

DISSERTATION

STATISTICAL METHODS FOR MODELING THE MOVEMENT AND SPACE-USE OF  
CARNIVORES

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

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Fort Collins, Colorado

Summer 2017

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## ABSTRACT

# STATISTICAL METHODS FOR MODELING THE MOVEMENT AND SPACE-USE OF CARNIVORES

Recent advancements in the ability to monitor animal locations through time has led to a rapidly expanding field focused on statistical models for animal movement. However, many of the existing methods are computationally time-consuming to fit, restricting their application to a few individuals, and inaccessible to wildlife management practitioners. In addition, existing movement models were developed for contemporary animal location data. Many previously collected telemetry data sets may provide important information on animal movement, but there may be additional challenges that are not present in data collected explicitly for movement modeling. For example, telemetry data collected for survival studies may have large temporal gaps, and long-term studies may have used multiple data collection methods, resulting in data points with different error structures. My goal is to develop and expand on methods for modeling individual- and population-level animal movement in a flexible and computationally accessible framework.

In Chapter 1, I discuss the role of carnivores in natural resource management and the habitat associations and movement ecology of two carnivores native to Colorado, Canada lynx and cougars. I describe the existing data sets, collected by Colorado Parks and Wildlife, that are available for analyzing Canada lynx and cougar movement ecology. I also discuss contemporary statistical methods for analyzing animal telemetry data. Finally, I conclude with my research objectives.

Chapter 2 presents a new framework for modeling the unobserved paths of telemetered individuals while accounting for measurement error. Many available telemetry data sets were

not collected for the purposes of movement modeling, making the use of existing methods challenging due to large temporal gaps and varying monitoring protocols. In contrast to the more traditional mechanistic movement models that appear in the literature, I propose a phenomenological functional model for animal movement. The movement process is approximated with basis functions (e.g., splines), which are an extremely flexible statistical tool that allows for complex, non-linear movement patterns at different temporal scales. In addition, the observed data contains complicated error structures that vary across telemetry type. I then apply this model to a case-study of two Canada lynx that were reintroduced to Colorado and show that inference about spatio-temporal movement behaviors can be obtained from the unobserved paths.

For Chapter 3, I apply a population-level version of the functional movement model, developed in Chapter 1, to 153 Canada lynx that were released in Colorado as part of a state reintroduction program. Twelve offspring of the reintroduced individuals were also included in the analysis. I perform a *post hoc* analysis of movement paths using spatial visualizations and linear mixed models, allowing the different movement behaviors to vary as a function of season, sex, reproductive status, and reintroduction timeline. This chapter represents one of the most comprehensive analyses of Canada lynx movement in the continental United States.

In Chapter 4, I discuss the fine-scale movement of cougars in the Colorado Front Range using a continuous-time discrete-space (CTDS) framework. The CTDS framework is computationally fast, flexible, and easily implemented in standard statistical programs. This chapter focuses on a population-level extension of the CTDS framework that can be used to model the population- and individual-level effect of landscape variables on movement rates and directionality. I use this model to determine potential drivers of cougar movement in

the Colorado Front Range, a rapidly urbanizing area in the foothills of the Rocky Mountains. This work also uses the functional model I developed in Chapter 1, but with an error structure more appropriate for small-error GPS data.

I conclude with a summary of findings, overarching themes, and potential future research directions in Chapter 5.

## ACKNOWLEDGEMENTS

First, I thank my advisor, Mevin Hooten, for providing me with guidance on my research, professional development, and beer selection, during the occasionally tumultuous research process. I also thank my committee members, Randy Boone, Kevin Crooks, and Jake Ivan, for their feedback on my dissertation. In particular, I would like to acknowledge Jake Ivan for his efforts as both a committee member and coauthor. Jake was always willing to be a sounding board on topics ranging from ecological mechanisms to idiosyncratic advisors. Tanya Shenk and Mat Alldredge also contributed suggestions that ultimately improved the quality of the manuscripts resulting from my research.

The Wagar community and the Hootenannies have been vital sources of intellectual feedback, emotional support, and good humor. I would like to specifically acknowledge lab members: Brian Brost, Kristin Brooms, Brian Gerber, Trevor Hefley, Shannon Kay, Viviana Ruiz-Guitierrez, Henry Scharf, John Tipton, and Perry Williams; past and present denizens of Wagar: Jeremy Dertien, Cooper Farr, Jared Laufenberg, Anna Mangan, Brittany Mosher, and Casey Setash; and faculty and staff: Larissa Bailey, Kevin Bestgen, Paul Doherty, Gabriele Engler, Kate Huyvaert, Bill Kendall, Joyce Pratt, Kim Samsel, and Dana Winkelman. I would also like to thank my parents, Kevin, and friends near and far, for their support (even when they didn't know what I was talking about or why I was annoyed).

Financial support for this research was provided by Colorado Parks and Wildlife (1304), the National Park Service (P12AC11099), Colorado Department of Transportation, and the National Science Foundation Division of Mathematical Sciences (1614392). Data were provided by Colorado Parks and Wildlife. This dissertation is typeset in L<sup>A</sup>T<sub>E</sub>X using a document class designed by Leif Anderson.

## TABLE OF CONTENTS

|  |      |
|--|------|
| ABSTRACT .....                                 | ii   |
| ACKNOWLEDGEMENTS.....                          | v    |
| LIST OF TABLES.....                            | xi   |
| LIST OF FIGURES.....                           | xiii |
| CHAPTER 1. Introduction.....                   | 1    |
| 1.1. Canada Lynx.....                          | 1    |
| 1.1.1. Distribution.....                       | 1    |
| 1.1.2. Habitat Associations.....               | 2    |
| 1.1.3. Dispersal and Movement Ecology.....     | 3    |
| 1.1.4. Colorado Reintroduction.....            | 5    |
| 1.1.5. Available Data.....                     | 5    |
| 1.2. Cougars.....                              | 6    |
| 1.2.1. Distribution.....                       | 6    |
| 1.2.2. Habitat Associations.....               | 6    |
| 1.2.3. Dispersal and Movement Ecology.....     | 8    |
| 1.2.4. Available Data.....                     | 10   |
| 1.3. Methods for Modeling Animal Movement..... | 11   |
| 1.3.1. Point Process Models.....               | 12   |
| 1.3.2. Discrete-Time Models.....               | 14   |
| 1.3.3. Continuous-Time Models.....             | 15   |
| 1.4. Objectives.....                           | 17   |

|  |    |
|--|----|
| CHAPTER 2. A functional model for characterizing long distance movement behavior | 18 |
| 2.1. Summary   | 18 |
| 2.2. Introduction  | 19 |
| 2.3. Methods   | 24 |
| 2.3.1. Data Model  | 25 |
| 2.3.2. Process Model   | 27 |
| 2.3.3. Characterizing Movement   | 31 |
| 2.3.4. Case Study: Canada Lynx Reintroduction in Colorado                        | 33 |
| 2.4. Results   | 34 |
| 2.5. Discussion  | 35 |
| 2.6. Declaration of Support  | 38 |
| 2.7. Tables and Figures  | 39 |
| CHAPTER 3. Large-scale movement behavior in a reintroduced predator population.  | 41 |
| 3.1. Summary   | 41 |
| 3.2. Introduction  | 42 |
| 3.2.1. Reintroduced Canada Lynx in Colorado                                      | 44 |
| 3.3. Materials and Methods   | 46 |
| 3.3.1. Movement Model  | 47 |
| 3.3.2. Characterizing Movement   | 49 |
| 3.4. Results   | 53 |
| 3.4.1. Movement Summary Statistics   | 53 |
| 3.4.2. Reintroduction and Exploratory Behavior                                   | 55 |
| 3.4.3. Correlations Between Vegetation and Movement                              | 56 |
| 3.4.4. Connectivity and Residence Area Identification                            | 56 |

|  |   |     |
|--|---|-----|
| 3.5.   | Discussion .....  | 58  |
| 3.5.1.   | Overview of Findings .....  | 58  |
| 3.5.2.   | Inference for Movement of Reintroduced Canada lynx in Colorado..... | 59  |
| 3.6.   | Declaration of Support .....  | 65  |
| 3.7.   | Tables and Figures.....   | 66  |
| CHAPTER 4. Drivers of Cougar Movement in a Wildland-Urban Interface..... |   | 74  |
| 4.1.   | Summary .....   | 74  |
| 4.2.   | Introduction .....  | 75  |
| 4.3.   | Methods .....   | 79  |
| 4.3.1.   | Data Collection.....  | 79  |
| 4.3.2.   | Continuous-Time Discrete-Space Framework .....                      | 80  |
| 4.3.3.   | Secondary Models for Movement Inference .....                       | 81  |
| 4.3.4.   | Landscape Covariates .....  | 83  |
| 4.4.   | Results .....   | 86  |
| 4.5.   | Discussion .....  | 89  |
| 4.6.   | Declaration of Support .....  | 94  |
| 4.7.   | Tables and Figures.....   | 95  |
| CHAPTER 5. Conclusion.....   |   | 109 |
| 5.1.   | Overarching Themes .....  | 109 |
| 5.1.1.   | Phenomenological Models for Animal Movement .....                   | 109 |
| 5.1.2.   | Multi-data Source Models.....                                       | 110 |
| 5.1.3.   | Population-Level Inference .....                                    | 111 |
| 5.2.   | Future Methodological Directions .....                              | 111 |

|   |     |
|---|-----|
| 5.3. Ecological Inference.....                        | 112 |
| REFERENCES .....                                      | 114 |
| APPENDIX A. Supplemental Material for Chapter 2 ..... | 142 |
| A.1. Prior Specifications.....                        | 142 |
| A.2. Deviance Information Criterion Calculation.....  | 143 |
| A.3. MCMC Algorithm.....                              | 144 |
| A.4. Spatial Quantities .....                         | 156 |
| A.4.1. Average Residence Time.....                    | 156 |
| A.4.2. Average Speed .....                            | 156 |
| A.4.3. Average Persistence in Direction.....          | 156 |
| A.5. Temporal Quantities .....                        | 158 |
| A.5.1. Average Residence Time.....                    | 158 |
| A.5.2. Average Speed .....                            | 158 |
| A.5.3. Average Persistence in Direction.....          | 158 |
| A.6. Case Study Tables.....                           | 160 |
| A.7. Simulations .....                                | 161 |
| A.8. References.....                                  | 162 |
| APPENDIX B. Supplemental Material for Chapter 3 ..... | 163 |
| B.1. Data Summary .....                               | 163 |
| B.2. Model Details .....                              | 175 |
| B.3. Spatial and Temporal Quantities .....            | 181 |
| B.3.1. Residence Time: Spatial.....                   | 181 |
| B.3.2. Residence Time: Temporal.....                  | 182 |

|             |   |     |
|-------------|---|-----|
| B.3.3.      | Average Speed: Spatial.....                                   | 182 |
| B.3.4.      | Average Speed: Temporal.....                                  | 183 |
| B.3.5.      | Average Tortuosity: Spatial.....                              | 184 |
| B.3.6.      | Average Tortuosity: Temporal.....                             | 185 |
| B.4.        | Spatial Quantities Standardized By Available Individuals..... | 187 |
| B.5.        | References.....   | 188 |
| APPENDIX C. | Supplemental Material for Chapter 4.....                      | 189 |
| C.1.        | Details on Continuous-Time Discrete-Space Model.....          | 189 |

## LIST OF TABLES

|       |   |     |
|-------|---|-----|
| 3.1   | Number of Canada lynx that used the same settlement area a given number of times, along with the range in the percentage of settlements occurring in the same area. Settlement areas were defined as those locations where an individual's relative speed was equal to or less than 50% of the contribution to total behavior for more than 30 consecutive days. A total of 29 individuals never settled more than once in the same location and one individual used more than one settlement area more than once (resulting in an additional "individual" in the table)..... | 66  |
| A.6.1 | Release and mortality dates for two Canada lynx, originally from a population in British Columbia, Canada, and released in the San Juan mountains, Colorado, in 2003. Contact was lost with BC03M04 in 2005, whereas BC03F03 died in 2005. .  | 160 |
| A.6.2 | Number of locations in each Argos error class and number of VHF locations for two Canada lynx, originally from a population in British Columbia, Canada, and released in the San Juan mountains, Colorado, in 2003. The Argos provided estimate of error increases from less than 250 m for class 3 to more than 1,500 m for class 0; no estimated error is provided for classes A and B (Collecte Localisation Satellites, 2014).....  | 160 |
| A.6.3 | Optimal variance terms for the regulator matrix and posterior means and 95% credible intervals for the covariance terms $c$ and $\rho$ for Canada lynx BC03M04 and BC03F03.....   | 160 |
| A.6.4 | Posterior means and 95% credible intervals for the measurement error standard error (m) for each data type for Canada lynx BC03M04 and BC03F03.....   | 160 |
| B.1.1 | Information related to the original population, sex, and release year of the Canada lynx used in the analysis. Original populations other than those designated as  |     |

|  |     |
|--|-----|
| “Colorado” were reintroduced individuals, whereas “Colorado” individuals were those encountered during the course of the study that were not reintroduced. . . .   | 163 |
| B.1.2 Details regarding each time series for the Canada lynx used in the movement analysis. I include the number of data points for each data type, date range (presented as month/day/year), and span (days) for each time series. After the functional movement model was fit, time series within an individual were analyzed as a single time series. . . . . | 164 |
| B.2.1 The covariance matrix in the data model allows us to model the non-elliptical Argos error as well as the elliptical VHF error. Note that these are the posterior mean and 95% credible intervals on the longitude scale and are not in meters. . . .   | 179 |

## LIST OF FIGURES

|     |  |    |
|-----|--|----|
| 2.1 | <p>Mean and 95% credible intervals of the marginal locations for two Canada lynx (BC03M04 (a) and BC03F03 (b)), with the observed locations. The posterior mean of each movement descriptor, shown with the counties of Colorado, for individuals BC03M04 (c) and BC03F03 (d) . The size of the point corresponds to spatial uncertainty and the transparency indicates the strength of the behavior at that location; for visualization purposes any value below 25% of the maximum value for that behavior is not shown. Coordinates correspond to Universal Transverse Mercator zone 13N.....</p> | 39 |
| 2.2 | <p>Mean relative movement descriptors through time and space for two Canada lynx reintroduced to Colorado (BC03M04 (a) and BC03F03 (b)). Coordinates correspond to Universal Transverse Mercator zone 13N.....</p>   | 40 |
| 3.1 | <p>Mean daily speeds, and 95% confidence intervals, for Canada lynx as a function of season and sex (Figure 3.1a). Mean daily speeds, and 95% confidence intervals, for female lynx (Figure 3.1b) as a function of season and reproductive status. The breeding season was defined as February-April, summer as May-September, and winter as October-January.....</p>  | 67 |
| 3.2 | <p>Mean daily tortuosity, and 95% confidence intervals, for Canada lynx as a function of sex and season (Figure 3.2a). For consistency, I present the results from the model with a sex-by-season interaction, although the addition of season did not significantly improve the model. Tortuosity of females (Figure 3.2b) was a function of both season and reproductive status. The breeding season was defined as February-April, summer as May-September, and winter as October-January... </p>   | 68 |

|     |   |    |
|-----|---|----|
| 3.3 | Mean duration, and 95% confidence intervals, of movement bouts made by Canada lynx as a function of sex and season (Figure 3.3a). For consistency, I present the results from the model with a sex-by-season interaction, although the addition of season did not significantly improve the model. I detected an interaction between season and reproductive status on the duration of movement bouts by female lynx (Figure 3.3b). The breeding season was defined as February-April, summer as May-September, and winter as October-January. .... | 69 |
| 3.5 | Proportion of the Canada lynx that made a movement bout in a given month across all years of the study (1999-2011). Light gray shading indicates breeding season, and dark gray indicates summer. ....  | 70 |
| 3.5 | Mean daily speed (Figure 3.5a) and tortuosity (Figure 3.5b) of Canada lynx as a function of years since their release. The decrease/increase in speed/tortuosity up to year 5 is likely a result of individual’s increasing familiarity with the landscape, while anecdotally older lynx (those that have survived 5+ years) tend to become nomadic. ....   | 71 |
| 3.6 | Mean daily speed (Figure 3.6a) and tortuosity (Figure 3.6b) of Canada lynx during their first year in Colorado as a function of years since the reintroduction program was initiated. ....  | 72 |
| 3.7 | Population-level spatial quantities of residence time (Figure 3.7a, Figure 3.7b), speed (Figure 3.7c, Figure 3.7d), and tortuosity (Figure 3.7e, Figure 3.7f). For reference, county boundaries and major roads are shown for Colorado (Figure 3.7a, Figure 3.7c, Figure 3.7e). Not included are rare movements to eastern states (Nebraska, Kansas, and Iowa). ....  | 73 |

|     |   |     |
|-----|---|-----|
| 4.1 | Map of Colorado counties, with the cougar movement study area plotted in gray (Figure 4.1a). Elevation (m; Figure 4.1b) and land classified as developed (dark gray is <10 acres/unit; Figure 4.1c)) is shown for the study area and surrounding area. ....   | 95  |
| 4.2 | Posterior means and 95% credible intervals for the individual- and population-level static effect of distance to nearest potential kill site on rate (Figure 4.2a) and directionality (Figure 4.2b) of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011.....                                | 96  |
| 4.4 | The mean and 95% credible intervals for the difference between the population-level posterior effects of landscape covariates on movement rates and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011; positive values indicate a stronger positive response in April..... | 97  |
| 4.5 | Posterior means and 95% credible intervals for the individual- and population-level static effect of heat loading on cougar movement rates in the Colorado Front Range for two-week periods in April and June, 2011. ....   | 98  |
| 4.6 | Posterior means and 95% credible intervals for the individual- and population-level static effect of distance to nearest roofed structure on cougar movement rates in the Colorado Front Range for two-week periods in April and June, 2011. ....   | 99  |
| 4.7 | Posterior means and 95% credible intervals for the individual- and population-level directional persistence of cougars in the Colorado Front Range for two-week periods in April and June, 2011.....  | 100 |
| 4.8 | Posterior means and 95% credible intervals for the individual-level time-varying effect of distance to nearest potential kill site on cougar movement rates in the  |     |

|      |   |     |
|------|---|-----|
|      | Colorado Front Range over two-week periods in April and June, 2011. A subset of two females and two males are shown. ....   | 101 |
| 4.9  | Posterior means and 95% credible intervals for the individual-level time-varying effect of distance to nearest roofed structure on cougar movement rates in the Colorado Front Range over two-week periods in April and June, 2011. A subset of two females and two males are shown. ....   | 102 |
| 4.10 | Posterior means and 95% credible intervals for the individual-level time-varying effect of distance to nearest road on cougar movement rates in the Colorado Front Range over a two-week periods in April and June, 2011. A subset of two females and two males are shown. ....   | 103 |
| 4.11 | Posterior means and 95% credible intervals for the individual- and population-level diel time-varying effect of distance to nearest potential kill site on cougar movement rates in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period). A subset of two females and two males are shown, along with the population-level effect. ....             | 104 |
| 4.12 | Posterior means and 95% credible intervals for the individual- and population-level diel time-varying effect of distance to nearest potential kill site on directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period). A subset of two females and two males are shown, along with the population-level effect. .... | 105 |
| 4.13 | Posterior means and 95% credible intervals for the population-level diel time-varying effect of elevation, distance to nearest road, and distance to nearest roofed   |     |

|       |  |     |
|-------|--|-----|
|       | structure on rate and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period).....   | 106 |
| 4.14  | Posterior means and 95% credible intervals for the population-level effect of distance to nearest potential kill site on rate and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011.....  | 107 |
| 4.15  | Posterior means and 95% credible intervals for the population-level diel time-varying effect of distance to nearest potential kill site on rate and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period).....   | 108 |
| A.7.1 | Mean and 95% credible intervals of the marginal location for three simulated individuals (a), (b), (c). The posterior mean of each movement descriptor, relative to the maximum value for that behavior where the size of the point corresponds to spatial uncertainty and the transparency indicates the strength of the behavior at that location; for visualization purposes any value below 25% of the maximum value for that behavior is not shown (d), (e), (f). Posterior means for relative movement descriptors through time and space (g), (h), (i)..... | 161 |
| B.1.1 | Argos and VHF locations from 1999-2011 for 165 Canada lynx that were reintroduced to Colorado. These locations were used to fit a functional movement model.....   | 174 |

B.2.1 Posterior mean trajectories for the 165 Canada lynx used in the movement analysis. Points are based on a daily interpolation and transparency reflects the concentration of points. .... 180

B.4.1 Population-level spatial quantities of residence time (B.4.1a), speed (B.4.1b), and tortuosity (B.4.1c) that have been scaled by the number of individuals using that grid cell. Posterior mean number of individuals observed in a grid cell over the observation period is also shown (B.4.1d). Not included are rare movements to eastern states (Nebraska, Kansas, and Iowa). .... 187

## CHAPTER 1

# INTRODUCTION

As top predators, carnivores exert a disproportionate influence on ecosystem structure and function (Treves & Karanth, 2003), despite being naturally rare (Ripple *et al.*, 2014). In addition, carnivores are particularly sensitive to habitat fragmentation and urbanization due to their large home ranges and low densities (Noss *et al.*, 1996). Their sensitivity and area requirements often make them conservation priorities, because conserving land for carnivores will inevitably encompass habitat for smaller species (Noss *et al.*, 1996). Recent technological advancements allow researchers to gain unprecedented insight into how carnivores are interacting with the landscape. In this chapter, I discuss the habitat associations, movement ecology, and available data for two carnivores native to Colorado: Canada lynx (*Lynx canadensis*) and cougars (*Puma concolor*). I also present details on the standard methods that are currently used to infer movement from telemetry data.

### 1.1. CANADA LYNX

#### 1.1.1. *Distribution*

Canada lynx are a North American habitat specialist, and their distribution is closely tied to the presence of boreal forest and snowshoe hares (*Lepus americanus*), which constitute the majority of their diet (as reviewed in Mowat *et al.*, 2000). The majority of research on Canada lynx has focused on populations in the Alaskan and Canadian taiga (Ruggiero & McKelvey, 2000). However, their range also extends south into the subalpine and boreal/hardwood forest ecotones of the contiguous states (McKelvey *et al.*, 2000a); lynx in these areas are typically referred to as “southern” lynx populations. Using multiple sources of

data from the 1800s to 1999, McKelvey *et al.* (2000b) found lynx were historically present in 24 states, primarily occurring in cool, coniferous high elevation forests in the Western U.S. In the Western U.S., 70% of occurrences were within elevations between 1,500-2,000 m and the distribution of occurrence shifts to higher elevations as one moves southward from Idaho and Montana (McKelvey *et al.*, 2000b). Observations also occurred disproportionate to availability in Rocky Mountain conifer forest, including areas consisting of Douglas-fir/western spruce fir and fir/hemlock (McKelvey *et al.*, 2000b).

Lynx habitat in the U.S. has been described as consisting of peninsular extensions of the northern boreal forest (McKelvey *et al.*, 2000b). McKelvey *et al.* (2000b) suggested that the dispersal rates between the Canadian lynx population and the populations in the contiguous U.S. are small and highly variable. It has been hypothesized that lynx on the southern edge of their range are a product of dispersing individuals from a population that has reached a recent high (Mech, 1973). Using historical presence data for the contiguous U.S., McKelvey *et al.* (2000b) found only 2% of lynx locations were >10 km from conifer forest; they viewed these as likely dispersal events and noted that long-distance dispersal, >100 km from conifer forest, was much rarer (0.01% of all locations, but 5% of dispersal locations). Dispersals are mostly described by long-distance movements that ended when the individual died (Aubry *et al.*, 2000).

### 1.1.2. *Habitat Associations*

In the contiguous U.S., much of the suitable lynx habitat likely contains few individuals. The available boreal forests have hare densities close to the lower limits required for lynx reproduction and varies with forest type and stand age (McKelvey *et al.*, 2000c). For a stable population, fluctuations in habitat quality lead to fluctuating sources and sinks; this

combined with the cyclic nature of lynx populations may cause unique patterns in local extinction and colonization in southern populations (McKelvey *et al.*, 2000c). On average, home range size in the U.S. corresponds to home ranges in the taiga when hares are scarce, with males having an annual home range of 151 km<sup>2</sup> and females having a home range of 72 km<sup>2</sup> (as reviewed in Aubry *et al.* 2000). Home range sizes tend to increase with decreasing lynx density (Mowat *et al.*, 2000). Lynx and snowshoe hare populations in the Western U.S. are more prone to metapopulation dynamics compared to the populations in the northern taiga, due to the fragmented landscape and the distribution of optimal habitat (Buskirk *et al.*, 2000b).

### 1.1.3. *Dispersal and Movement Ecology*

Exploratory movements (i.e., movements outside of a home range) have been documented during the summer for both male and female lynx, although dispersing individuals differed in age, time spent away from home range, and number of documented exploratory movements in Canada lynx (Squires & Laurion, 2000) and Eurasian lynx (Zimmermann *et al.*, 2005). Exploratory movements have not been documented in northern Canada or Alaska, which contains more homogeneous boreal habitat. Exploratory movements may be a response to high landscape heterogeneity, because the probability of successful dispersal would increase with increasing knowledge of the heterogeneous landscape (Aubry *et al.*, 2000). In addition, lynx have been known to travel through suitable habitat without establishing a home range; low prey density is the hypothesized cause of this behavior (Mech, 1973).

Long-range movements are more common during periods when snowshoe hare populations are declining (McKelvey *et al.*, 2000c). Lynx are highly dependent on snowshoe hares as a primary food source; in northwestern Montana, 96% of lynx prey biomass consisted

of snowshoe hares, and alternative prey (e.g., red squirrels [*Tamiasciurus hudsonicus*]) contributed little biomass despite low hare densities (Squires & Laurion, 2000). However, the degree of dependence on hares is highly variable, decreasing to as little as 35% of the diet in some regions (as reviewed in Ruggiero *et al.* 1994). In Colorado, red squirrels comprised up to 20% of lynx prey items in some years, potentially as a result of periods of low snowshoe hare density or high red squirrel abundance (Ivan & Shenk, 2016). Less prey specialization in more southern and western lynx populations can lead to a decoupling in the relationship between lynx and hare densities (Roth *et al.*, 2007).

In Canada, juveniles disperse in spring at age of independence, whereas mid-winter dispersal is indicative of nutritional duress (Mowat *et al.*, 2000). Little is known about natal dispersal of Canada lynx, and dispersal timing and behavior varies considerably (Mowat *et al.*, 2000, as reviewed in). At low hare densities (0.5 hares/ha) in the southwestern Yukon, some marked lynx became nomadic, with three females covering a minimum area of 60-255 km<sup>2</sup> over 2-4 months (Ward & Krebs, 1985). Straight line travel distance also increased from 2.2-2.7 km/day when there were 1.0 hares/ha to 5.5 km/day at 0.2 hares/ha (Ward & Krebs, 1985). Emigration out of study areas in Alaska and the Northwest Territories varied from 0-32%, with the majority of emigration occurring at the peak and decline of the hare cycle (O'Donoghue *et al.*, 1997). In the Yukon Territory, Canada, the lowest rate of emigration occurred in September-October (1%) and was highest in March-June (51%) (Slough & Mowat, 1996) with seasonality being stronger for females (Ferrerias *et al.* 2004). Forty-six percent of emigrants were between 1 and 5 years, 40.5% were yearlings, and 13.5% were kits (Slough & Mowat, 1996). No weight loss was observed in male lynx following their long-distance movements in Minnesota (Burdett *et al.*, 2007), although long-distance movements are often considered a response to low hare abundance (Ward & Krebs, 1985).

#### 1.1.4. *Colorado Reintroduction*

Due to the isolation of boreal habitat in Colorado relative to the nearest established populations of lynx, Colorado Division of Wildlife (now Colorado Parks and Wildlife; CPW) initiated a reintroduction effort in 1997 (Seidel *et al.*, 1998). Between 1999 and 2006, 218 wild-caught lynx were released in the San Juan Mountains within 40 km of the Rio Grande Reservoir; 30 individuals originated from Alaska, 48 from the Yukon Territory, 91 from British Columbia, 4 from Manitoba, and 45 from Quebec (Devineau *et al.*, 2010).

#### 1.1.5. *Available Data*

Individuals were released after being held at a rehabilitation center and equipped with either VHF devices (Telonics<sup>TM</sup>, Mesa, AZ, USA) or satellite/VHF collars (Sirtrack<sup>TM</sup>, Havelock North, New Zealand) with locations obtained using the Argos System operated by CLS Argos (<http://www.argos-system.org>, Devineau *et al.*, 2010). A total of 26 Colorado born lynx were also telemetered. Irregular location data were obtained from 1999-2011 due to one or both of the transmitter components failing, logistical constraints, or movement out of the study area. Post-release monitoring was conducted over a 20,684 km<sup>2</sup> area including the reintroduction area and surrounding high-elevation sites (>2,591 m; Devineau *et al.* 2010). During denning season (15 May-June 30) two flights per week were conducted to locate VHF-collared individuals throughout Colorado, Wyoming, and New Mexico; flights were performed weekly outside of denning season. VHF locations were also collected outside of the study area when the opportunity was available (Devineau *et al.*, 2010). Satellite collars activated once/week and were active for 12 hours/week. Individuals with failed transmitters were recaptured and re-collared if possible; when a mortality signal was detected, ground crews would locate and retrieve the carcass, usually within 3 weeks (Devineau *et al.*, 2010).

## 1.2. COUGARS

### 1.2.1. *Distribution*

The cougar (*Felis concolor*), also referred to as the “mountain lion” or “puma,” once had the largest geographic range of any native terrestrial mammal in the Western Hemisphere (Nowak, 2005). However, between European settlement and the early 1900s, the geographic distribution of cougars in North America had been reduced to one-quarter of the historical range (Logan & Sweanor, 2001). Most established cougar populations occur in the Western U.S. across a range of landscapes and elevations (Nowak, 2005).

### 1.2.2. *Habitat Associations*

On average, reported home range sizes are 48.6 km<sup>2</sup> (Gittleman & Harvey, 1982). However, there is significant variation among estimates due to local environmental conditions, intrinsic factors, and estimator choice (Anderson *et al.*, 1992). For example, Grigione *et al.* (2002) found that variation in home-range size can be attributed to intrinsic factors, such as sex and body mass, as well as extrinsic factors, such as relative deer abundance and season. In Utah, vacant home ranges of deceased resident females were filled by at least one of their independent female offspring or female offspring of adjacent resident females (Laing & Lindzey, 1993). Rarely did an immigrating female establish a home range in the vacated range, whereas vacated ranges by males were filled by immigrating males (Laing & Lindzey, 1993). This pattern of replacement results in clusters of related females and unrelated males.

Prey availability is a driving factor in cougar habitat selection. For example, cougars in western Washington used areas where suspected prey availability was high, such as low-elevation, early successional forests, and areas near water (Kertson *et al.*, 2011). Blecha (2015) also observed cougars foraging in areas with high mule deer utilization. In addition,

despite cougars demonstrating avoidance of high housing densities while foraging, hunting success was positively related to housing density (Blecha, 2015). Significant individual variation in resource selection has been observed, which may reflect the spatial distribution of prey items or the behavioral flexibility of a generalist predator (Kertson *et al.*, 2011; Wilmers *et al.*, 2013).

Cougars prefer riparian habitat for both their home-range and locations within their home-range (Dickson & Beier, 2002; Nicholson *et al.*, 2014). Whereas males demonstrate strong selection for riparian areas during feeding events, females avoid riparian areas (Benson *et al.*, 2016). Riparian areas contain abundant prey items and easily traversable terrain, but interactions with aggressive males may increase (Benson *et al.*, 2016). In addition, Wilmers *et al.* (2013) found that cougars were less likely to use areas near development when close to water sources, likely due to increased human activity near water.

Cougars tend to avoid human-dominated landscapes (Dickson & Beier, 2002; Nicholson *et al.*, 2014), but also avoid some natural landscapes, such as grasslands (Dickson & Beier, 2002; Wilmers *et al.*, 2013). Within developed areas, cougars use areas with the most abundant native land cover, greatest prey use, and the least amount of anthropogenic disturbance (Kertson *et al.*, 2011). Wilmers *et al.* (2013) found that female cougars avoid areas of high housing density less than males and exhibited greater individual variation. Location of predation events relative to developed areas also varied by sex in the greater Los Angeles metropolitan area, with females selecting mule deer feeding sites closer to developed areas (but not in them) than males (Benson *et al.*, 2016). Females may show less avoidance of human disturbance due to increased food limitation or the presence of offspring (Wilmers *et al.*, 2013).

Benson *et al.* (2016) observed a functional response to development, with feeding sites occurring closer to developed areas as the amount of development decreased within an individual's home range. Knopff *et al.* (2014) also observed a functional response to anthropogenic landscape features, with selection of some features increasing as availability increased. However, other studies found no functional response of habitat selection to anthropogenic disturbance (Burdett *et al.*, 2010; Kertson *et al.*, 2011; Wilmers *et al.*, 2013). Blecha (2015) found that while cougars avoided foraging in areas of high housing density, most of the inter-individual variation in foraging site selection was attributed to housing density in the surrounding area. Individuals may also show temporal variability in their response to development, such as avoiding areas of anthropogenic activity less at night, while avoiding contiguous forest habitat less during the day; this pattern has been observed to be stronger for cougars in rural, rather than wilderness, areas (Knopff *et al.*, 2014).

### 1.2.3. *Dispersal and Movement Ecology*

Logan & Sweanor (2001) define dispersal as beginning when a subadult makes its first movement outside of its natal range and did not return; the age of dispersal in Utah occurred between 16 and 19 months (Hemker *et al.*, 1984). After individuals become breeding adults, they typically do not emigrate from their home-range (Logan & Sweanor, 2001). In a study in the San Andres Mountains, New Mexico, 63% of progeny dispersed from their natal home range; based on the 27 progeny that dispersed, males dispersed 8.1 times the distance of females (Logan & Sweanor, 2001). In a study in southern Utah, 12 of 32 cubs were observed dispersing out of the study area and those that could be relocated were found 6-44 km from their natal home range (Hemker *et al.*, 1984).

One of the farthest documented dispersals of a cougar was of a VHF-collared sub-adult male in the Black Hills of South Dakota; the straight line distance from the cougar's last known location, which was 92.4 km from the capture site, to the mortality site was 1,067 km, traveled over the course of 266 days (Thompson & Jenks, 2005). In addition, a female from the Oquirrh Mountains, Utah, was harvested 357 km due east of her capture site; however, using available GPS locations, it traveled an actual distance closer to 1,341 km (Stoner *et al.*, 2008). Dispersing individuals have been shown to orient their movement parallel to mountain ridges and cross valleys at their narrowest point (Stoner *et al.*, 2008). Movements across unsuitable habitat are typically short and unidirectional (Sweanor *et al.*, 2000), and are more likely to be made by males (Sweanor *et al.*, 2000). Although individuals do cross highways (Sweanor *et al.*, 2000; Logan & Sweanor, 2001; Stoner *et al.*, 2008), highway expansion is shown to decrease connectivity (Sweanor *et al.*, 2000).

Traveling and hunting cougars in southern California move slowly through riparian vegetation and fastest through grassland and areas heavily utilized by humans (Dickson *et al.*, 2005). They also use paths that are less rugged than the surrounding area, including dirt roads, but avoid two lane paved roads (Dickson *et al.*, 2005). Canyon bottoms likely correlate with an abundance of prey items, and cougars may be minimizing energy expenses by utilizing less steep slopes (Dickson & Beier, 2007). Cougars that are monitored over both nocturnal and diel time periods are observed using a wider range of habitats than would be inferred from an analysis of daytime locations (Dickson *et al.*, 2005). Kertson *et al.* (2011) found that nocturnal movement rates are higher than diurnal and crepuscular movement rates, but there was not statistical support for movement rates differing between wildland and residential areas.

True transient cougars are likely rare, but possibly occur when the population is isolated or diffuse, the food source is patchy and migratory, or the individuals are unable to compete (Logan & Sweanor, 2001). Many transients may actually be non-residents making a foray or undergoing a home range shift (Logan & Sweanor, 2001). For example, a female subadult in the Santa Ana Mountains covered 342 km in 4 months without establishing a home range, eventually returning to her natal home range (Beier, 1995). The majority of documented dispersers in the Santa Ana Mountains explored habitat peninsulas, extensions of wildland habitat into urban areas, despite no monitored adult performing similar explorations (Beier, 1995). Likewise, females in the San Andres Mountains made exploratory movements up to 66 km from their natal home range only to return and settle nearby after a short period (Logan & Sweanor, 2001). Duration of transient behavior by males may be variable, with some individuals settling immediately and others using multiple temporary home ranges (Beier, 1995; Logan & Sweanor, 2001).

#### 1.2.4. *Available Data*

Colorado Parks and Wildlife (CPW) trapped cougars from 2006-2016, fitting them with global positioning system (GPS) collars, and releasing them along the Front Range of Colorado. CPW used three different GPS collar manufacturers over the duration of the study (Lotek Wireless Inc., Newmarket, Ontario, Canada; Northstar Science and Technology LLC, King George, VA, USA; Vectronics GmbH, Berlin, Germany), and collars were programmed to record fixes every three hours.

### 1.3. METHODS FOR MODELING ANIMAL MOVEMENT

The true movement process of an individual is never observed, because there is no available method for monitoring animal movement continuously and without error. While contemporary methods, such as very-high frequency (VHF) or satellite telemetry devices, are more adept at detecting both long-distance (Koenig *et al.*, 1996; Trakhtenbrot *et al.*, 2005) and fine-scale (Hebblewhite & Haydon, 2010) movement than traditional capture-recapture methods, the data are still imperfect and intermittent observations of the true process. VHF data are limited by the frequency and timing at which telemetered individuals are located using a hand-held receiver, but battery life is relatively long for these devices. Aerial location accuracy associated with VHF data may be affected by antenna accuracy, altitude, and observer skill (Mech, 1983). Furthermore, ground triangulation accuracy may be impacted by terrain, vegetation, power lines, weather, equipment, and observer skill (White & Garrott, 1990). In contrast, the intended fix rate for a satellite telemetry device is typically preprogrammed and is often regularly spaced in time, although fix rates can be influenced by canopy cover, terrain, climatic conditions, and behavior (e.g., Di Orio *et al.*, 2003; Heard *et al.*, 2008; DeCesare *et al.*, 2005; Mattisson *et al.*, 2010). The preceding factors, in addition to the telemetry device engineering (e.g., GPS or Argos System), can also influence accuracy of the observed locations, which can include anisotropic error structures (e.g., Vincent *et al.*, 2002; Heard *et al.*, 2008; Costa *et al.*, 2010; Patterson *et al.*, 2010; Douglas *et al.*, 2012). Battery life depends on the amount of time the device attempts to acquire satellites, with more time spent searching corresponding to shorter battery life; however, decreasing search time decreases the fix rate and the precision of the estimated location (Hansen & Riggs, 2008). Both VHF and satellite components can be programmed into the same device or

individuals can be outfitted with two separate devices, leading to some data sets consisting of both data types.

Statistical models for animal movement have to account for motion in both space and time. Various methods have been proposed for dealing with movement in multiple dimensions, however, most methods can be placed into one of three categories: point process models, discrete-time models, and continuous-time models (Hooten *et al.*, 2017). The discrete and continuous-time models can be further delineated by whether they deal with space in a discrete or continuous framework (McClintock *et al.*, 2014a). The choice of modeling framework can have implications for implementation and inference, and many variations of these models have been investigated in the literature; I focus on the more commonly referenced examples within each category.

Measurement error can be incorporated into any of the following modeling frameworks. While the term “hierarchical model” is now ubiquitous in ecology (Royle & Dorazio, 2008; Bolker *et al.*, 2009), it should be noted that hierarchical movement models are occasionally referred to as state-space models. Regardless of terminology, hierarchical models consist of two components: a model for the true, underlying process, and a model for the observed data conditioned on the true process. When measurement error is ignored, the observed data are assumed to be generated by the true, underlying process.

### 1.3.1. *Point Process Models*

Spatial point process models are typically used to estimate space-use and resource selection, as opposed to the movement process. However, space-use and resource selection result from the movement process (Hooten *et al.*, 2017). In a spatial point process model, the locations of the points in space are considered to be random variables. Space-use is

frequently quantified using a kernel density estimator, which can provide the probability density function at any location in space given the true locations of the individual (Hooten *et al.*, 2017). Resource selection is concerned with the underlying decisions that give rise to the space-use of an individual and is modeled using a resource selection function (Manly *et al.*, 2007). In practice, resource selection is defined as use that is disproportionate to availability (Manly *et al.*, 2007), such that the point process arises from a weighted distribution with two components: a selection function and an availability function.

The selection function quantifies the individual's response to landscape variables, while the availability function accounts for the landscape that is available to an individual at a given time. Typically, the availability function is assumed to be uniform over the sample space (Aarts *et al.*, 2008), meaning that the individual can occur with equal probability anywhere within the support of the sample space. The support can be arbitrary, however it is usually chosen according to some biological understanding of the study species (Johnson, 1980; Manly *et al.*, 2007), which may be informed by the kernel density estimate for space-use (Hooten *et al.*, 2017). When the availability function is considered to be uniform, the true locations arise from the selection function alone. The weighted distribution itself is analytically intractable, and resource selection functions are typically fit by taking a background sample of locations that approximate the unused available habitat. Traditional methods such as logistic and Poisson regression can then be used to estimate the selection coefficients (Hooten *et al.*, 2017).

More recent extensions to the point process model, termed spatio-temporal point process models, relax the assumption of uniform availability, which allows the density of the availability function to vary with the previous location and the elapsed time between observed locations (e.g., Christ *et al.*, 2008; Johnson *et al.*, 2013; Brost *et al.*, 2015). These methods

account for the inherent autocorrelation that is present in telemetry data (Fieberg *et al.*, 2010). Step-selection functions are an approximation to spatio-temporal point process models (e.g., Fortin *et al.*, 2005; Roever *et al.*, 2010; Avgar *et al.*, 2016). While accounting for time-varying availability is important in modeling the decision making process of an individual, only one of these methods (Brost *et al.*, 2015) also accounts for uncertainty in the true location of an individual.

