



Research Article

A Multi-State, Time-Removal Model for Population Dynamics of Cliff-Nesting Raptors

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ABSTRACT Cliff-nesting raptors present considerable challenges for population estimation due to their sparse distribution across remote landscapes and the multiple occupancy states (e.g., unoccupied, occupancy without breeding, breeding occupancy) through which we observe their nesting territory dynamics. To increase the efficiency and spatial inference of surveys, we developed 2 versions of a multi-state, time-removal model: 1 for long-term monitoring studies and the other for population inventories or single-season surveys in which there is no prior knowledge of nest locations. We focused our development of these methods in the context of a combined aerial and ground-based survey approach, which permits efficient surveying at landscape scales. The approach, however, is also applicable to designs restricted to ground surveys. For long-term monitoring of species with alternative nests, we formulated a version of the model that accounts for state uncertainty at the territory level caused by a failure to observe all nests within a territory. Simulations based on the long-term monitoring model indicated adequate (near nominal) coverage and low relative bias (<0.05) for nearly all parameters. In the simulation study for the inventory model, population size estimates showed negligible bias for a survey duration of 90 minutes. We applied our approach to a long-term study of golden eagles (*Aquila chrysaetos*) in Alaska and demonstrated that the maximum effort spent on any nesting territory could be reduced by up to almost 90% of that recommended by standard protocols. Published 2018. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS alternative nests, *Aquila chrysaetos*, golden eagle, long-term monitoring, multi-method, multi-state occupancy, rare species.

Landscape-scale monitoring is necessary for effective conservation of wildlife species. Sampling at large spatial scales for sparsely distributed species, however, presents considerable challenges. In such cases, the development of cost-effective approaches can be addressed in part through a thorough understanding of how the data are actually generated (the observation process, in part) and the application of sampling methods that attempt to maximize detection probability (Thompson 2004, Royle and Dorazio 2008, Nichols et al. 2009). When these populations are comprised of multiple states, multiple survey methods may be used to increase the probability of correct classification of individuals in each state.

Developing efficient sampling methods for cliff-nesting raptors is particularly challenging because of the large space usage of these species, their sparse distribution across remote landscapes, and the multiple occupancy states (e.g., unoccupied,

occupancy without breeding, occupied with breeding) through which we observe their population dynamics. In most studies of the dynamics of cliff-nesting raptor populations, territories or historical nests are visited with an intensive level of effort that is assumed to ensure that the occupancy state is known with certainty (Hardey et al. 2006). For example, the United States Fish and Wildlife Service (USFWS) recommends ≥ 2 , 4-hour ground observation occasions in each territory or ≥ 2 aerial survey visits for monitoring peregrine falcons (*Falco peregrinus*; USFWS 2003) and golden eagles (*Aquila chrysaetos*; Pagel et al. 2010). In a landscape-scale survey, allocating survey effort in this manner is impractical and inefficient, particularly in the Arctic and subarctic where logistical costs are often high.

Most studies of raptor population dynamics involve intensively monitoring 30–100 nesting territories within a single survey area (Steenhof et al. 1997, Pokrovsky et al. 2014). The spatial scale of inference from these studies is limited, leaving gaps in our understanding of cliff-nesting raptor population dynamics and distribution at the landscape scale. Single-season (or intermittent) surveys (i.e., population inventories) may be necessary to fill these information gaps and to protect breeding areas. Specifically, as lands are

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opened for energy development or are subject to other forms of disturbance, land managers must assess the potential effects on cliff-nesting raptors and their alternative nests (Millsap et al. 2015). These assessments will often be restricted to single-season surveys of landscapes for which little or no prior knowledge of nest locations exists. Despite a critical need for long-term monitoring and inventory studies of cliff-nesting raptors, the development of cost-effective methods that would permit sampling at larger spatial scales has received little study with few exceptions (Booms et al. 2010). Here, we take the approach that the compromise for survey efficiency involves abandoning the assumption of state certainty for a modeling framework in which state and observation processes are considered simultaneously.

The process by which we observe raptor population dynamics is complicated by several aspects of their breeding ecology. On breeding grounds, raptor populations are generally comprised of non-territorial individuals (i.e., floaters), breeders, and territorial non-breeders (Newton 2003, Steenhof et al. 2017). Studies of nesting territory occupancy typically make inference to the territorial population corresponding to the latter 2 groups of individuals. Prey availability or weather may limit the proportion of the population attempting breeding in a given year, whereas the composite territorial occupancy (occupancy with or without breeding) shows considerably less interannual variation (Newton 1979, Steenhof et al. 1997, McIntyre and Schmidt 2012; Fig. 1, box 3). Thus, for some raptor species, the breeding component on its own is likely to be a poor predictor of population size, particularly in years when prey densities are low. In such cases, estimates of the subset of the population comprised of territorial individuals that are not breeding (i.e., occupancy without breeding) are needed to make reliable inferences about population dynamics.

The tendency of cliff-nesting raptors to maintain nesting territories comprised of multiple, alternative nests results in additional complexity in how we observe their population dynamics (Fig. 1, box 2b). For example, in studies conducted in the Canadian High Arctic, rough-legged hawks (*Buteo lagopus*) maintained nesting territories comprised of an average of 1.6 nests (range = 1–4; Beardsell et al. 2016). Golden eagle nesting territories were comprised of 6.9 nests (range = 1–18) in southwestern Idaho, USA (Kochert and Steenhof 2012) and approximately 3 nests (range = 1–9) in Denali, Alaska, USA (C. L. McIntyre, U.S. National Park Service, unpublished data). In a long-term monitoring study, knowledge of the locations of nests is accumulated over many years until all nest locations within a territory are eventually known, although new nests are occasionally constructed. For species in which nesting territories may include alternative nests located 1–2 km apart, we would expect that incomplete knowledge of nests in the initial years of the study would result in failure to survey some nests that contained eggs. This could lead to negative bias in the estimate of the breeding component of the population.

Herein, we developed a framework that permits larger spatial inference about cliff-nesting raptor population dynamics under a variety of aerial and ground-based designs.

