



Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl

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Abstract: Land and resource managers often use detection-nondetection surveys to monitor the populations of species that may be affected by factors such as habitat alteration, climate change, and biological invasions. Relative to mark-recapture studies, using detection-nondetection surveys is more cost-effective, and recent advances in statistical analyses allow the incorporation of detection probability, covariates, and multiple seasons. We examined the efficacy of using detection-nondetection data (relative to mark-recapture data) for monitoring population trends of a territorial species, the California Spotted Owl (*Strix occidentalis occidentalis*). We estimated and compared the finite annual rates of population change (λ_t) and the resulting realized population change (Δ_t) from both occupancy and mark-recapture data collected over 18 years (1993–2010). We used multiseason, robust-design occupancy models to estimate that territory occupancy declined during our study ($\Delta_t = 0.702$, 95% CI 0.552–0.852) due to increasing territory extinction rates ($\hat{\epsilon}_{1993} = 0.019$ [SE 0.012]; $\hat{\epsilon}_{2009} = 0.134$ [SE 0.043]) and decreasing colonization rates ($\hat{\gamma}_{1993} = 0.323$ [SE 0.124]; $\hat{\gamma}_{2009} = 0.242$ [SE 0.058]). We used Pradel's temporal-symmetry model for mark-recapture data to estimate that the population trajectory closely matched the trends in territory occupancy ($\Delta_t = 0.725$, 95% CI 0.445–1.004). Individual survival was constant during our study ($\hat{\phi}_{1993} = 0.816$ [SE 0.020]; $\hat{\phi}_{2009} = 0.815$ [SE 0.019]), whereas recruitment declined slightly ($\hat{\jmath}_{1993} = 0.195$ [SE 0.032]; $\hat{\jmath}_{2009} = 0.160$ [SE 0.023]). Thus, we concluded that detection-nondetection data can provide reliable inferences on population trends, especially when funds preclude more intensive mark-recapture studies.

Keywords: dynamic occupancy model, population dynamics, Sierra Nevada, *Strix occidentalis occidentalis*, temporal-symmetry model

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Resumen: Los manejadores de tierras y recursos a menudo utilizan muestreos de detección-no detección para monitorear las poblaciones de especies que pueden ser afectadas por factores como la alteración del hábitat, cambio climático e invasiones biológicas. En relación con estudios de captura-recaptura, el uso de muestreos de detección-no detección es más rentable, y los avances recientes de los análisis estadísticos permiten la incorporación de la probabilidad de detección, covariables y múltiples temporadas. Examinamos la eficacia del uso de datos de detección-no detección (relativos a datos de captura-recaptura) para monitorear las tendencias poblacionales de una especie territorial, el búho moteado de California (*Strix occidentalis occidentalis*). Estimamos y comparamos las tasas finitas anuales de cambio poblacional (λ_t) y cambio poblacional realizado resultante (Δ_t) tanto para datos de ocupación y de captura-recaptura recolectados a lo largo de 18 años (1993–2010). Utilizamos modelos de ocupación multianuales de diseño robusto para estimar que la ocupación de territorio declinó durante nuestro estudio ($\Delta_t = 0.702$, 95% IC 0.552–0.852) debido al incremento en las tasas de extinción de ocupación de territorio ($\hat{\epsilon}_{1993} = 0.019$ [ES 0.012]; $\hat{\epsilon}_{2009} = 0.134$ [ES 0.043]) y el decremento de las tasas de colonización ($\hat{\gamma}_{1993} = 0.323$ [ES 0.124]; $\hat{\gamma}_{2009} = 0.242$ [ES 0.058]). Utilizamos el modelo de simetría temporal de Pradel para datos de captura-recaptura para estimar que la trayectoria de la población era similar a las tendencias de la ocupación de territorio ($\Delta_t = 0.725$, 95% IC 0.445–1.004). La supervivencia individual fue constante a lo largo de nuestro estudio ($\hat{\phi}_{1993} = 0.816$ [ES 0.020]; $\hat{\phi}_{2009} = 0.815$ [ES 0.019]), mientras que el reclutamiento declinó levemente ($\hat{\jmath}_{1993} = 0.195$ [ES 0.032]; $\hat{\jmath}_{2009} = 0.160$ [ES 0.023]). Por lo tanto, concluimos que los datos de detección-no detección pueden proporcionar

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inferencias confiables sobre las tendencias poblacionales, especialmente cuando los fondos excluyen estudios más intensivos de captura-recaptura.

Palabras Clave: dinámica de poblaciones, modelo de ocupación dinámica, modelo de simetría temporal, Sierra Nevada, *Strix occidentalis occidentalis*

Introduction

A primary responsibility of land and resource managers is to monitor (often over large spatial scales) the population trends of focal species that may be affected by changing future conditions, such as habitat change, climate change, and biological invasions. The use of detection-nondetection data (i.e., occupancy monitoring) may be a cost-effective, robust means of achieving this goal (Noon et al. 2012). Furthermore, recent advances in the statistical analyses of site-occupancy data allow the incorporation of imperfect detection, site- and survey-specific covariates, multiseason dynamics, and multiple states to assess a wide range of ecological and management questions, which enhances the utility of occupancy analyses (MacKenzie et al. 2006; Nichols et al. 2007).

