion of the Sierra study area and estimated $\hat{p}$ separately for the yr immediately following the expansion. We estimated $\hat{f}$ (recruitment) separately for intervals immediately preceding and following expansion of the Sierra study area.

[b] Key to model notation: K = no. of parameters; $QAIC_c$ = quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model; w_i = model wt based on model $QAIC_c$ compared to all other model $QAIC_c$ values; g = study-area effect (Eldorado, Lassen, Sierra, and Sequoia and Kings Canyon); t = yr effect.

landscape configuration and specific habitat types in terms of demographic performance. Other explanations, such as differences in topography, prey abundance, or other habitat- or population-level mechanisms need further exploration relative to explaining differences in territorial owl survival.

Reproduction.—We observed an even–odd year pattern (*EO*) in reproductive output for 3 study areas and a negative relationship between the proportion of subadults on the study area (*psub*) and reproductive output. Reproductive output of spotted owls appears to be strongly related to weather in the Sierra Nevada (Seamans and Gutiérrez 2007*a*) and elsewhere (Franklin et al. 2000, Seamans et al. 2002, Olson et al. 2004). However, weather during our study did not follow an even–odd year pattern (M. Seamans, University of Minnesota, personal observation).

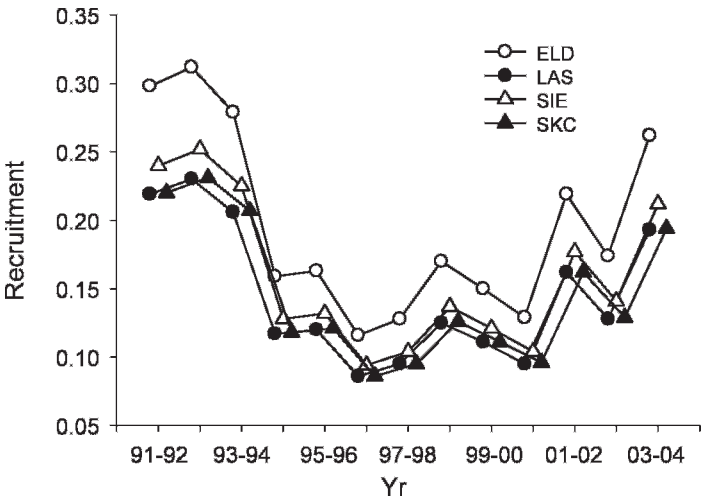

Figure 11. Annual estimates of recruitment rates (f; no. of new territorial individuals at time t/no. of territorial individuals at time $t - 1$) for California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 1992–2003, based on the model $\varphi(g)$, $p(g \times t)$, $f(g + t)$ where g = study-area effect; t = year effect.

Table 19. Estimated mean log of population growth rate [$\ln(\bar{\lambda})$] and temporal variation in $\ln(\lambda)$($\hat{\sigma}_{temporal}$, estimate and 95% CI) for California spotted owls on each of 4 study areas in the southern Cascades and Sierra Nevada, California, USA, 1992–2004.

				95% CI ($\hat{\sigma}_{temporal}$)	
Study area	$\ln(\bar{\lambda})$	SE[$\ln(\bar{\lambda})$]	$\hat{\sigma}_{temporal}$	Lower	Upper
Eldorado	0.007	0.029	0.081	0.000	0.188
Lassen	−0.027	0.014	0.000	0.000	0.094
Sierra	−0.008	0.014	0.000	0.000	0.085
Sequoia and Kings Canyon	0.006	0.031	0.083	0.018	0.195

Temporal trends in the primary prey species (northern flying squirrels [*Glaucomys sabrinus*] and woodrats [*Neotoma sp.*]; Williams et al. 1992) of the CASPO are unlikely to follow such patterns. However, Rosenberg et al. (2003) found that reproductive success of northern spotted owls in the Oregon Cascade Mountains was positively associated with deer mice (*Peromyscus* sp.) abundance, although deer mice accounted for <2% of prey biomass consumed by owls. Rosenberg et al. (2003) observed the same even–odd year pattern in owl reproduction that we observed