Specifically, we developed 2 versions of a multi-state, time-removal model: 1 applicable to long-term monitoring studies and the other to population inventories. In the context of the long-term monitoring model, we provide a method that accommodates incomplete surveying of alternative nests within territories without requiring repeat surveys to estimate nest-level detection. We focused our development of these methods in the context of a combined aerial and ground-based survey approach that permits efficient surveying at landscape scales. We also provide an extension of our model applicable to long-term monitoring studies restricted to ground surveys.

STUDY AREA

We based the development of our inference framework on a long-term monitoring study of golden eagles in Denali from 2007–2016. The 2,100-km² study area (centered near 63° 35'89"N, 149° 38'29"W) lies within the northern foothills of the Alaska Range and is primarily designated wilderness. Elevations of the foothill summits range from 607 m to 1,372 m and the higher peaks exceed 2,500 m and are permanently snow and ice covered (McIntyre and Adams 1999). Most of the study area is above treeline (>800 m) and is characterized by broad glacially carved valleys of shrub-tundra bordered by steep, disturbed slopes, and barren rock outcrops (McIntyre and Adams 1999). Vegetation types include upland coniferous forest, sparsely canopied woodland at treeline, dense riparian and upland shrublands, extensive riparian gravel bars, open shrublands near shrubline, and alpine tundra and fellfield. The key prey species of golden eagle within this landscape are snowshoe hare (*Lepus americanus*) and willow (*Lagopus lagopus*), rock (*L. mutus*), and white-tailed (*L. leucurus*) ptarmigan. Temperatures range from –47 °C to 32 °C and annual precipitation averages 38 cm with 200 cm of snowfall (McIntyre and Adams 1999).

METHODS

Long-Term Monitoring With Aerial and Ground-Based Surveys

Survey methods.—We monitored 104 golden eagle territories in Denali annually from 1988–2016 using a combination of aerial and ground-based surveys. We used a subset of these data (2007–2016) to illustrate our inference framework. We assumed the locations of all nests within each territory were known, although occasionally we located newly constructed and previously unobserved nests. Via helicopter, an observer (C. L. McIntyre) surveyed nests within all nesting territories in late April or early May (i.e., after most clutches were assumed to have been completed) and recorded the presence or absence of an incubating eagle, eggs, or eggshells. We also made observations that, in the absence of evidence of a breeding attempt, were considered indicative of occupancy without breeding including a recently refurbished nest, a mated pair of eagles, or some other territorial behavior. If we did not detect evidence of occupancy with or without breeding, the helicopter landed at a vantage point and we

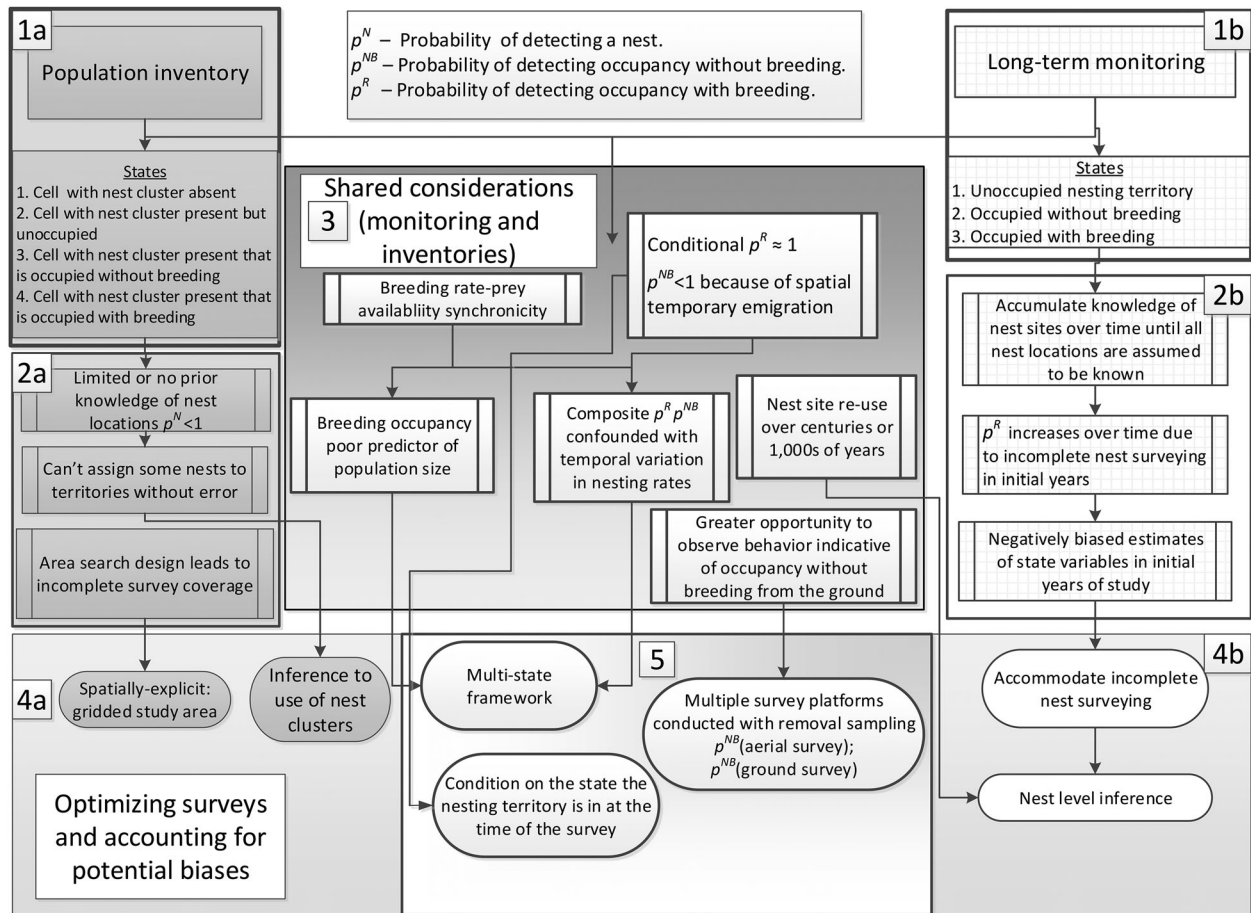


Figure 1. Conceptual diagram of inference framework for long-term monitoring and population inventories of cliff-nesting raptors. Boxes with the letter a appended are specific to population inventories and boxes with the letter b appended are specific to long-term monitoring designs. Boxes 1a and 1b include the occupancy states considered under the different designs. Boxes 2a and 2b contrast the extent of prior knowledge about nest locations under the 2 designs and list some implications for developing inference methods. Box 3 includes shared characteristics of state and observation processes in inventories and monitoring studies. Boxes 4a and 4b are characteristics of the inference methods developed here that are specific to inventory and monitoring studies, respectively. Box 5 includes aspects of the inference methods developed here that are shared under the 2 designs.

