

OPTIMIZING LANDBIRD SURVEYS FOR DETECTING POPULATION AND SPATIAL
DYNAMICS

By

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A Dissertation Submitted in Partial Fulfillment of the Requirements

for the Degree of

Doctor of Philosophy

in

Biological Sciences

University of Alaska Fairbanks

December 2017

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ABSTRACT

Landbird populations are undergoing concurrent changes in population size, spatial distribution, and phenology. The sensitivity of landbird monitoring programs to detect and distinguish these varied processes is of critical importance. Consequently, these efforts require inference methods that are efficient and fully leverage information about spatial, population, and phenological dynamics. The development of efficient inference methods can be addressed in part through a thorough understanding of how the data are actually generated, the application of sampling methods that attempt to maximize encounter probability, and the tailoring of sampling methods to maximize sensitivity to specific inference objectives.

Chapter one of this dissertation is concerned with accommodating temporary emigration in spatial distance sampling models. Model-based distance sampling is commonly used to understand spatial variation in the density of wildlife species. The standard approach is to assume that individuals are distributed uniformly in space and model spatial variation in abundance using plot-level effects. Thinned point process models for surveys of unmarked populations (spatial distance sampling) frame the sampling process in terms of the individual encounter in space and, consequently, are expected to offer greater sensitivity for understanding spatial processes. However, existing spatial distance sampling approaches are conditioned on the assumption that all individuals are present and available for sampling. Temporary emigration of individuals can therefore result in biased estimates of abundance. Herein, I extend spatial distance sampling models to accommodate temporary emigration. A simulation study indicated more precise and less biased estimation under the spatial distance sampling model compared to models that assume a uniform distribution of individuals and assess spatial variation in abundance using plot-level effects. An applied example involving two arctic-breeding passerines indicated considerably stronger inference under the spatial distance sampling model than standard distance sampling models.

Chapter two is concerned with the capacity of subarctic passerines to adjust their arrival timing to relatively extreme variation in spring conditions. I assessed interannual variation in passerine arrival timing in Denali National Park, Alaska from 1995-2015, a period that included both the warmest and coldest recorded mean spring temperatures for the park. Neotropical-Nearctic migrants varied in terms of the flexibility of their arrival timing, but generally showed

plastic phenologies, suggesting resilience under extreme spring conditions. In comparison, Nearctic-Nearctic migrants showed similar or greater plasticity in arrival timing. A majority of species showed synchronous-asynchronous fluctuation in arrival (i.e., synchronous arrival in some years, asynchronous in others) in combination with various levels of the mean response (i.e., early, average, and late arrival), suggesting the presence of interactions between environmental conditions at multiple scales and inter-individual variation. Overall, these findings suggest that monitoring of the mean-variance relationship may lead to a deeper understanding of the factors shaping phenological responses.

Chapter three is concerned with developing efficient inference methods for inventorying and monitoring cliff-nesting raptor populations. In nest occupancy studies of cliff-nesting raptors, the standard approach is to allocate a level of survey effort that is assumed to ensure that the occupancy state is known with certainty. However, allocating effort in this manner is inefficient, particularly at landscape scales, constraining our capacity for effective management of these species. To increase survey efficiency and expand the spatial inference of these studies, I developed two versions of a multi-state, time-removal model, one for long-term monitoring studies and another for population inventories or single-season surveys in which there is no prior knowledge of nest locations. For long-term monitoring of species with alternative nests, I 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. Simulation studies indicated generally low to moderate relative bias under the monitoring and inventory models. In addition, I applied the monitoring model to a long-term study of golden eagles (*Aquila chrysaetos*) in Alaska and demonstrate that the maximum effort spent on any nesting territory could be reduced by up to almost 90% of that recommended by standard protocols.

TABLE OF CONTENTS

	Page
TITLE PAGE	i
ABSTRACT.....	iii
TABLE OF CONTENTS.....	v
LIST OF FIGURES	ix
LIST OF TABLES.....	x
LIST OF APPENDICES.....	xi
ACKNOWLEDGEMENTS.....	xiii
INTRODUCTION	1
Literature cited.....	5
CHAPTER 1 ACCOMODATING TEMPORARY EMIGRATION IN SPATIAL DISTANCE	
SAMPLING MODELS.....	1
1.1 Abstract.....	1
1.2 Introduction.....	10
1.3 Methods.....	12
1.3.1 Model development	12
1.3.2 Simulation study	14
1.3.3 Application: Arctic passerines	16
1.4 Results.....	19
1.5 Discussion.....	20
1.6 Acknowledgements.....	22
1.7 Literature cited	23
CHAPTER 2 SUBARCTIC-BREEDING PASSERINES EXHIBIT PHENOLOGICAL	
RESILIENCE TO EXTREME SPRING CONDITIONS.....	43

2.1 Abstract	43
2.2 Introduction	44
2.3 Methods	47
2.3.1 Data collection	47
2.3.2 Analyses	47
2.4 Results	50
2.5 Discussion	51
2.6 Acknowledgments	55
2.7 Literature cited	55
CHAPTER 3_A MULTI-STATE, TIME-REMOVAL MODEL FOR INCREASING EFFICIENCY IN SURVEYS OF CLIFF-NESTING RAPTORS	71
3.1 Abstract	71
3.2 Introduction	72
3.2.1 Breeding ecology characteristics that influence how we observe raptor population dynamics	73
3.2.2 A multi-state, time-removal model for expanding spatial inference	74
3.2.2.1 Long-term monitoring using aerial and ground-based surveys	74
3.2.2.2 Long-term monitoring with ground-based surveys.....	75
3.2.2.3 Population inventories with aerial and ground-based surveys.....	75
3.3 Methods.....	75
3.3.1 Long-term monitoring with aerial and ground-based surveys.....	75
3.3.1.1 Survey methods.....	75
3.3.1.2 Model development	77
3.3.1.3 Case study	80
3.3.2 Long-term monitoring with ground-based surveys.....	81
3.3.3 Population inventories with aerial and ground-based surveys.....	81

3.3.3.1 Survey methods.....	81
3.3.3.2 Model development	83
3.3.4 Implementation	84
3.4 Results.....	85
3.4.1 Simulation study: long-term monitoring model with aerial-ground-based methods...	85
3.4.2 Case study: long-term monitoring with aerial and ground-based methods in Denali..	85
3.5 Discussion.....	85
3.6 Management implications.....	87
3.7 Acknowledgments.....	88
CONCLUSIONS.....	119
Literature cited	122

LIST OF FIGURES

	Page
Figure 1.1. A spatially correlated covariate simulated on a 10 x 10 pixel grid.	26
Figure 1.2. The sampling design implemented at a study site in Noatak NP, Alaska in 2016.	27
Figure 1.3. Posterior predictions of superpopulation point intensity (abundance per pixel) for American Tree Sparrow (top) and Savannah Sparrow (bottom).	28
Figure 2.1. Average April-May temperature (degrees C) from a weather station at Denali National Park Headquarters, 1926-2015.	62
Figure 2.2. Survey routes 1-3 along the park road in Denali National Park and Preserve (Denali), Alaska.	63
Figure 2.3. Year-specific, posterior means for the Julian date on which a) 50% and b) 5% of occupied sites had shown an arrival event.	64
Figure 2.4. Boxplot of year-specific standard deviations for migrants breeding in in Denali National Park, Alaska (1995-2015).	65
Figure 2.5. Arrival distributions of long-distance migrants in Denali National Park, Alaska (1995-2015).	66
Figure 2.6. Arrival distributions of short-distance migrants in Denali National Park, Alaska (1995-2015).	67
Figure 2.7. Arrival distributions of short-distance migrants in Denali National Park, Alaska (1995-2015).	68
Figure 3.1. Conceptual diagram of inference framework for population inventories and long-term monitoring of cliff-nesting raptors.	92
Figure 3.2. Long-term monitoring scenario implemented in the simulation study for the nest-level, multi-state model.	93

LIST OF TABLES

	Page
Table 1.1.1. Results from 500 simulations for Poisson TEDS, Poisson log-normal TEDS, and TPP models	29
Table 1.1.2. Parameter estimates and 95% credible intervals for Poisson log-normal TEDS and TPP models.	30
Table 3.1. Estimates from the long-term monitoring simulation study used to assess the performance of the nest-level, multi-state model.	94
Table 3.2. Estimates from long-term monitoring of golden eagles in Denali National Park, Alaska (2007-2016).	95

LIST OF APPENDICES

	Page
Appendix 1.1. Simulation and JAGS code for the TPP model.....	31
Appendix 1.2. Simulation and JAGS code for the log-normal TEDS model.....	35
Appendix 1.3. JAGS code for Savannah and American Tree Sparrow analyses using the TPP model.....	39
Appendix 2.1. Passerine species considered in analyses of arrival timing in Denali NP, Alaska from 1995-2015.	69
Appendix 2.2. Shift in annual mean arrival for species relative to the average April-May temperature.	70
Appendix 3.1. List of estimated parameters in the long-term monitoring (LTM) and population inventory (INV) models.....	96
Appendix 3.2. Model development for population inventories of cliff-nesting raptors and a simulation study to assess model performance.....	97
Appendix 3.3. Data generation and JAGS code used in the simulation study for the multi-state, time-removal model for long-term monitoring studies.....	102
Appendix 3.4. Data generation and JAGS code for the multi-state, time-removal model used for the population inventory simulation study.....	110
Appendix 3.5. JAGS model code for the multi-state, time-removal model for long-term monitoring designs restricted to ground surveys	115

ACKNOWLEDGEMENTS

This research was supported by the National Park Service's Inventory and Monitoring Program in Arctic (ARCN) and Central Alaska Networks (CAKN). I am grateful for the support of past and present managers of these programs including Jim Lawler (ARCN), Maggie MacCluskie (CAKN), and Eric Wald (ARCN).

Special thanks to my graduate advisory committee: Mark Lindberg for his mentorship and helping guide me through the writing of these manuscripts; Abby Powell and Greg Breed for their careful readings and insightful comments on each of these manuscripts; and Josh Schmidt for sharing his keen insight into population sampling. Josh has been critical to my development as an ecologist and our collaboration has deeply enriched my time working for the National Park Service.

Special thanks to my collaborators at the National Park Service: Stacia Backensto and Kumi Ratterbury for their constant support and help with logistics; Dave Swanson for his valuable help with GIS; and the many field technicians who worked on these projects particularly Jared Hughey, Sarah Swanson, and Shelli Swanson.

I would like to thank Carol McIntyre who has been my advocate throughout my passage from field technician to biologist. In addition, without her knowledge of raptor breeding ecology and her dedicated investigation of Golden Eagle population dynamics in Denali National Park, the chapter on raptor survey methods would not have been possible.

I would like to thank Steve Lewis (U.S. Fish and Wildlife Service) for his insight into raptor breeding ecology and leading the Golden Eagle population inventory detailed in this dissertation.

Lastly, I would like to thank my family for their endless support.

INTRODUCTION

Ecological monitoring programs have been beset by a lack of clear inference objectives at their outset, a poor understanding of how the data are actually being generated, a failure to fully leverage spatial and temporal information, and inefficient sampling methods (Lindenmayer and Likens 2009, 2010, Reynolds et al. 2011, Thompson et al. 2011, Schmidt et al. 2013). Landbird monitoring has been particularly problematic because these efforts have historically relied on unadjusted count data for inference (Nichols et al. 2009). However, recent decades have seen a greater recognition that variation in detection probability, if ignored, may confound estimates of variation in abundance (e.g., Farnsworth et al. 2002, Rosenstock et al. 2002, Alldredge et al. 2007, Nichols et al. 2009). Emphasis has been placed on the development of survey methodologies and hierarchical modeling approaches that permit simultaneous estimation of state variables and detection probability (Royle and Dorazio 2008). Despite such advances towards a form of inference that accommodates the hierarchical nature of population sampling, there remains substantial room for increased efficiency in studies of avian population ecology.

We require efficient inference methods in order to have the sensitivity to detect and distinguish the varied processes underlying landbird population dynamics. Landbird populations are undergoing concurrent changes in population size, spatial distribution, and arrival phenology (Root et al. 2003, Mizel et al. 2016). In particular, changes in spatial distribution may complicate the understanding of apparent changes in population size (e.g., Mizel et al. 2016). For example, apparent population declines could potentially result from species shifting distributions outside of the sampling frame (Mizel et al. 2016). In addition, changes in population size may drive changes in phenology (see chapter two), or, conversely, the decoupling of arrival phenology and seasonal food availability may drive population declines (Both and Visser 2001, Visser et al. 2004). The development of efficient inference methods is made all the more critical when sampling sparsely distributed species (e.g., cliff-nesting raptors) and for studies conducted in remote areas and/or at large spatial scales due to the logistical challenges involved in these efforts.

The development of efficient inference methods can be addressed in part through a thorough understanding of how the data are actually generated, the application of sampling methods that attempt to maximize encounter probability, and leveraging information during the sampling and the analysis phases (Royle and Dorazio 2008, Nichols et al. 2009). These ideas

have their basis in the hierarchical modeling approach to conducting ecological inference (Royle and Dorazio 2008). Hierarchical modeling approaches conceive population sampling in terms of explicit, probability-based state and observation processes unified by their conditional relationship to one another (Royle and Dorazio 2008). This approach naturally motivates decomposition of the constituent parts of both of these processes, which often may be advantageous for optimizing inference methods (Royle and Dorazio 2008). Specifically, decomposing the observation process into its constituent probabilities may serve as a starting point for developing a survey design that accounts for potential biases and maximizes encounter probability. The observation process can be decomposed into four primary components: 1) the probability the individual's home range overlaps the sampling unit, p_s ; 2) the probability the individual is present within the area that is exposed to sampling during the survey occasion, p_p ; 3) the probability the individual is available for detection during the survey occasion, p_a ; and 4) the probability that the individual is detected given that it is present and available, p_d (see Nichols et al. 2009).

A variety of survey methods are available for accommodating imperfect detectability including repeat surveys (Royle 2004), distance sampling (Buckland et al. 2001, 2004), time of detection methods (Farnsworth et al. 2002, Alldredge et al. 2007), double observer methods (Nichols et al. 2000), and various combinations of the aforementioned (Chandler et al. 2011, Amundson et al. 2014). However, the various inference methods differ in the composite of detection probability that they estimate (Nichols et al. 2009). Consequently, they provide inference to different subsets of the 'superpopulation'; i.e. all individuals having home ranges that overlap the area exposed to sampling (Kendall et al. 1997, Nichols et al. 2009). Each inference method carries with it the assumption that those components that are not estimated do not vary through space and time. Should this assumption prove untenable, then the sensitivity for monitoring programs to detect change may be reduced as variation in the unaddressed component(s) may be confounded to an unknown degree with that present in abundance. This is particularly relevant to studies of species that exhibit territorial movements and/or temporal variation in cue production where failure to accommodate these temporary emigration processes ($p_p p_a$) may result in biased estimates of abundance (Chandler et al. 2011).

Understanding both the assumptions and population of inference that are implicit in the choice of estimation methods is necessary for proper interpretation of results and for designing

studies with the sensitivity to detect changes in population size and distribution (Schmidt et al. 2013). Hayes and Monfils (2015) recommended the disuse of occupancy modeling (MacKenzie et al. 2005) for populations subject to temporary emigration. Alternatively, it is not the occupancy model that is at issue here, but the fact that inference (or interpretation of the occupancy parameter) is to the proportion of the study area that is used when populations are subject to temporary emigration (Kéry and Royle 2016). In such cases, the meaningfulness of the occupancy or abundance parameter is determined by the study design, specifically, its spatial and temporal resolution (Kéry and Royle 2016). Thus, rather than focusing on the (occupancy or N-mixture) model in general terms, it may be more useful to accept the presence of temporary emigration processes and attempt to accommodate these processes in the sampling design and analysis phases. Throughout this dissertation, I emphasize that decomposing the observation process in relation to a species' ecology motivates a clearer understanding of these processes, including temporary emigration, which in turn, provides the basis for developing efficient survey methods. I also emphasize that leveraging spatio-temporal information begins in the design phase through identification of inference objectives and tailoring sampling methods to maximize sensitivity to these objectives.

In chapter one, I use a spatial distance sampling approach for potentially stronger inference about spatial processes. Standard distance sampling methods do not fully leverage the spatial information underlying individual encounters for use in explaining variation in density. Standard approaches rely on plot-level effects for explaining spatial variation in density, inducing over-dispersion when density varies within plots. In contrast, spatial distance sampling describes the observed locations of individuals as arising from a spatial point process thinned through incomplete detection and, consequently, exploits the spatial information inherent in the location of encounter for potentially stronger inference about spatial processes (Hedley and Buckland 2004, Johnson et al. 2010, Kéry and Royle 2016, Yuan et al. 2016).

However, existing spatial distance sampling approaches are conditioned on the assumption that all individuals are present and available for sampling. Temporary emigration of individuals can therefore result in biased estimates of abundance. Herein, I extend spatial distance sampling models to accommodate temporary emigration. Extending these methods to accommodate temporary emigration is expected to be particularly useful for species that show large variation in cue production over a survey season and highly mobile species, including birds

(e.g., Nichols et al. 2009, Chandler et al. 2011, Schmidt et al. 2013), herpetofauna (e.g., O'Donnell et al. 2015), and insects (e.g., Kéry et al. 2009).

Also in chapter one of this dissertation, I detail a sampling method for off-road surveys that diverges considerably from the standard point count protocol of Ralph et al. (1993, 1995). Recently, Matsuoka et al. (2014) advocated standardization of landbird sampling methods, specifically a return to the time and distance-binning approach to point counts of Ralph et al. (1993, 1995). They argued that use of a consistent protocol will strengthen inference across datasets. However, implementing this protocol in off-road study areas will often be inefficient as it may require 25-30 minutes of 'off-effort' (transit) time for every 10-minute survey. Thus, I used a method in which the encounter locations of individuals are recorded from a continuous, fixed survey route. By remaining 'on-effort' throughout the survey day, this approach would be expected to maximize the population that is exposed to sampling on a given site-visit.

In chapter two, I used the open-population occupancy model of Roth et al. (2014) to estimate arrival events in a subarctic-breeding passerine community. This model provides an explicit rendering of the observation process into the probability of initial presence (i.e., arrival) at a site and the composite detection probability $p_p p_a p_d$. In doing so, it leverages information about arrival phenology from standard occupancy survey data. I apply this model to survey data for a community of subarctic-breeding passerines and document interannual variation in the mean and variance of the arrival distribution.

In chapter three, I develop a framework for inventorying and monitoring cliff-nesting raptor populations over landscape scales based upon an efficient combination of aerial and ground-based occupancy surveys. Surveys of cliff-nesting raptors present considerable challenges due to their sparse distribution across remote landscapes and the multiple occupancy states (e.g., unoccupied, non-breeding occupancy, and breeding occupancy) through which we observe their nesting territory dynamics. The standard approach in nesting territory surveys is to allocate a level of effort that is assumed to ensure that the occupancy state of each territory is known with certainty. However, this is logistically prohibitive at landscape scales, constraining our capacity for effective management of these species.

To develop a more efficient inference framework, I begin by detailing various aspects of cliff-nesting raptor breeding ecology which induce complexity in how we observe their population dynamics including: maintaining alternative nest sites, a tendency to exhibit

numerical reproductive responses, and the presence of multiple nesting occupancy states (unoccupied, occupied without breeding, and occupied with breeding) that differ in their detectability. I then develop a multi-method, multi-state approach that 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 non-breeding occupancy.

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CHAPTER ONE

ACCOMODATING TEMPORARY EMIGRATION IN SPATIAL DISTANCE SAMPLING MODELS¹

1.1 Abstract

The sensitivity of long-term monitoring programs to detect and distinguish population and spatial dynamics is of critical importance. Model-based distance sampling is commonly used to understand spatial variation in the density of wildlife species. The standard approach is to assume that individuals are distributed uniformly and model spatial variation in density using plot-level effects. Thinned point process models for surveys of unmarked populations (spatial distance sampling) more fully leverage the spatial information underlying individual encounters, and in the presence of within-plot variation in density, may explain a larger proportion of the spatial variation in density. However, existing spatial distance sampling approaches are conditioned on the assumption that all individuals are present and available for sampling. Temporary emigration of individuals can therefore result in biased estimates of abundance.

Herein, we extend spatial distance sampling models to accommodate temporary emigration (TPP model). Using simulations of a thinned inhomogeneous point process, we assessed the performance of the TPP model relative to the temporary emigration distance sampling (TEDS) model, which implies a uniform distribution of individuals. In addition, we compared inferences between TPP and TEDS models using data for two passerine species in Alaska.

Parameter estimates from the TPP model exhibited improved CI coverage and precision relative to the TEDS model including a 26% reduction in the CV of the population size estimate. In the applied example, the TEDS model indicated weak relationships between abundance and habitat covariates, whereas the TPP model indicated strong relationships for those same effects, suggesting that spatial distance sampling models can provide considerably stronger inference in

¹ Mizel, J. D., J. H. Schmidt, and M. S. Lindberg (*accepted*). Accommodating temporary emigration in spatial distance sampling models. *Journal of Applied Ecology*.

the presence of within-plot variation in density. In addition, the CV of the population size estimates for the two passerine species were 32% and 4% smaller under the TPP model.

We expect our extension accommodating temporary emigration will be a critical specification for spatial distance sampling models, particularly for studies confronted with large variation in the population available for sampling over multiple occasions. Our model will be of particular use for assessing changes in the distribution and abundance of highly mobile species including passerines.

1.2 Introduction

Conventional and model-based distance sampling are commonly used to estimate the density of wildlife species (Buckland et al. 2001; 2004). However, standard distance sampling methods do not fully leverage the spatial information underlying individual encounters for use in explaining variation in density. Standard model-based approaches rely on plot-level effects for explaining spatial variation in density, inducing over-dispersion when density varies within plots. In contrast, spatial distance sampling describes the observed locations of individuals as arising from a spatial point process thinned through incomplete detection and, consequently, exploits the spatial information inherent in the location of encounter for potentially stronger inference about spatial processes (Hedley & Buckland 2004; Johnson, Laake, & Ver Hoef 2010; Kéry & Royle 2016; Yuan et al. 2016).

However, existing spatial distance sampling approaches describe the observation process entirely in terms of the detection function (i.e., the decline in detectability as a function of individual distance from the transect) and, consequently, are conditioned on the assumption that all individuals are present and available for sampling. The limitations of this approach are best understood by decomposing the observation process into its four primary components: 1) the probability the individual's home range overlaps the sampling unit, p_s ; 2) the probability the individual is present within the area that is exposed to sampling during the survey occasion, p_p ; 3) the probability the individual is available for detection during the survey occasion, p_a ; and 4) the probability that the individual is detected given that it is present and available, p_d (see Nichols, Thomas & Conn 2009).

The various field methods used in wildlife surveys differ in the components of the detection process that they estimate and, consequently, provide inference to different subsets of the superpopulation; i.e., the population comprised of all individuals with a non-negligible

probability of being present in the sample unit over the survey period (Kendall, Nichols & Hines 1997). Single-visit distance sampling typically only addresses p_s (through the survey design) and p_d (through the detection function). By failing to address p_p and p_a directly, single visit approaches make the implicit assumption that these components of the detection process are relatively constant through space and time. Should this assumption prove untenable, then inference is limited to some unknown proportion of the superpopulation and abundance estimates are negatively biased (Nichols, Thomas & Conn 2009; Chandler, Royle & King 2011; Schmidt, McIntyre & MacCluskie 2013). Thus, estimates of superpopulation abundance require fewer implicit assumptions and, therefore, should have greater sensitivity for assessing population and spatial dynamics.

Chandler, Royle & King (2011) developed a model framework for explicitly accommodating non-Markovian temporary emigration in unmarked populations. Their model is applicable to a number of protocols including the combination of repeat surveys and distance sampling which allows separate estimation of p_d and the composite probability of availability $p_p p_a$. However, the temporary emigration distance-sampling (TEDS) version of their model implies that individuals are distributed uniformly in space and models spatial variation in abundance at the plot-level. Models with plot-level effects (e.g., the TEDS model) will often be a good description of variation in abundance when sample units are small or habitat gradients are gradual (Miller et al. 2013; Kéry & Royle 2016). However, an inhomogeneous distribution of individuals over a compressed habitat gradient would be expected to induce considerable within-plot variation in density. Under these conditions, properly specifying the distribution of individuals within plots as inhomogeneous may explain a larger proportion of the variation in density.

There have been several recent developments in spatial distance sampling inference. Using full likelihood approaches (i.e., the N_j as explicit parameters), Johnson, Laake, & Ver Hoef (2010) and Yuan et al. (2016) developed thinned point process models for continuous space. Kéry & Royle (2016) formulated a thinned point process model for discrete space using a data augmentation approach. While these methods allow fine-scale assessment of spatial variation in abundance, they do not address the temporary emigration process and, consequently, may yield biased estimates of abundance.

Herein, we unify the thinned point process formulation of the Kéry & Royle (2016) model and the full likelihood description of the temporary emigration process developed for N-mixture models (Chandler, Royle & King 2011). The development of these inference methods was motivated by a need to efficiently and effectively monitor arctic passerine populations, which are expected to undergo rapid changes in abundance and distribution in association with shrub expansion into open habitats and higher elevations (Sturm, Racine & Tape 2001; Tape, Sturm & Racine 2006; Dial et al. 2015; Mizel et al. 2016). Thus, it was important that we develop inference methods with the sensitivity to efficiently detect and distinguish population and spatial dynamics while also addressing all components of the detection process. We viewed accommodating temporary emigration as critical given the characteristics of sampling arctic passerine populations including territorial movements of individuals across plot boundaries between survey visits (i.e., spatial temporary emigration) and large variation in cue production over a highly compressed breeding season (i.e., random temporary emigration) (Kéry & Royle 2016). While motivated by our particular case study, the resulting framework will be broadly applicable in other situations where temporary emigration occurs. Our specific objectives in this manuscript were to: 1) develop a framework for accommodating temporary emigration in a spatial distance sampling context; 2) assess the precision and bias of estimates from our model relative to the TEDS model through simulation; and 3) demonstrate the advantages of our unified model through an application to field data for two passerine species.

1.3 Methods

1.3.1 Model development

Herein, we develop the temporary emigration, thinned point process (hereafter, TPP) model for a hierarchical sampling design where multiple line or point transect plots each comprise a grid of pixel centroids from an underlying habitat raster, and each plot is surveyed multiple times (e.g., separated by a day or a few days). The survey yields the locations of the observed individuals in continuous space, but these are subsequently assigned to the nearest pixel centroid for the data structure used in the analysis. For simplicity of presentation, we develop the model in the context of a single season.