### 1.3.2. *Discrete-Time Models*

When the movement process itself is of interest, one may want to explicitly model the movement of an individual. In a discrete-time model, the modeled process occurs at regularly spaced intervals. The most simplistic discrete-time model is a random walk, where the true location at the next time step is an autoregressive process of order one. However, animal movement is rarely adequately described by such a model; instead, many discrete-time movement models are, at their foundation, a correlated random walk.

In contrast to a simple random walk, a correlated random walk accounts for the tendency of an individual to continue moving in the direction it had been moving, which can result in a smoother, more realistic movement path (Hooten *et al.*, 2017). Correlated random walks can be used to model a number of parameters that give rise to the observed movement path; for example, Forester *et al.* (2009) modeled step lengths, Morales *et al.* (2005) modeled step lengths and turning angles independently, McClintock *et al.* (2012) and Langrock *et al.* (2012) modeled step length and bearing independently, and Jonsen *et al.* (2005) modeled the velocity (turning angle and speed). In the latter case, modeling velocity induces correlation between the turning angle and speed. Correlated random walks can also include points of attraction (e.g., Langrock *et al.*, 2012; McClintock *et al.*, 2012) and multiple behavioral states

(e.g., Jonsen *et al.*, 2005; Morales *et al.*, 2005; Forester *et al.*, 2007; Langrock *et al.*, 2012; McClintock *et al.*, 2012, 2013). These models are known as state-switching or change-point models, and the number of change-points is usually difficult to estimate and must be specified *a priori* (Jonsen *et al.*, 2005, 2007; Gurarie *et al.*, 2009; Hanks *et al.*, 2011). Except for the early movement models that relied on tag-recovery or mark-recapture data, discrete-time models tend to be continuous in space.

Discrete-time models are attractive because the methods used in time-series analysis can be applied to telemetry observations (Hooten *et al.*, 2017) and it is easier to conceptualize and implement models in discrete-time, as opposed to continuous-time (McClintock *et al.*, 2014a). However, the movement process in discrete-time occurs at regular intervals, while the data themselves often occur irregularly in time (the time difference between observations is not consistent). Therefore, the data have to be aligned with the desired scale of inference, which requires a process known as imputation (McClintock *et al.*, 2012) and can be time-intensive.

### 1.3.3. *Continuous-Time Models*

Despite the advantages of discrete-time models, animals move in continuous-time. Therefore, a more realistic representation of animal movement would be formulated in continuous-time, such that inference can be obtained for any point in time (Hooten & Johnson, In Press). The continuous-time equivalent to a random walk is known as Brownian motion, and the correlated random walk equivalent is the Ornstein-Uhlenbeck process (McClintock *et al.*, 2014a). The Ornstein-Uhlenbeck stochastic process contains a Brownian motion component, but adds an additional drift component to allow for attraction to a central point

in the parameter space (Hooten *et al.*, 2017). The Ornstein-Uhlenbeck process was traditionally used to model autocorrelation when calculating space-use (e.g., Dunn & Gipson, 1977; Blackwell, 1997), but like the discrete-time models, it can also be used to model step length and turning angle (e.g., Gurarie *et al.*, 2009), velocity (e.g., Johnson *et al.*, 2008a), attraction (e.g., Johnson *et al.*, 2008a), and multiple behavioral states (e.g., Gurarie *et al.*, 2009). However, the modeling of multiple behavioral states in a continuous-time framework is not as well developed (but see Gurarie *et al.*, 2009) as it is in the discrete-time framework (McClintock *et al.*, 2014a) and is performed using *post hoc* clustering methods (e.g., Hooten *et al.*, 2010; Hanks *et al.*, 2011).

While the aforementioned models are all continuous in space, it is not uncommon to discretize over the spatial support of the process in a continuous-time framework. Formulating the model in discrete-space is often used when the ultimate goal is continuous-time inference on resource selection. Spatial covariates are usually discrete in space, therefore it can be useful in terms of inference and computation time to match the support of the process to the spatial covariates, which are discrete in space (e.g., Hooten *et al.*, 2010; Hanks *et al.*, 2011, 2015).

The movement model that is most widely used is probably the continuous-time correlated random walk (CTCRW) model as implemented by Johnson *et al.* (2008a). The CTCRW model is a continuous-time version of the discrete-time correlated random walk model of Jonsen *et al.* (2005). While it is a useful and reasonable model for animal movement, the primary reason for the widespread adoption of the CTCRW framework is the availability of the corresponding R package `crawl`, which has made implementing a continuous-time model significantly easier for non-statisticians (Johnson, 2016).

#### 1.4. OBJECTIVES

As I have illustrated, the field of movement modeling is rapidly evolving. However, many of the aforementioned models are computationally time-consuming and challenging to fit, particularly for data that were not collected explicitly for movement modeling. Most movement model applications focus on a few individuals and are not intended to provide biological inference across a suite of individuals (Hooten *et al.*, 2016). My goal was to develop flexible, efficient, and easy to implement movement models for telemetry data sets that can be used for individual- and population-level inference on movement behavior. I used these models, with existing data, to learn about the movement and space-use of two carnivore species native to Colorado: Canada lynx and cougars.

## CHAPTER 2

# A FUNCTIONAL MODEL FOR CHARACTERIZING LONG DISTANCE MOVEMENT BEHAVIOR<sup>1</sup>

### 2.1. SUMMARY

Advancements in wildlife telemetry techniques have made it possible to collect large data sets of highly accurate animal locations at a fine temporal resolution. These data sets have prompted the development of a number of statistical methodologies for modeling animal movement. Telemetry data sets are often collected for purposes other than fine-scale movement analysis. These data sets may differ substantially from those that are collected with technologies suitable for fine-scale movement modeling, and may consist of locations that are irregular in time, are temporally coarse, or have large measurement error. These data sets are time consuming and costly to collect but may still provide valuable information about movement behavior. I developed a Bayesian movement model that accounts for error from multiple data sources as well as movement behavior at different temporal scales. The Bayesian framework allows us to calculate derived quantities that describe temporally varying movement behavior, such as residence time, speed, and persistence in direction. The model is flexible, easy to implement, and computationally efficient. I apply this model to data from Colorado Canada lynx (*Lynx canadensis*) and use derived quantities to identify changes in movement behavior.

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<sup>1</sup>The material in Chapter 2 is based on the following publication: Buderman, F.E., M.B. Hooten, J.S. Ivan, and T.M. Shenk. 2016. A functional model for characterizing long distance movement behavior. *Methods in Ecology and Evolution* 7(3):264-273.

## 2.2. INTRODUCTION

Data sets consisting of animal locations are often collected for purposes other than movement analysis (e.g., survival analysis, demographic studies; White & Shenk 2001; Winterstein *et al.* 2001) or with technology that prohibits long-term fine-scale movement modeling (Yasuda & Arai, 2005). For example, radio-telemetry may be used to estimate survival (Cowen & Schwarz, 2005), but the locations may not be used in the analysis (e.g., Hightower *et al.*, 2001; Buderman *et al.*, 2014). These data sets are costly and time consuming to collect, but often contain a wealth of unused spatial information. The ability to spatially characterize movement behaviors using datasets that are insufficient for fine-scale movement modeling may help management and conservation agencies identify critical areas for wildlife movement (Berger, 2004). In addition, with appropriate temporal data, researchers can also better understand mechanisms that regulate movement behavior (Hays *et al.*, 2014; Scott *et al.*, 2014).

Runge *et al.* (2014) divide long-distance movements into four categories: irruption (dispersal), migration, nomadism, and intergenerational relays (which I do not address). Such movement behavior can vary among individuals and over an individual's lifetime, though some species may be more inclined to exhibit one kind of long-distance movement behavior (LDMB) over another (Jonzén *et al.*, 2011; Mueller *et al.*, 2011; Singh *et al.*, 2012). For most organisms, the causes and costs of dispersal will vary by individual and in space and time (Bowler & Benton, 2005), resulting in a continuum of movement behaviors (Jonzén *et al.*, 2011). LDMB may contribute substantially to population dynamics because it is the main determinant of population spread and colonization rates (Greenwood & Harvey, 1982;

Shigesada & Kawasaki, 2002). Thus, LDMB is an important life history trait for many processes such as species invasions, range shifts and local extinctions, reintroduction programs, metapopulation dynamics, connectivity, and gene flow (Trakhtenbrot *et al.*, 2005).

The spatial location of these behaviors could inform conservation efforts for species capable of long-distance movements, as some behaviors may be more important than others for population persistence (Runge *et al.*, 2014). In addition, comparing contemporary movement data with properly analyzed historical data may identify changes in movement behavior resulting from natural and anthropogenic disturbances. Changes in migratory behavior could have wide-ranging consequences in cases where the species contributes significantly to the biological assemblage (Robinson *et al.*, 2009). Species are usually limited in their range by dispersal ability, foraging ecology, or available habitat (Wood & Pullin, 2002; Hays & Scott, 2013), and as habitat fragmentation and climate variability increase, the ability of species to traverse long distance will become critical (Bowler & Benton, 2005). Species that have the capability for long-distance movement may be able to track habitat as environmental conditions change. However, individuals usually depend on a network of suitable habitats for different behaviors (e.g., breeding or migration; Robinson *et al.*, 2009). Long-term survival of the species can be reduced when the distance between patches exceeds dispersal ability (Trakhtenbrot *et al.*, 2005), or when suitable habitat is not available for all of the behaviors that occur during an annual cycle (Robinson *et al.*, 2009).

Although dispersal, migration, and nomadism are all LDMBs, they may differ in characteristics that can be quantitatively measured, such as residence time, speed, and persistence in direction (described using the turning angle). For example, areas where individuals are foraging or maintaining a home range may be identified by longer residence times or slower speeds (Schofield *et al.*, 2013) and undirected motion (Morales *et al.*, 2004). In contrast,

movement may be faster (Dickson *et al.*, 2005) and more directed (Haddad, 1999) within corridors. Nomadic individuals may exhibit similar speeds as migrators and dispersers, but they would appear to be perpetually dispersing, with no consistent activity center and a turning angle independent of previous movements (Lidicker Jr & Stenseth, 1992). Dispersal and migration may have similar speed and directional characteristics, but migration is a seasonally repeated movement between the same areas (Berger, 2004) by individuals within a population (Sawyer *et al.*, 2005), whereas dispersal is a one-way movement (Lidicker Jr & Stenseth, 1992).

Movement behavior is typically monitored using very-high frequency (VHF) or satellite telemetry devices. These monitoring devices are more effective at detecting LDMB than plot-based studies, which may underestimate long-distance movement (Koenig *et al.*, 1996). The frequency of VHF data is determined by how often an individual can be located and are spatially restricted to the actively searched area. Aerial location accuracy associated with VHF data may be affected by antenna type, altitude, and observer skill, while ground triangulation accuracy may be additionally impacted by terrain, vegetation, power lines, and weather (Mech, 1983). In contrast, the intended fix rate for a satellite telemetry device is preprogrammed and often regularly spaced in time. Fix success rates and accuracy can be influenced by animal behavior, such as diving behavior, canopy cover, terrain, and climatic conditions (e.g., Di Orio *et al.*, 2003; Heard *et al.*, 2008; Mattisson *et al.*, 2010; Dujon *et al.*, 2014). The device's satellite system (GPS or Argos Satellite maintained by Service Argos) can also influence accuracy of the location observations (Vincent *et al.*, 2002; Heard *et al.*, 2008; Costa *et al.*, 2010; Patterson *et al.*, 2010; Dujon *et al.*, 2014). In addition, fix success rate, battery life, and accuracy may all depend on transmitter manufacturer and model. Both VHF and satellite components can be placed into the same device or individuals can

be outfitted with two separate devices, resulting in data sets consisting of multiple data types.

Movement modeling often seeks to spatially characterize an individual's location as a function of time; however, this function may be highly complex and non-stationary. In addition, measurement error varies among monitoring methods and can be large enough to overwhelm small-scale movement patterns (Kuhn *et al.*, 2009; Breed *et al.*, 2011). Coupled with temporal irregularity and missing data, these attributes may prohibit the use of contemporary movement models. I have found that many available methods do not readily accommodate multiple sources of data and must impute missing data to obtain locations at regular intervals (e.g., Hooten *et al.*, 2010; Hanks *et al.*, 2011; Johnson *et al.*, 2011; Hanks *et al.*, 2015). For example, the continuous-time correlated random walk model presented by Johnson *et al.* (2008a) only accounts for elliptical error distributions. Breed *et al.* (2012) incorporated an augmented particle smoother into a CRW process model to allow for time-varying parameters, however their method does not account for multiple data sources and its effectiveness was only demonstrated on highly accurate GPS data at a fine temporal scale (10-30 locations/day). Winship *et al.* (2012) incorporated multiple data sources (Argos, GPS, and geolocation data) into a state-space model, but the method performed poorly when there were data gaps, relied heavily on the estimates of Argos precision presented in Jonsen *et al.* (2005), and treated the GPS data as equivalent to the best Argos location class. Change-point models require specifying or estimating the number of change-points, and the change-points are discrete in time (Jonsen *et al.*, 2005, 2007; Gurarie *et al.*, 2009; Hanks *et al.*, 2011); modeling smooth transitions in the change-point framework is more difficult. Given that one individual may exhibit many different LDMBs, I seek a model that is flexible enough to detect different types and degrees of movement behavior, without specifying or

estimating the number of change points. Brownian bridge movement models, a method commonly used with high-resolution telemetry data, have been shown to work well only when the measurement error is negligible (Pozdnyakov *et al.*, 2013) making them unsuitable for data sets obtained with VHF or Argos technology, which can be subject to substantial error. Recent applications of wavelet analyses also do not account for location error or uncertainty in the change-point identification and are not feasible with sparse and irregular data sets (Lavielle, 1999; Sur *et al.*, 2014).

Basis functions are a useful set of tools for approximating continuous functions, such as movement paths, when ordinary polynomials are inadequate to describe the behavior of the function (Rice, 1969). Commonly used basis functions include wavelets, Fourier series, and splines. Approximating a function with splines is computationally easy because the function is just a weighted sum of simpler functions (Wold, 1974), and such tools have been incorporated into standard statistical software. Wold (1974) recognized that splines may be most useful in low information settings where the ultimate goal is to compare individual estimates of a few characteristic parameters that describe the curve. Basis functions have been used extensively in fields such as physics (e.g., Sapirstein & Johnson, 1996), medicine (e.g., Gray, 1992) and medical imaging (e.g., Carr *et al.*, 1997), and climate science (e.g., Sáenz-Romero *et al.*, 2010). However, basis functions and associated statistical methods are less commonly used in ecology. Most applications focus on modeling species distributions (e.g., Leathwick *et al.*, 2005; Lawler *et al.*, 2006) and population dynamics (e.g., Bjørnstad *et al.*, 1999), though splines have broad applicability in generalized additive models (Hastie & Tibshirani, 1990; Wood & Augustin, 2002). For example, Hanks *et al.* (2015) used B-splines to model spatial transition rates as a function of location and direction-based covariates and time-varying coefficients. In addition, recent efforts have used B-splines to estimate

density functions associated with movement-related behavioral states (Langrock *et al.*, 2014). Tremblay *et al.* (2006) used Bezier, hermite, and cubic splines as strict interpolators of irregular telemetry data from ocean-obligate species; however, they assumed the filtered Argos locations were the true locations. There is also precedent in the statistical literature for the equivalence between stochastic movement processes, such as the Wiener process, and smoothing polynomial splines (Wahba, 1978; Wecker & Ansley, 1983).

I describe a functional approach to movement modeling using basis functions within a Bayesian model that accounts for multiple data types and their associated error, recognizing that the observed locations are not the true location. The basis functions allow us to account for temporal variation in the continuous underlying movement path without specifying movement mechanisms. I then use derived quantities, such as residence time, speed, and persistence in direction, to characterize movement behavior. In addition, the model is multi-scale, allowing for movement behavior at multiple biologically relevant temporal scales. I use this model to describe how reintroduced Canada lynx (*Lynx canadensis*) moved throughout Colorado. The two data collection methods, along with their measurement error and the sampling irregularity, make this an ideal data set to demonstrate the utility of my model.

### 2.3. METHODS

Conventional functional data analysis (FDA) assumes that there is a continuous underlying process, but the observations are temporally discrete, may be subject to error, and are temporally irregular (Ramsay & Dalzell, 1991; Ramsay & Silverman, 2002, 2005). Unlike traditional time series analysis, FDA does not assume stationarity or regularity of time intervals (Levitin *et al.*, 2007). The continuous function of interest is approximated using basis functions, which are a set of patterns that capture the main shape of the curve (Ramsay &

Silverman, 2005; Ferraty & Vieu, 2006; Hastie *et al.*, 2009). In my case, different sets of basis functions account for complexity in the process at different temporal scales, allowing us to detect both large and small-scale movement. In addition, FDA is useful when the objectives of an analysis are to estimate the derivatives of a function (Ramsay & Dalzell, 1991; Levitin *et al.*, 2007). In my framework, functions of temporal derivatives, such as residence time, speed, and persistence in direction, are derived quantities that can characterize the movement path. The Bayesian framework allows for inference concerning these derived quantities and their associated uncertainty while incorporating multiple data sources; for my purposes, I incorporated VHF and Argos data into a single model.

### 2.3.1. Data Model

I consider each observed (centered and scaled) location,  $\mathbf{s}_j(t)$  for a time  $t \in \mathcal{T}$  associated with data type  $j$  ( $j = 1, \dots, 6$  are Argos error classes and  $j = 7$  denotes VHF), to arise from a multivariate normal mixture model with mean,  $\mathbf{z}(t)$ , representing the true location at time  $t$ , and a covariance matrix  $\Sigma_j$  such that

$$(1) \quad \mathbf{s}_j(t) \sim \begin{cases} N(\mathbf{z}(t), \Sigma_j), & \text{if } w_j(t) = 1 \\ N(\mathbf{z}(t), \tilde{\Sigma}_j), & \text{if } w_j(t) = 0. \end{cases}$$

The covariance matrix,  $\Sigma_j \equiv \sigma_j^2 \mathbf{R}_j$ , represents the error variance associated with each data type where the correlation matrix is

$$(2) \quad \mathbf{R} \equiv \begin{bmatrix} 1 & \sqrt{c}\rho \\ \sqrt{c}\rho & c \end{bmatrix},$$

for  $j = 1, \dots, 6$ , and  $\mathbf{R} \equiv \mathbf{I}$  for  $j = 7$ . The prior distribution for the measurement error variance,  $\sigma_j^2$ , was modeled as an inverse gamma,  $\text{IG}(q, r)$ , where  $q$  is the shape parameter and  $r$  is the rate parameter. Argos error for all error classes has been shown to be larger than reported by Argos and greater in the longitudinal direction (Costa *et al.*, 2010; Hoenner *et al.*, 2012; Boyd & Brightsmith, 2013); therefore I use the parameter  $c$ , where  $c \sim \text{Beta}(\alpha_c, \beta_c)$ , to scale the error variance to be less in latitude than longitude. The  $\rho$  parameter scales the degree of covariance between latitude and longitude and is modeled as  $\text{Beta}(\alpha_\rho, \beta_\rho)$ .

The indicator  $w_j(t)$  determines which mixture component gives rise to the observed location and is modeled as  $\text{Bern}(0.5)$ . The covariance matrix of the rotated distribution,  $\tilde{\Sigma}_j$ , is calculated as  $\mathbf{H}_j \Sigma_j \mathbf{H}_j'$  where  $\mathbf{H}_j$  is a transformation matrix equal to

$$(3) \quad \mathbf{H} \equiv \begin{bmatrix} 1 & 0 \\ 0 & -1 \end{bmatrix}$$

for  $j = 1, \dots, 6$ , and  $\mathbf{H} \equiv \mathbf{I}$  (the identity matrix) for  $j = 7$ . The mixture model accounts for the fact that Argos error locations do not follow a symmetric distribution around the true location, but are more likely to be found in an x-pattern, due to the polar orbit of the satellites (Costa *et al.*, 2010; Douglas *et al.*, 2012). In preliminary analyses not presented here, the multivariate normal mixture model fit the data better than a multivariate normal non-mixture model. Argos locations are commonly modeled with a  $t$ -distribution to account for extreme outliers (following Jonsen *et al.* 2005), however the mixture model allows us to model anisotropic outliers. Though the aforementioned studies have modeled or estimated Argos error, the information is not directly applicable in the form of priors because the mixture model is a novel method for modeling Argos error and there is significant variability in reported estimates of Argos error (Costa *et al.*, 2010). Beginning in 2011, the Argos system

implemented a new algorithm that provides an error ellipse, as opposed to a radius, for each location (Lopez *et al.*, 2014). Recent work by McClintock *et al.* (2014b) used the ellipse parameters provided by the Argos system and a bivariate normal distribution to model the data.

### 2.3.2. Process Model

In the FDA paradigm, a continuous process for a set of times  $t$  ( $t \in \mathcal{T}$ ) is written as an expansion of  $M$  basis functions of order  $k$ :

$$(4) \quad z(t) = \sum_{m=1}^M c_m \phi_{m,k}(t),$$

where  $z(t)$  is the curve of interest,  $c_m$  is a coefficient that determines the weight of each basis function in the construction of the curve, and  $\phi_m(t)$  is a particular basis function (Levitin *et al.*, 2007). The type of pattern present in the data dictates the best choice of basis function; for example, splines are often used for non-periodic data, Fourier series for periodic data, and wavelet bases for data with sharp localized patterns. I employed the B-spline basis, which is commonly used in semi-parametric regression because it has local support and stable numerical properties when the number of knots (the points at which the basis functions connect) is large (Ruppert *et al.*, 2003; Keele, 2008). However, the model I present is general enough to accommodate any type of basis functions. B-spline basis functions are defined recursively according to the Cox-de Boor formula (see De Boor 1978). Let  $x_{m,k}$  denote the  $m$ th B-spline basis function of order  $k$  (cubic B-splines are 4th order and 3rd degree) for the knot sequence  $\tau$ , where  $k \leq K$ . Then for  $m = 1, \dots, N + 2K - k$ ,

$$(5) \quad x_{m,k}(t) = \frac{t - \tau_m}{\tau_{m+k-1} - \tau_m} B_{m,k-1}(t) + \frac{\tau_{m+k} - t}{\tau_{m+k} - \tau_{m+1}} B_{m+1,k-1}(t),$$

where  $N$  is the number of interior knots (Hastie *et al.*, 2009).

In the spatial statistics and signal processing framework, a continuous stochastic process is often written as a convolution, or a moving average, of a smoothing kernel function,  $k(\tau - t)$ , and a latent process (e.g., white noise),  $\eta(\tau)$ :

$$(6) \quad z(t) = \int_{\mathcal{T}} k(\tau - t)\eta(\tau)d\tau,$$

for  $\tau \in \mathcal{T}$  (Higdon, 2002; Lee *et al.*, 2002; Calder, 2007). When discretized, (6) takes on a general formulation (4) (Higdon, 2002; Lee *et al.*, 2002; Calder, 2007). Non-stationary processes can be modeled by allowing the kernel to be a function of time (or space) and not just distance (Higdon *et al.*, 1999; Higdon, 2002; Cressie & Wikle, 2011). In the context of animal movement, one can consider the smoothing kernel as some function that imposes temporal dependence on the observed locations (the latent process) to create a continuous and smooth movement path.

In my case, the location of an individual at time  $t$  in each direction,  $z(t)$ , is a function of an individual's geographic mean in that direction,  $\beta_0$ , and the summation of  $M$  cubic B-splines evaluated at time  $t$ ,  $x_{m,4}(t)$ , and the regularized, direction-specific coefficient,  $\beta_m$ , for that B-spline. The location in longitude and latitude is

$$(7) \quad z_{lon}(t) = \beta_{0_{lon}} + \sum_{m=1}^M x_{m,4}(t)\beta_{m_{lon}},$$

$$(8) \quad z_{lat}(t) = \beta_{0_{lat}} + \sum_{m=1}^M x_{m,4}(t)\beta_{m_{lat}}.$$

Using matrix notation, I can write (7) and (8) jointly as

$$(9) \quad \mathbf{z}(t) = \boldsymbol{\beta}_0 + \mathbf{X}(t)\boldsymbol{\beta},$$

where  $\mathbf{z}(t)$  is a vector describing the location in space at time  $t$ . The matrix  $\mathbf{X}(t)$ , is a 2-by- $2M$  matrix where  $\mathbf{x}(t)'$  is a row vector containing all of the B-splines evaluated at time  $t$ , such that

$$(10) \quad \mathbf{X}(t) \equiv \begin{pmatrix} \mathbf{x}(t)' & \mathbf{0}' \\ \mathbf{0}' & \mathbf{x}(t)' \end{pmatrix}.$$

As such, it can be multiplied by a single  $2M$ -by-1 vector of regularized coefficients

$$(11) \quad \boldsymbol{\beta} \equiv \begin{pmatrix} \boldsymbol{\beta}_{lon} \\ \boldsymbol{\beta}_{lat} \end{pmatrix}.$$

The regularized coefficients for higher order splines are not generally interpreted (Weisberg, 2014), but can be thought of as the contribution, or the directional forcing, of that basis function to the process at that time. The intercept,  $\boldsymbol{\beta}_0$ , can be interpreted as the geographic center of mass for each individual, for which I specified a relatively uninformative dimensional normal prior (Appendix A.1). I specified a normal prior with mean  $\mathbf{0}$  and covariance matrix  $\boldsymbol{\Sigma}_{\boldsymbol{\beta}}$  for the coefficients such that

$$(12) \quad \boldsymbol{\beta} \sim N(\mathbf{0}, \boldsymbol{\Sigma}_{\boldsymbol{\beta}}).$$

I selected three sets of B-splines and varied the number of knots to align with temporal scales I believe are biologically important for lynx movement: year, season (3 months), and month. Including multiple sets of basis functions allows the continuous function to capture behavior at different temporal scales without losing predictive capability when there is an absence of fine-scale temporal data. However, the required number of knots results in a large design matrix of coefficients that is difficult to visualize; for example, there were 36 and 41

basis functions for the two Canada lynx presented in the case study. The number of basis functions will increase as the length of the time series increases. I used the covariance matrix

$$(13) \quad \Sigma_{\beta} \equiv \begin{pmatrix} \sigma_{\beta_{lon}}^2 \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \sigma_{\beta_{lat}}^2 \mathbf{I} \end{pmatrix}$$

as a regulator in the ridge regression framework to shrink the coefficients  $\beta$ . The variance terms,  $\sigma_{\beta_{lon}}^2$  and  $\sigma_{\beta_{lat}}^2$ , control the smoothing in each dimension; a very small variance leads to underfitting, whereas a large variance can lead to overfitting (Eilers & Marx, 1996). I selected the variance components by calculating the Deviance Information Criterion (DIC; Spiegelhalter *et al.*, 2002) over 10,000 MCMC iterations and optimizing the DIC over 400 pairs of variance components (Appendix A.2). In simulation, I found that DIC and K-fold cross-validation methods performed similarly. The details of regularization and ridge regression are beyond the scope of this paper, and are explored in more detail in Hastie *et al.* (2009) and Hooten & Hobbs (2015).

The model described above yields the posterior distribution

$$(14) \quad [\beta_0, \beta, \sigma^2, \rho, c, \mathbf{w} | \mathbf{S}] \propto \prod_{j=1}^J \prod_{t \in \mathcal{T}} [s_j(t) | \beta_0, \beta, \sigma_j^2, \rho, c, w_j(t)] [\beta_0] [\beta] [\sigma^2] [\rho] [c] [\mathbf{w}],$$

where  $\sigma^2 \equiv [\sigma_1^2, \dots, \sigma_J^2]$ ,  $\mathbf{w}$  is a vector of the indicators  $w_j(t)$ , and  $\mathbf{S}$  is a matrix of observed locations. This is the form of a typical “integrated” model where multiple data sources provide information about the same underlying processes. Similar multi-data source models have become popular in demographic studies (e.g., Burnham, 1993; Barker, 1997; Nasution *et al.*, 2001; Schaub & Abadi, 2011), but have not been as common in movement studies (but see Winship *et al.*, 2012). If inference for multiple individuals is desired, the data model can be shared among individuals while the process model parameters  $(\beta_0, \beta)$  and regulator  $(\Sigma_{\beta})$

can be allowed to vary by individual. This model can be extended to account for additional stochasticity using a first-order Gaussian process, such that  $\mathbf{z}(t) \sim N(\boldsymbol{\beta}_0 + \mathbf{X}(t)\boldsymbol{\beta}, \sigma_\mu^2 \mathbf{R})$ , where  $\sigma_\mu^2 \mathbf{R}$  accounts for process error separately. Such Gaussian processes are commonly used as statistical emulators of complicated non-linear mechanistic models (O’Hagan & Kingman, 1978; Hooten *et al.*, 2011).

See Appendix A.1 for prior specifications. The model was fit using Markov Chain Monte Carlo (MCMC) and a Gibbs sampler was constructed to sample from the posterior using the full-conditional distributions for all parameters except  $\rho$  and  $c$ , because they were not conjugate. Metropolis-Hastings was used to sample  $\rho$  and  $c$ . See Appendix A.3 for R code (R Core Team, 2013).

### 2.3.3. *Characterizing Movement*

I am interested in quantities derived from  $\mathbf{z}(t)$  that can be used as movement descriptors. I describe three relevant derived quantities; however, my framework can be extended to other systems and conservation questions by modifying these quantities. These derived quantities represent the physical outcome in the movement path from various movement behaviors. The Bayesian framework allows us to obtain inference for derived quantities through Monte Carlo integration. These quantities can be visualized both temporally and spatially. All quantities are calculated in the MCMC algorithm using techniques described in Appendix A.4 and A.5.

To describe the quantities of interest spatially, I define a grid of equally sized regions,  $\mathcal{A}_l$  for  $l = 1, \dots, L$ , that comprise the area for which I desire inference. This method is similar to that used by Johnson *et al.* (2011) to describe diving behavior of northern fur seals (*Callorhinus ursinus*). The first derived quantity I describe is residence time,  $r_l$ , and

is calculated on each MCMC iteration as a per area frequency of locations in region  $\mathcal{A}_l$ :

$$(15) \quad r_l = \lim_{\Delta t \rightarrow 0} \sum_{t \in \mathcal{T}} \Delta t I_{\{\mathbf{z}(t) \in \mathcal{A}_l\}},$$

where the indicator  $I$  identifies whether location  $\mathbf{z}(t)$  was in region  $\mathcal{A}_l$ .

The second derived quantity of interest is speed. To calculate the average speed per unit of area, I first need the velocity between the location at time  $\mathbf{z}(t)$  and the location at time  $\mathbf{z}(t - \Delta t)$ . When  $\Delta t$  is sufficiently small, the first derivative of  $\mathbf{z}(t)$  with respect to  $t$  can be approximated by

$$(16) \quad \frac{d\mathbf{z}(t)}{dt} \approx \boldsymbol{\delta}(t),$$

where

$$(17) \quad \boldsymbol{\delta}(t) = \frac{\mathbf{z}(t) - \mathbf{z}(t - \Delta t)}{\Delta t}.$$

In practice,  $\Delta t$  is constant for the entire time series, and velocity is related to speed  $\nu(t)$  such that

$$(18) \quad \nu(t) = \sqrt{\boldsymbol{\delta}(t)' \boldsymbol{\delta}(t)}.$$

The average speed in  $\mathcal{A}_l$ , given a positive residence time, is

$$(19) \quad \bar{\nu}_l = \frac{\lim_{\Delta t \rightarrow 0} \sum_{t \in \mathcal{T}} \Delta t \nu(t) I_{\{\mathbf{z}(t) \in \mathcal{A}_l\}}}{r_l}.$$

A large average speed describes areas where the individual was moving quickly and spending little time. Therefore, large average speeds (19) identify areas that individuals may use to travel.

Persistence in direction is the third metric of interest and may be useful for describing directed, as opposed to nomadic, movement. I can describe persistence in direction by deriving the turning angle,  $\theta$ , using the velocity calculated in (17),

$$(20) \quad \theta(t) = \left| \arccos \left( \frac{\boldsymbol{\delta}(t+1)\boldsymbol{\delta}(t)}{\sqrt{\boldsymbol{\delta}(t)\boldsymbol{\delta}(t)}\sqrt{\boldsymbol{\delta}(t+1)\boldsymbol{\delta}(t+1)}}} \right) \right|.$$

Given that residence time is positive, the average turning angle,  $\theta(t)$ , in region  $\mathcal{A}_l$  is

$$(21) \quad \bar{\theta}_l = \frac{\lim_{\Delta t \rightarrow 0} \sum_{t \in \mathcal{T}} \Delta t \theta(t) I_{\{\mathbf{z}(t) \in \mathcal{A}_l\}}}{r_l}.$$

Alternatively, I can describe these quantities temporally, negating the need for a spatially defined grid. This decreases computation time and allows the quantities to be visualized temporally and spatially. Speed and persistence in direction can be calculated as they were in (18) and (20) and residence time can be calculated as the inverse of speed:

$$(22) \quad r(t) = \frac{1}{\nu(t)}.$$

#### 2.3.4. Case Study: Canada Lynx Reintroduction in Colorado

Colorado Division of Wildlife (now Colorado Parks and Wildlife) initiated a reintroduction program for Canada lynx (*Lynx canadensis*) in 1997. Between 1999 and 2006, 218 wild-caught lynx from Alaska, Yukon Territory, British Columbia, Manitoba, and Quebec were released in the San Juan Mountains within 40 km of the Rio Grande Reservoir (Devineau *et al.*, 2010). Individuals were fitted with either VHF collars (Telonics<sup>TM</sup>, Mesa, AZ, USA)

that were active for 12 hours per day or satellite/VHF collars (Sirtrack<sup>TM</sup>, Havelock North, New Zealand) that were active for 12 hours per week with locations obtained using the Argos system (Devineau *et al.*, 2010). Weekly airplane flights were conducted over a 20,684 km<sup>2</sup> area, which included the reintroduction area and surrounding high-elevation sites (>2,591 m; Devineau *et al.* 2010); attempts were made to locate each VHF-collared individual in the study area once every 2 weeks. Additional flights outside of the study area were conducted when feasible and during denning season (Devineau *et al.*, 2010). Accuracy of VHF locations were self-reported as 50-500 m (Devineau *et al.*, 2010). Irregular location data were obtained from 1999-2011 due to one or both of the transmitter components failing, logistical constraints, or movement out of the study area precluding VHF data collection. Therefore, data for each individual varies in the length of the time series, the temporal regularity of locations, and the number of locations from each data type and error class. I have analyzed the telemetry data from two Canada lynx (Appendix A.6).

I obtained 10,000 MCMC iterations, with a burn-in period of 1,000 iterations. Additional results from fitting the model to simulated data are available in Appendix A.7.

## 2.4. RESULTS

To visualize the fit of the model to the data, I calculated standard posterior quantities, such as means and 95% credible intervals for the marginal location in each direction (Figure 2.1a, 2.1b). Increasing uncertainty is evident during long periods of missing data (Figure 2.1a, 2.1b). The derived quantities were scaled relative to the maximum value for that quantity over the individual's lifetime and plotted both spatially, on a map of Colorado (Figure 2.1c, 2.1d, 2.2), and temporally (Figure 2.2). These relative values are useful for visualizing the degree of each behavior at a given time point, despite the quantities having

different units; the degree of shading represents the strength of that behavior, with the size corresponding to the spatial uncertainty (Figure 2.1c, 2.1d, 2.2). The optimal variance terms for the regulator matrix (13) and mean and 95% credible intervals for the covariance matrix (23) are presented in Appendix A.6.

Both individuals had multiple periods of fast speeds, large turning angles, and high residence times (Figure 2.1c, 2.1d, 2.2). For these individuals, high residence time often indicated a corresponding large turning angle, however these behavioral quantities were not always concurrent (Figure 2.2). For example, individual BC03M04 displayed periods early in the time series where the turning angle was the strongest quantity, while speed and residence time were fairly low, suggesting a searching or nomadic behavior (Figure 2.2a). Both time series culminated with the individuals residing in two specific counties (Clear Creek and Summit), which includes an area that is considered important lynx habitat (Loveland Pass; Colorado Parks and Wildlife, personal communication). These results also indicate that lynx are capable of consistent long-term movement across large distances without establishing an area of high residence time. For example, within a period of two months, individual BC03F03 traveled approximately 480 km (posterior mean), from the southern portion of Colorado (Mineral County) to southern Wyoming (Medicine Bow National Forest, specifically the area located within Carbon and Albany counties; Figure 2.2b).

## 2.5. DISCUSSION

The process model I propose falls within the same class of models as statistical emulators, functional data models, and process convolutions, and I showed that it can be written in much the same way. The model presented could be written as a hierarchical model, by allowing the latent process to be stochastic. However, it is well-known that hierarchical

models with two sources of unstructured error and lacking replication will have identifiability issues (Hobbs & Hooten, 2015). Given a situation where there are strong constraints on the movement process, it may be possible to separate data and process error. For example, Brost *et al.* (2015) were able to separately estimate data and process error in a resource selection framework by constraining the spatial domain of the process. However, their study focused on a marine mammal and therefore the process can be constrained to the marine environment (Brost *et al.*, 2015). Constraining movement in a terrestrial environment may be possible but is less intuitive and will impose strong assumptions.

In addition, one of the benefits of using a functional data approach is its flexibility, in contrast to more constrained mechanistic models. The simplicity of the process model results in greater computational efficiency than other available methods for movement modeling. For example, my model can be fit on the order of minutes for each individual, compared to other models that require on the order of days (e.g., Hooten *et al.*, 2010; McClintock *et al.*, 2014a). Although small-scale movement patterns may be difficult to detect given the coarse temporal resolution and the large amount of measurement error associated with Argos locations, large-scale movement patterns are easily discernible and informative. However, researchers analyzing data at a finer temporal scale could discern small-scale movement with properly scaled basis functions (e.g., daily or weekly).

The model can be used to estimate an animal's movement path alone, but is especially useful for learning about movement behaviors that describe how individuals are utilizing the landscape. For example, persistence in direction may be used to infer when and where an individual is migrating or dispersing, whereas variation in direction may indicate habitat suitable for a home range (Haddad, 1999; Morales *et al.*, 2004). In the data I analyzed, the movement descriptors corresponded with anecdotal evidence of lynx movement behavior.

Many existing methods for analyzing location data explicitly model the quantities that give rise to the movement path (e.g., speed, turning angle, residence time, velocity), such that the quantities must be estimated while fitting the model (mechanistic models; e.g., Morales *et al.*, 2004; Jonsen *et al.*, 2005; Johnson *et al.*, 2008a; Breed *et al.*, 2012; McClintock *et al.*, 2012; Winship *et al.*, 2012). In contrast, I use the equivariance property of MCMC to calculate derived quantities as well as the proper uncertainty associated with each behavior (Hobbs & Hooten, 2015). Alternative *ad hoc* methods could be used, such as calculating derived quantities based on the mean predicted path, but to ensure the validity of those quantities as estimators with proper uncertainty, a procedure like the one I describe is necessary. Quantities of interest beyond those presented can be derived, such as bearing or tortuosity, or summarized with respect to temporal and spatial features. However, my model would need to be adjusted to accommodate other sources of measurement error (e.g., GPS data).

The model that I developed may be particularly well-suited for analyzing data sets that have not been collected explicitly for movement analysis. These data sets may contain multiple data types, have large amounts of error, and have been collected at a coarse temporal resolution. As such, they may not be conducive for fine-scale mechanistic movement modeling. I used a data set that embodied these characteristics, the telemetry data from the Canada lynx reintroduction to Colorado, to demonstrate that the FDA approach can be used to estimate movement paths and associated movement descriptors. The biological inference from the derived movement descriptors can also be extended beyond what I show here. For example, my framework could be extended to incorporate spatial and temporal covariates into the process model, similar to the approach described by Hanks *et al.* (2015). In addition, the spatial distribution of the movement descriptors can be used to summarize movement behavior across linear landscape features such as roads. Likewise, movement

behavior through non-linear landscape features, such as National Parks, can be described with the average posterior mean of a movement descriptor within a spatial boundary. My model can also be generalized for use with multiple individuals. In this case, the derived quantities can be aggregated to describe population-level movement. This type of population movement model allows the Argos and VHF covariance matrices to borrow strength across individuals, potentially improving parameter estimates. Such extensions are the subject of ongoing research.

## 2.6. DECLARATION OF SUPPORT

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Funding was provided by Colorado Parks and Wildlife (1304) and the National Park Service (P12AC11099). Data were provided by Colorado Parks and Wildlife (CPW ACUC #04-2000). The authors would like to thank the anonymous reviewers for their constructive commentary that helped improve the manuscript.

