

Using integrated population models to improve conservation monitoring: California spotted owls as a case study



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ABSTRACT

Integrated population models (IPMs) constitute a relatively new approach for estimating population trends and demographic parameters that makes use of multiple, independent data sources (e.g., count and mark-recapture data) within a unified statistical framework. In principle, IPMs offer several advantages over more conventional modeling approaches that rely on a single source of data, including greater precision in parameter estimates and the ability to estimate demographic parameters for which no explicit data are available. However, to date, the IPM literature has focused primarily on model development and evaluation, and few “real-world” applications have demonstrated that IPMs can strengthen inferences about population dynamics in a species of conservation concern. Here, we combined 23 years of count, occupancy, reproductive, and mark-recapture data into an IPM framework to estimate population trends and demographic rates in a population of California spotted owls (*Strix occidentalis occidentalis*). Using this framework, we observed a significant population decline, as evidenced by the geometric mean of the finite annual rate of population change ($\hat{\lambda}_t = 0.969$, 95% CRI 0.957–0.980) and the resulting realized population change (proportion of the initial population present in 2012; $\hat{\Delta}_{2012} = 0.501$, 95% CRI 0.383–0.641). The estimated decline was considerably greater than the approximately 30% decline estimated using conventional mark-recapture and occupancy approaches (Tempel and Gutiérrez, 2013). The IPM likely yielded a greater decline because it allowed for the inclusion of three years of data from the beginning of the study that were omitted from previous analyses to meet the assumptions of mark-recapture models. The IPM may also have yielded a greater estimate of decline than occupancy models owing to an increase in the number of territories occupied by single owls over the study period. All demographic parameters (adult and juvenile apparent survival, reproductive rate, immigration rate) were positively correlated with $\hat{\lambda}_t$, but immigration was fairly high ($\widehat{imm}_t = 0.097$, 95% CRI 0.055–0.140) and contributed most to temporal variation in $\hat{\lambda}_t$, suggesting that changes in owl abundance were influenced by processes occurring outside of our study area. More broadly, our results indicated that the IPM framework has the potential to strengthen inference in population monitoring and demographic studies, particularly for those involving long-lived species whose abundance may be slowly declining. In our case, the conservation implications from the results of the IPM suggested a decline in the population of owls that was steeper than previously thought.

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1. Introduction

Many species are endangered by anthropogenic factors such as habitat loss and fragmentation, introduced species, climate change, and overexploitation (Wilcove et al., 1998; Fahrig, 2003; Moritz and Agudo, 2013), but detecting population declines and estimating rates of decline in rare species can be challenging (Thompson,

2004). Rare species are often widely distributed at low densities, which can lead to low precision in estimates of abundance and population trends because of small sample sizes. In addition, species of conservation concern are often characterized by “slow” life-history strategies where longevity has been selected at the expense of reproduction (Cardillo et al., 2005). Detecting population declines in such species can be challenging because long life spans and low mortality in adults can result in slow, but biologically important, declines. As a consequence, the status of many species of conservation concern remains uncertain despite the implementation of large-scale and labor-intensive population monitoring

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programs (e.g., Cam et al., 2003; Kendall et al., 2009; Blakesley et al., 2010).

Conventional approaches for estimating population trends typically make use of a single source of information such as mark-recapture, count, or presence–absence data (Williams et al., 2002; MacKenzie et al., 2006). For example, population growth can be estimated from mark-recapture data using “robust designs” when a study area has been surveyed on more than one occasion within primary sampling periods (Otis et al., 1978) or using a temporal symmetry model when only one survey has been conducted per primary sampling period (Pradel, 1996). In contrast, integrated population models (IPMs) represent a more recent analytical approach that can combine multiple data sources, including count, occupancy, mark-recapture, and reproductive data, into a unified framework (Besbeas et al., 2002; Abadi et al., 2010a). This approach offers several potential advantages over separate analysis of each dataset, including more precise estimates of population growth and the ability to estimate demographic parameters for which no explicit data are available (Schaub and Abadi, 2011). For example, IPMs can provide estimates of immigration rates without explicit data on the movements of individuals into a study area or population (Abadi et al., 2010). Reliable estimates of immigration are notoriously elusive, yet essential to determine if a population of interest is a sink population that would decline in the absence of recruitment from other populations or if regional processes affect local population dynamics (Pulliam, 1988; Thomas and Kunin, 1999; Peery et al., 2006). However, thus far, the IPM literature has been primarily about model development and evaluation, with few “real-world” applications demonstrating that IPMs can improve conservation monitoring (Gauthier et al., 2007; Schaub et al., 2007, 2010).

The California spotted owl (*Strix occidentalis occidentalis*) is a subspecies of conservation concern because it inhabits old forests which have high economic value. Thus, logging of these forests is a conservation concern because it may negatively affect the owl. However, the status (i.e., population trend) of California spotted owls in the Sierra Nevada has been uncertain for more than two decades despite the results of large-scale mark-recapture studies, partly because of a lack of precision for estimates of population change (Franklin et al., 2004; Blakesley et al., 2010; Tempel and Gutiérrez, 2013). A previous occupancy analysis of our study population indicated a decline in the number of occupied territories (Tempel and Gutiérrez, 2013), but this simple occupancy model did not account for factors that may impact population size (e.g., the proportion of territories occupied by single owls). Uncertainty about population status as a result of imprecise estimation contributed to decisions not to list the California spotted owl as a threatened species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2003, 2006). Moreover, uncertainty in the population trend of California spotted owls has challenged the assessment of two major forest-management plans implemented to protect owls and their habitat on public lands in the Sierra Nevada (Verner et al., 1992; U.S. Forest Service, 2004).

Here, we developed an IPM to estimate finite annual rates of population change (λ_t) and realized population change (Δ_t) over a 23-year period in a demographically open population of California spotted owls in the central Sierra Nevada (Seamans et al., 2001; Franklin et al., 2004; Blakesley et al., 2010). Our IPM incorporated data on population counts, mark-recapture histories, and reproduction, but it differed from previous IPM applications in that we first used a multi-state occupancy model to obtain annual “counts” of the number of adults and young produced, rather than using naïve counts that did not account for imperfect detection. This approach would produce stronger inferences about population trends if, for example, researchers became more proficient over time at locating individuals on their study area. In addition, incorporating these

different sources of data into an IPM differed from all previous studies of spotted owl demographics that relied solely upon either mark-recapture or occupancy data to estimate population change (e.g., Gutiérrez, 1994; Forsman et al., 2011; Tempel and Gutiérrez, 2013). We structured the IPM such that it contained annual random effects for apparent adult and juvenile survival, reproductive rate, and immigration rate, which allowed us to evaluate the sensitivity of population growth to changes in vital rates. By using an IPM framework, we strove to improve precision in estimates of population change, understand the role of immigration to local population dynamics, and reduce uncertainty about the status of California spotted owls in the Sierra Nevada.