Following Kéry & Royle (2016), plot-level abundance is a Poisson outcome of a point intensity function integrated over a grid of points. However, in order to accommodate a replicated count protocol and temporary emigration in the generalized N-mixture framework

(i.e., Chandler, Royle & King 2011), we use a full likelihood formulation with a conditional multinomial observational model (Royle, Dawson & Bates 2004; Kéry & Royle 2016). Data from the replicated count-spatial distance sampling protocol is organized as a series of counts of unmarked individuals within each pixel $i = 1, 2, \dots, I$, in plot $j = 1, 2, \dots, J$, and visit $k = 1, 2, \dots, K$. This is amenable to formulating the observation model in terms of multinomial probabilities and leads to an implicit binning of distances (Kéry & Royle 2016). The focus is on estimating the superpopulation point intensity function for a Poisson point process of the individual locations (Kéry & Royle 2016):

$$\log(\lambda_{ij}) = \beta_0 + \beta_1 x_{ij}, \quad (\text{Eq. 1.1})$$

where λ_{ij} is the superpopulation intensity function for each pixel, x_{ij} is the pixel covariate value, and β_0 and β_1 are parameters to be estimated. Integrating over the grid of points in each plot yields the expected plot-level superpopulation sizes Λ_j (Kéry & Royle 2016). By the rectangular rule, this integral is approximated for the discretized region using summation (Kéry & Royle 2016):

$$\Lambda_j = \sum_i \exp(\beta_0 + \beta_1 x_{i,j}). \quad (\text{Eq. 1.2})$$

The local superpopulation sizes are specified as Poisson random variables:

$$M_j \sim \text{Poisson}(\Lambda_j). \quad (\text{Eq. 1.3})$$

The populations available for detection on a given plot-visit are binomial outcomes of the superpopulation sizes and the probability of availability ϕ (i.e., the product of p_p and p_a) which is the complement of the temporary emigration probability (Chandler, Royle & King 2011):

$N_{j,k} \sim \text{Binomial}(M_j, \phi)$. Models for time- and plot-dependent ϕ could also be considered including random effects parameterizations which account for over-dispersion and/or temporal correlation in repeated counts (Buckland, Oedekoven & Borchers 2016). Here we assume ϕ is constant for simplicity of presentation.

The hierarchical distance sampling (HDS) model of Royle, Dawson & Bates (2004) and other standard model-based formulations (Buckland, Oedekoven & Borchers 2016) imply that the within-plot distribution of individuals is uniform. In the HDS model, the observed counts follow a multinomial distribution where the vector of cell probabilities are the product of

detection probability and of occurring in a particular distance class, which is specified as uniform across distance classes (adjusted for annulus area in the point transect case). In the TPP model, the multinomial observation probabilities are the product of detection probability and the probability of occurring in a particular pixel $\theta_{i,j}$. The latter is derived using the point intensity function for each pixel, conditional on the plot-specific total (Kéry & Royle 2016):

$$\theta_{i,j} = \frac{\lambda_{i,j}}{\sum_i \lambda_{i,j}}. \quad (\text{Eq. 1.4})$$

Using a half-normal detection function as an example, the multinomial observation cell probabilities are:

$$\pi_{i,j} = \exp\left(-\frac{d_{i,j}^2}{2\sigma^2}\right) * \theta_{i,j}, \quad (\text{Eq. 1.5})$$

where d is the distance from the transect to the pixel centroid and σ is the scale parameter of the detection function. The probability of not being detected at all is $\pi_{0,j} = 1 - \sum_i \pi_{i,j}$ and the conditional multinomial cell probabilities are (Royle, Dawson & Bates 2004; Kéry & Royle 2016):

$$\pi_{i,j}^c = \frac{\pi_{i,j}}{1 - \pi_{0,j}}. \quad (\text{Eq. 1.6})$$

The model for the observations is decomposed into multinomial and binomial components in order to avoid specifying the multinomial index as a random variable (Royle, Dawson & Bates 2004; Kéry & Royle 2016). Conditional on the observed count, the number of individuals observed in a pixel on each plot-visit follows a multinomial distribution. The observed counts $n_{j,k}$ are binomial outcomes of the latent $N_{j,k}$ and the total probability of detection $1 - \pi_{0,j}$:

$$y_{i,j,k} | n_{j,k} \sim \text{Multinomial}(n_{j,k}, \pi_{i,j}^c) \quad (\text{Eq. 1.7})$$

$$n_{j,k} \sim \text{Binomial}(N_{j,k}, 1 - \pi_{0,j}). \quad (\text{Eq. 1.8})$$

1.3.2 Simulation study

We designed our simulations in the context of passerine bird monitoring in an open arctic habitat. We began by simulating a spatially correlated covariate (i.e., a continuous measure of

habitat) on a grid of 10 x 10 pixels, replicated over 150 plots under a line transect sampling design (Fig. 1.1). Each plot-specific vector of covariate values x was generated as a series of multivariate random variables using the Cholesky decomposition of the variance-covariance matrix $V^{1/2}$ and its product with a compatible vector of *iid* normal random variables $e \sim N(0,1)$ (Kéry & Royle 2016). We simulated point intensity for each discretized plot as $\log(\lambda_{i,j}) = \beta_0 + \beta_1 x_{i,j}$ where $\beta_0 = -5.8$ and $\beta_1 = 2$, corresponding to an inhomogeneous point process. The local superpopulation sizes were generated from a Poisson distribution with an expected value equal to $\sum_i \exp(\beta_0 + \beta_1 x_{i,j})$ (Kéry & Royle 2016). We used the plot-specific, conditional intensity probabilities to allocate individuals to pixels for each plot-visit. A vertical line transect bisected the center of each plot resulting in a maximum distance of 4.5 to any pixel centroid (Fig. 1.1). Observations were simulated over four replicated counts using $\phi = 0.6$ and a half-normal detection function with $\sigma = 3$.

We fit the TPP model to the simulated data to assess whether it could recover the data-generation parameter values. We also investigated model performance relative to the TEDS model (Chandler, Royle & King 2011; Kéry & Royle 2016). Observations for the TEDS model were generated as above (i.e., the TPP model was the data generating model) except that data structure was reduced to the number of individuals for each plot-visit in distance class $i = 1, 2, \dots, 5$ rather than pixel $i = 1, 2, \dots, 100$. We used five distance classes corresponding to the sequence of centroid distances in the discretized plots, paralleling the implicit binning of the TPP model. We used the conditional multinomial formulation of the TEDS model (Kéry & Royle 2016) making it structurally similar to the TPP model. However, the TEDS model assumes a uniform distribution of individuals across distance classes. The TEDS model is made spatially-explicit by a model for variation in local superpopulation abundance, which we specified as $\log(\lambda_j) = \beta_0 + \beta_1 \bar{x}_j$, where \bar{x}_j is the mean covariate value over all grid points in a plot. Because this represented a reduced information summary of the data generating process, we assumed that there was unexplained variation in the model. Thus, we included both Poisson and Poisson log-normal versions of the TEDS model in comparison to the TPP model.

We ran 500 simulations for each of the three models. To improve mixing of chains in the TPP and TEDS models, we removed the binomial model for the $N_{j,k}$ and described the observations a binomial outcomes with M_j sample size and probability $(1 - \pi_{0,j}) * \phi$ (Kéry & Royle 2016). 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 Team 2015). We specified vague normal priors for all regression coefficients, a uniform prior for σ from 0 to the plot truncation distance, and a uniform (0,1) prior for ϕ . We used uniform (0,100) priors for the standard deviations of the random effects. Summaries of the posterior distribution were calculated from one Markov chain run for 21,500 iterations with a 6,500 iteration burn-in and thinning every five draws with the exception of the log-normal TEDS model, which we ran for 58,000 iterations with a 28,000 iteration burn-in. We 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). See Appendices 1.1 and 1.2 for simulation and JAGS model code.

1.3.3 Application: Arctic passerines

We applied the TPP model to data collected in the Noatak National Preserve, Alaska between May 21 and June 19 2016 for two species of passerines, American tree sparrow (*Spizella arborea*) and savannah sparrow (*Passerculus sandwichensis*). Our study site represents one of three long-term, landbird monitoring sites in the U.S. National Park Service's Arctic Inventory and Monitoring Network and covers an elevational gradient from lowland to alpine habitats with open and riparian shrublands, *Dryas* and/or mixed dwarf shrub tundra, and barren slopes. Habitat types are distributed non-uniformly, presumably influencing the distribution of bird territories. We adopted a route-based, continuous-effort survey design to maximize encounter rates (i.e., exposure to sampling) and study area coverage. We centered a 10.8 x 9.6 km grid comprising 600 m x 600 m cells on the airstrip at which we located our basecamp. We used this grid to establish a series of fixed survey routes (Fig. 1.2). Routes were designed to be completed in a single day and were allowed to change direction (Hiby & Krisha 2001) in part to return observers close to their original starting point. In general, routes were located such that they intersected the centroid of each cell and then were deflected at an angle of 0 or 90 degrees (i.e., followed a parallel or perpendicular direction; Fig. 1.2). In some cases, we shifted routes off of the central axis of the cell due to the presence of terrain features (e.g., cliffs and high flow creeks).

We walked along the survey line using the image of the route displayed on our GPS units as an aid. We conducted the survey as if it was one continuous line transect, recording one observation per individual bird during a given route-visit, but we restricted the analysis to

detections of singing males because females are much more difficult to detect and singing males can be reasonably expected to represent the breeding population. Upon detecting a bird, we took a bearing and waypoint from our location along the line and used a laser range-finder to estimate the distance to the bird. The final plots used for analyses were created by buffering the route by a species-specific truncation distance (Buckland et al. 2001) and clipping the buffered area using the grid cell boundaries (Fig. 1.2). Following the field season, observations were associated with plots by projecting them over the plot polygons in ArcGIS. We established 17 routes and a total of 150 plots, each of which we surveyed three times on average.

We expected that normalized difference vegetation index (NDVI) would be a good predictor of bird distribution given the relatively distinct and simple structural characteristics of vegetation in our study area including barren slopes, low-shrub tundra, and tall shrub thickets. Using a Landsat 8 image of our study area, we discretized plots using the image's original 30-m resolution and attributed each pixel with its underlying NDVI value. This resulted in an average of 328 pixels per plot. We also extracted the elevation at these grid points from a 5-m digital terrain model. Bird locations were subsequently assigned to the nearest pixel centroid based on the bearing, distance, and waypoint information recorded in the field.

Although data were collected for the entire bird community, we selected the American tree sparrow and savannah sparrow for use as examples because these they had sufficient data for analysis and represented contrasting patterns of distribution which could affect the strength of inference under the TPP model. American tree sparrow is associated with medium-tall shrub thickets and consequently has a clumped distribution, whereas savannah sparrow is associated with open, low shrub-tundra and is more widespread in our study area. For American tree sparrow, we discarded ~5% of the singing observations at the furthest distances, resulting in a 250-m strip width and a total of 325 detections. For savannah sparrow, discarding ~5% of the furthest singing observations resulted in plots defined by a 200-m strip width and 1188 total detections.

For savannah sparrow, we specified the model for the superpopulation point intensity as:

$$\log(\lambda_{i,j}) = \beta_0 + \beta_1 * NDVI_{i,j} + \beta_2 * NDVI_{i,j}^2 + \beta_3 * Elev_{i,j} + \beta_4 * Elev_{i,j}^2 + \varepsilon_{subplot},$$

where $\varepsilon_{subplot}$ is a mean zero random effect for the 300 x 300-m quarter sections underlying each plot. We included the random effects term because unexplained variation in the point intensity function may lead to bias in spatial effect, abundance, and variance estimates (Cressie 1993;

Yuan et al. 2016). Due to the comparatively sparse distribution of American tree sparrow, we fit a simplified model with the effect of NDVI, linear and quadratic effects of elevation, and a plot-level random effect.

For savannah sparrow, we described the probability of availability $\phi_{j,k}$ as a linear function of time after 02:00 AM, $time_{j,k}$, linear and quadratic effects of date, a survey-level random effect $\delta_{j,k}$, and the duration of the plot-visit, $effort_{j,k}$:

$$\text{logit}(\phi_{j,k}) = \alpha_0 + \alpha_1 * time_{j,k} + \alpha_2 * date_{j,k} + \alpha_3 * date_{j,k}^2 + \alpha_4 * effort_{j,k} + \delta_{j,k},$$

assuming that as survey effort increases (e.g., time or route length), the population that is exposed to sampling during a survey occasion will approach the ‘true’ population size (Royle & Dorazio 2006). We used 02:00 AM to calculate the survey timing covariate because there is no sunrise/sunset in June for our study area and this hour corresponds to the initiation of singing for many species. We included the linear and quadratic effects of survey date to account for variation in the probability of availability over a survey period that began prior to the arrival of a subset of individuals and then extended past peak singing (Kéry et al. 2009, Schmidt, McIntyre & MacCluskie 2013). Lastly, we included a survey-level random effect $\delta_{j,k}$, assuming that there was unexplained variation in the model (Oedekoven, Laake & Skaug 2015, Buckland, Oedekoven & Borchers 2016), in part due to variation in weather and among plots in their degree of spatial overlap with territories. For the smaller American tree sparrow dataset, we fit a reduced model that included only the fixed effects of time and effort.

We also fit a similarly parameterized log-normal TEDS model (with 10 distance classes), except that the spatial effects were reduced to the plot mean and we included an offset (i.e., $\log(plot\ area_j)$) in the model for variation in local abundance. We report estimates from both TPP and log-normal TEDS models as posterior means with 95% credible intervals. We also present predictive maps of point intensity from the TPP model.

We fit all models using JAGS (Plummer 2003). We specified vague priors for all parameters as described in the simulation study section. Summaries of the posterior distribution were calculated from two independent Markov chains run for 100,000 and 75,000 iterations (savannah and American tree sparrow, respectively) with a 25,000 iteration burn-in and thinning every five draws. We used the Gelman-Rubin diagnostic (Brooks & Gelman 1998) to assess convergence and scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. See Appendix 1.3 for JAGS model code.

1.4 Results

Based on data generated under the TPP model, the Poisson TEDS model exhibited negative bias in population estimates and poor credible interval coverage for all parameters (Table 1.1). Bias in parameter and abundance estimates was relatively low for both the log-normal TEDS model (-3.5 – 5.6%) and the TPP model (-0.1 – 1.9%). In contrast to the log-normal TEDS model, credible interval coverage for all parameters estimated under the TPP model was approximately nominal (Table 1.1). Under the log-normal TEDS model, coverage for σ was particularly poor (0.73). In addition, the RMSE of the σ estimates (truth = 3) was larger for the log-normal TEDS model (0.30 vs. 0.17). Lastly, the average coefficient of variation (CV) of the total population estimate was 26% smaller for the TPP model compared to the log-normal TEDS model.

For the arctic passerine application, the log-normal TEDS model explained very little of the spatial variation in abundance for both savannah and American tree sparrow, in strong contrast to inferences from the TPP model. Between both species, all but one of the 95% CIs for the spatial effects from the log-normal TEDS model covered 0, whereas none of 95% CIs for the same effects from the TPP model covered 0 (Table 1.2). In addition, the CVs for the population estimates from the TPP were 32% and 4% smaller for savannah and American tree sparrow, respectively. For both species, population estimates from the TPP model were smaller than those from the log-normal TEDS model (Table 1.2). Lastly, there was considerable variation in the available population across survey occasions that was apparently well explained by temporal and search intensity covariates (Table 1.2). That is, the survey-specific expected $\phi_{j,k}$ ranged from 0.20-0.89 and 0.17-0.95 for savannah and American tree sparrow, respectively.

The fine spatial grain of the TPP model revealed strong and contrasting habitat relationships between American tree sparrow and savannah sparrow (Fig. 1.3). As expected, American tree sparrow exhibited a clumped distribution, corresponding to the non-uniform distribution of their preferred habitat, medium to tall shrub thickets. In contrast, savannah sparrow was more uniformly distributed in a landscape largely composed of lower vegetative growth forms (Fig. 1.3). The TEDS model generally failed to identify patterns of habitat association in either species (Table 1.2), and permitted inference about variation in abundance at a much coarser spatial grain (i.e., the plot).

1.5 Discussion

Ecological studies are inherently spatial, integrating spatial processes in sampling design, encounter probability, and population dynamics (Royle et al. 2013; Borchers & Marques 2017). However, the sensitivity of studies to spatial processes may be affected by choice of inference method including their assumptions about the observation process (Nichols, Thomas & Conn 2009). Herein, we used an approach that frames the sampling design and analysis in terms of individual encounters in space rather than aggregating counts at the plot-level (Kéry & Royle 2016). While distance sampling models that incorporate plot-level spatial effects will often be a good description of variation in abundance (Miller et al. 2013), our application demonstrates that spatial distance sampling models that accommodate temporary emigration can provide considerably stronger inference in the presence of within-plot variation in density.

The lower precision (i.e., a 36% larger average CV for the population estimate) of the Poisson log-normal TEDS model relative to the TPP model in our simulation study was expected given that the model for variation in the local population sizes was a reduced information summary of the data generating process and there was greater uncertainty in explaining the remaining variation in abundance as random noise. The negative bias of population size estimates from the Poisson TEDS model lacking an overdispersion term was likely due to a failure to fit some local population sizes that were larger than would be expected under the estimated Poisson mean. In addition, our simulation study indicated that the improper assumption of a homogeneous point pattern may result in relatively poor estimation of σ .

In the applied examples, TEDS and TPP models provided contrasting inference. For both species, the log-normal TEDS model indicated weak relationships between plot-level abundance and habitat, whereas the TPP model indicated strong relationships for those same effects on point intensity, suggesting the existence of relatively strong within-plot variation in density (i.e., inhomogeneous distribution of vegetation). In open landscapes like those in our Alaskan study area, within-plot variation in bird density may be considerable due to the need to establish plots that are sized appropriately relative to a large effective sampling area coupled with variation in vegetation that is compressed along steep elevational gradients. Under these situations, the TPP model would be expected to provide improved inference due to properly specifying an inhomogeneous distribution of individuals within plots and leveraging the spatial information inherent in the location of encounter.

In addition to explicitly addressing spatial processes affecting the distribution of individuals, our approach also accommodates non-Markovian temporary emigration. In single-visit distance sampling surveys, abundance and detection probability are conditional on p_p and p_a . However, variation in the temporary emigration composite process, $p_p p_a$, may be confounded to an unknown degree with that present in abundance, negatively biasing abundance estimates (Chandler, Royle & King 2011; Schmidt, McIntyre & MacCluskie 2013). Temporary emigration processes are particularly problematic for surveys of species that show large variation in cue production over a survey season and highly mobile species, including: birds (e.g., Nichols, Thomas & Conn 2009; Chandler, Royle & King 2011; Schmidt, McIntyre & MacCluskie 2013), herpetofauna (e.g., O'Donnell, Thompson & Semlitsch 2015), and insects (e.g., Kéry et al. 2009). For example, in our study, the proportion of American tree and savannah sparrows that were available for sampling on a given visit ranged from approximately 0.2 to nearly 1. Using repeat surveys with inference to the superpopulation allowed us to directly estimate $p_p p_a$ and, thereby, make minimal untested assumptions regarding the observation process. Theoretically, the thinned point process model described here could be combined with the distance sampling-time removal model of Amundson, Royle & Handel (2014) to explicitly estimate all of the primary components of detection. However, for our arctic passerine application, it is unlikely that the combined model could fully separate p_p and p_a . Much of the information about temporary emigration, particularly, seasonal variation in song frequency, comes from visits spaced several days apart (rather than the time intervals within a visit) in part due to the Markovian nature of birdsong (Collins 2004). Consequently, we would expect that the estimated p_p under this combined model would still be some version of a composite $p_p p_a$ comprising some proportion of the seasonal variation in song frequency that cannot be fully explained by the time-removal model for p_a . For our application, we would expect that directly accommodating individual heterogeneity in p_p , in the form of variation in the proximity of home ranges to the survey transect, would be necessary for separate estimation of p_a . This type of inference would be possible within the framework of the spatial count model (Chandler & Royle 2013) which extends the spatial point process underlying spatial capture-recapture models (Efford 2004; Borchers & Efford 2008; Royle & Young 2008) to unmarked and partially marked populations.

Studies of population dynamics in remote areas face considerable logistical challenges, making it critical to develop efficient survey designs for these landscapes. Particularly in rugged

terrain, a completely randomized design, as required under the uniformity assumption of conventional distance sampling, will often lead to inefficiency (Marques, Buckland, Borchers, Tosh, & McDonald 2010). Spatial distance sampling inference permits non-standard designs where the focus can be on maximizing the population that is exposed to sampling in an efficient manner. For our study, this consideration was particularly important given that many arctic passerines are sparsely distributed and the terrain is not amenable to a completely random and efficient transect configuration. Thus, configuring transects such that we limited our time spent “off-effort” greatly increased the amount of data we were able to collect within the limited breeding season.

Framing inference in terms of the individual encounter in space offers greater sensitivity for understanding spatial processes particularly in the presence of within-plot variation in density (Royle et al. 2013). However, in many ecological studies, investigators are confronted with large variation in the available population across survey occasions. Thus, we expect that accounting for temporary emigration in spatial distance sampling models may be a critical specification for many species. That is, to fully realize the spatial information inherent in the location of encounter, it may be necessary to directly estimate $p_p p_a$ or p_p , as in related spatial capture-recapture models (Efford 2004; Borchers & Efford 2008; Royle & Young 2008). We expect that the methods described here will be particularly applicable to monitoring of species undergoing concurrent changes in distribution and abundance, particularly the study of populations subject to changes in abundance that are being driven by changes in habitat distribution.

1.6 Acknowledgements

We thank J.B. Hughey, S.A. Swanson, S.C. Swanson, and E. Burk for conducting surveys. We thank J.A. Royle for initially suggesting a point pattern approach and J.P. Lawler for his support during the development of the landbird monitoring program. We also wish to thank G.A. Breed, A.N. Powell, E.J. Wald, and two anonymous reviewers for valuable comments on an earlier version of this manuscript. Funding for this work was provided through the U.S. National Park Service’s Inventory and Monitoring Program and the Arctic Network. Any reference to trade names or commercial products are for descriptive purposes only and do not imply endorsement by the U.S. government and the research conducted in this study is in compliance with its current laws.

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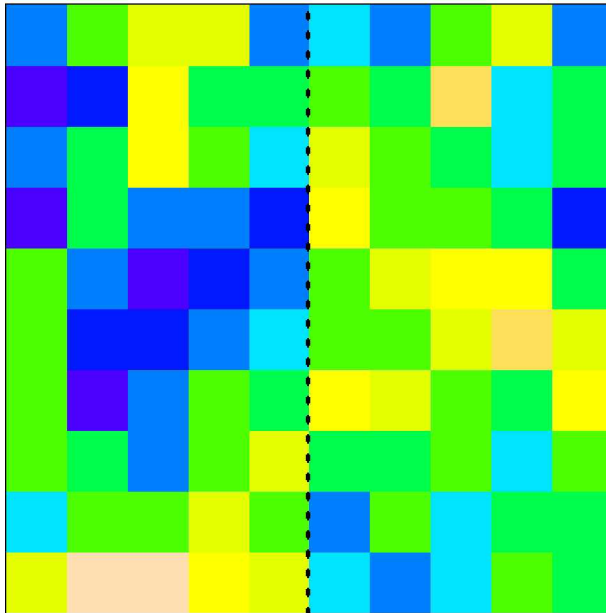


Figure 1.1. A spatially correlated covariate simulated on a 10 x 10 pixel grid. Each plot in the simulation study was bisected by a line transect (dashed line).

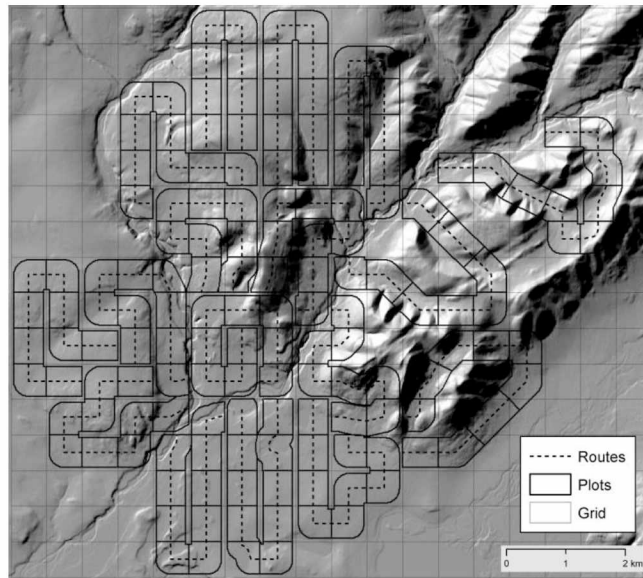


Figure 1.2. The sampling design implemented at a study site in Noatak National Preserve, Alaska in 2016. Plots (solid borders) and routes (dashed lines) are shown for a species with a 250 m truncation distance.

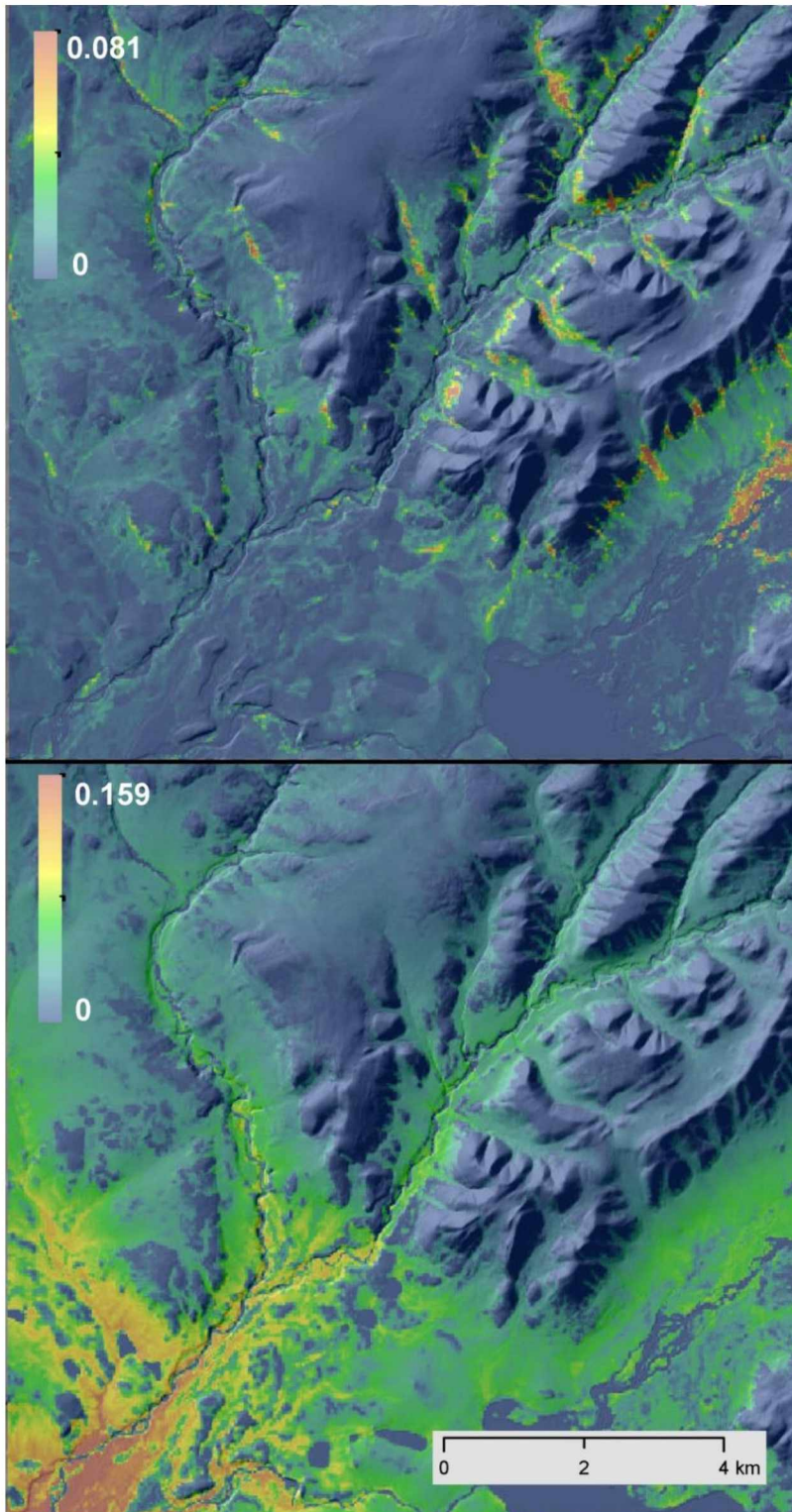


Figure 1.3. Posterior predictions of superpopulation point intensity (abundance per pixel) for American Tree Sparrow (top) and Savannah Sparrow (bottom).