## 2.7. TABLES AND FIGURES

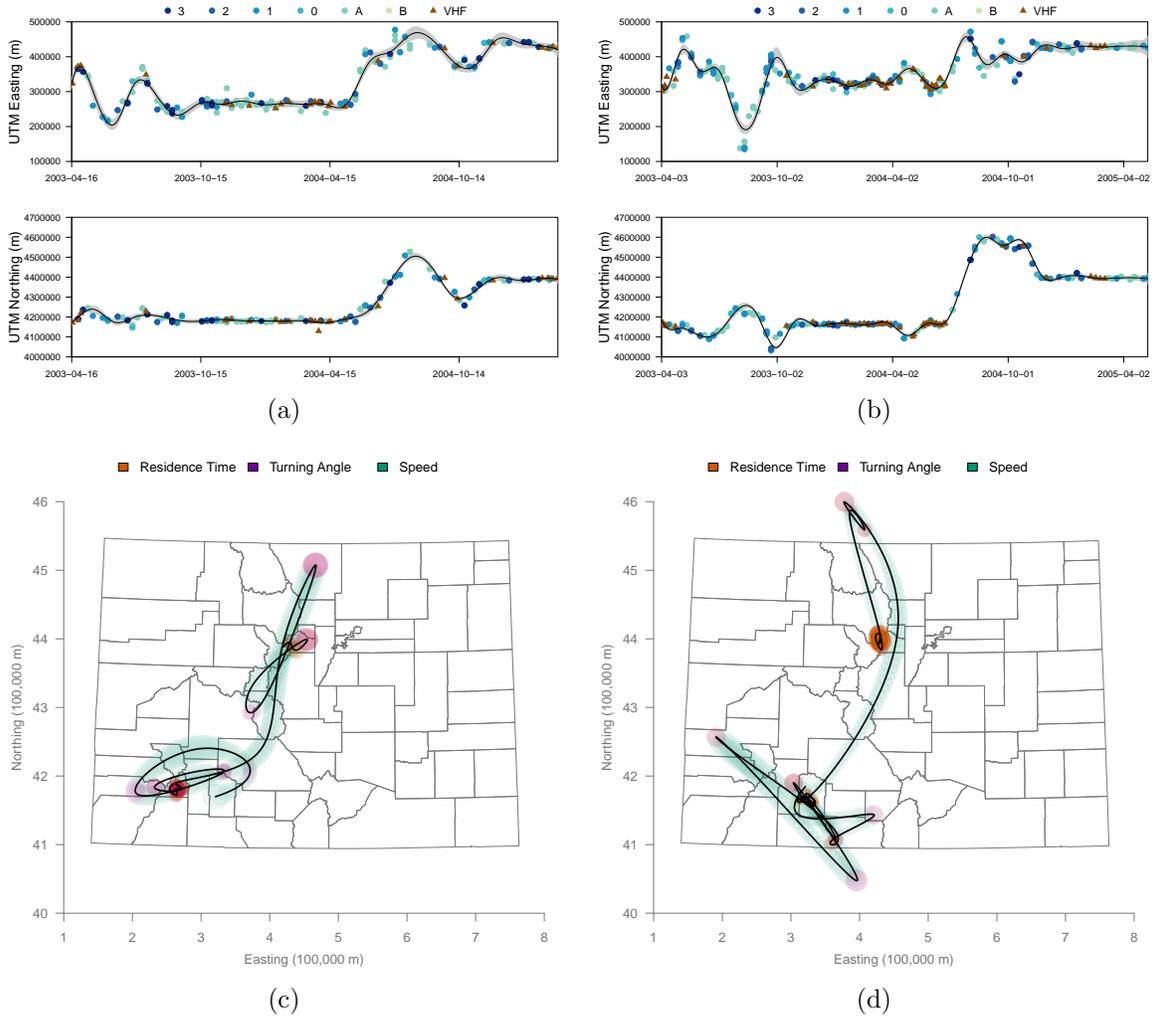
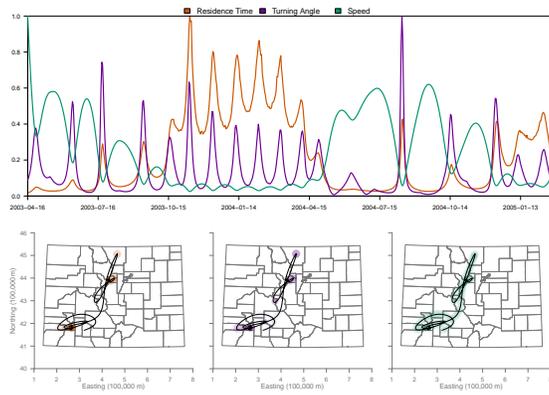
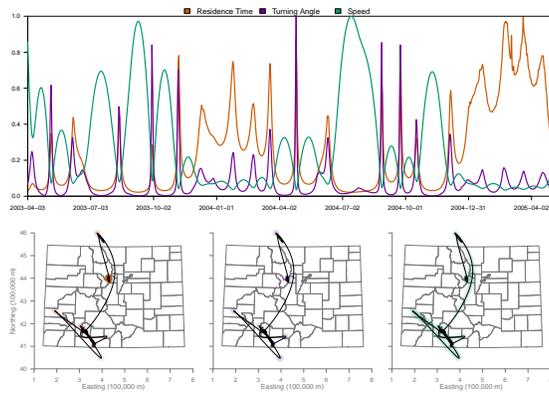


FIGURE 2.1. Mean and 95% credible intervals of the marginal locations for two Canada lynx (BC03M04 (a) and BC03F03 (b)), with the observed locations. The posterior mean of each movement descriptor, shown with the counties of Colorado, for individuals BC03M04 (c) and BC03F03 (d). The size of the point corresponds to spatial uncertainty and the transparency indicates the strength of the behavior at that location; for visualization purposes any value below 25% of the maximum value for that behavior is not shown. Coordinates correspond to Universal Transverse Mercator zone 13N.



(a)



(b)

FIGURE 2.2. Mean relative movement descriptors through time and space for two Canada lynx reintroduced to Colorado (BC03M04 (a) and BC03F03 (b)). Coordinates correspond to Universal Transverse Mercator zone 13N.

## CHAPTER 3

# LARGE-SCALE MOVEMENT BEHAVIOR IN A REINTRODUCED PREDATOR POPULATION<sup>1</sup>

### 3.1. SUMMARY

Understanding movement behavior and identifying areas of landscape connectivity is critical for the conservation of many species. However, collecting fine-scale movement data can be prohibitively time consuming and costly, especially for rare or endangered species, whereas existing data sets may provide the best available information on animal movement. Contemporary movement models may not be an option for modeling existing data due to low temporal resolution and large or unusual error structures, but inference can still be obtained using a functional movement modeling approach. I use a functional movement model to perform a population-level analysis of telemetry data collected during the reintroduction of Canada lynx to Colorado. Little is known about southern lynx populations compared to those in Canada and Alaska, and inference is often limited to a few individuals due to their low densities. Our analysis of a population of Canada lynx fills significant gaps in the knowledge of Canada lynx behavior at the southern edge of its historical range. I analyzed functions of individual-level movement paths, such as speed, residence time, and tortuosity, and identified a region of connectivity that extended north from the San Juan Mountains, along the continental divide, and terminated in Wyoming at the northern edge of the Southern Rocky Mountains. Individuals were able to traverse large distances across non-boreal habitat, including exploratory movements to the Greater Yellowstone area and

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<sup>1</sup>The material in Chapter 3 is based on the following publication: Buderman, F.E., M.B. Hooten, J.S. Ivan, and T.M. Shenk. In Revision. Large-scale movement behavior in a reintroduced predator population. *Ecography*

beyond. I found evidence for an effect of seasonality and breeding status on many of the movement quantities and documented a potential reintroduction effect. Our findings provide the first analysis of Canada lynx movement in Colorado and substantially augment the information available for conservation and management decisions. The functional movement framework can be extended to other species and demonstrates that information on movement behavior can be obtained using existing data sets.

### 3.2. INTRODUCTION

Functional connectivity, the degree to which the landscape facilitates or impedes movement among resource patches (Taylor *et al.*, 1993), is of critical importance for a number of ecological processes, such as gene flow (Coulon *et al.*, 2004; Keyghobadi *et al.*, 2005), metapopulation dynamics (Hanski, 1999), migration (Sawyer *et al.*, 2005), and range expansion (Safranyik *et al.*, 2010). Given the importance of connectivity for wildlife population persistence, its preservation and restoration have become conservation priorities. Many methods exist for identifying areas of high connectivity, but few of these methods are capable of quantifying realized functional connectivity of the landscape (Calabrese & Fagan, 2004). Whereas structural connectivity focuses on the spatial arrangement of the landscape in isolation of animal behavior, functional connectivity incorporates the behavior of the individual (Crooks & Sanjayan, 2006), either through knowledge about their physiology and dispersal capabilities (structural functional connectivity) or by observing individuals moving through a landscape (realized functional connectivity; Calabrese & Fagan 2004). The movement path of an individual arises from sequential decisions regarding their needs and perceptions of the surrounding habitat, and it is these decisions that ultimately give rise to the functional connectivity of the landscape (Tracey, 2006).

Despite the priority on maintaining and increasing connectivity, few methods for evaluating connectivity explicitly incorporate animal movement (but see Tracey, 2006; Tracey *et al.*, 2013). Realized functional connectivity can be difficult and labor intensive to measure because it requires long-term monitoring of individual movements (Ferrari *et al.*, 2007). However, the locations of individuals are often collected in conjunction with other monitoring data; existing data sets may contain a wealth of spatial information but were not explicitly collected to monitor movement across the landscape. Utilizing existing data on animal movement, despite its potential deficiencies, may provide the best available information for landscape-level management decisions intended to improve connectivity.

Connectivity planning, particularly the delineation and maintenance of corridors, is often associated with high costs and risks (Morrison & Reynolds, 2006). In an ideal scenario, connectivity planning would allow for data collection to explicitly identify optimal management decisions, such as corridor placement. Logistically, however, there are often time or budget constraints that preclude collecting data explicitly for the decision under consideration (Clevenger *et al.*, 2002). In addition, basic species-specific information, such as habitat requirements, movement abilities, movement behaviors (e.g., seasonality, age, and sex differences in movement), and facilitators or impediments to movement, is critical for informing management decisions, but is often lacking during the decision making process (Bennett, 1999). Given the costly and political nature of connectivity planning, existing data sets on animal movement may provide the best available information at a time when a decision needs to be made, particularly for rare or endangered species at low densities. However, novel methods may be necessary to deal with unique factors of existing data, such as irregular time intervals, missing data, and multiple data types.

I extended the approach presented by Buderman *et al.* (2016) to simultaneously model the movement paths of a population of individual animals using data that were not collected with the intention of modeling animal movement, but that contain valuable spatial information. The functional movement modeling approach is flexible and can be modified to account for other types of measurement error beyond the combination of Argos (a polar-orbiting satellite system) and radio-telemetry data presented here. I used the modeled movement paths to identify temporal and demographic patterns in movement behavior across a threatened population of reintroduced Canada lynx (*Lynx canadensis*). Spatial patterns in movement behavior were used to identify areas that suggest high landscape connectivity. I obtained inference for movement behavior using derived quantities that can be modified to fit the species and system in question and are not constrained to those presented here.

### 3.2.1. Reintroduced Canada Lynx in Colorado

Canada lynx were designated as an endangered species in Colorado in 1973, although the last verified Canada lynx record occurred in 1974 (Halfpenny *et al.*, unpublished manuscript). The boreal habitat in Colorado is isolated from similar habitat in Montana (Findley & Anderson, 1956), making a natural recolonization from source populations unlikely. Therefore, Colorado Division of Wildlife (CDOW; now Colorado Parks and Wildlife) initiated a reintroduction program for Canada lynx in 1997 (Seidel *et al.*, 1998). Between 1999 and 2006, 218 wild-caught lynx from Alaska and Canada were fitted with radio-telemetry/Argos collars and released in the San Juan Mountains (Devineau *et al.*, 2010).

The southern Rocky Mountains consist of “boreal islands” separated by large areas of non-boreal vegetation, in contrast to the relatively homogeneous boreal zone in Canada (McKelvey *et al.*, 2000a). Snowshoe hares (*Lepus americanus*), the primary prey source for

lynx, have been observed in Colorado at densities equivalent to those during the low phase of population cycles in the northern boreal forests of Canada (Hodges, 2000; Ivan *et al.*, 2014), potentially due to the patchy and heterogeneous nature of spruce-fir habitat in the mountainous regions of Colorado (Wolff, 1980). The natural patchiness of optimal habitat may cause lynx in southern boreal forests to travel farther and more frequently to access an adequate amount of habitat (Aubry *et al.*, 2000). Evidence also exists for large exploratory movements of lynx in southern boreal forests, a behavior that has not been observed in northern populations (Aubry *et al.*, 2000).

Much of the published literature on Canada lynx focuses on northern populations, and Buskirk *et al.* (2000a) caution against extrapolating this information to southern boreal populations, as climate, topography, and vegetation differ significantly over the broad geographic range. The available information on lynx dispersal and long distance movement in southern boreal forests is typically unpublished, consists of small sample sizes, or has incomplete spatial coverage. The reintroduction effort in Colorado has produced an extensive data set of spatial and demographic information for Canada lynx in southern boreal forests, a data set that is nearly impossible to replicate today.

Given that Canada lynx are endangered in the state of Colorado and Federally threatened (United States Fish and Wildlife Service, 2014), information on their movement behavior can be of critical importance for management decisions. For example, the U.S. Forest Service and U.S. Fish and Wildlife Service have a Conservation Agreement that necessitated the identification of linkage areas for lynx that facilitate movement between and among parcels of lynx habitat (Claar *et al.*, 2003). However, the linkage areas in Colorado have not been modified since 2002, shortly after the reintroduction program was initiated. Information from the reintroduced population, over the course of ten years, can be used to modify linkage

area delineation. In addition to identifying temporal, spatial, and demographic patterns in movement behavior, I also explored the effect of the reintroduction on individual behavior.

### 3.3. MATERIALS AND METHODS

Reintroduced individuals were released in the spring and fitted with either radio-telemetry radio collars (hereafter referred to as VHF collars; Telonics<sup>TM</sup>, Mesa, AZ, USA) or VHF/Argos collars (Sirtrack<sup>TM</sup>, Havelock North, New Zealand). Satellite transmitters were active for 12 consecutive hours per week, during which time several locations over those 12 hours could be obtained using the Argos System (Devineau *et al.*, 2010). Weekly airplane flights were conducted over a 20,684 km<sup>2</sup> area, which included the reintroduction area and surrounding high-elevation sites (>2,591 m; Devineau *et al.* 2010); attempts were made to obtain a VHF location from each radio-collared individual in the study area once every 2 weeks. Additional flights outside of the study area were conducted when feasible and during the denning season (May-June; Devineau *et al.* 2010). Irregular location data were obtained from 1999-2011 due to one or both of the transmitter components failing, logistical constraints, or movement out of the study area that precluded consistent VHF data collection. Each winter, efforts were made to recapture reintroduced individuals and capture Colorado-born individuals to maintain an adequate sample of working telemetry devices throughout the study period.

There were sufficient data for modeling the movements of 153 of the 218 reintroduced Canada lynx, in addition to 12 Colorado-born lynx that were collared as adults (N=165, Appendix B.1). For certain individuals, time periods with missing data were large enough to cause computational stability issues; thus, based on preliminary analyses, I identified those cases and split the data into separate time series. The 216 resulting time series spanned 59-3,947 days (mean=756) and contained 26-1,257 data points (mean=202; Appendix B.1).

Argos class Z locations, which are conventionally deemed invalid, were removed from the data prior to analysis. Reproductive status of females was determined during denning season (May-June) through intense telemetry and den searches to locate females with dependent kittens each year; the breeding season was defined as February-April, summer as May-September, and winter as October-January.

### 3.3.1. *Movement Model*

Our lynx data contains multiple data sources, large measurement error, temporal irregularities, and a coarse temporal resolution. These characteristics result in a data set that may not be amenable to analysis with contemporary mechanistic movement models (e.g., Jonsen *et al.*, 2005; Johnson *et al.*, 2008a; McClintock *et al.*, 2012). To overcome these challenges, I extended a Bayesian model developed by Buderman *et al.* (2016) for telemetry data that were collected at coarse spatial and temporal resolutions.

As an alternative to a mechanistic movement model, the process model developed by Buderman *et al.* (2016) approximates the underlying non-linear and complex movement behavior with linear combinations of basis functions. A basis function is a continuous function that can either transform an existing covariate in space or time, or act as a covariate itself; in ecology, basis functions are often used in generalized additive models (Wood & Pullin, 2002), but are also used to model autocorrelated data (Hefley *et al.*, 2017). In a movement context, multiple sets of basis functions operate as covariates that push or pull the movement process away from the geographic mean to create a representation of the underlying true path. The multiple sets of basis functions allow the movement behavior to change according to different temporal scales and allows for time-varying heterogeneity in movement without specifying or estimating the number of behavioral change-points or states (e.g., Jonsen *et al.*, 2005, 2007;

Gurarie *et al.*, 2009; Hanks *et al.*, 2011). The data component of the model presented by Buderman *et al.* (2016) uses multiple data sources to contribute to learning about the same underlying process, allowing us to use both VHF and Argos data, in contrast to other movement models that have been developed for use with a single error structure (e.g., Johnson *et al.*, 2008a; Breed *et al.*, 2012; McClintock *et al.*, 2014b). Additionally, the model allows for data at irregular time intervals, alleviating the conventional need to impute missing data (e.g., Hooten *et al.*, 2010; Hanks *et al.*, 2011; Johnson *et al.*, 2011; Hanks *et al.*, 2015). These characteristics result in a flexible, phenomenological model for animal movement that correctly accounts for multiple data sources and allows for temporally irregular and sparse data.

I generalized the model developed by Buderman *et al.* (2016) to allow for statistically rigorous population-level inference by simultaneously modeling the independent movement processes for multiple individuals (153 reintroduced and 12 Colorado-born lynx) using a shared data model component; this is in contrast to Buderman *et al.* (2016), where the two individuals were modeled completely independently from one another. The process model variance components were tuned at an individual level using predictive scoring over a two-step grid search of the parameter space. I fit the population-level model using a Markov Chain Monte Carlo (MCMC) algorithm written in R (R Core Team, 2013), and posterior inference was based on 9,000 MCMC iterations. Appendix B.2 contains additional details for the model specification, estimated measurement error, and posterior mean trajectories of individuals.

### 3.3.2. *Characterizing Movement*

In what follows, I use the word “locations” to refer to modeled locations (the daily locations derived from the functional modeling framework). As the foundation for characterizing lynx movement behavior, I used the three quantities proposed by Buderman *et al.* (2016): residence time, speed, and tortuosity. Residence time was defined as the amount of time spent in a grid cell (the number of daily locations observed), and relative speed was calculated as the distance between sequential locations (because the modeled locations are regular in time, the distance is proportional to daily speed). I defined tortuosity as the degree to which individual’s orientation at time  $t$  deviates from time  $t - \Delta t$ , where large values indicate larger directional changes from one time to the next (I modeled locations daily, such that  $t - \Delta t$  is equal to one day). Spatial and temporal derivations of each quantity are presented in Appendix B.3, as well as a guide to which analyses correspond to each quantity. The Bayesian framework allowed us to obtain posterior inference for derived quantities using Monte Carlo integration (e.g., Hobbs & Hooten, 2015). Because the underlying movement process is modeled in continuous space and time, the derived quantities can be summarized spatially or temporally at any desired resolution. I calculated the temporal versions of speed and tortuosity at a daily resolution and used the posterior means as response variables in subsequent analyses.

An additional quantity was calculated by scaling speed and residence time by their maximum values and then dividing each by the sum of the two scaled quantities, such that the quantities can be viewed as the contribution to total behavior at that time. I describe three discretized behavioral modes based on the posterior means of these relative quantities: movement bouts, settlement locations, and exploratory movements. A movement bout was any time an individual’s relative speed exceeded 50% of the contribution to total behavior

(residence behavior is the complement). Settlement areas were identified as those locations where an individual's relative speed was equal to or less than 50% of the contribution to total behavior for more than 30 consecutive days, with initial settlement being the first location that resulted in a settlement (i.e., an initial home range). Exploratory movements were those locations that occurred between settlement locations following initial settlement.

I used linear mixed models with an individual random intercept for any analysis with multiple measurements per individual (R package `lme4`; Bates *et al.* 2014). Individuals that were split into separate time series for fitting the movement model were considered as the same individual in subsequent analysis. In all cases, the response variable was log-transformed and the mean and 95% Wald confidence interval for the fixed effects were presented on the real scale (due to the transformation, this results in geometric, not arithmetic, means). For analyses with a single response variable per individual I present the sample arithmetic mean and range across individuals. Likelihood ratio tests were used for model comparison.

3.3.2.1. *Movement Summary Statistics.* Daily speed, daily tortuosity, and duration of completed movement bouts were modeled as a function of sex, season, and reproductive status (for females). Patterns in movement initiation dates were determined by calculating the proportion of individuals that performed movement bouts compared to the number that could have performed a movement bout at that time. Finally, total distance moved from first to last location for each individual was calculated as the sum of the daily posterior mean speeds.

3.3.2.2. *Reintroduction and Exploratory Movement.* Of the 153 reintroduced individuals with sufficient data, 18 had large gaps between the reintroduction date and first modeled location, three had subsequent missing data before initial settlement, and four settled within a day of their release. These individuals were removed from the analysis of movement

from reintroduction to initial settlement, resulting in 128 individuals. To determine the immediate post-reintroduction behavior of lynx, given that they did not settle immediately after release, I calculated time from reintroduction to initial settlement, total distance moved from reintroduction to initial settlement, and straight-line distance from reintroduction to initial settlement as response variables in linear mixed models.

Temporal duration and distance of exploratory movements for reintroduced individuals following initial settlement were modeled as functions of sex. An additional 36 of the 128 individuals only completed an initial settlement and three had missing values during their only exploratory movement, leaving 89 individuals who performed a total of 196 exploratory movements (excluding those with missing data).

To investigate the effect of reintroduction on movement behavior, I compared annual 6-month periods that corresponded to the same date range as the first 6-months after an individual's release (e.g., January 1, 1999 to June 1, 1999 vs. January 1, 2000 to June 1, 2000, etc.). I analyzed a subset of individuals with multiple years of data and compared speed and tortuosity across years. I modeled data up to 7 years following release because few individuals remained telemetered longer than that. To account for the increasing population size as the reintroduction progressed, I modeled daily speed and tortuosity during the first 6-month period following an individual's release as a function of the year since the reintroduction was initiated (1999).

To quantify the return rate to a previous settlement location, I modified the `clusGap` function (R package `cluster`; Maechler *et al.* 2013) to use the Haversine formula for great-circle distance (R package `cluster`; Hijmans 2015) and calculated the optimal number of geographic clusters among settlement locations. Of 165 individuals (153 reintroduced individuals plus 12 Colorado-born individuals), nine individuals were never observed settling

in a location for more than 30 days and 40 only settled once (including two Colorado-born lynx). A remaining 40 individuals had inconclusive clustering results, which were indicated by the algorithm separating a single residence period into multiple geographic clusters (likely caused by slow unidirectional movement). Inference for return rates was obtained for the remaining 77 individuals that were observed settling more than once.

3.3.2.3. *Correlations Between Vegetation and Movement.* I used LANDFIRE (2008) data to assess correlations between habitat characteristics and movement bouts (indicating connectivity) and non-movement locations. Because of the large extent of the study area, I reclassified the 120 relevant LANDFIRE classes into 16 categories: agriculture, urban/developed, riparian willow, riparian non-willow (e.g., cottonwood, poplar, sedge, exotic), grassland/rangeland, water, barren (rock/snow/ice/talus), alpine/subalpine tundra/meadow, montane shrubland (e.g., Gambel oak, mesic mountain shrub, serviceberry, snowberry), xeric shrubland (e.g., sagebrush, saltbrush, greasewood), spruce-fir, mixed spruce-fir (e.g., spruce with Douglas fir, lodgepole, or aspen), pinyon-juniper, aspen, lodgepole pine, and montane mixed forest. I then extracted the raster values for times when individuals were and were not performing a movement bout.

3.3.2.4. *Connectivity and Residence Area Identification.* To identify areas of connectivity, I divided the western United States into equally sized grid cells (0.15 degree<sup>2</sup>) with boundaries determined by the minimum and maximum location values. The grid cell representation of the spatial surface facilitates computation, with smaller grid cells more closely approximating a continuous surface. To obtain population-level spatial quantities, I calculated the sum across individuals of the per grid cell posterior mean, such that the quantity represents the total mean behavior for any of the 165 individuals that entered that grid cell from 1999-2011. For example, cells with large values for speed indicated areas where lynx moved quickly (i.e.,

what I assume represent long distance movement behavior and thus indicates connectivity), or areas where many slow moving lynx aggregated (see Appendix B.4 for population averaged quantities). Assessing speed and residence time together can highlight those areas used for high-speed movements. Connectivity areas were indicated by areas of high speed and low residence time behavior, whereas residence areas were identified by large values for residence time.

### 3.4. RESULTS

#### 3.4.1. *Movement Summary Statistics*

Using a random effect for individual, I did not observe a statistically significant effect of sex on daily speed ( $\chi^2(1)=2.28$ ,  $p=0.12$ ): average daily speed was 0.93 km/day (CI=0.85-1.03). However, a season effect was statistically significant ( $\chi^2(2)=13,778$ ,  $p<0.0001$ ), and a season by sex interaction improved the model over just a season effect ( $\chi^2(3)=463$ ,  $p<0.0001$ ; Figure 3.1a). Using the season-by-sex interaction model, I found that both females and males exhibited greater daily speeds during the summer months (Figure 3.1a). On average, males moved slightly faster than females, but this difference was greatest during the summer months (Figure 3.1a). An interaction between season and female reproductive status was significant ( $\chi^2(3)=6,476$ ,  $p<0.0001$ ; Figure 3.1b), with non-reproductive lynx consistently moving faster than reproductive lynx. Speeds during the winter months were similar, regardless of reproductive status, but non-reproductive individuals moved significantly faster during the breeding and summer months (when the difference between groups was greatest; Figure 3.1b).

Using a random effect for individual, I found that sex did not have a statistically significant effect on daily tortuosity ( $\chi^2(1)=1.15$ ,  $p=0.28$ ): average daily tortuosity was 2.9 degrees/day (CI=2.81-2.99). I found that adding season as a fixed effect significantly improved the model ( $\chi^2(2)=1,739$ ,  $p<0.0001$ ), while an additional interaction between season and sex did not ( $\chi^2(3)=4.21$ ,  $p=0.24$ ). Average daily tortuosity, using the model with a season-by-sex interaction, showed that values for tortuosity were lowest in the summer for both sexes (Figure 3.2a). Female movement paths varied in tortuosity by reproductive status and season, with reproductive individuals having more tortuous movements, particularly in the summer ( $\chi^2(3)=477$ ,  $p<0.0001$ ; Figure 3.2b).

Accounting for sex marginally improved the model for duration of movement bouts ( $\chi^2(1)=3.73$ ,  $p=0.05$ ). On average, the duration of movement bouts was 25 days for females (CI=23-27) and 28 days for males (CI=26-30). One female and one male spent over 200 days in a continuous movement bout. I did find a seasonal effect on the duration of movement ( $\chi^2(3)=736$ ,  $p<0.0001$ ), but a model with a season by sex interaction did not perform better than a model with just a season effect ( $\chi^2(3)=4.46$ ,  $p=0.22$ ). The average duration of a male movement bout lasted slightly longer than a female's, but the difference was greatest during the breeding season and summer (Figure 3.3a). I found evidence for an interaction between season and reproductive status on duration of movement bouts for females ( $\chi^2(3)=8.73$ ,  $p=0.03$ ; Figure 3.3b). During breeding season, reproductive females made shorter movement bouts than non-reproductive females (Figure 3.3b).

Aggregating across years for each sex, I found a slight difference in the proportion of males and females performing movement bouts, particularly in April, May, and June (Figure 3.5). From reintroduction to last location (either mortality or collar failure, excluding the distance

potentially moved between non-modeled time periods), females moved, on average, a total distance of 1,322 km (range=139-4,116) and males moved 1,367 km (range=136-5,841).

### 3.4.2. *Reintroduction and Exploratory Behavior*

On average, given that they did not settle within one day of release, females and males spent over 5 months moving before establishing an initial settlement area (females: mean=157 days, range=4-571; males: mean=179 days, range=3-624). Mean total distance traveled from the reintroduction site to first settlement was 449 km for females (range=4-2,805) and 519 km for males (range=4-1,414). Standardizing by the number of days available to move, females and males moved, on average, 2.8 km/day (females: range=0.4-6.4; males: range=0.5-6.6). The reintroduction site and the initial settlement site were 96 km apart for females (range=2-766) and 126 km apart for males (range=6-643).

On average, given that an individual settled more than once, each individual performed 2.2 exploratory movements. Sex was not a significant predictor for the duration of exploratory movements ( $\chi^2(1)=1.96$ ,  $p=0.16$ ), which was, on average, 72 days (CI=62-85). Sex was also not a significant predictor for the total distance moved during exploratory movements ( $\chi^2(1)=1.63$ ,  $p=0.2$ ), which was, on average, 107 km (CI=82-139). Of the 196 exploratory movements, 44% were in the summer, 35% were in the breeding season, and 21% were in winter.

Daily speed decreased steadily over the first four years following an individual's release but then increased (Figure 3.5a). I also saw increasing values for daily tortuosity, which indicates that an individual is covering less ground from one day to the next (constrained movement within an area; Figure 3.5b). Accounting for the year since the reintroduction was initiated significantly improved the model for daily speed and tortuosity during the first

6 months following an individual's release ( $\chi^2(6)=107$ ,  $p<0.0001$  and  $\chi^2(6)=354$ ,  $p<0.0001$ , respectively). Although the 95% confidence intervals overlap, there is a suggestion that speed was higher (Figure 3.6a) and tortuosity lower (Figure 3.6b) as time since the reintroduction increased.

Of the 77 individuals that settled more than once, 26 never settled in the same location more than once. The remaining individuals used the same location for a settlement area 2-10 times, and those reused settlement areas often constituted a large percentage of their total settlements (Table 3.1). In addition, one individual used two separate settlement areas more than once.

#### 3.4.3. *Correlations Between Vegetation and Movement*

Approximately 56% of non-movement bout locations occurred in spruce/fir habitat, with an additional 12% and 10% occurring in aspen and alpine/subalpine habitat, respectively. Habitat designated as barren contained 10% of non-movement bout locations. All other habitat was associated with less than 3% of the residence locations. Movement bout locations also occurred predominately in spruce/fir habitat (40%), aspen (15%), and alpine/subalpine habitat (9%). Barren habitat contained 8% of movement bout locations. However, a greater proportion of movement locations occurred in alternative habitat compared to non-movement locations. For example, 7% of movement locations occurred in xeric shrublands, and 4% occurred in each of lodgepole pine habitat and montane mixed forest.

#### 3.4.4. *Connectivity and Residence Area Identification*

Values for residence time were largest in the San Juan Mountains of southwest Colorado, between the towns of Silverton and Creede (this area encompasses the reintroduction area; Figure 3.7a). Large values for residence time, compared to the surrounding area, can also

be seen in the Sawatch Range in the central part of the State, approximately 40 km east of Aspen (Figure 3.7a). At a population-level, individuals spent little time outside of the reintroduction area in Colorado (Figure 3.7b).

Within Colorado, population-level speeds were highest in the San Juan Mountains in southwest Colorado (Figure 3.7c). The overlap with areas of high residence time was likely because the summation will result in similarly large speeds if a grid cell contained a small number of fast individuals or a large number of slow individuals. Therefore, areas of high residence time may also be areas of high speeds (see Appendix B.4 for alternative quantities that account for the number of individuals using a cell and the posterior mean number of individuals that were observed in a cell). However, peak speeds in areas with low residence time (e.g., connectivity areas) occurred northeast of the town of Creede (i.e., east of the area where residence time peaked) at the base of a population-level path that extended along the Continental Divide through the Sawatch, Mosquito, and Front Ranges of Colorado before entering Wyoming (Figure 3.7c). From southern Wyoming, trajectories fork and dissipate as they move westward toward the Wind River, Wyoming, and Uinta Ranges and northward toward the Bighorn Mountains (Figure 3.7d). Multiple individuals that left Colorado used an area in the southern portion of Wyoming with individual paths intersecting at multiple points along the western border of Wyoming, but, proportionally, only a few individuals utilized these areas (Figure 3.7d).

The largest values for tortuosity correspond to the same areas as for residence time (Figure 3.7e). However, large values for population-level tortuosity also extended beyond the high residence time area (to the northwest and to the northeast along portions of the path to Wyoming), suggesting a boundary area where individuals spent time exploring but not settling (Figure 3.7e).

## 3.5. DISCUSSION

### 3.5.1. *Overview of Findings*

Generally, lynx moved at greater speeds and with lower tortuosity during summer compared to winter. Males moved slightly faster than females in summer, and non-reproductive females moved faster and in less tortuous paths than reproductive females during the breeding and summer seasons. Proportionally more individuals engaged in movement bouts during summer compared to other seasons. I found that reintroduced lynx spent an average of 5 months in a movement bout, given that they did not settle within one day of release, before establishing an initial settlement area (i.e., an initial home range). Locations of initial settlement areas averaged approximately 100 km from the release site. After initial settlement, more than half of the individuals engaged in at least one exploratory movement that lasted an average of 72 days, covered an average of 107 km, and occurred mostly during the breeding and summer seasons. Many individuals returned to the same settlement area after making an exploratory movement. Areas traversed during movement bouts generally encompassed larger proportions of alternative habitat (e.g., xeric shrublands, lodgepole pine forest, montane mixed conifer forest) than those used during non-movement bouts (e.g., spruce/fir forest, aspen, alpine or subalpine meadows). Residence behavior occurred mostly in southwest and central Colorado; however, I observed a population-level corridor of high-speed movement that extended from the southwest part of Colorado, through the central mountain ranges, and dissipated in southern Wyoming. While I can compare these findings to what has been seen in other southern lynx populations (e.g., Poole, 1997; Burdett *et al.*, 2007; Squires *et al.*, 2013), our study is unique in that the inference directly relates to conditions following a reintroduction.

### 3.5.2. *Inference for Movement of Reintroduced Canada lynx in Colorado*

Squires *et al.* (2013) found that lynx movement rates in the Northern Rocky Mountains averaged 6.9 km/day, which is considerably higher than those reported in northern populations during periods of high hare density but similar to those during cyclic lows. I found lower daily speeds, however the fine-scale movement information obtained by Squires *et al.* (2013) may account for this difference. There are many small-scale movements made by lynx that our model would fail to detect, because speed was calculated as the difference between daily locations. Our estimates of tortuosity represent the difference in direction of movement from one day to the next, therefore, as with speed, these estimates do not include the many fine-scale directional changes that lynx perform within a 24-hour period. Due to the resolution of the data, the splines used in this analysis were not intended to detect movement at a fine scale. However, the relative values of these estimates are still informative for distinguishing between behaviors that occur at relevant time-scales (e.g., days as opposed to hours). Directed movement paths (low tortuosity), such as those observed in Colorado, are typical for populations in marginal or patchy habitat, and may indicate that these lower elevation montane zones are facilitating movements between primary habitat blocks (Ruediger *et al.*, 2000). Fuller & Harrison (2010) found similar results for Canada lynx in northwestern Maine, where paths were more tortuous in habitat with greater densities of snowshoe hares. Comparable patterns have also been observed in other species; for example, Davies *et al.* (2013) found that koalas demonstrated highly torturous paths within habitat patches, and more linear paths when moving between patches.

While Poole (1997) considered dispersal in the Northwest Territories to occur when an individual Canada lynx moved  $\geq 5$  km from the boundary of a home range, and anything less to be an exploratory movement, I found that individuals often returned to a settlement

location after traveling distances larger than 5 km. However, similar to Poole (1997), I did not find that sex was an important factor in the total distance moved by lynx. I did find a difference in the duration of movement bouts by season, with both males and females spending more time in a continuous movement bout in the breeding season and summer compared to winter. Burdett *et al.* (2007) also found that some male lynx in Minnesota exhibited increased movements during the month of March, which was encompassed by our designated breeding season, while female lynx had the smallest home ranges during the summer months, when they were more closely associated with the den site. Therefore, I expected non-reproductive females to exhibit more movement behavior, because they are not spatially constrained. While the uncertainty in mean duration of a summer movement bout was large for reproductive females, I did find that non-reproductive females engaged in longer movement bouts during the breeding season.

In addition, some individuals traveled extremely large distances (e.g., >1,000 km). The majority of these individuals, particularly those moving east, were unlikely to be reproductively successful because there are no lynx populations in the central United States. Some individuals did move through potential lynx habitat in Montana where individuals could have encountered other lynx. Individuals that moved large distances traveled across significant stretches of marginal habitat, however their mortality risk may have been higher than individuals that did not leave the reintroduction area. For example, 20% of reintroduced Colorado lynx mortalities were due to vehicle collisions (Devineau *et al.*, 2010), similar to the 19% seen following their reintroduction to the Adirondack Mountains (Aubry *et al.*, 2000).

Our analysis suggests that individuals make longer movements at faster speeds during the first few years following release; this is not an uncommon finding for reintroduction programs. For example, Rosatte & MacInnes (1989) found that exploratory movements and

home ranges were many times greater for relocated urban raccoons (*Procyon lotor*) compared to non-relocated individuals. In addition, individuals that were relocated to a rural area, as opposed to a town, had a stronger response to the relocation, possibly due to a lack of familiarity with the surrounding area (Rosatte & MacInnes, 1989). The boreal habitat in Colorado is known to be more patchy and heterogeneous than boreal habitat in Canada and Alaska (McKelvey *et al.*, 2000a). These habitat differences may be sufficient to result in exploratory movements. In a reintroduced population of Eurasian lynx (*Lynx lynx*), Vandel *et al.* (2006) found that some individuals made exploratory movements during the first three months of being released, a behavior that gradually declined and ended with the individuals establishing a home range near or centered on the release site. In contrast, very few lynx in our study settled at the release site, and many individuals moved a large distance before initial settlement, often geographically far from the release site. This could be due to the large number of individuals released at a limited number of release sites.

Time since release has been shown to be an important factor in determining movement behaviors (e.g., distance between release and settlement sites, tortuosity) across species (Wear *et al.*, 2005). For example, while 13% of a reintroduced black bear (*Ursus americanus*) population returned to their capture site (approximately 160 km away) the non-homing individuals reduced their mean daily movements during the first month post-reintroduction (Wear *et al.*, 2005). del Mar Delgado *et al.* (2009) found that eagle owls (*Bubo bubo*) in the wandering phase of dispersal had less tortuous paths than individuals in the stop phase of dispersal (initiated after an individual finds a temporary settlement area), which, in turn, had less tortuous paths than territorial individuals; they suspected that changes in tortuosity are a function of familiarity with the landscape. Lynx exhibited a similar pattern, exhibiting decreased daily speed and increased tortuosity as they had been present on the landscape

for longer. The reintroduction effect in our study may also be confounded with individual age. Anecdotally, older age classes of lynx in Colorado are more likely to become nomadic, which is corroborated by the increase in daily lynx speeds at 5+ years since being released (Jake Ivan, CPW, personal observation). In addition, this population was reproductively successful, therefore the effect of reintroduction on movement was not ubiquitous enough to hinder the success of the reintroduction.

Squires *et al.* (2013) assumed that lynx respond similarly to the landscape during a dispersal event as they would within their home-range. However, habitat selection depends on the resources available to the individual (Johnson, 1980) and the costs associated with a particular habitat (Morris, 1992), which may vary across behaviors. For example Killeen *et al.* (2014), found that dispersing elk (*Cervus canadensis*) did not respond to NDVI (a measure of landscape productivity), whereas resident elk showed a strong positive relationship to NDVI. Similarly, Morrison *et al.* (2015) found that selection for open water, roads, and elevation differed between cougars (*Puma concolor*) establishing temporary home ranges and those making exploratory movements. While I found some similarities in the habitat types used by lynx during movement and non-movement behavior, a greater proportion of movement bout locations occurred in xeric shrublands, lodgepole pine, and montane mixed forest compared to non-movement bout locations.

Based on the modeled movement of individuals from 1999-2011, I identified an area of high connectivity at the population-level in the Front Range. Our results indicate that a substantial subset of individuals ventured beyond the reintroduction area, predominately to the north, both before and after initial settlement into a home range. However, the area of connectivity (indicated by high speed) I identified within Colorado is very wide, due to uncertainty in the individual movement paths and large amounts of individual variation.

Therefore, it is unlikely that the concept of a linear corridor connecting habitat patches is applicable for Canada lynx in Colorado. Cushman *et al.* (2009) believed that the concept of a corridor is limiting to the idea of connectivity, and connectivity should be considered broadly as the ability of an individual to traverse a landscape with variable resistance. Lynx were also observed using diffuse corridors, similar to those I observed north of Colorado, through varying habitat quality near the southern limit of their range in Canada, indicating that this type of behavior may be a function of the patchy landscape (Walpole *et al.*, 2012).

The area of high connectivity I identified along the Front Range from 1999-2011 may have changed as a function of intraspecific interactions (e.g., long-term settlement in areas previously used for movement between high quality habitats), although the population density is likely still low due to the population being at the southern periphery of their range where boreal forest is naturally patchy (Aubry *et al.*, 2000). Although uncertainty was high, I found evidence for new individuals making movements of higher speeds and lower turning angles as the number of years since the reintroduction was initiated increased, which may be a function of increasing lynx density at the reintroduction sites. Additionally, I did not explicitly account for temporal changes to the landscape (e.g., weather patterns at the reintroduction sites, amount of understory vegetation), therefore I cannot assume that the changes in lynx behavior over time are solely a function of lynx density. However, evidence for reintroduced lynx and their offspring using specific areas of Colorado can still inform where conservation efforts should be focused, while acknowledging that no single corridor will provide connectivity across all individuals.

Some movement analyses explicitly link movement to resource selection, typically using step-selection functions. However, most step-selection function models do not account for measurement error (e.g., Fortin *et al.*, 2005; Forester *et al.*, 2009; Avgar *et al.*, 2016).

While the spatio-temporal point process of Brost *et al.* (2015) is more general and incorporates measurement error into a resource selection framework, it is computationally intensive (Hooten *et al.*, 2017). The continuous-time discrete-space model developed by Hanks *et al.* (2015) could be used for analyzing drivers of lynx movement over short temporal spans, but the memory requirements for fitting the model across multiple years would exceed the current storage capabilities of most statistical software. In addition, the large amount of path uncertainty introduced by both the Argos error and the large temporal gaps in the time-series would inflate the uncertainty associated with inference on movement drivers. However, linking contemporary lynx movements to spatial covariates would provide natural resource agencies with additional information that could be incorporated into predictive models for evaluating impacts of landscape-level management actions and should be the subject of future research.

I demonstrated that extensions to the modeling framework presented by Buderman *et al.* (2016) were able to provide insight into movement of Canada lynx following their reintroduction to the Colorado. Using a statistical model for telemetry locations properly accounts for measurement error, which is present in the raw locations, and allows for continuous-time inference on how the animal is moving, not just where it was observed. While the Canada lynx data set uses a generalized form of the data model presented in Buderman *et al.* (2016), other data models, such as those for GPS locations, can be used in place of the one presented here, which is specific to combinations of Argos and VHF data. A version of the functional movement modeling approach with a simplified data model has been implemented in standard statistical software (R package `ctmcmove`; Hanks 2016). In addition, if locations are collected more frequently in time than the lynx data were, then fine-scale basis functions can be used to detect smaller changes in movement behavior. I also note that our definitions for

movement bouts, settlement locations, and exploratory movements can be modified to either match the definitions used by other studies or to reflect a different quantity of interest.

