Movement analytics: A data-driven approach to quantifying space-time variation in grizzly bear

(Ursus arctos L.) near-road movement patterns

By

Robin Olive Kite

B.Sc., University of Victoria, 2013
B.Sc., University of Alberta, 2006

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ABSTRACT

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Improvements in GPS tracking technologies have resulted in the collection of high resolution movement datasets for a range of wildlife species. In combination with new high resolution remote sensing products, researchers now have the ability to ask complex questions regarding animal movement in heterogeneous landscapes. However, there currently exists a dearth of analytical approaches to combine movement data with environmental variables. Developing methods to examine wildlife movement-environment interactions are particularly relevant given our unprecedented access to high resolution data; however, the analytical and technical challenges of integrating two disparate data types have yet to be effectively overcome. In the analyses presented in this thesis, I examine current approaches for linking wildlife movement to the physical environment, and introduce a data-driven method for examining wildlife movement-environment interactions. The first analysis consists of a review of existing tools in wildlife movement analysis, specifically tools supported within R statistical software, to highlight any existing methodological opportunities and limitations associated with relating movement to landscape features. The review highlights R’s strengths as an integrated toolbox for exploratory analyses, and the current lack of applications for linking high density telemetry datasets with environmental variables. AdehabitatLT was the most functional package available, offering the greatest variety of analysis options. Due to the comprehensive nature of adehabitatLT, I
recommend that future method development be implemented through its package specific framework. Extending the first analysis, the second portion of this research introduces a data-driven method, based in semivariogram modelling, for quantifying wildlife movement patterns relative to linear features. The semivariogram-based method is applied to grizzly bear telemetry data to quantify how grizzly bear movement patterns change in relation to roads. The semivariogram-based method demonstrated that the bears’ spatial scale of response ranged from 35 m- 90 m from roads but varied by age, sex, and season. Applying the scales of response to link near-road movement patterns to survival and mortality, revealed that bears that were killed displayed less-risk adverse movements near roads than bears that survived (i.e., longer step lengths and more day light movements around roads). Given this pattern, my data suggest a minimum vegetation buffer of 90 m to serve as screening cover along roadsides to help mitigate the effects of roads on grizzly bear populations in west-central Alberta, Canada. Through the development of data-driven methods in wildlife movement analysis, I can realize the full potential of high resolution telemetry datasets. Data-driven methods reduce the subjectivity within movement analyses, providing more relevant measures of wildlife response to environment. The semivariogram-based method can identify definitive zones of influence around linear disturbance features in any wildlife system, thereby, providing managers with spatially explicit, data-driven insights to reduce impacts on wildlife in multi-use landscapes.
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CO-AUTHORSHIP STATEMENT

This thesis is the combination of two scientific manuscripts for which I am the lead author. The initial project structure was provided by Dr. Trisalyn Nelson, for which the development of data driven methods for analyzing wildlife movements in a disturbed landscape was identified as a key research opportunity. For these two scientific journal articles, I performed all research, data analysis, initial interpretation of results, and final manuscript presentations. Dr. Chris Darimont and Dr. Gordon Stenhouse provided assistance with defining research questions and interpretation of results. Dr. Stenhouse provided the data. Dr. Nelson, Dr. Darimont and Dr. Stenhouse supplied editorial comments and suggestions incorporated into the final manuscript.
1.0 INTRODUCTION

1.1 Research context

Spatial data have become a key component of environmental monitoring, as innovations in spatial data collection and processing techniques have provided a means of systematically sampling environmental processes through time (Robertson et al., 2007). Within the disciplines of wildlife conservation and management, these innovations have come in the form of Global Positioning System (GPS) tracking technologies for monitoring wildlife movements. Prior to GPS technology, researchers relied on very high frequency (VHF) tracking techniques to characterize movement; however, these techniques were limited in that they relied upon triangulation to determine position, and sampling schedules were dependent on field conditions (Tomkiewicz et al., 2010). GPS collars are an improvement on previously used techniques, as they permit continuous regular sampling of animal movement with high positional accuracy. Further refinements to battery life, data storage and transmission capabilities have generated temporally dense movement datasets (Cagnacci et al., 2010; Demšar et al., 2015; Tomkiewicz et al., 2010). Consequently, high resolution movement datasets now exist for a range of species from migratory birds to pelagic fish to large terrestrial mammals (Dettki et al., 2004; Gutenkunst et al., 2007; Thiebault and Tremblay, 2013).