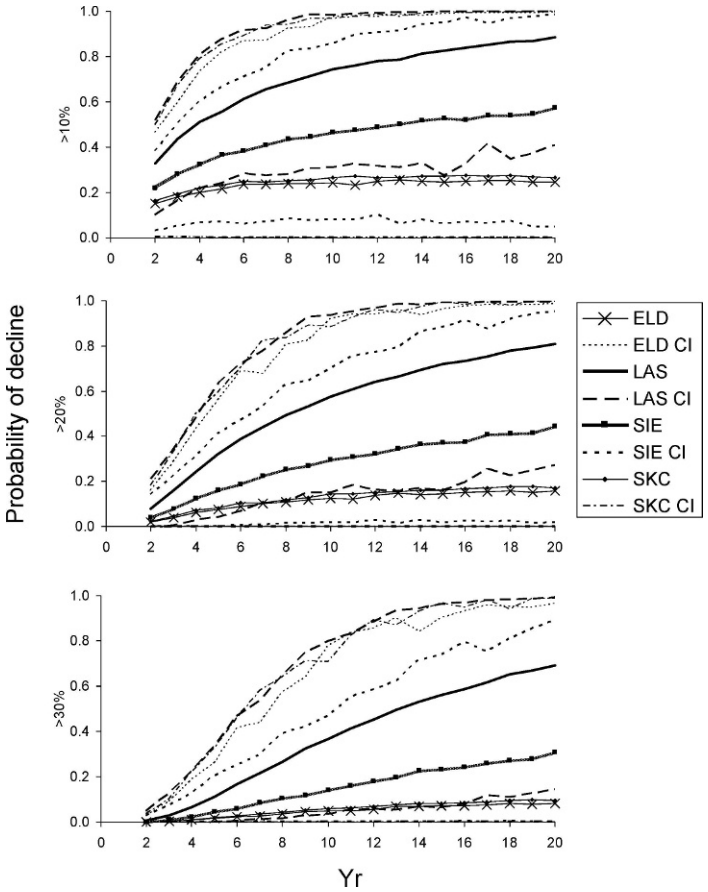

Figure 12. Probability of detecting >10%, >20%, and >30% declines in populations of California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 2–20 years into the future, given estimates of population trend and associated estimated temporal process variance from 1992 to 2002.

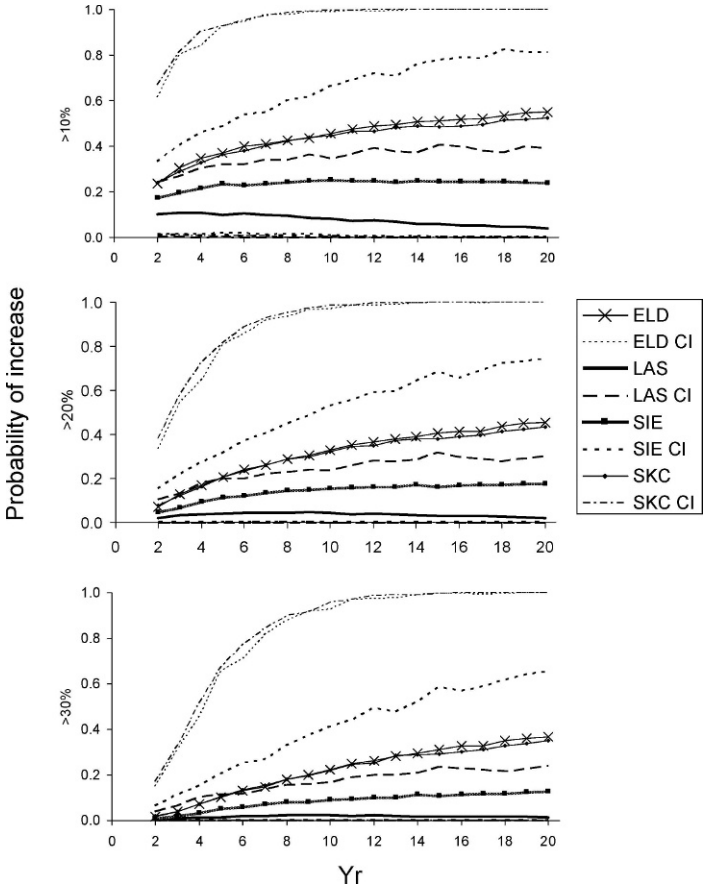

Figure 13. Probability of detecting >10%, >20%, and >30% increases in populations of California spotted owls on 4 study areas (LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia and Kings Canyon) in the southern Cascades and Sierra Nevada, California, USA, 2–20 years into the future, given estimates of population trend and associated estimated temporal process variance from 1992 to 2002, and assuming habitat is not limiting.

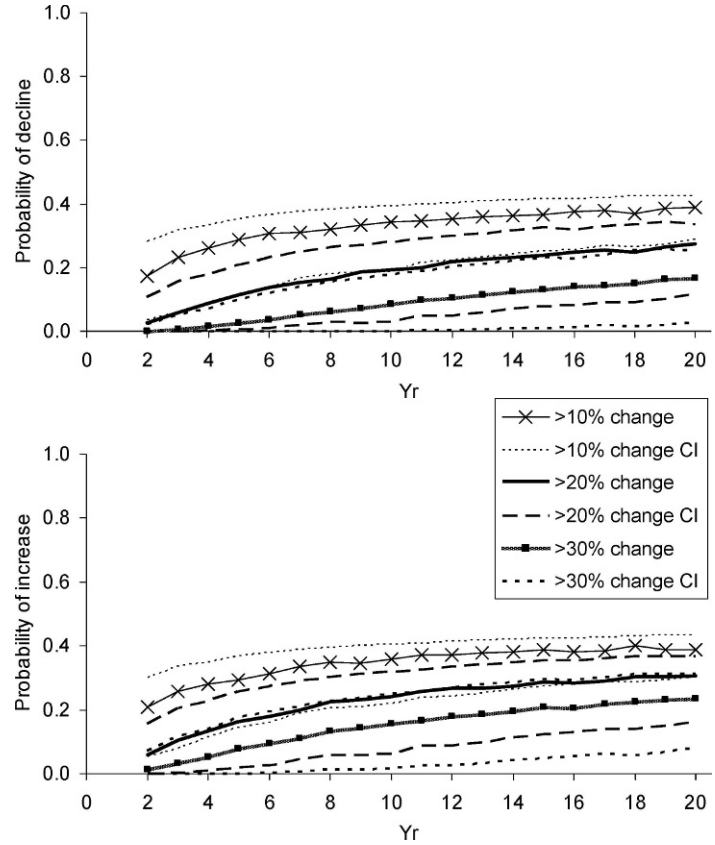

Figure 14. Probability of decrease and increase in a hypothetical population 2–20 years into the future, given $\lambda = 1.0$ (λ is defined as the finite rate of population change) and estimated temporal process variance equal to that we observed for California spotted owls in the southern Cascades and Sierra Nevada, California, USA, from 1992 to 2002.