This data set is one of the largest for a population of Canada lynx in the lower United States and augments the available information on movement behavior and connectivity of southern boreal lynx populations. While many of the summary statistics were focused on increasing our understanding of movement behavior (e.g., timing, duration), the spatial summary of lynx movement behavior from existing data may be particularly useful for Federal and State agencies that are required to consider lynx space use in their project planning. As with many retrospective studies, complete information regarding Canada lynx movement behavior in Colorado is unavailable. However, inference can still be obtained by using flexible modeling approaches that relax the constraints of fine-scale movement models. While fine-scale movement data are preferable when developing a new study, a large investment was made in gathering existing movement data. Despite the potential need for novel methods to analyze existing data sets, they allow for invaluable inference for movements of rare and low-density species.

### 3.6. DECLARATION OF SUPPORT

Funding was provided by Colorado Parks and Wildlife (1304), the National Park Service (P12AC11099), Colorado Department of Transportation, and NSF DMS 1614392. Data were provided by Colorado Parks and Wildlife (CPW ACUC #04-2000). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

### 3.7. TABLES AND FIGURES

TABLE 3.1. Number of Canada lynx that used the same settlement area a given number of times, along with the range in the percentage of settlements occurring in the same area. Settlement areas were defined as those locations where an individual’s relative speed was equal to or less than 50% of the contribution to total behavior for more than 30 consecutive days. A total of 29 individuals never settled more than once in the same location and one individual used more than one settlement area more than once (resulting in an additional “individual” in the table).

|                           | Number of Times A Settlement Area Was Reused |        |     |        |     |     |    |    |     |  |
|---------------------------|--|--------|-----|--------|-----|-----|----|----|-----|--|
|                           | 2  | 3      | 4   | 5      | 6   | 7   | 8  | 9  | 10  |  |
| Returning Individuals     | 22   | 9      | 7   | 6      | 5   | 1   | 0  | 0  | 1   |  |
| Percentage of Settlements | 40-100                                       | 60-100 | 100 | 83-100 | 100 | 100 | NA | NA | 100 |  |

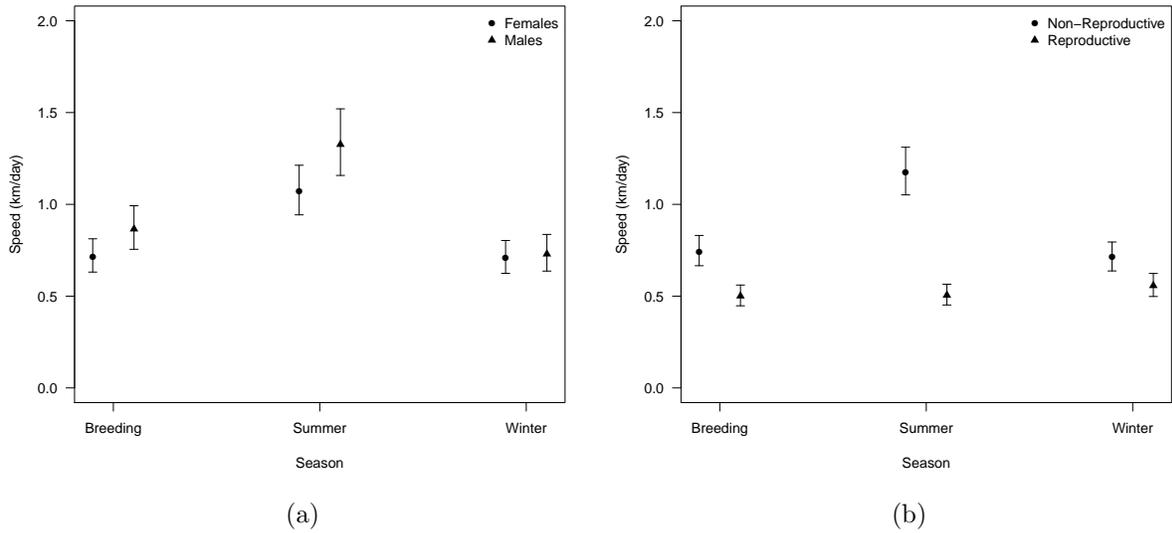


FIGURE 3.1. Mean daily speeds, and 95% confidence intervals, for Canada lynx as a function of season and sex (Figure 3.1a). Mean daily speeds, and 95% confidence intervals, for female lynx (Figure 3.1b) as a function of season and reproductive status. The breeding season was defined as February-April, summer as May-September, and winter as October-January.

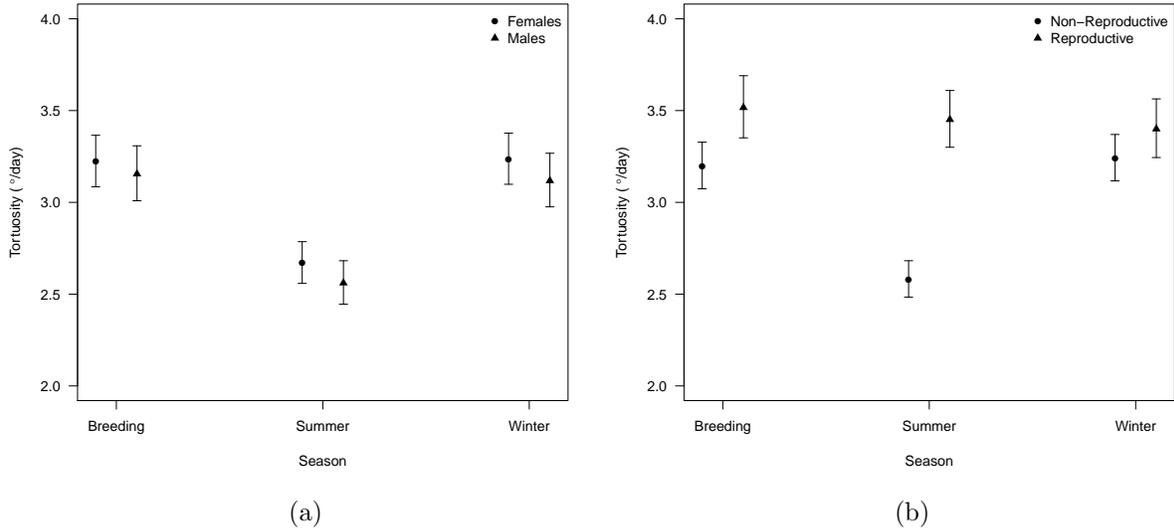


FIGURE 3.2. Mean daily tortuosity, and 95% confidence intervals, for Canada lynx as a function of sex and season (Figure 3.2a). For consistency, I present the results from the model with a sex-by-season interaction, although the addition of season did not significantly improve the model. Tortuosity of females (Figure 3.2b) was a function of both season and reproductive status. The breeding season was defined as February-April, summer as May-September, and winter as October-January.

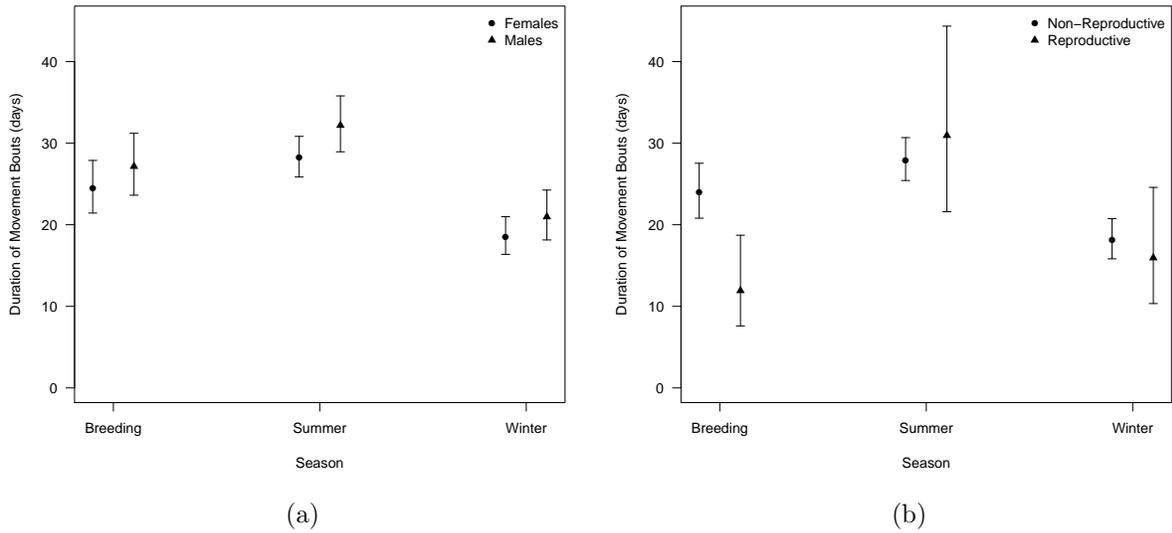


FIGURE 3.3. Mean duration, and 95% confidence intervals, of movement bouts made by Canada lynx as a function of sex and season (Figure 3.3a). For consistency, I present the results from the model with a sex-by-season interaction, although the addition of season did not significantly improve the model. I detected an interaction between season and reproductive status on the duration of movement bouts by female lynx (Figure 3.3b). The breeding season was defined as February-April, summer as May-September, and winter as October-January.

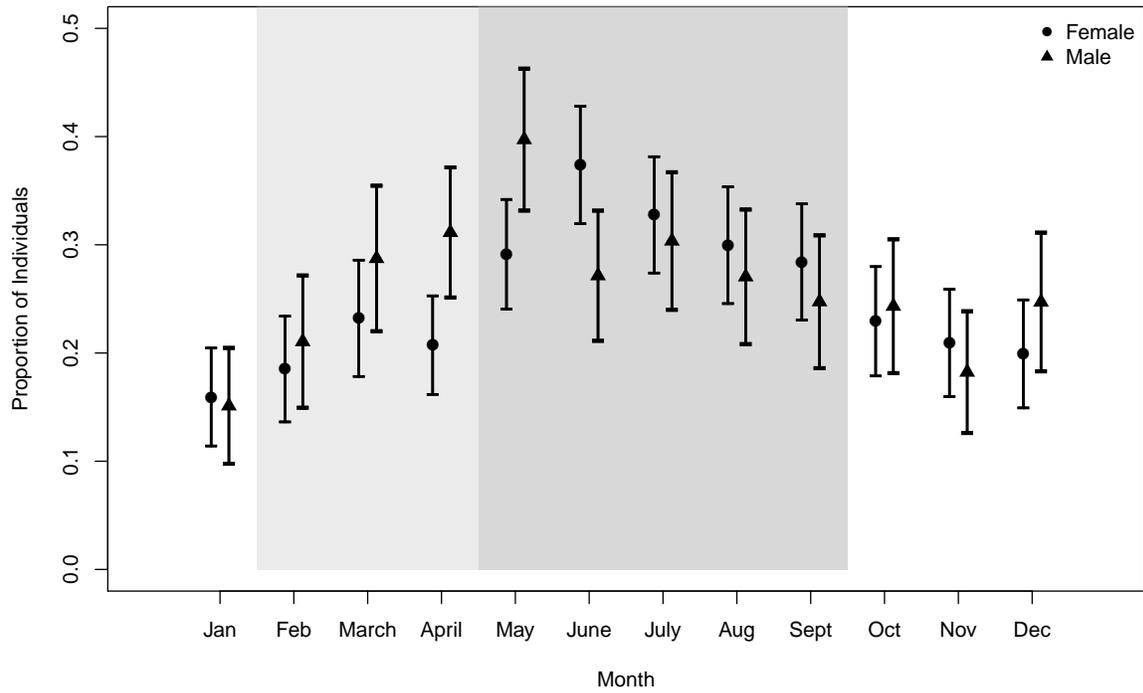
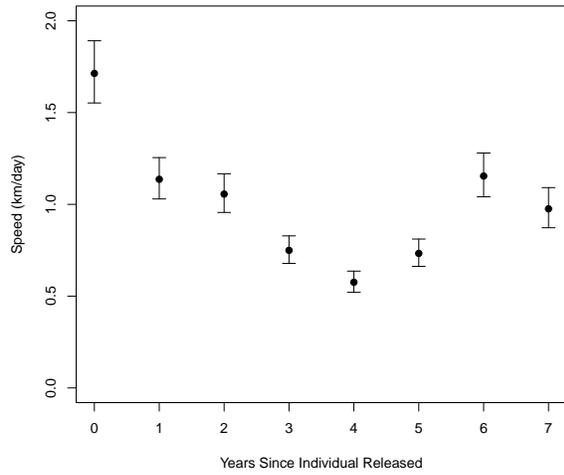
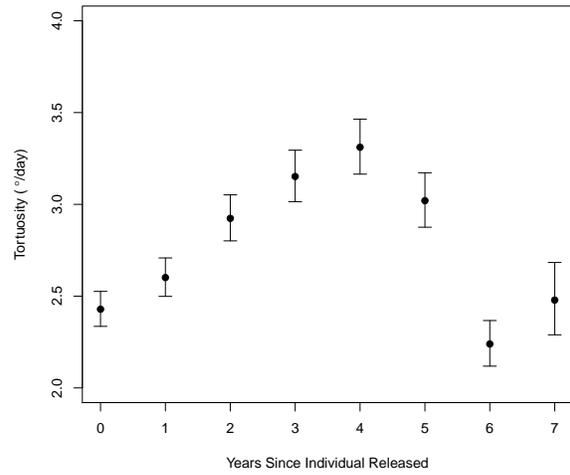


FIGURE 3.5. Proportion of the Canada lynx that made a movement bout in a given month across all years of the study (1999-2011). Light gray shading indicates breeding season, and dark gray indicates summer.

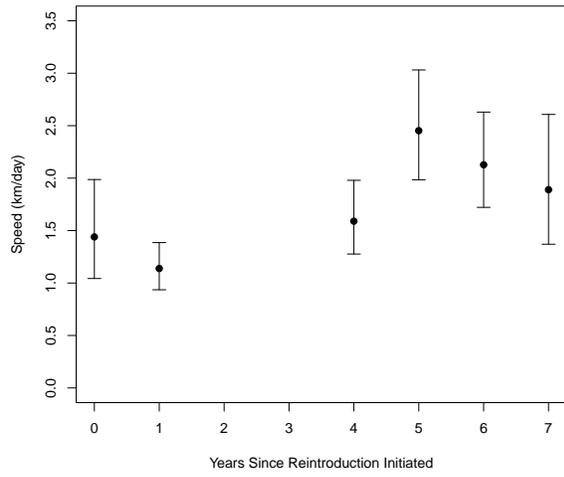


(a)

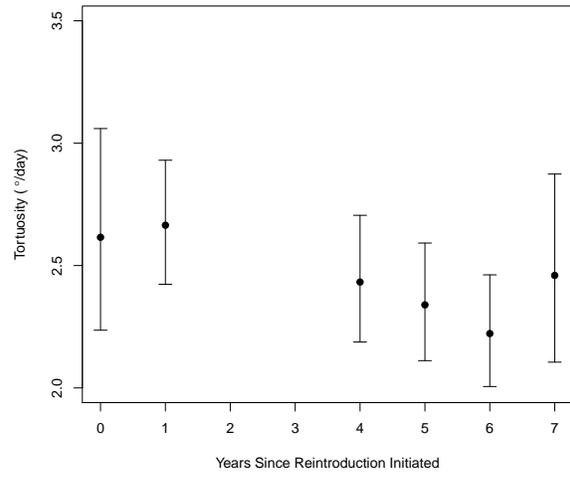


(b)

FIGURE 3.5. Mean daily speed (Figure 3.5a) and tortuosity (Figure 3.5b) of Canada lynx as a function of years since their release. The decrease/increase in speed/tortuosity up to year 5 is likely a result of individual's increasing familiarity with the landscape, while anecdotally older lynx (those that have survived 5+ years) tend to become nomadic.

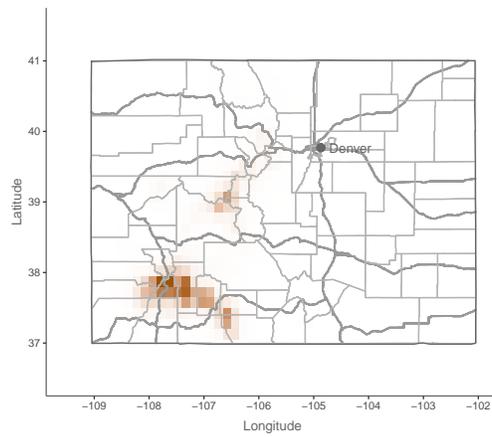


(a)

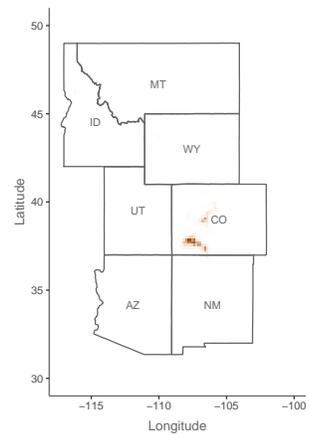


(b)

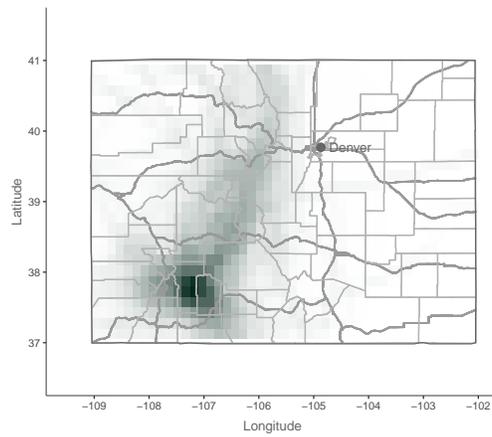
FIGURE 3.6. Mean daily speed (Figure 3.6a) and tortuosity (Figure 3.6b) of Canada lynx during their first year in Colorado as a function of years since the reintroduction program was initiated.



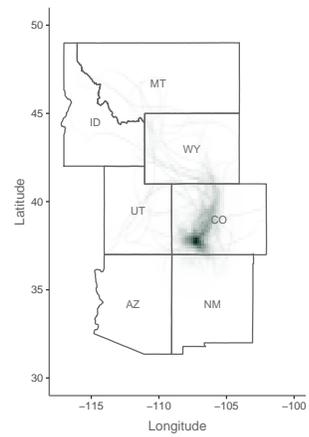
(a)



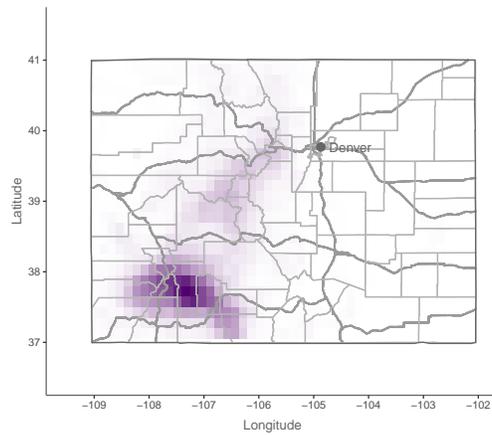
(b)



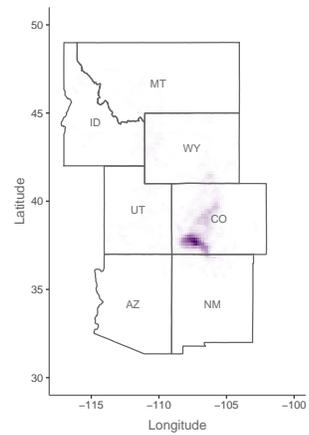
(c)



(d)



(e)



(f)

FIGURE 3.7. Population-level spatial quantities of residence time (Figure 3.7a, Figure 3.7b), speed (Figure 3.7c, Figure 3.7d), and tortuosity (Figure 3.7e, Figure 3.7f). For reference, county boundaries and major roads are shown for Colorado (Figure 3.7a, Figure 3.7c, Figure 3.7e). Not included are rare movements to eastern states (Nebraska, Kansas, and Iowa).

## CHAPTER 4

# DRIVERS OF COUGAR MOVEMENT IN A WILDLAND-URBAN INTERFACE<sup>1</sup>

### 4.1. SUMMARY

Assessing preferential use of the landscape is important for managing wildlife and can be particularly useful in transitional habitats, such as at the wildland-urban interface. Human-wildlife interactions increase risk for wildlife, particularly large carnivores, but human-modified habitat may be sources of increased prey availability. While many species have suffered from the detrimental impacts of increasing human population growth, some species, such as cougars (*Puma concolor*), have been observed using human-modified landscapes. I characterized preferential habitat selection by a population of cougars inhabiting the Front Range of Colorado, an area exhibiting rapid population growth and increased recreational use.

Preferential use is often evaluated using resource selection functions (RSFs), but RSFs do not account for the habitat available to an individual at a given time and may mask conflict or avoidance behavior. Contemporary approaches to account for availability based on movement include spatio-temporal point process models, step-selection functions, and continuous-time discrete-space (CTDS) models; in contrast to the other methods, the CTDS model allows for explicit inference on animal movement. I exploited the flexibility of the CTDS framework to model speed and directionality of movement, individual variation, and time-varying responses to landscape covariates. I found that there was significant individual-

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<sup>1</sup>The material in Chapter 4 is similar to a manuscript that will be submitted to the Journal of Animal Ecology: Buderman, F.E., M.B. Hooten, M.W. Alldredge, E.M. Hanks, and J.S. Ivan. In Preparation. Drivers of Cougar Movement in a Wildland-Urban Interface. Journal of Animal Ecology

and temporal-variability in cougar response to landscape characteristics. Distance to nearest kill site and heat loading emerged as important drivers of movement; cougars moved quickly when far from kill sites and in areas with high heat loading (south-facing slopes). Distance to nearest kill site was also an important directional driver of movement, with individuals moving toward areas closer to kill sites. In addition, I found that behavior was a function of development, with cougars moving faster as distance to kill site increased and with stronger directional bias toward a kill site in less developed areas.

#### 4.2. INTRODUCTION

Quantifying variability in habitat selection by individuals, while simultaneously estimating population-level patterns, can be important for management and conservation issues where resources are heterogeneous or cause points of conflict (Kertson *et al.*, 2011). Some large carnivores, such as cougars (*Puma concolor*), have undergone recent range expansions into human-modified landscapes (Knopff *et al.*, 2014), but they rarely use the heavily modified landscapes in urban and suburban areas, instead relying on the rural and exurban areas at the wild-urban interface (Burdett *et al.*, 2010; Kertson *et al.*, 2011). Along with increased risk from human interactions (Burdett *et al.*, 2010), human-modified landscapes may contain greater numbers of both primary (ungulates, e.g., Torres *et al.*, 2011) and secondary (domestic animals, e.g., Torres *et al.*, 1996) prey for carnivores compared to adjacent wild-land areas. Even as early as 1998, the frequency of human-cougar interactions along portions of the Front Range, a mountain range extending north-south from Casper, Wyoming to Pueblo, Colorado, had increased due to encroaching residential development, increasing cougar populations, and increasing prey densities near human populations (Manfredo *et al.*, 1998). The Front Range Urban Corridor runs along the eastern edge of the Front

Range, while the Front Range itself contains a matrix of towns and areas that are managed for recreational use by county, state, and federal agencies. Due to their desirable qualities, human populations around protected areas have demonstrated more growth than expected compared to growth in rural, non-protected areas (Wittemyer *et al.*, 2008), increasing the potential for human-wildlife conflict (White & Ward, 2011).

Individual-level movement decisions are one of the underlying processes that give rise to population-level patterns such as species' distributions or their density and abundance on the landscape (Wiens *et al.*, 1993). Movement decisions are a function of a number of variables, including the current location of the individual and the alternative available landscape choices (Wiens *et al.*, 1993). Therefore, a central theme of animal ecology is the assessment of an individual's preference for habitat, given what is available on the landscape (Johnson, 1980). Habitat preference is typically characterized using resource selection functions (RSF), which are often fit using logistic regression to compare the locations used by an individual or population to a random sample taken across some area defined as "available" (Manly *et al.*, 2007). Use that is disproportionate to availability implies that the individual has a preference for, or aversion to, that habitat (Manly *et al.*, 2007). However, inference on preference depends on what components are considered available to the animal (Johnson, 1980). For example, an animal may use a resource disproportionately less than is available in its home range, however it may have chosen its home range because the resource was abundant (Johnson, 1980).

In addition, availability is constrained by an individual's range of movement. To account for this, spatio-temporal point process models simultaneously estimate the resource selection and time-varying availability kernels, where the kernel is the area an individual is capable of moving to over a given period of time (Christ *et al.*, 2008; Johnson *et al.*, 2008b; Brost

*et al.*, 2015). The more commonly used method, a step-selection function, approximates the availability kernel by fitting a conditional logistic regression using a sample of “available” steps that an individual could have taken (e.g., Boyce *et al.*, 2003; Fortin *et al.*, 2005; Forester *et al.*, 2009). Recent methods have attempted to use conditional logistic regression to separately approximate the movement and time-varying availability kernels, in the vein of spatio-temporal point process models (Avgar *et al.*, 2016). However, because all of these methods are formulated in discrete time, inference is made only when data were observed and not on the unobserved path. In addition, besides the spatio-temporal point process of Brost *et al.* (2015), none of these methods account for measurement error.

In contrast to many resource selection studies, one of the primary goals of continuous-time movement models is to estimate the true path of an individual when it was unobserved (Brost *et al.*, 2015; Johnson *et al.*, 2008a; Patterson *et al.*, 2008; Buderman *et al.*, 2016; Hooten *et al.*, 2017). Continuous-time movement models can also incorporate measurement error and irregular observations in time. However, movement models are typically time consuming and computational intensive to fit, making it difficult to obtain inference on multiple individuals (Hooten *et al.*, 2016). If inference on multiple individuals were attainable, then it may be possible to identify a population-level response to a feature of the landscape that is consistent across individuals, which would provide a rigorous link between individual choices and population-level patterns (Wiens *et al.*, 1993). In addition, understanding individual variability may help identify individuals that associate more strongly with certain features of the landscape (Aune, 1991).

A recently developed method, continuous-time discrete-space (CTDS) modeling, incorporates an explicit movement model to obtain information on travel speeds. Travel speeds

give indirect inference on resource selection (Dickson *et al.*, 2005) and avoid absolute statements about preference (Johnson, 1980). The CTDS method, developed by Hanks *et al.* (2015), is fit in two stages, where the first stage uses a continuous-time movement model to obtain inference on where the individual was when it was unobserved, while the second stage allows for evaluation of landscape drivers of animal movement. The second-stage of the analysis uses a Poisson likelihood with an offset to model transition rates; therefore, any statistical model that uses a Poisson likelihood can be used in the CTDS framework (Hanks *et al.*, 2015). The flexibility of the CTDS framework can account for time-varying responses to landscape drivers by allowing coefficients to vary temporally (Hanks *et al.*, 2015), and it can also be implemented in a Bayesian hierarchical framework, allowing for inference on individual- and population-level drivers.

Given the increasing potential for human-wildlife conflict as development permeates rural and wildland areas along the Front Range and elsewhere in the West, I sought to extend previous work by explicitly modeling cougar movement to identify key drivers of their behavior, and in doing so, better understand their use of the wildland-urban landscape in both space and time. Information on cougar movement and resource selection is surprisingly limited, especially for movement and selection at a fine temporal scale and over the duration of an entire day. Most studies have inferred selection and movement patterns for cougars using approximately one or fewer locations per day; these locations were sometimes obtained only during daylight (e.g., Beier, 1995; Anderson *et al.*, 1992; Dickson & Beier, 2002), obtained during night and day but were treated equivalently (e.g., Hemker *et al.*, 1984), or obtained at unspecified times (e.g., Ruth *et al.*, 1998; Sweanor *et al.*, 2000). Inference on time-varying behavior has been limited to separate analyses on discretized temporal periods (e.g., Dickson *et al.*, 2005; Knopff *et al.*, 2014). Some studies have also focused exclusively on kill

site and hunting locations (e.g., Blecha, 2015) or non-kill site locations (e.g., Dickson *et al.*, 2005; Knopff *et al.*, 2014). In contrast to previous studies, I used the CTDS framework to model individual- and population-level cougar responses to landscape features in continuous time, which allowed for direct inference on how behavior varies through time, given what is available.

### 4.3. METHODS

#### 4.3.1. *Data Collection*

Colorado Parks and Wildlife (CPW) trapped cougars from 2006-2016, fit them with global positioning system (GPS) collars, and released them along the Front Range of Colorado (Figure 4.1). CPW used three different GPS collar manufacturers over the duration of the study (Lotek Wireless Inc., Newmarket, Ontario, Canada; Northstar Science and Technology LLC, King George, VA, USA; Vectronics GmbH, Berlin, Germany), and collars were programmed to achieve fixes every three hours. For this analysis I selected a subset of 20 adult individuals (M=6, F=14) that were monitored with Vectronics collars during April 2011 and 21 adult individuals (M=7, F=14) that were monitored during June 2011. We expected that cougar behavior would vary between April and June, because mule-deer fawns, a primary prey source for cougars, are born in June (Pojar & Bowden, 2004). Mule deer constitute a large proportion of cougar diets (Anderson Jr & Lindzey, 2003), and fawns are at a disproportionately high for predation (Hornocker, 1970). April and June of 2011 had a large number of males and females available for monitoring. Eighteen individuals were monitored during both April and June, allowing us to perform population-level comparisons

between the two months. The area of inference was restricted to the area for which covariates were available.

#### 4.3.2. *Continuous-Time Discrete-Space Framework*

I used a Bayesian hierarchical CTDS model to evaluate drivers of cougar movement; this model is an extension of the model proposed by Hanks *et al.* (2015) and allows for inference on movement rates and directional bias, as opposed to resource selection, in continuous time. The initial step in the CTDS framework is to estimate a continuous movement path from the observed data points. I used the functional movement model proposed by Buderman *et al.* (2016) with fixed measurement error to predict locations every ten minutes for the first two weeks of each month. A random subset of paths from the posterior predictive distribution of the movement model were spatially discretized to a latent variable formulation with a cell size of 100-m<sup>2</sup>, which was the largest cell size among the available covariates (Appendix C.1). In the latent variable formulation, each transition corresponds to four data points (the four neighboring grid cells); the response variable is equal to one if the neighboring grid cell is the cell that the individual transitioned into and zero otherwise. The latent variable formulation results in a Poisson likelihood where the offset is the amount of time an individual spent in that grid cell, and the covariates are landscape variables that correspond to the position of that cell on the landscape (Hanks *et al.*, 2015). I used the R package `ctmcmove` to facilitate creation of the CTDS latent variable data (Hanks, 2016).

Using multiple imputed paths accounts for the uncertainty in the true path of the individual and is a process version of multiple imputation (Hanks *et al.*, 2015; Hooten *et al.*, 2016; Scharf *et al.*, In Press), a method frequently used for missing data (Rubin, 1987). I generated 30 imputations for each individual, using 15 imputations for *a priori* selection of

regularization terms (which shrinks the effect of unimportant covariates toward zero to prevent over-fitting) and 15 imputations to fit the models for individual- and population-level inference on transition rates.

### 4.3.3. *Secondary Models for Movement Inference*

I assessed cougar response, as measured by movement rates and directional bias, to landscape features, including measures of anthropogenic activity. Because cougars and humans are active at different times throughout the day, I proposed three models for drivers of cougar movement: a hierarchical generalized linear model (H-GLM) for individual- and population-level inference on average cougar behavior, a non-hierarchical generalized additive model (GAM) for individual-level time-varying behavior over a two-week period, and a hierarchical generalized additive model (H-GAM) to account for individual- and population-level diel time-varying behavior. Covariates were centered and scaled to the individual, meaning that the coefficients are relative to the mean and standard deviation of the values that each individual encountered during a given two-week period. This is similar to the idea proposed by Johnson (1980), where preference was determined by comparing some measure of usage and availability of a landscape feature on an individual basis.

On average, I expected cougars to respond similarly to landscape covariates. Therefore, I developed a H-GLM for the latent variable formulation of the CTDS framework. In the CTDS framework, the response variables,  $z_{ij}$ , are a sequence of zeros and ones, where  $z_{ij} \sim \text{Poisson}(\lambda_{ij})$ , for  $i = 1, \dots, T$  and  $j = 1, \dots, J$ , where  $T$  is the total number of cell transitions, and  $J$  is the number of individuals. Landscape covariates are incorporated using the log link function, such that  $\log(\lambda_{ij}) = \log(\tau_{ij}) + \mathbf{x}'_{ij}\boldsymbol{\beta}_j$ . The residence times are represented by the constants  $\tau_{ij}$ , and the landscape variables by  $\mathbf{x}_{ij}$ . The parameter  $\boldsymbol{\beta}_j$  is a vector

of  $p$  individual-level coefficients and is drawn from the population-level distribution  $\beta_j \sim \mathcal{N}(\boldsymbol{\mu}_\beta, \boldsymbol{\Sigma}_\beta)$ . The covariance matrix,  $\boldsymbol{\Sigma}_\beta \equiv \text{diag}(\sigma_\beta^2 \boldsymbol{\phi})$ , where the vector  $\boldsymbol{\phi}$  scales the value  $\sigma_\beta^2$  to each individual, allows us to sample from one parameter space, as opposed to  $J$  parameter spaces (a  $\sigma_\beta^2$  for each individual). The population-level distribution has a mean that is modeled with a multivariate normal distribution  $\boldsymbol{\mu}_\beta \sim \mathcal{N}(\mathbf{0}, \sigma_\mu^2 \mathbf{I})$ . Both  $\sigma_\beta^2$  and  $\sigma_\mu^2$  are used as regularization terms to shrink the coefficients toward zero; this prevents over-fitting and allows for correlated predictors (Hooten & Hobbs, 2015).

The GAM is formulated as a varying coefficient model (Hastie & Tibshirani, 1993), where the response to covariates varies over space or time. By expanding the landscape covariates with a basis function (Hefley *et al.*, 2017), I created a new vector,  $\mathbf{v}_{ij}$ , that is the Kronecker product of the  $p$  length vector of covariates,  $\mathbf{x}_{ij}$ , and the  $q$  length vector of the values of the basis at the time of transition  $i$ ,  $\mathbf{w}(i)$ . The GAM for movement over a two-week period is similar to the GLM, except  $\log(\lambda_{ij}) = \log(\tau_{ij}) + \mathbf{v}'_{ij} \boldsymbol{\alpha}_j$ , where  $\boldsymbol{\alpha}_j$  is a vector of length  $pq$ . Each parameter in  $\boldsymbol{\alpha}_j$  is the collective effect of the basis function and the corresponding covariate at the time of transition  $i$ . Using the vector  $\mathbf{w}(i)$ ,  $\boldsymbol{\alpha}_j$  can be back-transformed to obtain the time-varying effect of the covariate. I used cubic splines as the basis for the non-hierarchical GAM. The model is fit independently for each individual and  $\boldsymbol{\alpha}_j \sim \mathcal{N}(\mathbf{0}, \sigma_\alpha^2 \mathbf{I})$ , where  $\sigma_\alpha^2$  is selected via a one-dimensional grid search.

The final model is a H-GAM that allows us to account for diel time-varying behavior that I hypothesize is shared across individuals. The model is the same as above, but with an additional level that allows for population-level inference. In the hierarchical framework  $\boldsymbol{\alpha}_j \sim \mathcal{N}(\boldsymbol{\mu}_\alpha, \boldsymbol{\Sigma}_\alpha)$ , where  $\boldsymbol{\Sigma}_\alpha \equiv \text{diag}(\sigma_\alpha^2 \boldsymbol{\phi})$ . However, for diel movement, I used cubic cyclic splines as the basis ( $\mathbf{w}(i)$ ), because they constrain the start and end points of the varying coefficients to be equal, which is an important property for time spans that are cyclic in

nature. As in the GLM,  $\phi$  reduces the number of parameters I need to select *a priori* by scaling the  $\sigma_\alpha^2$  term to each individual, and  $\boldsymbol{\mu}_\alpha \sim \mathcal{N}(\mathbf{0}, \sigma_\mu^2 \mathbf{I})$ . Both  $\sigma_\alpha^2$  and  $\sigma_\mu^2$  act as regularization terms and are selected *a priori*.

Models were fit using a Markov Chain Monte Carlo (MCMC) algorithm written in R (R Core Team, 2013). I performed adaptive tuning over an initial 15,000 MCMC iterations. I used the selected tuning parameters as constants in the subsequent 15,000 iterations that were used to calculate the out-of-sample information criterion for the *a priori* regulator grid-search. The final models were fit using 100,000 MCMC iterations with a burn-in period of 10%.

#### 4.3.4. *Landscape Covariates*

Each covariate can be included as either a motility or directional driver of movement in the CTDS model. Motility covariates are based on the value of the grid cell that the individual is in currently and control the absolute rate of movement. Directional covariates account for the correlation between a movement and the gradient of a covariate and contribute to the probability that an individual moves toward a grid cell. The directional drivers were calculated such that a positive coefficient indicates that individuals move predominantly in the direction that the covariate decreases, whereas a negative coefficient indicates that individuals move in the direction that the covariate increases. All rasters were aggregated to a 100-m<sup>2</sup> resolution, which is within the distance that a cougar might typically move over a ten-minute interval (Dickson *et al.*, 2005).

I hypothesized that a number of landscape covariates may contribute to transition rates and directional bias of cougars: mule deer utilization (as a proxy for availability), distance to nearest potential kill site, distance to nearest structure, distance to nearest road, elevation,

heat insolation load index, and topographic wetness. I also used an autoregressive parameter to account for an individual's tendency to move in the direction it was already moving (directional persistence, Hanks *et al.*, 2015).

Distance to nearest structure (m) was calculated as the Euclidean distance to the nearest man-made roofed structure (Blecha, 2015). Distance to road was calculated using major roads data (i.e., a major highway primarily for through traffic usually on a continuous route and streets whose primary purpose is to serve the internal traffic movement within an area) obtained from Colorado Department of Transportation. Due to increased human activity around structures and roads, I expected cougar transition rates to decrease with distance to nearest roofed structure and distance to nearest road (Dickson & Beier, 2002; Dickson *et al.*, 2005; Nicholson *et al.*, 2014). However, females were expected to respond less to structures and roads than males, given that there may be additional factors, such as food limitation and offspring, that drive them to tolerate human-modified landscapes (Wilmers *et al.*, 2013; Benson *et al.*, 2016).

We approximated prey availability using two covariates: mule deer utilization and potential kill site. The model averaged prediction for mule deer utilization (Blecha, 2015) approximates prey availability given a suite of landscape covariates. I hypothesized that cougars would move slower in areas with high values for mule deer utilization and orient toward areas of high mule deer use during crepuscular and nocturnal movements (Anderson Jr & Lindzey, 2003; Kertson *et al.*, 2011; Blecha, 2015). Potential kill sites were determined using a clustering algorithm on the GPS points. Knopff *et al.* (2009) classified a location as a potential kill site if two or more GPS locations were found within 200 m of the site within a six-day period. Hanks *et al.* (2015) modified the algorithm such that at least one location had to occur between 9:00 pm and 6:00 am. I further modified the algorithm such that all

locations had to occur between 7:30 pm and 6:30 am during April and 8:30 pm and 5:30 am during June, which is the average time of sunset and sunrise for the months of April and June. I then calculated the distance (m) to nearest potential kill site across the study area. I expected individuals to move faster as distance to potential kill site increased, because decreasing distance would indicate that an individual was returning to a cached kill, and caches are more often located in areas of high vegetation cover (Husseman *et al.*, 2003).

Elevation was estimated using a digital elevation model. Blecha (2015) found that cougars avoided foraging in higher elevations, but Wilmers *et al.* (2013) observed cougars selecting for higher elevations in developed areas. We expect cougars to show high temporal variability in their directional response to elevation, with cougars moving toward lower elevations when they are hunting (crepuscular and nocturnal movement) and toward increasing elevations at other times. I used a raster based on the continuous heat insolation load index (CHILI, Theobald *et al.*, 2015), modified from McCune & Keon (2002) to measure the accumulation of solar radiation at that location over the course of a year (MJ/cm<sup>2</sup>/yr). Heat insolation will be high on south-facing slopes which are more xeric and open than north-facing slopes (Veblen & Donnegan, 2005). Cougars have been observed using less rugged terrain for travel (Dickson *et al.*, 2005), selecting for south-facing slopes containing shrubs (Knopff *et al.*, 2014), and avoiding foraging on north-facing slopes (Blecha, 2015). Therefore, we expect that cougars may orient toward areas of high heat insolation, but move quickly through them. The topographic wetness plus metric (TWI+) predicts soil moisture based on slope, as originally described by Beven & Kirkby (1979), and aspect, as modified by Theobald (2007). Because cougars have been observed selecting for and hunting in riparian areas (Dickson & Beier, 2002; Kertson *et al.*, 2011; Nicholson *et al.*, 2014; Benson *et al.*, 2016), we expected cougars to move slowly in areas of high topographic wetness and demonstrate

temporal variability in their directional response (toward areas of increasing topographic wetness when hunting).

I also analyzed a subset of individuals and the interaction between housing density and their response to deer utilization and distance to nearest kill site. These are the two variables that I expected to vary most with housing density due to the potential trade-offs between increased prey abundance but increased mortality risk (Blecha, 2015). The landscape was discretized into either developed (<10 acres/unit) or undeveloped areas. Only 15 individuals (with 11 that were available for both months; F=8, M=3) were used in the secondary analysis for both April and June because the remaining individuals did not spend any time in developed areas.

#### 4.4. RESULTS

Distance to potential kill site was the primary driver of both motility and directionality in the GLM framework for April and June (Figure 4.2). As individuals increased their distance from a potential kill site, their transition rate increased (Figure 4.2a). In addition, individuals oriented their movements toward their potential kill site (Figure 4.2b). I did detect a slight difference between months in the directional response to distance from potential kill sites, with a more positive response in June. However, this difference was not significantly different from zero (Figure 4.4).

