Investigating the population dynamics of California spotted owls without marked individuals

D. I. MacKenzie · M. E. Seamans · R. J. Gutiérrez · J. D. Nichols

Abstract Understanding population dynamics is of great interest in many different contexts. Traditionally, population dynamics have often been considered in terms of individual-based demographic parameters (e.g., abundance, survival, and reproductive rates), estimation of which generally requires information from marked individuals. Alternatively, in some situations, it may be appropriate to consider population dynamics at a landscape level where the focus is shifted from numbers of individuals to the status of the population at places on the landscape. One consequence of doing so is that information from marked individuals is no longer required. Recently developed methods allow the estimation of landscape-level population vital rates in the realistic situation where the current status of the population might be misclassified via field methods (e.g., because of imperfect detection). Here, we consider the case of the California spotted owl (*Strix occidentalis occidentalis*) at the Eldorado study area in central Sierra Nevada, California, USA, where interest is in the occupancy rate of potential nesting territories, and in whether owls in an occupied territory successfully reproduced each year during 1997–2004. We analyzed the data using multistate occupancy models and found no evidence of annual variation in dynamic occupancy probabilities. There was strong evidence of annual variation in successful reproduction, with the pattern of variation being different depending on whether there was successful reproduction in the territory in the previous year. Of the three environmental variables considered, the Southern Oscillation Index appeared to be most important and explained some of the annual variation in reproduction probabilities.

Keywords California spotted owl · Detection · Multistate · Occupancy models

D. I. MacKenzie (✉)
Proteus Wildlife Research Consultants, PO Box 5193,
Dunedin 9058, New Zealand
e-mail: darryl@proteus.co.nz

M. E. Seamans
Division of Migratory Bird Management, USFWS,
Laurel, MD, USA

R. J. Gutiérrez
Department of Fisheries, Wildlife and Conservation Biology,
University of Minnesota, St Paul, MN, USA

J. D. Nichols
Patuxent Wildlife Research Center, USGS, Laurel, MD, USA

Introduction

Population dynamic processes determine how the status of a population changes through time. Understanding these processes and the rate at which they occur will often be of great interest in many applications; whether it is from a solely scientific perspective, or the perspective of ongoing conservation or management of the species. Traditionally, the study of population dynamics has often focused on the individual level, e.g., abundance, survival probabilities and reproductive rates. Estimation of these demographic parameters typically involves collecting reliable information from animals that can be individually identified using either natural or artificial markings. Such studies can be relatively expensive, particularly at moderately large spatial scales. They may also require certain technical field skills that may be unavailable in some regions. For some species of special conservation concern, there may also be

some resistance about handling individuals; hence the application of artificial marks may be undesirable.

In such situations, it may often be appropriate to consider population dynamics at a coarser, landscape level. At defined locations on the landscape, the status of the population can be assigned into one of multiple, biologically meaningful, mutually exclusive states. Population dynamics can thus be defined in terms of the rate at which status of the locations changes over time. The exact nature of the states is flexible and can vary among different applications, e.g., presence/absence of the species, levels of relative abundance, or whether the species is reproducing at certain locations. One advantage of such an approach is that often the information required to determine the status of the population does not require individuals to be uniquely identifiable. Such approaches may therefore be reasonable to consider where logistically, legally, or ethically the use of marked individuals may not be possible. However, an important consideration is that it may not always be possible to observe the true status of the population at a location. For example, successful reproduction may have occurred at a location, but the required evidence (e.g., detection of young) may not be observed. Hence, without accounting for the observation process, inferences about population dynamics may be misleading.

Recently, MacKenzie et al. (2009) have developed such an approach by extending multi-season occupancy models (MacKenzie et al. 2003, 2006) beyond the case of presence/absence-type data. As above, they consider situations where each location (or sampling unit) of interest could be in one of multiple discrete states, with some potential for observation error. A key assumption is that any observation error or misclassification error is one-way. For example, if reproduction is truly occurring at a location then it is possible to miss the evidence of reproduction so the location appears to have no reproduction, but it is not possible to falsely observe reproduction if no reproduction is truly occurring at the location. To account for the potential misclassification, the method of MacKenzie et al. (2009) requires that multiple surveys be conducted at each location at each time point to determine the current status of the location.