and found the pattern to be much stronger for the proportion of owls that attempted to nest than for the number of young/territory. We observed unusually high densities of deer mice on LAS during the 2 years of highest spotted owl reproduction (1992 and 2002; J. A. Blakesley, Rocky Mountain Bird Observatory, personal observation). Therefore, it is possible that prey abundance was responsible for the exceptionally high reproduction in 1992 and 2002, and may in part explain the even–odd year trend in reproductive output. Anthony et al. (2006) reported an even–odd trend on some northern spotted owl study areas during the early years of their studies, but the trend apparently disappeared in later years. Thus, such synchrony may be transitory in spotted owl populations. The relationship between proportions of subadults and reproductive output is likely less complicated. The negative slope suggests that as the proportion of subadults increases in the population, mean annual reproductive output declines because subadults have a lower reproductive output than adults and this lower rate reduces the estimate of mean annual reproductive output (Anthony et al. 2006).

Beyond these common patterns in reproductive output, the negative linear trend in reproductive output on ELD is of potential concern. However, it is likely that the few exceptional years of reproductive output early in the study and the few low years toward the end of the study were related to weather and were largely responsible for this trend because reproductive output appears to be strongly influenced by weather on ELD (Seamans and Gutiérrez 2007*a*). Further, until about 1999, ELD had considerably higher reproductive output than the other study areas. The low years following 1999 show reproductive outputs more similar to the other areas; it is possible that the decline reflects more typical reproductive outputs, after a series of exceptionally good years (e.g., 1991–1997).

Recruitment.—We observed 2 peaks in recruitment, one at the beginning of our study and one at the end. We suspected that recruitment of new individuals into areas we sampled was a function of the availability of sites for occupancy and the extant pool of recruits. Trends in recruitment (Fig. 11) were similar to trends in survival (Fig. 4) but were not similar to trends in reproductive output (Fig. 6). Population growth rate, λ, can be viewed as the sum of apparent survival probability (φ) and per capita recruitment rate (f; $\lambda_i = \varphi_i + f_i$; Nichols and Hines 2002). Consequently, we expected density dependence to act upon these 2 vital rates, and both appeared to generally support the argument that density dependence was operating in these populations, as discussed above. Reproductive output, on the other hand, was probably more related to environmental and physiological influences. The number of young produced may not have been

density-dependent, but the number that was successfully recruited may have been.

Spotted owls recruited into the territorial population comprise owls hatched on the study area that subsequently established a territory within the boundary of the population and owls immigrating from outside the boundary of the study area. Median estimated breeding dispersal distance (distance moved by previously territorial individuals) for spotted owls at LAS was 7 km (Blakesley et al. 2006), whereas median natal dispersal distance (distance moved from the natal site to the first territorial site) was 23 km (n = 36; J. A. Blakesley, unpublished data). For northern spotted owls, median breeding dispersal distance was 3.5 km and median natal dispersal distance was 14 km (Forsman et al. 2002). Probabilities of moving also varied between juveniles and adult territorial owls. Probability of dispersal from natal territories was approximately 100% for juveniles (they are obligate dispersers [Gutiérrez et al. 1995, Forsman et al. 2002]), whereas only about 7% of territorial owls dispersed (switched sites) annually on LAS (Blakesley et al. 2006). Blakesley et al. (2006) also found that subadult territorial owls were more likely to disperse than adults. Therefore, most owls immigrating onto our study areas were likely natal dispersers rather than breeding dispersers because low breeding dispersal rates and short movement distances would have negligible impact on estimates of λ given the sizes of these study areas (Zimmerman et al. 2007).

Population growth rate.—Three of the 4 populations (ELD, SIE, and SKC) had estimates of mean annual growth rates (λ) close to 1.0 (Table 19). Given the number of years these populations were monitored, if estimates of λ were not close to 1.0, there would have been noticeably growing or declining populations of owls. Still, that all populations had estimates of λ not statistically different from 1.0 was interesting.

The spotted owl is a long-lived species whose population growth rate is closely linked to nonjuvenile survival, and nonjuvenile survival exhibits low temporal variability (Noon and Biles 1990, Franklin et al. 2000, Seamans and Gutiérrez 2007*a*). Therefore, it can be very difficult to detect statistically any long-term declines in such species because annual population declines tend to be very small and, given sampling variability, estimates of λ cannot be differentiated from those of a stationary population. Our PVA results highlight the low probability of detecting a decline or increase (10–30%) on ELD and SKC in near future (20 yr). Thus, even if populations gradually declined or increased on ELD and SKC, we would be unlikely to detect these changes over the short time frame of our study.