Mark-recapture studies offer an alternative means of monitoring populations and provide more detailed data on demographic vital rates, such as survival and recruitment (Armstrup et al. 2005). However, mark-recapture studies are labor intensive, relatively costly, and generally encompass a small geographic area due to these constraints. In contrast, occupancy studies require surveying for only the presence or absence of a species and generally allow a larger area to be surveyed at a lower cost (Noon et al. 2012). Furthermore, metapopulation models and species-abundance distributions describe a fundamental, theoretical relation between occupancy and abundance so that site occupancy should provide a useful index for population status (Royle et al. 2005; Borregaard & Rahbek 2010). The results of some empirical research support the theoretical relation between occupancy and abundance. For example, Zuckerberg et al. (2009) found strong correlations between regional occupancy and relative abundance for a wide range of bird species in the state of New York (U.S.A.) over 2 periods. For these reasons, researchers have recently used detection-nondetection data, rather than mark-recapture data, to monitor the population status of species over large spatial extents (e.g., Burton et al. 2011; Karanth et al. 2011; Thorn et al. 2011). However, we were unaware of existing studies in which annual trends in site occupancy were compared with annual population trends (estimated with mark-recapture data from the same study population), a comparison that would more convincingly demonstrate a close relation between occupancy and abundance.

The California Spotted Owl (*Strix occidentalis occidentalis*) is a focal management species in the Sierra Nevada because it uses late-seral forests for nesting and

roosting (Gutiérrez et al. 1992). The U.S. Forest Service (USFS) considers the owl a “sensitive” species, which motivated the USFS to develop a Sierra-wide forest management plan (U.S. Forest Service 2004). The owl is highly territorial, displays strong site fidelity, and breeds irregularly, typically producing 1–2 young in years when it reproduces (Gutiérrez et al. 1995). Currently, the USFS monitors owl populations in the Sierra Nevada with long-term, mark-recapture studies designed to detect territorial adults (i.e., those responding to vocal surveys) (Franklin et al. 2004; Blakesley et al. 2010). The vital rates of those individuals are then quantified annually. These studies require intensive survey effort over large areas because California Spotted Owls have large home ranges (mean = 555 ha [SE 100] on the basis of data collected within and near our study area) (Williams et al. 2011). Thus, occupancy studies on a regional scale could be an ideal complement to the mark-recapture studies.

To test the efficacy of using occupancy studies to infer population status, we compared long-term trends (1993–2010), estimated from both occupancy and mark-recapture data, in a California Spotted Owl population in the central Sierra Nevada. We considered each owl territory a site, so the sampling population was similar for both types of data (i.e., all territorial adults on our study area vs. all owl territories). Thus, we expected annual trends in owl site occupancy should be similar to population trends estimated from the mark-recapture data.

Study Area

We conducted our study on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California. The Eldorado Density Study Area (EDSA) has been the site of a long-term mark-recapture study of California Spotted Owls (Seamans et al. 2001; Franklin et al. 2004; Blakesley et al. 2010). We surveyed the entire area each year without regard to land cover, topography, access, or land ownership. Approximately 60% of the EDSA was public land managed by the USFS, and 40% was private land managed by timber companies.

The primary vegetation type on the EDSA was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Common understory species included California black oak (*Quercus kelloggii*), bigleaf maple (*Acer macrophyllum*), and tanoak

(*Lithocarpus densiflorus*). Red-fir (*Abies magnifica*) forest, dominated by red fir and lodgepole pine (*Pinus contorta*), was present at higher elevations. Other local vegetation types and landscape features included chaparral, black oak woodland, and barren rock. Elevations on the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

Methods

Spotted Owl Surveys

We conducted surveys annually for spotted owls from 1986–2010 during the owl breeding season (1 April to 31 August). We did not conduct complete surveys over the entire EDSA in the early years of the study because funding constraints limited our survey effort. Hence, we examined survey coverage of the EDSA (see Survey Coverage of Study Area below) to determine when our survey effort was adequate to include data for analyses. In our surveys we imitated spotted owl vocalizations (vocal lure) for 10 minutes at a survey station or used vocal lures while walking along a survey route. We determined sex of a responding owl by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected on nocturnal surveys, we conducted diurnal surveys to band unmarked owls, resight marked owls, assess reproduction, and band fledglings (Franklin et al. 1996). We banded owls with a numbered locking metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al. 1996). We included both nocturnal and diurnal surveys in our occupancy analyses. We considered sites a territory where owls responded to vocal lures and were subsequently observed either roosting or nesting.