2. Materials and methods

2.1. Study area

We conducted our study on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California, which 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; Tempel and Gutiérrez, 2013). We surveyed the entire area each year regardless of land cover, topography, access, or land ownership. Approximately 60% of the study area was public land managed by the USFS, and 40% was private land managed by timber companies. The primary vegetation type on our study area was mixed-conifer forest, elevations ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

2.2. Spotted owl surveys

We conducted annual surveys for spotted owls from 1986 to 2012 during their breeding season (1 April–31 August). Although the entire study area was not fully surveyed until 1993 because of funding constraints (Tempel and Gutiérrez, 2013), we used all data from 1990 to 2012 because our analytical approach could accommodate data from years where we had lower survey effort. For example, we used a Bayesian analysis for the multi-state occupancy model (see Section 2.3.1) and imputed the true state of each sampling unit (i.e., territory) for each iteration of the Markov chain (MacKenzie et al., 2009). Thus, the number of adults and the number of young that they produced were estimated at territories that were not surveyed in a given year.

Spotted owl surveys consisted of imitating owl vocalizations (vocal lures) for 10 min at designated survey stations or while walking along survey routes. We determined the sex of spotted owls responding to vocal lures by the pitch of their 4-note territorial calls; males have a lower-pitched call than females (Forsman et al., 1984). If we detected spotted owls on nocturnal surveys, we then conducted diurnal surveys to locate and band unmarked individuals, resight marked individuals, and assess reproduction (Franklin et al., 1996). We banded adult owls with a locking, numbered metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al., 1996). We banded juvenile owls with a numbered metal band on one leg and a non-unique cohort band on the other leg, but we replaced the cohort band with a unique band and tab combination if we later recaptured the juvenile as an adult.

2.3. Analytical design

We used an age-structured population IPM structurally identical to the model developed by Abadi et al. (2010a) for the little owl (*Athene noctua*). The data used in the IPM consisted of annual population counts of adults (y), annual counts of the number of young

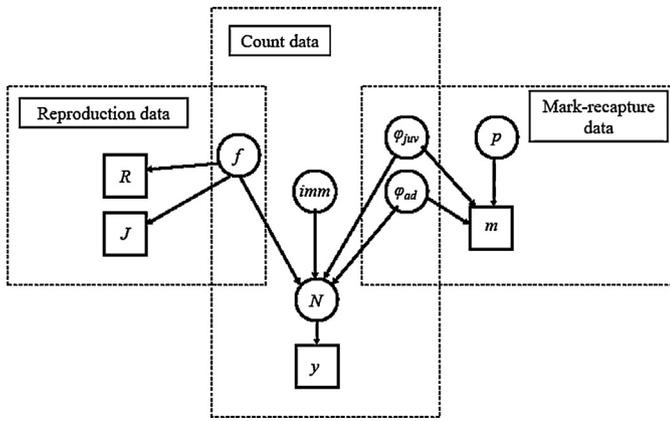


Fig. 1. Graphic representation of an integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012 (modeling framework adapted from Abadi et al., 2010a). R = number of adults assessed for reproduction; J = number of young produced, f = number of young produced per adult, imm = immigration rate (number of immigrants per adult), ϕ_{juv} = juvenile apparent survival probability, ϕ_{ad} = adult apparent survival probability, m = capture–recapture data, p = recapture probability, y = population count data, N = population size.

produced (J), and mark–recapture data for fledglings and adults (m) (Fig. 1). The IPM provided estimates of adult and juvenile apparent survival, reproductive rates, immigration rates, and population size. Immigration rates can be estimated within this framework despite the lack of explicit data on immigration. Rather than using raw counts of the number of owls detected each year, we first used a multi-state occupancy model that incorporated imperfect detection (MacKenzie et al., 2009) to obtain annual estimates of the number of adults (y) and number of young produced (J). As a result, R (the number of adults for which reproduction was assessed) in Fig. 1 was equal to y . We then used the estimates of y and J from the multi-state occupancy model as input data for the IPM, along with the mark–recapture data.

2.3.1. Multi-state occupancy model

We implemented a state-space modeling approach similar to MacKenzie et al. (2009). State-space models contain two components—a submodel for the latent, state process (e.g., the occupancy model described below) and a submodel for the observation process in which the observed data are conditional on the unobserved or partially observed state process (Buckland et al.,

2004). The sampling units for the multi-state occupancy model were the owl territories; we considered a territory to be a site where spotted owls were observed either roosting or nesting at some point during the study. Each territory could be in one of five states: 0 = no spotted owls present; 1 = single adult present; 2 = adult pair present, no young produced; 3 = adult pair present, one young produced; 4 = adult pair present, two young produced.

Three young were rarely produced (four times in 23 years), so we did not include a sixth state with three young. Instead, we categorized these occasions as state 4 (i.e., two young produced). Surveys in which no spotted owls were detected had to be ≥ 30 min in total duration to be considered adequate for inclusion in the database. We did not include nocturnal detections that were >400 m from the edge of long-term core use areas (Berigan et al., 2012) because these individuals may have been individuals from a neighboring territory or non-territorial “floaters.”

We divided each breeding season into 10 bimonthly survey periods (1–15 April, 16–30 April, 1–15 May, 16–31 May, etc.). During each survey period, we recorded the highest occupancy state (0, 1, 2, 3, or 4) observed at each territory; the observed occupancy state may have been less than or equal to the true value. On surveys conducted before 1 June, we constrained the probabilities of detecting reproduction (states 3 and 4) to 0 because young were observed before this date on only 5 occasions during the 23-year study period. If a territory was not surveyed during a bimonthly survey period, we treated it as a missing observation. The primary sampling periods were breeding seasons (i.e., years), and the secondary sampling periods were the bimonthly periods within each breeding season.