The California spotted owl (*Strix occidentalis occidentalis*) is a relatively long-lived species that exhibits a very high degree of fidelity to nesting territories (Blakesley et al. 2006; Seamans and Gutiérrez 2006, 2007). It would therefore be expected that the rate at which potential nesting territories are occupied in successive years should be highly correlated with adult survival. As for many territorial species, the number of breeding pairs of California spotted owls within a region that produce young during a breeding season should be correlated with the fraction of occupied nesting territories where young are produced. Hence, rather than consider population dynamics in terms of number of breeding pairs

and number of young produced (with vital rates of adult survival probabilities and per-capita reproductive rates), it may be reasonable to approach the situation in terms of number of occupied potential territories and number of occupied territories where young were produced (with vital rates of occupancy and reproduction probabilities). Therefore, the intent is to classify each potential nesting territory as: unoccupied, occupied without successful reproduction, or occupied with successful reproduction. We define successful reproduction for a pair in our study when at least one owlet has left the nest; hence, we do not distinguish non-breeding attempts from other nest failures. While capture–recapture methods have commonly been used to estimate parameters associated with population dynamics of all three spotted owl subspecies (Anthony et al. 2006; Franklin et al. 2004; Seamans et al. 1999), they are relatively expensive and time consuming to implement. Landscape-level surveys of potential California spotted owl territories are comparatively inexpensive and have been conducted by various agencies; hence they represent a potentially useful source of information, though imperfect detection must be accounted for. Here, we apply the methods of MacKenzie et al. (2009) to estimate landscape-level population dynamic parameters and the degree of annual variation in these parameters that can be explained by environmental variables.

Methods

Statistical methods

We first offer a brief overview of the statistical methods used; see MacKenzie et al. (2009) for additional details. The region of interest comprises S, suitably defined, geographic units. Units may be arbitrarily defined (e.g., grid cells or quadrats) or naturally occurring (e.g., habitat patches or ponds), depending upon the situation. The status of the species at each unit is in one of multiple discrete states, though it is considered that, generally, the state may not be observed perfectly. Hence, repeated surveys of each unit are required to enable detection and misclassification probabilities to be estimated and accounted for (although if states are observed perfectly, repeated surveys are not required and the methods can still be used to provide estimates by setting detection probabilities to 1.0). A sample of s units is selected in such a manner that enables the results of the sample to be applied to all S units in the region of interest, or that is otherwise conducive to the objectives of the study. The selected units are surveyed at systematic points in time (e.g., each breeding season) that are separated by appropriate intervals that reflect the timescale of interest for the dynamics (e.g., annually or 6-monthly). At each of these times (sampling season), the

sample units are surveyed repeatedly, and the true status of the units is assumed not to change across these repeated surveys. The series of surveys results in a detection history.

For example, suppose a unit may be in one of three possible states: species absent, species present without reproduction, or species present with reproduction; denoted as states 0, 1 and 2, respectively. There is a maximum of 3 possible outcomes for any single survey of a unit: species is not detected, species is detected but with no evidence of reproduction, or species is detected and evidence of reproduction is detected. These outcomes may be recorded as the observations 0, 1 and 2, respectively. If the unit is surveyed for three years with two surveys per year, the resulting detection history (h) could be represented as 21 00 01. This history indicates that in the first year the species was detected with evidence of reproduction in the first survey, then detected but without evidence of reproduction in the second survey. As it is assumed that the status of the unit does not change during the period of the surveys within a year, given that evidence of reproduction was observed at least once, reproduction must have occurred at the unit in the first year. In year 2, the species was not detected in either survey; however, it cannot be concluded that the species was absent if we admit imperfect detection, the species may actually have been present with or without reproduction. In the final year, the species was not detected in the first survey, but was detected in the second without evidence of reproduction. This precludes the possibility that the species is absent from the unit, but reproduction may or may not be occurring.