Concurrently, advances in remote sensing technologies have also produced environmental datasets with improved spatial and temporal resolutions. As a result, remotely sensed imagery and derived products are available to characterize landcover, disturbance, terrain, climate and productivity at resolutions more suited for use in wildlife movement analysis (Neumann et al., 2015). For example, phenomenon such as forest disturbance events can be characterized bi-monthly using Landsat and MODIS imagery (Gaulton et al., 2011; Hilker et al.,
2009), or the timing of vegetation phenology can be assessed using time lapse photography (Nijland et al., 2013).

Despite the abundance of new wildlife movement and environmental datasets, methods to effectively integrate these two data types are limited. Reconciling differences in spatial representation and resolution between movement and environmental variables is a major hurdle that will require innovative analytical and technical approaches to solve. In the absence of effective analysis techniques, the information obtainable from these detailed datasets are underutilized, limiting the scope of testable hypotheses when investigating wildlife movement-environment interactions.

Examining how wildlife movement patterns vary in response to the physical environment is a major avenue of research (Schick et al., 2008). The emphasis of movement-environment research questions has shifted to focus on the effects of disturbance on wildlife movement patterns, as anthropogenic activities are overlapping more and more into wildlife habitats. For example, Latham et al. (2011) and Ehlers et al. (2014) examined how disturbance features affected wolf movement patterns and associated predator-prey relationships, Graham et al. (2010) examined spatial temporal changes in grizzly bear movement rates around roads and probabilities of road crossing, and Dyer et al. (2001) examined how caribou movement patterns change relative to human developments. Understanding how wildlife movement patterns vary in relation to disturbance features is a key component of wildlife conservation and management, as it is can be used to inform future land-use planning decisions to balance human activities and healthy wildlife populations in multi-use landscapes.

Individual movement trajectories are a complex collection of movement patterns created by spatial-temporal variations in the processes influencing movement (Fleming et al., 2014;
Investigating the drivers of wildlife movement is challenging, as a combination of internal and external factors work to create variation in movement patterns across space, through time, and between individuals (Mueller and Fagan, 2008). However, because these processes are operating at a range of spatial and temporal scales, the granularity, or sampling interval, of movement data determines the complexity of research questions possible (Fleming et al., 2014). Fine granularities provide a detailed representation of movement, while coarse granularities provide a more generalized representation (Long and Nelson, 2013a). The value of high density movement data is that they permit the investigation of more specific hypotheses around spatial-temporal variations in wildlife movement (Cagnacci et al., 2010). Yet, there is a balance between detail and over-sampling since too fine a granularity can result in movement patterns being masked by data noise (Long and Nelson, 2013b). Movement trajectories sampled at fine granularities include a high degree of spatial and temporal dependency between locations. Dependency between locations may violate the assumptions of traditional statistical approaches; however, animals do not move randomly across a landscape, so failing to incorporate autocorrelation into movement analyses can limit the relevancy of resulting insights (Boyce et al., 2010; De Solla et al., 1999; Dray et al., 2010; Wittemyer et al., 2008).

Data driven methods are advantageous when working with high density telemetry data, as they provide a means of exploiting the built-in spatial and temporal autocorrelation properties of the data. Quantifying the spatial autocorrelation in movement parameters relative to the physical environment creates a link between observable patterns of wildlife movement, and underlying environmental and biological processes. The benefit of these approaches is that they reduce the number of subjective decisions or a priori knowledge required when analyzing movement data. For example, in the context of wildlife movement patterns in disturbed landscapes, subjective
distance thresholds are commonly used to define an animal’s proximity to human-related
features; however, their application can limit analyses when the spatial scale of the thresholds do
not match the scale of movement processes. Alternatively, animal movement can be quantified
using mathematical models (i.e., correlated random walks, levy flights or area restricted
searches) (Schick et al., 2008). However, prior knowledge of relevant movement processes are
needed to select the appropriate model for the behaviour of interest and avoid misleading results
(Nams, 2014). In other words, data driven methods aim to quantify pattern to connect to process;
whereas, alternative approaches, use knowledge of process in order to quantify pattern.