We used the model parameterization that contained parameters for initial occupancy, transition probability, and detection probability (MacKenzie et al., 2009). We denoted the probability that a territory was in state m in the initial year as $\phi^{[m]}$, and defined the initial occupancy vector as follows:

$$\phi_0 = [1 - \phi^{[1]} - \phi^{[2]} - \phi^{[3]} - \phi^{[4]} \quad \phi^{[1]} \quad \phi^{[2]} \quad \phi^{[3]} \quad \phi^{[4]}]$$

We denoted the probability of a territory transitioning from state m in year t to state n in year $t + 1$ as $\phi_t^{[m,n]}$, and defined the transition probability matrix as follows:

$$\phi_{t+1} = \begin{bmatrix} 1 - \phi_t^{[0,1]} - \phi_t^{[0,2]} - \phi_t^{[0,3]} - \phi_t^{[0,4]} & \phi_t^{[0,1]} & \phi_t^{[0,2]} & \phi_t^{[0,3]} & \phi_t^{[0,4]} \\ 1 - \phi_t^{[1,1]} - \phi_t^{[1,2]} - \phi_t^{[1,3]} - \phi_t^{[1,4]} & \phi_t^{[1,1]} & \phi_t^{[1,2]} & \phi_t^{[1,3]} & \phi_t^{[1,4]} \\ 1 - \phi_t^{[2,1]} - \phi_t^{[2,2]} - \phi_t^{[2,3]} - \phi_t^{[2,4]} & \phi_t^{[2,1]} & \phi_t^{[2,2]} & \phi_t^{[2,3]} & \phi_t^{[2,4]} \\ 1 - \phi_t^{[3,1]} - \phi_t^{[3,2]} - \phi_t^{[3,3]} - \phi_t^{[3,4]} & \phi_t^{[3,1]} & \phi_t^{[3,2]} & \phi_t^{[3,3]} & \phi_t^{[3,4]} \\ 1 - \phi_t^{[4,1]} - \phi_t^{[4,2]} - \phi_t^{[4,3]} - \phi_t^{[4,4]} & \phi_t^{[4,1]} & \phi_t^{[4,2]} & \phi_t^{[4,3]} & \phi_t^{[4,4]} \end{bmatrix}$$

Similarly, we denoted the probability of observing a territory in state l during survey period j of year t when its true state was m as $p_{j,t}^{[l,m]}$, and defined the detection probability matrix as follows (assuming that a territory could not be observed in a state higher than its true state):

True state	Observed state				
	0	1	2	3	4
0	1	0	0	0	0
1	$1 - p_{j,t}^{[1,1]}$	$p_{j,t}^{[1,1]}$	0	0	0
2	$1 - p_{j,t}^{[1,2]} - p_{j,t}^{[2,2]}$	$p_{j,t}^{[1,2]}$	$p_{j,t}^{[2,2]}$	0	0
3	$1 - p_{j,t}^{[1,3]} - p_{j,t}^{[2,3]} - p_{j,t}^{[3,3]}$	$p_{j,t}^{[1,3]}$	$p_{j,t}^{[2,3]}$	$p_{j,t}^{[3,3]}$	0
4	$1 - p_{j,t}^{[1,4]} - p_{j,t}^{[2,4]} - p_{j,t}^{[3,4]} - p_{j,t}^{[4,4]}$	$p_{j,t}^{[1,4]}$	$p_{j,t}^{[2,4]}$	$p_{j,t}^{[3,4]}$	$p_{j,t}^{[4,4]}$

2004). The sampling units for the multi-state occupancy model were the owl territories; we considered a territory to be a site where spotted owls were observed either roosting or nesting at some point during the study. Each territory could be in one of five states: 0 = no spotted owls present; 1 = single adult present; 2 = adult pair present, no young produced; 3 = adult pair present, one young produced; 4 = adult pair present, two young produced.

Related sets of parameters (initial occupancy probabilities, detection and transition probabilities for a specific state) were constrained to sum to 1. For example, the individual probabilities that a territory in state m in year t was in one of the five states in year $t + 1$ ($\phi_t^{[m,0]}$, $\phi_t^{[m,1]}$, $\phi_t^{[m,2]}$, $\phi_t^{[m,3]}$, $\phi_t^{[m,4]}$) must sum to 1. Similarly, the individual detection probabilities for a territory in state l during a given year and survey period must sum to 1, keeping in mind that

a territory cannot be observed in a state higher than its true state. Thus, if a territory was in true state 3 during year t , then $p_{j,t}^{[0,3]}$, $p_{j,t}^{[1,3]}$, $p_{j,t}^{[2,3]}$, and $p_{j,t}^{[3,3]}$ must sum to 1 for each survey period j .

We used Markov chain Monte Carlo (MCMC) methods within a Bayesian framework to estimate the model parameters (Link et al., 2002; MacKenzie et al., 2009). We considered the true state of each territory each year to be a latent (unknown) variable and predicted or imputed its true state from the observed data. As noted by MacKenzie et al. (2009), an advantage of this approach is that relevant summaries of the system (e.g., the number of territories in each state) can be calculated easily. Thus, we estimated the number of fledglings produced each year (J) and the number of adults in the population each year (y) as:

$$J = \text{no. of territories in state 3} + [2 \times (\text{no. of territories in state 4})]$$

$$y = \text{no. of territories in state 1} \\ + [2 \times (\text{no. of territories in states 2, 3, or 4})]$$

For related model parameters that were constrained to sum to 1 (see above), a Dirichlet prior distribution was appropriate. The Dirichlet is a multivariate generalization of the beta distribution and the conjugate prior for multinomial distributions (McCarthy, 2007). However, the parameters of a Dirichlet distribution cannot be stochastic nodes in OpenBUGS software, so we induced a Dirichlet distribution (Spiegelhalter et al., 2003). For each model parameter (i), we specified an associated variable (β_i) with a gamma distribution. Then for a group of related model parameters, we set each parameter, i , equal to $(\beta_i / \sum_{k=1}^N \beta_k)$ where N was the total number of parameters within the group; this ensured that their sum was 1 (Spiegelhalter et al., 2003). The gamma distributions were characterized by a shape parameter (r) and a rate parameter (θ) (Spiegelhalter et al., 2003). We incorporated annual random effects for all detection and transition probabilities by specifying uninformative distributions for the parameters of the gamma distribution within a related group of β_i 's, where $r \sim \text{Uniform}(0.5, 10)$ and $\theta \sim \text{Gamma}(1, 1)$. In addition, when a territory's true state was 1, there were only two possible outcomes for the detection probability (0 = no detection, 1 = single owl detected). Therefore, we specified that $\text{logit}(p_{j,t}^{[1,1]}) = \mu + \varepsilon$, where $\mu \sim \text{Normal}(0, 10,000)$ and $\varepsilon \sim \text{Normal}(0, \sigma)$. We used a hyperprior ($\sigma \sim \text{Uniform}[0,10]$) in the error term to incorporate annual random effects into the estimation of $p_{j,t}^{[1,1]}$. We held within-year detection probabilities constant to keep the number of estimated parameters at a manageable level, except we constrained the probability of detecting reproduction before 1 June to 0 (see above; MacKenzie et al., 2009).