conducted a ground survey. The ground survey included visually searching the area for eagles engaged in territorial behavior such as nest building, territorial defense, or courtship and generally lasted ≤ 4 hours or until we observed a behavior indicative of occupancy. We conducted a subset of surveys entirely on foot, which occasionally included multiple observers.

Because the Denali monitoring program is focused on inference at the park-level and not larger spatial scales, we used an intensive level of effort to ensure that the occupancy state is known with certainty. Ground surveys occasionally lasted > 4 hours and sometimes we made additional aerial and ground visits. Here, our primary objective was to expand spatial inference through a more efficient application of this protocol (i.e., reduce the max. effort spent on any nesting territory to a single aerial visit followed by a 1–2-hour ground survey). Therefore, in our case study, we used only the first aerial visit to nesting territories and censored (*post hoc*) all ground surveys at 2 hours to specify a time-removal model for this component of the observation process. Because golden eagle breeding is related to prey abundance, we also

compiled an index of 2 primary prey species, snowshoe hare and willow ptarmigan, based on counts made during routine field work from mid-April through late June (McIntyre and Adams 1999).

Model-development.—We developed a dynamic multi-state, time-removal occupancy model in a state-space framework, describing the probability of each nesting territory existing in 1 of 3 mutually exclusive states: unoccupied; occupied without breeding; and occupied with breeding (Fig. 1). We specified the observations y_{it} for territory $i = 1, 2, \dots, I$ and year $t = 1, 2, \dots, T$ as multinomial random variables conditional on the true states z_{it} with cell probabilities π_{ik} for cell $k = 1, 2, \dots, K$:

$$y_{it} \sim \text{Multinomial}(\pi_{ik}[z_{it}, \dots], 1) \quad (1)$$

We described our observations as arising from a state-dependent, removal sampling process. The rows of the state detection matrix were dependent on the true state m with probabilities that summed to 1 and the columns k corresponded to the probabilities of observing state l (i.e., $k^{[l]}$; MacKenzie et al. 2009). The first 2 columns

corresponded to the aerial survey:

$$1^{[3]} \quad 2^{[2]} \\ 1 \begin{bmatrix} 0 & 0 \\ 0 & p^{NB,A} \\ S_{it} & (1 - S_{it}) \times p^{NB,A} \end{bmatrix} \quad (2)$$

$k = 3, 4, \dots, K-1$ were the individual intervals of the time-removal survey:

$$K^{[2]} \\ 1 \begin{bmatrix} 0 \\ (1 - p^{NB,A}) \times p^{NB,G} \times (1 - p^{NB,G})^{k-3} \\ (1 - S_{it}) \times (1 - p^{NB,A}) \times p^{NB,G} \times (1 - p^{NB,G})^{k-3} \end{bmatrix} \quad (3)$$

and K was the cell containing the probability of failing to observe occupancy at the end of the combined aerial-ground survey:

$$K^{[1]} \\ 1 \begin{bmatrix} 1 \\ (1 - p^{NB,A}) \times (1 - p^{NB,G})^{K-1} \\ (1 - S_{it}) \times (1 - p^{NB,A}) \times (1 - p^{NB,G})^{K-1} \end{bmatrix} \quad (4)$$

The parameters of the state detection matrix were the probability of detecting occupancy without breeding during the aerial survey ($p^{NB,A}$), the probability of detecting occupancy without breeding during the ground survey for some time interval ($p^{NB,G}$), and a binary indicator of whether the nest in which eggs were laid was surveyed (S_{it}).

In our single-visit approach, we assume the territorial population is closed but condition on the territory's state at the time of the survey (Fig. 1, box 5). Given that a nest contains eggs at the time of the survey and its contents are observed during the aerial survey, we assume that the (conditional) probability of detection is 1 (Fig. 1, box 3). We make the distinction between surveying an individual nest (i.e., directly observing its contents) and surveying a nesting territory. For example, one could visit a known nesting territory and unknowingly fly past a particular nest in 1 year and then find and observe the contents of the nest in a subsequent year, in which case the territory is surveyed in both visits, but the nest is recorded as surveyed only in the latter visit. Although we assume the conditional probability of detecting breeding is 1, we allow for incomplete surveying of individual nests in a territory. In long-term studies of species with territories comprised of alternative nests, the probability of detecting breeding in a territory that ignores incomplete surveying of nests increases over time until all nest locations are known (although new nests are occasionally constructed). This process can induce negative bias in estimates of occupancy for the initial part of the study and potentially confound temporal effects on occupancy. Although we did not apply the nest-level version of the model in the Denali long-term monitoring case study, we develop it here because we expect it could be used to improve inferences from other monitoring efforts.

In the nest-level formulation of the long-term monitoring model, we specified a model for the expected frequency of use λ_{gi} for nest $g = 1, 2, \dots, G_i$ in territory i :

$$\log(\lambda_{gi}) = \delta_1 \times x_{gi} \quad (5)$$

where G_i is the known number of nests in territory i , x_{gi} is a covariate for each nest (e.g., nest condition, distance to some disturbance), and δ_1 is a parameter to be estimated (Royle and Converse 2014). We did not include an intercept in this model because it would be confounded with the probability of breeding (i.e., δ_1 is the effect on nest use frequency conditional on the territory existing in the breeding state; Royle and Converse 2014). The model for nest use frequency serves a dual purpose, accounting for incomplete surveying of nests within territories and permitting ecological inferences about the use of individual nests for breeding.