Individuals also moved faster than average in areas where heat-loading was high in April, but not in June (Figure 4.5); however, the 95% credible intervals still included zero and the difference was not significant (Figure 4.4). There was a slight trend for slower movements with increasing distance from a roofed structure (Figure 4.6). Finally, I detected significantly more directional persistence in April than in June (Figure 4.7, Figure 4.4).

I observed significant individual variation, both across and within individuals, for the two-week periods of both months (GAM). Given that distance to nearest potential kill site was the primary driver for motility in the time-homogeneous GLM framework, I expected this parameter to be significantly different from zero in the GAM time-varying framework, however I observed significant variability within certain individuals across the two weeks (Figure 4.8). This behavior also varied by month for some individuals (Figure 4.8). I also observed temporal deviations from zero for covariates that were not significant in the GLM framework. For example, while the 95% credible intervals often included zero for much of the two weeks, the response to distance from nearest roofed structure (Figure 4.9) and distance to nearest road (Figure 4.10) oscillated between positive and negative for some individuals, with inconsistent individual-level responses between the two months.

Distance to nearest potential kill site was the predominant motility and directionality driver in the diel time-varying framework (H-GAM; Figures 4.11 and 4.12). However, the strength of the positive relationship to distance to nearest potential kill site varied over time, with the strongest response occurring around dawn, decreasing steadily during daylight hours, and then increasing around dusk (Figure 4.11). Some individuals' behavior shifted slightly, either temporally, or in magnitude depending on the month (Figure 4.11). The strength of the directional bias toward potential kill sites also varied through time, with the 95% credible intervals for the population mean and the mean response for a subset of individuals suggesting that individuals tended to move away from their potential kill sites during daylight hours (Figure 4.12).

While the 95% credible intervals overlapped zero for much of the day, there were modest temporal responses in both motility and directionality to elevation, distance to nearest road, and distance to nearest structure (Figure 4.13). At dawn, individuals moved faster at lower

elevations, while during mid-day and evening individuals moved faster at higher elevations. In addition, during mid-day, individuals moved toward areas of higher elevations, while during other hours they moved toward lower elevations. The population-level pattern was for a more negative motility response to distance to nearest structure and road during dawn and dusk (i.e., being closer to roads and structures is correlated to an increase in transition rates), with less negative or even positive responses during the day (Figure 4.13). While the directional response to distance to nearest road was negligible, there was a negative directional response mid-day, meaning that individuals oriented toward areas farther away from the nearest road (Figure 4.13). The remaining covariates showed little temporal variation at the population-level or contained large amounts of individual heterogeneity.

I did not see evidence for an interaction between development and deer utilization, which remained a statistically insignificant driver of cougar movement rates and directionality in both the H-GLM and H-GAM models. There was a stronger positive effect of distance to potential kill site on speed (faster as distance to kill site increases) and directional bias (more direct orientation toward the kill site) in less developed areas, compared to developed areas (H-GLM; Figure 4.14). In the H-GAM framework, the general pattern for the effect of potential kill site on speed was the same between the two areas, but there was a stronger positive effect of kill site in undeveloped areas (Figure 4.15). The effect of distance to kill site on directionality was less conclusive; in general, with cougars showed a slight tendency to move away from a kill site in daylight (Figure 4.15), something that was not observed when I did not address the interaction between kill site and development (Figure 4.12). Cougars in undeveloped areas had a much more variable temporal response to the direction of a potential kill site (Figure 4.15), and were likely driving the pattern I saw in the model without the interaction (Figure 4.12).

## 4.5. DISCUSSION

The varying coefficient modeling framework, implemented in the study as a GAM, can reveal hidden process dynamics (Fan & Zhang, 2008) and allows for complex non-linear patterns that would be difficult to model in a traditional framework (e.g., Polansky & Robbins, 2013). Conventional generalized linear models can mask time-varying responses to covariates (e.g., Cheng *et al.*, 2009), because the response variable is essentially averaged over the time period of interest. Therefore, if the response of an individual switches between positive and negative (faster or slower movement rates), the estimated response will be approximately zero.

Studies have found that cougars use a broader range of habitats for nocturnal movements than for daybed locations (Dickson *et al.*, 2005) and demonstrate temporal variability in their response to anthropogenic landscape features (Knopff *et al.*, 2014). Therefore, restricting analysis of locations to a particular temporal subset may not be indicative of all behavior (Comiskey *et al.*, 2002). I expanded each parameter into the temporal space, however one could make each covariate a function of another parameter, either a different temporal predictor (e.g., time since kill) or another parameter in the model (e.g., distance to structure).

The strong response to distance to nearest potential kill site is likely due to returning visits to the carcass and unmeasured fine-scale covariates related to landscape features that increase the likelihood of a successful hunting attempt. Blecha (2015) found that hunting success was greater in areas with higher housing densities and lower topographic positions, such as drainage areas, despite drainage areas having lower prey availability. I did not measure hunting success, but I did find that cougars moved to lower elevations at dusk, when cougars are likely to hunt or return to a carcass. In addition, Benson *et al.* (2016) found that male and female cougars selected for different site-level characteristics for their

mule deer predation sites. The complex interaction between the probability of encountering and successfully killing prey is likely best captured in my model by the potential kill site location. I found that individual response to nearest potential kill site was variable within the two-week period and across individuals; this is likely a function of timing of successful kills and the size of the prey item, with stronger positive responses being correlated with larger prey. I also observed individuals having an increasingly strong positive response to distance to kill site from dusk to dawn, implying that, from dusk to dawn, individuals moved increasingly faster the farther away they were from a potential kill site.

I found that cougars moved slightly faster in areas with a higher heat insolation load index. These areas correspond to xeric, south-facing slopes, which, in the montane zone of the Front Range, mostly consist of open stands of ponderosa pine, compared to the more dense north-facing slopes (Veblen & Donnegan, 2005). The more open forest floor may facilitate cougars using south-facing slopes as travel corridors, leading to greater transition rates. Similarly, Dickson *et al.* (2005) found that cougars used less rugged terrain than the surrounding area while traveling, while Knopff *et al.* (2014) found that cougars selected for south-facing slopes and areas with shrub habitat. The monthly difference in effect size for the response to heat loading may be related to seasonal changes in vegetation (shrub cover may be denser in June, reducing speed) or a product of unobserved weather patterns (e.g., more snow on north-facing slopes in April could lead to a larger difference in speed). The speed and directionality of the transitions in response to elevation indicate that individuals are moving quickly to higher elevations during the day, and then moving quickly toward lower elevations at other times. Blecha (2015) found that predation events were more successful at lower elevations, which could explain the temporal pattern I observed.

The response of cougars to disturbed and developed landscapes varies in the literature, and is likely a function of the level of disturbance encountered. For example, Kertson *et al.* (2011) found no difference in cougar movement rates in wildland and residential areas throughout the day. However, Knopff *et al.* (2014) observed that cougars avoid developed landscapes, while also documenting a temporal shift in usage of those areas, with cougars avoiding areas near buildings and roads more during the day than at night. On average, I observed a more negative relationship to distance from structures and roads around dawn and dusk compared to mid-day and evening (i.e., individuals moved faster when closer to structures and roads during dawn and dusk than mid-day and evening), which could be explained by increased human activity level caused by the start and end of the work-day. In addition, I observed individuals orienting away from areas near roads mid-day. However, the uncertainty was fairly large for the diel effect of elevation, distance to nearest roofed structure, and distance to nearest road, particularly at the individual level.

Dickson *et al.* (2005) found that cougars moved fastest through developed areas, however I observed that cougar speeds are less sensitive to distance to potential kill site when they are in developed areas. In other words, cougars moved faster with increasing distance to nearest potential kill site when in undeveloped areas compared to developed areas. When in developed areas, cougars may maintain a more consistent travel speed and are responding more to fine-scale obstructions (e.g., trails, vehicles, light sources) than when their movements are unconstrained by development. Likewise, I saw more directional avoidance (or a non-response) to kill sites in developed areas, which would be expected if the potential kill sites are in heavily trafficked areas. Again, possibly due to the absence of movement constraints in undeveloped areas, cougars showed a less temporally consistent directional temporal response to a potential kill site.

I did not see consistent patterns for distance to structures or roads over the two-week period of observation, either within, or among, individuals, which could be explained by unmeasured spatial and temporal relationships, such as individual interactions and fine-scale temporally variable human disturbance (e.g., recreational activities, noise, construction). For example, Wilmers *et al.* (2013) found that cougars show stronger avoidance of more consistent sources of anthropogenic disruption, such as neighborhoods, than intermittent sources, such as low-traffic roads. However, because these fine-scale variables were not measured, we may fail to detect a consistent avoidance of structures and roads.

Other studies have detected significant individual variation (Kertson *et al.*, 2011; Wilmers *et al.*, 2013), and Benson *et al.* (2016) and Wilmers *et al.* (2013) found that selection differed between males and females. I did not see consistent sex-specific responses to covariates, which could be due to the timing of the observations; for example, females may respond differently to males when breeding, but similarly at other times. Some of the unexplained individual variation could be due to the amount of anthropogenic landscape features each individual was likely to encounter in their movements Benson *et al.* (2016); Knopff *et al.* (2014), as opposed to the amount of development in the available habitat during a given movement. Benson *et al.* (2016) hypothesized that the amount of development in many studies of cougar habitat selection has been too low to cause cougar behavioral changes, which may also explain the lack of a significant response to the covariates that act as proxies for anthropogenic use. I did not detect a link between response to development (either roads or buildings structures) and cougars that were considered nuisance individuals (Colorado Parks and Wildlife, personal communication). Cougars have demonstrated different second and third-order selection to roads in previous studies (Dickson & Beier, 2002), therefore, individuals that become nuisance individuals may select for, or end up in, home ranges near

human development, but do not select for areas that are closer to development within their home range (Linnell *et al.*, 1999).

In the CTDS modeling framework, the autocorrelation variable not only accounts for an individual's tendency to continue moving in the same direction, but absorbs unexplained dependence in the transitions. Given that few landscape variables were statistically significant, the autocorrelation parameter is capturing both of the aforementioned characteristics. However, Dickson *et al.* (2005) found that cougars tend to continue moving in a straight line, implying that some of the effect size of the autocorrelation term is due to behavior and not unexplained heterogeneity in the response variable. This supports the hypothesis that the subset of cougars in this analysis may not have a strong response to the level of landscape heterogeneity present in the Front Range during the months of May and June.

While I observed a trend in the mean response to certain drivers, and stronger responses in some individuals than others, many of the hypothesized movement drivers did not have a consistent statistically significant relationship with movement. However, studies on cougars in the same geographic area have found strong effects for landscape variables on cougar resource use (Blecha, 2015). It is important to keep in mind that the CTDS framework is measuring the effect of landscape variables on speed and directionality, not habitat preference. For example, cougars may select for areas with high mule deer use (Blecha, 2015), but cougars may not alter their speed based on the amount of mule deer usage. I propose that the lack of statistically significant drivers of movement may have four potential causes. First, cougars are generalists, therefore, they are expected to demonstrate less habitat selection at the landscape scale than would a habitat specialist (Katnik & Wielgus, 2005). For example, Dickson & Beier (2002) also failed to detect significant selection to topographic variables. Second, despite the cougars occupying heterogeneous urban-wildland habitat, it is possible

that covariate values in the Front Range are not variable enough to detect a significant response in behavior. Third, cougars may be responding to the landscape at a much finer scale than researchers are currently able to measure at such a large spatial extent. Fourth, it may be possible that movements measured in other months of the year, or different years, may have revealed stronger and more consistent responses.

I did learn that cougars exhibit heterogeneity amongst individuals in their responses to landscape features, but they consistently show a strong motility and directional response to distance to nearest potential kill site. In addition, some individuals respond relatively strongly to roads, structures, and elevation at various times of day; a non time-varying GLM would miss these temporally varying responses. Future studies could compare behavior across a wider range of seasons when cougars may respond differently to the landscape. In addition, very few of the observed locations occurred in developed areas; if comparing movement behavior between developed and undeveloped areas is of primary interest, capturing efforts should focus on individuals closest to urban areas. The CTDS framework represents an important step forward in detecting nuanced temporal patterns in animal movement than was previously possible and is especially useful when behavior is known to vary in time.

#### 4.6. DECLARATION OF SUPPORT

Funding was provided by Colorado Parks and Wildlife (1304), the National Park Service (P12AC11099), Colorado Department of Transportation, and NSF DMS 1614392. Data were provided by Colorado Parks and Wildlife (CPW ACUC #01-2008). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## 4.7. TABLES AND FIGURES

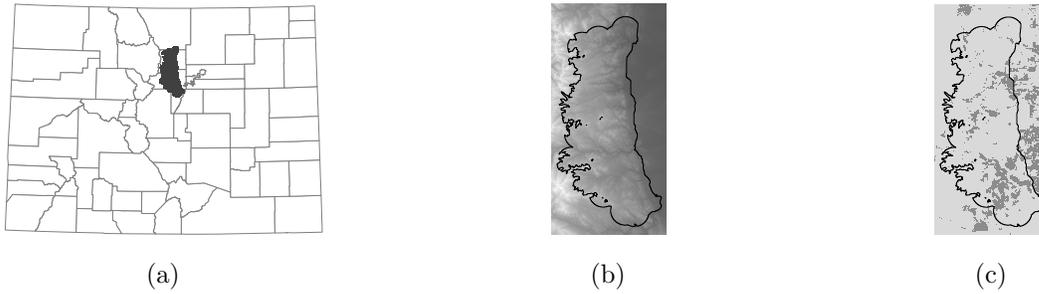


FIGURE 4.1. Map of Colorado counties, with the cougar movement study area plotted in gray (Figure 4.1a). Elevation (m; Figure 4.1b) and land classified as developed (dark gray is  $<10$  acres/unit; Figure 4.1c) is shown for the study area and surrounding area.

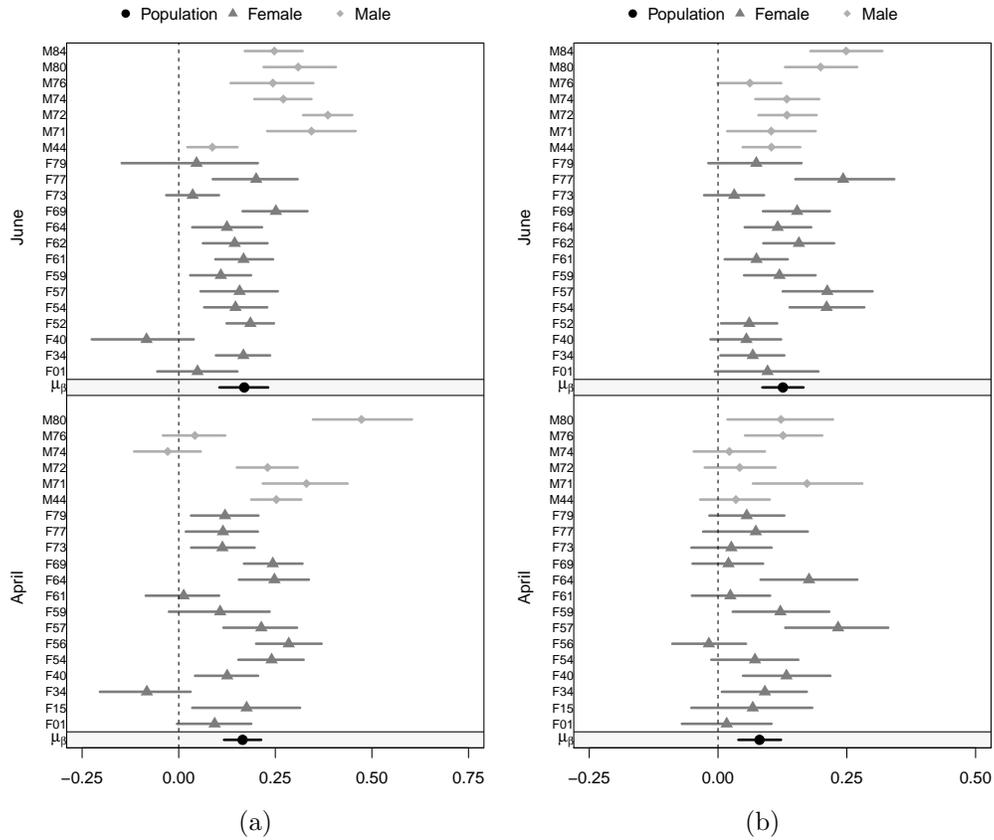


FIGURE 4.2. Posterior means and 95% credible intervals for the individual- and population-level static effect of distance to nearest potential kill site on rate (Figure 4.2a) and directionality (Figure 4.2b) of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011.

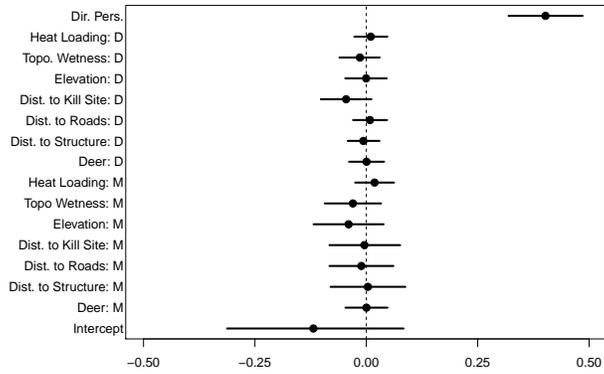


FIGURE 4.4. The mean and 95% credible intervals for the difference between the population-level posterior effects of landscape covariates on movement rates and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011; positive values indicate a stronger positive response in April.

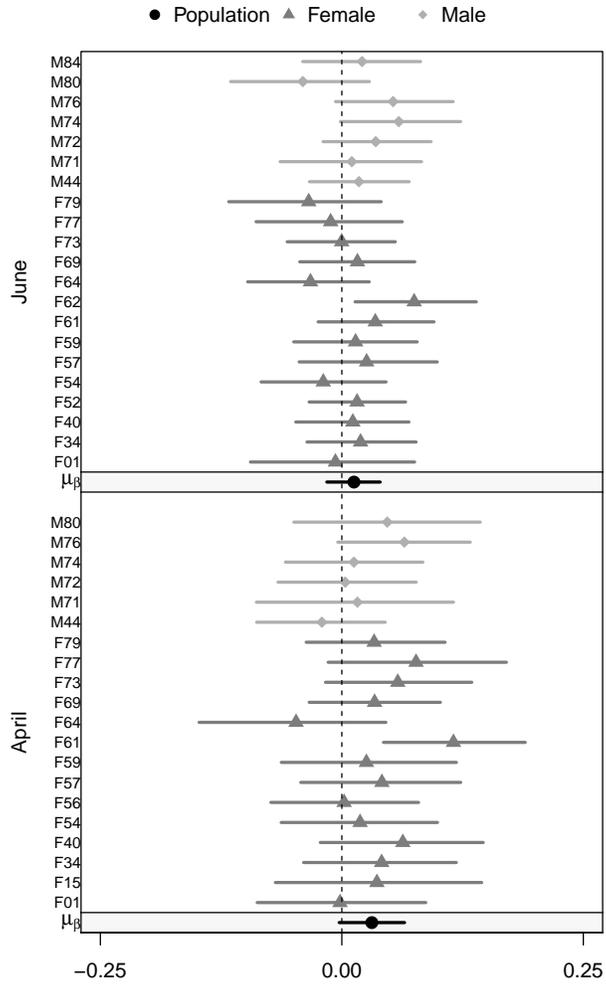


FIGURE 4.5. Posterior means and 95% credible intervals for the individual- and population-level static effect of heat loading on cougar movement rates in the Colorado Front Range for two-week periods in April and June, 2011.

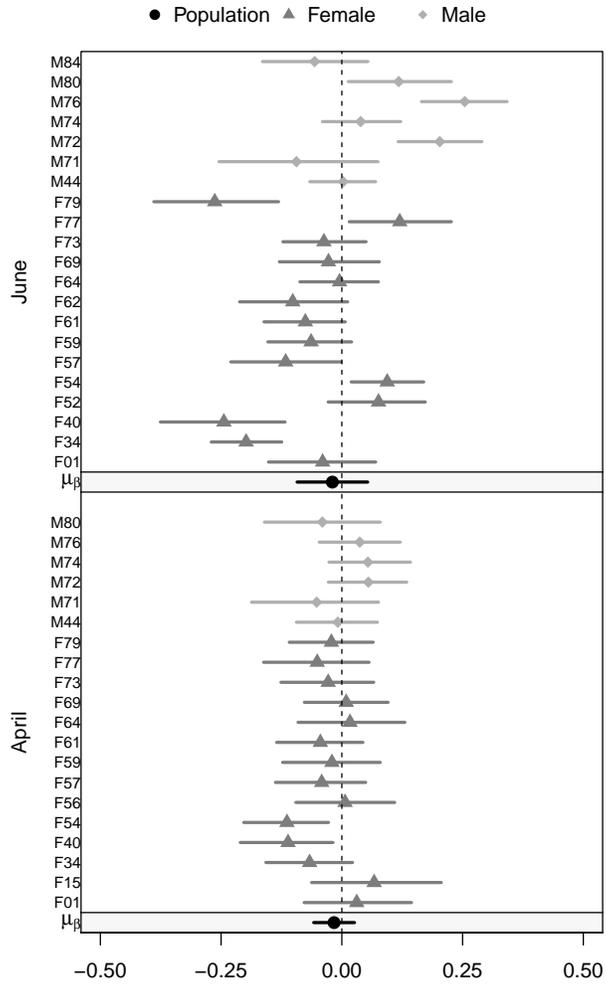


FIGURE 4.6. Posterior means and 95% credible intervals for the individual- and population-level static effect of distance to nearest roofed structure on cougar movement rates in the Colorado Front Range for two-week periods in April and June, 2011.

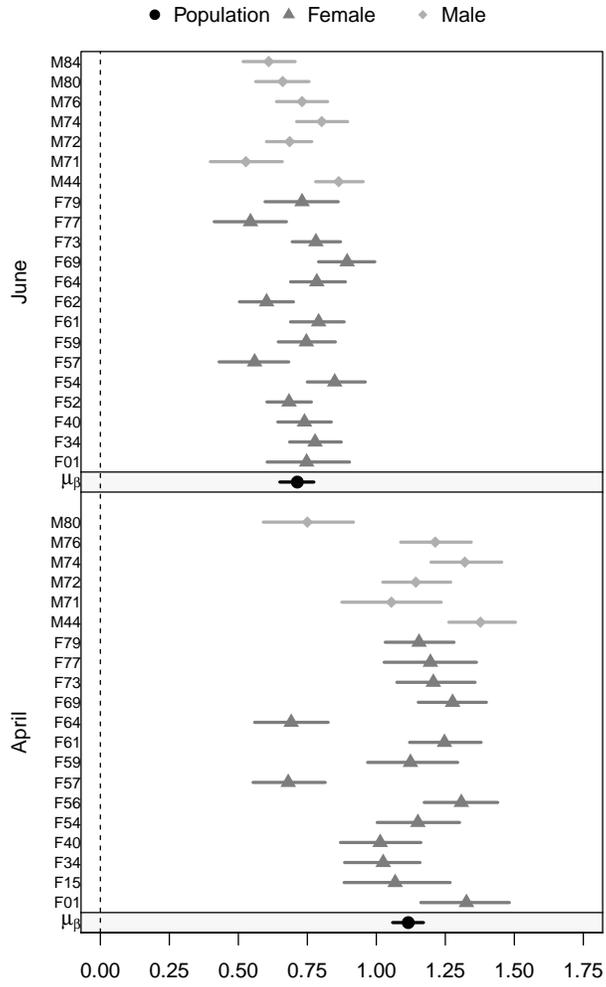


FIGURE 4.7. Posterior means and 95% credible intervals for the individual- and population-level directional persistence of cougars in the Colorado Front Range for two-week periods in April and June, 2011.

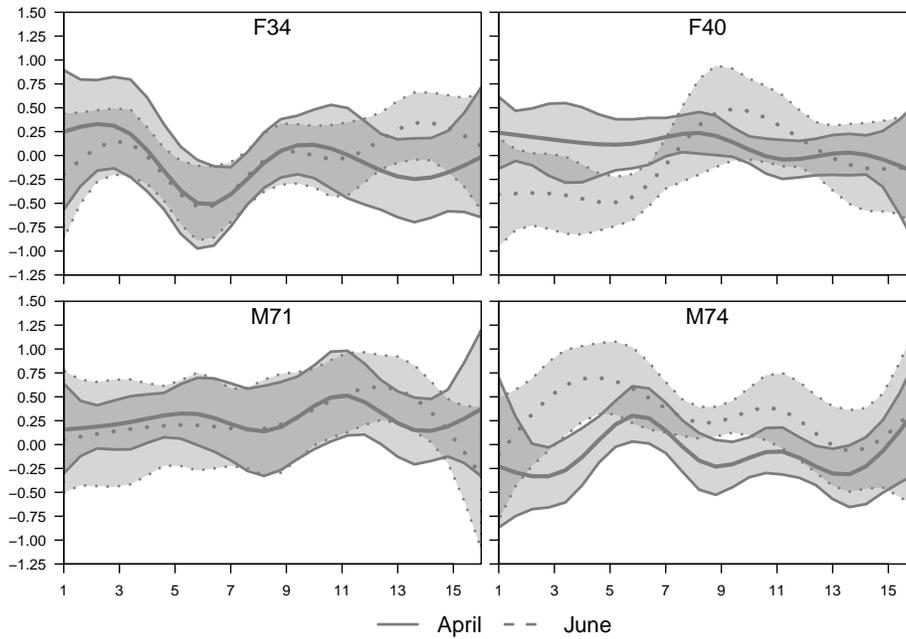


FIGURE 4.8. Posterior means and 95% credible intervals for the individual-level time-varying effect of distance to nearest potential kill site on cougar movement rates in the Colorado Front Range over two-week periods in April and June, 2011. A subset of two females and two males are shown.

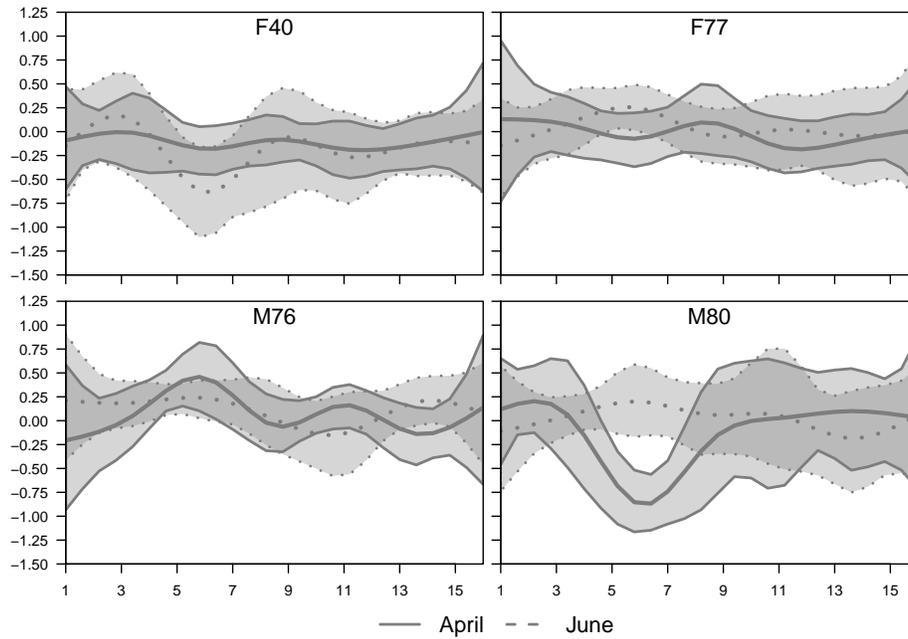


FIGURE 4.9. Posterior means and 95% credible intervals for the individual-level time-varying effect of distance to nearest roofed structure on cougar movement rates in the Colorado Front Range over two-week periods in April and June, 2011. A subset of two females and two males are shown.

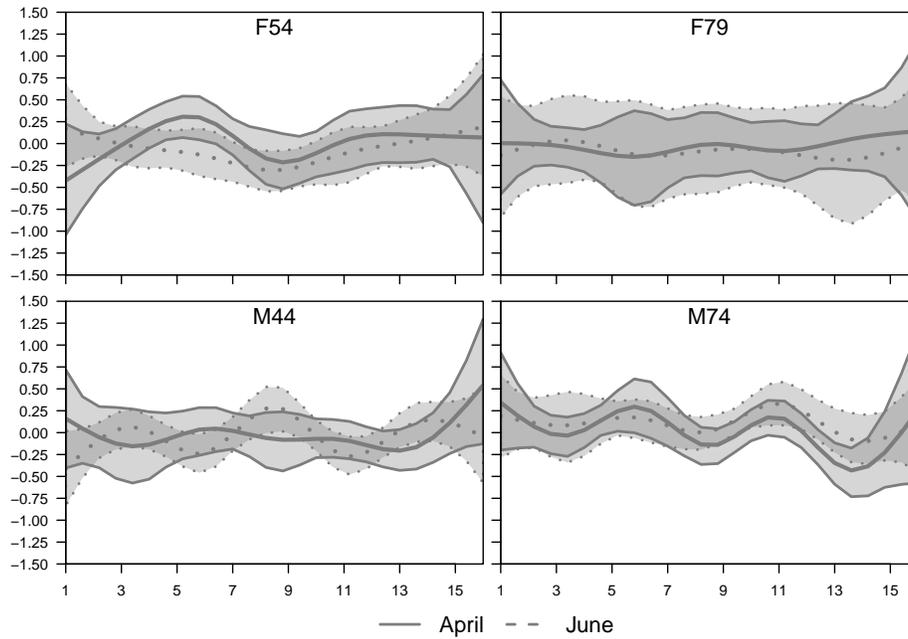


FIGURE 4.10. Posterior means and 95% credible intervals for the individual-level time-varying effect of distance to nearest road on cougar movement rates in the Colorado Front Range over a two-week periods in April and June, 2011. A subset of two females and two males are shown.

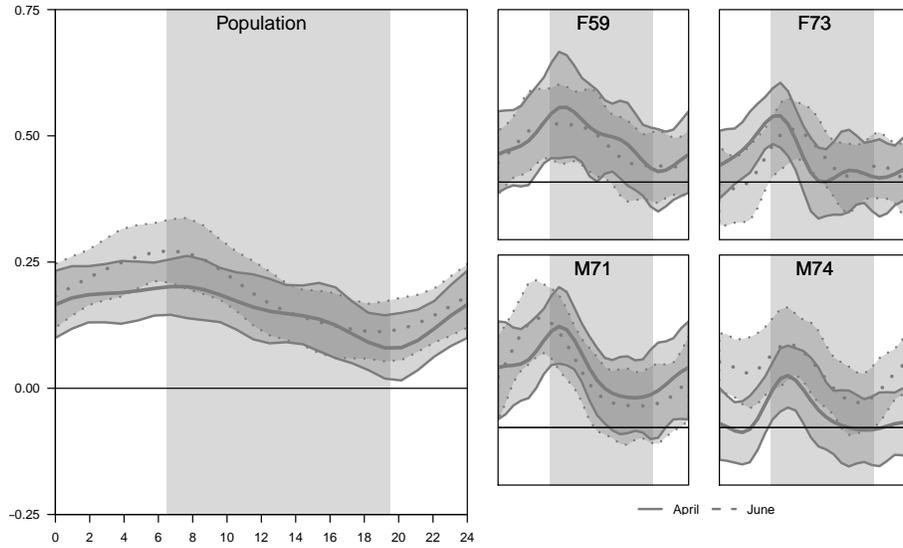


FIGURE 4.11. Posterior means and 95% credible intervals for the individual- and population-level diel time-varying effect of distance to nearest potential kill site on cougar movement rates in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period). A subset of two females and two males are shown, along with the population-level effect.

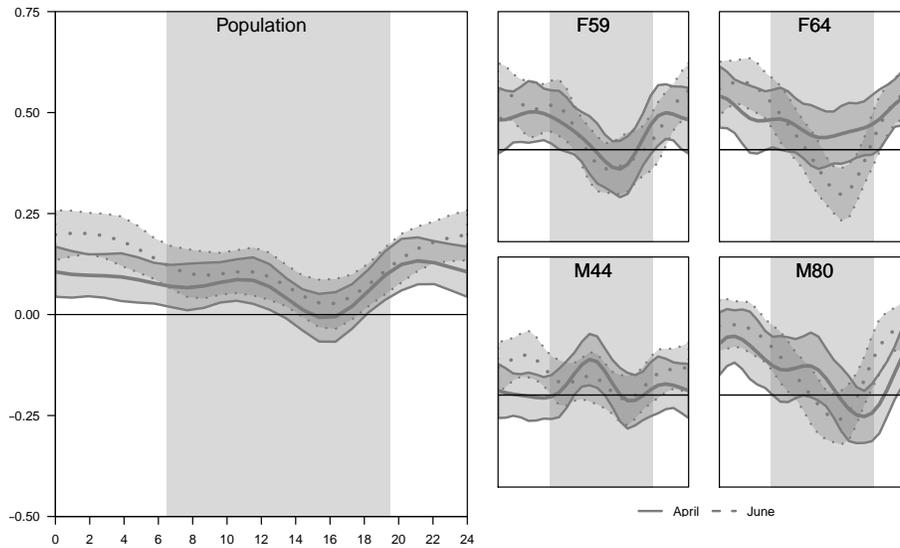


FIGURE 4.12. Posterior means and 95% credible intervals for the individual- and population-level diel time-varying effect of distance to nearest potential kill site on directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period). A subset of two females and two males are shown, along with the population-level effect.

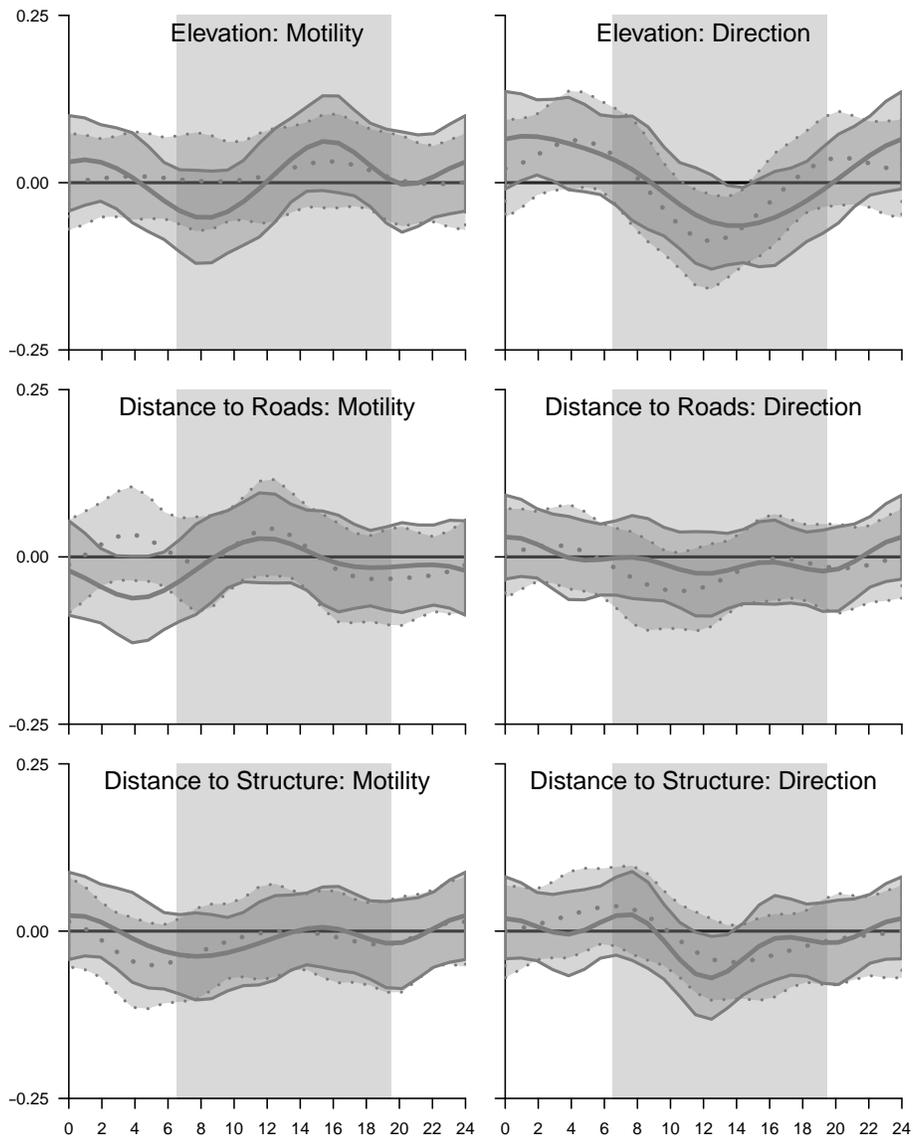


FIGURE 4.13. Posterior means and 95% credible intervals for the population-level diel time-varying effect of elevation, distance to nearest road, and distance to nearest roofed structure on rate and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period).

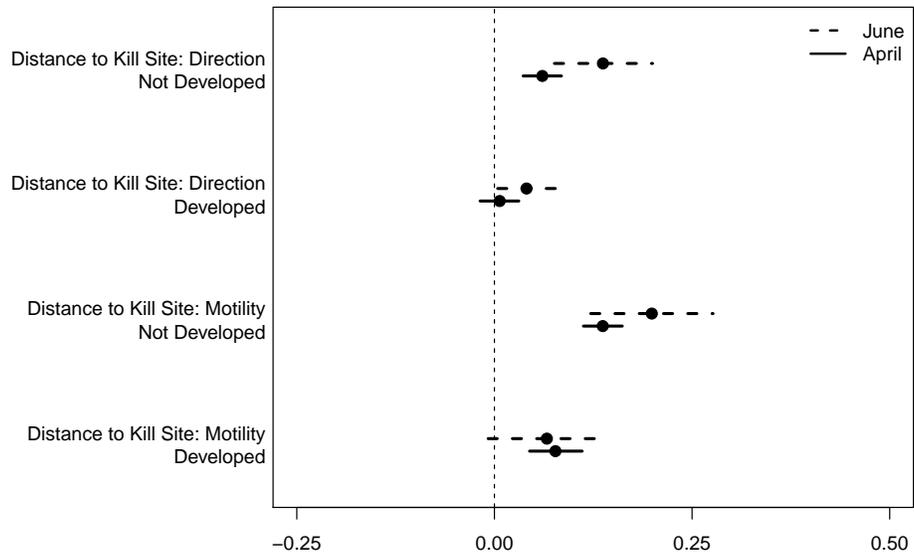


FIGURE 4.14. Posterior means and 95% credible intervals for the population-level effect of distance to nearest potential kill site on rate and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011.

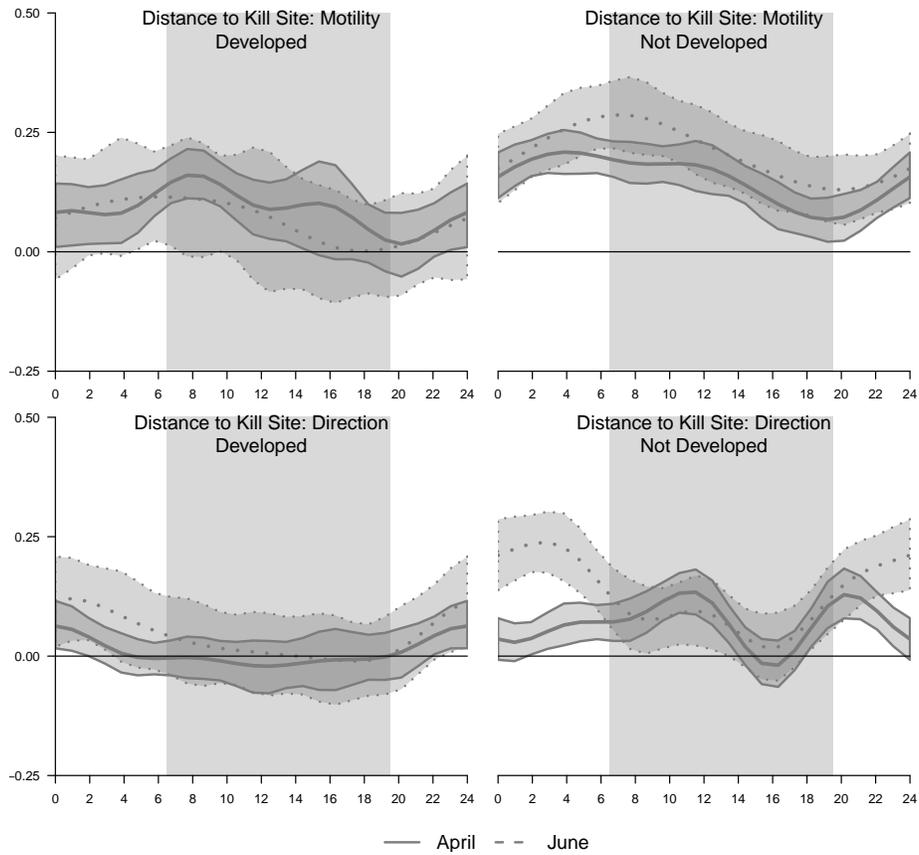


FIGURE 4.15. Posterior means and 95% credible intervals for the population-level diel time-varying effect of distance to nearest potential kill site on rate and directionality of cougar movement in the Colorado Front Range for two-week periods in April and June, 2011. The gray box represents 0630 hours to 1930 hours (the approximate period of daylight during the study period).

## CHAPTER 5

# CONCLUSION

My research has contributed to advancing the field of movement modeling and increasing our understanding of how carnivores move across the landscape. For both Canada lynx and cougars, rigorous movement modeling provided fine-scale temporal or spatial details on movement behavior that was previously unattainable. I will conclude by discussing the overarching themes that I explored in my dissertation, future methodological directions, and the ecological inference we have gained using the methods I developed.