We conducted the analysis using OpenBUGS (Lunn et al., 2009; see Appendix A for model code). We ran three chains of 20,000 iterations to approximate the posterior distributions of the model parameters after discarding the initial 10,000 iterations of each chain as a burn-in period. After the burn-in period, the chains were well-mixed as the Gelman–Rubin convergence statistic (\hat{R}) was <1.1 for all parameters (Gelman and Hill, 2007; see trace history plots for y and J in Appendix C).

2.3.2. Integrated population model

The modeled population consisted of three age classes (juvenile, 1 year old, ≥ 2 years old). We hereafter refer to any owls at least 1 year old as adults. Non-juvenile spotted owls can be distinguished into 3 age classes (1 year old, 2 years old, and ≥ 3 years old) based on the appearance of their rectrices (Moen et al., 1991). However, prior analyses using Cormack–Jolly–Seber models (Seber, 1982) showed that differences in annual survival among these three age classes were small (<0.10 ; unpublished data); 1- and 2-year-olds also comprised $<10\%$ of the total population on average (unpublished data).

Furthermore, we did not use a female-only model because single spotted owls at territories were typically males and a potentially important component of the total population size. We modeled the total population of males and females combined, instead of separate population components for each sex, because another occupancy state would have been required to distinguish between single males and single females, but data were sparse for single females.

As noted above, we used the estimates of y and J provided by the multi-state occupancy model, rather than naïve counts of young and adults, to account for imperfect detection. The mark-recapture data were summarized as m -arrays (Burnham et al., 1987) for juveniles and adults. This format allowed much faster computation but reduced the flexibility of the modeling (i.e., individual covariates could not be used). The data sets were not independent, which is an assumption of the IPM, but Abadi et al. (2010b) demonstrated with simulations that using non-independent data for a structurally identical IPM resulted in minimal bias in the parameter estimates. In addition, they observed increased precision and accuracy in parameter estimation when all three sources of data were analyzed simultaneously, rather than individually.

We again used a state-space approach where the state process was described by the following distributions:

$$N_{1,t+1} \sim \text{Poisson}([N_{1,t} + N_{2,t}] \times f_t \times \varphi_{juv,t})$$

$$N_{2,t+1} \sim \text{Binomial}([N_{1,t} + N_{2,t}], \varphi_{ad,t}) + \text{Poisson}([N_{1,t} + N_{2,t}] \times \text{imm}_t)$$

where $N_{1,t}$ was the number of 1-year-old spotted owls at time t ; $N_{2,t}$ was the number of spotted owls ≥ 2 years old at time t ; φ_{juv} and φ_{ad} were the apparent survival probabilities of juveniles and adults, respectively, from time t to $t+1$; f_t was the number of young produced per adult at time t ; and imm_t was the immigration rate (number of immigrant adult spotted owls into the population at time $t+1$ per adult in the population at time t). Thus, the expected number of 1-year-old spotted owls at time $t+1$ was the product of the number of young produced at time t and juvenile apparent survival from t to $t+1$. The expected number of spotted owls ≥ 2 years old at time $t+1$ had two components: (i) the number of adults at time t multiplied by adult apparent survival from t to $t+1$, and (ii) the number of adults at time t multiplied by the immigration rate from t to $t+1$. As noted by Abadi et al. (2010a), immigrants were assumed to enter the population as individuals ≥ 2 years old, but the results would be identical if they were assumed to enter as 1-year-olds. The total population size (N_t) was the sum of $N_{1,t}$ and $N_{2,t}$. We estimated the finite rate of population change (λ_t) as N_{t+1}/N_t and the realized population change (Δ_t) as N_t/N_{t-1} .

We specified Poisson distributions for the “count” data (y , J), which allowed the absolute observation error to change proportionally with population size and reproductive output: $y_t \sim \text{Poisson}(N_t)$

$$J_t \sim \text{Poisson}(R_t \times f_t).$$

Kéry and Schaub (2012) noted for an IPM having the same structure as ours that the Poisson distribution produced faster convergence of the Markov chains and identical parameter estimates when compared to the lognormal or normal distribution. We used a normal distribution to describe the initial population sizes of owls that were 1 year old, ≥ 2 years old, and immigrants; the priors for each class were $\sim \text{Normal}(100, 10,000)$. For the mark-recapture data formatted as m -arrays, we used the Cormack–Jolly–Seber (CJS) model with a product multinomial distribution for the estimation of φ_{juv} and φ_{ad} (Kéry and Schaub, 2012). Recapture probabilities (p ; not to be confused with detection probability in the occupancy model) were also estimated within the CJS model. We incorporated annual random effects by assuming that the demographic

Table 1
Posterior means (95% credible interval [CRI]) of parameters from a multi-state occupancy model of California spotted owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1990–2012. The territory states are: 0 = no spotted owls present; 1 = single adult present; 2 = pair of adults present, no young produced; 3 = pair of adults present, one young produced; 4 = pair of adults present, two young produced.

Parameter	Territory state				
	0	1	2	3	4
Initial occupancy ^a					
$\phi^{[m]}$	0.02 (0.00–0.15)	0.02 (0.00–0.17)	0.52 (0.22–0.75)	0.03 (0.00–0.30)	0.41 (0.19–0.66)
Detection probabilities ^b					
$p^{l,1}$	0.72 (0.64–0.80)	0.28 (0.20–0.36)	–	–	–
$p^{l,2}$	0.25 (0.21–0.29)	0.25 (0.22–0.29)	0.50 (0.45–0.55)	–	–
$p^{l,3}$ (early) ^c	0.28 (0.23–0.33)	0.29 (0.25–0.34)	0.43 (0.37–0.49)	–	–
$p^{l,3}$ (late) ^c	0.20 (0.16–0.25)	0.22 (0.18–0.27)	0.33 (0.27–0.39)	0.25 (0.20–0.30)	–
$p^{l,4}$ (early) ^c	0.25 (0.21–0.30)	0.24 (0.20–0.28)	0.51 (0.46–0.56)	–	–
$p^{l,4}$ (late) ^c	0.13 (0.10–0.16)	0.16 (0.13–0.20)	0.23 (0.18–0.28)	0.14 (0.11–0.17)	0.34 (0.30–0.38)
Transition probabilities ^d					
$\phi^{[0,n]}$	0.31 (0.24–0.38)	0.24 (0.19–0.29)	0.16 (0.13–0.20)	0.15 (0.12–0.19)	0.14 (0.11–0.18)
$\phi^{[1,n]}$	0.25 (0.21–0.30)	0.23 (0.18–0.28)	0.19 (0.15–0.23)	0.17 (0.13–0.21)	0.16 (0.13–0.20)
$\phi^{[2,n]}$	0.15 (0.12–0.18)	0.16 (0.12–0.19)	0.25 (0.20–0.31)	0.19 (0.15–0.23)	0.25 (0.21–0.30)
$\phi^{[3,n]}$	0.17 (0.13–0.21)	0.17 (0.14–0.21)	0.24 (0.19–0.29)	0.20 (0.16–0.25)	0.22 (0.17–0.27)
$\phi^{[4,n]}$	0.14 (0.11–0.17)	0.14 (0.11–0.18)	0.27 (0.22–0.33)	0.21 (0.16–0.26)	0.24 (0.19–0.30)

^a Probability that a territory was in state m in the initial year.