Survey Coverage of Study Area

To determine the initial year of complete survey coverage of the EDSA, we used ArcGIS 9.3 (ESRI, Redlands, California) to examine annual survey coverage of the EDSA. We drew a 0.80-km (0.5 mile) circle around each survey point where owls were not detected and a 1.61-km (1 mile) circle around each nest or roost location. We chose the 0.80-km distance because we expected surveyors to be able to hear any owls within this distance that responded during the surveys. We chose the 1.61-km distance because it was unlikely that other territorial owls would occur so close to a given territory (mean nearest-neighbor distance between owl territory centers from 1993–2010 was equal to 2.26 km). We then overlaid these circled areas on a map of the EDSA and calculated the proportion of the EDSA contained within the estimated areas of survey coverage each year. We chose 1993 as the starting year for our analyses because it was the first year

that >90% of the EDSA land area was surveyed and >1 survey was conducted at >90% of the owl territories. The surveys conducted prior to 1993 served to develop survey protocols and identify owl territories. Our approach was consistent with previous mark-recapture analyses for the EDSA that did not use data collected prior to 1990 because it was subjectively determined that survey effort was inadequate from 1986–1989 (Franklin et al. 2004; Blakesley et al. 2010).

Occupancy Modeling

We used a multiseason, robust-design occupancy model (MacKenzie et al. 2003) to assess occupancy trends of owls. We divided each breeding season into 10 bimonthly periods (1–15 April, 16–30 April, 1–15 May, 16–31 May, etc.). This approach provided greater biological meaning to the survey occasions at individual territories, relative to sequentially using all surveys conducted at a territory each year. For example, if one territory was first surveyed in early April and another in late May, we believed that it was inappropriate to model the detection probability for the first survey occasion at each site with the same parameter. We chose bimonthly periods to retain as much data as possible without having too many missing observations within a given sampling period. If a territory was not surveyed during a bimonthly period, we treated it as a missing observation. If multiple surveys were conducted within the same period, we assigned a zero to the survey history if no owls were detected during any survey and a one if at least one owl was detected during any survey. Our primary sampling periods were breeding seasons (i.e., years), and our secondary sampling periods were the bimonthly periods within each breeding season.

Our statistical model contained parameters for initial occupancy (ψ_1), local extinction (ε_t), local colonization (γ_t), and detection probability ($p_{t,j}$) (MacKenzie et al. 2003). We used PRESENCE (version 3.1) (Hines 2006) to compare models with Akaike's information criterion (AIC) (Burnham & Anderson 2002). We used MARK (version 6.1) (White & Burnham 1999) to obtain model-averaged parameter estimates that were based on Akaike weights (ω_i) (Burnham & Anderson 2002). Both programs also provided annual estimates of occupancy ($\hat{\psi}_t$) and rates of change in occupancy ($\hat{\lambda}_t$), which were derived recursively from $\hat{\psi}_1$, $\hat{\varepsilon}_t$, and $\hat{\gamma}_t$ (MacKenzie et al. 2003). We then calculated the geometric mean for the rate of change in occupancy ($\hat{\lambda}$) and estimated the realized change in occupancy (Δ_t) as

$$\Delta_t = \prod_{i=1}^{t-1} \hat{\lambda}_i. \quad (1)$$

Thus, Δ_t was the product of $\hat{\lambda}_{1993} \times \hat{\lambda}_{1994} \times \dots \times \hat{\lambda}_{2009}$ and represented the proportion of the initial population (i.e., the number of occupied territories) remaining in

2010. We obtained variance estimates for $\hat{\lambda}$ and Δ_t with the delta method (Powell 2007).

We conducted the modeling in 2 stages. First, we used the fully parameterized model ($\psi_1, \varepsilon_t, \gamma_t, p_{t,j}$) to model within-season p . We developed 16 models containing covariates that we hypothesized affect p on survey occasion j during year t (Supporting Information). We used month as a covariate because each month corresponded to a different stage of the owl's breeding cycle and breeding-cycle stage affects owl behavior (April, incubation period; May, brooding; June, young fledged from nest; July, fledglings and adults typically near nest tree; August, fledglings and adults typically farther from nest tree) (Gutiérrez et al. 1995). We separated the survey season into pre fledging (1 April to 31 May) and post fledging (1 June to 31 August) periods because the fledging period affects owl behavior. We included time trends (linear, quadratic, and log linear) because Seamans and Gutiérrez (2007) found that p varied in a log-linear trend over the survey season on the EDSA. We specified that p was different on survey occasions after the survey when owls were initially detected at a territory because observers intensified their efforts to relocate detected birds in order to resight or capture birds and assess reproduction (Riddle et al. 2010). Because we expected nesting owls to be more easily detected than non-nesting owls (Nichols et al. 2007; MacKenzie et al. 2009), we used reproductive status as a covariate. Nesting owls may defend their territories more aggressively (i.e., respond more readily to vocal surveys) or spend more time in the territory core area, where most of our survey effort occurred. We did not include any covariates for survey effort because multiple surveys were often conducted within a sampling period at sites where owls were known to be present (i.e., for the demographic study), which created a spurious, positive relation between survey effort and p . We also did not include a covariate for survey type because surveys of different types were often conducted within the same period.