### 5.1. OVERARCHING THEMES

#### 5.1.1. *Phenomenological Models for Animal Movement*

The discrete- and continuous-time models that I summarized in Chapter 1 are considered mechanistic movement models. Mechanistic movement models connect the stochastic movements of individual animals to their movement decisions (Patterson *et al.*, 2008). However, the resolution of the telemetry data must be able to provide inference at the scale of individual decision making (McClintock *et al.*, 2014a). In addition, these models may require assumptions about the number of behavioral states an animal exhibits (e.g., Jonsen *et al.*, 2005; Morales *et al.*, 2005; Forester *et al.*, 2007; Langrock *et al.*, 2012; McClintock *et al.*, 2012, 2013).

I developed a phenomenological model using basis functions that can accommodate large temporal gaps between observations, allows for continuous inference on behavioral states, and accounts for measurement error. Using basis functions allows for complex non-linear patterns that would be difficult to model in a traditional framework (e.g., Polansky & Robbins, 2013)

and can be used in a number of ecological applications (Hefley *et al.*, 2017). A significant benefit of this model is that it scales with the data. For example, the temporal coarseness of the Canada lynx data meant that the basis functions that I used were also at a coarse scale. As in any statistical model, there is a trade-off between fit and prediction; if I had used a finer-scale set of basis functions, the uncertainty in the location of the individual would be large in the absence of data. However, with finer-scale temporal data, a finer-scale set of basis functions can be used and appropriate inference can be obtained.

The phenomenological model is also deceptively simple, because it takes the form of a regression. While the model may appear complicated, the majority of the complexity is attributed to the error structure. The model’s simplicity also makes it easy and computationally efficient to fit. The same model, with a simple isotropic error structure, had been implemented in the `ctmcmove` package, which was used in the analysis of cougar movement (Hanks, 2016).

### 5.1.2. *Multi-data Source Models*

Researchers often collect multiple kinds of data on the same population. In some cases, it may be beneficial to link data types that contribute to the same process; models of this type are often called “integrated” models. Integrated data modeling is a popular and active area of research (e.g., Burnham, 1993; Barker, 1997; Nasution *et al.*, 2001; Schaub & Abadi, 2011; Tempel *et al.*, 2014), because auxiliary data sets can correct for estimator bias (e.g., Buderman *et al.*, 2014) and can sometimes improve precision of shared estimates (e.g., Besbeas *et al.*, 2002).

Multiple types of telemetry data are not often considered separate data sources, because they both provide information about where the individual is on the landscape. However,

when the telemetry device produces locations with differing amounts of uncertainty, it may be important to model these locations as arising from different data processes, but contributing to the same true process of interest. The data type containing more information, or less uncertainty, helps to minimize the uncertainty in the true process (as reviewed in Schaub & Abadi, 2011).

### 5.1.3. *Population-Level Inference*

Movement models can be time-consuming to fit due to the number of estimated parameters and the amount of data necessary to gain inference on animal movement (Hooten *et al.*, 2017). Discrete-time models can add additional computation time due to the data imputation process that is necessary to obtain temporally regular observations (McClintock *et al.*, 2014a). It is often computationally infeasible to fit the model to more than a few individuals. However, the speed at which the functional movement model is fit makes it relatively easy to perform population-level analyses, which is often the ultimate goal in applied wildlife management research (Hooten *et al.*, 2016).

## 5.2. FUTURE METHODOLOGICAL DIRECTIONS

The primary drawback to using a phenomenological model for animal movement is the disconnect between movement and the landscape. At this time, it is not obvious how to incorporate landscape variables into the continuous-time movement process directly, though it can be done in the discrete-time spatial point-process framework (Johnson *et al.*, 2013; Brost *et al.*, 2015). Incorporating landscape variables could improve location estimation, particularly for specialists that are dependent on specific landscape features. At the current stage of development, linking movement to the landscape is done through secondary analyses

(Hooten *et al.*, 2017). However, spatial and temporal covariates could be incorporated by letting a potential function contribute to the true location of an individual in space (Hooten *et al.*, 2017). Potential functions have previously been implemented as the drift component in a stochastic differential equation for velocity (e.g., Brillinger *et al.*, 2001; Brillinger, 2010).

Many of the landscape variables that we treat as static are also varying in time, either over long periods, like land use, or short periods, like kill sites. Incorporating time-varying covariates adds an additional layer of complexity, however time-varying covariates could strengthen inference on the effect of the landscape. For example, the algorithm used to fit the model could reference a temporally indexed covariate for subsets of the data. A series of covariates that correspond to different time-periods would be more representative of what the individual was responding to at a given time.

### 5.3. ECOLOGICAL INFERENCE

There have been many studies on Canada lynx populations in Alaska and Canada, where they are an abundant fur-bearer. However, due to their low densities in the continental U.S., few extensive studies have been performed on the “southern” lynx populations (Buskirk *et al.*, 2000a). Many of the preexisting studies have been plagued by small sample sizes and minimal temporal coverage. Due to the number of individuals and the span of temporal coverage, my study of lynx movement behavior is a significant contribution to the available information on Canada lynx movement at the southern extent of their historical range. In addition, this study is unique in its focus on a reintroduced population; we found that daily speed and turning angle does vary as a function of the year since an individual was reintroduced, potentially resulting in long-term behavioral effects. Similar methodology, as presented in Chapters 2 and 3, could be used to model reintroduced Iberian lynx (*Lynx pardinus*) and

Eurasian lynx (*Lynx lynx*). Many recent studies have used technology that obtains high-frequency data (e.g., Blazquez-Cabrera *et al.*, 2016; Gastón *et al.*, 2016); however, older data sets (e.g., Vandel *et al.*, 2006) may provide useful information on historical movement behavior.

In contrast, habits of cougars are well-studied due to their relative abundance and their general habitat requirements, which are in contrast to the specialized requirements of Canada lynx. Large carnivores are often used as indicators of habitat integrity because of their large home-ranges (Noss *et al.*, 1996). However, I found that cougars are not particularly sensitive to anthropogenic disturbances on the landscape. The insensitivity to the level of human disturbance present in the Colorado Front Range may make them poor ecological proxies for non-generalist species. However, the strong effect of potential kill site locations may indicate that cougars are sensitive to fine-scale landscape features that increase the probability of them locating and successfully killing a prey item (Blecha, 2015). These fine-scale landscape features are currently impossible to observe at large spatial scales, but could provide more informative inference on movement dynamics for cougars and other perceived generalists.

Technological advancements in wildlife monitoring allow researchers to collect incredible amounts of information on individual animal movements with relative ease (Hebblewhite & Haydon, 2010). The study of animal movement can offer insights into evolutionary adaptations (Fahrig, 2007), demographic impacts of habitat fragmentation (Shepard *et al.*, 2008), and population dynamics, such as survival, emigration, and immigration (Morales *et al.*, 2010). Developing efficient and easy to implement movement models can help biologists connect the wealth of spatial data to the dynamics that are most often used for population management and conservation.

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## APPENDIX A

### SUPPLEMENTAL MATERIAL FOR CHAPTER 2

#### A.1. PRIOR SPECIFICATIONS

$w_j(t) \sim \text{Bern}(0.5)$  for  $j = 1, \dots, J$  and  $t \in \mathcal{T}$

$\sigma_j^2 \sim \text{IG}(0.0001, 1000)$  for  $j = 1, \dots, J$

$\rho \sim \text{Beta}(13.31, 4.44)$

$$E[\rho] = 0.75$$

$$\text{VAR}[\rho] = 0.01$$

$c \sim \text{Beta}(7.2, 0.8)$

$$E[c] = 0.90$$

$$\text{VAR}[c] = 0.01$$

$\beta_0 \sim N(\mathbf{0}, 100\mathbf{I})$

$$\beta \sim N\left(\mathbf{0}, \begin{bmatrix} \sigma_{\beta_{lon}}^2 \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \sigma_{\beta_{lat}}^2 \mathbf{I} \end{bmatrix}\right)$$

Priors for  $\rho$  and  $c$  were selected to approximate the shape of the Argos error structure reported by Costa *et al.* (2010) and Brost *et al.* (2015). Alternatively, one could use  $\text{Beta}(1, 1)$  as a flat prior for both parameters. Posterior inference for the Canada lynx data was not very sensitive to the choice of priors for  $\rho$  and  $c$ .

## A.2. DEVIANCE INFORMATION CRITERION CALCULATION

$$DIC = \hat{D} + 2p_D$$

$$p_D = \bar{D} - \hat{D}$$

Deviance computed at the posterior mean of the parameters:

$$\hat{D} = -2\log[\mathbf{S}|\hat{\boldsymbol{\beta}}_0, \hat{\boldsymbol{\beta}}, \hat{\boldsymbol{\sigma}}^2, \hat{\rho}, \hat{c}, \hat{\mathbf{w}}]$$

Posterior mean deviance:

$$\bar{D} = E(-2\log[\mathbf{S}|\boldsymbol{\beta}_0, \boldsymbol{\beta}, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}]|\mathbf{S})$$

### A.3. MCMC ALGORITHM

MCMC algorithm for fitting the spline-based movement model and calculating derived behavioral quantities.

```
fda.movement <- function(S.0,S.1,S.2,S.3,S.A,S.B,S.V,X.0,X.1,X
.2,X.3,X.A,X.B,X.V,X.pred,s2.beta,n.mcmc,pred=TRUE){
# longitude is always [,1], latitude [,2]
# S.0, S.1, S.2, S.3, S.A, S.B, S.V: scaled locations for each
  data type
# X.0, X.1, X.2, X.3, X.A, X.B, X.V: the B-splines evaluated at
  times corresponding to the locations for each data tume
# X.pred: B-splines evaluated at prediction times
# s2.beta: variance terms for regularization matrix
# pred: if TRUE, derived quantities are calculated
# Note: this code calculates the temporal versions of the
  derived quantities, not the spatial (grid cell) versions
# Note: if plotting on the original landscape is desired, MU
  should be back-transformed before calculating derived
  quantities
####
#### Libraries and Subroutines
####
library(mvtnorm)
####
#### Setup Variables
####
n.burn=round(.1*n.mcmc)
T=dim(X.pred)[1]
p=dim(X.pred)[2]
T.0<-ifelse (is.null(nrow(S.0)), 1, nrow(S.0)[1])
T.1<-ifelse (is.null(nrow(S.1)), 1, nrow(S.1)[1])
T.2<-ifelse (is.null(nrow(S.2)), 1, nrow(S.2)[1])
T.3<-ifelse (is.null(nrow(S.3)), 1, nrow(S.3)[1])
T.A<-ifelse (is.null(nrow(S.A)), 1, nrow(S.A)[1])
T.B<-ifelse (is.null(nrow(S.B)), 1, nrow(S.B)[1])
T.V<-ifelse (is.null(nrow(S.V)), 1, nrow(S.V)[1])
s.0=c(S.0)
s.1=c(S.1)
s.2=c(S.2)
s.3=c(S.3)
s.A=c(S.A)
s.B=c(S.B)
s.V=c(S.V)
data.all<-cbind(rbind(S.0,S.1,S.2,S.3,S.A,S.B,S.V),rep(1:7,c(T
.0,T.1,T.2,T.3,T.A,T.B,T.V)),rep(1:sum(T.0,T.1,T.2,T.3,T.A,T
.B,T.V)))
if (length(S.0>0)) {X.big.0<-diag(2)%x%matrix(X.0,nrow=length(S
.0)/2)} else {X.big.0<-diag(2)%x%X.0}
if (length(S.1>0)) {X.big.1<-diag(2)%x%matrix(X.1,nrow=length(S
.1)/2)} else {X.big.1<-diag(2)%x%X.1}
if (length(S.2>0)) {X.big.2<-diag(2)%x%matrix(X.2,nrow=length(S
.2)/2)} else {X.big.2<-diag(2)%x%X.2}
if (length(S.3>0)) {X.big.3<-diag(2)%x%matrix(X.3,nrow=length(S
.3)/2)} else {X.big.3<-diag(2)%x%X.3}
```

```

if (length(S.A>0)) {X.big.A<-diag(2)%x%matrix(X.A,nrow=length(S
.A)/2)} else {X.big.A<-diag(2)%x%X.A}
if (length(S.B>0)) {X.big.B<-diag(2)%x%matrix(X.B,nrow=length(S
.B)/2)} else {X.big.B<-diag(2)%x%X.B}
if (length(S.V>0)) {X.big.V<-diag(2)%x%matrix(X.V,nrow=length(S
.V)/2)} else {X.big.V<-diag(2)%x%X.V}
X.big.full=diag(2)%x%X.pred
####
#### Storage
####
beta.save=matrix(0,2*p,n.mcmc)
beta.0.save=matrix(0,2,n.mcmc)
w.save=matrix(0,sum(T.0,T.1,T.2,T.3,T.A,T.B,T.V),n.mcmc)
s2.0.save=rep(0,n.mcmc)
s2.1.save=rep(0,n.mcmc)
s2.2.save=rep(0,n.mcmc)
s2.3.save=rep(0,n.mcmc)
s2.A.save=rep(0,n.mcmc)
s2.B.save=rep(0,n.mcmc)
s2.V.save=rep(0,n.mcmc)
MU=matrix(0,T,2)
MU.save=array(0,c(T,2,n.mcmc))
rho.save=rep(0,n.mcmc)
c.save=rep(0,n.mcmc)
####
#### Derived Quantities
####
MU.us=matrix(0,T,2)
MU.save.us=array(0,c(T,2,n.mcmc))
speed.save=matrix(0,T-1,n.mcmc)
res.save=matrix(0,T-1,n.mcmc)
theta.save=matrix(0,T-2,n.mcmc)
####
#### Priors and Starting Values
####
#### Priors for beta_0
mu.0=rep(0,2)
Sig.0=100*diag(2)
Sig.0.inv=solve(Sig.0)
#### Prior for beta
Sig.beta.inv=diag(1/c(rep(s2.beta[1],p),rep(s2.beta[2],p)))
#### Priors for s2.j
r.0=1000
q.0=.0001
r.1=1000
q.1=.0001
r.2=1000
q.2=.0001
r.3=1000
q.3=.0001
r.A=1000
q.A=.0001
r.B=1000
q.B=.0001
r.V=1000
q.V=.0001
#### Priors for rho and c
betamoments<-function(mu,sigma){
  alpha<-mu*((mu*(1-mu))/sigma^2-1)

```

```

beta<-(1-mu)*((mu*(1-mu))/sigma^2-1)
list(alpha=alpha,beta=beta)
}
rho.alpha<-betamoments(mu=0.75,sigma=0.1)$alpha
rho.beta<-betamoments(mu=0.75,sigma=0.1)$beta
c.alpha<-betamoments(mu=0.9,sigma=0.1)$alpha
c.beta<-betamoments(mu=0.9,sigma=0.1)$beta
rho.tune=0.1
c.tune=0.1
#### Priors for w
p.ARGOS<-0.5
p.VHF<-1
#### Starting Value for beta and beta_0
beta.0=apply(rbind(S.0,S.1,S.2,S.3,S.A,S.B,S.V),2,mean)
beta=rep(0,2*p)
#### Starting Value for s2.j
if (length(s.0)>0) {s2.0<-1} else {s2.0<-0}
if (length(s.1)>0) {s2.1<-1} else {s2.1<-0}
if (length(s.2)>0) {s2.2<-1} else {s2.2<-0}
if (length(s.3)>0) {s2.3<-1} else {s2.3<-0}
if (length(s.A)>0) {s2.A<-1} else {s2.A<-0}
if (length(s.B)>0) {s2.B<-1} else {s2.B<-0}
if (length(s.V)>0) {s2.V<-1} else {s2.V<-0}
#### Starting Value for rho and c
rho<-0.5
rho.acc<-0
c<-0.5
c.acc<-0
#### k Matrix and Covariance Matrix for VHF
K.argos=matrix(c(1,0,0,-1),2,2,byrow=T)
t.K.argos=t(K.argos)
K.vhf=matrix(c(1,0,0,1),2,2,byrow=T)
t.K.vhf=t(K.vhf)
R.vhf=matrix(c(1,0,0,1),2,2,byrow=T)
R.vhf.inv=solve(R.vhf)
R.vhf.star=matrix(c(1,0,0,1),2,2,byrow=T)
#### Lists for Sigma
Sigma<-list()
Sigma.tilda<-list()
Sigma.inv<-list()
Sigma.tilda.inv<-list()
####
#### Begin MCMC Loop
####
for(k in 1:n.mcmc){
  if(k%%100==0) cat(k,"□")
  ####
  #### Calculate Sigma_j and associated matrices
  ####
  R.argos=matrix(c(1,sqrt(c)*rho,sqrt(c)*rho,c),2,2,byrow=T)
  R.argos.inv=solve(R.argos)
  if (length(S.0)>0) {Sigma[[1]]<-matrix(s2.0*R.argos,2,2,byrow=
    T)} else {Sigma[[1]]<-matrix(rep(0,4),2,2)}
  if (length(S.1)>0) {Sigma[[2]]<-matrix(s2.1*R.argos,2,2,byrow=
    T)} else {Sigma[[2]]<-matrix(rep(0,4),2,2)}
  if (length(S.2)>0) {Sigma[[3]]<-matrix(s2.2*R.argos,2,2,byrow=
    T)} else {Sigma[[3]]<-matrix(rep(0,4),2,2)}
}

```

```

if (length(S.3)>0) {Sigma[[4]]<-matrix(s2.3*R.argos,2,2,byrow=
T)} else {Sigma[[4]]<-matrix(rep(0,4),2,2)}
if (length(S.A)>0) {Sigma[[5]]<-matrix(s2.A*R.argos,2,2,byrow=
T)} else {Sigma[[5]]<-matrix(rep(0,4),2,2)}
if (length(S.B)>0) {Sigma[[6]]<-matrix(s2.B*R.argos,2,2,byrow=
T)} else {Sigma[[6]]<-matrix(rep(0,4),2,2)}
if (length(S.V)>0) {Sigma[[7]]<-matrix(s2.V*R.vhf,2,2,byrow=T)
} else {Sigma[[7]]<-matrix(rep(0,4),2,2)}
Sigma.tilda[[1]]<-K.argos%%Sigma[[1]]%%t.K.argos
Sigma.tilda[[2]]<-K.argos%%Sigma[[2]]%%t.K.argos
Sigma.tilda[[3]]<-K.argos%%Sigma[[3]]%%t.K.argos
Sigma.tilda[[4]]<-K.argos%%Sigma[[4]]%%t.K.argos
Sigma.tilda[[5]]<-K.argos%%Sigma[[5]]%%t.K.argos
Sigma.tilda[[6]]<-K.argos%%Sigma[[6]]%%t.K.argos
Sigma.tilda[[7]]<-K.vhf%%Sigma[[7]]%%t.K.vhf
X.0.x.beta<-matrix(c(X.big.0%%beta),ncol=2)
X.1.x.beta<-matrix(c(X.big.1%%beta),ncol=2)
X.2.x.beta<-matrix(c(X.big.2%%beta),ncol=2)
X.3.x.beta<-matrix(c(X.big.3%%beta),ncol=2)
X.A.x.beta<-matrix(c(X.big.A%%beta),ncol=2)
X.B.x.beta<-matrix(c(X.big.B%%beta),ncol=2)
X.V.x.beta<-matrix(c(X.big.V%%beta),ncol=2)
X.x.beta.all<-cbind(rbind(X.0.x.beta,X.1.x.beta,X.2.x.beta,X
.3.x.beta,X.A.x.beta,X.B.x.beta,X.V.x.beta),rep(1:7,c(T.0,T
.1,T.2,T.3,T.A,T.B,T.V)))
beta.0.all<-cbind(rep(beta.0[1],nrow(X.x.beta.all)),rep(beta
.0[2],nrow(X.x.beta.all)))
tmp.mean<-NULL
tmp.diff<-NULL
tmp.mean<-cbind(beta.0.all+X.x.beta.all[,1:2],X.x.beta.all
[,3],data.all[,4])
tmp.diff<-cbind(data.all[,1:2]-tmp.mean[,1:2],X.x.beta.all
[,3],data.all[,4])
rownames(tmp.mean)<-data.all[,4]
rownames(tmp.diff)<-data.all[,4]
tmp.diff.subset<-tmp.diff[,1:2]
####
#### Sample w
####
p.tmp.ARGOS<-NULL
for (n in unique(tmp.diff[,3][tmp.diff[,3]!=7])){
p.tmp.ARGOS<-rbind(p.tmp.ARGOS,cbind(p.ARGOS*dmvnorm(tmp.diff
.subset[tmp.diff[,3]==n,],c(0,0),Sigma[[n]])/(p.ARGOS*
dmvnorm(tmp.diff.subset[tmp.diff[,3]==n,],c(0,0),Sigma[[n
]]))+
(1-p.ARGOS)*dmvnorm(tmp.diff.subset[tmp.diff[,3]==n,],c(0,0)
,Sigma.tilda[[n]])),as.numeric(rownames(tmp.diff[tmp.diff
[,3]==n,],drop=FALSE))))
}
w.ARGOS<-if (is.null(p.tmp.ARGOS)) {NULL} else {cbind(rbinom(
nrow(p.tmp.ARGOS),1,p.tmp.ARGOS[,1]),p.tmp.ARGOS[,2])}
p.tmp.VHF<-cbind(rep(1,nrow(tmp.diff[tmp.diff[,3]==7,]))
w.VHF<-cbind(rbinom(nrow(p.tmp.VHF),1,p.tmp.VHF[,1]),tmp.diff[
tmp.diff[,3]==7,4])
w<-rbind(w.ARGOS,w.VHF)

```

```

w<-cbind(w,tmp.diff[tmp.diff[,4]==w[,2],3])
w.save[,k]<-w[,1]
w.0<-sum(w[w[,3]==1,1])
w.1<-sum(w[w[,3]==2,1])
w.2<-sum(w[w[,3]==3,1])
w.3<-sum(w[w[,3]==4,1])
w.A<-sum(w[w[,3]==5,1])
w.B<-sum(w[w[,3]==6,1])
w.V<-sum(w[w[,3]==7,1])
### Factor out k, 2nd column becomes negative
tmp.diff.neg<-tmp.diff
tmp.diff.neg[w[,1]==0,2]<--tmp.diff[w[,1]==0,2]
tmp.s.0.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==1,1:2])*
%R.argos.inv*tmp.diff.neg[tmp.mean[,3]==1,1:2]))
tmp.s.1.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==2,1:2])*
%R.argos.inv*tmp.diff.neg[tmp.mean[,3]==2,1:2]))
tmp.s.2.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==3,1:2])*
%R.argos.inv*tmp.diff.neg[tmp.mean[,3]==3,1:2]))
tmp.s.3.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==4,1:2])*
%R.argos.inv*tmp.diff.neg[tmp.mean[,3]==4,1:2]))
tmp.s.A.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==5,1:2])*
%R.argos.inv*tmp.diff.neg[tmp.mean[,3]==5,1:2]))
tmp.s.B.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==6,1:2])*
%R.argos.inv*tmp.diff.neg[tmp.mean[,3]==6,1:2]))
tmp.s.V.inner<-sum(rowSums(tmp.diff.neg[tmp.mean[,3]==7,1:2])*
%R.vhf.inv*tmp.diff.neg[tmp.mean[,3]==7,1:2]))
#### Sample s2.0
tmp.r=(1/r.0+.5*tmp.s.0.inner)^(-1)
tmp.q=T.0+q.0
s2.0=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.0)==0) {s2.0<-0}
#### Sample s2.1
tmp.r=(1/r.1+.5*tmp.s.1.inner)^(-1)
tmp.q=T.1+q.1
s2.1=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.1)==0) {s2.1<-0}
#### Sample s2.2
tmp.r=(1/r.2+.5*tmp.s.2.inner)^(-1)
tmp.q=T.2+q.2
s2.2=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.2)==0) {s2.2<-0}
#### Sample s2.3
tmp.r=(1/r.3+.5*tmp.s.3.inner)^(-1)
tmp.q=T.3+q.3
s2.3=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.3)==0) {s2.3<-0}
#### Sample s2.A
tmp.r=(1/r.A+.5*tmp.s.A.inner)^(-1)
tmp.q=T.A+q.A
s2.A=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.A)==0) {s2.A<-0}
#### Sample s2.B
tmp.r=(1/r.B+.5*tmp.s.B.inner)^(-1)
tmp.q=T.B+q.B

```

```

s2.B=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.B)==0) {s2.B<-0}
#### Sample s2.V
tmp.r=(1/r.V+.5*tmp.s.V.inner)^(-1)
tmp.q=T.V+q.V
s2.V=1/rgamma(1,tmp.q,,tmp.r)
if (length(s.V)==0) {s2.V<-0}
#### Save Samples
s2.0.save[k]=s2.0
s2.1.save[k]=s2.1
s2.2.save[k]=s2.2
s2.3.save[k]=s2.3
s2.A.save[k]=s2.A
s2.B.save[k]=s2.B
s2.V.save[k]=s2.V
#### Recalculate sigmas
Sigma[[1]]<-matrix(s2.0*R.argos,2,2,byrow=T)
Sigma[[2]]<-matrix(s2.1*R.argos,2,2,byrow=T)
Sigma[[3]]<-matrix(s2.2*R.argos,2,2,byrow=T)
Sigma[[4]]<-matrix(s2.3*R.argos,2,2,byrow=T)
Sigma[[5]]<-matrix(s2.A*R.argos,2,2,byrow=T)
Sigma[[6]]<-matrix(s2.B*R.argos,2,2,byrow=T)
Sigma[[7]]<-matrix(s2.V*R.vhf,2,2,byrow=T)
Sigma.tilda[[1]]<-K.argos%%Sigma[[1]]%%t.K.argos
Sigma.tilda[[2]]<-K.argos%%Sigma[[2]]%%t.K.argos
Sigma.tilda[[3]]<-K.argos%%Sigma[[3]]%%t.K.argos
Sigma.tilda[[4]]<-K.argos%%Sigma[[4]]%%t.K.argos
Sigma.tilda[[5]]<-K.argos%%Sigma[[5]]%%t.K.argos
Sigma.tilda[[6]]<-K.argos%%Sigma[[6]]%%t.K.argos
Sigma.tilda[[7]]<-K.vhf%%Sigma[[7]]%%t.K.vhf
####
#### Sample rho
####
#### Propose rho.star
rho.star=rnorm(1,rho,rho.tune)
#### Calculate mh ratio
if (rho.star>=0 & rho.star<=1){
  R.argos.star=matrix(c(1,sqrt(c))*rho.star,sqrt(c)*rho.star,c)
  ,2,2,byrow=T)
  Sigma.star<-list()
  Sigma.tilda.star<-list()
  Sigma.star[[1]]=s2.0*R.argos.star
  Sigma.star[[2]]=s2.1*R.argos.star
  Sigma.star[[3]]=s2.2*R.argos.star
  Sigma.star[[4]]=s2.3*R.argos.star
  Sigma.star[[5]]=s2.A*R.argos.star
  Sigma.star[[6]]=s2.B*R.argos.star
  Sigma.star[[7]]=s2.V*R.vhf.star
  Sigma.tilda.star[[1]]=K.argos%%Sigma.star[[1]]%%t.K.argos
  Sigma.tilda.star[[2]]=K.argos%%Sigma.star[[2]]%%t.K.argos
  Sigma.tilda.star[[3]]=K.argos%%Sigma.star[[3]]%%t.K.argos
  Sigma.tilda.star[[4]]=K.argos%%Sigma.star[[4]]%%t.K.argos
  Sigma.tilda.star[[5]]=K.argos%%Sigma.star[[5]]%%t.K.argos
  Sigma.tilda.star[[6]]=K.argos%%Sigma.star[[6]]%%t.K.argos
  Sigma.tilda.star[[7]]=K.vhf%%Sigma.star[[7]]%%t.K.vhf

```

```

mh1<-dbeta(rho.star,rho.alpha,rho.beta,log=TRUE)
mh2<-dbeta(rho,rho.alpha,rho.beta,log=TRUE)
for (n in unique(w[,3][w[,3]!=7])){
  if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])!=0 & length(
    tmp.diff[w[,3]==n & w[,1]==0,1:2])!=0){
    mh1.tmp<-(sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
      (0,0),Sigma.star[[n]],log=TRUE))+sum(dmvnorm(tmp.diff[w
        [,3]==n & w[,1]==0,1:2],c(0,0),Sigma.tilda.star[[n]],log
          =TRUE)))
  }
  if (length(tmp.diff[w[,3]==n & w[,1]==0,1:2])==0){
    mh1.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
      (0,0),Sigma.star[[n]],log=TRUE))
  }
  if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])==0){
    mh1.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==0,1:2],c
      (0,0),Sigma.tilda.star[[n]],log=TRUE))
  }
  mh1<-mh1+mh1.tmp
  if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])!=0 & length(
    tmp.diff[w[,3]==n & w[,1]==0,1:2])!=0){
    mh2.tmp<-(sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
      (0,0),Sigma[[n]],log=TRUE))+sum(dmvnorm(tmp.diff[w[,3]==
        n & w[,1]==0,1:2],c(0,0),Sigma.tilda[[n]],log=TRUE)))
  }
  if (length(tmp.diff[w[,3]==n & w[,1]==0,1:2])==0){
    mh2.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
      (0,0),Sigma[[n]],log=TRUE))
  }
  if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])==0){
    mh2.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==0,1:2],c
      (0,0),Sigma.tilda[[n]],log=TRUE))
  }
  mh2<-mh2+mh2.tmp
}
mhratio=exp(mh1-mh2)
if(mhratio > runif(1)){
  rho=rho.star
  rho.acc=rho.acc+1
  ##### Recalculate sigmas
  R.argos=matrix(c(1,sqrt(c)*rho,sqrt(c)*rho,c),2,2,byrow=T)
  Sigma[[1]]<-matrix(s2.0*R.argos,2,2,byrow=T)
  Sigma[[2]]<-matrix(s2.1*R.argos,2,2,byrow=T)
  Sigma[[3]]<-matrix(s2.2*R.argos,2,2,byrow=T)
  Sigma[[4]]<-matrix(s2.3*R.argos,2,2,byrow=T)
  Sigma[[5]]<-matrix(s2.A*R.argos,2,2,byrow=T)
  Sigma[[6]]<-matrix(s2.B*R.argos,2,2,byrow=T)
  Sigma[[7]]<-matrix(s2.V*R.vhf,2,2,byrow=T)
  Sigma.tilda[[1]]<-K.argos%%Sigma[[1]]%%t.K.argos
  Sigma.tilda[[2]]<-K.argos%%Sigma[[2]]%%t.K.argos
  Sigma.tilda[[3]]<-K.argos%%Sigma[[3]]%%t.K.argos
  Sigma.tilda[[4]]<-K.argos%%Sigma[[4]]%%t.K.argos
  Sigma.tilda[[5]]<-K.argos%%Sigma[[5]]%%t.K.argos
  Sigma.tilda[[6]]<-K.argos%%Sigma[[6]]%%t.K.argos
  Sigma.tilda[[7]]<-K.vhf%%Sigma[[7]]%%t.K.vhf
}

```

```

}
rho.save[k]<-rho
####
#### Sample c
####
#### Propose c.star
c.star=rnorm(1,c,c.tune)
if (c.star>=0 & c.star<=1){
  R.argos.star=matrix(c(1,sqrt(c.star)*rho,sqrt(c.star)*rho,c.
    star),2,2,byrow=T)
  Sigma.star<-list()
  Sigma.tilda.star<-list()
  Sigma.star[[1]]=s2.0*R.argos.star
  Sigma.star[[2]]=s2.1*R.argos.star
  Sigma.star[[3]]=s2.2*R.argos.star
  Sigma.star[[4]]=s2.3*R.argos.star
  Sigma.star[[5]]=s2.A*R.argos.star
  Sigma.star[[6]]=s2.B*R.argos.star
  Sigma.star[[7]]=s2.V*R.vhf.star
  Sigma.tilda.star[[1]]=K.argos%%Sigma.star[[1]]%%t.K.argos
  Sigma.tilda.star[[2]]=K.argos%%Sigma.star[[2]]%%t.K.argos
  Sigma.tilda.star[[3]]=K.argos%%Sigma.star[[3]]%%t.K.argos
  Sigma.tilda.star[[4]]=K.argos%%Sigma.star[[4]]%%t.K.argos
  Sigma.tilda.star[[5]]=K.argos%%Sigma.star[[5]]%%t.K.argos
  Sigma.tilda.star[[6]]=K.argos%%Sigma.star[[6]]%%t.K.argos
  Sigma.tilda.star[[7]]=K.vhf%%Sigma.star[[7]]%%t.K.vhf
  mh1<-dbeta(c.star,c.alpha,c.beta,log=TRUE)
  mh2<-dbeta(c,c.alpha,c.beta,log=TRUE)
  for (n in unique(w[,3][w[,3]!=7])){
    if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])!=0 & length(
      tmp.diff[w[,3]==n & w[,1]==0,1:2])!=0){
      mh1.tmp<-(sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
        (0,0),Sigma.star[[n]],log=TRUE))+sum(dmvnorm(tmp.diff[w
          [,3]==n & w[,1]==0,1:2],c(0,0),Sigma.tilda.star[[n]],log
            =TRUE)))
    }
    if (length(tmp.diff[w[,3]==n & w[,1]==0,1:2])==0){
      mh1.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
        (0,0),Sigma.star[[n]],log=TRUE))
    }
    if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])==0){
      mh1.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==0,1:2],c
        (0,0),Sigma.tilda.star[[n]],log=TRUE))
    }
    mh1<-mh1+mh1.tmp
    if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])!=0 & length(
      tmp.diff[w[,3]==n & w[,1]==0,1:2])!=0){
      mh2.tmp<-(sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
        (0,0),Sigma[[n]],log=TRUE))+sum(dmvnorm(tmp.diff[w[,3]==
          n & w[,1]==0,1:2],c(0,0),Sigma.tilda[[n]],log=TRUE)))
    }
    if (length(tmp.diff[w[,3]==n & w[,1]==0,1:2])==0){
      mh2.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==1,1:2],c
        (0,0),Sigma[[n]],log=TRUE))
    }
  }
  if (length(tmp.diff[w[,3]==n & w[,1]==1,1:2])==0){

```

```

    mh2.tmp<-sum(dmvnorm(tmp.diff[w[,3]==n & w[,1]==0,1:2],c
      (0,0),Sigma.tilda[[n]],log=TRUE))
  }
  mh2<-mh2+mh2.tmp
}
mhratio=exp(mh1-mh2)
if(mhratio > runif(1)){
  c=c.star
  c.acc=c.acc+1
  ##### Recalculate sigmas
  R.argos=matrix(c(1,sqrt(c)*rho,sqrt(c)*rho,c),2,2,byrow=T)
  Sigma[[1]]<-matrix(s2.0*R.argos,2,2,byrow=T)
  Sigma[[2]]<-matrix(s2.1*R.argos,2,2,byrow=T)
  Sigma[[3]]<-matrix(s2.2*R.argos,2,2,byrow=T)
  Sigma[[4]]<-matrix(s2.3*R.argos,2,2,byrow=T)
  Sigma[[5]]<-matrix(s2.A*R.argos,2,2,byrow=T)
  Sigma[[6]]<-matrix(s2.B*R.argos,2,2,byrow=T)
  Sigma[[7]]<-matrix(s2.V*R.vhf,2,2,byrow=T)
  Sigma.tilda[[1]]<-K.argos%%Sigma[[1]]%%t.K.argos
  Sigma.tilda[[2]]<-K.argos%%Sigma[[2]]%%t.K.argos
  Sigma.tilda[[3]]<-K.argos%%Sigma[[3]]%%t.K.argos
  Sigma.tilda[[4]]<-K.argos%%Sigma[[4]]%%t.K.argos
  Sigma.tilda[[5]]<-K.argos%%Sigma[[5]]%%t.K.argos
  Sigma.tilda[[6]]<-K.argos%%Sigma[[6]]%%t.K.argos
  Sigma.tilda[[7]]<-K.vhf%%Sigma[[7]]%%t.K.vhf
}
}
c.save[k]<-c
#####
##### Calculate Sigma inverse
#####
if (length(S.0)>0) {Sigma.inv[[1]]<-solve(Sigma[[1]]); Sigma.
  tilda.inv[[1]]<-K.argos%%Sigma.inv[[1]]%%t.K.argos} else
  {Sigma.inv[[1]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[1]]
  <-matrix(rep(0,4),2,2)}
if (length(S.1)>0) {Sigma.inv[[2]]<-solve(Sigma[[2]]); Sigma.
  tilda.inv[[2]]<-K.argos%%Sigma.inv[[2]]%%t.K.argos} else
  {Sigma.inv[[2]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[2]]
  <-matrix(rep(0,4),2,2)}
if (length(S.2)>0) {Sigma.inv[[3]]<-solve(Sigma[[3]]); Sigma.
  tilda.inv[[3]]<-K.argos%%Sigma.inv[[3]]%%t.K.argos} else
  {Sigma.inv[[3]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[3]]
  <-matrix(rep(0,4),2,2)}
if (length(S.3)>0) {Sigma.inv[[4]]<-solve(Sigma[[4]]); Sigma.
  tilda.inv[[4]]<-K.argos%%Sigma.inv[[4]]%%t.K.argos} else
  {Sigma.inv[[4]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[4]]
  <-matrix(rep(0,4),2,2)}
if (length(S.A)>0) {Sigma.inv[[5]]<-solve(Sigma[[5]]); Sigma.
  tilda.inv[[5]]<-K.argos%%Sigma.inv[[5]]%%t.K.argos} else
  {Sigma.inv[[5]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[5]]
  <-matrix(rep(0,4),2,2)}
if (length(S.B)>0) {Sigma.inv[[6]]<-solve(Sigma[[6]]); Sigma.
  tilda.inv[[6]]<-K.argos%%Sigma.inv[[6]]%%t.K.argos} else
  {Sigma.inv[[6]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[6]]
  <-matrix(rep(0,4),2,2)}

```

```

if (length(S.V)>0) {Sigma.inv[[7]]<-solve(Sigma[[7]]); Sigma.
  tilda.inv[[7]]<-K.vhf%%Sigma.inv[[7]]%%t.K.vhf} else {
  Sigma.inv[[7]]<-matrix(rep(0,4),2,2); Sigma.tilda.inv[[7]]
  <-matrix(rep(0,4),2,2)}
####
#### Sample beta
####
Sigma.0.big<-matrix(rep(0,T.0),nrow=2*T.0,ncol=2*T.0)
Sigma.1.big<-matrix(rep(0,T.1),nrow=2*T.1,ncol=2*T.1)
Sigma.2.big<-matrix(rep(0,T.2),nrow=2*T.2,ncol=2*T.2)
Sigma.3.big<-matrix(rep(0,T.3),nrow=2*T.3,ncol=2*T.3)
Sigma.A.big<-matrix(rep(0,T.A),nrow=2*T.A,ncol=2*T.A)
Sigma.B.big<-matrix(rep(0,T.B),nrow=2*T.B,ncol=2*T.B)
Sigma.V.big<-matrix(rep(0,T.V),nrow=2*T.V,ncol=2*T.V)
Sigma.big<-list(Sigma.0.big,Sigma.1.big,Sigma.2.big,Sigma.3.
  big,Sigma.A.big,Sigma.B.big,Sigma.V.big)
S.times<-list(T.0,T.1,T.2,T.3,T.A,T.B,T.V)
for (n in 1:7){
  tmp.w<-w[w[,3]==n,,drop=FALSE]
  diag.1<-rep(Sigma.inv[[n]][1,1],S.times[n])
  diag.2<-rep(Sigma.inv[[n]][2,2],S.times[n])
  offdiag<-rep(0,S.times[n])
  offdiag[tmp.w[,1]==1]<-Sigma.inv[[n]][2,1]
  offdiag[tmp.w[,1]==0]<-Sigma.tilda.inv[[n]][2,1]
  delta<-row(Sigma.big[[n]])-col(Sigma.big[[n]])
  diag(Sigma.big[[n]])<-c(diag.1,diag.2)
  Sigma.big[[n]][abs(delta)==S.times[n]]<-offdiag
}
#### Cholesky decomposition
b.tmp<-t(X.big.0)%%Sigma.big[[1]]%%(c(S.0)-kronecker(c(beta
  .0),rep(1,T.0)))+
  t(X.big.1)%%Sigma.big[[2]]%%(c(S.1)-kronecker(c(beta.0),rep
    (1,T.1)))+
  t(X.big.2)%%Sigma.big[[3]]%%(c(S.2)-kronecker(c(beta.0),rep
    (1,T.2)))+
  t(X.big.3)%%Sigma.big[[4]]%%(c(S.3)-kronecker(c(beta.0),rep
    (1,T.3)))+
  t(X.big.A)%%Sigma.big[[5]]%%(c(S.A)-kronecker(c(beta.0),rep
    (1,T.A)))+
  t(X.big.B)%%Sigma.big[[6]]%%(c(S.B)-kronecker(c(beta.0),rep
    (1,T.B)))+
  t(X.big.V)%%Sigma.big[[7]]%%(c(S.V)-kronecker(c(beta.0),rep
    (1,T.V)))
A.tmp.chol<-chol(t(X.big.0)%%Sigma.big[[1]]%%X.big.0+
  t(X.big.1)%%Sigma.big[[2]]%%X.big.1+t(X.big.2)%%Sigma.big
    [[3]]%%X.big.2+
  t(X.big.3)%%Sigma.big[[4]]%%X.big.3+t(X.big.A)%%Sigma.big
    [[5]]%%X.big.A+
  t(X.big.B)%%Sigma.big[[6]]%%X.big.B+t(X.big.V)%%Sigma.big
    [[7]]%%X.big.V+Sig.beta.inv)
beta<-backsolve(A.tmp.chol,backsolve(A.tmp.chol,b.tmp,
  transpose=TRUE)+rnorm(2*p))
#### Save samples
beta.save[,k]=beta
####

```

```

#### Sample beta.0
####
sum.0.tmp<-colSums(matrix(c(Sigma.big[[1]]%*(c(S.0)-X.big.0%*
%beta)),nrow=T.0,ncol=2))
sum.1.tmp<-colSums(matrix(c(Sigma.big[[2]]%*(c(S.1)-X.big.1%*
%beta)),nrow=T.1,ncol=2))
sum.2.tmp<-colSums(matrix(c(Sigma.big[[3]]%*(c(S.2)-X.big.2%*
%beta)),nrow=T.2,ncol=2))
sum.3.tmp<-colSums(matrix(c(Sigma.big[[4]]%*(c(S.3)-X.big.3%*
%beta)),nrow=T.3,ncol=2))
sum.A.tmp<-colSums(matrix(c(Sigma.big[[5]]%*(c(S.A)-X.big.A%*
%beta)),nrow=T.A,ncol=2))
sum.B.tmp<-colSums(matrix(c(Sigma.big[[6]]%*(c(S.B)-X.big.B%*
%beta)),nrow=T.B,ncol=2))
sum.V.tmp<-colSums(matrix(c(Sigma.big[[7]]%*(c(S.V)-X.big.V%*
%beta)),nrow=T.V,ncol=2))
mult.0.tmp<-w.0*Sigma.0.inv+(T.0-w.0)*Sigma.tilda.0.inv
mult.1.tmp<-w.1*Sigma.1.inv+(T.1-w.1)*Sigma.tilda.1.inv
mult.2.tmp<-w.2*Sigma.2.inv+(T.2-w.2)*Sigma.tilda.2.inv
mult.3.tmp<-w.3*Sigma.3.inv+(T.3-w.3)*Sigma.tilda.3.inv
mult.A.tmp<-w.A*Sigma.A.inv+(T.A-w.A)*Sigma.tilda.A.inv
mult.V.tmp<-w.V*Sigma.B.inv+(T.B-w.B)*Sigma.tilda.B.inv
mult.V.tmp<-w.V*Sigma.V.inv+(T.V-w.V)*Sigma.tilda.V.inv
#### Cholesky decomposition
b.tmp<-sum.0.tmp+sum.1.tmp+sum.2.tmp+sum.3.tmp+sum.A.tmp+sum.V
.tmp+Sig.0.inv**mu.0
A.tmp.chol<-chol(mult.0.tmp+mult.1.tmp+mult.2.tmp+mult.3.tmp+
mult.A.tmp+mult.V.tmp+Sig.0.inv)
beta.0=t(backsolve(A.tmp.chol,backsolve(A.tmp.chol,b.tmp,
transpose=TRUE)+rnorm(2)))
beta.0.save[,k]=beta.0
####
#### Save Derived Quantities
####
MU=t(matrix(beta.0,2,T))+matrix(X.big.full**beta,T,2)
MU.save[,k]=MU
if (pred){
  if(k > n.burn){
    MU.diff=apply(MU,2,diff)
    speed=sqrt(diag(MU.diff**t(MU.diff)))
    theta=rep(NA,T-2)
    for(t in 1:(T-2)){
      theta[t]=abs(acos(pmin((MU.diff[t+1,]**MU.diff[t,])/(sqrt(
MU.diff[t,]**MU.diff[t,])*sqrt(MU.diff[t+1,]**MU.diff[
t+1,])),1)))
    }
    speed.save[,k]=speed
    res.save[,k]=1/speed
    theta.save[,k]=theta
  }
}
}
cat("\n")
list(s2.beta=s2.beta,beta.0.save=beta.0.save,beta.save=beta.
save,c.save=c.save,rho.save=rho.save,

```

```
s2.0.save=s2.0.save,s2.1.save=s2.1.save,s2.2.save=s2.2.save,s2
.3.save=s2.3.save,s2.A.save=s2.A.save,s2.B.save=s2.B.save,s2
.V.save=s2.V.save,
MU.save=MU.save,speed.save=speed.save,res.save=res.save,theta.
save=theta.save,n.mcmc=n.mcmc,n.burn=n.burn)
}
```

#### A.4. SPATIAL QUANTITIES

To describe movement behavior, I derived quantities from the movement path. These quantities can be described across a spatial extent of interest. Using the equivariance property of MCMC, I can calculate the posterior mean of these quantities for a cell within a grid,  $\mathcal{A}_l$  for  $l = 1, \dots, L$ , which spans the area for which I desire inference.