^b Probability of observing a territory in state l given that its true state was 0, 1, 2, 3, or 4. For example, the entry for $p^{l,1}$ and territory state = 0 indicates the value for parameter $p^{0,1}$.

^c Early = surveys conducted prior to 1 June; late = surveys conducted on and after 1 June.

^d Probability that a territory in state 0, 1, 2, 3, or 4 in year t was in state n in year $t + 1$. For example, the entry for $\phi^{[2,n]}$ and territory state = 0 indicates the value for parameter $\phi^{[2,0]}$.

parameters (apparent adult survival, apparent juvenile survival, immigration rate, reproductive rate) and recapture probability were realized from normally distributed variables that we transformed to real values using the logit link function for survival and recapture probability and using the log link function for reproductive and immigration rates (Abadi et al., 2010a; Kéry and Schaub, 2012). For each variable that would be transformed into the appropriate demographic parameter or p , we estimated the mean (μ) and error (ε) as hyperparameters from normal distributions where $\mu \sim \text{Normal}(0, 10,000)$ and $\varepsilon \sim \text{Normal}(0, \sigma)$ with $\sigma \sim \text{Uniform}(0, 10)$ (Kéry and Schaub, 2012).

We again used MCMC methods in a Bayesian framework to estimate the model parameters. We conducted the IPM analyses using R2WinBUGS (Sturtz et al., 2005), a package available in program R 2.15 (R Core Team, 2013) that calls WinBUGS (Lunn et al., 2000) for processing the data and model script in batch mode (see Appendix B for model code). We ran three chains of 50,000 iterations to approximate the posterior distributions of the model parameters and discarded the initial 10,000 iterations of each chain as a burn-in period. The chains were well-mixed after the burn-in period ($\hat{R} < 1.1$ for all parameters; see trace history plots in Appendix D). No goodness-of-fit tests are currently available for IPMs (Abadi et al., 2010a; M. Schaub, personal communication). However, we used Program MARK (White and Burnham, 1999) to assess the goodness-of-fit for the mark-recapture data within a CJS model where apparent survival varied by age (juvenile or adult) and year and detection probability varied by year. We found some evidence of overdispersion within the data ($\hat{c} = 1.32$), but Lebreton et al. (1992) suggested that values of $\hat{c} < 3$ indicate adequate fit.

3. Results

3.1. Multi-state occupancy

We identified 45 spotted owl territories on our study area from 1990 to 2012, so the maximum potential population size of territorial spotted owls was 90 individuals (i.e., if all territories were occupied by a pair of owls). Survey coverage increased during the early years of the study, as evidenced by the number of territories that were surveyed at least once each year (≤ 37 territories from

1990 to 1992, ≥ 41 from 1993 to 1995, ≥ 44 from 1997 to 2012). In the initial year (1990), nearly all surveyed territories were occupied by pairs ($\hat{\phi}^{[0]} = 0.02$, 95% CRI 0.00–0.15; $\hat{\phi}^{[1]} = 0.02$, 95% CRI 0.00–0.17; Table 1). The estimated number of territorial adults in the population declined steadily from a maximum of 88 (95% CRI 76–90) in 1990 to a minimum of 42 (95% CRI 39–49) in 2012 (Fig. 2). The estimated number of young produced varied more substantially but also declined over the study, which was expected given the declining number of adults available to breed.

The probability of detecting at least one spotted owl on a survey (i.e., 1 – probability of not detecting any spotted owls) was ≥ 0.72 for all occupancy states except territories with single spotted owls where non-detection rates were high ($\hat{p}^{0,1} = 0.72$, 95% CRI 0.64–0.80). Additionally, the probability of detecting at least one spotted owl increased with the state of a territory (Table 1). The probability of a territory being unoccupied depended upon the territory's state in the previous year, ranging from 0.31 (95% CRI

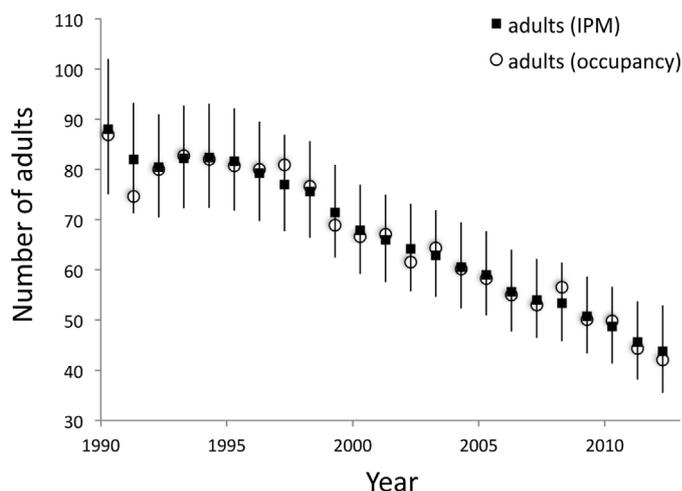


Fig. 2. Posterior means (95% CRI) of the estimated annual number of territorial adults from a Bayesian integrated population model (IPM) for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012. The posterior means of the estimated number of adults from a multi-state occupancy model are also shown; these values were used as “count” data for the IPM.