Let ψ_1 be the probability a unit is occupied (either state 1 or 2; i.e., species is present) in the first season and R_1 be the probability that successful reproduction occurred at a unit, given the unit was occupied (i.e., in state 2). The probabilities of being in each of the 3 states in the first season are, therefore, $1 - \psi_1$, $\psi_1(1 - R_1)$ and $\psi_1 R_1$,

respectively. For subsequent seasons, similar probabilities can be defined, though now these can also be allowed to vary by state in the previous season, i.e., $\psi_t^{[m]}$ and $R_t^{[m]}$ for $t = 2, 3,\ldots, T$, and m denotes state at time $t - 1$. These probabilities can be used to describe the population dynamics; how units change from being in one particular state to another. For example, the probability of a unit changing from a place where the species is absent to having successful reproduction in the next year would be $\psi_t^{[0]} R_t^{[0]}$, while the probability of changing from a location with reproduction to a place that is occupied but without reproduction is $\psi_t^{[2]}\left(1 - R_t^{[2]}\right)$. As noted by MacKenzie et al. (2009), such a parameterization is very flexible and allows interesting biological hypotheses to be explored.

To account for imperfect detection, let $p_{t,j}^{[1]}$ and $p_{t,j}^{[2]}$ be the probability of detecting the species in the jth survey of season t given that the unit is truly in state 1 or 2, respectively (with probability of detecting the species given the species is absent equal to 0), and $\delta_{t,j}$ be the probability of observing the evidence of successful reproduction given the species has been detected and reproduction has occurred. Therefore, at a unit with successful reproduction, the probability of detecting the species and finding the required evidence of reproduction in a survey (i.e., observe a 2) would be $p_{t,j}^{[2]}\delta_{t,j}$, and the probability of detecting the species but not finding the evidence of reproduction (i.e., observe a 1) would be $p_{t,j}^{[2]}\left(1 - \delta_{t,j}\right)$. At a unit without successful reproduction, there is no chance of observing reproduction (hence no δ term has been defined), while the probability of detecting the species is $p_{t,j}^{[1]}$.

In combination, these defined probabilities can be used to express the probability of observing any particular detection history. For example, consider again the detection history 21 00 01. By translating our previous verbal description into a mathematical expression we obtain:

$$\Pr(\mathbf{h} = 21\ 00\ 01) = \psi_1 R_1 p_{1,1}^{[2]}\delta_{1,1}p_{1,2}^{[2]}\left(1 - \delta_{1,2}\right)$$

$$\times \left\{ \begin{array}{l} \left(1 - \psi_2^{[2]}\right)\left[\begin{array}{l} \psi_3^{[0]}\left(1 - R_3^{[0]}\right)\left(1 - p_{3,1}^{[1]}\right)p_{3,2}^{[1]} \\ + \psi_3^{[0]}R_3^{[0]}\left(1 - p_{3,1}^{[2]}\right)p_{3,2}^{[2]}(1 - \delta_{3,2}) \end{array} \right] \\ + \psi_2^{[2]}\left(1 - R_2^{[2]}\right)\left(1 - p_{2,1}^{[1]}\right)\left(1 - p_{2,2}^{[1]}\right)\left[\begin{array}{l} \psi_3^{[1]}\left(1 - R_3^{[1]}\right)\left(1 - p_{3,1}^{[1]}\right)p_{3,2}^{[1]} \\ + \psi_3^{[1]}R_3^{[1]}\left(1 - p_{3,1}^{[2]}\right)p_{3,2}^{[2]}(1 - \delta_{3,2}) \end{array} \right] \\ + \psi_2^{[2]}R_t^{[2]}\left(1 - p_{2,1}^{[2]}\right)\left(1 - p_{2,2}^{[2]}\right)\left[\begin{array}{l} \psi_3^{[2]}\left(1 - R_3^{[2]}\right)\left(1 - p_{3,1}^{[1]}\right)p_{3,2}^{[1]} \\ + \psi_3^{[2]}R_3^{[2]}\left(1 - p_{3,1}^{[2]}\right)p_{3,2}^{[2]}(1 - \delta_{3,2}) \end{array} \right] \end{array} \right\}.$$

Where there is ambiguity in the true state, the probabilities associated with the multiple possibilities are added together. The three main lines within the large brackets represent the three possible true states in the second season, and the two lines within each of the square brackets represent the two possible true states in the third season. More generally, it is more convenient to express the probability for any observed history using a matrix formulation (MacKenzie et al. 2006, 2009). The model likelihood for the entire set of collected data is the product of the probability statements across all of the units. Estimates of the population dynamic probabilities can be obtained using either maximum likelihood or Bayesian techniques.