##### A.4.1. Average Residence Time

Posterior mean:

$$E(r_l|\mathbf{S}) = \int \cdots \int r_l[\beta_0, \beta, \sigma^2, \rho, c, \mathbf{w}|\mathbf{S}] d\beta_0 d\beta d\sigma^2 d\rho dc d\mathbf{w}$$

MCMC approximation:

$$E(r_l|\mathbf{S}) \approx \sum_{k=1}^K \frac{r_l^{(k)}}{K}$$

##### A.4.2. Average Speed

Posterior mean:

$$E(\bar{v}_l|\mathbf{S}) = \int \cdots \int \bar{v}_l[\beta_0, \beta, \sigma^2, \rho, c, \mathbf{w}|\mathbf{S}] d\beta_0 d\beta d\sigma^2 d\rho dc d\mathbf{w}$$

MCMC approximation:

$$E(\bar{v}_l|\mathbf{S}) \approx \sum_{k=1}^K \frac{\bar{v}_l^{(k)}}{K}$$

##### A.4.3. Average Persistence in Direction

Posterior mean:

$$E(\bar{\theta}_l|\mathbf{S}) = \int \cdots \int \bar{\theta}_l[\beta_0, \beta, \sigma^2, \rho, c, \mathbf{w}|\mathbf{S}] d\beta_0 d\beta d\sigma^2 d\rho dc d\mathbf{w}$$

MCMC approximation:

$$E(\bar{\theta}_l | \mathbf{S}) \approx \sum_{k=1}^K \frac{\bar{\theta}_l^{(k)}}{K}$$

## A.5. TEMPORAL QUANTITIES

To describe movement behavior, I derived temporal quantities from the continuous-time movement path. To obtain the posterior mean of a quantity for a given  $t \in \mathcal{T}$  I can use the equivariance property of MCMC.

### A.5.1. Average Residence Time

Posterior mean:

$$E(r(t)|\mathbf{S}) = \int \cdots \int r(t)[\boldsymbol{\beta}_0, \boldsymbol{\beta}, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}|\mathbf{S}]d\boldsymbol{\beta}_0d\boldsymbol{\beta}d\boldsymbol{\sigma}^2d\rho dc d\mathbf{w}$$

MCMC approximation:

$$E(r(t)|\mathbf{S}) \approx \sum_{k=1}^K \frac{r(t)^{(k)}}{K}$$

### A.5.2. Average Speed

Posterior mean:

$$E(\nu(t)|\mathbf{S}) = \int \cdots \int \nu(t)[\boldsymbol{\beta}_0, \boldsymbol{\beta}, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}|\mathbf{S}]d\boldsymbol{\beta}_0d\boldsymbol{\beta}d\boldsymbol{\sigma}^2d\rho dc d\mathbf{w}$$

MCMC approximation:

$$E(\nu(t)|\mathbf{S}) \approx \sum_{k=1}^K \frac{\nu(t)^{(k)}}{K}$$

### A.5.3. Average Persistence in Direction

Posterior mean:

$$E(\theta(t)|\mathbf{S}) = \int \cdots \int \theta(t)[\boldsymbol{\beta}_0, \boldsymbol{\beta}, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}|\mathbf{S}]d\boldsymbol{\beta}_0d\boldsymbol{\beta}d\boldsymbol{\sigma}^2d\rho dc d\mathbf{w}$$

MCMC approximation:

$$E(\theta(t)|\mathbf{S}) \approx \sum_{k=1}^K \frac{\theta(t)^{(k)}}{K}$$

## A.6. CASE STUDY TABLES

TABLE A.6.1. Release and mortality dates for two Canada lynx, originally from a population in British Columbia, Canada, and released in the San Juan mountains, Colorado, in 2003. Contact was lost with BC03M04 in 2005, whereas BC03F03 died in 2005.

| ID      | Release Date (y/m/d) | End Date (y/m/d) | Span (days) |
|---------|----------------------|------------------|-------------|
| BC03M04 | 2003/04/11           | 2005/03/03       | 687         |
| BC03F03 | 2003/04/03           | 2005/05/10       | 768         |

TABLE A.6.2. Number of locations in each Argos error class and number of VHF locations for two Canada lynx, originally from a population in British Columbia, Canada, and released in the San Juan mountains, Colorado, in 2003. The Argos provided estimate of error increases from less than 250 m for class 3 to more than 1,500 m for class 0; no estimated error is provided for classes A and B (Collecte Localisation Satellites, 2014).

| ID      | Class 3 | Class 2 | Class 1 | Class 0 | Class A | Class B | VHF | Total |
|---------|---------|---------|---------|---------|---------|---------|-----|-------|
| BC03M04 | 22      | 19      | 24      | 3       | 80      | 0       | 26  | 174   |
| BC03F03 | 10      | 21      | 65      | 16      | 112     | 0       | 42  | 266   |

TABLE A.6.3. Optimal variance terms for the regulator matrix and posterior means and 95% credible intervals for the covariance terms  $c$  and  $\rho$  for Canada lynx BC03M04 and BC03F03.

| ID      | $\sigma_{\beta_{lon}}^2$ | $\sigma_{\beta_{lat}}^2$ | $c$                   | $\rho$                 |
|---------|--------------------------|--------------------------|-----------------------|------------------------|
| BC03M04 | 0.0225                   | 0.0119                   | 0.94 (0.804-0.9991)   | 0.7714 (0.6453-0.8702) |
| BC03F03 | 0.0225                   | 0.0205                   | 0.768 (0.6061-0.9577) | 0.7618 (0.6526-0.8412) |

TABLE A.6.4. Posterior means and 95% credible intervals for the measurement error standard error (m) for each data type for Canada lynx BC03M04 and BC03F03.

| Parameter      | BC03M04 (m)             | BC03F03 (m)             |
|----------------|-------------------------|-------------------------|
| $\sigma_3$     | 12,703 (9,436-16,943)   | 13,403 (8,815-19,875)   |
| $\sigma_2$     | 15,981 (12,061-21,395)  | 18,306 (14,242-23,585)  |
| $\sigma_1$     | 24,091 (18,434-31,810)  | 21,1169 (18,004-25,070) |
| $\sigma_0$     | 37,927 (17,504-80,746)  | 22,142 (16,123-30,074)  |
| $\sigma_A$     | 19,150 (16,626-22,326)  | 20,077 (17,543-23,088)  |
| $\sigma_B$     | NA                      | NA                      |
| $\sigma_{VHF}$ | 13,389 (10,568-17,056)) | 12,298 (10,195-14,878)  |

## A.7. SIMULATIONS

Data were generated to mimic data patterns that may appear as a result of movement behaviors and to determine if the model could detect changes in movement quantities.

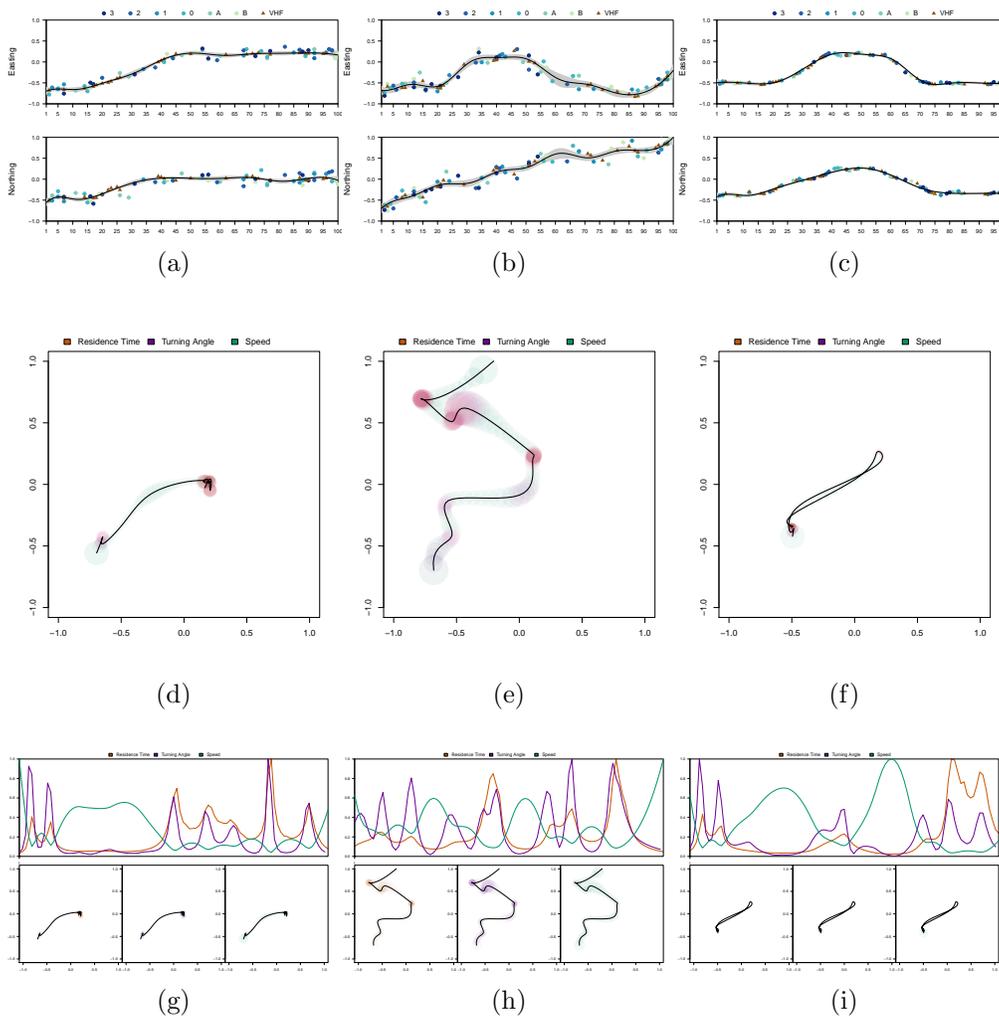


FIGURE A.7.1. Mean and 95% credible intervals of the marginal location for three simulated individuals (a), (b), (c). The posterior mean of each movement descriptor, relative to the maximum value for that behavior where the size of the point corresponds to spatial uncertainty and the transparency indicates the strength of the behavior at that location; for visualization purposes any value below 25% of the maximum value for that behavior is not shown (d), (e), (f). Posterior means for relative movement descriptors through time and space (g), (h), (i).

## A.8. REFERENCES

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APPENDIX B

SUPPLEMENTAL MATERIAL FOR CHAPTER 3

B.1. DATA SUMMARY

TABLE B.1.1. Information related to the original population, sex, and release year of the Canada lynx used in the analysis. Original populations other than those designated as “Colorado” were reintroduced individuals, whereas “Colorado” individuals were those encountered during the course of the study that were not reintroduced.

| Population       | Sex    | Release/Marking Year |      |      |      |      |      |      |      |      |      |      |
|------------------|--------|----------------------|------|------|------|------|------|------|------|------|------|------|
|                  |        | 1999                 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 |
| Alaska           | Male   | 1                    | 1    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| Alaska           | Female | 6                    | 3    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    |
| British Columbia | Male   | 3                    | 6    | 0    | 0    | 9    | 10   | 7    | 4    | 0    | 0    | 0    |
| British Columbia | Female | 1                    | 8    | 0    | 0    | 9    | 6    | 3    | 4    | 0    | 0    | 0    |
| Colorado         | Male   | 0                    | 0    | 0    | 0    | 0    | 3    | 2    | 0    | 1    | 0    | 0    |
| Colorado         | Female | 0                    | 0    | 0    | 0    | 0    | 4    | 0    | 0    | 1    | 0    | 1    |
| Manitoba         | Male   | 0                    | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0    |
| Manitoba         | Female | 0                    | 0    | 0    | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 0    |
| Quebec           | Male   | 0                    | 0    | 0    | 0    | 3    | 6    | 6    | 0    | 0    | 0    | 0    |
| Quebec           | Female | 0                    | 0    | 0    | 0    | 6    | 8    | 7    | 0    | 0    | 0    | 0    |
| Yukon            | Male   | 1                    | 6    | 0    | 0    | 0    | 0    | 3    | 3    | 0    | 0    | 0    |
| Yukon            | Female | 2                    | 13   | 0    | 0    | 0    | 0    | 2    | 2    | 0    | 0    | 0    |

TABLE B.1.2. Details regarding each time series for the Canada lynx used in the movement analysis. I include the number of data points for each data type, date range (presented as month/day/year), and span (days) for each time series. After the functional movement model was fit, time series within an individual were analyzed as a single time series.

| ID       | Series | Argos Error Class |    |    |    |      |    |     | Total      | Start      | End        | Span |
|----------|--------|-------------------|----|----|----|------|----|-----|------------|------------|------------|------|
|          |        | 3                 | 2  | 1  | 0  | A    | B  | VHF |            |            |            |      |
| AK00F02  | 1      | 0                 | 0  | 0  | 0  | 0    | 0  | 29  | 29         | 06/12/2001 | 07/17/2002 | 401  |
|          | 2      | 0                 | 0  | 0  | 0  | 0    | 0  | 35  | 35         | 11/07/2002 | 08/19/2003 | 286  |
|          | 3      | 20                | 39 | 76 | 43 | 1220 | 86 | 386 | 04/20/2004 | 09/29/2007 | 1258       |      |
| AK00F03  | 1      | 0                 | 0  | 2  | 6  | 5    | 0  | 68  | 81         | 05/03/2000 | 05/16/2003 | 1109 |
| AK00F05  | 1      | 5                 | 11 | 21 | 14 | 50   | 0  | 51  | 152        | 03/02/2005 | 11/01/2006 | 610  |
|          | 2      | 32                | 50 | 42 | 22 | 84   | 18 | 43  | 291        | 03/06/2007 | 03/02/2009 | 728  |
| AK00M011 |        | 6                 | 9  | 27 | 9  | 30   | 0  | 15  | 96         | 05/03/2000 | 05/22/2001 | 385  |
| AK99F02  | 1      | 0                 | 0  | 0  | 0  | 0    | 0  | 35  | 35         | 05/07/1999 | 04/18/2000 | 348  |
|          | 2      | 0                 | 0  | 0  | 0  | 0    | 0  | 60  | 60         | 07/06/2001 | 07/30/2003 | 755  |
| AK99F03  | 1      | 0                 | 0  | 0  | 0  | 0    | 0  | 33  | 33         | 10/04/1999 | 06/19/2000 | 260  |
| AK99F05  | 1      | 13                | 14 | 14 | 3  | 49   | 0  | 92  | 185        | 07/19/2000 | 10/17/2003 | 1186 |
|          | 2      | 19                | 24 | 28 | 12 | 44   | 0  | 12  | 139        | 04/10/2005 | 12/26/2005 | 261  |
| AK99F15  | 1      | 0                 | 0  | 0  | 0  | 0    | 0  | 26  | 26         | 05/14/1999 | 11/17/1999 | 188  |
| AK99F25  | 1      | 0                 | 0  | 0  | 0  | 0    | 0  | 45  | 45         | 05/07/1999 | 08/02/2000 | 454  |
| AK99FX   | 1      | 0                 | 0  | 0  | 0  | 0    | 0  | 136 | 136        | 05/07/1999 | 01/14/2003 | 1349 |
| AK99M011 |        | 0                 | 0  | 0  | 0  | 0    | 0  | 75  | 75         | 05/14/1999 | 03/12/2002 | 1034 |
| BC00F05  | 1      | 14                | 8  | 18 | 10 | 36   | 0  | 23  | 109        | 04/02/2000 | 08/03/2001 | 489  |
| BC00F06  | 1      | 3                 | 5  | 8  | 18 | 23   | 0  | 19  | 76         | 04/02/2000 | 05/22/2001 | 416  |
| BC00F07  | 1      | 11                | 9  | 16 | 7  | 32   | 0  | 13  | 88         | 04/02/2000 | 02/09/2001 | 314  |

|         |   |    |    |    |    |      |   |     |     |            |            |      |
|---------|---|----|----|----|----|------|---|-----|-----|------------|------------|------|
| BC00F08 | 1 | 12 | 7  | 14 | 7  | 38   | 0 | 22  | 100 | 04/02/2000 | 06/28/2001 | 453  |
|         | 2 | 0  | 0  | 0  | 0  | 0    | 0 | 121 | 121 | 10/18/2001 | 08/19/2004 | 1037 |
|         | 3 | 0  | 0  | 0  | 0  | 0    | 0 | 26  | 26  | 05/12/2005 | 11/17/2005 | 190  |
| BC00F10 | 1 | 8  | 10 | 14 | 5  | 20   | 0 | 8   | 65  | 04/02/2000 | 09/17/2000 | 169  |
| BC00F14 | 1 | 28 | 42 | 61 | 22 | 1190 |   | 65  | 337 | 04/02/2000 | 02/05/2004 | 1405 |
| BC00F18 | 1 | 10 | 10 | 21 | 11 | 46   | 0 | 8   | 106 | 04/02/2000 | 01/17/2001 | 291  |
|         | 2 | 5  | 7  | 18 | 11 | 61   | 0 | 167 | 269 | 09/26/2001 | 07/12/2005 | 1386 |
|         | 3 | 10 | 7  | 12 | 9  | 22   | 0 | 24  | 84  | 01/03/2007 | 08/07/2007 | 217  |
| BC00F19 | 1 | 12 | 21 | 19 | 4  | 28   | 0 | 141 | 225 | 04/02/2000 | 03/25/2004 | 1454 |
| BC00M02 | 1 | 5  | 10 | 11 | 5  | 31   | 0 | 5   | 67  | 04/02/2000 | 10/15/2000 | 197  |
|         | 2 | 4  | 2  | 4  | 1  | 25   | 0 | 39  | 75  | 03/16/2005 | 03/20/2007 | 735  |
| BC00M04 | 1 | 3  | 10 | 15 | 19 | 24   | 0 | 2   | 73  | 04/02/2000 | 09/18/2000 | 170  |
|         | 2 | 0  | 0  | 0  | 0  | 0    | 0 | 46  | 46  | 06/19/2001 | 04/11/2003 | 662  |
|         | 3 | 14 | 23 | 45 | 27 | 78   | 0 | 39  | 226 | 01/16/2004 | 07/13/2006 | 910  |
| BC00M09 | 1 | 13 | 19 | 21 | 8  | 95   | 0 | 122 | 278 | 04/02/2000 | 04/03/2006 | 2193 |
| BC00M11 | 1 | 14 | 12 | 19 | 11 | 53   | 0 | 120 | 229 | 04/02/2000 | 07/28/2005 | 1944 |
|         | 2 | 2  | 10 | 10 | 6  | 29   | 0 | 9   | 66  | 04/03/2006 | 10/21/2006 | 202  |
| BC00M15 | 1 | 13 | 17 | 9  | 3  | 45   | 0 | 20  | 107 | 04/02/2000 | 03/08/2001 | 341  |
|         | 2 | 0  | 0  | 0  | 0  | 0    | 0 | 27  | 27  | 04/25/2001 | 02/15/2002 | 297  |
| BC00M16 | 1 | 4  | 14 | 24 | 11 | 25   | 0 | 7   | 85  | 04/02/2000 | 12/27/2000 | 270  |
|         | 2 | 3  | 3  | 14 | 7  | 18   | 0 | 32  | 77  | 09/30/2004 | 07/12/2005 | 286  |
| BC03F01 | 1 | 58 | 80 | 82 | 78 | 1670 |   | 143 | 608 | 04/11/2003 | 11/24/2007 | 1689 |
| BC03F02 | 1 | 25 | 36 | 73 | 41 | 1390 |   | 164 | 478 | 04/11/2003 | 01/31/2008 | 1757 |

|         |   |    |    |    |    |      |     |     |            |            |            |      |
|---------|---|----|----|----|----|------|-----|-----|------------|------------|------------|------|
| BC03F03 | 1 | 10 | 21 | 65 | 16 | 1120 | 42  | 266 | 04/03/2003 | 05/10/2005 | 769        |      |
| BC03F05 | 1 | 2  | 2  | 7  | 2  | 18   | 0   | 3   | 34         | 04/23/2003 | 09/17/2003 | 148  |
| BC03F06 | 1 | 9  | 15 | 25 | 15 | 78   | 0   | 6   | 148        | 04/16/2003 | 07/22/2005 | 829  |
| BC03F07 | 1 | 4  | 3  | 6  | 15 | 17   | 0   | 5   | 50         | 04/16/2003 | 09/19/2003 | 157  |
| BC03F08 | 1 | 9  | 11 | 24 | 19 | 75   | 0   | 35  | 173        | 04/23/2003 | 07/06/2005 | 806  |
|         | 2 | 2  | 2  | 0  | 1  | 5    | 0   | 69  | 79         | 01/23/2006 | 11/23/2007 | 670  |
| BC03F09 | 1 | 15 | 15 | 32 | 13 | 79   | 0   | 76  | 230        | 04/23/2003 | 06/06/2006 | 1141 |
| BC03F10 | 1 | 13 | 32 | 47 | 23 | 1260 | 165 | 406 | 04/23/2003 | 10/30/2007 | 1652       |      |
| BC03M01 | 1 | 10 | 16 | 32 | 13 | 60   | 0   | 22  | 153        | 04/11/2003 | 01/15/2005 | 646  |
| BC03M02 | 1 | 13 | 27 | 28 | 19 | 1110 | 76  | 274 | 04/16/2003 | 04/20/2007 | 1466       |      |
| BC03M03 | 1 | 1  | 7  | 9  | 8  | 21   | 0   | 4   | 50         | 04/23/2003 | 10/14/2003 | 175  |
| BC03M04 | 1 | 22 | 19 | 24 | 3  | 80   | 0   | 26  | 174        | 04/16/2003 | 03/03/2005 | 688  |
| BC03M06 | 1 | 4  | 28 | 35 | 23 | 90   | 0   | 37  | 217        | 04/23/2003 | 07/15/2005 | 815  |
|         | 2 | 29 | 42 | 36 | 5  | 81   | 0   | 44  | 237        | 09/21/2005 | 01/31/2008 | 863  |
| BC03M07 | 1 | 16 | 36 | 55 | 29 | 92   | 0   | 44  | 272        | 04/11/2003 | 06/30/2005 | 812  |
| BC03M08 | 1 | 4  | 7  | 11 | 2  | 16   | 0   | 5   | 45         | 04/03/2003 | 08/05/2003 | 125  |
|         | 2 | 42 | 46 | 54 | 30 | 65   | 0   | 18  | 255        | 01/06/2004 | 03/23/2005 | 443  |
| BC03M09 | 1 | 19 | 31 | 74 | 52 | 1020 | 6   | 284 | 04/11/2003 | 01/03/2005 | 634        |      |
| BC03M10 | 1 | 18 | 21 | 23 | 13 | 86   | 0   | 31  | 192        | 04/11/2003 | 05/15/2005 | 766  |
|         | 2 | 24 | 39 | 44 | 14 | 89   | 0   | 12  | 222        | 04/17/2006 | 11/08/2007 | 571  |
|         | 3 | 1  | 6  | 13 | 5  | 14   | 27  | 6   | 72         | 02/19/2008 | 09/27/2008 | 222  |
| BC04F01 | 1 | 21 | 21 | 51 | 46 | 99   | 0   | 160 | 398        | 04/17/2004 | 06/18/2009 | 1889 |
| BC04F02 | 1 | 9  | 16 | 55 | 26 | 60   | 0   | 24  | 190        | 04/19/2004 | 09/23/2005 | 523  |

|         |   |             |                    |      |            |            |      |
|---------|---|-------------|--------------------|------|------------|------------|------|
| BC04F03 | 1 | 83          | 160300132294147141 | 1257 | 04/19/2004 | 03/15/2011 | 2522 |
| BC04F04 | 1 | 90          | 13518768 294267164 | 1205 | 04/19/2004 | 04/13/2011 | 2551 |
| BC04F05 | 1 | 7           | 11 16 14 35 0 30   | 113  | 04/17/2004 | 10/26/2005 | 558  |
| BC04F08 | 1 | 3           | 10 16 13 25 0 7    | 74   | 04/19/2004 | 01/11/2005 | 268  |
| BC04M01 | 1 | 4           | 6 14 26 41 0 11    | 102  | 04/26/2004 | 03/22/2005 | 331  |
|         | 2 | 2           | 3 4 0 11 0 20      | 40   | 06/27/2005 | 02/06/2007 | 590  |
|         | 3 | 18619625391 | 25124532           | 1254 | 07/19/2007 | 04/09/2011 | 1361 |
| BC04M02 | 1 | 0           | 8 14 36 65 0 95    | 218  | 04/18/2004 | 03/16/2009 | 1794 |
| BC04M03 | 1 | 4           | 11 37 63 79 0 34   | 228  | 04/26/2004 | 04/17/2006 | 722  |
| BC04M05 | 1 | 5           | 8 19 19 39 0 16    | 106  | 04/26/2004 | 03/05/2005 | 314  |
| BC04M06 | 1 | 10          | 16 19 18 55 0 14   | 132  | 04/26/2004 | 07/11/2006 | 807  |
| BC04M08 | 1 | 7           | 13 24 19 35 0 2    | 100  | 04/05/2004 | 02/28/2006 | 695  |
|         | 2 | 8           | 8 27 17 49 0 5     | 114  | 02/15/2007 | 01/04/2008 | 324  |
| BC04M09 | 1 | 31          | 30 30 8 82 0 23    | 204  | 04/17/2004 | 04/10/2006 | 724  |
|         | 2 | 80          | 14522010019321720  | 975  | 03/11/2008 | 02/16/2011 | 1073 |
| BC04M10 | 1 | 9           | 12 33 32 77 0 28   | 191  | 04/18/2004 | 08/08/2006 | 843  |
|         | 2 | 47          | 46 48 8 77 79 21   | 326  | 02/19/2008 | 10/15/2009 | 605  |
| BC04M11 | 1 | 17          | 21 17 5 49 0 22    | 131  | 04/17/2004 | 04/10/2006 | 724  |
|         | 2 | 5           | 11 26 25 42 18 40  | 167  | 11/17/2006 | 05/18/2009 | 914  |
| BC04M13 | 1 | 28          | 26 39 22 58 0 16   | 189  | 04/19/2004 | 11/04/2005 | 565  |
| BC05F01 | 1 | 13          | 17 29 9 57 0 98    | 223  | 04/19/2005 | 07/10/2008 | 1179 |
| BC05F02 | 1 | 4           | 12 16 10 47 0 64   | 153  | 04/01/2005 | 07/10/2008 | 1197 |
| BC05F04 | 1 | 12          | 27 40 8 75 0 40    | 202  | 04/09/2005 | 07/09/2007 | 822  |

|           |    |    |    |    |      |    |     |     |            |            |      |
|-----------|----|----|----|----|------|----|-----|-----|------------|------------|------|
| BC05M01 1 | 5  | 14 | 26 | 12 | 74   | 0  | 22  | 153 | 04/19/2005 | 04/04/2007 | 716  |
| BC05M02 1 | 17 | 20 | 29 | 15 | 56   | 0  | 20  | 157 | 04/11/2005 | 02/06/2007 | 667  |
| BC05M03 1 | 10 | 23 | 50 | 38 | 65   | 0  | 4   | 190 | 04/01/2005 | 03/20/2007 | 719  |
| BC05M04 1 | 10 | 26 | 44 | 13 | 78   | 0  | 11  | 182 | 04/01/2005 | 04/03/2007 | 733  |
| BC05M05 1 | 8  | 15 | 19 | 8  | 65   | 0  | 6   | 121 | 04/05/2005 | 06/03/2006 | 425  |
| BC05M07 1 | 8  | 11 | 32 | 40 | 73   | 0  | 23  | 187 | 04/11/2005 | 03/20/2007 | 709  |
| BC05M09 1 | 12 | 13 | 24 | 15 | 61   | 0  | 14  | 139 | 04/05/2005 | 04/03/2007 | 729  |
| BC06F05 1 | 14 | 19 | 28 | 8  | 31   | 0  | 2   | 102 | 04/01/2006 | 10/28/2006 | 211  |
| BC06F06 1 | 6  | 17 | 27 | 41 | 46   | 0  | 4   | 141 | 04/01/2006 | 11/27/2006 | 241  |
| BC06F07 1 | 10 | 21 | 31 | 43 | 41   | 0  | 1   | 147 | 04/01/2006 | 01/07/2007 | 282  |
| BC06F09 1 | 2  | 8  | 24 | 22 | 30   | 0  | 8   | 94  | 04/03/2006 | 11/12/2006 | 224  |
| 2         | 29 | 74 | 75 | 17 | 90   | 79 | 28  | 392 | 01/19/2009 | 08/10/2010 | 569  |
| BC06M11 1 | 23 | 32 | 55 | 32 | 98   | 0  | 13  | 253 | 04/01/2006 | 12/17/2007 | 626  |
| BC06M12 1 | 7  | 7  | 19 | 17 | 36   | 0  | 1   | 87  | 04/03/2006 | 01/08/2007 | 281  |
| BC06M13 1 | 10 | 22 | 61 | 72 | 96   | 0  | 1   | 262 | 04/03/2006 | 09/29/2007 | 545  |
| BC06M14 1 | 13 | 19 | 25 | 22 | 53   | 0  | 7   | 139 | 04/03/2006 | 04/15/2007 | 378  |
| BC99F15 1 | 0  | 0  | 0  | 0  | 0    | 0  | 93  | 93  | 03/12/1999 | 02/22/2001 | 714  |
| BC99M03 1 | 0  | 0  | 0  | 0  | 0    | 0  | 56  | 56  | 03/12/1999 | 05/15/2000 | 431  |
| 2         | 21 | 26 | 41 | 30 | 1030 |    | 153 | 374 | 01/24/2001 | 03/27/2006 | 1889 |
| BC99M04 1 | 0  | 0  | 0  | 0  | 0    | 0  | 63  | 63  | 03/12/1999 | 08/10/2000 | 518  |
| BC99M10 1 | 0  | 0  | 0  | 0  | 0    | 0  | 55  | 55  | 03/19/1999 | 06/19/2000 | 459  |
| CO04F07 1 | 0  | 0  | 0  | 0  | 0    | 0  | 56  | 56  | 04/12/2005 | 10/31/2006 | 568  |
| CO04F15 1 | 3  | 3  | 16 | 7  | 39   | 0  | 72  | 140 | 01/20/2005 | 11/17/2006 | 667  |

|          |   |             |          |       |          |         |       |    |      |            |            |      |
|----------|---|-------------|----------|-------|----------|---------|-------|----|------|------------|------------|------|
|          | 2 | 9           | 20       | 44    | 35       | 50      | 43    | 45 | 246  | 01/20/2008 | 06/04/2009 | 502  |
| CO04F18  | 1 | 10          | 12       | 23    | 18       | 83      | 0     | 75 | 221  | 04/29/2005 | 11/24/2007 | 940  |
|          | 2 | 63          | 13796    | 38    | 14218022 |         |       |    | 678  | 11/18/2008 | 04/09/2011 | 873  |
| CO04F19  | 1 | 48          | 48       | 73    | 42       | 1160    | 161   |    | 488  | 01/20/2005 | 06/29/2009 | 1622 |
| CO04M101 |   | 23          | 51       | 10324 | 72       | 94      | 7     |    | 374  | 04/20/2009 | 08/10/2010 | 478  |
| CO04M121 |   | 20          | 32       | 77    | 42       | 13111   | 37    |    | 350  | 04/29/2005 | 05/14/2009 | 1477 |
| CO04M161 |   | 6           | 24       | 15    | 10       | 37      | 0     | 16 | 108  | 03/15/2005 | 06/27/2006 | 470  |
| CO05M031 |   | 7           | 18       | 32    | 9        | 60      | 0     | 45 | 171  | 02/23/2006 | 04/02/2008 | 770  |
|          | 2 | 3           | 7        | 13    | 15       | 30      | 45    | 16 | 129  | 06/30/2008 | 09/21/2009 | 449  |
| CO05M081 |   | 57          | 77       | 72    | 48       | 1021098 |       |    | 473  | 02/22/2009 | 08/20/2010 | 545  |
| CO07AF01 |   | 10015219164 | 22924475 |       |          |         |       |    | 1055 | 03/06/2007 | 04/08/2011 | 1495 |
| CO07AM01 |   | 2           | 1        | 10    | 10       | 11      | 0     | 12 | 46   | 02/06/2007 | 11/24/2007 | 292  |
| CO09AF01 |   | 34          | 64       | 62    | 26       | 71      | 87    | 19 | 363  | 04/06/2009 | 07/10/2010 | 461  |
| MB03M011 |   | 30          | 23       | 36    | 16       | 1040    | 33    |    | 242  | 04/16/2003 | 06/30/2005 | 807  |
| MB05F01  | 1 | 13          | 29       | 71    | 51       | 91      | 0     | 10 | 265  | 05/07/2005 | 11/21/2006 | 564  |
|          | 2 | 24          | 37       | 75    | 27       | 74      | 11118 |    | 366  | 01/19/2009 | 07/22/2010 | 550  |
| MB05F02  | 1 | 20          | 24       | 35    | 20       | 78      | 0     | 10 | 187  | 07/14/2005 | 02/06/2007 | 573  |
| MB05F03  | 1 | 8           | 17       | 36    | 29       | 60      | 0     | 11 | 161  | 04/27/2005 | 10/24/2006 | 546  |
| QU03F01  | 1 | 13          | 24       | 41    | 26       | 99      | 0     | 50 | 253  | 04/23/2003 | 07/15/2005 | 815  |
|          | 2 | 0           | 0        | 0     | 0        | 0       | 0     | 34 | 34   | 05/11/2007 | 07/29/2008 | 446  |
| QU03F03  | 1 | 23          | 51       | 52    | 32       | 90      | 0     | 29 | 277  | 04/03/2003 | 12/04/2004 | 612  |
| QU03F04  | 1 | 16          | 28       | 53    | 19       | 85      | 0     | 99 | 300  | 04/11/2003 | 02/06/2007 | 1398 |
|          | 2 | 0           | 0        | 0     | 0        | 0       | 0     | 42 | 42   | 05/09/2007 | 06/30/2008 | 419  |

|          |   |    |    |     |     |      |    |     |            |            |            |      |
|----------|---|----|----|-----|-----|------|----|-----|------------|------------|------------|------|
| QU03F05  | 1 | 21 | 39 | 61  | 26  | 86   | 0  | 186 | 419        | 04/11/2003 | 07/24/2008 | 1932 |
| QU03F06  | 1 | 5  | 9  | 30  | 13  | 67   | 0  | 114 | 238        | 04/16/2003 | 08/16/2007 | 1584 |
| QU03F07  | 1 | 14 | 46 | 68  | 55  | 1130 | 46 | 342 | 04/11/2003 | 09/11/2005 | 885        |      |
| QU03M011 |   | 11 | 13 | 49  | 32  | 86   | 0  | 23  | 214        | 04/03/2003 | 08/11/2005 | 862  |
| QU03M021 |   | 5  | 4  | 2   | 3   | 20   | 0  | 1   | 35         | 04/11/2003 | 08/31/2003 | 143  |
|          | 2 | 8  | 12 | 17  | 7   | 51   | 0  | 36  | 131        | 03/27/2005 | 04/20/2007 | 755  |
|          | 3 | 11 | 44 | 104 | 102 | 192  | 32 | 636 | 815        | 07/19/2007 | 04/13/2011 | 1365 |
| QU03M051 |   | 1  | 5  | 11  | 8   | 33   | 0  | 10  | 68         | 04/11/2003 | 11/10/2003 | 214  |
| QU04F01  | 1 | 6  | 18 | 46  | 33  | 56   | 0  | 2   | 161        | 04/05/2004 | 04/16/2006 | 742  |
| QU04F02  | 1 | 10 | 16 | 26  | 16  | 55   | 0  | 4   | 127        | 04/03/2004 | 04/11/2005 | 374  |
|          | 2 | 24 | 46 | 94  | 50  | 78   | 0  | 3   | 295        | 05/07/2005 | 10/31/2006 | 543  |
| QU04F03  | 1 | 1  | 3  | 1   | 0   | 7    | 0  | 26  | 38         | 04/03/2004 | 07/04/2005 | 458  |
|          | 2 | 1  | 2  | 2   | 0   | 9    | 0  | 33  | 47         | 09/30/2005 | 06/29/2007 | 638  |
|          | 3 | 0  | 0  | 0   | 0   | 0    | 0  | 29  | 29         | 10/01/2007 | 06/25/2009 | 634  |
| QU04F06  | 1 | 4  | 7  | 13  | 11  | 31   | 0  | 54  | 120        | 04/05/2004 | 04/10/2006 | 736  |
| QU04F07  | 1 | 8  | 8  | 9   | 4   | 21   | 0  | 2   | 52         | 04/05/2004 | 09/19/2004 | 168  |
| QU04F08  | 1 | 14 | 22 | 59  | 41  | 73   | 0  | 30  | 239        | 04/17/2004 | 09/25/2005 | 527  |
|          | 2 | 38 | 62 | 91  | 30  | 122  | 51 | 64  | 458        | 01/09/2007 | 06/29/2009 | 903  |
| QU04F09  | 1 | 12 | 24 | 20  | 5   | 64   | 0  | 33  | 158        | 04/18/2004 | 10/12/2006 | 908  |
| QU04F10  | 1 | 7  | 8  | 20  | 13  | 52   | 0  | 7   | 107        | 09/26/2004 | 03/12/2006 | 533  |
|          | 2 | 0  | 0  | 0   | 0   | 0    | 0  | 52  | 52         | 11/17/2006 | 05/28/2009 | 924  |
| QU04M011 |   | 7  | 19 | 18  | 12  | 42   | 0  | 15  | 113        | 04/05/2004 | 05/22/2005 | 413  |
| QU04M021 |   | 9  | 11 | 19  | 14  | 51   | 0  | 17  | 121        | 04/03/2004 | 04/03/2006 | 731  |