The identity of the nest used for breeding in territory i and year t is a multinomial random variable:

$$\text{nest}_{it} \sim \text{Multinomial}(\pi_{1i}, \pi_{2i}, \dots, \pi_{G_i i}, 1) \quad (6)$$

with cell probabilities π_{gi} conditional on the territory-specific sum of nest use intensities:

$$\pi_{gi} = \frac{\lambda_{gi}}{\sum_{g=1}^{G_i} \lambda_{gi}} \quad (7)$$

To describe nest use as a binary, we specified an indicator variable w_{git} that is an outcome of the relation of nest_{it} to the array index $j = 1, 2, \dots, G$, where G includes G_i (the real number of nests in territory i) padded with structural nests to the maximum number of nests known to exist in any territory:

$$w_{git} = \begin{cases} 1 & \text{when } \text{nest}_{it} = g \\ 0 & \text{when } \text{nest}_{it} \neq g \end{cases} \quad (8)$$

We described the detection of breeding at the nest-level as the outcome of whether the nest was used for breeding and whether its contents were observed in year t :

$$S_{git}^n = w_{git} \times \text{surveyed}_{git} \quad (9)$$

Re-use of nests by cliff-nesting raptors is thought to extend over generations or centuries (Newton 1979), with some evidence from radiocarbon-dating indicating that nests may be re-used over periods of several thousand years (Burnham et al. 2009; Fig. 1, box 3). Thus, we assumed that any nest recorded as unsurveyed in prior years was available for breeding and may have been used in prior years. Over the <10-year period in which knowledge of nests in the study area is incomplete, we expect that relatively few nests enter the population at locations where there is no prior evidence of use (i.e., that most of these nests have been in use for timescales much longer than our study period). If a nest is newly constructed, collapses, is absorbed by a different territory, or uncertainty exists about whether it was available for breeding in a prior year, however, it can be recorded as surveyed, precluding its potential imputation as used for breeding.

Finally, the indicator variable for detecting breeding is the binary outcome of summing the nest-level indicators within a territory $S_{it} = \sum_{g=1}^G S_{git}^n$. The latent true states z_{it} were specified as the outcome of conditional binomial probabilities using the parameterization of Nichols et al. (2007). The true states for the first year were multinomial random variables:

$$z_{i1} \sim \text{Multinomial}(\phi_0, 1) \quad (10)$$

with the probability vector:

$$\phi_0 = [1 - \psi \quad \psi \times (1 - R) \quad \psi \times R] \quad (11)$$

where ψ is the first-year probability of occupancy and R is the first-year probability of breeding (MacKenzie et al. 2009). The true states for subsequent years were multinomial random variables:

$$z_{it} | z_{it-1} \sim \text{Multinomial}(\phi_{t-1}[z_{it-1}, \dots], 1) \quad (12)$$

with cell probabilities ϕ_t defined in the transition probability matrix as follows:

$$\phi_t = \begin{bmatrix} 1 - \psi_{t+1}^{[1]} & \psi_{t+1}^{[1]} \times (1 - R_{t+1}^{[1]}) & \psi_{t+1}^{[1]} R_{t+1}^{[1]} \\ 1 - \psi_{t+1}^{[2]} & \psi_{t+1}^{[2]} \times (1 - R_{t+1}^{[2]}) & \psi_{t+1}^{[2]} R_{t+1}^{[2]} \\ 1 - \psi_{t+1}^{[3]} & \psi_{t+1}^{[3]} \times (1 - R_{t+1}^{[3]}) & \psi_{t+1}^{[3]} R_{t+1}^{[3]} \end{bmatrix} \quad (13)$$

where $\psi_{t+1}^{[m]}$ and $R_{t+1}^{[m]}$ are the probabilities of occupancy and breeding, respectively, in year $t+1$ given m , the state in year t (MacKenzie et al. 2009). Thus, each row corresponds to a vector of probabilities that sum to 1 and are conditional on m .

Simulation study.—We conducted a simulation study to assess whether the multi-state, time-removal model could recover the data-generating values under a scenario in which the population was declining over time and subject to synchronization of its breeding rate with fluctuation in prey abundance. For illustration, we used a relatively extreme example of cyclical prey that are strongly linked to golden eagle reproduction, but other influences of reproductive dynamics may be more appropriate in other species (e.g., weather conditions; Steenhof et al. 1997). We specified $I = 150$ territories and $T = 20$ years. We drew the number of nests in each territory from a zero-truncated Poisson distribution with mean = 3, corresponding approximately to the mean of the Denali population. We induced incomplete nest-level surveying by specifying the annual probabilities of a nest entering the sampled population as 0.75, 0.06, 0.05, 0.04, 0.03, and 0.02 for the first 6 years, with complete nest-level surveying thereafter. We based these entry probabilities on the accumulation of known territory locations from the Denali study (e.g., 0.66 for the first year) but adjusted them upwards for a more conservative entry process.

We coincided the initial years of the study with the low point of prey availability and later years with the high point of prey availability (Fig. 2). The result was a low proportion of the population in the breeding state in the initial years of the study and high proportion in the latter years (Fig. 2).

Consequently, under single-state inference in our scenario, the composite p from the aerial survey would be lower in early years and higher in later years, confounding the decreasing trend in occupancy. This would be compounded by incomplete nest-level surveying in the initial years, which would induce negative bias in estimates of occupancy in early years and positive bias in later years under approaches that ignore incomplete nest-level surveying.