California spotted owls

Data considered here were collected on 66 potential nesting territories in April–August from 1997 to 2004 at the Eldorado study site in the central Sierra Nevada, California. MacKenzie et al. (2009) conducted a cursory analysis of these data, but here a more complete analysis is conducted with particular emphasis on whether annual variation in the population dynamic rates can be well explained by climatic and environmental variables. The variables of interest were Southern Oscillation Index (SOI), level of precipitation during the incubation period (April; INCP) and energy expenditure during the incubation period (INCE). Metabolic equations developed by Weathers et al. (2001) for spotted owls were used to calculate the average daily resting energy expenditure below the owl's thermoneutral zone. Seamans and Gutiérrez (2007) found that annual variation in adult survival and per capita reproductive rates was well explained by these environmental predictor variables. The results from MacKenzie et al. (2009) clearly indicated that the dynamic occupancy parameters ($\psi_t^{[m]}$) depended upon state in the previous season, but provided essentially no indication of annual variation, while the successful reproduction probabilities ($R_t^{[m]}$) exhibited variation as a function of previous state and across years.

For the dynamic occupancy probabilities, we considered six different models with respect to annual variation (Table 1): (1) none; (2) linear relationship with SOI; (3) quadratic relationship with SOI; (4) linear trend over time; (5) unconstrained annual variation (i.e., a year effect); in each case, a 'state' effect was included as an additive effect (i.e., the nature of any annual variation was consistent regardless of state in the previous year); and (6) the sixth model allowed the effect of state in the previous year to be different for each year, that is, an interaction between state and year. MacKenzie et al. (2009) found little evidence of annual variation in occupancy transition probabilities; hence, we did not expect the models including annual variation to be well supported. If there was a relationship

Table 1 Summary of initial model selection on dynamic occupancy probabilities ($\psi_t^{[m]}$)

Model	ΔAICc	w	K	$-2l$
ψ(State)	0.00	0.48	45	2,826.26
ψ(State + SOI)	1.53	0.23	46	2,825.66
ψ(State + Trend)	1.98	0.18	46	2,826.11
ψ(State + SOI^2)	2.98	0.11	47	2,824.98
ψ(State + Year)	10.35	0.00	51	2,823.79
ψ(State × Year)	18.55	0.00	63	2,806.04

Reproduction probabilities were modeled such that annual variation could be different depending on reproductive state in the previous year. In additional to models with annual variation, a linear trend (*Trend*) or relationships with Southern Oscillation Index (*SOI*) were considered. Models are notated by the highest order terms included, inclusion of all lower order terms is implied. Given are the relative difference in Akaike's Information Criterion corrected for small samples (ΔAICc), the AICc model weight (w), total number of parameters (K) and twice the negative log-likelihood for each model ($-2l$). *State* denotes an effect for occupancy and reproductive state in the previous years

Effective sample size was assumed to be 1,500

with the dynamic occupancy probabilities, we predicted: a negative linear relationship with SOI; a negative quadratic relationship with SOI (i.e., a local optimum); or a negative linear trend. For the successful reproduction probabilities, we considered SOI, INCE and INCP as potential covariates, either individually or in combination (Table 2). A potential interaction between INCE and INCP was considered, as was a quadratic relationship with SOI, but no interaction was considered between SOI and the other variables. Primarily, the effect of the environmental variables was assumed to be consistent regardless of state in the previous year. The effects were allowed to vary for the different states in some models, but only where a single environmental variable was considered. Otherwise, the number of parameters to be estimated for each state would rival the number of years of data. In addition, we considered models with no annual variation, annual variation that was consistent for the different states, and unconstrained annual variation.