Table 1.1. Results from 500 simulations for Poisson TEDS, Poisson log-normal TEDS, and TPP models where σ is the scale parameter of the half-normal detection function, ϕ is the probability of availability, β_1 is a spatial effect on the point intensity, and M_{total} is the total superpopulation size (a derived parameter) which varied between simulation runs due to randomly drawing the local population sizes.

Parameter	Model	True value	Mean	RMSE	Bias	CI coverage
σ	TEDS	3	3.11	0.31	0.04	0.72
	Log-normal TEDS	3	3.11	0.30	0.04	0.73
	TPP	3	3.06	0.17	0.02	0.95
ϕ	TEDS	0.6	0.66	0.08	0.10	0.70
	Log-normal TEDS	0.6	0.58	0.06	-0.04	0.89
	TPP	0.6	0.60	0.04	0.00	0.96
β_1	TEDS	–	2.03	–	–	–
	Log-normal TEDS	–	2.11	–	–	–
	TPP	2	2.00	0.04	0.00	0.95
M_{total}	TEDS	–	303.84	30.55	-0.08	0.66
	Log-normal TEDS	–	354.74	32.58	0.06	0.93
	TPP	–	337.73	20.29	0.01	0.95

Table 1.2. Parameter estimates and 95% credible intervals for Poisson log-normal TEDS and TPP models. Estimates for α parameters correspond to effects on ϕ and are on the logit-scale. Estimates for β parameters correspond to effects on the point intensity and are on the log-linear scale. M_{total} is the total superpopulation and σ is the scale parameter of a half-normal detection function. Bold numbers indicate estimates with 95% credible intervals that do not include 0.

Species	Parameter	Log-normal TEDS		TPP	
		Mean	95% CI	Mean	95% CI
American Tree Sparrow					
	σ	135.93	(119.75, 157.44)	156.89	(132.54, 192.43)
	α_0	0.22	(-0.48, 1.02)	-0.01	(-0.61, 0.55)
	α_1*time	0.26	(-0.03, 0.59)	0.21	(-0.03, 0.46)
	$\alpha_2*effort$	0.80	(0.41, 1.35)	0.64	(0.34, 1.01)
	β_0	-1.93	(-5.23, 1.32)	-6.24	(-6.65, -5.81)
	β_1*NDVI	1.38	(0.73, 2.08)	1.93	(1.64, 2.22)
	β_2*elev	0.12	(-0.17, 0.41)	-0.33	(-0.62, -0.06)
	β_3*elev^2	-0.88	(-2.70, 0.92)	-0.488	(-0.79, -0.22)
	M_{total}	252.55	(202, 336)	243.826	(199, 321)
Savannah Sparrow					
	σ	113.20	(105.24, 122.24)	116.003	(107.52, 126.09)
	α_0	-0.49	(-1.07, 0.02)	-0.347	(-0.78, 0.07)
	α_1*time	-0.20	(-0.34, -0.08)	-0.22	(-0.36, -0.09)
	α_2*date	0.14	(0.00, 0.30)	0.225	(0.07, 0.40)
	α_3*date^2	0.19	(0.06, 0.33)	0.224	(0.09, 0.37)
	$\alpha_4*effort$	0.50	(0.32, 0.73)	0.515	(0.33, 0.73)
	β_0	-2.68	(-5.34, -0.02)	-4.186	(-4.44, -3.90)
	β_1*NDVI	-0.05	(-0.40, 0.29)	1.193	(1.00, 1.40)
	β_2*NDVI^2	-0.03	(-0.69, 0.62)	-0.497	(-0.69, -0.31)
	β_3*elev	0.11	(-0.07, 0.30)	-0.683	(-0.80, -0.57)
	β_4*elev^2	1.06	(-0.92, 3.05)	0.141	(0.02, 0.26)
	M_{total}	1368.80	(1045, 1947)	1233.76	(1018, 1558)

Appendix 1.1. Simulation and JAGS code for the TPP model.

```
#####  
#### Mizel, J.D., Schmidt, J.H. and Lindberg, M.S.  
#### Accommodating temporary emigration in spatial distance sampling models  
#####  
  
#####  
#### Simulation code adapted from Kéry and Royle (2016)  
#####  
  
library(jagsUI)  
  
e2dist<-  
function (x, y)  
{  
i <- sort(rep(1:nrow(y), nrow(x)))  
dvec <- sqrt((x[, 1] - y[i, 1])^2 + (x[, 2] - y[i, 2])^2)  
matrix(dvec, nrow = nrow(x), ncol = nrow(y), byrow = F)  
}  
  
sim.spatialHDS.TE <-  
function(nsites=100,dim=10,delta=1,b1=1,int.lam=2.5,T=4,adj.sigma=.6,phi=.6){  
  
n.pixels<-dim*dim  
B<-dim/2  
  
sigma<-adj.sigma*B # Default adj.sigma is .75 x radius B  
  
# Create coordinates for n.pixels x n.pixels grid  
grx <- seq(delta/2, 2*B - delta/2, delta) # mid-point coordinates  
gr <- expand.grid(grx,grx) # Create grid coordinates  
center<-matrix(B,nrow=1,ncol=2)  
  
tr<-cbind(rep(B,length(grx)),grx)  
d1<-e2dist(tr,gr)  
d<-apply(d1,2,min)  
  
V <- exp(-e2dist(gr,gr)/1)  
  
# Create spatially correlated covariate x and plot it  
b0<-log(int.lam/n.pixels)  
x<-probs<-array(NA,dim=c(n.pixels,nsites))  
M<-rep(NA,nsites)  
  
for (j in 1:nsites){
```

```

z<- t(chol(V))%*%rnorm(n.pixels)
x[,j]<- z
M[j]<- rpois(1, sum(exp(b0 + b1*x[,j])))
}

for (i in 1:n.pixels){
for (j in 1:nsites){
probs[i,j]<- exp(b1*x[i,j])/sum(exp(b1*x[,j]))
}}

Mind<-max(M)

superpop<-array(0,c(Mind,nsites))
for (j in 1:nsites){
ifelse(M[j]>0,superpop[1:M[j],j]<-1,superpop[,j]<-0)
}

# Simulate individual locations
pixel.id <-array(NA,dim=c(Mind,nsites,T))
for (i in 1:Mind){
for (j in 1:nsites){
for (k in 1:T){
pixel.id[i,j,k] <- sample(1:n.pixels, 1, replace=TRUE, prob=probs[,j])
}}}}

y1<-p<-array(NA,dim=c(Mind,nsites, T))
# Simulate observations
# p = real member of superpop x availability x detection function (half-normal)
for (i in 1:Mind){
for (j in 1:nsites){
for(k in 1:T){
p[i,j,k]<-superpop[i,j] * phi * exp(-d[pixel.id[i,j,k]]*d[pixel.id[i,j,k]]/(2*(sigma^2)))
y1[i,j,k]<-rbinom(1, 1, p[i,j,k])
}}}}
Counts<-apply(y1,2:3,sum,na.rm=TRUE)

pixel.id[y1==0]<-0 #not detected or not real individual

# Re-shape individual data structure into counts in site x pixel x visit array
y <- array(NA, dim = c(nsites, n.pixels,T),
dimnames = list(NULL, c(1:n.pixels)))
for(i in 1:nsites){
for (k in 1:T){
y[i,.,k] <- table(factor(paste(pixel.id[,i,k], sep = "")),
levels = c(1:n.pixels)))
}}

```

```

dim(y)<-c(nsites, n.pixels,T)

return(list(M=M,B=B,d=d,Habitat=x,B=B,T=T,n.pixels=n.pixels,nsites=nsites,y=y,Counts=Cou
nts))
}

str(tmp <- sim.spatialHDS.TE(nsites=150,int.lam=.3,b1=2,phi=.6,T=4))

y<- tmp$y
d <- tmp$d
B<-tmp$B
nobs<- tmp$Counts
Habitat <- tmp$Habitat
Habitat <- Habitat - mean(Habitat)
Habgrid <- tmp$grid
M<- tmp$M
nsites<-tmp$nsites
n.pixels<-tmp$n.pixels
T<-tmp$T
nind <- sum(M) #total superpop size

#####

sink("model.jags")
cat("
model {
sigma ~ dunif(0,5)
phi~dunif(0,1)
b1~dnorm(0,.01)
b0~dnorm(0,.01)

for (i in 1:n.pixels){
log(g[i])<--d[i]*d[i]/(2*sigma*sigma)
for (j in 1:nsites){
log(lam[i,j]) <- b0+b1*Habitat[i,j]
pix.probs[i,j]<-lam[i,j]/sum(lam[,j])
cellprobs[i,j]<-g[i]*pix.probs[i,j]
cellprobs.cond[i,j] <- cellprobs[i,j]/sum(cellprobs[1:n.pixels,j])
}}
for (j in 1:nsites) {
cellprobs[n.pixels+1,j]<- 1-sum(cellprobs[1:n.pixels,j])
M.lam[j]<-sum(lam[,j])
M[j] ~ dpois(M.lam[j])
pdet[j] <- sum(cellprobs[1:n.pixels,j])
pmarg[j] <- pdet[j]*phi # Marginal probability
for (k in 1:T) {

```

```

#N[j,k] ~ dbin(phi, M[j])
#nobs[j,k] ~ dbin(pdet[j,k], N[j,k])
nobs[j,k] ~ dbin(pmarg[j], M[j])
y[j,1:n.pixels,k]~dmulti(cellprobs.cond[1:n.pixels,j], nobs[j,k])
}}

total.M<-sum(M[])

} # end model

",fill = TRUE)
sink()

data <- list(y = y, d=d, nsites=nsites,Habitat=Habitat,nobs=nobs,n.pixels=n.pixels,T=T)

inits <- function(){ list (sigma=3,M=M,b1=2,phi=.6,b0=-5.8)}

params <- c("sigma","b0","b1","phi","total.M")

ni <-21500 ; nb <- 6500 ; nt <-5 ; nc <- 1

out <- jags(data, inits, params, "model.jags", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb,
parallel = TRUE)

```

Appendix 1.2. Simulation and JAGS code for the log-normal TEDS model.

```
#####
#### Mizel, J.D., Schmidt, J.H. and Lindberg, M.S.
#### Accommodating temporary emigration in spatial distance sampling models
#####

#####
#### Simulation code adapted from Kéry and Royle (2016)
#####
```

```
library(jagsUI)
```

```
e2dist<-
function (x, y)
{
i <- sort(rep(1:nrow(y), nrow(x)))
dvec <- sqrt((x[, 1] - y[i, 1])^2 + (x[, 2] - y[i, 2])^2)
matrix(dvec, nrow = nrow(x), ncol = nrow(y), byrow = F)
}
```

```
sim.spatialHDS.TE <-
function(nsites=100,dim=10,b1=1,int.lam=2.5,T=3,adj.sigma=.6,phi=.6){
```

```
n.pixels<-dim*dim
B<-dim/2
sigma<-adj.sigma*B #default is .6 x radius B
```

```
# Create coordinates for n.pixels x n.pixels grid
delta <- (2*B-0)/dim # '2D bin width'
grx <- seq(delta/2, 2*B - delta/2, delta) # mid-point coordinates
gr <- expand.grid(grx,grx) # Create grid coordinates
center<-matrix(B,nrow=1,ncol=2)
```

```
tr<-cbind(rep(B,length(grx)),grx)
d1<-e2dist(tr,gr)
d<-apply(d1,2,min)
```

```
M<-rep(NA,nsites)
V <- exp(-e2dist(gr,gr)/1)
# Create spatially correlated covariate x and plot it
x<-array(NA,dim=c(n.pixels,nsites))
for (j in 1:nsites){
z<- t(chol(V))*rnorm(n.pixels)
x[,j]<- z
}
```



```

# If true, keep only pixels within B and simulate as spatially-closed population

midpt <- seq(delta/2, B, delta) #
nD <- length(midpt)

b0<-log(int.lam/n.pixels)
probs<-array(NA,dim=c(n.pixels,nsites))

for (j in 1:nsites){
  # Note Poisson assumption which means in each pixel is also Poisson
  M[j]<- rpois(1, sum(exp( b0 + b1*x[,j])))
}
for (i in 1:n.pixels){
for (j in 1:nsites){
probs[i,j]<- exp(b1*x[i,j])/sum(exp(b1*x[,j]))
}}

Mind<-max(M)

superpop<-array(0,c(Mind,nsites))
for (j in 1:nsites){
ifelse(M[j]>0,superpop[1:M[j],j]<-1,superpop[,j]<-0)          #rbinom(1,1,psi.M[j])
}

pixel.id <-array(NA,dim=c(Mind,nsites,T))
for (i in 1:Mind){
for (j in 1:nsites){
for (k in 1:T){
pixel.id[i,j,k] <- sample(1:n.pixels, 1, replace=TRUE, prob=probs[,j]) ##simulate individual
locations
}}}}

y1<-p<-array(NA,dim=c(Mind,nsites, T))
for (i in 1:Mind){ #simulate observations
for (j in 1:nsites){
for(k in 1:T){
  p[i,j,k]<-superpop[i,j] * phi * exp(-d[pixel.id[i,j,k]]*d[pixel.id[i,j,k]]/(2*(sigma^2)))
#half-normal function          #prob of avail x cond prob of detection
(perceptibility)
  y1[i,j,k]<-rbinom(1, 1, p[i,j,k])
}}}}
Counts<-apply(y1,2:3,sum,na.rm=TRUE) #these are the site-visit counts

cutpoints<-seq(0,B,delta)
dclass<-as.numeric(cut(d[pixel.id],cutpoints, include.lowest=TRUE))
dclass[y1==0]<-0

```

```

dim(dclass)<-c(Mind,nsites,T)

y <- array(NA, dim = c(nsites, nD,T),
  dimnames = list(NULL, c(1:nD)))
for(i in 1:nsites){
for (k in 1:T){
  y[i,,k] <- table(factor(paste(dclass[,i,k], sep = ""),
  levels = c(1:nD)))
}}
dim(y)<-c(nsites, nD,T)

return(list(M=M,B=B,d=d,Habitat=x,B=B,T=T,n.pixels=n.pixels,nD=nD,midpt=midpt,delta=del
ta,nsites=nsites,y=y,Counts=Counts))
}

str(tmp <- sim.spatialHDS.TE(nsites=150,int.lam=.3,b1=2,phi=.6,T=4))

y<- tmp$y
nD<- tmp$nD
midpt<- tmp$midpt
B <- tmp$B
delta<-tmp$delta
d <- tmp$d
nobs<- tmp$Counts
Habitat <- tmp$Habitat
Habitat <- Habitat - mean(Habitat)
Habgrid <- tmp$grid
M<- tmp$M
nsites<-tmp$nsites
T<-tmp$T
nind <- sum(M) #total superpop size

habitat<-apply(Habitat,2,mean)

#####

sink("model.jags")
cat("
model {
# Prior distributions
beta0 ~ dnorm(0, 0.01) # Intercept for log(lambda)
mean.lam <- exp(beta0)
beta1 ~ dnorm(0, 0.01) # Coefficient of log transform of lambda on habitat
sigma ~ dunif(0,5) # Distance function parameter
phi~dunif(0,1)
tau.eps<-pow(sigma.eps,-2)

```

```

sigma.eps~dunif(0,100)
# Detection probs for each distance interval and related things
for(b in 1:nD){
  log(g[b]) <- -midpt[b]*midpt[b]/(2*sigma*sigma) # half-normal
  cellprobs[b] <- g[b]/nD
  cellprobs.cond[b] <- cellprobs[b]/sum(cellprobs[1:nD])
}
cellprobs[nD+1]<- 1-sum(cellprobs[1:nD])

for (s in 1:nsites) {
  for (k in 1:T) {
    pdet[s,k] <- sum(cellprobs[1:nD]) # Distance class probabilities
    pmarg[s,k] <- pdet[s,k]*phi # Marginal probability
    # Model part 4: distance class frequencies
    y[s,1:nD,k] ~ dmulti(cellprobs.cond[1:nD], nobs[s,k])
    # Model part 3: total number of detections:
    nobs[s,k] ~ dbin(pmarg[s,k], M[s])
    # nobs[s,k] ~ dbin(pdet[s,k], Navail[s,k]) # Alternative formulation
    # Model part 2: Availability. Not used in this model but simulated.
    #avail[s,k] ~ dbin(phi, M[s])
  } # end k loop
  # Model part 1: Abundance model
  M[s] ~ dpois(lambda[s])
  log(lambda[s]) <- beta0 + beta1*habitat[s]+eps[s]
  eps[s]~dnorm(0,tau.eps)
} # End s loop

# Derived quantities
Mtot <- sum(M[])

} # End model

",fill = TRUE)
sink()

data <- list(y = y, nsites=nsites,habitat=habitat,nobs=nobs,T=T,nD=nD,
midpt=midpt)

inits <- function(){ list (sigma=3,M=M,phi=.6)}

params <- c("sigma", "phi", "beta0", "beta1", "Mtot", "sigma.eps")

ni <-58000 ; nb <- 28000 ; nt <-10 ; nc <- 1

out <- jags(data, inits, params, "model.jags", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb,
parallel = TRUE)

```

Appendix 1.3. JAGS code for Savannah and American Tree Sparrow analyses using the TPP model.

```
#####  
#### Mizel, J.D., Schmidt, J.H. and Lindberg, M.S.  
#### Accommodating temporary emigration in spatial distance sampling models  
#####  
  
#####  
####As written, runs the model for SAVS.  
####To run the analysis for American Tree Sparrow (ATSP), 1) replace "SAVS" with "ATSP";  
####2) replace "200" with "250"; and 3) reduce the model as done in the paper.  
####The data from the arctic passerine application is available at the Dryad Digital Repository  
####https://doi.org/10.5061/dryad.90kp2 (Mizel, Schmidt, & Lindberg 2017).  
#####  
  
T<-5  
nsites<-150  
nsurveys<-466  
  
NDVIdf<-read.csv("NDVI_200.csv") #covariate grid  
SAVS<-read.csv("SAVS.csv") #individual encounter data  
pcov<-read.csv("pcovariates.csv") #survey-level covariates  
data<-read.csv("Counts2sp.csv") #Survey counts  
C<-data$SAVScounts  
dim(C)<-c(nsites,T)  
  
site<-NDVIdf$newsite  
sitepix<-as.vector(table(site))  
max.pix<-max(sitepix)  
d<-round(NDVIdf$NEAR_DIST,2)  
pixID<-NDVIdf$PointID2  
elev<-round(as.vector(scale(NDVIdf$elev)),5)  
elev2<-elev*elev  
elev2<-round(elev2,5)  
NDVI<-round(as.vector(scale(NDVIdf$NDVI)),5)  
subgrid<-NDVIdf$subplot  
nsubgrids<-max(subgrid)  
n.pixels<-length(NDVI)  
effort<-scale(pcov$effort)  
julian<-scale(pcov$juldate)  
julian2<-julian*julian  
time<-scale(pcov$reltime)  
effort<-effort[!is.na(as.vector(effort))]  
julian<-julian[!is.na(as.vector(julian))]  
julian2<-julian2[!is.na(as.vector(julian2))]
```

```

time<-time[!is.na(as.vector(time))]
ind.site<-SAVSS$Site
pixel.cap<-SAVSS$Pixel
ind.visit<-SAVSS$Visit
Mind<-max(C,na.rm=T)*2

site2<-C
for(j in 1:nsites){
for(k in 1:T){
  ifelse(is.na(C[j,k]),site2[j,k]<-NA,site2[j,k]<-j)
}}
site2<-site2[!is.na(as.vector(site2))]

nobs<-C[!is.na(as.vector(C))]
y2<-array(0,dim=c(Mind,nsurveys))
for(j in 1:nsurveys){
  ifelse(nobs[j]>0,y2[1:nobs[j],j]<-1,y2[j]<-0)
}
y.indices<-which(y2==1,arr.ind=TRUE)
ind<-y.indices[,1]

survey1<-C
survey1[!is.na(survey1)]<-1
survey2<-as.vector(survey1)
survey3 <- survey2
survey3[!is.na(survey2)] <- cumsum(survey3[!is.na(survey2)])
dim(survey3)<-c(nsites,T)
survey<-survey3

pixel<-array(0,dim=c(Mind,nsurveys))
for(i in 1:length(pixel.cap)){
  pixel[ind[i],survey[ind.site[i],ind.visit[i]]]<-pixel.cap[i]
}

y <- array(0, dim = c(nsurveys,max.pix),
  dimnames = list(c(1:nsurveys),c(1:max.pix)))
for(j in 1:nsurveys){
  y[j,] <- table(factor(paste(pixel[,j], sep = ""),
  levels = c(1:max.pix)))
}
dim(y)<-c(nsurveys,max.pix)

M<-apply(C,1,max,na.rm=T)+1

```

```

#####
####Model code          #####

```

```
#####
```

```
library(jagsUI)

sink("model.jags")
cat("
model {
sigma ~ dunif(0,200)
a0~dnorm(0,.01)
a1~dnorm(0,.01)
a2~dnorm(0,.01)
a3~dnorm(0,.01)
a4~dnorm(0,.01)
tau.eps<-pow(sigma.eps,-2)
sigma.eps~dunif(0,100)
tau.avail<-pow(sigma.avail,-2)
sigma.avail~dunif(0,100)
b0~dnorm(0,.01)
b1~dnorm(0,.01)
b2~dnorm(0,.01)
b3~dnorm(0,.01)
b4~dnorm(0,.01)
for (j in 1:nsubgrids) {
  eps[j]~dnorm(0,tau.eps)
}
for (i in 1:n.pixels){
  log(g[i])<--d[i]*d[i]/(2*sigma*sigma)
  log(lam[pixID[i],site[i]]) <b0 + b1*NDVI[i] + b2*NDVI2[i] + b3*elev[i] + b4*elev2[i] +
eps[subgrid[i]]
  pix.probs[pixID[i],site[i]]<-lam[pixID[i],site[i]]/sum(lam[1:sitepix[site[i]],site[i]])
  cellprobs[pixID[i],site[i]]<-g[i]*pix.probs[pixID[i],site[i]]
  cellprobs.cond[pixID[i],site[i]] <-
cellprobs[pixID[i],site[i]]/sum(cellprobs[1:sitepix[site[i]],site[i]])
}
for (j in 1:nsites) {
  cellprobs[sitepix[j]+1,j]<- 1-sum(cellprobs[1:sitepix[j],j]) #
  M.lam[j]<-sum(lam[1:sitepix[j],j])
  M[j] ~ dpois(M.lam[j])
}
for (i in 1:nsurveys) {
  logit(phi[i]) <-a0+a1*time[i]+a2*julian[i]+a3*julian2[i]+a4*effort[i]+e.avail[i]
  e.avail[i]~dnorm(0,tau.avail)
  pdet[i] <- sum(cellprobs[1:sitepix[site2[i]],site2[i]])
  pmarg[i] <- pdet[i]*phi[i] # Marginal probability
  nobs[i] ~ dbin(pmarg[i], M[site2[i]])
  y[i,1:sitepix[site2[i]]]~dmulti(cellprobs.cond[1:sitepix[site2[i]],site2[i]], nobs[i])
}
```

```

#N[i] ~ dbin(phi[i], M[site2[i]])
#nobs[i] ~ dbin(pdet[i], N[i])
}
total.M<-sum(M[])

} # end model

",fill = TRUE)
sink()

data <- list(y = y, d=d, nsites=nsites, NDVI=NDVI, nobs=nobs, n.pixels=n.pixels, plot=site,
nsubgrids=nsubgrids, pixID=pixID, julian=julian, subgrid=subgrid, NDVI2=NDVI2,
julian2=julian2, time=time, effort=effort, plot2=site2, nsurveys=nsurveys, plotpix=sitepix,
elev=elev,elev2=elev2)

inits <- function(){ list (sigma=114,M=M+1,b1=1)}

params <- c("sigma", "b0", "b1", "b2", "b3", "b4",
"a0", "a1", "a2", "a3", "a4", "sigma.avail", "total.M", "sigma.eps")

ni <-100000 ; nb <- 25000 ; nt <-5 ; nc <- 2

out <- jags(data, inits, params, "model.jags", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb,
parallel = TRUE)

```

CHAPTER 2

SUBARCTIC-BREEDING PASSERINES EXHIBIT PHENOLOGICAL RESILIENCE TO EXTREME SPRING CONDITIONS¹

2.1 Abstract

There has been relatively little study of the capacity of subarctic passerines to adjust their phenologies to rapid changes on their breeding grounds. Here we assess variation in passerine arrival timing in Denali National Park, Alaska from 1995-2015, a period that included both the warmest and coldest recorded mean spring temperatures for the park. Using an open-population occupancy modeling approach in which arrival events are random variables, we investigated interannual variation in the arrival distribution for 10 Nearctic-Nearctic migrants, three Nearctic-Neotropical migrants, and one Palearctic migrant. Neotropical-Nearctic migrants varied in terms of the flexibility of their arrival timing, but generally showed plastic phenologies, suggesting resilience under extreme spring conditions. In comparison, Nearctic-Nearctic migrants showed similar or greater plasticity in arrival timing. A majority of species showed synchronous-asynchronous fluctuation in arrival (i.e., synchronous arrival in some years, asynchronous in others) in combination with various levels of the mean response (i.e., early, average, and late arrival), suggesting the presence of interactions between environmental conditions at multiple scales and inter-individual variation. The presence of synchronous-asynchronous fluctuation in arrival suggests that weakening of the north-south temperature gradient under continued Arctic amplification may strongly affect arrival variances. Our results also suggest that complex interactions between distributional and phenological changes may be possible. For example, the arrival distribution of Fox Sparrow (*Passerella iliaca*) became more synchronized over time, a pattern that coincided with a dramatic increase in occupancy probability through expansion of its elevational distribution. Overall, our findings suggest that monitoring of the mean-variance relationship may lead to a deeper understanding of the factors shaping phenological responses.

¹ Mizel, J. D., J. H. Schmidt, C. L. McIntyre, and M. S. Lindberg. 2017. Subarctic-breeding passerines exhibit phenological resilience to extreme spring conditions. *Ecosphere* 8: e01680.