Studying wildlife movement is most relevant to conservation when investigated in the
context of survival and mortality. Wildlife movement provides a glimpse into the factors
influencing wildlife population sustainability, as requisite activities for survival (i.e., foraging,
predation, breeding, dispersal) can be linked back to movement behaviors. However, human
activities, both industrial and recreational, can have consequences for wildlife populations
through the alteration of landscape structure and the distribution of resources (Forman and
Alexander, 1998). Infrastructure construction and vegetation clearing can result in habitat or
population fragmentation and the direct loss of habitat (Ewers and Didham, 2006; Forman and
Alexander, 1998; Leu et al., 2008). Additionally, more human activity can lead to habitat loss
indirectly through avoidance behaviors (Dyer et al., 2001; Polfus et al., 2011). Linking variations
in wildlife movement patterns back to ecological and biological processes is therefore a key
component to understanding animal movements in heterogeneous landscapes, and their related
impacts on survival (Barraquand and Benhamou, 2008; Gurarie et al., 2009).
1.2 Research focus

For grizzly bear (*Ursus arctos*) populations in the foothills of west-central Alberta, the expansion of resource extraction activities since the 1990s has resulted in a steady encroachment of human activity into previously remote bear habitats (Laberee et al., 2014; Linke et al., 2005; Roever et al., 2008). Grizzly bear movement near roads is a particularly important wildlife-landscape interaction to understand as road networks are essential for the development and operation of resource extraction industries (Boulanger and Stenhouse, 2014). In the foothills region, both forestry and oil and gas industries are active, and require expanding road networks to connect resource extraction areas to major transportation corridors. However, establishing road networks through undeveloped landscape areas have a number of important consequences for bear populations. Roads facilitate human access to isolated areas of the landscape, which can adversely affect bear populations by increasing the chances of animal-vehicle collisions, and human-bear encounters ending in animal mortality. For example, expanding road networks heighten the risk of legal harvest by hunters, and illegal harvest by poachers through improved access to previously secure habitats (Benn and Herrero 2002; McLellan and Shackleton 1988; Nielsen et al. 2004; Roever et al. 2008). Boulanger and Stenhouse (2014) found that road densities have a substantive demographic impact on survival and reproductive rates for grizzly bear populations in Alberta. Based on their results of survival rates for females with dependent offspring, they recommended a road density threshold of 0.75 km/km² to ensure sustainable grizzly bear populations.

Despite the risks associated with roads, they can also act as attractants for bears (McLellan 1990, Gibeau et al. 2002a, Nielsen et al. 2004, Roever et al. 2008a). Road construction creates edges which promote the growth of understory and herbaceous vegetation.
by opening up the canopy and increasing light penetration to the forest floor. Road sides can provide valuable edge habitats rich in food resources during the spring, early summer green-up period when other food resources are still unavailable (Graham et al., 2010; Roever et al., 2008; Stewart et al., 2013). Habitats in proximity to roads are referred to as primary sinks or ecological traps as they represent high-risk, high-quality habitats available for selection by some wildlife (Bourbonnais et al., 2013; Ciarniello et al., 2007; Nielsen et al., 2006).

Due to the long term monitoring of grizzly bear populations in Alberta by the Foothills Research Institute Grizzly Bear Project, comprehensive movement and environmental datasets exist for the west-central region of the province. These datasets provide a unique opportunity to develop data-driven approaches for quantifying wildlife movement patterns in relation to linear disturbance features. Providing managers with spatially explicit information about how movement patterns change relative to disturbance features is essential for informed land-use planning and the maintenance of healthy wildlife populations within multi-use landscapes.

1.3 Thesis objective

This research is concerned with quantifying the effect of near-road movement patterns on grizzly bear seasonal mortality and survival. The goal of this research is to develop a data-driven approach for quantifying grizzly bear movement patterns relative to roads, and to examine the link between near-road movement patterns and survival. This aim will be addressed by accomplishing the following objectives:

1) Review of existing tools for conducting movement analysis, specifically tools supported within R statistical software, to highlight any existing methodological opportunities and limitations associated with relating movement to environmental variables.
2) Develop a data-driven approach to quantify the spatial scales of wildlife movement response to linear features, and apply it to quantify how grizzly bear near-road movements affect mortality and survival.