As it is very rare for spotted owls to establish a new territory and then breed in the same year, the probability of successful reproduction given the potential territory was unoccupied by owls in the previous year was assumed to be constant for the duration of the study and predicted to be near 0.0. MacKenzie et al. (2009) found very strong evidence of annual variation in the reproductive success probabilities; we were therefore interested in whether that annual variation could be well explained by the environmental variables. We predicted negative relationships with all the environmental variables. In all cases, we allowed detection and late-season classification probabilities to vary

Table 2 Summary of initial model selection on dynamic reproduction probabilities ($R_t^{[m]}$)

Model	ΔAICc	w	K	−2l
R(State × Year)	0.00	0.84	45	2,826.26
R(State × SOI^2)	5.55	0.05	37	2,848.73
R(State + SOI^2)	6.64	0.03	35	2,854.03
R(State + Year)	7.02	0.03	39	2,845.99
R(State + SOI^2 + INCP)	8.04	0.01	36	2,853.33
R(State + SOI^2 + INCE)	8.58	0.01	36	2,853.87
R(State + SOI + INCP)	9.31	0.01	35	2,856.70
R(State + SOI^2 + INCP + INCE)	9.82	0.01	37	2,853.00
R(State + SOI + INCP + INCE)	11.23	0.00	36	2,856.52
R(State + SOI + INCE)	11.49	0.00	35	2,858.88
R(State + SOI + INCP × INCE)	11.15	0.00	37	2,854.33
R(State + SOI)	12.50	0.00	34	2,861.98
R(State + SOI^2 + INCP × INCE)	11.69	0.00	38	2,852.77
R(State × SOI)	14.65	0.00	35	2,862.04
R(State × (INCP × INCE))	16.01	0.00	39	2,854.98
R(State)	18.92	0.00	33	2,870.50
R(State + INCP)	20.27	0.00	34	2,869.75
R(State + INCE)	20.75	0.00	34	2,870.23
R(State + INCP × INCE)	20.96	0.00	36	2,866.25
R(State × INCP)	22.03	0.00	35	2,869.42
R(State + INCP + INCE)	22.09	0.00	35	2,869.48
R(State × INCE)	22.80	0.00	35	2,870.19

In all cases, reproduction was constrained to be constant if the territory was unoccupied in previous year. Occupancy probabilities depended upon state in the previous year, but no annual variation. Covariates considered are Southern Oscillation Index (*SOI*), level of precipitation during the April incubation period (*INCP*) and energy expenditure during the incubation period (*INCE*). Models are notated by the highest order terms included, inclusion of all lower order terms is implied. Given are the relative difference in Akaike's Information Criterion corrected for small samples (ΔAICc), the AICc model weight (*w*), total number of parameters (*K*) and twice the negative log-likelihood for each model (−2 *l*). *State* denotes an effect for occupancy and reproductive state in the previous years

Effective sample size was assumed to be 1,500

annually, but not otherwise within season. Early-season classification probabilities were expected to be essentially zero; hence, made equal in all years.

Model fitting was conducted in two phases using maximum likelihood techniques, as implemented in Program PRESENCE. First, model selection was performed on the dynamic occupancy parameters. The six models were fit to the data and ranked according to Akaike's Information Criterion corrected for small samples (AICc). There is some debate as to the "correct" effective sample size with occupancy models (MacKenzie et al. 2006) and possible values here range from 528 (66 territories × 8 years) to 2,227 (total number of completed surveys). We arbitrarily selected a middling value of 1,500 as a compromise

between these extremes (results are relatively robust to the value used). For each of the models presented in Table 1, a general model with respect to successful reproduction was maintained where reproduction was constrained to be constant if a territory was unoccupied in the previous year, but no other constraints otherwise (i.e., values allowed to vary independently for the other states each year). Once the best model with respect to occupancy probabilities was identified, the second phase was to perform model selection on the successful reproduction probabilities. Some see this two-phase approach as less than ideal, and we generally agree. However, we view this as a reasonable pragmatic approach, because otherwise a large number of models would have to be fit to the data (representing different combinations of scientific hypotheses about occupancy and reproduction dynamics) increasing the possibility of obtaining a spurious result given our moderate sample sizes.

Results

There was no strong indication of any substantial annual variation in the dynamic occupancy probabilities (Table 1). The top-ranked model suggested that the dynamic occupancy probabilities were constant with time. While other models were ranked relatively closely, there was no substantial improvement in the fit of the models with the additional variables (as indicated by the log-likelihood values); hence, there was little evidence of a relationship between the dynamic occupancy probabilities and SOI. The probability of a potential nesting territory being occupied in 1997 was estimated as 0.89 (95% CI: 0.76–0.95), with the dynamic occupancy probabilities estimated to be 0.16 (0.10–0.25) if the territory was unoccupied in the previous year, 0.85 (0.78–0.90) if the territory had been occupied but without successful reproduction, and 0.94 (0.85–0.97) if occupied with successful reproduction.