2.2 Introduction

Advances in the breeding and migratory phenology of birds due to climate change are well documented (Parmesan and Yohe 2003, Root et al. 2003, Dunn 2004). The observed shifts are generally thought to be plastic phenotypic responses rather than micro-evolutionary responses to selection on heritable traits (Gienapp et al. 2007, Gienapp et al. 2008, Charmantier and Gienapp 2014). Trends towards earlier arrival appear to be more widespread and of greater magnitude in short-distance migrants (e.g., Butler 2003, Mills 2005, Travers et al. 2015) compared to long-distance migrants (but see; Hüppop and Hüppop 2003, Stervander et al. 2005, Zalakevicius et al. 2006, Jonzén et al. 2006). Long-distance migrants are thought to show relatively limited plasticity in migratory timing (e.g., Pulido and Widmer 2005, Miller-Rushing et al. 2008, Both et al. 2009), in part due to strong control of migratory onset by endogenous mechanisms (Berthold 1984, Gwinner 1996). On northern breeding grounds experiencing rapid warming, some long-distance migrants show insufficient adaptation of arrival timing relative to changes in the phenology of their invertebrate prey (Both and Visser 2001, Visser et al. 2004). The decoupling of arrival phenology and seasonal food availability has been linked to population declines in long-distance migrants (Both and Visser 2001, Visser et al. 2004).

While there appear to be constraints on the development of plastic migratory traits in long-distance migrants, many of these species fine-tune their migration speed in response to conditions encountered en route (Marra et al. 2005, Both 2010, Tøttrup et al. 2010) and some show variation in departure timing related to conditions on wintering grounds (Gordo et al. 2005, Saino et al. 2007, Studds and Marra 2007). Short-distance migrants, by virtue of wintering in seasonal climates, often show comparatively close tracking of spring phenology during migration and, consequently, tend to have more plastic phenologies (Alerstam and Högstedt 1980, Butler 2003). Our understanding of these relationships in passerines comes largely from studies of Palearctic migrants and from studies at North American mid-latitudes. There has been relatively little study of the potential capacity (or resilience) of passerines breeding in the subarctic to adjust their arrival phenologies to large variation in spring conditions (but see: Eeva et al. 2000, Gunnarsson and Tómasson 2011, Grabowski et al. 2013, Liebezeit et al. 2014, Ward et al. 2015). In addition, studies of avian arrival phenology have focused extensively on temporal trends in first or mean arrival dates, but have largely ignored temporal patterns in the variance of the arrival distribution (but see: Møller 1994b, Ptaszyk et al. 2003, Møller 2008, Møller et al. 2010).

Intraspecific phenotypic variation plays an integral role in ecological and evolutionary dynamics, and sole reliance on the mean trait for inference may underestimate the capacity of species to cope with environmental change (Bolnick et al. 2011, Violle et al. 2012). Assessments of the relationship between the mean and variance of the arrival distribution may lead to a deeper understanding of the factors shaping phenological responses and the capacity of species to adapt their phenologies in response to environmental change.

The costs and benefits of early arrival are phenotype-dependent, and optimization of individual arrival timing is thought to depend on individual condition, the individual-specific costs of early arrival, and the arrival timing of competing males that helps set the value of arriving on a given date (Møller 1994a, Kokko 1999). Carry-over effects often provide a mechanism for inter-individual variation in migratory and breeding timing (reviewed in Harrison et al. 2011). For example, individuals occupying poorer and/or more distant wintering habitat may arrive later on breeding grounds (e.g., Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004). Age- and sex-related differences in migration timing and stopover behavior are also well documented (Yong et al. 1998, Stewart et al. 2002, Vardanis et al. 2011, McKinnon et al. 2014). In addition to differing in their average arrival date, individuals may also differ in the capacity for phenotypic plasticity. Some individuals may show the capacity for adjustments beyond their optimal arrival date that are disproportionate to those exhibited by others. The presence of inter-individual variation in plasticity or an individual-by-environment interaction (Nussey et al. 2007) may be important factors underlying interannual variation in the spread of the arrival distribution (i.e., variance heterogeneity through time).

Previous studies have documented multiscale influences on arrival timing (e.g., Gordo et al. 2005, MacMynowski and Root 2007, Tøttrup et al. 2010) and the interactive effects of individual variation and environmental conditions on the arrival variance (e.g., Møller 1994b, Ptasyzk et al. 2003, Møller 2008). Interactions between environmental conditions at high- and mid-latitudes may affect the arrival distributions of subarctic migrants. Over recent decades, Arctic near-surface temperatures have increased at a rate almost twice that of the global average, and zonal-mean temperature anomalies show larger increases with increasing latitude (Serreze and Francis 2006, Serreze et al. 2009, Screen and Simmonds 2010). Given this weakening of the north-south temperature gradient or Arctic amplification, understanding the underlying

interactions between high- and mid-latitude environments within migration systems is critical for predicting the possible effects on passerine communities.

Migratory birds are under strong directional selection for earlier breeding (Both and Visser 2001, Visser et al. 2004, Dingemanse et al. 2004, Verhulst and Nilsson 2008). Competition for territories (e.g., Kokko 1999), seasonal variation in food availability (e.g., Both and Visser 2001), predation (e.g., Lank and Ydenberg 2003), and mortality risk during the early spring transition period (Newton 2007), all exert strong selective pressure on arrival and breeding timing. These pressures are likely to be particularly acute in Arctic and subarctic breeders due to heightened mortality risk during the spring arrival period and to the time demands of producing a brood, molting, and preparing for fall migration within a highly compressed breeding season (Eeva et al. 2000). Thus, understanding the potential capacity of passerines breeding in the subarctic to adjust their arrival timing in response to large interannual variation in spring conditions is of critical importance.

In this study, we investigated interannual variation in passerine arrival timing in Denali National Park, Alaska (hereafter, Denali) from 1995-2015. Our sampling period included both the warmest (1995) and coldest (2013) mean spring (April-May) temperatures recorded in Denali (1926-2015) (Fig. 2.2.1), providing the opportunity to assess the effects of a range of spring conditions on the arrival process. We used an open-occupancy modeling approach in which arrival events are random variables. Our objectives were to: 1) assess patterns of interannual variation in the mean and variance of the arrival distribution of individual species; and 2) compare and contrast the observed patterns between short- and long-distance migrants. We predicted that long-distance migrants would show limited variation in mean arrival, relatively homogenous variance across time, and compressed arrival distributions overall, because long-distance migrants generally exhibit smaller passage variances than short-distance migrants (Mills 2005, Van Buskirk et al. 2009, La Sorte et al. 2013) and high repeatability in arrival (e.g., Vardanis et al. 2011, Conklin and Battley 2011, Stanley et al. 2012). In contrast, we expected that short-distance migrants would show greater variation in the mean response and pronounced variance heterogeneity across time.

2.3 Methods

2.3.1 Data collection

We conducted passerine surveys along the easternmost 118 km of the 144 km Denali Park Road (DPR), a narrow, unpaved road transecting upland forest, treeline, shrubline, and open alpine habitats in the northeastern portion of Denali (63° 35.8'N, 149° 38.2'W) (Fig. 2.2). We established 3 roadside survey routes each comprising 50 points with 0.8 km spacing. Trained observers conducted repeated surveys from mid-April to early-July during twelve years (1995-1998, 2006, and 2009-2015), and routes were surveyed 2-18 times in each year (mean = 6.5 visits/year). Standard 3-minute point count surveys were conducted during favorable weather from 0.5 hours before sunrise to approximately 6 hours thereafter (Bystrack 1981). All birds seen or heard within ~400 m during the count period were recorded (Bystrack 1981), but only detections of singing males were used for our analyses. The same routes were generally surveyed by multiple observers in each year and some observers conducted surveys in multiple years (Schmidt et al. 2013, Mizel et al. 2016). For additional detailed descriptions of the study area and sampling scheme, see Schmidt et al. (2013) and Mizel et al. (2016).

2.3.2 Analyses

We restricted analysis to species detected at >10% of sites in most years to provide sufficient data to adequately model arrival, observation, and occupancy processes. We also excluded Lincoln's Sparrow (*Melospiza lincolnii*), which had detection probability <0.2 in all years, making it difficult to separate the arrival and observation processes. Our final data set included 14 species including: 10 Nearctic-Nearctic migrants, three Nearctic-Neotropical migrants, and one Palearctic migrant (Appendix 2.1). We classified species as short- or long-distance migrants if their wintering grounds lie primarily north or south of the Tropic of Cancer, respectively (Rappole et al. 1983).

We used the open-population occupancy modeling approach of Roth et al. (2014) to estimate arrival events. In this approach, arrival dates are random variables conditional on detection probability and the true occupancy state. In our data structure, the y_{ijt} observations corresponded to detection/non-detection of a given species at each point $i = 1, 2, \dots, I$, during each repeat survey $j = 1, 2, \dots, J$, in each year $t = 1, 2, \dots, T$. The true occupancy states z_{it} were Bernoulli random variables with occupancy probability ψ_{it} :

$$z_{it} \sim \text{Bernoulli}(\psi_{i,t}) \quad (\text{Eq. 2.1})$$

Based on the results of Mizel et al. (2016), we assumed ψ_{it} was a linear function of year, elevation (linear and quadratic), two interaction terms, and random site-level adjustments α_i around μ :

$$\text{logit}(\psi_{it}) = \mu + \alpha_i + \alpha_1 \text{year}_t + \alpha_2 \text{elev}_i + \alpha_3 \text{elev}_i^2 + \alpha_4 \text{year}_t * \text{elev}_i + \alpha_5 \text{year}_t * \text{elev}_i^2$$

Roth et al. (2014) treated arrival dates as overdispersed Poisson random variables. Given severe time constraints on breeding in the subarctic, we did not expect a need for accommodating additional variation in the right tail of the arrival distribution. In addition, given the relatively extreme interannual variation in spring conditions that occurred during our study period, we thought it necessary to account for variance heterogeneity across time. Therefore, we described arrival dates a_{it} as normal random variables with a year-specific variance and a random mean that varied by year:

$$a_{it} \sim \text{Normal}(\mu_t, \sigma_t^2) \quad (\text{Eq. 2.2})$$

We specified an arrival indicator variable I_{ijt} as an outcome of the relation of a_{it} to the survey date (i.e., $date_{ijt}$):

$$I_{ijt} = \begin{cases} 1 & \text{when } a_{it} \leq date_{ijt} \\ 0 & \text{when } a_{it} > date_{ijt} \end{cases} \quad (\text{Eq. 2.3})$$

The y_{ijt} observations were considered to be Bernoulli random variables with success probability specified such that detection probability p_{ijt} was conditional on the true occupancy state z_{it} and the arrival indicator I_{ijt} :

$$y_{ijt} \sim \text{Bernoulli}(z_{it} * p_{ijt} * I_{ijt}) \quad (\text{Eq. 2.4})$$

Based on the findings of Mizel et al. (2016), we assumed detection probability was a linear function of $date_{ijt}$ and time after sunrise, $time_{ijt}$:

$$\text{logit}(p_{ijt}) = \beta_0 + \beta_1 date_{ijt} + \beta_2 date_{ijt}^2 + \beta_3 time_{ijt} + \beta_4 time_{ijt}^2 \quad (\text{Eq. 2.5})$$

We included the linear and quadratic effects of survey timing (relative to sunrise) to account for variation in the probability of availability or diurnal patterns of singing frequency. We included

the linear and quadratic effects of survey date to account for variation in availability due to seasonal variation in singing frequency (Schmidt et al. 2013). See Roth et al. (2014) for additional details on model structure.

We were unable to estimate arrival in the years 1997 and 1998 because each of the three survey routes received ≤ 2 visits. However, we did not exclude data from these years as they contained detection and occupancy information. Instead, the arrival variance term for these years was fixed at 25, which corresponded to a mean standard deviation of 5 days in many species, and the year-specific random mean was set equal to the overall mean of this distribution. The surveys that did occur in these years were conducted in early June (between Julian dates 154-160), that is, after all arrival events were expected to occur for all short-distance migrants and most long-distance migrants. Thus, fixing arrival at reasonable values would be expected to have minimal effect on estimates of other parameters. However, we performed a series of sensitivity analyses on all long-distance migrants in which the arrival variance was set equal to 100 instead of 25. The effect was negligible in all cases.

We fit models using OpenBugs (Lunn et al. 2009) via the R2OpenBUGS package (Sturtz et al. 2005) in program R 3.2.2 (R Core Team 2015). We used diffuse priors on all occupancy and detection parameters (i.e., uniform distributions from 0 to 100 for the standard deviations of the random effects; uniform distributions -10 to 10 for all fixed occupancy and detection covariates). We used diffuse priors for all arrival parameters including uniform distributions from 0 to 30 for all standard deviations and normal distributions with mean 0 and precision 0.01 for the overall mean. Summaries of the posterior distribution were calculated from two independent Markov chains run for 60,000 iterations with a 10,000 iteration burn-in and thinning every four draws. We used the Gelman-Rubin diagnostic (Brooks and Gelman 1998) to assess convergence and scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. From posterior distributions for arrival dates at occupied sites, we calculated posterior distributions for the proportion of sites with an arrival event on or prior to each date within the survey season (i.e., cumulative arrival proportions). We also calculated the dates at which 5%, 50%, and 95% of occupied sites first showed an arrival event. This allowed us to assess the synchronicity of the arrival process (i.e., the interval between the arrival of the first and last 5% of individuals), as well as the timing of the bulk of the arrivals (i.e., arrival of 50% of the individuals). Estimates for the year-specific mean arrival dates μ_t were nearly equivalent to the

50 percentile estimates (i.e., the median) for all species. For clarity, we refer to the 50 percentile estimates as mean arrival. All estimates are presented as posterior means with 95% Bayesian credible intervals. We considered arrival to be synchronous in a particular year if the ratio of its standard deviation to the mean standard deviation for that species was <0.5 . Arrival was considered asynchronous if this ratio was >2.0 .

Lastly, we did not include weather covariates on arrival because our approach was to estimate the latent arrival events for each site in each year and a weather covariate would be expected to affect parts of this distribution differently, often with minimal effect on later arrival events. However, we accounted for interannual variation in weather by describing arrival in terms of a random mean and variance that varied by year. We also conducted a post-hoc linear regression of the annual arrival shift as a function of the average April-May temperature. The annual arrival shift for species i in year j was the mean arrival date for species i in year j minus the multiyear median for species j . We excluded Arctic Warbler (*Phylloscopus borealis*), a Palearctic migrant, from this analysis because this species did not appear to respond to spring temperatures (see Results).

2.4 Results

Long-distance migrants varied in terms of flexibility in arrival timing. Among Neotropical-Nearctic migrants, Orange-crowned (*Oreothlypis celata*) and Wilson's Warblers (*Wilsonia pusilla*) showed interannual variation in mean arrival that was comparable to that exhibited by short-distance migrants. i.e., estimates for their year-specific mean arrival dates spanned 13 and 17 days, respectively (Fig. 2.3a). The remaining Neotropical-Nearctic migrant, Swainson's Thrush (*Catharus ustulatus*) showed limited variation in mean arrival except for a relatively large advance in 2011 (Fig. 2.3a). However, contrary to theoretical predictions, all Neotropical-Nearctic migrants exhibited large interannual variation in arrival of the 5 percentile cohort, with year-specific estimates spanning 19-27 days for the three species (Fig. 2.3b). In addition, all Neotropical-Nearctic migrants showed unexpected and pronounced variance heterogeneity across time (Fig. 2.4), the result of synchronous-asynchronous fluctuation in arrival (i.e., synchronous arrival in some years, asynchronous in others) (Fig. 2.5a-c). Across these species, we observed asynchronous arrival and synchronous arrival in combination with all levels of the mean response (i.e., early, average, and late arrival) (Fig. 2.5a-c). In contrast, Arctic

Warbler, a Palearctic migrant, showed almost no interannual and intrapopulation variation in its arrival timing (Fig. 2.5d).

As predicted, short-distance migrants exhibited modest to large interannual variation in mean arrival and arrival of the 5 percentile cohort. Across the 10 short-distance migrants that we considered, interannual variations in mean arrival and arrival of the 5 percentile cohort spanned 13-26 and 14-32 days, respectively (Fig. 2.3). Short-distance migrants exhibited individualistic patterns of interannual variation in the dispersion of arrival dates (Fig. 2.4). Some species had small variances that were relatively homogenous across time and others showed pronounced variance heterogeneity across time (Fig. 2.4), the result of synchronous-asynchronous fluctuation in arrival (Fig. 2.6c-d and 2.7b, e). The arrival of Fox Sparrow (*Passerella iliaca*) became more synchronized over time (Fig. 2.7a) in concert with dramatic expansion of its elevational distribution at both low and high elevations (Mizel et al. 2016).

Arrival timing of Nearctic-Nearctic and Neotropical-Nearctic migrants showed an apparent relationship with local temperature (Appendix 2.2). Correspondingly, the extremely late spring of 2013 synchronized the arrival of the entire community. With the exception of Savannah Sparrow (*Passerculus sandwichensis*) and Arctic Warbler, mean arrival dates spanned only 3 and 5 days for long- and short-distance migrants, respectively (Fig. 2.3a). During the early spring of 1995, most species had advanced mean arrival, but the effect tended to be greatest in the 5 percentile cohort with advances (relative to each species' multiyear median) of 15, 18 and 20 days in Orange-crowned Warbler, Fox Sparrow, and Wilson's Warbler, respectively (Fig. 2.3b).

2.5 Discussion

Long-distance migrants are expected to have relatively inflexible phenologies, making them susceptible to trophic mismatches and corresponding population declines under climate change (e.g., Both and Visser 2001, Both et al. 2009). However, we found two Neotropical-Nearctic migrants, Orange-crowned and Wilson's Warblers, showed unexpectedly plastic phenologies, suggesting resilience under extreme spring conditions. Swainson's Thrush, the remaining Neotropical-Nearctic migrant, showed limited interannual variation in mean arrival, but greater variation in the arrival of the 5-percentile cohort, suggesting the capacity for plastic adjustments in arrival timing. Short-distance migrants showed similar or greater plasticity in arrival timing, indicating an ability to closely track the emergence of spring along their migration

routes. Overall, our findings suggest that both Neotropical-Nearctic and Nearctic-Nearctic migrants breeding in interior Alaska are able to adjust arrival in response to relatively large inter-annual variation in spring conditions.

The onset of spring in Denali is rapid and unpredictable in its timing. Further, it comprises large temperature variation and is often interrupted by periods of cold weather and snow, thereby representing substantial risk for early arriving individuals. Thus, all but the latest arriving species in our study area may have undergone selection for plasticity in arrival.

All Neotropical-Nearctic and several Nearctic-Nearctic migrants showed variance heterogeneity across time, the result of synchronous-asynchronous fluctuation in arrival. With the notable exception of Fox Sparrow, the degree of synchronicity in arrival did not appear to be strongly associated with annual occupancy, suggesting little support for interannual variation in density-dependent competition driving fluctuation in arrival variances. Instead, many species exhibited temporal trends in occupancy (Mizel et al. 2016) indicating the presence of temporal correlation in annual density amidst random interannual fluctuations in the arrival variance. Thus, the fact that we observed synchronous and asynchronous arrival in combination with various levels of the mean response (i.e., early, average, and late arrival) suggests the presence of interactions between environmental conditions at multiple scales and inter-individual variation in average arrival, and potentially, in phenotypic plasticity. That is, these interactions were likely involved in order for the variance to be large or small, irrespective of the mean response.

This may be conceptualized by decomposing the migration systems of high-latitude breeders into three basic environments: the wintering ground environment (E_W), the migration route or mid-latitude environment (E_R), and the near-breeding ground environment (E_B). Given its potential severity, the high-latitude environment (E_B) often mediates the conflated effect of the wintering ground-migration route environment ($E_W E_R$) on arrival timing. Early-asynchronous arrival may result when conditions on the $E_W E_R$ are near average, but an unusually favorable E_B releases the vanguard cohort to show a disproportionately large advance relative to the rest of the population. For example, in 1995, Wilson's and Orange-crowned warblers showed early arrival overall, but the shift in the 5-percentile cohort was disproportionate to that exhibited by the rest of their respective populations, resulting in early-asynchronous arrival.

Early-synchronous arrival may arise when a favorable $E_W E_R$ (e.g., mid-latitude conditions) relaxes the costs of early arrival sufficiently to induce early passage of most

individuals and E_B conditions also align favorably. In 2010 and 2015, Wilson's and Orange-crowned warblers exhibited early arrival overall, but the 5 percentile cohort did not realize a disproportionate response, resulting in early-synchronous arrival. The frequency dependence of migratory timing may also underlie early-synchronous arrival (Kokko 1999). Arrival timing is thought to be optimized on the basis of individual-specific costs and benefits, which themselves are a function of individual condition and the arrival timing of other males in the population (Møller 1994a, Kokko 1999). Thus, when spring conditions are ameliorated and risk is reduced to a certain degree, average and lower quality males may anticipate the early arrival of competing males, possibly through assessment along the migration route, triggering them to advance their arrival beyond their particular 'cost-minimizing date' (Kokko 1999) or optimal migratory timing, leading to early-synchronous arrival.

Because we lack data on individuals, our understanding of inter-individual variation in phenotypic plasticity in these populations is limited and further complicated by multiscale environmental interactions, the role of stochastic influences (e.g., wind patterns), and potential non-linear responses to environmental variation. However, the fact that we observed interannual changes in the mean-variance relationship including instances of early-synchronous and early-asynchronous arrival suggests the presence of an individual by environment interaction ($I \times E_W E_R \times E_B$), or inter-individual variation in phenotypic plasticity (Nussey et al. 2007). That is, in response to environmental variation, some males may make adjustments from their average arrival timing that are disproportionate to those made by other males. The shape of the arrival distribution may then depend on which individuals (e.g., high or average quality) make these adjustments and in which environment(s) they are made, $E_W E_R$ and/or E_B . At a minimum, the observed pattern suggests a population-level capacity in these species to adjust their arrival timing to large variation in spring conditions. If, hypothetically, the potential for a phenological mismatch exists in these species, then the affected segment of the migrant population could vary considerably on an annual basis given the observed variation in the mean-variance relationship.

In general, the arrival variances of short-distance migrants were not larger than those of Neotropical-Nearctic migrants. This was in contrast to studies conducted at North American mid-latitudes showing larger passage variances for short-distance migrants compared to Neotropical-Nearctic migrants (Mills 2005, Van Buskirk et al. 2009, La Sorte et al. 2013), potentially indicating that interactions between high and mid-latitude environments may alter the

shape of arrival distributions (Møller 2008). However, the arrival distributions of short-distance migrants were also individualistic. Several short-distance migrants showed pronounced variance heterogeneity across time or synchronous-asynchronous fluctuation. In contrast, a subset of short-distance migrants showed weak variance heterogeneity and relatively compressed arrival distributions. The latter pattern could be indicative of limited inter-individual variation in plasticity that would synchronize arrival (Kokko 1999). However, many other factors likely underlie interspecific variation in the behavior of the arrival variance including; the intensity of competition for territories (Kokko 1999, Jonzén et al. 2007), the breadth of a species' foraging niche, the temporal variance of resource availability (Jonzén et al. 2007), variation between migration routes in spatio-temporal patterns of vegetation phenology (La Sorte et al. 2013), the distance of the migratory journey, and species-specific flight strategies including the degree of selectivity for favorable winds in timing migration flights (Karlsson et al. 2011, Nilsson et al. 2014).

Fox Sparrow, a short-distance migrant, was unique in that its arrival distribution became more synchronized over time. This pattern coincided with a 250% increase in its abundance within the study area (Schmidt et al. 2013) and dramatic expansion of its elevational distribution (Mizel et al. 2016). Synchronization of its arrival phenology could have been driven by density-dependent intensification of competition for territories (Kokko 1999) although other explanations are possible. This unique pattern emphasizes the importance of considering other factors, such as changes in population size, when assessing variation in phenology to avoid possibly erroneous conclusions (Tryjanowski and Sparks 2001, Miller-Rushing et al. 2008).

In contrast to the rest of the species that we considered, Arctic Warbler, a Palearctic long-distance migrant, showed little plasticity in arrival timing. The entire local population arrived within a few days of June 6 each year, thereby circumventing variation in spring onset entirely but creating a highly compressed breeding season. Such inflexibility in their phenology would theoretically make them susceptible to trophic mismatches. However, the degree of specialization in their diet and the temporal breadth of peak prey availability are unknown in our study area, limiting our ability to make predictions about the potential for a phenological mismatch.

With the exception of Arctic Warbler, the arrival phenologies of the subarctic migrants that we considered appear to be relatively flexible. However, they were subject to synchronous-asynchronous fluctuation suggesting that arrival variances may respond strongly to weakening of

the north-south temperature gradient. We found that extremes in local spring temperatures have the potential to synchronize arrival across the bird community (as in the late spring of 2013) and to induce substantial advances in arrival among both long- and short-distance migrants (as in the early spring of 1995). Although the ultimate effects of climate warming on bird populations are unknown, our findings suggest that some Neotropical migrants breeding in the subarctic may have greater capacity for plastic arrival timing than was previously expected.

2.6 Acknowledgments

We thank J. Bouton, T. Koronkiewicz, J. Mason, E. Miller, P. Payton, S. Hoover-Paton, S. Springer, A. Wildman, and C. Witt (Alaska Bird Observatory) and M. Paulson, J. Reppert, and K. Bartecchi Rozell (NPS) for conducting surveys. We also wish to thank G. Breed, A. Powell, and two anonymous reviewers for valuable comments on an earlier version of this manuscript. Funding for this work was provided through the U.S. National Park Service Inventory and Monitoring Program, the Central Alaska and Arctic Inventory and Monitoring Networks, and Denali National Park and Preserve. Any reference to trade names or commercial products are for descriptive purposes only and do not imply endorsement by the U.S. government and the research conducted in this study is in compliance with its current laws.