References


2.0 A review of R packages for the analysis of wildlife movement

2.1 Abstract

Supported by advances in geographic information science (GIS), computing, and statistics, researchers are developing new methods to leverage high resolution telemetry data sets for investigating fine-scale questions regarding animal movement. Here I review the analytics currently available for wildlife movement research, where movement is defined by continuous point location data rather than habitat selection or use, and highlight opportunities and challenges in future research. I identify three themes in analytical approaches for research questions posed in wildlife movement analysis: 1) quantifying movement pattern, 2) linking movement to process and behaviour via trajectory segmentation, and 3) linking movement to process and behaviour using models. For each theme I review available analytical packages in R that implement state-of-the-art methods related to data preprocessing, available analysis options, and output formats. I illustrate these approaches using telemetry data from grizzly bears in west-central Alberta, Canada. I find that, whereas methods to quantify patterns are well developed, limited methods exist to integrate telemetry data with the increasingly available and important environmental covariates. Accordingly, an opportunity exists to develop data-driven approaches that take advantage of unique autocorrelation characteristics present in high density temporal datasets to quantify the interaction between wildlife movement and the environment and contribute to new theory in wildlife movement.

2.2 Introduction

Advances in global positioning satellite (GPS) tracking technologies have culminated in readily available and temporally dense datasets of wildlife movement. New methods are being
developed to analyze novel wildlife data sets (Long and Nelson, 2013a), and method innovation is fueled by collaborations among biologists, mathematicians, geographers and computer scientists (Cagnacci et al., 2010; Calenge et al., 2009). Supported by advances in geographic information science (GIS), computer science, and statistics, wildlife movement analysis is quickly developing powerful analytical tools to answer complex ecological questions regarding animal movement (Cagnacci et al., 2010; Long and Nelson, 2013a). Despite - and in part owing to this rapid proliferation of approaches – future work requires scholars and practitioners to consider carefully among options before them.

Strategic choices start with an understanding of movement data. Movement is defined as a continuous process that supports the fundamental requirements for wildlife survival such as feeding, security, or dispersal. Though movement is continuous, it is typically represented discretely in time and space by GPS telemetry data as a series of sequential x, y locations. At the individual level, movement is determined by a combination of four components: an animal’s internal state (e.g., body condition, reproductive status, energetic state and needs), its physiological capabilities (e.g., how does the animal move and orient itself), and a mixture of external biotic and abiotic factors (e.g., presence of food resource, presence of competitor, time of day, weather conditions) (Nathan et al., 2008). Thus, wildlife movement patterns reflect the complex interactions between biological and ecological processes operating across a range of spatial-temporal scales (Fleming et al., 2014; Gurarie et al., 2009; Martin et al., 2013; Nathan et al., 2008).

Wildlife movement analysis approaches fall into two categories: Eulerian and Lagrangian (Turchin, 1998). Eulerian methods describe movement patterns in terms of probable space use and are useful for investigating movement patterns and processes occurring over large spatial
and temporal scales (Smouse et al., 2010). For example, identification of migration routes and stop over sites (Kranstauber et al., 2012; Sawyer et al., 2009), and home range delineation. Lagrangian methods differ as they examine movement patterns at fine scales using discrete movement steps in time and space, and quantify patterns with descriptive parameters like step length, turning angle, and direction (Chetkiewicz et al., 2006; Smouse et al., 2010). Although both approaches can be applied to examine GPS tracking data, research questions focused on shifts in wildlife distributions and habitat use fall under the purview of Eulerian approaches; whereas, research questions focused on relating movement to behavior employ Lagrangian based approaches (Gurarie, 2008). In this paper I focus on Lagrangian based approaches, as they tend to be used to quantify movement from high telemetry datasets for individual animals (Smouse et al., 2010).

Given the increased computational complexity of many methodological advancements researchers applying these tools require software platforms to facilitate implementation. A variety of platforms exist (e.g., Geospatial Modelling Environment, WinBugs, ArcMET, MoveMine), but by and large, the greatest variety of analytical options is offered by packages run in R statistical software. R is a programming language and a free software platform for statistical computing and graphics (R Core Team, 2014). R packages frequently accompany academic journal articles, and establishment of a journal specifically aimed at showcasing new tools in R, are evidence of the importance of R as a tool for sharing scientific developments (Tufto and Cavallini, 2005; Van Moorter, 2014). R is highly accessible given that it is free, open source, and stands alone; however, the barrier to use tends to be a steep learning curve for new users (Van Moorter, 2014). Within the field of wildlife movement analysis, packages are available to examine home ranges (e.g. adehabitatHR, T-LoCoh); utilization distributions (e.g.
BBMM, mkde); wildlife interaction (e.g. wildlifeDI); marine mammal movement (e.g. diveMove, argosfilter) and movement visualization (e.g. animalTrack). However, due to the large number of packages available, potential users will require judicious thinking and guidance as to which packages best fit the research objectives.