The question remains as to why LAS shows evidence for continuing population declines relative to the stationary populations on the other 3 areas, especially compared to the 2001 meta-analysis (i.e., all other areas showed some improvement in λ). The strong additive area effect in meta-analysis results suggests that CASPO populations may be governed by bioregional factors, such as weather or large-scale vegetation patterns that may drive owl population dynamics and parameters. However, these large-scale patterns may be modified on a study-area- and territory-specific scale by habitat-quality issues and all associated factors (e.g., vegetation, prey, predators), which may explain the difference in LAS. The population decline in the LAS study area may have occurred because it is located near the edge of CSO range with many territories in suboptimal, drier, and higher elevation forest types compared to the other study areas, including areas east of the Cascade–Sierra Nevada crest. A second possible explanation is that there may have been more timber harvest in LAS; this possibility remains speculative because, unfortunately, timber harvest data are not readily available for all study areas. A third possible explanation is that timber harvest has had a greater negative effect on LAS relative to the other study areas. Timber harvest in lower elevation forests may have lesser negative effects on owls because openings may allow increases in numbers of woodrats or other mammalian prey. In contrast, timber harvest in higher elevation forests may reduce flying squirrel numbers without a concomitant increase in more open-habitat prey. Flying squirrels are a major component of the diet of spotted owls on LAS (>61% of biomass; Verner et al. 1992*a*). Thus, differences in study-area location and effects of management across study areas, operating separately or interactively, might be a plausible hypothesis for differences we observed between LAS and the other 3 study areas.

MANAGEMENT IMPLICATIONS

Our meta-analysis showed that spotted owls were not precipitously declining across the Sierra Nevada. This observation did not mean that the population was unaffected by forest management because, based on our PVA, it was unlikely that we would have detected modest declines during our 15-year study period. Moreover, we were unable to link owl population dynamics with changes in habitat because we had no compatible habitat map for all study areas. This lack of understanding about impacts of habitat change is of particular concern when evaluating potential impacts on spotted owls from the current management plan (the Sierra Framework) for Sierra Nevada National Forests (USFS 2004). Owls may be especially impacted within the wildland–urban-interface zones specified in the Sierra Framework because more aggressive tree thinning and greater reduction of canopy cover will be allowed in these zones. Approximately 50% of all known spotted owl sites in the Sierra Nevada are within or near wildland–urban-interface zones. In view of the Sierra Framework and its potential impact on forest landscapes of the Sierra Nevada, it is especially important that land management or regulatory agencies develop more reliable vegetation maps suitable for assessing habitat of spotted owls in relationship to the vital rates of populations.

The repository of information on our 4 study areas provides a template against which managers can monitor owl responses and then respond adaptively if there are negative effects of their actions on the owl. Therefore, we reiterate the recommendations of Franklin et al. (2004) that existing demographic studies continue to be coordinated with forest management activities, that accurate vegetation maps should be developed, and that landscape-scale experiments should be designed to assess the effects of forest management on spotted owl demographic rates. In addition, we think the latter can be accomplished by integrating our population studies with implementation of the new management regimes in the Sierra Nevada to assess their impacts on spotted owls.

SUMMARY

1) Temporal trends in survival, recruitment, and population rate of change were similar among 4 study populations of CASPOs in the Sierra Nevada and Cascade Range in California, but patterns of realized change appeared to be different among the study populations.
2) Apparent annual survival of adults was higher in one protected study area (SKC) than 3 study areas under forest management.
3) After a slight decline early in our studies (1990–1995), apparent survival of adults appeared to increase over the remainder of the studies (1995–2005).
4) After a steep decline (1991–1996), recruitment increased to the end of the study (1996–2004).
5) The strongest pattern in reproductive output was an even–odd year trend, with little consistency among study areas.
6) Trends in recruitment and survival were similar, but trends in recruitment were not similar to trends in reproductive output.
7) Mean estimated population growth rates were close to 1.0 for 3 of 4 study populations (except LAS).
8) Population viability analyses indicated that the probability of a >10% population decline in 7 years ranged from 0.23 to 0.64 on our 4 study areas, with the northernmost study area, Lassen National Forest population, exhibiting the greatest probability of decline.
9) We expect neither large declines in the owl's population nor an ability to detect gradual declines over short periods. Our study cannot be used by itself to directly assess the impact of future management plans (e.g., habitat changes under Sierra Framework) or whether the owl should be listed. However, our results can be considered in concert with other data during any future evaluation of the status of the CASPO in the southern Cascades and Sierra Nevada.

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APPENDIX A

Protocol for Error-Checking Data Sets

Data files for analyses of survival (capture-history files) and reproduction were error-checked by an independent contractor. Data files for rates of population change were condensed from the capture-history files after they were fully cleaned and verified.

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

We sent all survival (capture histories) and reproductive output records as field data sheets that we scanned to pdf files and attached to e-mails or sent as paper copies through overnight mail. When the verifier found any suspicious or unclear details in a record, the verifier contacted the biologist for clarification. If it was an issue of clarity (each biologist had unique methods to record their data and it took some experience to understand), a note was made and kept with the record. When errors were found in the first round of error-checking, another sample of 10 records was selected as described above, and the error-checking process was repeated. Had there been errors in a second sample, the entire file may have been checked (as specified in the verification protocol); however, no errors were found in the second-round data files that were independently checked. During this process, 2 files did not pass on the first round.

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

Certification of Data

Name of Study Area

_____

Location of Study Area _____

Number of Years of Banding _____

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

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

_____

(print and sign name

_____

Date:_____

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

_____

print and sign name

_____

Date:_____

We generated data files for input to Program MARK from database files for survival and population changes for each study area after the survival file was verified as free from errors. We imported the reproductive output files into Statistical Analysis Software (SAS) as Excel files after being verified as free from errors.