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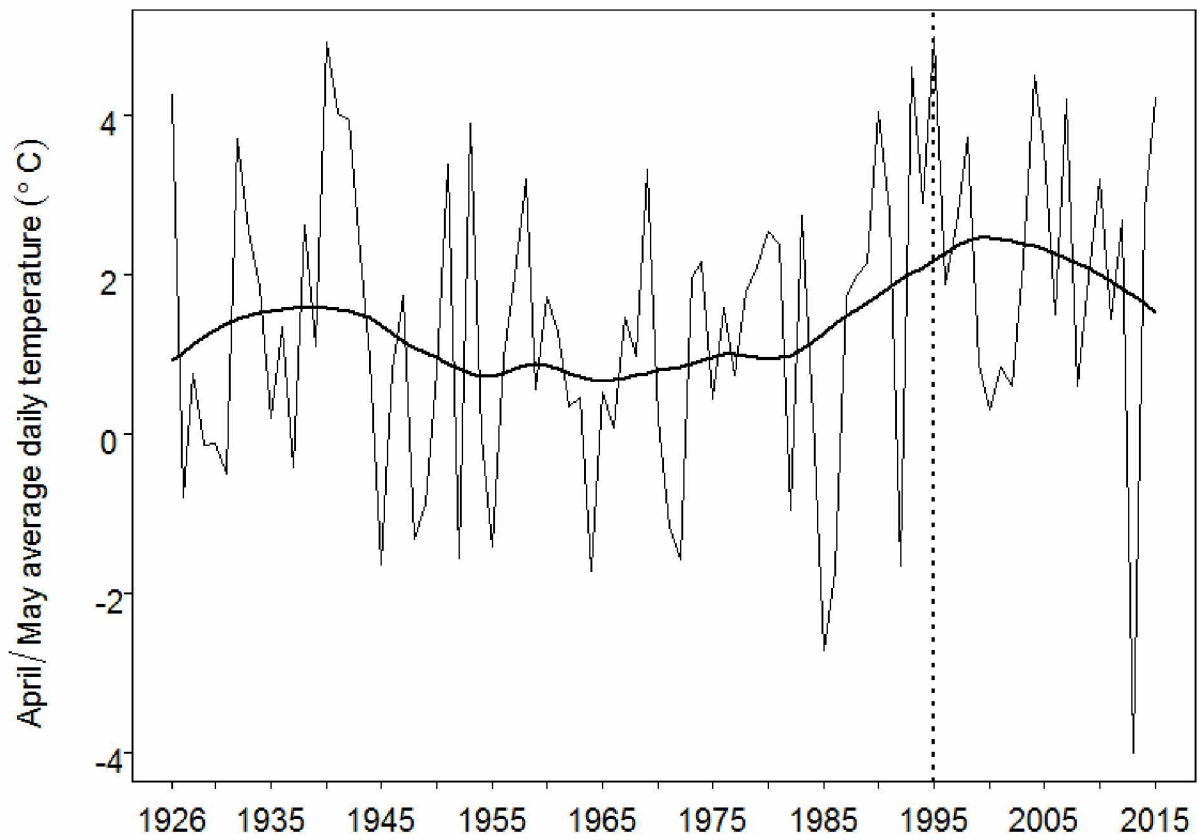


Figure 2.1. Average April-May temperature (degrees C) from a weather station at Denali National Park Headquarters, 1926-2015. The fitted (loess) curve is shown as a solid line. The dotted vertical line indicates the first year of our study.

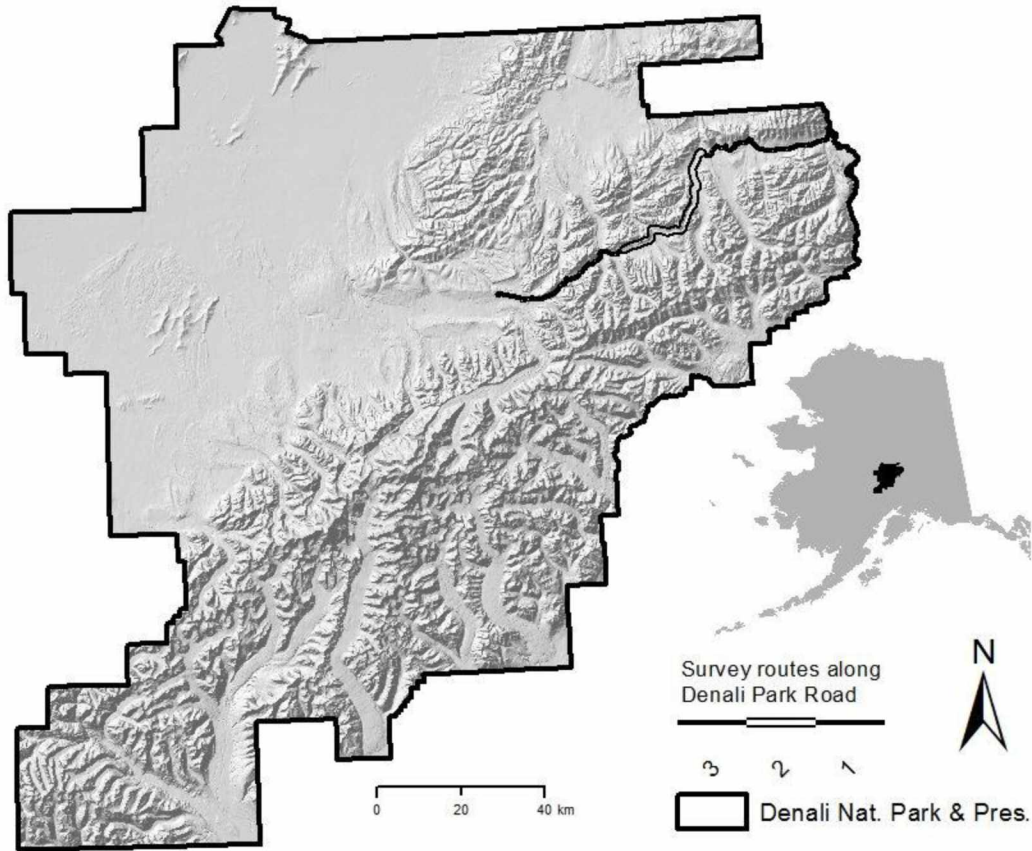


Figure 2.2. Survey routes 1-3 along the park road in Denali National Park and Preserve (Denali), Alaska (modified from Mizel et al. 2016).

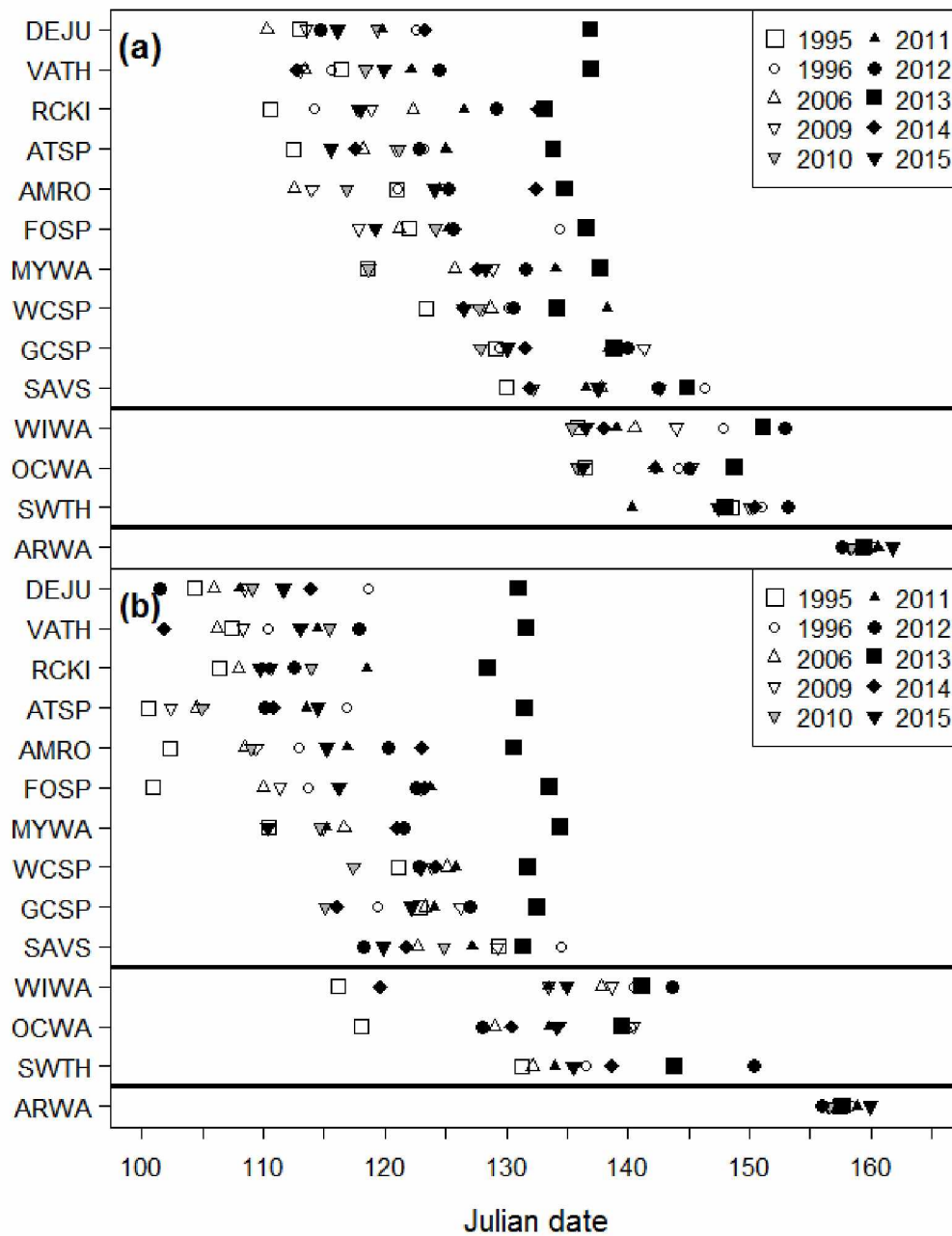


Figure 2.3. Year-specific, posterior means for the Julian date on which a) 50% and b) 5% of occupied sites had shown an arrival event. Thick black lines separate short-distance migrants (top), Neotropical-Nearctic migrants (middle), and a Palearctic migrant (bottom). Within migration groups, species were ordered according to their average arrival date. The symbols for 1995 (open squares) and 2013 (filled squares) were enlarged for emphasis. See Appendix 2.1 for species names and codes.

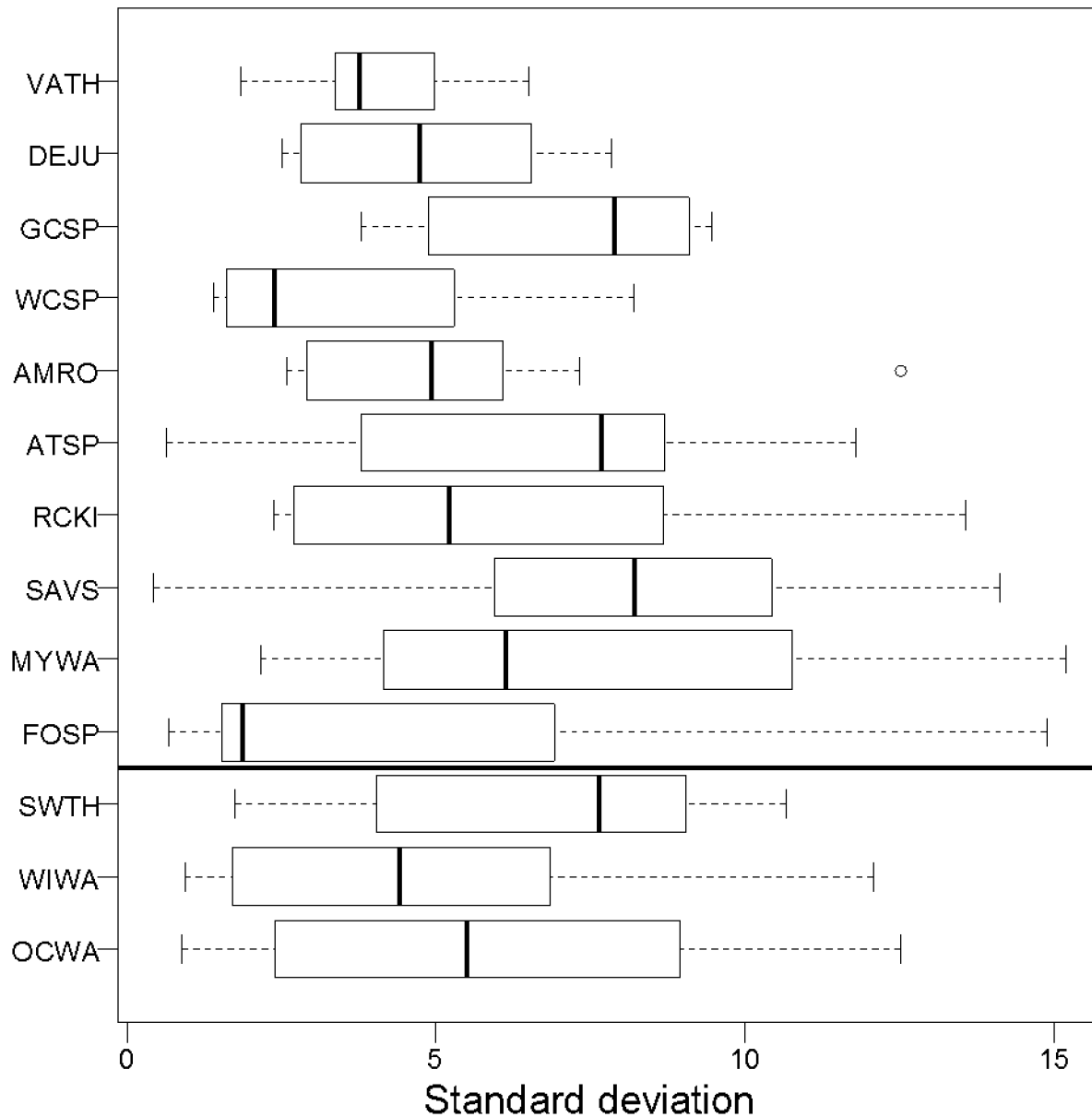


Figure 2.4. Boxplot of year-specific standard deviations for migrants breeding in Denali National Park, Alaska (1995-2015). The thick black line separates short-distance from long-distance migrants (bottom). Within migration groups, species were ordered according to the standard deviation of the year-specific standard deviations. Arctic Warbler is not shown because of a lack of variability in arrival dates.

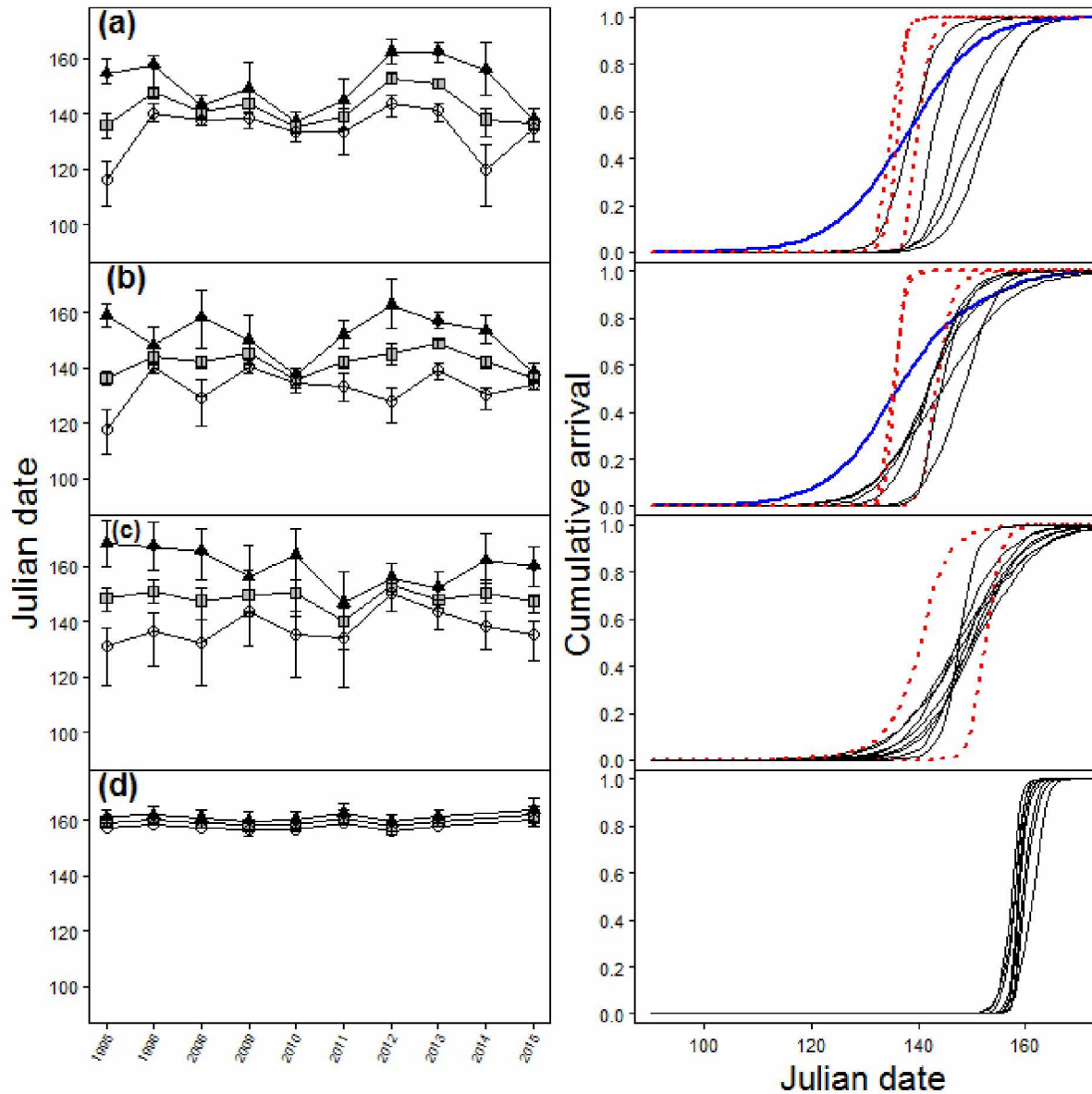


Figure 2.5. Arrival distributions of long-distance migrants in Denali National Park, Alaska (1995-2015). Only years in which sampling occurred and arrival was estimable are shown. Right panels show cumulative arrival curves and left panels show species-specific posterior means for the Julian dates in which 5% (open circles), 50% (gray squares), and 95% of occupied sites had shown an arrival event. Bayesian 95% credible intervals are also shown. Species include: a) Wilson’s Warbler; b) Orange-crowned Warbler; c) Swainson’s Thrush; and d) Arctic Warbler. We considered arrival to be synchronous (dashed red lines) if the ratio of the standard deviation of that year to the average standard deviation was <0.5 . Arrival was considered asynchronous (blue lines) if this ratio was >2.0 .

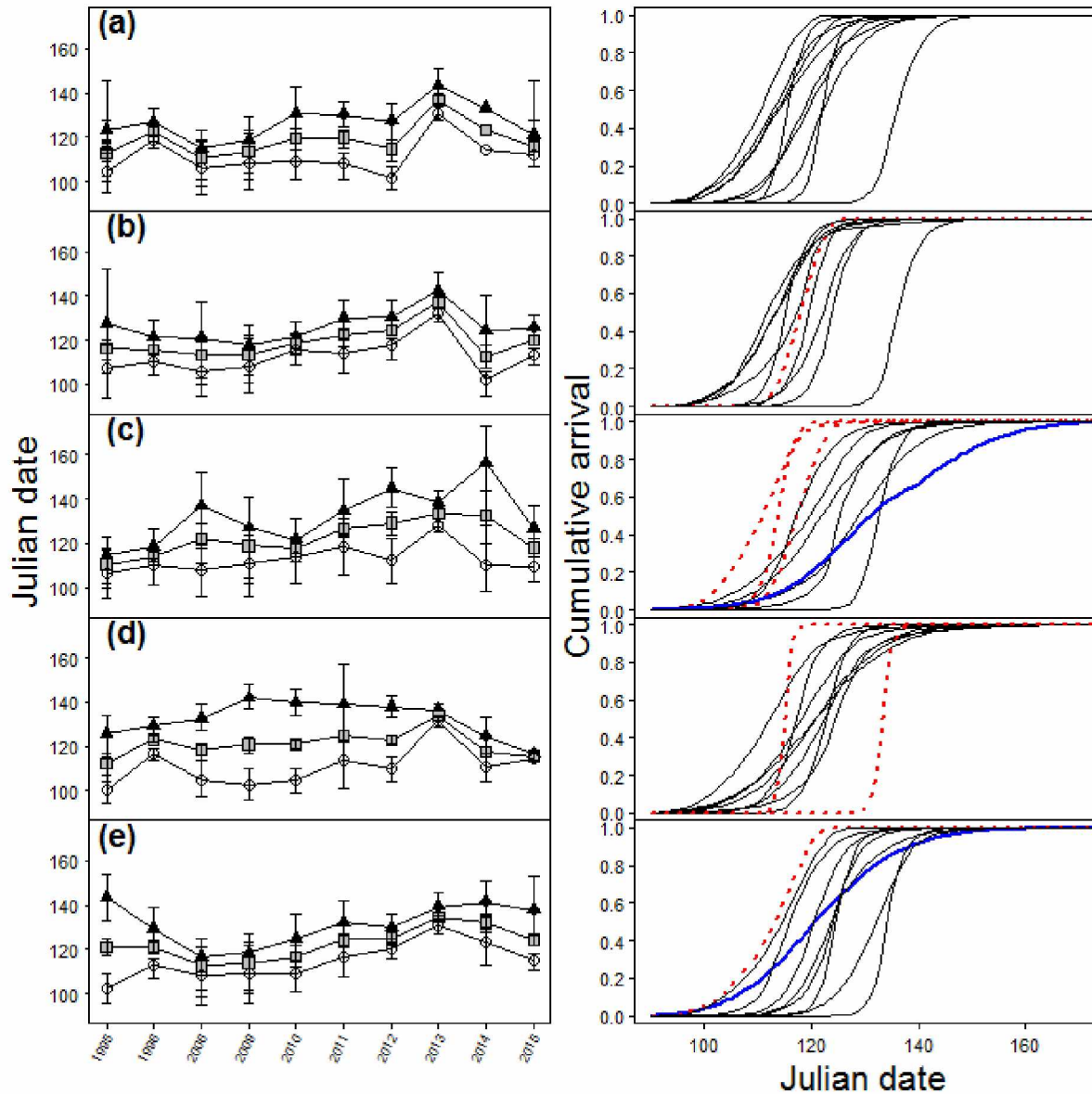


Figure 2.6. Arrival distributions of short-distance migrants in Denali National Park, Alaska (1995-2015). Only years in which sampling occurred and arrival was estimable are shown. Right panels show cumulative arrival curves and left panels show species-specific posterior means for the Julian dates in which 5% (open circles), 50% (gray squares), and 95% of occupied sites had shown an arrival event. Bayesian 95% credible intervals are also shown. Species include: a) Dark-eyed Junco; b) Varied Thrush; c) Ruby-crowned Kinglet; d) American Tree Sparrow; and e) American Robin. We considered arrival to be synchronous (dashed red lines) if the ratio of the standard deviation of that year to the average standard deviation was <0.5 . Arrival was considered asynchronous (blue lines) if this ratio was >2.0 .

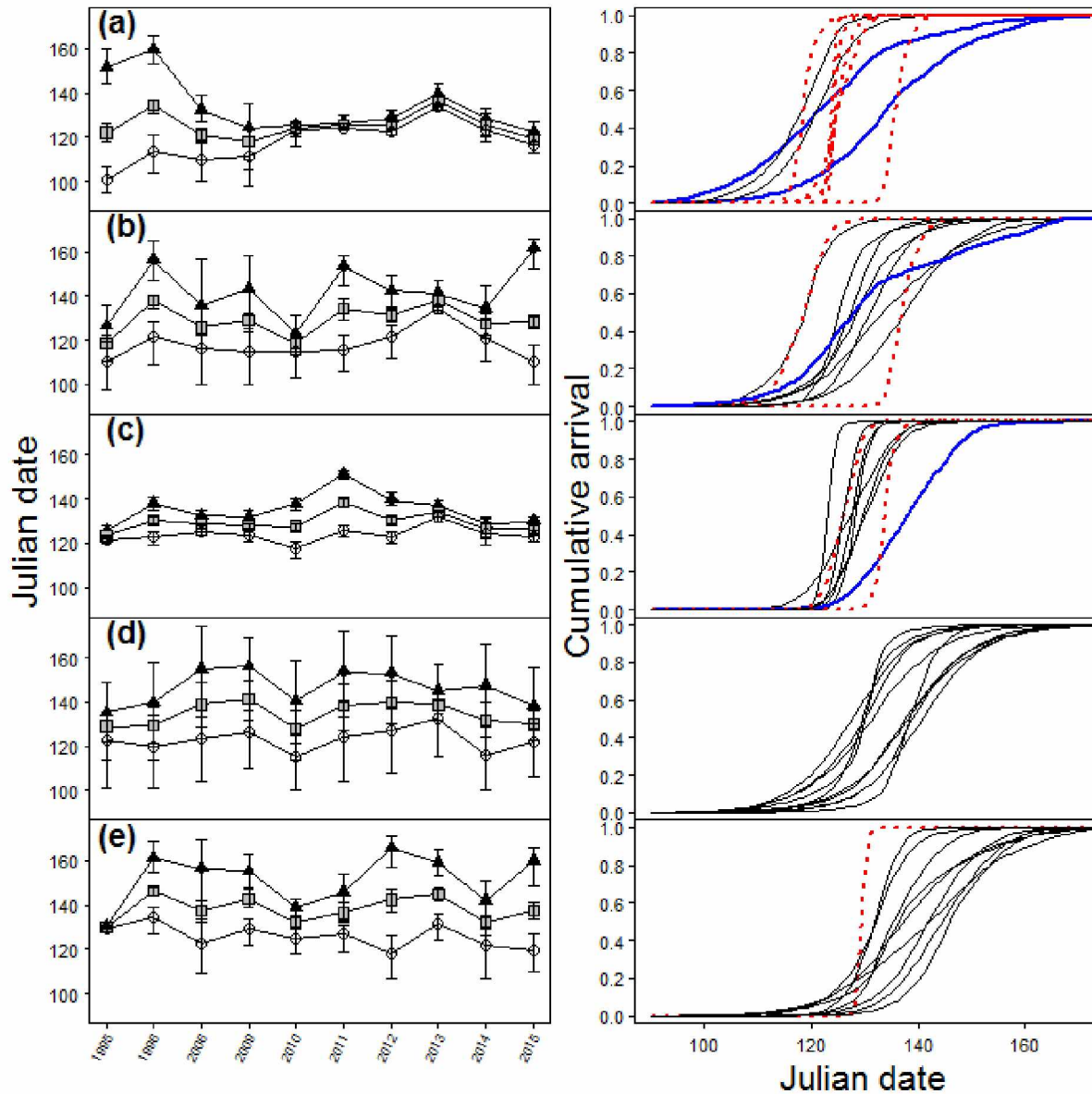
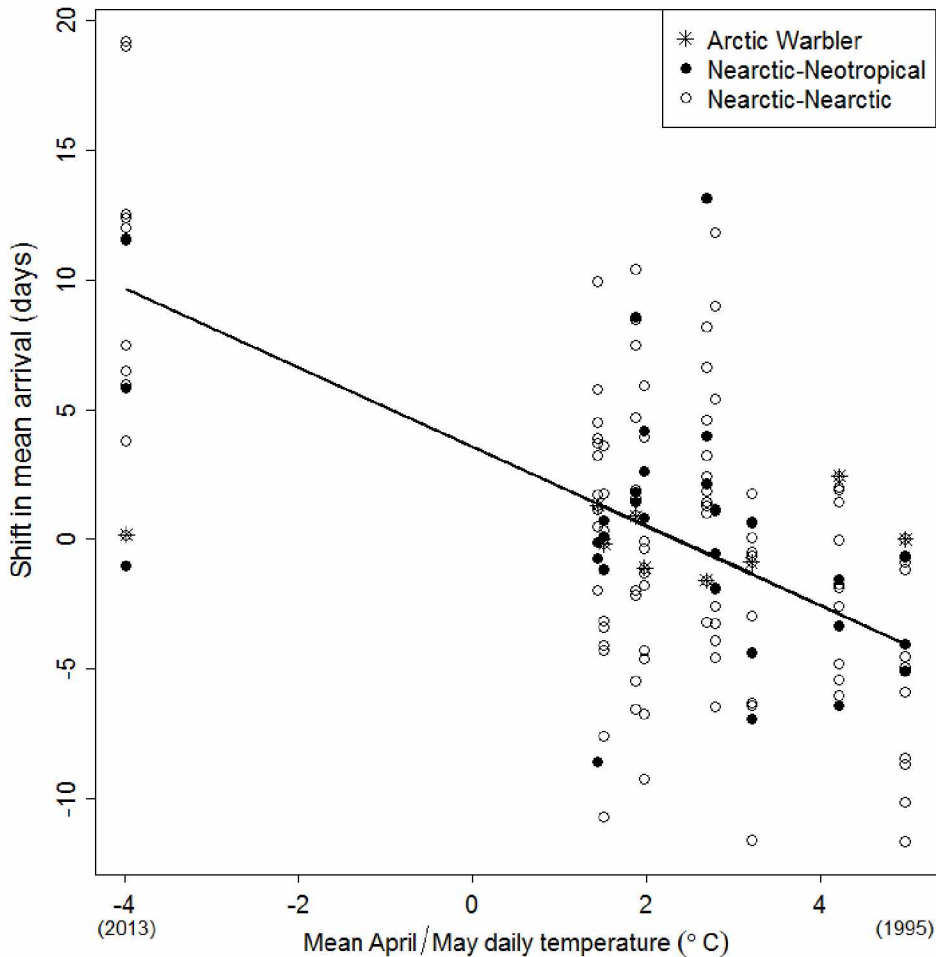


Figure 2.7. Arrival distributions of short-distance migrants in Denali National Park, Alaska (1995-2015). Only years in which sampling occurred and arrival was estimable are shown. Right panels show cumulative arrival curves and left panels show species-specific posterior means for the Julian dates in which 5% (open circles), 50% (gray squares), and 95% of occupied sites had shown an arrival event. Bayesian 95% credible intervals are also shown. Species include: a) Fox Sparrow; b) Yellow-rumped (Myrtle) Warbler; c) White-crowned Sparrow; d) Golden-crowned Sparrow; and e) Savannah Sparrow. We considered arrival to be synchronous (dashed red lines) if the ratio of the standard deviation of that year to the average standard deviation was <0.5 . Arrival was considered asynchronous (blue lines) if this ratio was >2.0 .