My goal is to review current methods for wildlife movement analysis in order to identify opportunities and gaps in the available analytics following these objectives. First, I review existing literature and identify three themes in Lagrangian-based approaches for addressing research questions posed in wildlife movement analyses: i) quantifying movement pattern, ii) linking movement to process and behaviour via trajectory segmentation, and iii) linking movement to process and behaviour using models. For each movement research theme I review R statistical software packages that support analysis based on three topic areas: data preprocessing, methods and analysis options, outputs. I then identify opportunities and challenges for developing theoretical approaches and software tools for movement analysis and emphasize the growing potential and importance of investigating movement as a function of environmental conditions. I limit my scope to R packages that support the analysis of individual movement patterns and focus on methods that quantify movement pathways, rather than space-use.

2.3 Methods

2.3.1 Inclusion criteria

The process of selecting wildlife movement packages to evaluate was guided by my interest in the analysis of terrestrial wildlife movement-environment interactions. My primary selection consideration was the package must have the capacity to analyze GPS location data. A
trajectory’s positional error structure is determined by the method of data collection. For example, in contrast, Argos data has higher positional errors due to the differences in how location is calculated (Argos Doppler shift versus GPS on-board triangulation) (Douglas et al., 2012; Tomkiewicz et al., 2010). Managing Argos positional errors requires specific data processing techniques, and the error structure can sometimes be built directly into functions for the analysis of Argos movement trajectories. Since GPS locational data do not share the same error characteristics in terms of the Argos classes and do not require the same processing techniques, packages that were designed specifically to manage and analyze Argos data were excluded (Figure 2.1).

My second consideration was that the package contained functions for trajectory analysis that quantified movement pattern in terms of movement structure (i.e., speed, tortuosity) rather than in terms of habitat selection or utilization distributions. Packages that quantify movement in terms of space use and selection were excluded as they pertain to research questions that quantify the link between movement and environment through changes in use rather than variations in movement pattern.

Packages that were primarily focused on the analysis of marine tracking data were also excluded due to the differences in environmental variables used in marine versus terrestrial systems. Marine environmental variables are generally collected at much coarser spatial and temporal resolutions, and can include data collected by the tracking device itself like depth and light levels (Tomkiewicz et al., 2010). Depth adds a 3D component to wildlife movement analysis that is not considered for terrestrial trajectories (Cagnacci et al., 2010).

My final consideration was that the packages had been updated since 2014 to ensure only actively maintained packages were included. Including only actively maintained packages was
deemed important because it implied that there would be available user resources, either through communication with the maintainer, associated package documentation, or established user base. Including only actively maintained packages also minimized the number of compatibility issues with package dependencies and R versions. Packages that deal strictly with data management or visualization were also excluded, as my focus is linking movement patterns to the spatial-temporal variation in underlying processes. These criteria narrowed my review to six prominent packages (Table 2.1).

2.3.2 Reviewing framework

Research questions in movement analysis at the population level can be partitioned into three categories: exploratory, explanatory and predictive (Calenge et al., 2015; Gurarie et al., 2015). These subdivisions, however, are also relevant at the individual trajectory level. As a result, selected R packages were divided into three analytical themes based on the framework used by Calenge et al. (2015): analytical methods for quantifying pattern (Table 2.2), analytical methods for linking movement to behavior using trajectory segmentation (Table 2.3), and linking movement to behavior using models (Table 2.4). Within each of the three themes, the capabilities of each package were reviewed with regards to three general aspects of wildlife data analysis: data pre-processing, analysis options, and output formats.

I define pre-processing as the steps needed to format GPS telemetry data for use with the analysis tools available in each category. Although GPS telemetry data are collected as a sequence of x/y locations attributed with a time stamp, pre-processing is required to convert these data into package specific R-object classes. Object classes support object-oriented programming, and are used to define the methods available to handle that object (Bivand et al., 2008). For example, the ltraj class used by adehabitatLT package stores data for multiple
individuals as a list of data frames with the coordinates, time stamps, additional attributes, and descriptive movement parameters for each trajectory (Calenge et al., 2009).