APPENDIX B

Protocol for Modeling Apparent Survival on Individual Study Areas Using Quasi-Akaike's Information Criterion Corrected for Small Sample Size and Lack of Model Fit ($QAIC_c$) Model-Selection Criteria in Program MARK

1. $\varphi(a \times s \times t)$, $p(a \times s \times t)$ is the global model using the Cormack–Jolly–Seber (CJS) model, where a = age, s = sex, and t = time (yr) Structure 6 sets of PIMs (parameter index matrices) with time-specific values separate for each sex and age class (1–2 yr old = Subadult1 or S1; 2–3 yr old = Subadult2 or S2; >3 yr old = Adult or Ad).
2. Determine goodness-of-fit using median $\hat{c}$ on global model. Use median $\hat{c}$ for $QAIC_c$ and model selection.

   Note: the global model would not converge in Program MARK for some study areas; in such cases, $\varphi(s \times t)$, $p(s \times t)$ was the global model.
3. Using $\varphi(a \times s \times t)$, model p as follows:
   a. $p(.)$
   b. $p(a)$
   c. $p(s)$
   d. $p(a + s)$
   e. $p(c)$, where c = choice of 1 covariate selected based on biologist's experience (e.g., survey effort, *TT*, etc., where *TT* is *a* quadratic time trend).
   f. $p(r)$, where r = reproductive output covariate
   g. $p(t)$, where t = categorical time effect
   h. $p(T)$, where T = linear time trend
   i. $p[\ln(T)]$, logarithmic linear, or pseudo-threshold time trend

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

   j. $p(r)$, where r = reproductive output covariate
   k. $p(t)$ unless the model fails to converge due to over-parameterization
   l. $p(T)$
   m. $p[\ln(T)]$
4. Using the best p structure from the models in step 3, model φ with the following age- and sex-structure models:

Structure	Coding
(S1, S2, Ad) + s	φ(a3 + s)
(S1, S2, Ad)	φ(a3)
(S1, S2 = Ad) + s	φ(a1 + s)
(S1, S2 = Ad)	φ(a1)
(S1 = S2, Ad) + s	φ(a2 + s)
(S1 = S2, Ad)	φ(a2)
(S1 = S2 = Ad) + s	φ(s)
(S1 = S2 = Ad)	φ(.)
(S1, S2 = Ad) × s	φ(a1 × s)
(S1 = S2, Ad) × s	φ(a2 × s)

by the following time models:

+ t,
+ T,
× T,
+ TT,
× TT,
+ ln(T),
× ln(T), and
no time effect.

Note: in models with a sex effect and a multiplicative time effect, we modeled φ[(age × time) + sex].

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

Note: Profile likelihood confidence interval will be used for estimates of φ at parameter boundaries, as needed.
Note: Best model(s) are defined as a maximum of the 3 lowest $QAIC_c$ models with $\Delta QAIC_c \leq 2$.

APPENDIX C

Protocol for Meta-Analysis Modeling of Apparent Survival Using $QAIC_c$ Model-Selection Criteria in Program MARK

1. φ($g \times s \times t$), p($g \times s \times t$) is the global model for Cormack–Jolly–Seber (CJS) model, where g = study area, s = sex, and t = year (time).
2. Determine goodness-of-fit using median $\hat{c}$ on global model. Use median $\hat{c}$ for quasi-Akaike's Information Criterion corrected for small sample size and lack of model fit ($QAIC_c$) and model selection.
3. Run the following models.

	Model	Description of φ structure	Description of p structure
1	φ(.), p($g \times t$)	No effects	Study-area and yr effects with interactions
2	φ(g), p($g \times t$)	Study-area effect	Study-area and yr effects with interactions
3	φ($g + t$), p($g \times t$)	Study-area effect with additive yr effects	Study-area and yr effects with interactions
4	φ($g + T$), p($g \times t$)	Study-area effect with additive linear time effect	Study-area and yr effects with interactions
5	φ($g + TT$), p($g \times t$)	Study-area effect with additive quadratic time effect	Study-area and yr effects with interactions
6	φ[g + ln(T)], p($g \times t$)	Study-area effect with additive log-time effect	Study-area and yr effects with interactions
7	φ($g \times t$), p($g + t + s$)	Study-area and yr effects with interactions	Additive study-area, yr, and gender effects
8	φ($g \times t$), p($g \times t$)	Study-area and yr effects with interactions	Study-area and yr effects with interactions
9	φ($g \times t$), p(r)	Study-area and yr effects with interactions	Annual reproductive output effect
10	φ($\gamma \times t$), p($r \times s$)	Study-area and yr effects with interactions	Annual reproductive output and gender effects with interactions
11	φ($g \times t$), p($g + t$)	Study-area and yr effects with interactions	Additive study-area and yr effects
12	φ($g \times t$), p($r + s$)	Study-area and yr effects with interactions	Additive annual reproductive output and gender effects
13	φ($g \times t$), p[($g + t$) × s]	Study-area and yr effects with interactions	Additive study-area and yr effects interacting with gender
14	φ($g \times T$), p($g \times t$)	Study-area and linear time effects with interactions	Study-area and yr effects with interactions
15	φ($g \times t + s$), p(r)	Study-area and yr effects with interactions and an additive gender effect	Annual reproductive output
16	φ($g \times t + s$), p($r + s$)	Study-area and yr effects with interactions and an additive gender effect	Annual reproductive output with an additive gender effect
17	φ($g \times t + s$), p($g \times t \times s$)	Study-area and yr effects with interactions and an additive gender effect	Study-area, yr, and gender effects with all interactions
18	φ($g \times t + s$), p($g \times t + s$)	Study-area and yr effects with interactions and an additive gender effect	Study-area and yr effects with interactions and an additive gender effect
19	φ($g \times t + s$), p[($g + t$) × s]	Study-area and yr effects with interactions and an additive gender effect	Additive study-area and yr effects interacting with gender
20	φ($g \times t + s$), p($g + t$)	Study-area and yr effects with interactions and an additive gender effect	Additive study-area and yr effects
21	φ($g \times t + s$), p($g + t + s$)	Study-area and yr effects with interactions and an additive gender effect	Additive study-area, yr, and gender effects
22	φ($g \times t + s$), p($g \times t$)	Study-area and yr effects with interactions and an additive gender effect	Study-area and yr effects with interactions
23	φ($g \times t + s$), p($r \times s$)	Study-area and yr effects with interactions and an additive gender effect	Annual reproductive output and gender effects with interactions
24	φ($g \times t \times s$), p($r + s$)	Study-area, yr, and gender effects with all interactions	Additive annual reproductive output and gender effects
25	φ($g \times t \times s$), p($r \times s$)	Study-area, yr, and gender effects with all interactions	Annual reproductive output and gender effects with interactions
26	φ($g \times t \times s$), p[($g + t$) × s]	Study-area, yr, and gender effects with all interactions	Additive study-area and yr effects interacting with gender
27	φ($g \times t \times s$), p($g + t$)	Study-area, yr, and gender effects with all interactions	Additive study-area and yr effects