In the second modeling stage, we used the best structure for within-season variation in p and compared models in which $\varepsilon_t, \gamma_t,$ and p_t varied in 5 ways: constant (\cdot), different in each year (t), linear trend (T), quadratic trend (TT), and log-linear trend ($\ln T$). We considered all possible combinations of temporal trends for $\varepsilon_t, \gamma_t,$ and p_t . We did not include additional covariates (e.g., habitat quality within a territory) because our main interest was to obtain the best estimate of temporal trends in occupancy, not to test biological hypotheses related to territory occupancy.

Mark-Recapture Modeling

In prior mark-recapture analyses of some of our data, a temporal-symmetry model (Pradel 1996) was used that

contained parameters for finite rate of population change (λ_t), annual survival (φ_t), and capture probability (p_t) and treated λ_t as a random effect (Franklin et al. 2004; Blakesley et al. 2010). Blakesley et al. (2010) used mark-recapture data from 1990–2005 on the EDSA, but they omitted the first 2 and last estimates of λ_t , which may have been confounded with p_t when the parameters were modeled with a categorical time covariate (i.e., a different parameter estimate for each year). We used data from only 1993–2010 in our analyses to maintain congruence with our occupancy modeling. Our top models did not include any categorical time covariates, so we did not omit any λ_t estimates from our results.

We also used a functional form of Pradel's temporal-symmetry model that contained parameters for recruitment (f_t), φ_t , and p_t , and treated all parameters as fixed effects. Although treating $\hat{\lambda}_t$ as a random effect allows the partitioning of process variance (i.e., variation in $\hat{\lambda}_t$ due to covariate effects) from sampling variance (i.e., variation in $\hat{\lambda}_t$ due to random sampling; Burnham & White 2002), we wished to maintain an approach consistent with our occupancy modeling. An additional benefit of our approach was the explicit modeling of both mechanisms (recruitment and survival) responsible for population change. For comparison with Blakesley et al. (2010), we also conducted a random-effects analysis with their methods (see Supporting Information).

We used MARK (version 6.1) to compare competing models with AIC_c and obtain model-averaged parameter estimates on the basis of ω_i . MARK provided annual estimates of finite rates of population change ($\hat{\lambda}_t$), which were derived from \hat{f}_t and $\hat{\varphi}_t$ (Pradel 1996). We then calculated $\hat{\lambda}, \Delta_t,$ and their variances as above (see Occupancy Modeling above).

As with the occupancy modeling, we conducted the mark-recapture modeling in 2 stages. First, we used the fully parameterized model (f_t, φ_t, p_t) to model p_t . In this case, p refers to the probability of recapturing a marked individual that was still alive during a given year, whereas p in the occupancy modeling referred to the probability of detecting an owl(s) at an occupied territory during a given survey. We developed 12 models containing covariates that we hypothesized could affect p (Supporting Information). Walk-in effort represented the amount of time spent conducting diurnal surveys in a given year. Relatively greater walk-in effort is positively correlated with p on the EDSA for survival analyses (Blakesley et al. 2010). Blakesley et al. (2010) also found that a bird's sex affected p on the EDSA. Finally, we included time trends (linear, quadratic, and log linear) because observer proficiency may have improved as our study progressed.

In the second modeling stage, we used the best structure for p_t and compared models in which f_t and φ_t varied temporally in 5 ways: constant (\cdot), different in each year (t), linear trend (T), quadratic trend (TT), and log-linear trend ($\ln T$). We considered all possible combinations of

Table 1. Top-ranked models for multiseason occupancy analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993–2010.

Model ^a	No. parameters	AIC ^b	ΔAIC^c	ω_i^d
$\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	8	3081.93	0.00	0.108
$\psi_1, \gamma_{\cdot}, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	8	3082.60	0.67	0.077
$\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	9	3082.82	0.89	0.069
$\psi_1, \gamma_{\ln T}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	9	3083.44	1.51	0.051
$\psi_1, \gamma_T, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	9	3083.50	1.57	0.049
$\psi_1, \gamma_{\cdot}, \varepsilon_{TT}, p_{T, \text{initial} + \text{repro}}$	9	3083.65	1.72	0.046
$\psi_1, \gamma_{\cdot}, \varepsilon_T, p_{TT, \text{initial} + \text{repro}}$	9	3083.74	1.81	0.044
$\psi_1, \gamma_{\ln T}, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	9	3084.04	2.11	0.038
$\psi_1, \gamma_T, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	9	3084.15	2.22	0.036
$\psi_1, \gamma_{\cdot}, \varepsilon_{TT}, p_{TT, \text{initial} + \text{repro}}$	10	3084.32	2.39	0.033
$\psi_1, \gamma_{\ln T}, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	10	3084.41	2.48	0.031
$\psi_1, \gamma_T, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	10	3084.46	2.53	0.030
$\psi_1, \gamma_{TT}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	10	3084.66	2.73	0.028
$\psi_1, \gamma_{\cdot}, \varepsilon_T, p_t, \text{initial} + \text{repro}$	24	3085.03	3.10	0.023
$\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_t, \text{initial} + \text{repro}$	24	3085.05	3.12	0.023
$\psi_1, \gamma_{TT}, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	10	3085.10	3.17	0.022
$\psi_1, \gamma_{\ln T}, \varepsilon_{TT}, p_{T, \text{initial} + \text{repro}}$	10	3085.20	3.27	0.021
$\psi_1, \gamma_{\ln T}, \varepsilon_T, p_{TT, \text{initial} + \text{repro}}$	10	3085.25	3.32	0.021
$\psi_1, \gamma_T, \varepsilon_{TT}, p_{T, \text{initial} + \text{repro}}$	10	3085.26	3.33	0.020
$\psi_1, \gamma_T, \varepsilon_T, p_{TT, \text{initial} + \text{repro}}$	10	3085.34	3.41	0.020
$\psi_1, \gamma_{TT}, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	11	3085.62	3.69	0.017