For successful reproduction probabilities, there was strong evidence of annual variation (Table 2). The top ranked model with 84% of the AICc model weight suggested that there was annual variation and that the pattern of that variation was different depending upon the reproductive status of the territory in the previous year. SOI featured prominently in the remaining top models, primarily as a negative quadratic relationship, suggesting some correlation with successful reproduction. While the second and third ranked models have low AICc weights, the difference in negative log-likelihood values compared to the model with only a state effect were 21.77 and 16.47 with an additional 4 and 2 parameters, respectively, indicating that those additional terms were explaining substantial variation in the data. There was essentially no support for the other environmental variables influencing
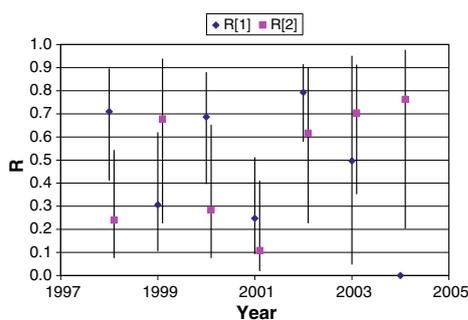
Fig. 1 Estimated probabilities of successful reproduction for California spotted owls (*Strix occidentalis occidentalis*) at the Eldorado study site in Sierra Nevada, California, USA, from the top model presented in Table 2. *R[1]* and *R[2]* indicate the estimates for territories without and with successful reproduction in the previous year, respectively
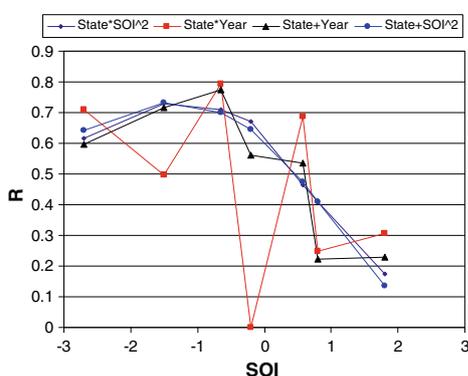

Fig. 2 Estimated probability of successful reproduction given no successful reproduction at territory in previous year from the top four models indicated in Table 2
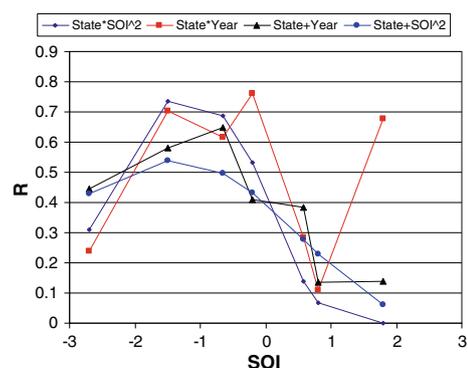

Fig. 3 Estimated probability of successful reproduction given successful reproduction at territory in previous year from top four models indicated in Table 2

the probabilities of successful reproduction. From the top model, the estimated probability of successful reproduction in 1997 was 0.47 (0.32–0.62), and, given a territory was unoccupied in the previous year, the probability of successful reproduction in subsequent years was estimated to be zero. We presented all remaining estimated probabilities of successful reproduction from the top model with associated 95% confidence intervals in Fig. 1. Similarly, we presented the estimated successful reproduction probabilities for territories without successful reproduction in the previous year for 1998–2007 from the top 4 models, plotted against SOI in Fig. 2. We presented the comparable estimates for territories that had successful reproduction in the previous year in Fig. 3. We only presented point estimates in Figs. 2 and 3 for clarity.