	Model	Description of φ structure	Description of p structure
28	$\varphi(g \times t \times s)$, $p(r)$	Study-area, yr, and gender effects with all interactions	Annual reproductive output effects
29	$\varphi(g \times t \times s)$, $p(g \times t)$	Study-area, yr, and gender effects with all interactions	Study-area and yr effects with interactions
30	$\varphi(g \times t \times s)$, $p(g \times t \times s)$	Study-area, yr, and gender effects with all interactions	Study-area, yr, and gender effects with all interactions
31	$\varphi(g \times t \times s)$, $p(g + t + s)$	Study-area, yr, and gender effects with all interactions	Additive study-area, yr, and gender effects
32	$\varphi(g \times t \times s)$, $p(g \times t + s)$	Study-area, yr, and gender effects with all interactions	Study-area and yr effects with interactions and an additive gender effect
33	$\varphi(g \times TT)$, $p(g \times t)$	Study-area and quadratic time effect with interactions	Study-area and yr effects with interactions
34	$\varphi[g \times \ln(T)]$, $p(g \times t)$	Study-area and log-linear time effect with interactions	Study-area and yr effects with interactions
35	φ(SKC, Rest), $p(g \times t)$	Group effect of SKC study area vs. other study areas	Study-area and yr effects with interactions
36	$\varphi(t)$, $p(g \times t)$	Yr effect	Study-area and yr effects with interactions
37	$\varphi(T)$, $p(g \times t)$	Linear time effect	Study-area and yr effects with interactions
38	$\varphi(TT)$, $p(g \times t)$	Quadratic time effect	Study-area and yr effects with interactions

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

Note: Profile likelihood confidence interval will be used for estimates of φ at parameter boundaries, as needed.
Note: Best model(s) are defined as a maximum of the 3 lowest AIC_c models with $\Delta QAIC_c \leq 2$.

APPENDIX D

Protocol for Modeling Reproductive Output of California Spotted Owls on Individual Study Areas

1. For known-age-class females, calculate the proportion of subadults for each study area each year. Use this proportion as a covariate in reproductive output estimation ($covariate_{psub}$). Analysis will include all females, regardless of whether age class was determined.
2. Estimate reproductive output using the following models with and without $covariate_{psub}$:

   Intercept-only

T	(linear time trend)
TT	(quadratic time trend)
$\ln(T)$	(log-linear or pseudo-threshold time trend)
EO	(Even–odd yr effect)
$EO + T$	(Even–odd yr effect with a linear time trend)

3. Site and year will each be modeled as a random effect.
4. Proc MIXED will be used to model reproductive output. The variance–covariance structures modeled include the following: first-order autoregressive [AR(1)]; AR(1) with EXP(YEAR); heterogeneous autoregressive [ARH(1)]; compound symmetric (CS); compound symmetric heterogeneous (CSH); log-linear variance (LOCAL = EXP[<*fixed year effects*>]); Toeplitz (TOEP); and a heterogeneous Toeplitz with estimates for the first 2 off-diagonal bands [TOEPH(3)]. Choice between variance–covariance structures will be made using AIC_c model selection based on restricted maximum-likelihood method (REML) in the T model without $covariate_{psub}$.
5. Estimate $\hat{\sigma}^2_{temporal}$ for reproductive output from the intercept-only model.

APPENDIX E

Protocol for Meta-Analysis of Reproductive Output of California Spotted Owls to Evaluate Time Effects

1. For known-age-class females, calculate the proportion of subadults for each study area each year. Use this proportion as a covariate in reproductive output estimation ($covariate_{psub}$). Analysis will include all females, regardless of whether age class was determined. Years for reproductive output meta-analysis will be 1991–2005.
2. Estimate reproductive output using the following models with and without $covariate_{psub}$:

   Intercept-only

T	(linear time trend)
TT	(quadratic time trend)
$\ln(T)$	(log-linear or pseudo-threshold time trend)
EO	(Even–odd yr effect)
$EO + T$	(Even–odd yr effect with a linear time trend)

