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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 ($\lambda_t = 0.969, 95\%$ 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 vielded 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 λ_t , but immigration was fairly high ($imm_t = 0.097$, 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,

http://dx.doi.org/10.1016/j.ecolmodel.2014.07.005 0304-3800/© 2014 Elsevier B.V. All rights reserved. 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 markrecapture, 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

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