Discussion

Predictions from ecological theory for long-lived species were that adult survival probabilities were likely to exhibit

less annual variation than reproductive rates (Pfister 1998; Gaillard et al. 2000). Seamans and Gutiérrez (2007) found this to be true for this population of California spotted owls using capture–recapture techniques. Using a landscape-level approach, we found similar results with essentially no evidence of substantial annual variation in occupancy dynamics, but very strong evidence of annual variation in successful reproduction dynamics. This suggested that the system may be in a state of equilibrium with respect to the distribution of spotted owls, but within that distribution, times and locations of successful reproduction were more variable.

Based upon the findings of Seamans and Gutiérrez (2007), we had expected that there would have been greater support for the environmental variables being important predictors of the successful reproduction probabilities, in particular SOI, but this was not the case. This may have been due to the fact that at the landscape scale, this relationship did not hold or was less marked. Or the weaker support could have been a consequence of fewer annual observations (7 years here vs 14 for Seamans and Gutiérrez 2007) and of the fact that the time period we considered here (1997–2004) only contained one notable El Nino event while that of Seamans and Gutiérrez (2007) contained three.

The best model indicates that the patterns of annual variation in successful reproduction probabilities are different depending upon the state of the territory in the previous year. That is, in some years the probability of successful reproduction in a territory is estimated to be higher if there was no reproduction in the previous year, whereas in other years territories that previously had successful reproduction had the higher estimated probability. If it was hypothesized that there was a significant energetic investment associated with successful reproduction, then it would be expected that the probability of successful reproduction should be consistently lower in territories that successfully reproduced the previous year compared to

territories at which successful reproduction did not occur. An alternative hypothesis about the system could be that some territories act as a source (frequent successful reproduction), while other territories are relative sinks (infrequent successful reproduction). Under this hypothesis, the reproduction probability for territories that had pairs that successfully produced young in the previous year would be expected to be consistently higher than for those pairs in territories where young were not successfully produced. In either case, a consistent difference between the respective probabilities would be expected. That there is such strong support for an inconsistent difference is in itself interesting, suggesting some other mechanisms may be driving the dynamics of the system and warranting further investigation. For example, in a year of low prey availability, it may be that birds that reproduced successfully the previous year might be at a disadvantage, leading to low probability of success. However, in a year of high prey availability, there may be no cost of successful reproduction in the previous year.

We also admit the possibility that the high ranking of the full time-specific model simply reflects the reality that some variable(s) other than those we investigated is also an important determinant of variation. While there tends to be a reasonable level of separation of the various confidence intervals (Fig. 1), the widths for many of the estimates are fairly wide, which is indicative of low sample sizes.

In addition to considering covariates to explain temporal variation in the dynamic rates, they could also be used to explain spatial variation amongst the territories. Measurable characteristics of the potential nesting territories (e.g., habitat or forest type, elevation and aspect) could be included in the models and fit to the data to explore potential relationships.

Despite our not finding any strong evidence of a relationship with the environmental variables considered here, we have shown that multi-state occupancy models provide a natural, and useful, framework for addressing questions of population dynamics at the landscape scale, without the need for marked individuals. In this application, landscape units have been defined in terms of potential nesting territories, though for other situations landscape units could be defined differently (e.g., arbitrarily-sized grid cells or forest fragment patches). The key consideration is to define landscape units in a manner that is most sensible given the objectives of the study. Similarly, the study objective is the prime consideration for determining the number and definition of the potential states. Data requirements must also be taken in account as they will increase in accordance with the number of states used.

The multi-state occupancy model used here has some similarities with multi-state mark–recapture models, in particular those that account for misclassification (e.g.,

Kendall et al. 2003; Nichols et al. 2004; Conn and Cooch 2009) or the multi-event model developed by Pradel (2005). Exploration of the similarities and differences may prove useful as tools that have been developed in these areas (e.g., software and methods for assessing model fit) could be applied to multi-state occupancy models with further development. All these methods are also special cases of hidden Markov models that are used in numerous other disciplines, hence wider reading of the relevant literature may be fruitful.

Finally, we recognize that for some objectives and situations, a landscape-level approach to population dynamics will be inappropriate, and that such questions can only be adequately addressed with more detailed individual-level information (e.g., from more intensive mark-recapture studies). Nevertheless, we believe the above methods are a valuable addition to the toolbox of options for studying many avian species, and species of other taxa, particularly because of their ability to account for imperfect detection, unequal surveying effort and investigate potential relationships with covariates or predictor variables.

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