   Study Area
   - Study Area + T
   - Study Area × T
   - Study Area + TT
   - Study Area × TT
   - Study Area + $\ln(T)$
   - Study Area × $\ln(T)$
   - Study Area + EO
   - Study Area × EO
   - Study Area + $T + EO$
   - Sequoia–Kings Canyon (SKC) versus other 3 study areas
   - Lassen (LAS) and Eldorado (ELD) versus Sierra (SIE) and SKC

   QUASI-POST HOC ANALYSIS to evaluate similarity in trends:
   - SKC versus other 3 study areas + best time structure from above
   - LAS and ELD versus SIE and SKC + best time structure from above

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

APPENDIX F

Protocol for Meta-Analysis of Reproductive Output of California Spotted Owls to Evaluate Effects of Male and Female Age (1–2 yr old = Subadult1 or S1; 2–3 yr old = Subadult2 or S2; >3 yr old = Adult or Ad)

1. Begin with data sets used in individual study area and meta-analyses of reproductive output. Eliminate all records in which age class of any owl is unknown. Eliminate all records of unpaired owls.
2. Define top models from results of meta-analyses of reproductive output with any covariate structure removed by the following criterion: maximum of top 3 models within $\Delta AIC_c = 2$ (i.e., within 2 AIC units). AIC_c = Akaike's Information Criterion corrected for small sample size and lack of model fit; ΔAIC_c = difference between the model listed and the AIC_c of the best model. Estimate reproductive output using the following models:

    a. Top models
    b. Top models + male age class [1 yr old (S1), 2 yr old (S2), Ad]
    c. Top models + male age class [S1, (S2 + Ad)]
    d. Top models + male age class [(S1 + S2), Ad]
    e. Top models + female age class [S1, S2, Ad]
    f. Top models + female age class [S1, (S2 + Ad)]
    g. Top models + female age class [(S1 + S2), Ad]
    h. Top model + best structure of male age class from models 2b–2d, and best structure of female age class among models 2e–2g (best based on ΔAIC_c).

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

APPENDIX G

Protocol for Modeling Population Change on Individual Study Areas Using the Pradel Model and Quasi-Akaike's Information Criterion Corrected for Small Sample Size and Lack of Model Fit ($QAIC_c$) Model-Selection Criteria in Program MARK

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

Model	No. parameters	No. parameters with adjustment for $\hat{c}$
$\lambda(t), \varphi(t), p(t)$	$3k - 4$	$(3k - 4) + 1$
$\lambda(s \times t), \varphi(s \times t), p(s \times t)$	$2(3k - 4)$	$[2(3k - 4)] + 1$
$\lambda(s \times t), \varphi(t), p(t)$	$4(k - 2) + 3$	$[4(k - 2) + 3] + 1$
$\lambda(t), \varphi(t), p(s \times t)$	$4(k - 2) + 5$	$[4(k - 2) + 5] + 1$

Note: we had originally proposed to construct the following 3 additional models, but upon further consideration, we deemed them biologically nonsensical because they constrained φ less than they constrained λ. This required that recruitment for each of the sexes must exactly compensate for the differences in φ to give the same λ value. (Furthermore, these models did not converge properly).

Nonsensical model	No. parameters	No. parameters with adjustment for $\hat{c}$
$\lambda(t), \varphi(s \times t), p(t)$	$4(k - 2) + 3$	$[4(k - 2) + 3] + 1$
$\lambda(t), \varphi(s \times t), p(s \times t)$	$5(k - 2) + 5$	$[5(k - 2) + 5] +1$
$\lambda(s + t), \varphi(s \times t), p(s \times t)$	$5(k - 2) + 6$	$[5(k - 2) + 6] + 1$

4. Select the best fixed-effects model from step 3 based on $QAIC_c$. If there is a sex effect in top models of any individual study, then incorporate the sex effect in the meta-analysis of population change.
5. Estimate variance components of the best model for ln(λ) using the following random-effects model structures. If the best fixed-effects model did not contain sex effects, constrain the parameter index matrices (PIMs) so that males = females for all parameters. Save the results (real parameter estimates) from each model. Do not include λ_1 (confounded, nonidentifiable), λ_2 (may be biased), and λ_{k-1} (confounded, nonidentifiable) from analysis. For studies with expansion areas, use the λ_i from the core area for the first year prior to and following the expansion.

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

6. Select the best random-effects model from Step 5 based on $QAIC_c$, and graph the predicted λ estimates.
7. Estimate $\bar{\lambda}$, SE($\bar{\lambda}$), and $\hat{\sigma}^2_{temporal}$ on the log scale (beta parameter estimates) from the intercept (mean) random-effects model. (This will provide a geometric mean rather than the arithmetic mean that comes from real estimates.) Back-transform $\bar{\lambda}$ and the confidence interval; use the Delta method to estimate the variance of the back-transformed $\bar{\lambda}$.

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

Parameterization of data from a study with an expansion area—see table below for an example.

These instructions pertain to a *t* model (*t* represents time as a categorical variable).

5Purpose: to ensure that λ estimates for the core area for intervals immediately prior to and the *p* and λ estimates immediately following an expansion are not confounded with data from the expansion area.