Appendix 2.1. Passerine species considered in analyses of arrival timing in Denali National Park, Alaska from 1995-2015.

Species	AOU code	Migration group
Dark-eyed Junco (<i>Junco hyemalis</i>)	DEJU	Nearctic-Nearctic
Varied Thrush (<i>Ixoreus naevius</i>)	VATH	Nearctic-Nearctic
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	RCKI	Nearctic-Nearctic
American Tree Sparrow (<i>Spizella arborea</i>)	ATSP	Nearctic-Nearctic
American Robin (<i>Ixoreus naevius</i>)	AMRO	Nearctic-Nearctic
Fox Sparrow (<i>Passerella iliaca</i>)	FOSP	Nearctic-Nearctic
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	WCSP	Nearctic-Nearctic
Yellow-rumped (Myrtle) Warbler (<i>Setophaga coronata coronate</i>)	MYWA	Nearctic-Nearctic
Golden-crowned Sparrow (<i>Zonotrichia atricapilla</i>)	GCSP	Nearctic-Nearctic
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	SAVS	Nearctic-Nearctic
Wilson's Warbler (<i>Wilsonia pusilla</i>)	WIWA	Nearctic-Neotropical
Orange-crowned Warbler (<i>Oreothlypis celata</i>)	OCWA	Nearctic-Neotropical
Swainson's Thrush (<i>Catharus ustulatus</i>)	SWTH	Nearctic-Neotropical
Arctic Warbler (<i>Phylloscopus borealis</i>)	ARWA	Paleartic

Appendix 2.2. Shift in annual mean arrival for species *i* in year *j* relative to the average April-May temperature (degrees C) from a weather station at Denali National Park Headquarters. The y-axis corresponds to the mean arrival date for species *i* in year *j* minus the multi-year median for species *j*. Positive values indicate a delay and negative values indicate an advance. We conducted a post-hoc linear regression of the annual arrival shift as a function of the average April-May temperature. We combined Nearctic-Nearctic and Neotropical-Nearctic species in this regression and excluded Arctic Warbler, a Palearctic migrant. The fitted line indicates the significant relationship between annual arrival shift and the average April-May temperature ($R^2 = 0.35$, $P < 0.0001$). The following years are indicated: 1995 (the warmest April-May temperature on record for Denali from 1926-2015) and 2013 (the coldest).



CHAPTER 3

A MULTI-STATE, TIME-REMOVAL MODEL FOR INCREASING EFFICIENCY IN SURVEYS OF CLIFF-NESTING RAPTORS¹

3.1 Abstract

Surveys of cliff-nesting raptors present considerable challenges due to their sparse distribution across remote landscapes and the multiple occupancy states (e.g., unoccupied, occupancy without breeding, and breeding occupancy) through which we observe their nesting territory dynamics. The standard approach in nesting territory surveys is to allocate an intensive level of effort that is assumed to ensure that the occupancy state of each territory is known with certainty. However, allocating effort in this manner is inefficient, particularly at landscape scales, constraining our capacity for effective management of these species. To increase survey efficiency and expand the spatial inference of these studies, we develop two versions of a multi-state, time-removal model, one for long-term monitoring studies and another for population inventories or single-season surveys in which there is no prior knowledge of nest locations. We focus our development of these methods in the context of a combined aerial and ground-based survey approach which permits efficient surveying at landscape scales. However, the approach is also applicable to designs restricted to ground surveys. For long-term monitoring of species with alternative nests, we formulate 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, all parameters showed low to moderate relative bias (≤ 0.07) for a survey duration of 90 minutes. We apply our approach to a long-term study of golden eagles (*Aquila chrysaetos*) in Alaska and demonstrate

¹ Mizel, J.D., C.L. McIntyre, S.B. Lewis, M.S. Lindberg, and J.H. Schmidt. (*under review*). A Multi-state, time-removal model for increasing efficiency in surveys of cliff-nesting raptors. *Journal of Wildlife Management*.

that the maximum effort spent on any nesting territory could be reduced by up to almost 90% of that recommended by standard protocols.

3.2 Introduction

Landscape-scale monitoring is necessary for effective conservation of wildlife species. However, sampling at large spatial scales for sparsely distributed species 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 (i.e., ecological and observation processes) and the application of sampling methods that attempt to maximize detection (Thompson 2004, Royle and Dorazio 2008, Nichols et al. 2009). When these populations are composed 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 due to the large space usage by 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 (e.g., Hardey et al. 2006). For example, the U.S. Fish and Wildlife Service (USFWS) recommends ≥ 2 , 4-hour ground observation occasions 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.

Consequently, most studies have focused on intensively monitoring 30-100 nesting territories within a single survey area (e.g., Steenhof et al. 1997, Pokrovsky et al. 2014). However, the spatial scale of inference from these studies is limited, leaving large gaps in our understanding of cliff-nesting raptor population dynamics and distribution at the landscape-scale. The development of cost-effective methods that would permit sampling at larger spatial scales has received little study (but see 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.

3.2.1 Breeding ecology characteristics that influence how we observe raptor population dynamics

On breeding grounds, raptor populations are generally composed of non-territorial individuals (i.e., floaters), breeders, and territorial, non-breeders (Newton 2003). Studies of nesting territory occupancy typically make inference to the territorial population corresponding to the latter two groups of individuals. The process by which we observe dynamics in the territorial population is complicated by several aspects of raptor breeding ecology. For example, prey availability and/or weather may limit the proportion of the population attempting breeding in a given year (Newton 1979, Steenhof et al. 1997) (Fig. 1, box 3). Numerical reproductive responses have been observed in a number of cliff-nesting raptor species including gyrfalcon (*Falco rusticolus*) (e.g., Nielsen 1999), rough-legged hawk (*Buteo lagopus*) (e.g., Pokrovsky et al. 2014), and golden eagle (e.g., Steenhof et al. 1997, McIntyre and Schmidt 2012). In a 23-year study of the golden eagle population in Denali National Park, Alaska (hereafter, Denali), breeding rates were highly variable, ranging from 0.14-0.88, and were strongly related to cyclical fluctuation in prey availability (McIntyre and Schmidt 2012). In contrast, the composite territorial occupancy (occupancy with or without breeding) has remained consistently high (range = 0.81-0.93) (McIntyre and Schmidt 2012). 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 composed of territorial individuals that are not breeding (i.e., occupancy without breeding) are needed in order to make reliable inferences about population dynamics.

There have been relatively few studies of cliff-nesting raptor breeding dynamics that account for state uncertainty, and those that have were generally done in a single-state framework under the assumption that detectability does not differ between states (Booms et al. 2010; but see Martin et al. 2009). Given that a nest contained eggs at the time of the survey and is surveyed (i.e., its contents are observed), the probability of detecting occupancy with breeding is ~ 1 . In contrast, territorial individuals that are not breeding may move in and out of proximity to the nesting territory (i.e., spatial temporary emigration), which leads to the probability of detecting occupancy without breeding being < 1 . Consequently, in the framework of a single state occupancy model in which a composite detection probability, p , is estimated, a decrease in the nesting rate could lead to negative bias in occupancy; i.e., p could be confounded with changes

in the nesting rate. This confounding would be exacerbated by fluctuations in drivers such as prey abundance or weather conditions, resulting in a subset of years in which breeding is either pervasive or extremely uncommon.

The tendency of longer-lived, 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 maintained nesting territories composed of an average of 1.6 nests (range = 1–4) (Beardsell et al. 2016). Golden eagle nesting territories were composed of 6.9 nests (range = 1–18) in southwestern Idaho (Kochert and Steenhof 2012) and an average of ~3 nests (range = 1–9) in Denali. 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. However, for species in which nesting territories may be composed of 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.

3.2.2 A multi-state, time-removal model for expanding spatial inference

3.2.2.1 Long-term monitoring using aerial and ground-based surveys

Herein, we develop a multi-state, time-removal model for long-term monitoring studies of cliff-nesting raptors that permits increased survey efficiency and, consequently, larger spatial inference (i.e., monitoring more territories). We focus our development of these methods in the context of a combined aerial and ground-based survey approach which permits efficient surveying at landscape scales. We investigate the performance of this model through simulation and a case study involving long-term monitoring of a golden eagle nesting population. The complex breeding ecology of golden eagles, including the potential for extreme fluctuation in nesting rate and use of alternative nests, presents a suitable basis for generalizing inference methods to other cliff-nesting raptor species. While there are numerous differences in the breeding ecology of these species (e.g., nesting substrates), we expect that the methods described here will have strong relevance to those species in which a proportion of the population is composed of territorial individuals that do not breed some in some years.

3.2.2.2 Long-term monitoring with ground-based surveys

While our focus is on applying the aerial-ground survey protocol at large spatial scales, the development of these methods can be viewed as part of a broader, more efficient framework that permits larger spatial inference for a variety of designs. Towards this objective, we provide an extension of our multi-state, time-removal model to studies restricted to ground surveys. 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 (mean = 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.

3.2.2.3 Population inventories with aerial and ground-based surveys

Long-term studies are necessary to understand the population dynamics of cliff-nesting raptors. However, such efforts are often not feasible over the vast, roadless areas that comprise much of these species' ranges. Consequently, single-season (or intermittent) surveys (i.e., population inventories) may be necessary to fill gaps in our knowledge of the distribution of these species. In addition, as lands are 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. These assessments will often be restricted to single-season surveys of landscapes for which little or no prior knowledge of nest locations exists. Herein, we develop a modified version of the aerial-ground survey methods and multi-state, time-removal model used for long-term monitoring that can be used to inventory populations over landscapes in which the number of nesting territories is unknown. Through simulation, we investigate the sampling design conditions (i.e., sample size and ground survey duration) under which the inventory model is applicable.

3.3 Methods

3.3.1 Long-term monitoring with aerial and ground-based surveys

3.3.1.1 Survey methods

We based our development of inference methods on a long-term monitoring study of golden eagles in Denali National Park and Preserve, Alaska (hereafter, Denali). The study area lies

within the northern foothills of the Alaska Range primarily 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 et al. 2006).

We monitored 104 golden eagle territories in Denali annually from 2007-2016 using a combination of aerial and ground-based surveys. The locations of all nests within each territory were assumed to be known although occasionally newly constructed and previously unobserved nests were located. Via helicopter, an observer (C. McIntyre), surveyed nests within all nesting territories in late April or early May and recorded the presence or absence of an incubating eagle, eggs, or eggshells. The observer also made observations that, in the absence of egg laying evidence, were considered indicative of occupancy without breeding including: a recently refurbished nest, a mated pair of eagles, or some other territorial behavior. If no evidence of occupancy with or without breeding was detected, the helicopter landed at a vantage point and the observer 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. It generally lasted up to four hours or until a behavior indicative of occupancy was observed. A subset of surveys was also conducted entirely on foot and occasionally included multiple observers.

Because the Denali monitoring program is focused on inference at the park level and not larger spatial scales, an intensive level of effort is used to ensure that the occupancy state is known with certainty. Ground surveys occasionally lasted >4 hours and sometimes additional aerial and ground visits were made. However, our primary objective was to expand spatial inference through a more efficient application of this protocol; i.e., reduce the maximum 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 a single aerial visit to nesting territories and censored (post-hoc) all ground surveys at 2 hours in order 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 two primary prey species, snowshoe hare (*Lepus americanus*) and willow ptarmigan (*Lagopus lagopus*) based on counts of made during routine field work from mid-April through late June (see McIntyre and Adams 1999 for further details).

3.3.1.2 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 one of three mutually exclusive states: 1) unoccupied; 2) occupied without breeding; and 3) occupied with breeding (Fig. 1). We specified the observations $y_{i,t}$ for territory $i = 1, 2, \dots, I$ and year $t = 1, 2, \dots, T$ as multinomial random variables conditional on the true states $z_{i,t}$ with cell probabilities $\pi_{i,t,k}$ for cell $k = 1, 2, \dots, K$:

$$y_{i,t} \sim \text{Multinomial}(\pi_{i,t,k} [z_{i,t}, \dots], 1) \quad (\text{Eq. 3.1})$$

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 (MacKenzie et al. 2009). The columns corresponded to the cell-specific probabilities of observing state l (i.e., $k^{[l]}$) where the first two corresponded to the aerial survey;

$$1 \begin{matrix} 1^{[3]} & 2^{[2]} \\ \left[\begin{array}{cc} 0 & 0 \\ 0 & p^{NB,A} \\ S_{i,t} & (1 - S_{i,t}) * p^{NB,A} \end{array} \right] \end{matrix} \quad (\text{Eq. 3.2})$$

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

$$1 \begin{matrix} k^{[2]} \\ \left[\begin{array}{c} 0 \\ (1 - p^{NB,A}) * p^{NB,G} * (1 - p^{NB,G})^{k-3} \\ (1 - S_{i,t}) * (1 - p^{NB,A}) * p^{NB,G} * (1 - p^{NB,G})^{k-3} \end{array} \right] \end{matrix}$$

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

$$1 \begin{matrix} K^{[1]} \\ \left[\begin{array}{c} 1 \\ (1 - p^{NB,A}) * (1 - p^{NB,G})^{K-1} \\ (1 - S_{i,t}) * (1 - p^{NB,A}) * (1 - p^{NB,G})^{K-1} \end{array} \right] \end{matrix}$$

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

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 one year and then find and observe the contents of the nest in a subsequent year, in which case, the nest is recorded as surveyed only in the latter visit while the territory is surveyed in both. 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 composed of alternative nests, the probability of detecting breeding 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 while also potentially confounding temporal effects on occupancy. While 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 Poisson process model for the expected frequency of use $\lambda_{g,i}$ for nest $g = 1, 2, \dots, G_i$ in territory i :

$$\log(\lambda_{g,i}) = \delta_1 * x_{g,i} \quad (\text{Eq. 3.3})$$

where G_i is the known number of nests in territory i , $x_{g,i}$ is a covariate for each nest (e.g., nest condition, distance to some disturbance, etc.), 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 (Royle and Converse 2014); i.e., δ_1 is the effect on nest use frequency conditional on the territory existing in the breeding state. 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 latent multinomial random variable:

$$nest_{i,t} \sim Multinomial(\pi_{1,i}, \pi_{2,i}, \dots, \pi_{G_i,i}, \mathbf{1}) \quad (\text{Eq. 3.4})$$

with cell probabilities $\pi_{g,i}$ conditional on the territory-specific sum of nest use intensities:

$$\pi_{g,i} = \frac{\lambda_{g,i}}{\sum_{g=1}^{G_i} \lambda_{g,i}} \quad (\text{Eq. 3.5})$$

We specified an indicator variable $w_{g,i,t}$ that is an outcome of the relation of the nest identity 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 (i.e., non-existent) nests to the maximum number of nests known to exist in any territory. In doing so, we describe nest use in each territory as binary and also account for the fact that the number of real nests in a territory G_i :

$$w_{g,i,t} = \begin{cases} 1 & \text{when } nest_{i,t} = g \\ 0 & \text{when } nest_{i,t} \neq g \end{cases} \quad (\text{Eq. 3.6})$$

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

$$S_{g,i,t}^n = w_{g,i,t} * surveyed_{g,i,t} \quad (\text{Eq. 3.7})$$

Re-use of nests by cliff-nesting raptors is thought to extend over generations or centuries (Newton 1979), with some evidence from radiocarbon-dating guano 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. However, 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, it can be recorded as surveyed, precluding its potential imputation as used for breeding.

Finally, the probability of detecting breeding within the territory is the binary outcome of summing the nest-level exposure variables:

$$p_{i,t}^R = \sum_{g=1}^M p_{g,i,t}^n \quad (\text{Eq. 3.8})$$

The latent true states $z_{i,t}$ 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:

$$z_{i,1} \sim \text{Multin}(\phi_0, \mathbf{1}) \quad (\text{Eq. 3.9})$$

with the probability vector:

$$\phi_0 = [1 - \psi \quad \psi * (1 - R) \quad \psi * R] \quad (\text{Eq. 3.10})$$

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:

$$z_{i,t} | z_{i,t-1} \sim \text{Multin}(\phi_{t-1}[z_{i,t-1}, \dots], \mathbf{1}) \quad (\text{Eq. 3.11})$$

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

$$\phi_t = \begin{bmatrix} 1 - \psi_{t+1}^{[1]} & \psi_{t+1}^{[1]} * (1 - R_{t+1}^{[1]}) & \psi_{t+1}^{[1]} R_{t+1}^{[1]} \\ 1 - \psi_{t+1}^{[2]} & \psi_{t+1}^{[2]} * (1 - R_{t+1}^{[2]}) & \psi_{t+1}^{[2]} R_{t+1}^{[2]} \\ 1 - \psi_{t+1}^{[3]} & \psi_{t+1}^{[3]} * (1 - R_{t+1}^{[3]}) & \psi_{t+1}^{[3]} R_{t+1}^{[3]} \end{bmatrix} \quad (\text{Eq. 3.12})$$

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 . See Appendix 3.1 for a list of estimated parameters in the long-term monitoring model.

3.3.1.3 Case study

In the monitoring case study in Denali, we did not use nest-level data and assumed that all nests had been located in the 20 years prior to the period we used to illustrate our model. Thus, we applied the model described above under the assumption $S_{i,t} = 1$ 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 three surveys which 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. Because a subset of surveys was conducted entirely on foot and, consequently, did not include an aerial survey, it was necessary to specify two different detection matrices.

Previous work in Denali indicated that both hare and ptarmigan abundance are important drivers 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):

$$\text{logit}(\psi_{t+1}^{[m]}) = \alpha_0^{[m]} + \alpha_1^{[m]} * \text{year}_{t+1} \quad (\text{Eq. 3.13})$$

$$\text{logit}(R_{t+1}^{[m]}) = \beta_0^{[m]} + \beta_1^{[m]} * \text{prey}_{t+1} \quad (\text{Eq. 3.14})$$

where hares_{t+1} and ptarmigan_{t+1} were indices of the annual abundance of adult hares and ptarmigan. In other populations, appropriate drivers of reproductive dynamics, such as winter weather conditions (Steenhof et al. 1997), could be substituted for the prey indices we used here.

3.3.2 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 (see JAGS code in Appendix 3.5).

3.3.3 Population inventories with aerial and ground-based surveys

3.3.3.1 Survey methods

Population inventories differ from long-term monitoring designs in terms of three key considerations (Fig. 1, boxes 2a and 4a):

- 1) Knowledge of nest locations is incomplete;
- 2) Nests are most efficiently located using area search methods, unconstrained by any predetermined search path, making incomplete study area coverage highly likely;

- 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 observer crew conducts an initial area search of a series of grid-blocks (e.g., 17 km x 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 minutes). 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 two independent surveys was 0.98, indicating that two area search surveys are sufficient for inventorying a golden eagle population. However, additional pilot studies would likely be needed to determine the optimal number of surveys necessary for other species that do not restrict nesting to stick nests (e.g., gyrfalcon).

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 at that particular level of clustering 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. However, for species in which alternative nests

may be located on multiple cliff faces, 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 positive 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 composed of 250 x 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 furthest allowed distance from any two nests in a cluster). While 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.

3.3.3.2 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 we have 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 one of four mutually exclusive states: 1) nest cluster absent; 2) nest cluster present but unoccupied; 3) nest cluster present and occupied without breeding; and 4) nest cluster present and occupied with breeding. 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. We included both of these parameters because we expected that nest cluster detection could differ due to the availability of stronger cues around occupied nest clusters (e.g., fresh whitewash, the presence of birds within the nesting territory, refurbishment materials, etc.). 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 that 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 one nest in which eggs were laid. However, these territories 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. In Appendix B, we provide further details of model structure and of a simulation study used to assess model performance at different survey durations and sample sizes.

3.3.4 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 Team 2015). 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, summaries of the posterior distribution were calculated from two Markov chains run for 85,000 iterations with a 10,000 iteration burn-in and thinning every 3 draws. For the simulation study, summaries of the posterior distribution were calculated from one 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 (mean = 0, SD = 1) 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). See Appendices 3.4 and 3.5 for data generation and JAGS code from the monitoring and inventory simulation studies.

3.4 Results

3.4.1 Simulation study: long-term monitoring model with aerial and ground-based methods

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 3.3.1). The latter group of effects showed moderate relative bias between 0.06–0.08, likely due to relatively few territories transitioning from the unoccupied state (Table 3.3.1).

3.4.2 Case study: long-term monitoring with aerial and ground-based methods in Denali

In the long-term monitoring case study, ptarmigan and hare abundance strongly affected the probability of breeding, as expected (Table 3.3.2). Consequently, fluctuation in prey availability resulted in highly variable nesting rates ranging from 0.11 (95% CI: 0.06, 0.16) in 2013 to 0.72 (95% CI: 0.68, 0.76) in 2009. However, composite occupancy 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 two 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 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.

3.5 Discussion

We developed a framework for expanding spatial inference in inventory and monitoring studies of cliff-nesting raptor populations based upon a more efficient allocation of effort and the application of a multi-state, time-removal model. While 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 minute ground survey compared to ≥ 2 , 4-hour 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. While standard approaches estimate the probability of breeding in a given year, 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.

Established long-term monitoring programs for cliff-nesting raptors, including the one in Denali, optimize effort over time through the accumulation of knowledge about individual nest locations. In such scenarios, using repeated surveys to estimate the probability of detecting an individual nest would be inefficient. Instead, we developed a model that accommodates incomplete nest surveying based on the fact that nests are often reused over long timescales (Newton 1979, Burnham et al. 2009) and that the probability of detecting breeding is ~ 1 given that a nest contains eggs at the time of the survey and its contents are observed. This approach serves a dual purpose, accounting for imperfect observation of the breeding state and allowing inferences about variation in the frequency of nest use which may be of interest for predicting potential impacts on individual nests.

We extended our multi-method approach to population inventories while also accommodating incomplete knowledge of nest locations. Our 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 (see Appendix 3.2). However, the sample sizes necessary for unbiased estimation of occupancy without breeding may prove challenging for some inventory applications (see Appendix 3.2), primarily due to parsing of this sample size from multiple survey platforms and states. In our 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 and/or the use of an informative prior that reflects our

knowledge about this parameter (McCarthy and Masters 2005). Based on our estimates for golden eagle and an experienced observer, a suitable prior for the logit-scale intercept of the probability of detecting occupancy without breeding during a 10-minute interval of the ground survey would be *Normal*(mean = -1.98 , SD = 0.09), or, less informatively, *Uniform*(0.10, 0.14) on the real scale. For other species, existing monitoring studies could be reanalyzed to derive a suitable informative prior for new inventory surveys.

Interspecific differences in distribution and detectability of nests and the occupancy states will necessitate adjustments of the sampling protocol when applied to species other than golden eagle. For example, Kéry and Royle (2016) assessed occupancy of peregrine falcon breeding cliffs using a continuous-time observation model and found that detection probability approached 1 after ~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 200-1000 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 that by necessity must assume the presence of state uncertainty. Lastly, we reiterate that our approach has the strongest relevance for species and populations in which the breeding component, alone, is not a reliable predictor of the territorial population size.

3.6 Management implications

Existing methods for cliff-nesting raptors are often inefficient and provide limited spatial inference. Consequently, limited trend and distributional data exists for many cliff-nesting raptor species particularly over the vast, remote sections of their ranges. This lack of information constrains our capacity for effective management of these species (Kochert and Steenhof 2002). We expect that 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. However, there exists additional room for increasing the efficiency of these surveys. For example, in population inventory studies, integrating fixed-wing aircraft (roughly a quarter the cost of a helicopter) into the design may greatly reduce costs. We could envision a hybrid approach in which fixed-wing aircraft locate nests in an area search-removal design, followed by a combined aerial-ground survey accomplished via helicopter to assess the occupancy state of the observed nest clusters. Additional studies are needed to assess the effectiveness of using fixed-wing aircraft to determine the occupancy state (but see Booms et al. 2010). We expect that the first step in optimizing these surveys 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.

3.7 Acknowledgments

We thank J. Shook, M. Paulson, P. Owen, J. Bryant, L. Phillips and R. Swisher for conducting surveys. We also wish to thank M. Kéry, R. Steidl, G.A. Breed, and A.N. Powell for valuable comments on drafts of the manuscript. Funding for this work was provided through the U.S. National Park Service's Inventory and Monitoring Program, the U.S. Fish and Wildlife Service, and the U.S. Army and Air Force. Any reference to trade names or commercial products are for descriptive purposes only and do not imply endorsement by the U.S. government and the research conducted in this study is in compliance with its current laws.