^aModel variables are defined in Methods.

^bAkaike's information criterion.

^cDistance in AIC units from the model with the lowest AIC value.

^dAkaike weight.

temporal trends for f_t and φ_t . As with the occupancy modeling, we did not include additional biological covariates because our goal was to obtain the best estimate of temporal trends in population size, not to test biological hypotheses related to individual survival or recruitment.

Results

Territory Occupancy

We located 45 owl territories from 1993–2010, and owls had been detected at least once at all sites by 1997. Reproduction by owls was observed at 39 of 45 territories at least once during the study, which indicated we had identified biologically relevant territories. At least 1 owl was detected at 40 of 45 (90.0%) territories in 1993, but at only 26 of 45 (57.8%) territories surveyed in 2010. Thus, naïve territory occupancy estimates, which did not account for imperfect detection, indicated occupancy declined by 31% (14/45) during our study.

In the first modeling stage, model $\{\psi_1, \gamma_t, \varepsilon_t, p_{t, \text{initial} + \text{repro}}\}$ had 100.0% of the Akaike weight among the 16 candidate models. Therefore, we used $p_{t, \text{initial} + \text{repro}}$ in all second-stage models, of which $\{\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}\}$ was the top-ranked model (Table 1). However, considerable uncertainty existed regarding which model best fit the data as the top 7 models were

within 2.0 AIC units of each other (Burnham & Anderson 2002). Parameter estimates from model $\{\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}\}$ indicated that within-year detection probability of owls was higher on surveys following the initial detection of an owl at a territory ($\hat{\beta}_{\text{initial}} = 1.20$ [SE 0.11]) and higher for nesting owls ($\hat{\beta}_{\text{repro}} = 1.63$ [SE 0.14]). Annual detection probabilities were generally high, particularly for nesting owls (Supporting Information).

Due to model-selection uncertainty, we obtained model-averaged estimates for $\hat{\gamma}_t$, $\hat{\varepsilon}_t$, and $\hat{\psi}_t$ with the 21 models that had >80% of the Akaike weight (Fig. 1). We used the top 80% because all models outside of this set had low support ($\omega_i \leq 0.02$). When a model contained a temporal covariate for either $\hat{\gamma}_t$ or $\hat{\varepsilon}_t$, the indicated trend was always negative for $\hat{\gamma}_t$ and positive for $\hat{\varepsilon}_t$. Thus, territory extinction increased over time ($\hat{\varepsilon}_{1993} = 0.019$ [SE 0.012]; $\hat{\varepsilon}_{2009} = 0.134$ [SE 0.043]), whereas territory colonization decreased over time ($\hat{\gamma}_{1993} = 0.323$ [SE 0.124]; $\hat{\gamma}_{2009} = 0.242$, SE = 0.058). As a result, territory occupancy declined during the study ($\hat{\psi}_{1993} = 0.957$ [SE 0.045]; $\hat{\psi}_{2010} = 0.671$ [SE 0.069]). The model-averaged estimates of ψ corresponded well with the naïve estimates of occupancy, despite a decline in the annual estimates of p during the study (Fig. 1). The estimated and naïve occupancy estimates did not diverge because p remained relatively high throughout our study, and we conducted sufficient surveys at a territory each year (average number of surveys per territory = 3.9) to detect owls reliably.