Steps:

1. The design matrix for the core area is unchanged.
2. Add 2 new columns to the design matrix to calculate λ estimates for the expansion area for the intervals immediately before and after the expansion.
3. For the expansion group, insert zeros in the cells corresponding to the λ estimate for the interval prior to the expansion and the λ estimate for the interval immediately following the expansion. This removes the expansion area data from the λ calculations for the core area.
4. Insert a 1 in the corresponding cells in the new columns added in step 2 (above) to calculate λ estimates for the expansion area for the intervals immediately prior to and following the expansion.
5. Follow steps 2–4 for the *p* estimate for the interval immediately following the expansion, except add only one new column rather than two. Also, set *p* for the year of and years prior to the expansion equal to zero (the fix parameters option in Program MARK).
6. See example below: hypothetical study with 8 years data and an expansion in year 4. Parameter Index Matrix constrained for this example as follows: φ(*t*), *p*(*t*), λ(*t*); core = original (core) study area; exp = expansion study area. Design matrix shown is for model φ(*T*), *p*(*T*), λ(*t*). Blank cells below would contain zeros in Mark.

	β1	**β2**	**β3**	**β4**	**β5**	**β6**	**β7**	**β8**	**β9**	**β10**	**β11**
	φ *T*	***p T***	**λ1**	**λ2**	**λ3**	**λ4**	**λ5**	**λ6**	**λ7**	**λ4 exp**	**λ5 exp**
φ M & F core yr 1	1										
φ M & F core yr 2	2										
φ M & F core yr 3	3										
φ M & F core yr 4	4										
φ M & F core yr 5	5										
φ M & F core yr 6	6										
φ M & F core yr 7	7										
φ M & F exp yr 1	1										
φ M & F exp yr 2	2										
φ M & F exp yr 3	3										
φ M & F exp yr 4	4										
φ M & F exp yr 5	5										
φ M & F exp yr 6	6										
φ M & F exp yr 7	7										
p M & F core yr 2		1									
p M & F core yr 3		2									
p M & F core yr 4		3									
p M & F core yr 5		4									
p M & F core yr 6		5									
p M & F core yr 7		6									
p M & F core yr 8		7									
p M & F exp yr 2		1									
p M & F exp yr 3		2									
p M & F exp yr 4		3									
p M & F exp yr 5		4									
p M & F exp yr 6		5									
p M & F exp yr 7		6									
p M & F exp yr 8		7									
λ M & F core yr 1			1								
λ M & F core yr 2				1							
λ M & F core yr 3					1						
λ M & F core yr 4						1					
λ M & F core yr 5							1				
λ M & F core yr 6								1			
λ M & F core yr 7									1		
λ M & F exp yr 1			1								
λ M & F exp yr 2				1							
λ M & F exp yr 3										1	
λ M & F exp yr 4											1
λ M & F exp yr 5							1				
λ M & F exp yr 6								1			
λ M & F exp yr 7									1		

APPENDIX H

Protocol for Meta-Analysis of Population Change Using the Pradel Model and Quasi-Akaike's Information Criterion Corrected for Small Sample Size and Lack of Model Fit ($QAIC_c$) Model-Selection Criteria in Program MARK

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

Model no.	Model	Model structure
1	$\varphi(g \times t), p(g \times t), f(g)$	All variation is in φ
2	$\varphi(g), p(g \times t), f(g \times t)$	All variation is in f
3	$\varphi(g \times t), p(g \times t), f(g \times t)$	Variation is in φ and f
4	$\varphi(g), p(g \times t), f(g)$	No variation in φ or f
5	$\varphi(g + t), p(g \times t), f(g)$	Variation in φ is parallel across study areas
6	$\varphi(g), p(g \times t), f(g + t)$	Variation in f is parallel across study areas
7	$\varphi(g + t), p(g \times t), f(g + t)$	Variation in f and φ are parallel across study areas
8	$\varphi(.), p(g \times t), f(.)$	No study area effect

To evaluate whether population growth rate (λ) for male and female subadult and adult territorial owls are correlated across study areas, use the $\varphi(g \times t)$, $p(g \times t)$, $\lambda(g \times t)$ for variance components (random-effects) models with the following structures:

Model no.	Model	Model structure
1	$\varphi(g \times t), p(g \times t), \lambda(t)$	Time only
2	$\varphi(g \times t), p(g \times t), \lambda(g \times t)$	Study area and time interaction
3	$\varphi(g \times t), p(g \times t), \lambda(g + t)$	Study area and time additive
4	$\varphi(g \times t), p(g \times t), \lambda(g)$	Study area only
5	$\varphi(g \times t), p(g \times t), \lambda$(SKC-vs.-Others)	Is SKC different than other study areas?

We will not report one λ for all 4 study areas. Rather, we will report a λ for each study area from the analysis of individual study areas from the best random-effects model (see protocol for individual study areas). If the model λ Sequoia–Kings Canyon (SKC)-versus-Others is a top model, we will also report a single λ for (Lassen [LAS], Eldoardo [ELD], Sierra [SIE]).

Notes:

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

APPENDIX I

Protocol for Population Viability Analysis (PVA)

Replicate Franklin's 2005 PVA for United States Fish and Wildlife Service with the following changes:

1. Include λ estimates from 2006 (this week's results).
2. Use log-transformed estimates of λ and standard error.
3. Eliminate probability of any decline. Estimate probability of >30%, >20%, and >10% declines over 20 years.
4. Estimate probability of >30%, >20%, and >10% increases over 20 years.
5. Compare results to hypothetical study area with $\lambda = 1.0$ and process variation from each of Lassen, Eldorado, Sierra, Sequoia–Kings Canyon. Overlay hypothetical study population projections with results from 3 above. (Note: cite Lewontin and Cohen [1969], Proceedings of the National Academy of Science of the United States of America)
6. Further expand PVA philosophy and applicability in discussion.