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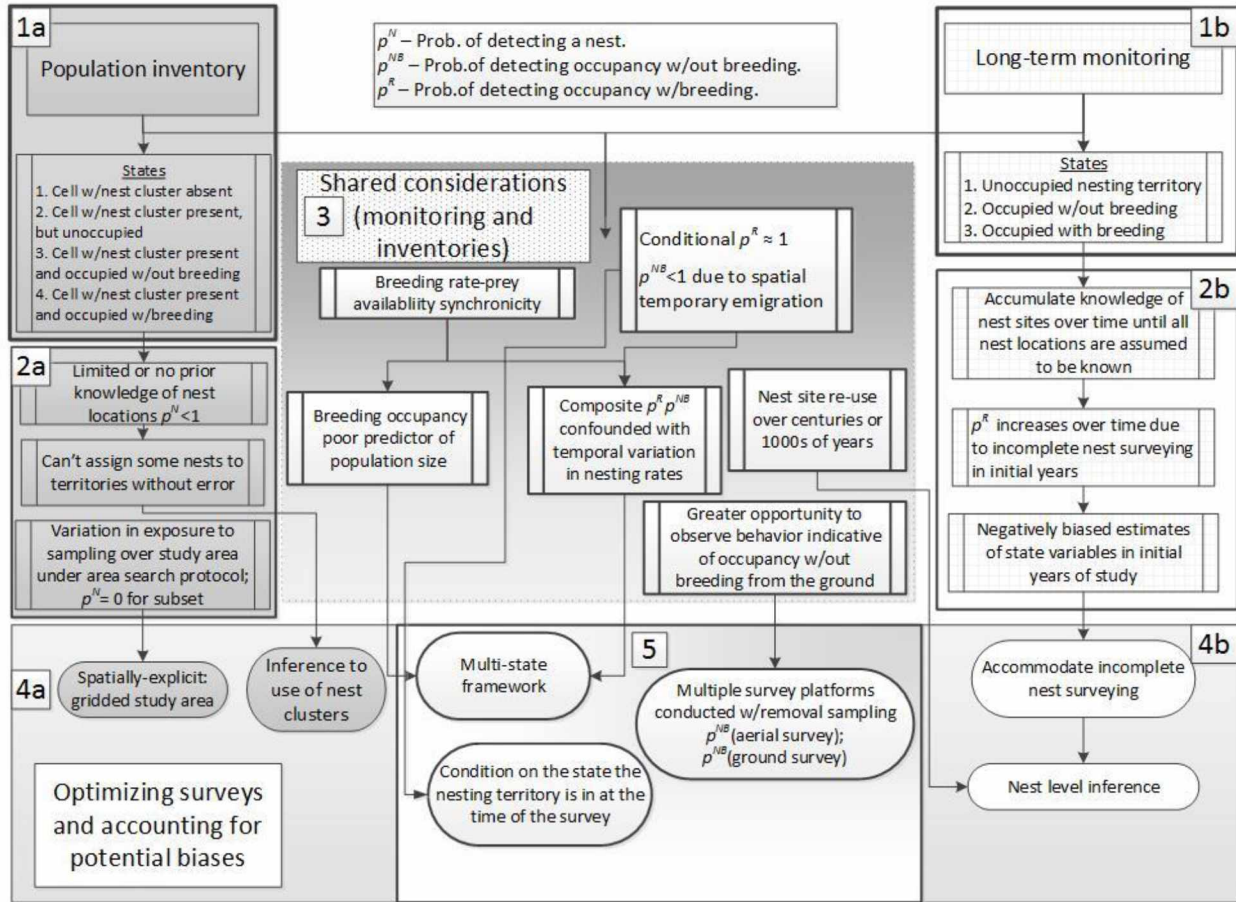


Figure 3.1. Conceptual diagram of inference framework for population inventories and long-term monitoring of cliff-nesting raptors.

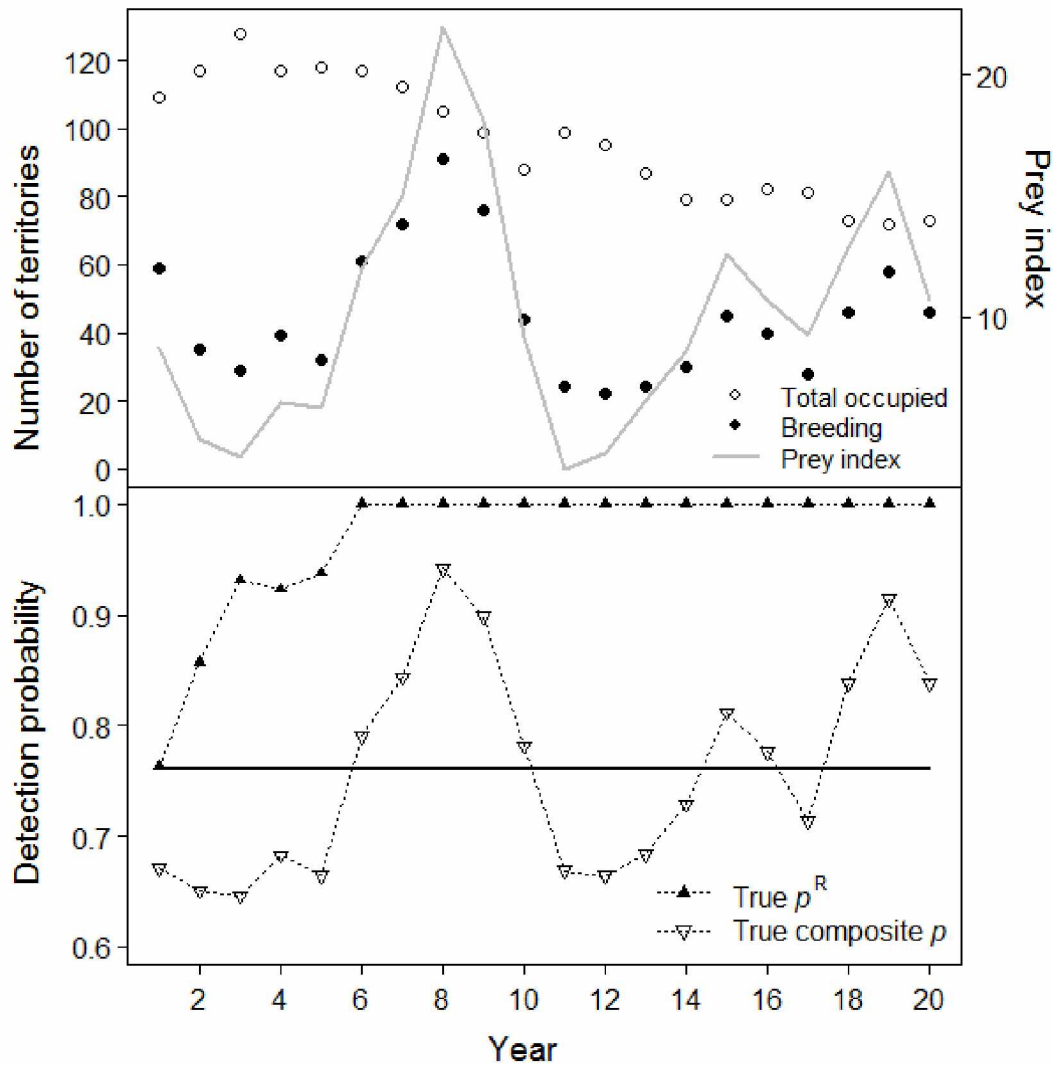


Figure 3.2. Scenario implemented in the simulation study for the long-term monitoring model involving a declining population with a nesting rate that is synchronized with fluctuation in prey abundance (top panel). The bottom panel shows the confounding that would arise under single-state inference between a constant, composite p (the probability of detecting non-breeding or breeding occupancy for the aerial survey; flat 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.

Table 3.1. Estimates from the long-term monitoring simulation study used to assess the performance of the nest-level, multi-state model. The bracketed superscript corresponds to the state in the previous year. Estimates are based on 500 simulations.

Parameter	True value	Mean	RMSE	Bias	CI coverage
$p^{NB,A}$	0.56	0.56	0.06	-0.01	0.93
$p^{NB,G}$	0.12	0.12	0.03	-0.01	0.93
R	0.60	0.57	0.15	-0.05	0.94
ψ	0.70	0.70	0.10	0.00	0.94
$\alpha_0^{[1]}$	0.61	0.65	0.31	0.07	0.93
$\alpha_0^{[2]}$	-0.58	-0.59	0.21	0.02	0.96
$\alpha_0^{[3]}$	0.26	0.25	0.20	-0.04	0.94
$\alpha_1^{[1]}*prey_t$	1.71	1.85	0.39	0.08	0.96
$\alpha_1^{[2]}*prey_t$	0.68	0.69	0.20	0.00	0.95
$\alpha_1^{[3]}*prey_t$	0.61	0.63	0.16	0.02	0.94
$\beta_0^{[1]}$	-0.25	-0.26	0.18	0.04	0.95
$\beta_0^{[2]}$	1.00	1.04	0.24	0.04	0.96
$\beta_0^{[3]}$	1.25	1.29	0.21	0.06	0.94
$\beta_1^{[1]}*year_t$	-0.40	-0.40	0.17	0.00	0.95
$\beta_1^{[2]}*year_t$	-0.40	-0.42	0.27	0.04	0.95
$\beta_1^{[3]}*year_t$	-0.40	-0.41	0.24	0.04	0.95
δ_1	1.00	1.00	0.20	0.00	0.95

Table 3.2. Estimates from long-term monitoring of golden eagles in Denali National Park, Alaska (2007-2016). The bracketed superscript corresponds to the state in the previous year. Bold numbers indicate estimates with 95% credible intervals that do not include 0.

Parameter	Mean	SD	95% CI
$p^{NB,A}$	0.56	0.03	(0.51, 0.61)
$p^{NB,G}$	0.12	0.01	(0.10, 0.14)
R	0.74	0.05	(0.64, 0.83)
ψ	0.89	0.04	(0.81, 0.95)
$\alpha_0^{[1]}$	0.61	0.84	(-0.92, 2.39)
$\alpha_0^{[2]}$	-0.58	0.13	(-0.84, -0.32)
$\alpha_0^{[3]}$	0.26	0.13	(0.01, 0.51)
$\alpha_1^{[1]}*hars_t$	0.12	1.25	(-2.51, 2.46)
$\alpha_1^{[2]}*hars_t$	0.34	0.16	(0.03, 0.66)
$\alpha_1^{[3]}*hars_t$	0.40	0.16	(0.09, 0.71)
$\alpha_2^{[1]}*ptarmigan_t$	1.71	1.33	(-0.48, 4.80)
$\alpha_2^{[2]}*ptarmigan_t$	0.68	0.14	(0.41, 0.96)
$\alpha_2^{[3]}*ptarmigan_t$	0.61	0.17	(0.29, 0.95)
$\beta_0^{[1]}$	-1.03	0.33	(-1.69, -0.39)
$\beta_0^{[2]}$	8.21	1.32	(5.22, 9.93)
$\beta_0^{[3]}$	8.43	1.18	(5.70, 9.94)
$\beta_1^{[1]}*hars_t$	0.10	0.44	(-0.77, 1.00)
$\beta_1^{[2]}*hars_t$	-0.29	2.42	(-4.91, 4.86)
$\beta_1^{[3]}*hars_t$	0.39	2.35	(-3.93, 5.22)
$\beta_2^{[1]}*ptarmigan_t$	-0.22	0.49	(-1.24, 0.68)
$\beta_2^{[2]}*ptarmigan_t$	0.03	2.67	(-4.25, 5.91)
$\beta_2^{[3]}*ptarmigan_t$	0.74	2.05	(-2.80, 5.22)

Appendix 3.1. List of estimated parameters in the long-term monitoring (LTM) and population inventory (INV) models.

Model	Parameter	Description
LTM	$p^{NB,A}$	Probability of detecting occupancy without breeding during the aerial survey.
	$p^{NB,G}$	Probability of detecting occupancy without breeding during a time-removal interval of the ground survey.
	$S_{i,t}$	A binary indicator of whether the nest in which eggs were laid was surveyed.
	ψ	The first-year probability of occupancy.
	R	The first-year probability of breeding.
	δ_1	A covariate on the frequency of use ($\lambda_{g,i}$) for nest g in territory i .
	$\pi_{g,i}$	The probability that eggs were laid in nest g in territory i .
	$\psi_{t+1}^{[m]}$	Probability of occupancy in year $t+1$ given m , the state in year t .
	$R_{t+1}^{[m]}$	Probability of breeding in year $t+1$ given m , the state in year t .
INV	p^{NU}	Probability of detecting an unoccupied nest cluster.
	p^{NO}	Probability of detecting an occupied nest cluster (with or without breeding).
	$p^{NB,A}$	Probability of detecting occupancy without breeding during the aerial survey.
	$p^{NB,G}$	Probability of detecting occupancy without breeding during a time-removal interval of the ground survey.
	ψ	Probability of nest cluster presence in a cell.
	U	Probability of occupancy.
	R	Probability of breeding.

Appendix 3.2. Model development for population inventories of cliff-nesting raptors and a simulation study to assess model performance at different sample sizes and survey durations.

Model development

We developed a single-season, multi-state occupancy model for a combined aerial and ground (time-removal) survey conducted over a gridded study area for which we have 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 one of four mutually exclusive states: 1) nest cluster absent; 2) nest cluster present but unoccupied; 3) nest cluster present and occupied without breeding; and 4) nest cluster present and occupied with breeding.

We described the observations as arising from a state-dependent, removal sampling process and used an expanded version of the state detection matrix from the long-term monitoring model. The observations y_i for *grid* cell $i = 1, 2, \dots, I$ were multinomial random variables with probabilities π_k for cell $k = 1, 2, \dots, K$ conditional on the true states z_i :

$$y_i \sim \text{Multinomial}(\pi_k [z_i, \dots], 1) \quad \text{Eq. 16}$$

The rows of the state detection matrix were dependent on the true state m with probabilities that summed to 1 (MacKenzie et al. 2009). The columns corresponded to the cell-specific probabilities of observing of state l (i.e., $k^{[l]}$). For a 9-interval time-removal survey and 2-pass aerial removal survey, the state detection matrix is:

$$\begin{array}{c} \begin{array}{ccc} 1^{[4]} & 2^{[3]} & k^{[3]} = 3, 4, \dots, 11 \end{array} \\ \begin{array}{c} 1 \\ 2 \\ 3 \\ 4 \end{array} \left[\begin{array}{ccc} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & p^{NO} * p^{NB,A} & p^{NO} * (1 - p^{NB,A}) * p^{NB,G} * (1 - p^{NB,G})^{k-3} \\ p^{NO} & 0 & 0 \end{array} \right] \end{array} \quad \text{Eq. 17}$$

$$\begin{array}{c} \begin{array}{ccc} 12^{[2]} & 13^{[4]} & 14^{[3]} \end{array} \\ \begin{array}{c} 1 \\ 2 \\ 3 \\ 4 \end{array} \left[\begin{array}{ccc} 0 & 0 & 0 \\ p^{NU} & 0 & 0 \\ p^{NO} * (1 - p^{NB,A}) * (1 - p^{NB,G})^9 & 0 & p^{NO} * (1 - p^{NO}) * p^{NB,G} \\ 0 & p^{NO} * (1 - p^{NO}) & 0 \end{array} \right] \end{array}$$

$$\begin{array}{c}
k^{[3]} = 15, 16, \dots, 23 \\
\begin{array}{l}
1 \\
2 \\
3 \\
4
\end{array}
\left[\begin{array}{c}
0 \\
0 \\
(1 - p^{NO}) * p^{NO} * (1 - p^{NB,A}) * p^{NB,G} * (1 - p^{NB,G})^{k-15} \\
0
\end{array} \right] \\
\\
\begin{array}{c}
24^{[2]} \qquad \qquad \qquad 25^{[1]} \\
\begin{array}{l}
1 \\
2 \\
3 \\
4
\end{array}
\left[\begin{array}{cc}
0 & 1 \\
p^{NU} * (1 - p^{NU}) & (1 - p^{NU}) * (1 - p^{NU}) \\
(1 - p^{NO}) * p^{NO} * (1 - p^{NB,A}) * (1 - p^{NB,G})^9 & (1 - p^{NO}) * (1 - p^{NO}) \\
0 & (1 - p^{NO}) * (1 - p^{NO})
\end{array} \right]
\end{array}
\end{array}$$

where p^{NU} is the probability of detecting a nest cluster given it is unoccupied, p^{NO} is the probability of detecting a nest cluster given that it is occupied, $p^{NB,A}$ is the probability of detecting occupancy without breeding during the aerial survey (given detection of the nest cluster), and $p^{NB,G}$ is the probability of detecting occupancy without breeding during a time interval of the ground survey (given detection of the nest cluster). We included the probabilities of detecting unoccupied and occupied nest clusters, p^{NU} and p^{NO} , respectively, because we expected that nest cluster detection could differ due to the availability of stronger cues around occupied nest clusters (e.g., recent whitewash, the birds themselves, etc.).

Unlike the long-term monitoring model, we assume complete surveying of nests within a cluster. In a few cases, we may detect a nest cluster, but not detect the one nest in which eggs were laid. However, these territories 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.

The true states z_i are multinomial random variables with state probabilities ϕ :

$$z_i \sim \text{Multin}(\phi, 1) \tag{Eq. 18}$$

The vector of state probabilities are:

$$\phi = [1 - \psi \quad \psi * (1 - U) \quad \psi * U * (1 - R) \quad \psi * U * R] \tag{Eq. 19}$$

where ψ is the probability of nest cluster presence in a cell, U is the probability of occupancy, and R is the probability of breeding. The probability of nest cluster presence ψ_i could also be modeled as a function of covariates indicative of cliff-nesting habitat (e.g., slope and elevation).

Simulation study

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 three (nest cluster present with occupancy without breeding) and the duration of the time-removal survey (60 or 90 minutes). We set p^{NU} , p^{NO} , and $p^{NB,A}$ equal to their respective estimates from a pilot inventory study that we conducted for golden eagle in the central Alaska Range. We set $p^{NB,G}$ equal to its estimate from the long-term monitoring case study.

Implementation

We fit 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 2015). We specified vague normal priors for all regression coefficients and uniform (0, 1) priors for all parameters on the real scale. Summaries of the posterior distribution were calculated from one Markov chain run for 18,000 iterations with a 6,000 burn-in and thinning every 2 draws. We used the Gelman-Rubin diagnostic (Brooks and Gelman 1998) to assess convergence and scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. We ran 500 simulations for each scenario 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

Estimates of the probability of detecting non-breeding occupancy during the time-removal 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 3.2-1). Under scenarios with 90-minute ground surveys, estimates for $p^{NB,G}$ showed moderate relative bias (≤ 0.07) and near nominal coverage (Table 3.2-1). 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 (breeding and nonbreeding nest clusters) showed negligible relative bias (≤ 0.01), but the RMSE for these estimates was lower under scenarios with 90-minute ground surveys (Table 3.2-1).

Table 3.2-1. Estimates from the population inventory simulation study using the single-season, multi-state removal model. The derived parameter $N_{occupied}$ is the sum of the grid cells containing an occupied nest cluster (with or without breeding). Estimates are based on 500 simulations.

Nonbreeding clusters	Duration (minutes)	Parameter	True value	Mean	RMSE	Bias	CI coverage
300	60	p^{NO}	0.55	0.61	0.06	0.10	0.93
		p^{NU}	0.86	0.85	0.02	0.00	0.94
		$p^{NB,A}$	0.44	0.45	0.04	0.03	0.97
		$p^{NB,G}$	0.12	0.15	0.03	0.19	0.96
		$N_{occupied}$	500	494.15	22.19	-0.01	0.97
400	60	p^{NO}	0.55	0.62	0.07	0.12	0.94
		p^{NU}	0.86	0.85	0.01	0.00	0.97
		$p^{NB,A}$	0.44	0.46	0.04	0.04	0.97
		$p^{NB,G}$	0.12	0.14	0.03	0.16	0.97
		$N_{occupied}$	600	591.59	25.10	-0.01	0.96
300	90	p^{NO}	0.55	0.60	0.05	0.09	0.91
		p^{NU}	0.86	0.85	0.02	0.00	0.94
		$p^{NB,A}$	0.44	0.44	0.03	0.01	0.96
		$p^{NB,G}$	0.12	0.13	0.02	0.07	0.96
		$N_{occupied}$	500	500.73	17.06	0.00	0.96
400	90	p^{NO}	0.55	0.61	0.06	0.10	0.93
		p^{NU}	0.86	0.85	0.01	0.00	0.96
		$p^{NB,A}$	0.44	0.44	0.03	0.00	0.96
		$p^{NB,G}$	0.12	0.13	0.02	0.06	0.96
		$N_{occupied}$	600	601.96	19.19	0.00	0.96

Appendix 3.3. Data generation and JAGS model code used in the simulation study for the multi-state, time-removal model for long-term monitoring studies using aerial and ground-based surveys. Includes the nest-level model.

```
# zero-truncated Poisson
rtpois <-
function(N, lambda=NA)
{
  if (is.na(lambda) == TRUE) return(NA)
  qpois(runif(N, dpois(0, lambda), 1), lambda)
}

#Ptarmigan annual abundance index data
prey<-c(5.00, 4.25, 6.50, 6.25, 12.00, 15.00, 22.00, 18.10, 9.20, 3.75, 4.36, 6.54, 8.60, 12.60,
10.70, 9.25, 12.87, 16.00, 10.70)
prey<- scale(pre y)

nyears<-20
T<-2

nterr<- 150 #number of territories
lam.nests<-3 #mean number of alternative nests in a territory
max.nests<-8 #max number of nests in a territory (use in padded matrix)
n.states<-3 #[1] not occupied [2] non-breeding occupancy [3] breeding occupancy

PSI.STATE1<- c(.3,.3,.4) #year one state probabilities

# Generation of simulated data
# Define mean survival, transitions, recapture, as well as number of occasions, states,
observations and released individuals
alpha2.T<-alpha1.T<-alpha0.T<-alpha2.R<-alpha1.R<-alpha0.R<-rep(NA,n.states)

alpha0.R[1]<-0.606 #intercept for reprod
alpha0.R[2]<--.581
alpha0.R[3]<-.261

alpha1.R[1]<-1.71 #prey effect on reprod
alpha1.R[2]<-0.684
alpha1.R[3]<-0.614

alpha0.T[1]<--.25 #int occ
alpha0.T[2]<-1
alpha0.T[3]<-1.25

alpha1.T[1]<--.4 #trend on occ
```

```

alpha1.T[2]<--.4
alpha1.T[3]<--.4
year0<-1:19
year1<-as.vector(scale(year0[1:nyears]))
psiT0<-psiT1<-psiT2<-psiR0<-psiR1<-psiR2<-rep(NA,nyears-1)
for (t in 1:(nyears-1)){
psiT0[t]<-1/(1+exp(-(alpha0.T[1]+alpha1.T[1]*year1[t])))
psiT1[t]<-1/(1+exp(-(alpha0.T[2]+alpha1.T[2]*year1[t])))
psiT2[t]<-1/(1+exp(-(alpha0.T[3]+alpha1.T[3]*year1[t])))
psiR0[t]<-1/(1+exp(-(alpha0.R[1]+alpha1.R[1]*prey[t])))
psiR1[t]<-1/(1+exp(-(alpha0.R[2]+alpha1.R[2]*prey[t])))
psiR2[t]<-1/(1+exp(-(alpha0.R[3]+alpha1.R[3]*prey[t])))
}
PSI.STATE <- array(NA, dim=c(n.states, n.states, nterr, nyears-1))
for (i in 1:nterr){
  for (t in 1:(nyears-1)){
    PSI.STATE[,i,t] <- matrix(c(
      1-psiT0[t],psiT0[t]*(1-psiR0[t]),psiT0[t]*psiR0[t],
      1-psiT1[t],psiT1[t]*(1-psiR1[t]),psiT1[t]*psiR1[t],
      1-psiT2[t],psiT2[t]*(1-psiR2[t]),psiT2[t]*psiR2[t]), nrow = n.states, byrow = TRUE)
  } #t
} #i

#simulate number of nests in each territory as zero-truncated Poisson
n.nests<-rtpois(nterr,lam.nests)
n.nests[n.nests>max.nests]<-max.nests #left truncate

#entry probs is the proportion of nests found in each year
entry.probs<-c(.75,.07,.06,.05,.04,0.03,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0)
#entry.probs<-c(1,rep(0,nyears-1)) #if found all nests in 1st year

found<-w.nest<-array(0,c(max.nests,nterr))
surveyed.nest<-array(0,c(max.nests,nterr,nyears))
for (j in 1:nterr){
  w.nest[1:n.nests[j],j]<-1 #w.nest is structural indicator if real nest
  found[1:n.nests[j],j]<-sample(1:nyears, n.nests[j], replace=TRUE, prob=entry.probs)
}
found[found==0]<-nyears+1 #if never found this nest

#create surveyed.nest array with trailing 0s until found nest
for (i in 1:max.nests){
  for (j in 1:nterr){
    for (t in 1:nyears){
      ifelse(found[i,j]<=t,surveyed.nest[i,j,t]<-1,surveyed.nest[i,j,t]<-0)
    }
  }
}

```

```
terr.surveyed<-apply(surveyed.nest,c(2,3),max,na.rm=T) #some territories may have 0 nests
found in a year(s)
```

```
lam<-x<-nest.probs<-matrix(0,nrow=max.nests,ncol=nterr)
znest<-array(0,dim=c(max.nests,nterr,nyears))
```

```
#create binary covariate for nest use intensity (e.g., poor or good condition nest, assumed
#constant across time for simplicity)
```

```
for (i in 1:max.nests){
  for (j in 1:nterr){
    x[j]<-rbinom(max.nests,1,.6)
  }
}
b1<-1
```

```
#expected nest use intensity
```

```
for (i in 1:max.nests){
  for (j in 1:nterr){
    lam[i,j]<-(exp(b1*x[i,j]))*w.nest[i,j]
  }
}
n.lam<-rep(NA,nterr)
for (j in 1:nterr){
  n.lam[j]<-sum(lam[,j])
}
```

```
#conditional nest use intensity
```

```
for (i in 1:max.nests){
  nest.probs[i,j]<-lam[i,j]/n.lam[j]
}
}
```

```
#simulate 1 nest used in each territory
```

```
for (j in 1:nterr){
  for (k in 1:nyears){
    znest[,j,k]<-rmultinom(1,1,nest.probs[,j])
  }
}
R.nest<-which(znest == 1, arr.ind=T)
R.nest2<-array(NA,dim=c(nterr,nyears))
```

```
for (i in 1:nrow(R.nest)){
  R.nest2[R.nest[i,2],R.nest[i,3]]<-R.nest[i,1]
}
}
```

```
# Multinomial trials for state transitions
```

```
CH.TRUE <- matrix(nrow=nterr,ncol=nyears)
for (i in 1:nterr){
  CH.TRUE[i,1] <- which(rmultinom(1, 1, PSI.STATE1)==1)
  for (t in 2:nyears){
    state <- which(rmultinom(1, 1, PSI.STATE[CH.TRUE[i,t-1],i,t-1])==1)
  }
}
```

```

    CH.TRUE[i,t] <- state
  }}
CH.TRUE.2<-CH.TRUE.2_3<-CH.TRUE.3<-CH.TRUE
CH.TRUE.3[CH.TRUE!=3]<-0
CH.TRUE.3[CH.TRUE.3==3]<-1
Nbreed<-colSums(CH.TRUE.3)

CH.TRUE.2_3[CH.TRUE==1]<-0
CH.TRUE.2_3[CH.TRUE==2]<-3
N23<-colSums(CH.TRUE.2_3)/3

CH.TRUE.2[CH.TRUE==1]<-0
CH.TRUE.2[CH.TRUE==3]<-0
CH.TRUE.2[CH.TRUE==2]<-1

#detection of breeding occupancy dependent on if you surveyed the 1 nest used for breeding
mu.pR<-array(NA,dim=c(max.nests,nterr,nyears))
for (i in 1:max.nests){
  for (j in 1:nterr){
    for (t in 1:nyears){
      mu.pR[i,j,t]<-CH.TRUE.3[j,t]*znest[i,j,t]*surveyed.nest[i,j,t] #breeding=1 * which nest
      w/eggs * surveyed that nest
    }}}
mu.pR2<-apply(mu.pR,2:3,sum) #detection prob
nest.missed<-CH.TRUE.3-mu.pR2

#create multinomial probs for time-removal process for state 2 (occupancy with no breeding)
C<-6 #6, 10 minute periods
pNB<-c(.563,.122) #pNB[1] (aerial survey), pNB[2] (ground survey; for a 10 min interval)
occprobs<-rep(0,C+2)
occprobs[1]<-pNB[1] #detected in aerial survey
occprobs[C+2]<-(1-pNB[1])*((1-pNB[2])^C) # 1...1 not detected in aerial survey or any ground
survey time interval
for (i in 2:(C+1)){
  occprobs[i]<-(1-pNB[1])*pNB[2]*((1-pNB[2])^(i-2)) #1..2..not detected in aerial survey, but
detected on ground in time interval i-1
}
y.occ<-array(0,dim=c(nterr,nyears,C+2))

#simulate observations of occupancy with no breeding
#if missed breeding in aerial survey, can still detect occupancy with no breeding on ground
survey
for (i in 1:nterr){
  for (t in 1:nyears){
    if(CH.TRUE.2[i,t]==1){y.occ[i,t]<-rmultinom(n=1, size=1, prob = occprobs)}
    if(CH.TRUE.2[i,t]==0 & CH.TRUE.3[i,t]==0){y.occ[i,t,C+2]<-1}
  }
}