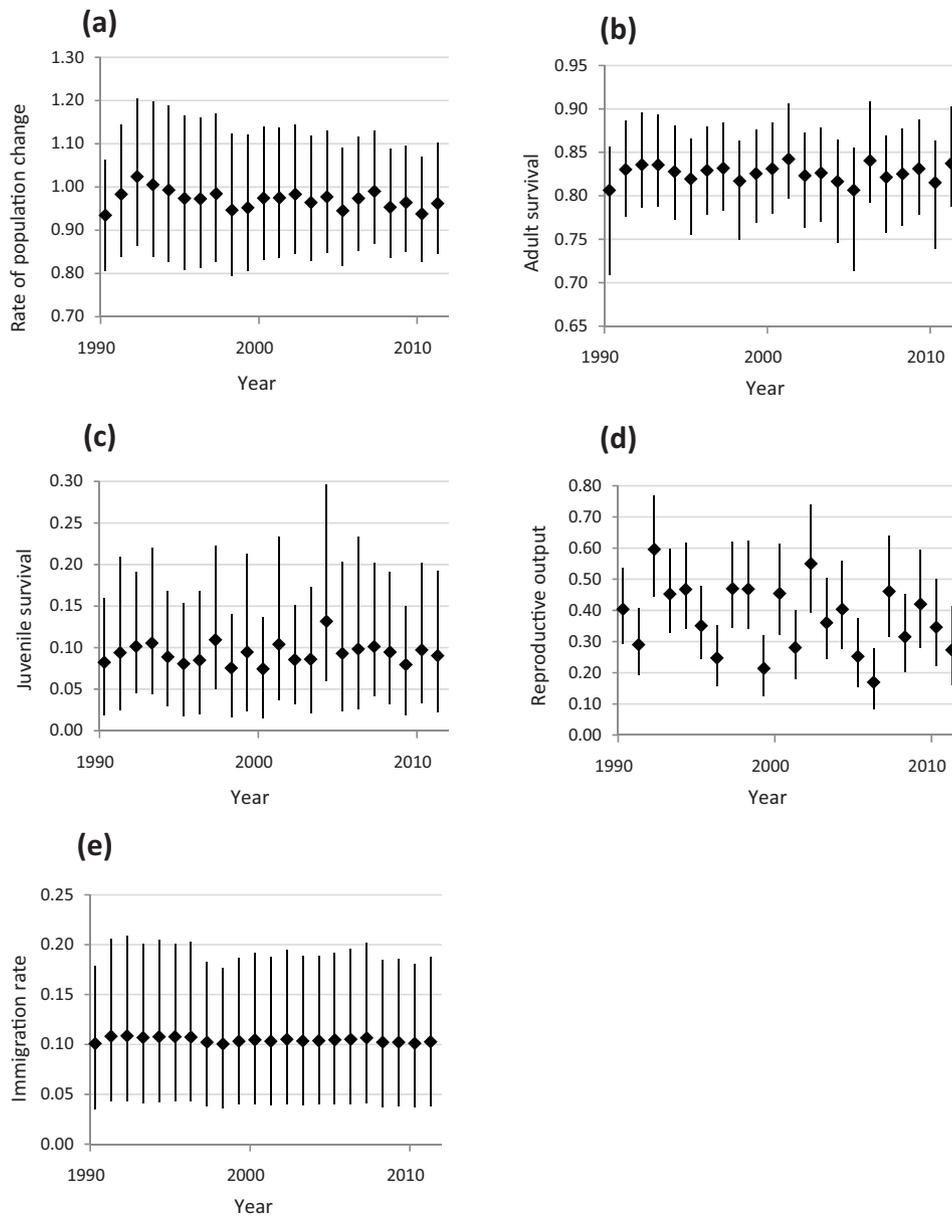


Fig. 3. Posterior means (95% CRI) of estimates for (a) finite rate of population change (λ), (b) apparent adult survival, (c) apparent juvenile survival, (d) reproductive rate, and (e) immigration rate from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2011.

0.24–0.38) for a territory that was unoccupied in the previous year to 0.14 (95% CRI 0.11–0.17) for a territory occupied by a pair that produced two young in the previous year (Table 1). Conversely, a territory was more likely to be occupied by a pair (states 2, 3, and 4) if the territory was also occupied by a pair in the previous year (Table 1).

3.2. Integrated population model

The annual estimates of population size were close to the “counts” provided by the occupancy model (Fig. 2). Thus, the observation error was small, which was expected given that the “counts” had already been rigorously modeled to account for imperfect detection. The finite rate of population change ($\hat{\lambda}_t$) was <1.0 in every year except for two years (1992, 1993) early in the study period (Fig. 3), and the geometric mean of $\hat{\lambda}_t$ was clearly <1.0 ($\hat{\lambda}_t = 0.969$, 95% CRI 0.957–0.980). This translated to a population decline of 50% from 1990 to 2012 ($\hat{\Delta}_{2012} = 0.501$, 95% CRI 0.384–0.642; Fig. 4).

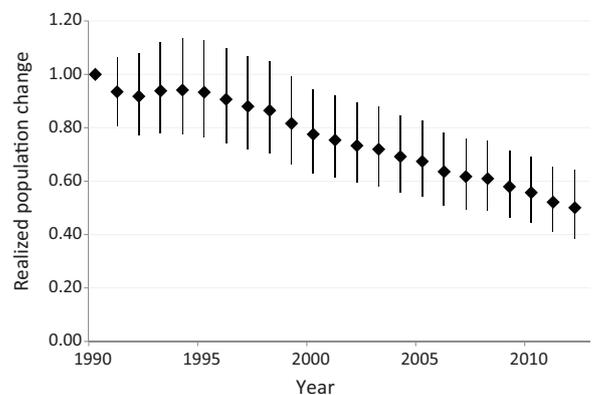


Fig. 4. Posterior means (95% CRI) of realized population change from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012.