The state probabilities for the first year were 0.3, 0.3, and 0.4 for states 1, 2, and 3, respectively. We generated data for subsequent years using the following logit-linear models:

$$\text{logit}(\psi_{t+1}^{[m]}) = \alpha_0^{[m]} + \alpha_1^{[m]} \times \text{year}_{t+1} \quad (14)$$

$$\text{logit}(R_{t+1}^{[m]}) = \beta_0^{[m]} + \beta_1^{[m]} \times \text{prey}_{t+1} \quad (15)$$

To create a declining population, we set $\alpha_0^{[m]}$ at -0.25 , 1.0 , and 1.25 for $m = 1, 2$, and 3 , respectively, and $\alpha_1^{[m]}$ was -0.4 for all m . We set the parameters of the breeding probabilities, $\beta_0^{[m]}$ and $\beta_1^{[m]}$, to values based on our knowledge of the Denali population. For the prey availability covariate, we used the real values of the ptarmigan index data over a 20-year period. We set $p^{NB,A}$ and $p^{NB,G}$ to 0.56 and 0.12, respectively, based

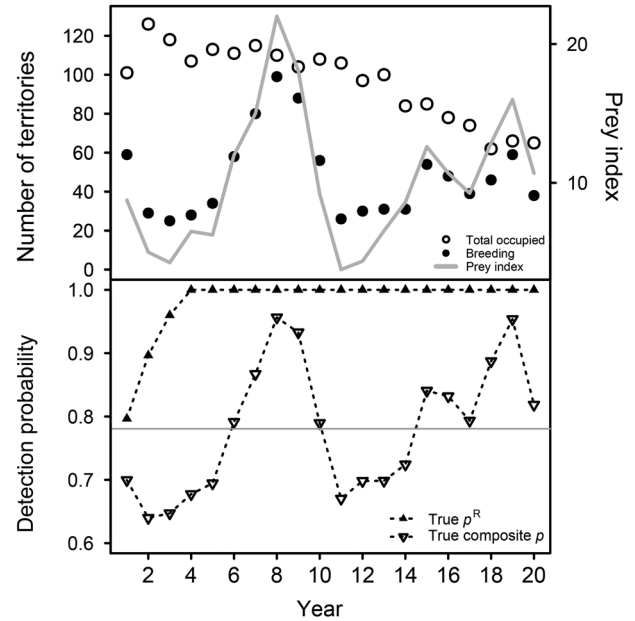


Figure 2. Scenario implemented in the simulation study for the long-term monitoring model for cliff-nesting raptors involving a declining population with a nesting rate that is synchronized with fluctuation in prey abundance (top panel). We generated data for 150 territories and a 20-year time period. The bottom panel shows the confounding that would arise under single-state inference between a constant, composite p (the probability of detecting non-breeding or breeding occupancy for the aerial survey; flat gray line) and the breeding rate. The true p (dashed line with unfilled triangles) accounts for the actual proportion of breeding and non-breeding territories in each year and their corresponding detection probabilities. The data-generating values for detecting occupancy without breeding and detecting occupancy with breeding (given observation of the nest contents) were 0.56 and 1, respectively. The probability of detecting breeding p^R was simulated <1 in the initial years (dashed line with filled triangles) to reflect the accumulation of known nest locations.

on our knowledge of the Denali population. To reflect the logistical considerations of a landscape-scale survey, we used 6, 10-minute time intervals for the time-removal ground survey.

Case study.—In the Denali case study, we did not use nest-level data and assumed that all nests were located in the 19 years prior (1988–2006) to the period we used to illustrate our model (2007–2016). Thus, we applied the model described above under the assumption $S_{it} = 1$ for all territories and years. We censored all surveys at 2 hours, corresponding with the minimum duration for a survey in which occupancy was not detected (with the exception of 3 surveys that we treated as missing data). We used 12, 10-minute removal intervals for the ground survey component of the state detection matrix, although finer intervals could be used to approximate continuous-time models (Garrard et al. 2008). Because a subset of surveys were conducted entirely on foot and, consequently, did not include an aerial survey, it was necessary to specify 2 different detection matrices.

Previous work in Denali indicated that both hare and ptarmigan abundance are important influences of golden eagle reproductive dynamics (McIntyre and Adams 1999, McIntyre and Schmidt 2012). Therefore, we specified the following logit-linear models for the probabilities of occupancy and reproduction in year $t+1$ conditional on the state in year t (m):

$$\text{logit}(\psi_{t+1}^{[m]}) = \alpha_0^{[m]} + \alpha_1^{[m]} \times \text{hares}_{t+1} + \alpha_2^{[m]} \times \text{ptarmigan}_{t+1} \quad (16)$$

$$\text{logit}(R_{t+1}^{[m]}) = \beta_0^{[m]} + \beta_1^{[m]} \times \text{hares}_{t+1} + \beta_2^{[m]} \times \text{ptarmigan}_{t+1} \quad (17)$$

where hares_{t+1} and ptarmigan_{t+1} were indices of the annual abundance of adult hares and ptarmigan.

Long-Term Monitoring with Ground-Based Surveys

Often monitoring studies are restricted to ground surveys, but the desire for increasing survey efficiency and expanding the spatial scale of the inference may exist. Extending the multi-state, time-removal model described above to these sampling designs is straightforward (Supplement 1, available online in Supporting Information). We do not consider designs that only include an aerial survey component based on a pilot study that found that the probability of detecting occupancy without breeding was poorly estimated in the absence of ground surveys ($\bar{x} = 0.438$, 95% CI = 0.192, 0.721). However, aerial survey (only) designs may be efficient when the breeding component alone is a reliable indicator of the territorial population size.