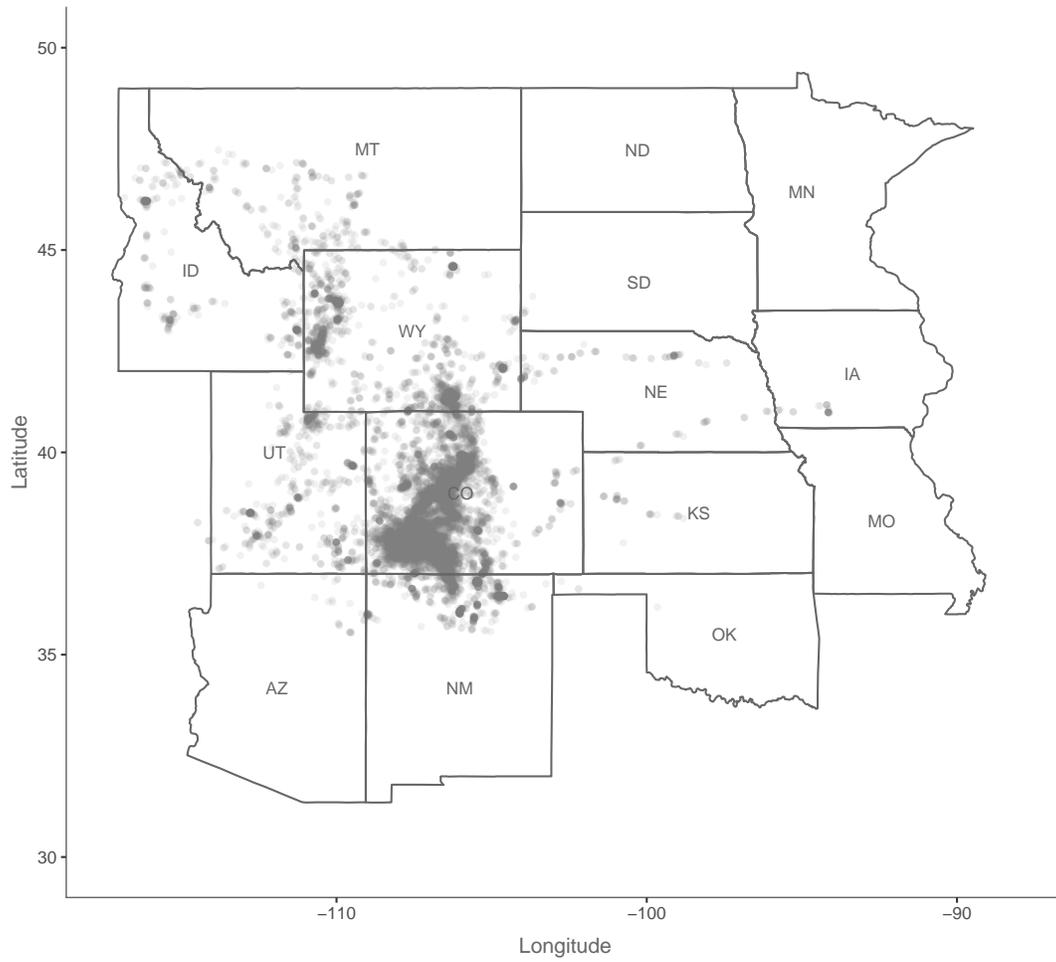
|           |    |     |     |    |      |      |     |     |            |            |      |
|-----------|----|-----|-----|----|------|------|-----|-----|------------|------------|------|
| QU04M031  | 28 | 18  | 26  | 7  | 73   | 0    | 39  | 191 | 04/03/2004 | 03/15/2006 | 712  |
| QU04M041  | 50 | 62  | 88  | 29 | 1260 |      | 16  | 371 | 04/05/2004 | 12/05/2006 | 975  |
| 2         | 5  | 7   | 9   | 7  | 11   | 0    | 5   | 44  | 01/20/2007 | 03/19/2007 | 59   |
| QU04M051  | 4  | 6   | 30  | 41 | 59   | 0    | 10  | 150 | 04/03/2004 | 01/15/2006 | 653  |
| QU04M071  | 7  | 6   | 10  | 1  | 15   | 0    | 2   | 41  | 04/05/2004 | 09/13/2004 | 162  |
| QU05F01 1 | 1  | 10  | 5   | 1  | 17   | 0    | 17  | 51  | 04/24/2006 | 02/21/2007 | 304  |
| QU05F03 1 | 10 | 13  | 29  | 10 | 40   | 0    | 6   | 108 | 04/01/2005 | 02/07/2007 | 678  |
| QU05F04 1 | 23 | 57  | 48  | 27 | 1060 |      | 2   | 263 | 04/01/2005 | 01/30/2007 | 670  |
| QU05F05 1 | 23 | 43  | 81  | 66 | 1429 |      | 69  | 433 | 04/03/2005 | 06/25/2009 | 1545 |
| QU05F06 1 | 7  | 11  | 37  | 11 | 56   | 0    | 34  | 156 | 04/05/2005 | 11/08/2007 | 948  |
| QU05F07 1 | 13 | 24  | 39  | 18 | 86   | 0    | 52  | 232 | 04/09/2005 | 12/05/2007 | 971  |
| QU05F08 1 | 25 | 41  | 57  | 20 | 89   | 0    | 2   | 234 | 04/09/2005 | 02/13/2007 | 676  |
| QU05M021  | 2  | 2   | 7   | 5  | 16   | 0    | 5   | 37  | 10/10/2005 | 08/14/2006 | 309  |
| 2         | 77 | 144 | 158 | 34 | 152  | 1738 |     | 746 | 03/29/2009 | 04/10/2011 | 743  |
| QU05M031  | 12 | 20  | 22  | 13 | 28   | 0    | 1   | 96  | 04/01/2005 | 09/26/2005 | 179  |
| QU05M051  | 8  | 23  | 30  | 9  | 80   | 0    | 11  | 161 | 04/03/2005 | 01/09/2007 | 647  |
| QU05M061  | 2  | 3   | 17  | 17 | 37   | 0    | 13  | 89  | 04/05/2005 | 10/17/2006 | 561  |
| QU05M081  | 13 | 24  | 24  | 16 | 32   | 0    | 2   | 111 | 04/09/2005 | 11/25/2005 | 231  |
| 2         | 9  | 8   | 9   | 7  | 22   | 0    | 1   | 56  | 04/18/2006 | 09/30/2006 | 166  |
| QU05M091  | 12 | 8   | 36  | 32 | 76   | 0    | 24  | 188 | 04/09/2005 | 03/20/2007 | 711  |
| YK00F01 1 | 12 | 27  | 36  | 30 | 86   | 0    | 169 | 360 | 04/02/2000 | 08/17/2006 | 2329 |
| YK00F02 1 | 11 | 7   | 35  | 23 | 39   | 0    | 59  | 174 | 04/02/2000 | 08/02/2002 | 853  |
| 2         | 0  | 0   | 0   | 0  | 0    | 0    | 33  | 33  | 09/23/2003 | 06/24/2004 | 276  |

|          |   |    |     |     |    |      |     |     |      |            |            |      |
|----------|---|----|-----|-----|----|------|-----|-----|------|------------|------------|------|
| YK00F03  | 1 | 3  | 3   | 10  | 1  | 8    | 0   | 3   | 28   | 04/02/2000 | 06/19/2000 | 79   |
| YK00F04  | 1 | 6  | 15  | 22  | 21 | 39   | 0   | 11  | 114  | 04/02/2000 | 04/02/2001 | 366  |
| YK00F05  | 1 | 4  | 8   | 38  | 34 | 48   | 0   | 105 | 237  | 04/02/2000 | 01/13/2004 | 1382 |
| YK00F07  | 1 | 19 | 25  | 58  | 38 | 1010 |     | 210 | 451  | 04/02/2000 | 12/12/2006 | 2446 |
|          | 2 | 10 | 20  | 21  | 2  | 26   | 0   | 2   | 81   | 01/20/2007 | 07/30/2007 | 192  |
| YK00F08  | 1 | 16 | 21  | 32  | 13 | 36   | 0   | 4   | 122  | 04/02/2000 | 12/21/2000 | 264  |
| YK00F09  | 1 | 7  | 12  | 7   | 9  | 26   | 0   | 7   | 68   | 04/02/2000 | 01/11/2001 | 285  |
| YK00F10  | 1 | 11 | 30  | 35  | 39 | 94   | 0   | 236 | 445  | 04/02/2000 | 06/29/2006 | 2280 |
| YK00F11  | 1 | 2  | 0   | 0   | 0  | 1    | 0   | 97  | 100  | 04/17/2000 | 05/14/2004 | 1489 |
|          | 2 | 13 | 30  | 35  | 14 | 61   | 0   | 41  | 194  | 01/18/2005 | 11/15/2006 | 667  |
| YK00F14  | 1 | 0  | 0   | 0   | 0  | 0    | 0   | 91  | 91   | 05/22/2000 | 08/02/2002 | 803  |
| YK00F15  | 1 | 39 | 106 | 113 | 65 | 239  | 206 | 304 | 1072 | 04/17/2000 | 02/06/2011 | 3948 |
| YK00F16  | 1 | 24 | 27  | 36  | 16 | 94   | 0   | 117 | 314  | 04/17/2000 | 10/05/2003 | 1267 |
| YK00M011 |   | 2  | 6   | 12  | 5  | 23   | 0   | 19  | 67   | 04/02/2000 | 06/20/2001 | 445  |
|          | 2 | 0  | 0   | 0   | 0  | 0    | 0   | 120 | 120  | 10/17/2001 | 06/30/2005 | 1353 |
| YK00M021 |   | 3  | 11  | 23  | 9  | 27   | 0   | 19  | 92   | 04/02/2000 | 06/06/2001 | 431  |
|          | 2 | 5  | 10  | 9   | 5  | 30   | 0   | 111 | 170  | 09/27/2001 | 12/21/2004 | 1182 |
| YK00M031 |   | 21 | 17  | 9   | 8  | 48   | 0   | 13  | 116  | 04/02/2000 | 04/26/2001 | 390  |
| YK00M041 |   | 7  | 14  | 20  | 9  | 49   | 0   | 18  | 117  | 04/02/2000 | 06/20/2001 | 445  |
| YK00M061 |   | 11 | 15  | 24  | 15 | 32   | 0   | 42  | 139  | 04/02/2000 | 05/07/2002 | 766  |
| YK00M071 |   | 0  | 0   | 0   | 0  | 0    | 0   | 128 | 128  | 08/24/2000 | 07/07/2005 | 1779 |
| YK05F02  | 1 | 6  | 12  | 17  | 10 | 46   | 0   | 73  | 164  | 04/21/2005 | 03/11/2008 | 1056 |
|          | 2 | 0  | 0   | 0   | 0  | 0    | 0   | 37  | 37   | 05/12/2008 | 06/29/2009 | 414  |

|           |    |    |    |    |    |   |     |     |            |            |      |
|-----------|----|----|----|----|----|---|-----|-----|------------|------------|------|
| YK05F03 1 | 17 | 26 | 58 | 28 | 83 | 0 | 21  | 233 | 04/21/2005 | 07/31/2007 | 832  |
| YK05M011  | 1  | 12 | 30 | 47 | 65 | 0 | 2   | 157 | 04/11/2005 | 11/07/2006 | 576  |
| YK05M021  | 8  | 37 | 45 | 24 | 73 | 0 | 7   | 194 | 04/19/2005 | 01/02/2007 | 624  |
| 2         | 12 | 28 | 25 | 12 | 35 | 0 | 3   | 115 | 02/02/2007 | 08/06/2007 | 186  |
| YK05M031  | 6  | 1  | 12 | 17 | 28 | 0 | 1   | 65  | 04/27/2005 | 11/08/2005 | 196  |
| YK06F01 1 | 18 | 34 | 16 | 8  | 30 | 0 | 1   | 107 | 04/12/2006 | 10/08/2006 | 180  |
| YK06F02 1 | 9  | 12 | 22 | 19 | 30 | 0 | 7   | 99  | 04/19/2006 | 02/11/2007 | 299  |
| YK06M011  | 12 | 20 | 20 | 8  | 24 | 0 | 2   | 86  | 04/12/2006 | 12/03/2006 | 236  |
| YK06M021  | 17 | 19 | 52 | 34 | 66 | 0 | 3   | 191 | 04/19/2006 | 12/17/2007 | 608  |
| YK06M031  | 20 | 27 | 55 | 30 | 72 | 0 | 42  | 246 | 04/19/2006 | 06/15/2009 | 1154 |
| YK99F01 1 | 10 | 12 | 25 | 8  | 77 | 0 | 243 | 375 | 07/23/1999 | 06/14/2005 | 2154 |
| YK99F05 1 | 0  | 0  | 0  | 0  | 0  | 0 | 97  | 97  | 05/10/1999 | 10/12/2001 | 887  |
| YK99M031  | 0  | 0  | 0  | 0  | 0  | 0 | 74  | 74  | 05/13/1999 | 06/28/2001 | 778  |

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FIGURE B.1.1. Argos and VHF locations from 1999-2011 for 165 Canada lynx that were reintroduced to Colorado. These locations were used to fit a functional movement model.



## B.2. MODEL DETAILS

I developed a model that is similar to the functional model presented by Buderman *et al.* (2016), however the data model is shared among individuals (I am using “individual” to refer to a time series) and all individuals are modeled simultaneously. The observed locations,  $\mathbf{s}_{ij}(t)$ , for individual  $i$  at a time  $t \in \mathcal{T}$  associated with data type  $j$  ( $j = 1, \dots, 6$  are Argos error classes and  $j = 7$  denotes VHF), arise from a multivariate normal mixture with mean,  $\mathbf{z}_i(t)$ , representing the true location at time  $t$ . The covariance matrix represents the error variance associated with each location and is either  $\Sigma_j$  or  $\tilde{\Sigma}_j$  (where  $\tilde{\Sigma}_j$  is  $\Sigma_j$  rotated about the y-axis). An indicator,  $w_{ij}(t)$ , determines which mixture component gives rise to the location. The covariance matrix,  $\Sigma_j \equiv \sigma_j^2 \mathbf{R}_j$ , where  $\sigma_j^2$  is the variance associated with a particular data type, allows us to model elliptical errors through the scale matrix,  $\mathbf{R}_j$ :

$$(23) \quad \mathbf{R}_j \equiv \begin{pmatrix} 1 & \sqrt{c}\rho \\ \sqrt{c}\rho & c \end{pmatrix},$$

for  $j = 1, \dots, 6$ . Argos error for all error classes has been shown to be greater in the longitudinal direction (Costa *et al.*, 2010; Hoenner *et al.*, 2012; Boyd & Brightsmith, 2013), therefore I use the parameter  $c$  to scale the error variance in latitude to be less than it is in longitude. The  $\rho$  parameter scales the degree of covariance between longitude and latitude. For  $j = 7$ ,  $\mathbf{R}_j \equiv \mathbf{I}$ . The parameters in the data model are shared among individuals, unlike in Buderman *et al.* (2016).

As in Buderman *et al.* (2016), the location of an individual at time  $t$ ,  $\mathbf{z}_i(t)$ , is a function of an individual’s geographic mean,  $\beta_{0_i}$ , basis functions evaluated at time  $t$ ,  $\mathbf{X}(t)$ , and a vector of coefficients,  $\beta_i$ . I selected three sets of B-splines to serve as our basis functions and varied the number of knots, or breakpoints, to align with biologically important temporal

scales: annually, seasonally (3 months), and monthly. The covariance matrix  $\Sigma_{\beta_i}$  acts as a regulator to shrink the coefficients  $\beta_i$  toward zero (Hooten & Hobbs, 2015). The variance terms  $\sigma_{\beta_{i_{lon}}}^2$  and  $\sigma_{\beta_{i_{lat}}}^2$  vary by individual and control the smoothing in each dimension. The underlying process is continuous, but for computational purposes I discretized at the daily scale.

For  $J$  data sources, the model described above yields the posterior distribution:

$$(24) \quad [\{\beta_{0_i}, \beta_i, \mathbf{w}_i, \forall i\}, \sigma^2, \rho, c | \{\mathbf{S}_i, \forall i\}] \propto \prod_{i=1}^n \prod_{j=1}^J \prod_{t \in \mathcal{T}} [s_{ij}(t) | \beta_{0_i}, \beta_i, w_{ij}(t), \sigma_j^2, \rho, c] [\beta_{0_i}] [\beta_i] [\mathbf{w}_i] [\sigma^2] [\rho] [c],$$

where  $\mathbf{w}_i$  is a vector of indicator variables (corresponding to the data for individual  $i$ ),  $\sigma^2 \equiv (\sigma_1^2, \dots, \sigma_J^2)'$ , and  $\mathbf{S}_i$  is a matrix of observed locations for each individual. The model was fit in R using Markov Chain Monte Carlo (MCMC). As a within sample regulator,  $\sigma_{\beta_{i_{lon}}}^2$  and  $\sigma_{\beta_{i_{lat}}}^2$  were tuned using predictive scoring over a two-step grid search of the parameter space.

The full model, divided into the data, process, and prior components, can be written as follows:

### Data Model

$$\mathbf{s}_{ij}(t) \sim \begin{cases} N(\mathbf{z}_i(t), \Sigma_j), & \text{if } w_{ij}(t) = 1 \\ N(\mathbf{z}_i(t), \tilde{\Sigma}_j), & \text{if } w_{ij}(t) = 0 \end{cases}$$

$$\Sigma_j \equiv \sigma_j^2 \mathbf{R}_j$$

$$\tilde{\Sigma}_j \equiv \mathbf{H}_j \Sigma_j \mathbf{H}_j'$$

$$\sigma_j^2 \sim \text{IG}(q, r)$$

$$\mathbf{H} \equiv \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix} \text{ for } j=1, \dots, 6$$

$$\mathbf{H} \equiv \mathbf{I} \text{ for } j=7$$

$$\mathbf{R} \equiv \begin{pmatrix} 1 & \sqrt{c}\rho \\ \sqrt{c}\rho & c \end{pmatrix} \text{ for } j=1, \dots, 6$$

$$\mathbf{R} \equiv \mathbf{I} \text{ for } j=7$$

$$c \sim \text{Beta}(\alpha_c, \beta_c)$$

$$\rho \sim \text{Beta}(\alpha_\rho, \beta_\rho)$$

$$w_{ij}(t) \sim \text{Bern}(0.5)$$

## Process Model

$$\mathbf{z}_i(t) = \boldsymbol{\beta}_{0_i} + \mathbf{X}(t)\boldsymbol{\beta}_i$$

$$\boldsymbol{\beta}_{0_i} \sim \text{N}(\boldsymbol{\mu}_{0_i}, \sigma_{0_i}^2 \mathbf{I})$$

$$\boldsymbol{\beta}_i \sim \text{N}(\mathbf{0}, \boldsymbol{\Sigma}_{\boldsymbol{\beta}_i})$$

$$\boldsymbol{\Sigma}_{\boldsymbol{\beta}_i} = \begin{pmatrix} \sigma_{\boldsymbol{\beta}_{i_{lon}}}^2 \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \sigma_{\boldsymbol{\beta}_{i_{lat}}}^2 \mathbf{I} \end{pmatrix}$$

## Priors

$$w_{ij}(t) \sim \text{Bern}(0.5) \text{ for } i = 1, \dots, N, j = 1, \dots, J \text{ and } t \in \mathcal{T}$$

$$\sigma_j^2 \sim \text{IG}(0.0001, 1000) \text{ for } j = 1, \dots, J$$

$$\rho \sim \text{Beta}(13.31, 4.44)$$

$$E(\rho) = 0.75$$

$$\text{Var}(\rho) = 0.01$$

$$c \sim \text{Beta}(7.2, 0.8)$$

$$E(c) = 0.90$$

$$\text{Var}(c) = 0.01$$

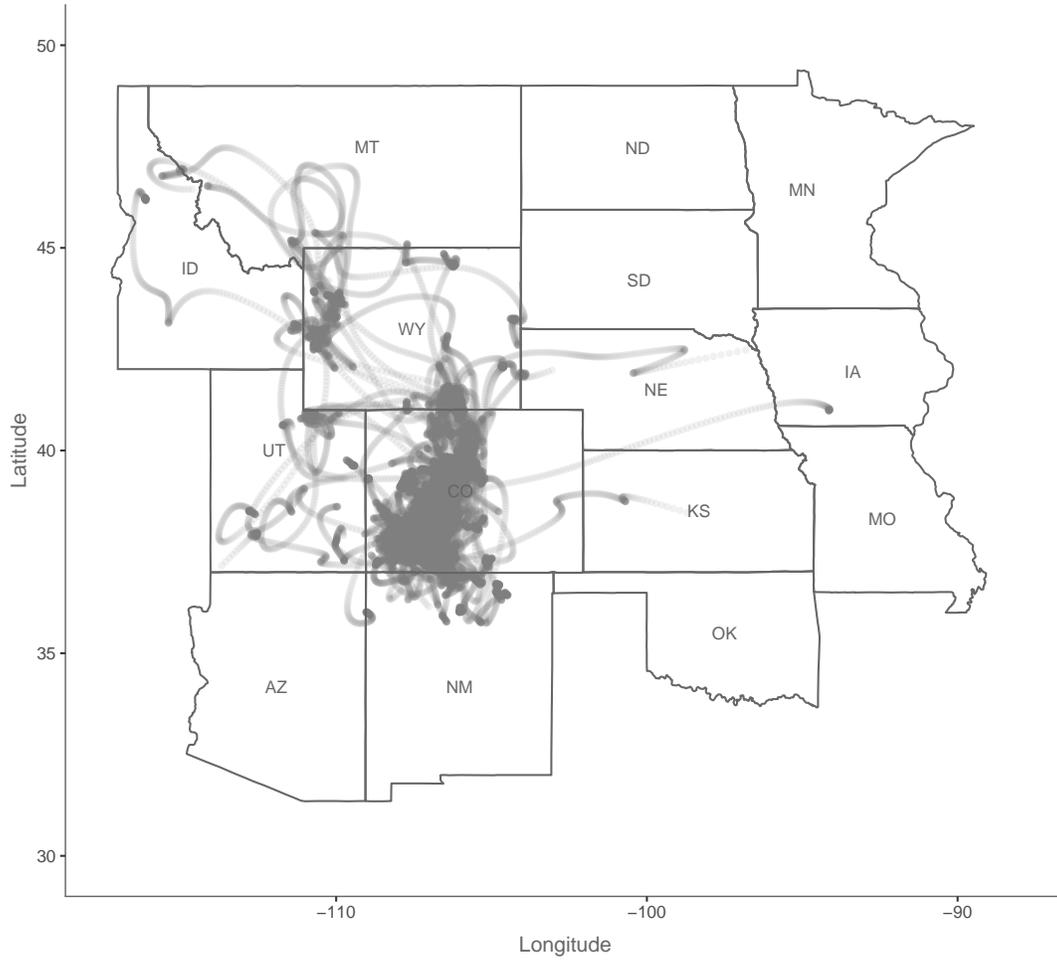
$$\beta_{0_i} \sim N(\mathbf{0}, \mathbf{100(I)})$$

$$\beta_i \sim N\left(\mathbf{0}, \begin{pmatrix} \sigma_{\beta_{i_{lon}}}^2 \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \sigma_{\beta_{i_{lat}}}^2 \mathbf{I} \end{pmatrix}\right)$$

TABLE B.2.1. The covariance matrix in the data model allows us to model the non-elliptical Argos error as well as the elliptical VHF error. Note that these are the posterior mean and 95% credible intervals on the longitude scale and are not in meters.

| Parameter  | Posterior Mean (95% CI) |
|------------|-------------------------|
| $\sigma_3$ | 0.516 (0.509-0.523)     |
| $\sigma_2$ | 0.585 (0.578-0.590)     |
| $\sigma_1$ | 0.590 (0.585-0.596)     |
| $\sigma_0$ | 0.684 (0.677-0.692)     |
| $\sigma_A$ | 0.612 (0.608-0.617)     |
| $\sigma_B$ | 0.862 (0.851-0.873)     |
| $\sigma_V$ | 0.358 (0.363-0.368)     |
| $c$        | 0.241 (0.235-0.245)     |
| $\rho$     | 0.752 (0.738-0.764)     |

FIGURE B.2.1. Posterior mean trajectories for the 165 Canada lynx used in the movement analysis. Points are based on a daily interpolation and transparency reflects the concentration of points.



### B.3. SPATIAL AND TEMPORAL QUANTITIES

To describe the quantities spatially, I defined a grid of equally sized regions,  $\mathcal{A}_l$  for  $l = 1, \dots, L$ , which comprised the area for which I desired inference. This method is similar to the one used by Johnson *et al.* (2011) to describe diving behavior of northern fur seals (*Callorhinus ursinus*). Alternatively, I can describe these metrics temporally, which implies they do not need to be averaged within a region. Calculating the temporal versions of the quantities decreases computation time, negates the need for a spatially defined grid, and allows for continuous-time inference. Spatial versions of residence time, speed, and tortuosity were used for the sections on connectivity and residence area identification, whereas the temporal versions of speed and tortuosity (or derivations of) were used for the sections on movement summary statistics, reintroduction and exploratory movement, and correlations between vegetation and movement. The temporal version of residence time was not used, because it is the inverse of the temporal version of speed (the spatial versions are not related as such, which is why both spatial residence time and speed are presented).

#### B.3.1. Residence Time: Spatial

*Metric calculation:*

$$r_{il} = \lim_{\Delta t \rightarrow 0} \sum_{t \in \mathcal{T}} \Delta t I_{\{\mathbf{z}_i(t) \in \mathcal{A}_l\}}$$

*Posterior mean:*

$$E(r_{il} | \mathbf{S}_i) = \int \cdots \int r_{il}[\boldsymbol{\beta}_{0_i}, \boldsymbol{\beta}_i, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}_i | \mathbf{S}_i] d\boldsymbol{\beta}_{0_i} d\boldsymbol{\beta}_i d\boldsymbol{\sigma}^2 d\rho dc d\mathbf{w}_i$$

*MCMC approximation:*

$$E(r_{il} | \mathbf{S}_i) \approx \sum_{k=1}^K \frac{r_{il}^{(k)}}{K}$$

### B.3.2. Residence Time: Temporal

*Metric calculation:*

$$r_i(t) = \frac{1}{\nu_i(t)}$$

*Posterior mean:*

$$E(r_i(t)|\mathbf{S}_i) = \int \cdots \int r_i(t)[\boldsymbol{\beta}_{0_i}, \boldsymbol{\beta}_i, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}_i|\mathbf{S}_i]d\boldsymbol{\beta}_{0_i}d\boldsymbol{\beta}_id\boldsymbol{\sigma}^2d\rho dc d\mathbf{w}_i$$

*MCMC approximation:*

$$E(r_i(t)|\mathbf{S}_i) \approx \sum_{k=1}^K \frac{r_i(t)^{(k)}}{K}$$

### B.3.3. Average Speed: Spatial

*Metric calculation:* When  $\Delta t$  is sufficiently small, the first derivative of  $\mathbf{z}(t)$  with respect to  $t$  (the instantaneous velocity) can be approximated by the average velocity  $\boldsymbol{\delta}_i(t)$  where

$$\frac{d\mathbf{z}_i(t)}{dt} \approx \boldsymbol{\delta}_i(t),$$

and

$$\boldsymbol{\delta}_i(t) = \frac{\mathbf{z}_i(t) - \mathbf{z}_i(t - \Delta t)}{\Delta t}.$$

In practice,  $\Delta t_i$  was constant for the entire time series. To account for the curvature of the earth I used the Haversine formula (R package `cluster`; Hijmans 2015) to approximate the daily distance moved (which is equivalent to speed):

$$\nu_i(t) = 2r \arcsin \left( \sqrt{\sin^2 \left( \frac{\phi_2 - \phi_1}{2} \right) + \cos(\phi_1) \cos(\phi_2) \sin^2 \left( \frac{\lambda_2 - \lambda_1}{2} \right)} \right),$$

where  $r=6,378,137$  m and  $\phi_1$  and  $\phi_2$  are  $\mathbf{z}_i(t)_{lat}$  and  $\mathbf{z}_i(t - \Delta t)_{lat}$  and  $\lambda_1$  and  $\lambda_2$  are  $\mathbf{z}_i(t)_{lon}$  and  $\mathbf{z}_i(t - \Delta t)_{lon}$ . The spatial representation is then

$$\bar{\nu}_{il} = \frac{\lim_{\Delta t \rightarrow 0} \sum_{t \in \mathcal{T}} \Delta t \nu_i(t) I_{\{\mathbf{z}_i(t) \in \mathcal{A}_l\}}}{r_{il}}.$$

*Posterior mean:*

$$E(\bar{\nu}_{il} | \mathbf{S}_i) = \int \cdots \int \bar{\nu}_{il} [\boldsymbol{\beta}_{0_i}, \boldsymbol{\beta}_i, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}_i | \mathbf{S}_i] d\boldsymbol{\beta}_{0_i} d\boldsymbol{\beta}_i d\boldsymbol{\sigma}^2 d\rho dc d\mathbf{w}_i$$

*MCMC approximation:*

$$E(\bar{\nu}_{il} | \mathbf{S}) \approx \sum_{k=1}^K \frac{\bar{\nu}_{il}^{(k)}}{K}$$

#### B.3.4. Average Speed: Temporal

*Metric calculation:* When  $\Delta t$  is sufficiently small, the first derivative of  $\mathbf{z}(t)$  with respect to  $t$  (the instantaneous velocity) can be approximated by the average velocity  $\boldsymbol{\delta}_i(t)$  where

$$\frac{d\mathbf{z}_i(t)}{dt} \approx \boldsymbol{\delta}_i(t),$$

and

$$\boldsymbol{\delta}_i(t) = \frac{\mathbf{z}_i(t) - \mathbf{z}_i(t - \Delta t)}{\Delta t}.$$

In practice,  $\Delta t_i$  was constant for the entire time series. To account for the curvature of the earth I used the Haversine formula (R package `cluster`; Hijmans 2015) to approximate the daily distance moved (which is equivalent to speed):

$$\nu_i(t) = 2r \arcsin \left( \sqrt{\sin^2 \left( \frac{\phi_2 - \phi_1}{2} \right) + \cos(\phi_1) \cos(\phi_2) \sin^2 \left( \frac{\lambda_2 - \lambda_1}{2} \right)} \right),$$

where  $r=6,378,137$  m and  $\phi_1$  and  $\phi_2$  are  $\mathbf{z}_i(t)_{lat}$  and  $\mathbf{z}_i(t - \Delta t)_{lat}$  and  $\lambda_1$  and  $\lambda_2$  are  $\mathbf{z}_i(t)_{lon}$  and  $\mathbf{z}_i(t - \Delta t)_{lon}$ .

*Posterior mean:*

$$E(\nu_i(t)|\mathbf{S}_i) = \int \cdots \int \nu_i(t)[\beta_{0_i}, \boldsymbol{\beta}_i, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}_i|\mathbf{S}_i]d\beta_{0_i}d\boldsymbol{\beta}_id\boldsymbol{\sigma}^2d\rho dc d\mathbf{w}_i$$

*MCMC approximation:*

$$E(\nu_i(t)|\mathbf{S}_i) \approx \sum_{k=1}^K \frac{\nu_i(t)^{(k)}}{K}$$

### B.3.5. Average Tortuosity: Spatial

*Metric calculation:* I first calculated the initial bearing, which takes an individual from the starting location to the ending location if followed in a straight line along a great-circle arc:

$$B_i(t)_{rad} = \text{atan2}(\sin(\lambda_2 - \lambda_1) \cos(\phi_2), \cos(\phi_1) \sin(\phi_2) - \sin(\phi_1) \cos(\phi_2) \cos(\lambda_2 - \lambda_1)),$$

where  $\phi_1$  and  $\phi_2$  are  $\mathbf{z}_i(t)_{lat}$  and  $\mathbf{z}_i(t - \Delta t)_{lat}$  and  $\lambda_1$  and  $\lambda_2$  are  $\mathbf{z}_i(t)_{lon}$  and  $\mathbf{z}_i(t - \Delta t)_{lon}$ .

I then converted radians to degrees:  $B_i(t)_{deg} = B_i(t)_{rad} \left(\frac{180}{\pi}\right)$  and calculated the absolute difference between subsequent bearings, to obtain a measure of tortuosity (I used the absolute difference because I am more interested in deviation from a given direction rather than actual direction):

$$\theta_i(t) = |(B_i(t)_{deg} - B_i(t - \Delta t)_{deg})|.$$

Finally, I subtracted all values greater than 180 from 360, to obtain our final quantity for  $\theta_i(t)$ . Spatially:

$$\bar{\theta}_{il} = \frac{\lim_{\Delta t \rightarrow 0} \sum_{t \in \mathcal{T}} \Delta t \theta_i(t) I_{\{\mathbf{z}_i(t) \in \mathcal{A}_l\}}}{r_{il}}.$$

*Posterior mean:*

$$E(\bar{\theta}_{il}|\mathbf{S}_i) = \int \cdots \int \bar{\theta}_{il}[\boldsymbol{\beta}_{0_i}, \boldsymbol{\beta}_i, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}_i|\mathbf{S}_i]d\boldsymbol{\beta}_{0_i}d\boldsymbol{\beta}_i d\boldsymbol{\sigma}^2 d\rho dc d\mathbf{w}_i$$

*MCMC approximation:*

$$E(\bar{\theta}_{il}|\mathbf{S}_i) \approx \sum_{k=1}^K \frac{\bar{\theta}_{il}^{(k)}}{K}$$

### B.3.6. Average Tortuosity: Temporal

*Metric calculation:* I first calculated the initial bearing, which will take an individual from the starting location to the ending location if followed in a straight line along a great-circle arc:

$$B_i(t)_{rad} = \text{atan2}(\sin(\lambda_2 - \lambda_1) \cos(\phi_2), \cos(\phi_1) \sin(\phi_2) - \sin(\phi_1) \cos(\phi_2) \cos(\lambda_2 - \lambda_1)),$$

where  $\phi_1$  and  $\phi_2$  are  $\mathbf{z}_i(t)_{lat}$  and  $\mathbf{z}_i(t - \Delta t)_{lat}$  and  $\lambda_1$  and  $\lambda_2$  are  $\mathbf{z}_i(t)_{lon}$  and  $\mathbf{z}_i(t - \Delta t)_{lon}$ . I then converted radians to degrees:  $B_i(t)_{deg} = B_i(t)_{rad} \left(\frac{180}{\pi}\right)$  and calculated the absolute difference between subsequent bearings, to obtain a measure of tortuosity (I used the absolute difference because I am more interested in deviation from a given direction rather than actual direction):

$$\theta_i(t) = |(B_i(t)_{deg} - B_i(t - \Delta t)_{deg})|.$$

Finally, due to how the bearing is calculated, I subtracted all values greater than 180 from 360, to obtain our final quantity for  $\theta_i(t)$ .

*Posterior mean:*

$$E(\theta_i(t)|\mathbf{S}_i) = \int \cdots \int \theta_i(t)[\boldsymbol{\beta}_{0_i}, \boldsymbol{\beta}_i, \boldsymbol{\sigma}^2, \rho, c, \mathbf{w}_i|\mathbf{S}_i]d\boldsymbol{\beta}_{0_i}d\boldsymbol{\beta}_i d\boldsymbol{\sigma}^2 d\rho dc d\mathbf{w}_i$$

*MCMC approximation:*

$$E(\theta_i(t)|\mathbf{S}) \approx \sum_{k=1}^K \frac{\theta_i(t)^{(k)}}{K}$$

#### B.4. SPATIAL QUANTITIES STANDARDIZED BY AVAILABLE INDIVIDUALS

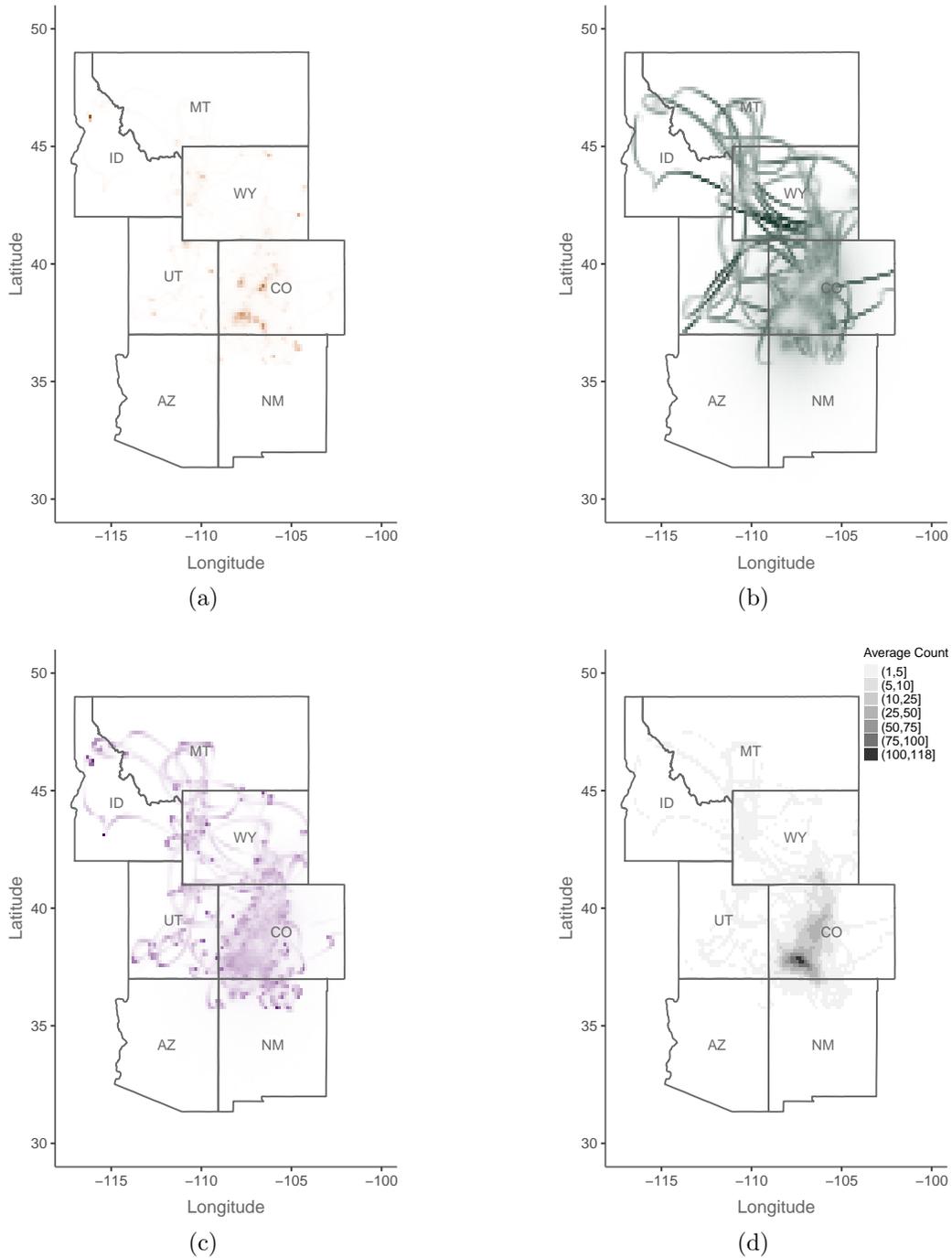


FIGURE B.4.1. Population-level spatial quantities of residence time (B.4.1a), speed (B.4.1b), and tortuosity (B.4.1c) that have been scaled by the number of individuals using that grid cell. Posterior mean number of individuals observed in a grid cell over the observation period is also shown (B.4.1d). Not included are rare movements to eastern states (Nebraska, Kansas, and Iowa).

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## APPENDIX C

### SUPPLEMENTAL MATERIAL FOR CHAPTER 4

#### C.1. DETAILS ON CONTINUOUS-TIME DISCRETE-SPACE MODEL

A posterior predictive continuous path from the movement model is spatially discretized to the resolution of the rasters of interest and decomposed into two elements:  $\mathbf{c}$ , a state sequence consisting of the sequential grid cells (of  $N$  possible grid cells) visited by the individual, and  $\boldsymbol{\tau}$ , a vector of residence times that describe how long the individual spent in each grid cell. We then describe the path in terms of the transition rates  $\boldsymbol{\alpha}$  where  $\alpha_{ij}$  is a parameter controlling movement from cell  $i$  to cell  $j$  that can be a function of spatial covariates:

$$(25) \quad \alpha_{ij} = e^{\mathbf{x}'_{ij}\boldsymbol{\beta}}$$

If we designate  $t$  as the  $t^{\text{th}}$  observation in the state-sequence ( $t \in T$ ), then the residence time  $\tau_t$  is exponentially distributed with a rate equal to the sum of all  $\alpha_{ij}$  (the total transition rate):

$$(26) \quad [\tau_t | \boldsymbol{\beta}] = \left( \sum_{j=1}^N \alpha_{ij} \right) e^{-\tau_k \sum_{j=1}^N \alpha_{ij}}.$$

We assume that it is impossible to move directly to non-neighboring cells, and therefore  $\alpha_{ij} = 0$  for all  $j$  except for the cells adjacent to cell  $i$ .

When an individual transitions to a neighboring cell, the probability of transitioning to cell  $c_{t+1} = l$  is

$$(27) \quad [c_{t+1} = l | c_t = i] = \frac{\alpha_{il}}{\sum_{j=1}^N \alpha_{ij}}.$$

Assuming independence, the joint likelihood is the product of the transition probabilities and the residence times in the state sequence  $\mathbf{c}$  is:

$$(28) \quad [\tau_t, c_{t+1} = l | c_t = i, \boldsymbol{\beta}] = \frac{\alpha_{il}}{\sum_{j=1}^N \alpha_{ij}} \left( \sum_{j=1}^N \alpha_{ij} \right) e^{-\tau_t \sum_{j=1}^N \alpha_{ij}}$$

$$(29) \quad = \alpha_{il} e^{-\tau_t \sum_{j=1}^N \alpha_{ij}}$$

Using a latent variable representation, where

$$(30) \quad z_{ij} = \begin{cases} 1, & \text{if } j = c_{t+1} \\ 0, & \text{if } j \neq c_{t+1} \end{cases}$$

and

$$(31) \quad [z_{ij}, \tau_t | \boldsymbol{\beta}] \propto \alpha_{ij}^{z_{ij}} e^{-\tau_t \alpha_{ij}},$$

then the product of  $[z_{c_t k}, \tau_t | \boldsymbol{\beta}]$  over all  $N$  is proportional to the likelihood of the observed transition:

$$(32) \quad [z_{ij}, \tau_t | \boldsymbol{\beta}] \propto \sum_{t=1}^T \sum_{j=1}^N \alpha_{ij}^{z_{ij}} e^{-\tau_t \alpha_{ij}}.$$

The above process is parameterized with a single realization from the movement model, however, we have failed to account for the uncertainty in the animal's path. To avoid

computational storage limitations, we use multiple imputation to account for the uncertainty in the path and make approximate posterior predictive inference on transition rates.