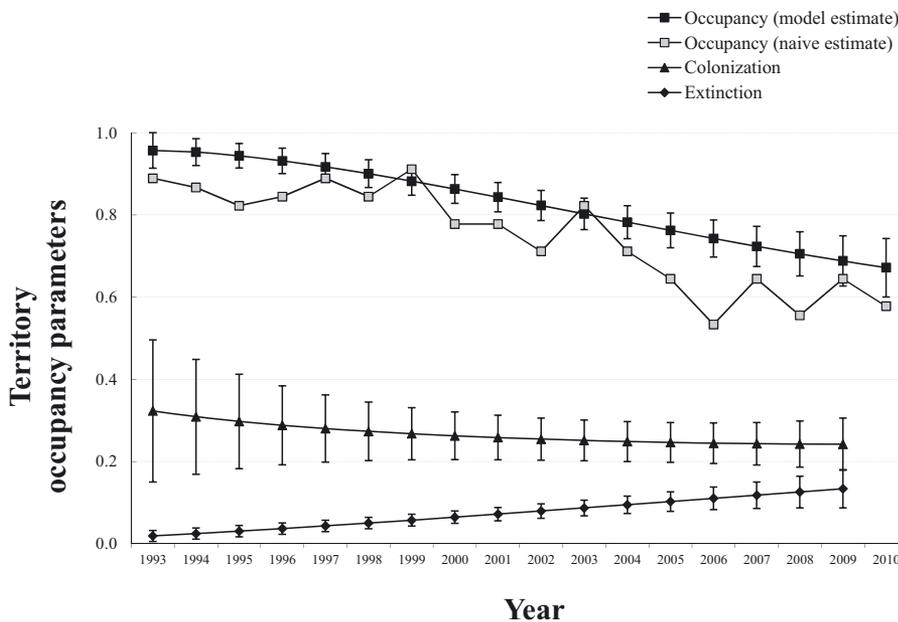


Figure 1. Annual estimates (SE) of territory extinction, colonization, and occupancy at California Spotted Owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993–2010.

Table 2. Top-ranked temporal-symmetry models with recruitment and survival for mark-recapture analysis of a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993–2010.

Model ^a	No. parameters	AIC _c ^b	ΔAIC _c ^c	ω _i ^d
$\varphi_{\cdot}, f_{\cdot}, p_{\text{sex} + \text{effort}}$	5	2326.29	0.00	0.186
$\varphi_{\cdot}, f_{\text{inT}}, p_{\text{sex} + \text{effort}}$	6	2326.86	0.57	0.139
$\varphi_{\cdot}, f_{\text{T}}, p_{\text{sex} + \text{effort}}$	6	2327.56	1.27	0.099
$\varphi_{\cdot}, f_{\text{TT}}, p_{\text{sex} + \text{effort}}$	7	2327.60	1.31	0.096
$\varphi_{\text{inT}}, f_{\cdot}, p_{\text{sex} + \text{effort}}$	6	2328.25	1.96	0.070
$\varphi_{\text{T}}, f_{\cdot}, p_{\text{sex} + \text{effort}}$	6	2328.30	2.01	0.068
$\varphi_{\text{T}}, f_{\text{inT}}, p_{\text{sex} + \text{effort}}$	7	2328.88	2.59	0.051
$\varphi_{\text{inT}}, f_{\text{inT}}, p_{\text{sex} + \text{effort}}$	7	2328.89	2.60	0.051
$\varphi_{\text{T}}, f_{\text{T}}, p_{\text{sex} + \text{effort}}$	7	2329.58	3.29	0.036
$\varphi_{\text{inT}}, f_{\text{T}}, p_{\text{sex} + \text{effort}}$	7	2329.59	3.30	0.036
$\varphi_{\text{T}}, f_{\text{TT}}, p_{\text{sex} + \text{effort}}$	8	2329.60	3.31	0.035
$\varphi_{\text{inT}}, f_{\text{TT}}, p_{\text{sex} + \text{effort}}$	8	2329.61	3.32	0.035
$\varphi_{\text{TT}}, f_{\cdot}, p_{\text{sex} + \text{effort}}$	7	2330.26	3.97	0.025

^aModel variables are defined in Methods.

^bAkaike's information criterion adjusted for small sample size.

^cDistance in AIC_c units from the model with the lowest AIC_c value.

^dAkaike weight.

Mark-Recapture Abundance

In the first modeling stage, model $\{\varphi_t, f_t, p_{\text{sex} + \text{effort}}\}$ was the top-ranked model and had 35.7% of the Akaike weight among the 12 candidate models, so we used $p_{\text{sex} + \text{effort}}$ for detection probability in all second-stage models. In the second modeling stage, model $\{\varphi_{\cdot}, f_{\cdot}, p_{\text{sex} + \text{effort}}\}$ was the top-ranked model (Table 2). Parameter estimates from model $\{\varphi_{\cdot}, f_{\cdot}, p_{\text{sex} + \text{effort}}\}$ indicated that φ and f were constant during our study period and that p was higher for male owls ($\hat{\beta}_{\text{sex}} = 0.54$ [SE 0.25]) and positively correlated with annual walk-in survey effort ($\hat{\beta}_{\text{effort}} = 1.46$ [SE 0.67]). However, the top 6 models were within 2.0 AIC units of each other.

Due to model-selection uncertainty, we obtained model-averaged estimates for $\hat{\varphi}_t$, \hat{f}_t , and $\hat{\lambda}_t$ with the 14 models that had $\geq 95.0\%$ of the Akaike weight (Fig. 2). The top 4 models specified that φ was constant; when a model contained a temporal covariate for $\hat{\varphi}_t$, the trend was weakly negative. The top model specified that f was constant; when a model contained a temporal covariate for \hat{f}_t , the trend was negative. Thus, survival was nearly constant over time ($\hat{\varphi}_{1993} = 0.816$ [SE = 0.020]; $\hat{\varphi}_{2009} = 0.815$ [SE 0.019]), whereas recruitment decreased slightly ($\hat{f}_{1993} = 0.195$ [SE 0.032]; $\hat{f}_{2009} = 0.160$ [SE 0.023]). As a result, the finite rate of population change slightly declined during the study ($\hat{\lambda}_{1993} = 1.011$ [SE 0.035]; $\hat{\lambda}_{2009} = 0.975$ [SE 0.024]).