Population Inventories With Aerial and Ground-Based Surveys

Survey methods.—Population inventories differ from long-term monitoring designs in terms of 3 key considerations (Fig. 1, boxes 2a and 4a): 1) knowledge of nest locations is incomplete throughout the study period; 2) nests are most efficiently located using area search methods, unconstrained

by any predetermined search path, making incomplete study area coverage inevitable; and 3) multiple years of surveys are necessary for the spatial structure of the nesting territories to become evident, making it difficult in a single-season survey to determine the territory identity of individual nests without error. We developed a population inventory approach that addresses the above considerations in the framework of combining the aerial-ground survey protocol from the long-term monitoring application with area search methods to locate nests. Under this protocol, the area is overlain with a grid and the observers conduct an initial area search of a series of grid-blocks (e.g., 17 km $\times$ 17 km) via helicopter. If a nest cluster (i.e., ≥ 1 nests located closely together) is located, it would be assessed for evidence of occupancy with or without breeding using previously described criteria. If no such evidence is found, the helicopter would land and the observer(s) would conduct a ground survey, remaining at that location until behavior indicative of occupancy without breeding is observed or the pre-determined maximum survey duration is reached (e.g., 90 min). Following the initial survey, the observer crew would identify areas of the block in which habitat exists but no nests were located. They would then return to the block to conduct a targeted search of the identified areas (i.e., a 2-pass area search removal survey). Locating a new nest cluster in the second pass would trigger the aerial and ground assessments of its occupancy state. In a pilot inventory study that we conducted adjacent to Denali, the estimated probability of detecting an occupied (with or without breeding) golden eagle nest cluster after 2 independent surveys was 0.98, indicating that 2 area search surveys are sufficient for inventorying a golden eagle population. Additional pilot studies would likely be needed, however, to determine the optimal number of surveys necessary for other species that do not restrict nesting to stick nests (e.g., gyrfalcon [*Falco rusticolus*]).

After the survey is completed, we would group nests into clusters such that all nests within a cluster were within a specified distance from its centroid (e.g., ≤ 350 m). The choice of this distance threshold would ensure that detection of nests in a cluster would be highly correlated (Martin et al. 2011), but that individual nest clusters would be detected independently of one another. In addition, in a population inventory for a species with alternative nests, basing inference on nest clusters avoids the potential for misclassification of the territory identity of an individual nest. For species in which alternative nests are generally clustered on a single cliff face, the estimated population of occupied nest clusters may closely correspond to the number of occupied territories. For species in which alternative nests may be located on multiple cliff faces, however, the estimated population of occupied nest clusters technically corresponds to the number of nest clusters used in the study area because an actual nesting territory may overlap multiple nest clusters, each of which could show evidence of use in a given year (e.g., refurbishment).

The area searches for nests would not be constrained by a predetermined search path, which would result in incomplete coverage of the study area. Failure to account for incomplete

survey coverage could result in negative bias in population estimates. Therefore, we would adopt a spatial sampling approach by gridding the study area at a resolution at which topographic variation is predictive of the distribution of nest clusters (e.g., a grid comprised of 250×250 -m cells) and that precludes the overlap of multiple nest clusters in a single grid cell. Nest cluster presence would be determined by the intersection of its centroid with the grid cell. We would determine whether a cell was surveyed if the survey track approached within a specified distance (e.g., the farthest allowed distance from any 2 nests in a cluster). Although our accounting of incomplete survey coverage is admittedly coarse, we expect it will capture much of the variation in the probability of detecting a nest cluster by specifically identifying those areas where the probability of detecting a nest cluster is 0. If a cell is not surveyed, then observations for these cell visits are treated as missing data. In addition, gridding of the study area allows incorporation of spatial covariates related to nest cluster distribution.

Model development.—We developed a single-season, multi-state occupancy model for a combined aerial and ground survey conducted over a gridded study area for which there is limited or no prior knowledge of nest locations. We formulated the model in a state-space framework, describing the probability of each grid cell existing in 1 of 4 mutually exclusive states: nest cluster absent, nest cluster present but unoccupied, nest cluster present and occupied without breeding, and nest cluster present and occupied with breeding (Supplement 2 [Model Development], available online in Supporting Information). We described the observations as arising from a removal sampling process and used an expanded version of the state detection matrix from the long-term monitoring model. This version of the matrix includes the additional probabilities of detecting unoccupied and occupied nest clusters, p^{NU} and p^{NO} , respectively (Table S1, available online in Supporting Information). We included both of these parameters because we expected that nest cluster detection could differ because of the availability of stronger cues around occupied nest clusters (e.g., fresh whitewash, the presence of birds within the nesting territory, refurbishment materials). In addition, this version differs from its long-term monitoring counterpart in that we assume complete sampling of all nests within a cluster. We make this assumption because we are making inference at the level of the nest cluster, not the nesting territory, which may contain multiple nest clusters located >1 km apart. Presumably, we have delineated the nest clusters in a manner that ensures that detections of individual nests within nest clusters are highly correlated. In a few cases, we may detect a nest cluster but not detect the 1 nest in which eggs were laid. These territories, however, may be still classified as members of the population, albeit in the non-breeding state. For population inventories, we lack a temporal context in which to place the estimated nesting rate, making estimation of the composite population (nest clusters occupied with and without breeding) the overriding objective.

Simulation Study: Population Inventory Model with Aerial and Ground-Based Surveys

To test the conditions under which our inventory methods would be applicable, we conducted a simulation study in which we varied the number of cells (300 or 400) in state 3 (nest cluster present with occupancy without breeding) and the duration of the ground survey (60 min or 90 min). We set p^{NU} and p^{NO} , the probabilities of detecting an unoccupied and occupied nest cluster, respectively, equal to their respective estimates from a pilot inventory study that we conducted for golden eagle in the central Alaska Range. We set $p^{NB,A}$ and $p^{NB,G}$ equal to estimates from the Alaska Range inventory and the Denali long-term monitoring case study, respectively.

Implementation

We fit all models in a Bayesian framework using JAGS version 4.0.0 (Plummer 2003) via the jagsUI package (Kellner 2016) in program R 3.2.2 (R Core Development Team 2017; Supplements 3 and 4 [data generation and model code], available online in Supporting Information). We specified vague normal priors for all regression coefficients and uniform (0, 1) priors for all parameters on the real scale. For the long-term monitoring case study, we calculated summaries of the posterior distribution from 2 Markov chains run for 85,000 iterations with a 10,000 iteration burn-in and thinning every 3 draws. For the simulation study, we calculated summaries of the posterior distribution from 1 Markov chain run for 14,000 iterations with a 4,000 burn-in and thinning every 2 draws. We used the Gelman–Rubin diagnostic (Brooks and Gelman 1998) to assess convergence and scaled continuous covariates to improve convergence properties. We ran 500 simulations and report the average parameter estimates, average relative bias, root mean squared error (RSME), and coverage (percentage of 95% Bayesian credible intervals for parameters that overlap the true values).