```

```

  if(CH.TRUE.3[i,t]==1 & nest.missed[i,t]==1){y.occ[i,t]<-rmultinom(n=1, size=1, prob =
occprobs)} #if missed nest, can still detect occ
}}

```

```

#determine if missed any breeding nests
y.B<-array(0,dim=c(nterr,nyears))
for (i in 1:nterr){
for (t in 1:nyears){
  if(CH.TRUE.3[i,t]==1 & nest.missed[i,t]==0){y.B[i,t]<-mu.pR2[i,t]}
  if(CH.TRUE.3[i,t]==0){y.B[i,t]<-0}
}}

```

```

zst<-CH.TRUE #inits for latent states

```

```

#create matrix for observed nests(within territory ID) used for breeding - NAs for no nest
observed either b/c missed or not breeding

```

```

R.nest3<-R.nest2
R.nest3[y.B==0]<-0
nest<-R.nest3
nest[nest==0]<-NA

```

```

#####create cumulative offset relating territory ID to vector of nests

```

```

terr2<-w.nest
for (i in 1:max.nests){
for (j in 1:nterr){
  ifelse(w.nest[i,j]==1,terr2[i,j]<-j,terr2[i,j]<-NA)
}}
x[is.na(terr2)]<-NA
x<-x[!is.na(as.vector(x))]
terr2<-terr2[!is.na(as.vector(terr2))]
nest.offset1<-nest.offset<-cumsum(n.nests)
nest.offset<-c(1,nest.offset1+1)
M.nests<-sum(n.nests)

```

```

#create final multinomial observation data structure with C+3 cells

```

```

#cell 1 is all observations of breeding territories (state3)
#cell 2 is obs of occupancy w/out breeding (state2) from aerial survey.
#cell 3:C+2 is obs of occupancy w/out breeding (state2) from ground survey.
#cell C+3 is no occupancy detected in any survey

```

```

y<-array(0,dim=c(nterr,nyears,C+3))
y[,1]<-y.B
y[,2:(C+3)]<-y.occ

```

```

y[terr.surveyed==0]<-NA
zst[nest.missed==1]<-3

```

```

#Must specify initial values for nest latent variable that are compatible with initial values for
territory occupancy
#if zst == 3 and y == 1, then nestst is the true nest used (and the one you missed)
nestst <- nest
I<-which(is.na(nest))
for (i in 1:nterr){
for (t in 1:nyears){
  if(is.na(nest[i,t])){nestst[i,t]<-R.nest2[i,t]}
}}
nestst[-I] <- NA

```

```

#####
## Model code #####
#####

```

```

library(jagsUI)
sink("model.jags")
cat("
model {
b1~dnorm(0,0.01)
pNB[1]~dunif(0,1)
pNB[2]~dunif(0,1)
pTTD<-1-(1-pNB[2])^C #There are C time intervals in the ground survey
psiR.1~dunif(0,1)
psiT.1~dunif(0,1)

for (s in 1:3){
alpha0.R[s]~dnorm(0,0.01)T(-10,10)
alpha1.R[s]~dnorm(0,0.01)T(-10,10)
alpha0.T[s]~dnorm(0,0.01)T(-10,10)
alpha1.T[s]~dnorm(0,0.01)T(-10,10)
}

for (i in 1:M.nests){
  log(lam[i])<-b1*x[i] #x is a covariate on the log-transform of nest use frequency
  nest.probs[i]<-lam[i]/sum(lam[nest.offset[terr2[i]]:(nest.offset[terr2[i]+1]-1)]) #conditional
intensity probs
}
for (i in 1:nterr){
  ps.1[i,1]<-1-psiT.1
  ps.1[i,2]<-psiT.1*(1-psiR.1)
  ps.1[i,3]<-psiT.1*psiR.1
  z[i,1]~dcat(ps.1[i,])
}

```



```

for (t in 1:(nyears-1)){
  logit(psiT1[t])<-alpha0.T[1]+ alpha1.T[1]*year1[t]
  logit(psiT2[t])<-alpha0.T[2]+ alpha1.T[2]*year1[t]
  logit(psiT3[t])<-alpha0.T[3]+ alpha1.T[3]*year1[t]
  logit(psiR1[t])<-alpha0.R[1] + alpha1.R[1]*prey[t]
  logit(psiR2[t])<-alpha0.R[2] + alpha1.R[2]*prey[t]
  logit(psiR3[t])<-alpha0.R[3] + alpha1.R[3]*prey[t]

  phi[1,t,1] <- 1-psiT1[t]
  phi[1,t,2] <- psiT1[t]*(1-psiR1[t])
  phi[1,t,3] <- psiT1[t]*psiR1[t]
  phi[2,t,1] <- 1-psiT2[t]
  phi[2,t,2] <- psiT2[t]*(1-psiR2[t])
  phi[2,t,3] <- psiT2[t]*psiR2[t]
  phi[3,t,1] <- 1-psiT3[t]
  phi[3,t,2] <- psiT3[t]*(1-psiR3[t])
  phi[3,t,3] <- psiT3[t]*psiR3[t]
}

for (i in 1:max.nests){
for (j in 1:nterr){
for (t in 1:nyears){
  mu.pRn[i,j,t]<-equals(i,nest[j,t])*surveyed.nest[i,j,t]
}}
for (i in 1:nterr){
for (t in 1:nyears){
  nest[i,t]~dcat(nest.probs[nest.offset[i]:(nest.offset[i+1]-1)])
  mu.pRt[i,t]<-state3[i,t]*sum(mu.pRn[1:max.nests,i,t]) #will be 0 or 1 if surveyed the
actual nest used for breeding

  mu[1,i,t,1]<-0
  mu[2,i,t,1]<-0
  mu[3,i,t,1]<-mu.pRt[i,t] #surveyed nest used for breeding 0 or 1

  mu[1,i,t,2]<-0
  mu[2,i,t,2]<-pNB[1] #detect occupancy w/out breeding in aerial survey
  mu[3,i,t,2]<-(1-mu.pRt[i,t])*pNB[1] #miss breeding nest, but detect occupancy w/out
breeding in aerial survey

  mu[1,i,t,(C+3)]<-1
  mu[2,i,t,(C+3)]<-(1-pNB[1])*((1-pNB[2])^C) #occupancy not detected
  mu[3,i,t,(C+3)]<-(1-mu.pRt[i,t])*(1-pNB[1])*((1-pNB[2])^C) #occupancy not detected

for (k in 3:(C+2)){
  mu[1,i,t,k]<-0

```

```

    mu[2,i,t,k]<-(1-pNB[1])*pNB[2]*((1-pNB[2])^(k-3))           #detect occupancy w/out
breeding in interval k-2 time-removal survey
    mu[3,i,t,k]<-(1-mu.pRt[i,t])*(1-pNB[1])*pNB[2]*((1-pNB[2])^(k-3)) #missed breeding nest,
but detect occupancy w/out breeding in interval k-2 time-removal survey
  }
  y[i,t,1:(C+3)]~dmulti(mu[z[i,t],i,t,],1)
}}
for (i in 1:nterr){
for (t in 2:nyears){
  z[i,t] ~ dcat(phi[z[i,t-1],t-1,])#
}}

for (i in 1:nterr){
for(t in 1:nyears){
  state1[i,t] <- equals(z[i,t], 1)
  state2[i,t] <- equals(z[i,t], 2)
  state3[i,t] <- equals(z[i,t], 3)
}}

for(t in 1:nyears){
  sum.state1[t]<-sum(state1[,t])
  sum.state2[t]<-sum(state2[,t])
  sum.state3[t]<-sum(state3[,t])
  N.occupied[t]<-sum.state2[t]+sum.state3[t]
}

} # end model
",fill = TRUE)
sink()
# Bundle data
data <- list(y = y,surveyed.nest=surveyed.nest,C=C,nest=nest,prey=prey,x=x,year1=year1,
max.nests=max.nests,nterr=nterr,nyears=nyears,M.nests=M.nests,terr2=terr2,
nest.offset=nest.offset)

inits <- function(){ list(z=zst,nest=nestst)}

params <- c("N.occupied", "pNB", "psiR.1", "psiT.1", "alpha0.R", "alpha0.T", "b1",
"alpha1.R", "alpha1.T", "sum.state2", "sum.state3", "alpha2.T", "alpha2.R")

ni <- 14000 ; nb <- 4000 ; nt <- 2 ; nc <- 1

out <- jags(data, inits, params, "model.jags", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb,
parallel = TRUE)

```

Appendix 3.4. Data generation and JAGS model code for the multi-state, time-removal model used for the population inventory simulation study with a 9-interval time-removal survey and 2-pass aerial removal survey.

```

ncells<-700 #number of grid cells in study area
nstates<-4 #[1] nest cluster not present in grid cell [2] unoccupied nest cluster present in cell
#[3] nest cluster present with non-breeding occupancy [4] nest cluster present with breeding

CH.TRUE <- c(rep(1,0),rep(2,200),rep(3,300),rep(4,200))

C<-9 #number of time intervals in ground survey

#pN [1] prob of detecting unoccupied nest cluster, pN [2] prob of detecting occupied nest cluster
pN<-c(.554,.856)
#pNB[1] (aerial survey) = .45, pNB[2] (ground survey 10 min interval) = .14
pNB<-c(.438,.122)
probs<-array(0,dim=c(nstates,(2*C)+7))

#columns - 1

#given grid cell nest cluster absent
probs[1,1:(2*C)+6]<-0
probs[1,(2*C)+7]<-1 #no misclassification

#given grid cell w/nest cluster present and unoccupied
probs[2,1]<-0
probs[2,2]<-0
probs[2,C+3]<-pN[1] #found nest first pass
probs[2,C+4]<-0
probs[2,C+5]<-0
probs[2,(2*C)+6]<-pN[1]*(1-pN[1]) #found nest 2nd pass
probs[2,(2*C)+7]<-(1-pN[1])*(1-pN[1]) #did not find nest after both passes

#given grid cell with nest cluster present with occupancy w/out breeding
#see model code below for further annotation of cell probabilities

probs[3,1]<-0
probs[3,2]<-pN[2]*pNB[1]
probs[3,C+3]<-pN[2]*(1-pNB[1])*((1-pNB[2])^C)
probs[3,C+4]<-0
probs[3,C+5]<-pN[2]*(1-pN[2])*pNB[1]
probs[3,(2*C)+6]<-pN[2]*(1-pN[2])*(1-pNB[1])*((1-pNB[2])^C)
probs[3,(2*C)+7]<-(1-pN[2])*(1-pN[2])

```

```

#given grid cell with nest cluster present with occupancy with breeding
probs[4,1]<-pN[2]
probs[4,2]<-0
probs[4,C+3]<-0
probs[4,C+4]<-pN[2]*(1-pN[2])
probs[4,C+5]<-0
probs[4,(2*C)+6]<-0
probs[4,(2*C)+7]<-(1-pN[2])*(1-pN[2])

#time removal probs after finding nest on 1st pass and not detecting occupancy w/out breeding
during the aerial survey
for (k in 3:(C+2)){
  probs[1,k]<-0
  probs[2,k]<-0
  probs[3,k]<-pN[2]*(1-pNB[1])*pNB[2]*((1-pNB[2])^(k-3))
  probs[4,k]<-0
}
#time removal probs after finding nest on 2nd pass and not detecting occupancy w/out breeding
during the aerial survey
for (k in (C+6):((2*C)+5)){
  probs[1,k]<-0
  probs[2,k]<-0
  probs[3,k]<-pN[2]*(1-pN[2])*(1-pNB[1])*pNB[2]*((1-pNB[2])^(k-(C+6)))
  probs[4,k]<-0
}

CH<-rep(0,ncells)
y<-array(0,dim=c(ncells,(2*C)+7))
for (i in 1:ncells){
  # Multinomial trials for observation process
  event <- which(rmultinom(1, 1, probs[CH.TRUE[i,]])==1)
  CH[i] <- event
}
for (i in 1:ncells){
  y[i,CH[i]]<-1
}
zst <- CH.TRUE

#####
Model code#####
#####
require(jagsUI)
sink("model.jags")
cat("
model {

```

```

psiR~dunif(0,1)
psiU~dunif(0,1)
psiT~dunif(0,1)

pN[1]~dunif(0,1)
pN[2]~dunif(0,1)
pNB[1]~dunif(0,1)
pNB[2]~dunif(0,1)

phi[1]<-1-psiT
phi[2]<-psiT*(1-psiU)
phi[3]<-psiT*psiU*(1-psiR)
phi[4]<-psiT*psiU*psiR

for (i in 1:ncells){
  z[i]~ dcat(phi[])
  mu[1,i,1]<-0
  mu[2,i,1]<-0
  mu[3,i,1]<-0
  mu[4,i,1]<-pN[2] #find breeding nest cluster, 1st pass

  mu[1,i,2]<-0
  mu[2,i,2]<-0
  mu[3,i,2]<-pN[2]*pNB[1] #find nest cluster 1st search and detect occupancy
w/out breeding during aerial survey
  mu[4,i,2]<-0

  mu[1,i,12]<-0
  mu[2,i,12]<-pN[1]
  mu[3,i,12]<-pN[2]*(1-pNB[1])*((1-pNB[2])^C) #found nest cluster, but don't detect
occupancy in aerial or time-removal survey; C is the number of intervals in the time-removal
(ground) survey
  mu[4,i,12]<-0

  mu[1,i,13]<-0
  mu[2,i,13]<-0
  mu[3,i,13]<-0
  mu[4,i,13]<-pN[2]*(1-pN[2]) #miss breeding nest cluster 1st aerial pass and find it
during 2nd aerial pass

  mu[1,i,14]<-0
  mu[2,i,14]<-0
  mu[3,i,14]<-pN[2]*(1-pN[2])*pNB[1] #miss nest cluster 1st aerial pass, find it during
2nd pass, detect occupancy w/out breeding during aerial survey
  mu[4,i,14]<-0

```

```

mu[1,i,24]<-0
mu[2,i,24]<-pN[1]*(1-pN[1]) #miss nest cluster on 1st pass, find it on 2nd pass
mu[3,i,24]<-pN[2]*(1-pN[2])*(1-pNB[1])*((1-pNB[2])^C) #miss nest cluster on 1st pass,
but don't detect occupancy without breeding during ground survey
mu[4,i,24]<-0

mu[1,i,25]<-1
mu[2,i,25]<-(1-pN[1])*(1-pN[1])
mu[3,i,25]<-(1-pN[2])*(1-pN[2]) #don't find the nest cluster in either aerial pass
mu[4,i,25]<-(1-pN[2])*(1-pN[2])

for (k in 3:11){
  mu[1,i,k]<-0
  mu[2,i,k]<-0
  mu[3,i,k]<-pN[2]*(1-pNB[1])*pNB[2]*((1-pNB[2])^(k-3)) #find nest cluster on 1st pass,
detect occupancy w/out breeding during the ground survey
  mu[4,i,k]<-0
}
for (k in 15:23){
  mu[1,i,k]<-0
  mu[2,i,k]<-0
  mu[3,i,k]<-pN[2]*(1-pN[2])*(1-pNB[1])*pNB[2]*((1-pNB[2])^(k-15)) #miss nest cluster 1st
aerial pass, find during 2nd aerial pass, detect occupancy w/breeding during the ground survey
  mu[4,i,k]<-0
}
y[i,1:25]~dmulti(mu[z[i],i,],1)
}

for(i in 1:ncells){
  state1[i] <- equals(z[i], 1)
  state2[i] <- equals(z[i], 2)
  state3[i] <- equals(z[i], 3)
  state4[i] <- equals(z[i], 4)
}
sum.state2<-sum(state2[])
sum.state3<-sum(state3[])
sum.state4<-sum(state4[])

N.occupied<-sum.state3+sum.state4

} # end model
",fill = TRUE)
sink()

win.data <- list(y = y,ncells=ncells,C=C)

```

```
inits <- function() list(z= zst)

params <- c("pNB", "pN", "sum.state2", "sum.state3", "sum.state4",
"N.occupied", "psiT", "psiR", "psiU")

ni <- 18000 ; nb <- 6000 ; nt <- 2 ; nc <- 1

out <- jags(win.data, inits, params, "model.jags", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin =
nb, parallel = TRUE)
```

Appendix 3.5. JAGS model code for the multi-state, time-removal model for long-term monitoring designs restricted to ground surveys. Includes the nest-level model.

```
#####
## Model code #####
#####

model {
b1~dnorm(0,0.01)
pNB~dunif(0,1)
pTTD<-1-(1-pNB)^C #There are C time intervals in the ground survey
psiR.1~dunif(0,1)
psiT.1~dunif(0,1)

for (s in 1:3){
  alpha0.R[s]~dnorm(0,0.01)T(-10,10)
  alpha1.R[s]~dnorm(0,0.01)T(-10,10)
  alpha0.T[s]~dnorm(0,0.01)T(-10,10)
  alpha1.T[s]~dnorm(0,0.01)T(-10,10)
}

for (i in 1:M.nests){
  log(lam[i])<-b1*x[i] #x is a covariate on the log-transform of nest use frequency
  nest.probs[i]<-lam[i]/sum(lam[nest.offset[terr2[i]]:(nest.offset[terr2[i]+1]-1)]) #conditional
intensity probs
}
for (i in 1:nterr){
  ps.1[i,1]<-1-psiT.1
  ps.1[i,2]<-psiT.1*(1-psiR.1)
  ps.1[i,3]<-psiT.1*psiR.1
  z[i,1]~dcat(ps.1[i,])
}
for (t in 1:(nyears-1)){
  logit(psiT1[t])<-alpha0.T[1]+ alpha1.T[1]*year1[t]
  logit(psiT2[t])<-alpha0.T[2]+ alpha1.T[2]*year1[t]
  logit(psiT3[t])<-alpha0.T[3]+ alpha1.T[3]*year1[t]
  logit(psiR1[t])<-alpha0.R[1] + alpha1.R[1]*prey[t]
  logit(psiR2[t])<-alpha0.R[2] + alpha1.R[2]*prey[t]
  logit(psiR3[t])<-alpha0.R[3] + alpha1.R[3]*prey[t]

  phi[1,t,1] <- 1-psiT1[t]
  phi[1,t,2] <- psiT1[t]*(1-psiR1[t])
  phi[1,t,3] <- psiT1[t]*psiR1[t]
  phi[2,t,1] <- 1-psiT2[t]
  phi[2,t,2] <- psiT2[t]*(1-psiR2[t])

```



```

    phi[2,t,3] <- psiT2[t]*psiR2[t]
    phi[3,t,1] <- 1-psiT3[t]
    phi[3,t,2] <- psiT3[t]*(1-psiR3[t])
    phi[3,t,3] <- psiT3[t]*psiR3[t]
  }

for (i in 1:max.nests){
for (j in 1:nterr){
for (t in 1:nyears){
  mu.pRn[i,j,t]<-equals(i,nest[j,t])*surveyed.nest[i,j,t]
}}
for (i in 1:nterr){
for (t in 1:nyears){
  nest[i,t]~dcat(nest.probs[nest.offset[i]:(nest.offset[i+1]-1)])
  mu.pRt[i,t]<-state3[i,t]*sum(mu.pRn[1:max.nests,i,t]) #will be 0 or 1 if surveyed the
  actual nest used for breeding

  mu[1,i,t,1]<-0
  mu[2,i,t,1]<-0
  mu[3,i,t,1]<-mu.pRt[i,t] #surveyed nest used for breeding 0 or 1

  mu[1,i,t,(C+2)]<-1 #no misclassification
  mu[2,i,t,(C+2)]<-(1-pNB)^C #occupancy not detected
  mu[3,i,t,(C+2)]<-(1-mu.pRt[i,t])*((1-pNB)^C) #occupancy not detected

for (k in 2:(C+1)){
  mu[1,i,t,k]<-0
  mu[2,i,t,k]<-pNB*((1-pNB)^(k-2)) #detect occupancy in interval k-1 of time-
  removal survey
  mu[3,i,t,k]<-(1-mu.pRt[i,t])*pNB*((1-pNB)^(k-2)) #missed breeding nest, but detect
  occupancy w/out breeding in interval k-1 of time-removal survey
}
  y[i,t,1:(C+2)]~dmulti(mu[z[i,t],i,t,],1)
}}
for (i in 1:nterr){
for (t in 2:nyears){
  z[i,t] ~ dcat(phi[z[i,t-1],t-1,])
}}

for (i in 1:nterr){
for(t in 1:nyears){
  state1[i,t] <- equals(z[i,t], 1)
  state2[i,t] <- equals(z[i,t], 2)
  state3[i,t] <- equals(z[i,t], 3)
}}

```

```
for(t in 1:nyears){
  sum.state1[t]<-sum(state1[,t])
  sum.state2[t]<-sum(state2[,t])
  sum.state3[t]<-sum(state3[,t])
  N.occupied[t]<-sum.state2[t]+sum.state3[t]
}

} # end model
```


CONCLUSIONS

Arctic- and subarctic-breeding passerines are undergoing concurrent changes in population size and elevational distribution due in part to the rapid expansion of woody vegetation (e.g., erect shrubs) across open landscapes (Sturm et al. 2001, 2005, Tape et al. 2006) and into higher elevations (Stueve et al. 2011, Mizel et al. 2016). The work described in this dissertation was motivated by a need to efficiently detect and distinguish population and spatial dynamics in these populations.

I developed inference methods for these sampling landbirds in the context of understanding how the data are actually generated (Royle and Dorazio 2008). This led to a more efficient allocation of effort and the capacity to more fully leverage the underlying spatial and temporal information. In chapter one, I used a spatial distance sampling approach which frames the sampling process in terms of the individual encounter in space and, consequently, leverages the underlying spatial information to a greater extent than standard distance sampling approaches (Kéry and Royle 2016). In addition, I developed a formulation of the spatial distance sampling model that accommodates temporary emigration permitting greater sensitivity to the underlying spatial processes compared to single-visit approaches, which are conditioned on the assumption that all individuals are present and available for sampling. I expect that my extension accommodating temporary emigration will be a critical specification for spatial distance sampling models, particularly for studies confronted with large variation in the population available for sampling over multiple occasions. This extension may be particularly useful for highly mobile species such as birds and insects (e.g., Kéry et al. 2009, Nichols et al 2009, Chandler et al. 2011, Schmidt et al. 2013) and species that exhibit random temporary emigration including within-season variation in cue production (e.g., singing) or burrowing and hiding behaviors (e.g., herpetofauna; O'Donnell et al. 2015).

In chapter two, I used the open-population occupancy model of Roth et al. (2014) to estimate arrival patterns in Denali's passerine community. This model provides an explicit rendering of the observation process into the probability of initial presence (i.e., arrival) at a site and detection probability. In doing so, it leverages information about arrival phenology from standard occupancy survey data. In addition, inclusion of the arrival date as a random variable allowed me to make inferences about the relationship between the mean and variance of the arrival distribution. Studies of avian arrival phenology have focused extensively on temporal

trends in first or mean arrival dates, but have largely ignored temporal patterns in the variance of the arrival distribution (but see: Møller 1994, Ptaszyk et al. 2003, Møller 2008, Møller et al. 2010). Assessments of the relationship between the mean and variance of the arrival distribution may lead to a deeper understanding of the factors shaping phenological responses and the capacity for species to adapt their phenologies in response to environmental change.

In chapter three, I developed an efficient framework for inventorying and monitoring cliff-nesting raptor populations over landscape scales. Surveys of cliff-nesting raptors present considerable challenges due to their sparse distribution across remote landscapes and the multiple occupancy states (e.g., unoccupied, occupied without breeding, and occupied with breeding) through which we observe their nesting territory dynamics. The standard approach in nesting territory surveys is to allocate a level of effort that is assumed to ensure that the occupancy state of each territory is known with certainty. However, this is logistically prohibitive at landscape scales, constraining our capacity for effective management of these species.

To increase survey efficiency and expand the spatial inference of these studies, I developed two versions of a multi-state, time-removal model, one for long-term monitoring studies and another for population inventories or single-season surveys in which there is no prior knowledge of nest locations. I focused my development of these methods in the context of a combined aerial and ground-based survey approach which permits efficient surveying at landscape scales.

In addition, established long-term monitoring programs for cliff-nesting raptors optimize effort over time through the accumulation of knowledge about individual nest locations. In such scenarios, using repeated surveys to estimate the probability of detecting an individual nest site would be inefficient. However, the standard approach does not accommodate incomplete surveying of alternative nests within a territory. Therefore, I formulated a version of the long-term monitoring model that accounts for state uncertainty at the territory-level caused by a failure to observe all nests within a territory. The nest-level formulation also provides inference about the mechanisms of variation in the frequency of nest use.

I demonstrated that the maximum effort spent on any nesting territory could be reduced by up to almost 90% of that recommended by standard protocols. I expect the inference framework developed here will have the capacity to greatly extend the spatial inference in

studies of cliff-nesting raptors. Interspecific differences in distribution and detectability of nests and the occupancy states will necessitate adjustments of the sampling methods when applied to species other than golden eagle. Regardless, the approach has strong relevance for species and populations in which the breeding component, alone, is not a reliable predictor of the territorial population size.

The development of efficient inference methods is critical when sampling over large, roadless landscapes and/or for sparsely distributed species. The need for efficiency may become all the more important when making inferences about the mechanisms of change in populations that are subject to interacting population, spatial, and phenological dynamics over multiple scales (e.g., arctic- and subarctic breeding populations of migratory birds; Mizel et al. 2016). In such cases, understanding how the data are actually generated may help provide a path towards optimizing survey methods (Royle and Dorazio 2008). Specifically, decomposing the observation process into its constituent probabilities may serve as a starting point for developing a survey design that accounts for potential biases and maximizes encounter probability.

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