Occupancy versus Abundance

The realized change in occupancy ($\Delta_t = 0.702$, 95% CI 0.552–0.852) (Fig. 3) and the geometric mean of annual change in occupancy ($\hat{\lambda} = 0.979$, 95% CI 0.967–0.992) both suggested that territory occupancy declined from 1993–2010. Changes in occupancy within our study area should reflect changes in abundance unless the average number of owls detected at a territory also changed over time (i.e., more or fewer single owls). Thus, we performed a linear regression of the number of owls detected per territory versus year, and the slope was not significantly different from 0.0 ($\beta = -0.004$, $F_{1,16} = 1.13$, $p = 0.30$).

The realized change in population size ($\Delta_t = 0.725$, 95% CI 0.445–1.004) (Fig. 3) and the geometric mean of the finite rate of population change ($\hat{\lambda} = 0.981$, 95% CI 0.959–1.004) also suggested that population size declined from 1993–2010, but the 95% CI slightly

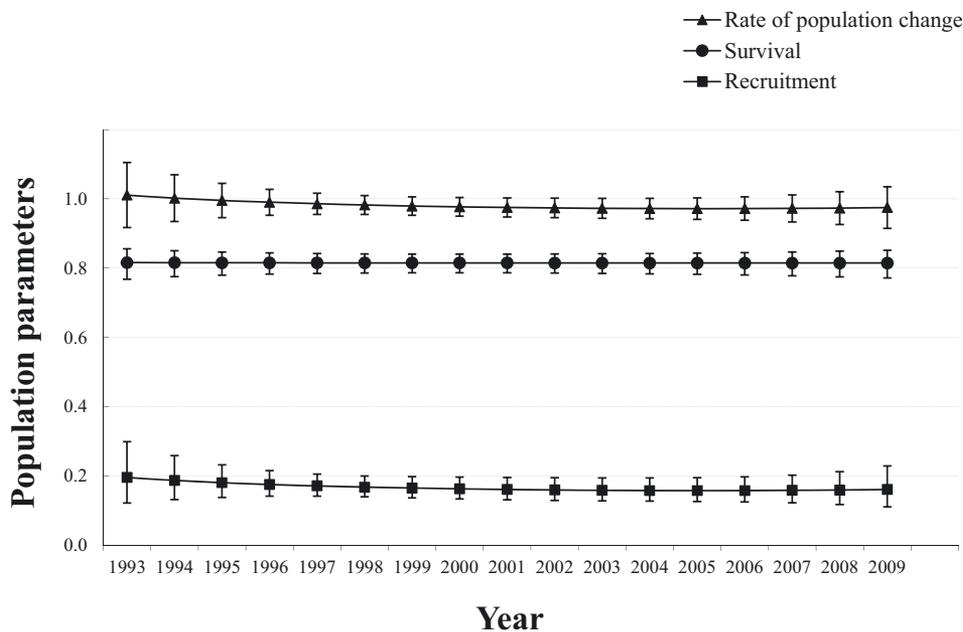


Figure 2. Annual estimates (SE) of survival, recruitment, and finite rate of population change for a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2009.

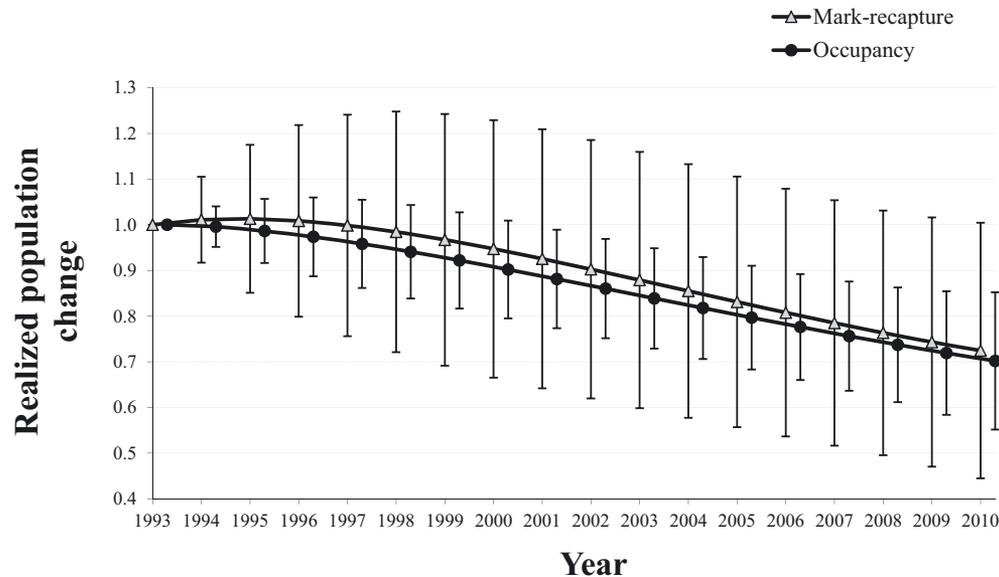


Figure 3. Realized population change (95% CI) with both occupancy and mark-recapture data for a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2010.

overlapped 1.0 for both parameters. The realized change in territory occupancy closely matched the realized population change estimated from mark-recapture data, although the realized population change estimates were less precise (Fig. 3).