RESULTS

For the long-term monitoring model, simulations indicated adequate (near nominal) coverage and low relative bias (<0.05) for all parameters except the covariate effects on the transition probabilities for the unoccupied state (Table 1). The latter group of effects showed moderate relative bias between 0.06–0.08, likely because relatively few territories transitioned from the unoccupied state (Table 2).

In the long-term monitoring case study, ptarmigan and hare abundance strongly affected the probability of breeding, as expected (Table 2). Consequently, fluctuation in prey availability resulted in highly variable breeding occupancy ranging from 0.11 (95% CI = 0.06, 0.16) in 2013 to 0.72 (95% CI = 0.68, 0.76) in 2009. Composite occupancy, however, was stable over the study period ranging from 0.88 to 0.92. During the ground survey, the probability of detecting occupancy without breeding after 2 hours of observation was 0.79 (95% CI = 0.73, 0.84), suggesting that 2 hours of observation from the ground would be adequate for long-term monitoring studies of golden eagles lacking an

Table 1. Estimates from the simulation study used to assess the performance of the nest-level, multi-state model for monitoring cliff-nesting raptors. We generated data for a combined aerial-ground survey of 150 territories and a 20-year time period over which the population was declining and subject to synchronization of breeding rate with fluctuating prey availability. The bracketed superscript corresponds to the state in year t : [1] = unoccupied; [2] = occupied without breeding; and [3] = occupied with breeding. Estimates are based on 500 simulations.

Par. ^a	True value	$\bar{x}$	RMSE	Bias	CI cover	Description
$p^{NB,A}$	0.56	0.56	0.06	-0.01	0.93	Aerial survey detection pr. ^b
$p^{NB,G}$	0.12	0.12	0.03	-0.01	0.93	Detection pr. during time interval
R	0.60	0.57	0.15	-0.05	0.94	First year pr. of breeding
ψ	0.70	0.70	0.10	0.00	0.94	First year pr. of occupancy
$\alpha_0^{[1]}$	0.61	0.65	0.31	0.07	0.93	Occupancy intercept given [1] in t
$\alpha_0^{[2]}$	-0.58	-0.59	0.21	0.02	0.96	Occupancy intercept given [2] in t
$\alpha_0^{[3]}$	0.26	0.25	0.20	-0.04	0.94	Occupancy intercept given [3] in t
$\alpha_1^{[1]}$	1.71	1.85	0.39	0.08	0.96	Prey effect on occupancy given [1] in t
$\alpha_1^{[2]}$	0.68	0.69	0.20	0.00	0.95	Prey effect on occupancy given [2] in t
$\alpha_1^{[3]}$	0.61	0.63	0.16	0.02	0.94	Prey effect on occupancy given [3] in t
$\beta_0^{[1]}$	-0.25	-0.26	0.18	0.04	0.95	Breeding intercept given [1] in t
$\beta_0^{[2]}$	1.00	1.04	0.24	0.04	0.96	Breeding intercept given [2] in t
$\beta_0^{[3]}$	1.25	1.29	0.21	0.06	0.94	Breeding intercept given [3] in t
$\beta_1^{[1]}$	-0.40	-0.40	0.17	0.00	0.95	Prey effect on breeding given [1] in t
$\beta_1^{[2]}$	-0.40	-0.42	0.27	0.04	0.95	Prey effect on breeding given [2] in t
$\beta_1^{[3]}$	-0.40	-0.41	0.24	0.04	0.95	Prey effect on breeding given [3] in t
δ_1	1.00	1.00	0.20	0.00	0.95	Covariate on nest use frequency

^a Parameter.

^b Probability.

aerial survey component. After the combined aerial-ground survey, the probability of detecting occupancy without breeding was 0.91 (95% CI = 0.88, 0.93), suggesting that monitoring studies of golden eagles using the combined method approach could reduce the ground observation period to 60–90 minutes.

In the inventory simulation study, estimates of the probability of detecting occupancy without breeding during a time interval of the ground survey ($p^{NB,G}$) showed high relative bias (≥ 0.16) under scenarios with 60-minute ground surveys, regardless of the sample size of nonbreeding nest clusters (Table S2, available online in Supporting Material). Under scenarios with 90-minute ground surveys, estimates for $p^{NB,G}$ showed moderate relative bias (≤ 0.07) and near nominal coverage. Estimates for the probability of detecting an occupied nest cluster (p^{NO}) were unbiased under all scenarios. In contrast, the probability of detecting an unoccupied nest cluster (p^{NU}) showed high relative bias (≥ 0.09) under all scenarios. However, the estimated number of unoccupied nest clusters is not part of the estimate for the territorial population. Under all scenarios, estimates for the territorial population size (nest clusters occupied with or without breeding) showed negligible relative bias (≤ 0.01). The root mean square error for these estimates was lower under scenarios with 90-minute ground surveys (Table S2).

DISCUSSION

Although our model can be applied to designs restricted to ground surveys, the combination of aerial and ground-based occupancy surveys are optimal for surveying at large spatial scales. Specifically, our multi-method approach leverages the fact that aerial surveys are optimal for detecting nests,

breeding, and refurbishment of nests, but ground surveys provide a greater opportunity for observing behaviors indicative of occupancy without breeding. Under our combined aerial-ground survey protocol, the maximum effort spent on any known nesting territory or cluster could be reduced by up to almost 90% of that recommended by standard protocols (i.e., a single, 60–90 min ground survey compared to ≥ 2 , 4-hr surveys; USFWS 2003, Pagel et al. 2010).

Given our focus on population estimation, we expect that our instantaneous view of the occupancy state will be more efficient. Standard approaches estimate the probability of breeding in a given year (Postupalsky 1974, Martin et al. 2009, Steenhof et al. 2017), whereas we assume the territorial population is closed but condition on the territory's state at the time of the survey. If surveys are conducted after clutches are initiated in most territories, we would expect minimal loss of sensitivity for understanding temporal variation in nesting rates in long-term monitoring applications. For population inventories, we lack a temporal context in which to place the estimated nesting rate, making estimation of the composite population (occupancy with or without breeding) the overriding objective.