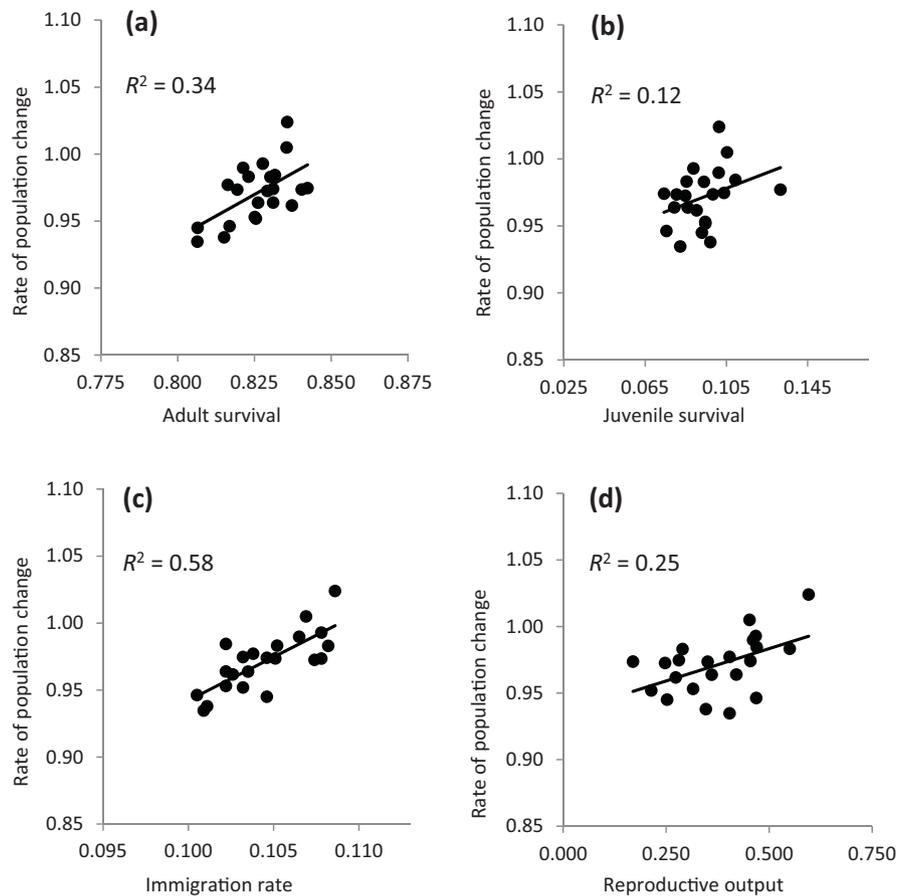


Fig. 5. Posterior means of the estimated finite rate of population change (λ) plotted against the posterior means of the estimates for (a) apparent adult survival, (b) apparent juvenile survival, (c) immigration rate (number of immigrants per adult), and (d) reproductive rate (number of young produced per adult) from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012. A best-fit regression line is shown on each graph.

We banded 229 non-juvenile owls and 252 juveniles from 1990 to 2012; twenty of the juveniles were later recaptured and banded as one of the 229 non-juvenile owls. Annual estimates of adult apparent survival ($\hat{\varphi}_{ad,t}$) ranged from 0.806 to 0.842 (Fig. 3); mean adult survival over the entire study period was 0.828 (95% CRI 0.801–0.854). In contrast, annual estimates of juvenile apparent survival ($\hat{\varphi}_{juv,t}$) ranged from 0.074 to 0.132 (Fig. 3) with a mean value of 0.087 (95% CRI 0.048–0.129). Immigration rates (\hat{imm}_t) were similar to juvenile survival rates, ranging from 0.100 to 0.109 with a mean value of 0.100 (95% CRI 0.059–0.144; Fig. 3). The reproductive rate (number of young produced per adult) ranged from 0.170 to 0.600 (Fig. 3), and the mean reproductive rate was 0.351 (95% CRI 0.280–0.425). Annual recapture probabilities were high ($\hat{p} = 0.868$, 95% CI 0.820, 0.911) and exhibited low temporal variation.

We calculated the correlation coefficients between the population growth rate and each of the demographic rates using the mean values provided by the IPM. All demographic rates were positively correlated with $\hat{\lambda}_t$ (Fig. 5). The correlation was strongest for \hat{imm}_t ($\beta_{slope} = 6.49$, 95% CI 4.056, 8.92; $R^2 = 0.58$) and weakest for $\hat{\varphi}_{juv,t}$ ($\beta_{slope} = 0.58$, 95% CI –0.112, 1.27; $R^2 = 0.12$). The correlations with $\hat{\varphi}_{ad,t}$ ($\beta_{slope} = 1.28$, 95% CI 0.50, 2.07; $R^2 = 0.34$) and \hat{f}_t ($\beta_{slope} = 0.10$, 95% CI 0.02, 0.17; $R^2 = 0.25$) were intermediate in strength. The magnitude of the regression slope was also greatest for immigration rate, which further suggested that $\hat{\lambda}_t$ was most sensitive to changes in immigration rate. In addition, we examined correlations between \hat{f}_t and \hat{imm}_t at 1- to 4-year time lags to assess whether good reproductive years resulted in increased immigration rates in

future years. All correlations were weak ($R^2 < 0.07$) except for the 3-year time lag ($\beta_{slope} = 0.008$, 95% CI –0.001, 0.017; $R^2 = 0.15$).

4. Discussion

We developed an integrated population model to assess population trends of territorial spotted owls in the central Sierra Nevada. Our approach was novel in that we first used a multi-state occupancy model to obtain annual “counts” of the number of adults and young produced, rather than using naïve counts that did not account for imperfect detection. This approach would produce stronger inferences about population trends if detection probabilities exhibited temporal variation (e.g., researchers became more proficient over time at locating individuals on their study area). We found a large decline in owl abundance on our study area from 1990 to 2012 ($\hat{\Delta}_{2012} = 0.501$, 95% CRI 0.384–0.642). Annual rates of population change were generally only slightly below 1.0 (Fig. 3), but the cumulative effect of small annual declines resulted in the loss of almost half of the initial population over the 23-year period. The approximately 50% decline in abundance was considerably greater than declines estimated for our study population based on separate analyses of mark-recapture ($\hat{\Delta}_{2011} = 0.725$, 95% CI 0.445–1.004) and occupancy ($\hat{\Delta}_{2011} = 0.702$, 95% CI 0.552–0.852) data collected from 1993 to 2011 (Tempel and Gutiérrez, 2013). We suspect that declines were greater when population growth was estimated with the IPM than with previous approaches for at least two reasons. First, the IPM allowed for the inclusion of an additional three years (1990–1992) of data at the beginning

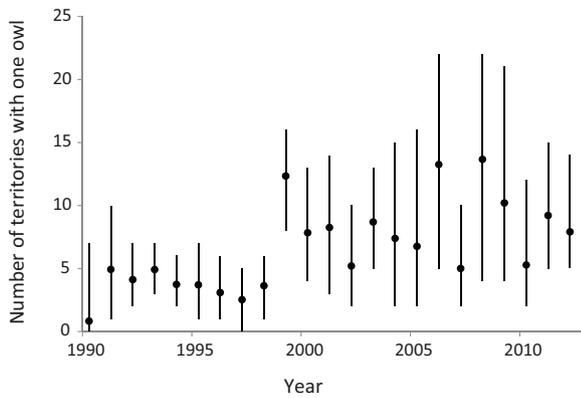


Fig. 6. Posterior means (95% CRI) of the number of California spotted owl (*Strix occidentalis occidentalis*) territories occupied by a single adult from a Bayesian multi-state occupancy model for a population in the central Sierra Nevada, 1990–2012.