Discussion

The realized change in population we estimated on the basis of occupancy closely matched the realized population change estimated from mark-recapture data. This

result suggests occupancy monitoring may offer an accurate, cost-effective means to monitor the population trends of territorial species over large spatial extents. The relation between occupancy and abundance may be less strong for nonterritorial species (e.g., semicolonial; Estrada & Arroyo 2012), so we encourage assessments of the occupancy-abundance relation for such species. Occupancy models that incorporate observed counts of individuals and imperfect detection should be well suited for such applications (Royle et al. 2005).

We obtained more-precise parameter estimates with occupancy modeling relative to mark-recapture

modeling. The determination of the effective sample size in occupancy studies has not been fully resolved (J. Nichols, personal communication). However, we apparently obtained a larger sample size with our occupancy data because the robust-design occupancy model accommodated multiple surveys (i.e., data points) at a territory each year, whereas we used a mark-recapture model that used a single datum each year for the marked individuals in our population. Robust-design models that accommodate missing observations are available for mark-recapture data (Pollock 1982), but we believe a site-based occupancy approach offers greater flexibility. For example, if the entire study area is not surveyed during each secondary sampling period, it is unclear how one would generally determine which individuals were not sampled during that period. Alternatively, the size of the study area can be increased to add more individuals, but this again requires substantial survey effort for species with large home ranges. In contrast, additional sampling units can be more easily added with occupancy surveys because the sampling unit is the site (whether defined as quadrats, territories, etc.), not the individual.

For the occupancy modeling, territory extinction increased over time, and colonization rates were insufficient to maintain occupancy at its initial level. Annual territory extinction was low during our study, but its effects were significant because most territories were occupied at the study's onset and colonization rates were also low. Territories may not have been colonized because habitat alteration during the study (e.g., logging, high-intensity wildfire) may have affected the quality of vacant owl territories (Seamans & Gutiérrez 2007). In addition, the mark-recapture modeling showed a declining trend in individual recruitment, so the population may have produced an insufficient number of owls to colonize vacant territories and maintain occupancy at its initial level.

We identified 2 factors that greatly affected the detection probability (p) in our occupancy analysis. First, p increased after the initial detection of owls at a territory during a given year (see Riddle et al. 2010). Owl demographic studies are designed to capture birds (either by banding unmarked birds or resighting marked birds) and to determine reproductive activity (Franklin et al. 1996), so observers intensify their efforts to locate birds after initial detection. This phenomenon suggests that future occupancy analyses for studies originally designed to collect mark-recapture data should include a within-year, initial-detection effect in the model structure. Second, we found that nesting spotted owls were more likely to be detected, which confirmed the results of prior analyses (Nichols et al. 2007; MacKenzie et al. 2009). Our results also supported the need to model detection probability appropriately during occupancy analyses to reduce bias in site-occupancy estimates (Mackenzie et al. 2006).

Our results suggested that occupancy data can provide reliable information on wildlife population trends,

as evidenced by the concurrent declines in territory occupancy and population size of California Spotted Owls. Therefore, managers may be justified in using less costly, occupancy-based study designs to monitor spotted owls and other species of management concern over large geographic areas. Our occupancy models also provided more precise parameter estimates than our mark-recapture models because we conducted multiple surveys at each territory per primary sampling period. A robust-design mark-recapture model could have been used, but it was unclear to us how one would determine whether individuals were sampled during a defined secondary sampling period. We caution, however, that occupancy data may be more suitable for inferring the population status of territorial species than those with clumped spatial distributions, unless data collection also includes counts of individual organisms (in addition to the simple detection or nondetection of the target species) and researchers use occupancy models that incorporate such data (Royle et al. 2005).

We encourage future research that incorporates ecological covariates (e.g., habitat quality, habitat change) to elucidate site-occupancy dynamics and inform management decisions that may affect the California Spotted Owl. For example, managers need information on how timber harvest affects territory extinction and colonization, reproductive output, and individual survival (U.S. Forest Service 2004). We also recognize that mark-recapture studies provide important demographic information not provided by occupancy studies, which may allow the identification of life-history stages that are limiting a population. Thus, the choice of study design will depend on the specific research or management objectives for a given wildlife population.

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Supporting Information

The methods and results for our random-effects mark-recapture modeling for which we used the methods of Blakesley et al. (2010) (Appendix S1), our a priori models for detection probability (occupancy modeling) and capture probability (mark-recapture modeling) (Appendix S2), and the annual detection probabilities for our occupancy modeling (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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