For the inventory version of our model, the simulation results indicated that a 90-minute ground survey was sufficient to yield relatively unbiased estimates of the probability of detecting occupancy without breeding for golden eagles (Table S2). However, the sample sizes necessary for unbiased estimation of occupancy without breeding may prove challenging for some inventory applications, primarily because this sample size will be parsed into multiple survey platforms and states. In our

Table 2. Estimates from long-term monitoring of golden eagles in Denali National Park, Alaska, USA, 2007–2016, using aerial and ground-based surveys. The bracketed superscript corresponds to the true state in year t : [1] = unoccupied; [2] = occupied without breeding; and [3] = occupied with breeding.

Parameter	Parameter description	$\bar{x}$	95% CI
$p^{NB,A}$	Pr. ^a of detecting [2] on the aerial survey	0.56	0.51, 0.61
$p^{NB,G}$	Pr. of detecting [2] in a time-removal interval	0.12	0.10, 0.14
R	First year prob. of breeding	0.74	0.64, 0.83
ψ	First year prob. of occupancy	0.89	0.81, 0.95
$\alpha_0^{[1]}$	Occupancy intercept given [1] in t	0.61	−0.92, 2.39
$\alpha_0^{[2]}$	Occupancy intercept given [2] in t	−0.58	−0.84, −0.32
$\alpha_0^{[3]}$	Occupancy intercept given [3] in t	0.26	0.01, 0.51
$\alpha_1^{[1]} \times \text{hares}_t$	Hare effect on occupancy given [1] in t	0.12	−2.51, 2.46
$\alpha_1^{[2]} \times \text{hares}_t$	Hare effect on occupancy given [2] in t	0.34	0.03, 0.66
$\alpha_1^{[3]} \times \text{hares}_t$	Hare effect on occupancy given [3] in t	0.40	0.09, 0.71
$\alpha_2^{[1]} \times \text{ptarmigan}_t$	Ptarmigan effect given [1] in t	1.71	−0.48, 4.80
$\alpha_2^{[2]} \times \text{ptarmigan}_t$	Ptarmigan effect given [2] in t	0.68	0.41, 0.96
$\alpha_2^{[3]} \times \text{ptarmigan}_t$	Ptarmigan effect given [3] in t	0.61	0.29, 0.95
$\beta_0^{[1]}$	Breeding intercept given [1] in t	−1.03	−1.69, −0.39
$\beta_0^{[2]}$	Breeding intercept given [2] in t	8.21	5.22, 9.93
$\beta_0^{[3]}$	Breeding intercept given [3] in t	8.43	5.70, 9.94
$\beta_1^{[1]} \times \text{hares}_t$	Hare effect on breeding given [1] in t	0.10	−0.77, 1.00
$\beta_1^{[2]} \times \text{hares}_t$	Hare effect on breeding given [2] in t	−0.29	−4.91, 4.86
$\beta_1^{[3]} \times \text{hares}_t$	Hare effect on breeding given [3] in t	0.39	−3.93, 5.22
$\beta_2^{[1]} \times \text{ptarmigan}_t$	Ptarmigan effect given [1] in t	−0.22	−1.24, 0.68
$\beta_2^{[2]} \times \text{ptarmigan}_t$	Ptarmigan effect given [2] in t	0.03	−4.25, 5.91
$\beta_2^{[3]} \times \text{ptarmigan}_t$	Ptarmigan effect given [3] in t	0.74	−2.80, 5.22

^a Probability.

long-term monitoring case study, monitoring of 104 territories over a 10-year period yielded only 241 ground surveys. The problem of an insufficient sample size for estimating the probability of detecting occupancy without breeding during the ground survey in a population inventory could be resolved by committing to multiple seasons of surveys or the use of an informative prior that reflects our knowledge about this parameter (McCarthy and Masters 2005). Based on our estimates for golden eagles and an experienced observer, a suitable prior for the probability of detecting occupancy without breeding during a 10-minute interval would be *Normal* (−1.98, 0.09) on the logit-scale, or alternatively, *Beta* ($\alpha = 161$, $\beta = 1160$), corresponding to mean = 0.12 and standard deviation = 0.009 on the real scale. For other species, existing monitoring studies could be reanalyzed to come up with a suitable informative prior for new inventory surveys.

Interspecific differences in distribution and detectability of nests and territory occupancy will necessitate adjustments of the sampling protocol when applied to species other than golden eagle. For example, Kéry and Royle (2016:617–621) assessed occupancy of peregrine falcon breeding cliffs using a continuous-time observation model and reported that detection probability approached 1 after approximately 20 minutes. We also expect that the nest-level component of our model may be unnecessary for species in which alternative nests are generally clustered on a single cliff face (e.g., falcons). In addition, we expect that some species may be poorly suited for inventorying in a single season. For

example, in suitable habitat in Alaska, gyrfalcons are found at densities of 1 pair per 200–1,000 km² (Swem et al. 1994). In addition, gyrfalcons and peregrine falcons do not build or refurbish nests but instead use nests constructed by other species or simply lay their eggs in a bowl-shaped depression on a cliff ledge (i.e., a scrape; Burnham et al. 2009). Scrapes may be less detectable than the stick nests constructed by some cliff-nesting raptor species. The sparse distribution and presumably lower detectability of gyrfalcon nests may necessitate accumulating the sample of nests over time. Despite these challenges, the sparse distribution of gyrfalcon is emblematic of the need to apply efficient designs for landscape-scale surveys of cliff-nesting raptors, which by necessity must assume the presence of state uncertainty.

MANAGEMENT IMPLICATIONS

Our inference framework for population inventories and long-term monitoring will be broadly applicable across breeding assemblages of cliff-nesting raptor species and has the capacity to expand the scale of spatial inference of these efforts. These methods have the strongest relevance for species and populations in which the breeding component alone is not a reliable predictor of the territorial population size. We expect that the first step in optimizing surveys of cliff-nesting raptors involves abandoning the intensive level of effort necessary to assume state certainty. Additional steps will often be study-area-specific decisions about how best to integrate the various survey platforms.

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