of the study when funding constraints prevented us from surveying the entire study area; population growth was negative during these years as well. A basic assumption of the mark-recapture model was that the size of the study area remained constant over time (Pradel, 1996), but the effective size of the study area increased in 1993. In contrast, the multi-state occupancy model that we used to obtain annual “counts” for the IPM imputed the true state of unsurveyed territories during each Markov chain iteration (MacKenzie et al., 2009), and the IPM utilized the mark-recapture data solely to estimate adult survival. Second, the larger decline estimated with the IPM, as least compared to the occupancy-based estimate, can also be attributed to an increasing number of territories that were occupied by single owls during the study (Fig. 6). The loss of one member of a territorial pair without replacement does not affect occupancy status (as defined in Tempel and Gutiérrez, 2013), but clearly reduces population growth rates. An additional advantage of the IPM was that it provided a much more precise estimate of the total change in population size than the mark-recapture analysis and a somewhat more precise estimate of change than the occupancy analysis. Although the gain in precision over the occupancy analysis was not large, even modest improvements in the precision of trend estimates can facilitate conservation decisions about endangered species when there are contentious issues. Moreover, as discussed above, IPMs can provide more direct measures of population growth than analogous occupancy-based metrics and should register the signal associated with changes in the number of territories occupied by a single individual.

Adult spotted owl apparent survival was high 0.828 (95% CRI 0.801–0.854) and had low temporal variation, which was consistent with prior results for both California and northern (*S. o. caurina*) spotted owls (LaHaye et al., 2004; Blakesley et al., 2010; Forsman et al., 2011). In contrast, juvenile apparent survival was only 0.087 (95% CRI 0.048–0.129), which was markedly lower than the estimate reported by LaHaye et al. (2004) ($\hat{\phi}_{juv} = 0.368$, SE 0.038). The primary reason for this difference was that LaHaye et al. (2004) studied an insular population of spotted owls, so their estimates of juvenile apparent survival were unaffected by juvenile emigration. Thus, we suspected that the true survival rate of juveniles born on our study area was substantially higher than apparent survival, but the difference was unknown because we did not have information on emigration rates of juveniles (see Burnham et al., 1996). However, juvenile apparent survival was the appropriate parameter for the IPM because we studied an open population in which immigration and emigration were components of population change (i.e., emigration is equivalent to death when estimating the rate of population change within study area boundaries). Although adult

spotted owl apparent survival varied less than the reproductive rate, the two parameters made similar contributions to variation in population change. This finding was consistent with the results of Seamans and Gutiérrez (2007b), who found that adult apparent survival exhibited low temporal variation relative to reproduction but had a similar influence on λ , which was more sensitive to changes in adult survival. Our results supported the hypothesis that spotted owls have evolved a life-history strategy that favors longevity to increase the likelihood of experiencing favorable years for reproduction, which can be strongly influenced by annual climatic conditions (Franklin et al., 2000; Seamans and Gutiérrez, 2007b).

While our findings of the relative importance of survival and reproduction were similar to previous studies, the IPM provided novel insights into the spatial population dynamics of spotted owls. The mean annual immigration rate indicated that immigration was fairly high (almost 10% of individuals present in a given year were immigrants) and immigration contributed more to annual variation in population growth than survival or reproduction. One potential explanation was that our study area contained sink habitat and the population was maintained by immigration of individuals from the larger regional population. If habitat quality declined on our study area, some territories may have become unsuitable over the past 20 years. For example, Seamans and Gutiérrez (2007a) found that loss of spotted owl habitat was negatively correlated with territory colonization and positively correlated with dispersal of breeding individuals to other territories. An alternative explanation was that conditions on our study area were similar to those in the greater region and that the observed importance of immigration was largely an artifact of juvenile dispersal distances being large relative to the size of our study area. In other words, spotted owl emigration rates from our study area may have been equivalent to, or even exceeded, immigration rates onto the study area. If this were the case, then the observed population decline would have been indicative of overall trends in the larger regional population. Furthermore, if reproduction on our study area was indicative of reproduction adjacent to our study area, then years of high reproductive output should have resulted in years of higher immigration at some future point in time. Indeed, we found some evidence that immigration was positively correlated with the reproductive rate three years prior (see Section 3.2). Regardless, the estimate of almost 10% annual immigration, as well as the tight correlation between immigration and population growth, suggested that factors impacting owls in one region could impact other regions by affecting immigration rates. Our inability to distinguish between these alternatives underscored the need for additional research that assesses the directionality of owl movements on the landscape.

The literature on IPMs thus far has been mainly concerned with model development and evaluation (Schaub and Abadi, 2011), but our results illustrated the value of using IPMs to assess the status of species of conservation concern. In conjunction with recent estimates of population decline within two other regions of the Sierra Nevada (Conner et al., 2013), our finding of a large, long-term decline in a spotted owl population has potential important ramifications for forest management in the Sierra Nevada, where a primary goal of U.S. Forest Service management is to maintain viable spotted owl populations (U.S.D.A. Forest Service, 2004). Thus, it becomes imperative to understand the causes of population decline and to determine whether current management actions are sufficient to maintain spotted owls or even if they are partially responsible for the decline. For example, we recently found that the amount of high-canopy-cover ($\geq 70\%$) forest within owl territories was highly correlated with population growth rate and site occupancy and that the amount of this vegetation type on our study area declined by 7.4% from 1993 to 2012 (Tempel et al., in press).

Finally, our results suggest that rigorous monitoring of this species should continue.

Integrated population models offer important advantages over the traditional approach of conducting separate analyses for each available data source. First, IPMs can improve the precision of population estimates, and achieving sufficient statistical power is critical for the implementation of successful monitoring programs (Lindenmayer et al., 2013). Annual population declines in previously spotted owl studies had been difficult to detect (Blakesley et al., 2010), but we demonstrated the utility of IPMs for detecting population change in the spotted owl. Although we analyzed a long-term and relatively large dataset, the improved precision afforded by IPMs should be even more important in situations where data are sparse (Schaub et al., 2007). Second, IPMs provide a unified framework for estimating immigration rates, as opposed to ad hoc approaches that rely on comparing vital rates obtained from separate analyses (Peery et al., 2006). IPMs, however, do not enable one to determine whether a population is a sink or source population (Pulliam, 1988) unless one also has information on emigration derived from radio- or GPS-marked individuals. Nevertheless, knowing the extent to which a local population is open and thus affected by regional processes will be useful for making appropriate conservation decisions. Finally, the IPM accommodates the use of data from years of reduced survey effort, a situation that often occurs because of limited budgets, unexpected budget reductions, and other logistical limitations. The use of IPMs does require multiple data sources, which can require greater field effort, but occupancy data are often collected incidentally during mark-recapture studies of territorial species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2014.07.005>.

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