Analysis options are defined by the analytics and methods supported by functions in the selected packages. I list the available methods, and highlight any unique features that set the packages apart. Accordingly, functions contained in the packages that do not fit into my review categories, such as functions for data management and visualization, are not covered. No method parameterization is discussed, as parameter selection is a major topic within wildlife movement analysis and more comprehensively covered in reviews expressly focused on method comparisons (e.g., Codling et al., 2008; Thurfjell et al., 2014).

Outputs of each analysis tool are summarized in terms of file formats produced. Output formats are discussed to provide more detail on the results of analysis, and to provide information on how the results could be integrated into subsequent analyses.

2.4 Review of Packages

2.4.1 Quantifying Movement Patterns

Quantifying pattern is an important component of wildlife movement analysis, as it facilitates the comparison of movement trajectories across space, through time, and between individuals (e.g., Fryxell et al., 2008; Graham and Stenhouse, 2014). Trajectories are often described in terms of steps, the straight line distance between successive relocations, and characterized using linear and angular descriptive parameters (Calenge et al., 2009). Patterns can be quantified in terms of individual steps (e.g., Root and Kareiva, 1984), or in terms of how steps relate to one another (e.g., Kareiva and Shigesada, 1983). Individual step descriptors include step length, x/y displacement and movement direction; while relative descriptors include turning angle and squared net displacement. These methods are often applied to exploratory research questions
where the goal is to examine the spatial and temporal variation in movement patterns along a trajectory, or how the distribution of movement parameter values varies between individuals (e.g., Fryxell et al., 2008; Graham and Stenhouse, 2014; Mueller et al., 2011). Since steps are the most basic unit in movement analysis, analytical tools for quantifying pattern also form the first step in more complex analyses.

Five of the selected R packages had tools for quantifying movement patterns (Table 2.2). In each case, the GPS telemetry data required pre-processing to transform the coordinates and associated time stamps into package specific R-object classes. Generally, pre-processing required combining the x/y locations into coordinate pairs and coercing time into a POSIXct class. *AdehabitatLT* required the trajectories to be regular for some analyses, so missing fixes were replaced by NA values as part of the pre-processing steps (Clément Calenge et al., 2015). Similarly, the *move* package requires x/y locations to be projected in Azimuthal Equidistant, so transforming the bear data from UTM to latitude/longitude was also considered as pre-processing (Kranstauber et al., 2015).

Although all the packages contained functions to calculate at least one linear and one angular movement parameter; *AdehabitatLT, move,* and *bcpa* have the greatest variety of analysis options for quantifying pattern. For example, the *move* package can be used to calculate step length, speed, direction, turning angle and time interval. Beyond calculating movement parameters, only *AdehabitatLT* and *move* have additional built in functions for examining the distributions of movement parameters within a given trajectory. The *move* package calculates summary statistics for the various parameters, and *AdehabitatLT* provides graphical descriptions of variation in movement parameters through time (Figure 2.2). *AdehabitatLT* is also unique as it offers analysis options for quantifying the autocorrelation in movement parameters, and the
occurrence of missing fixes. The `acfdist.ltraj` and `acfang.ltraj` functions compute correlograms to identify the temporal scales at which autocorrelation is present for linear or angular movement parameters; `runsNAltraj` and `plotNAltraj` provide information on the dependence structure and distribution of missing fixes in a trajectory.

Vectors or data frames of calculated movement metrics were used to output results. Movement metrics were calculated for each step resulting in a vector of values, one for each pair of successive GPS locations. For example, `AdehabitatLT` and `bcpa` output data frames with multiple descriptive parameters where the values were assigned to the first point in the pair of consecutive GPS locations forming the step. In contrast, the trajectories package output a data frame with the descriptive parameter value associated with the step itself. The `trip` and `move` packages output vectors of values that required the user to associate them back to the corresponding step or GPS location. `AdehabitatLT` was the only package to have value added graphics for histograms of movement descriptors, graphical summaries of how descriptors and missing fixes varied with time, and correlograms displaying any significant autocorrelation present in the data (Calenge, 2006; Dray et al., 2010). Functions for assessing autocorrelation also output test statistics that could be used to quantify autocorrelation structure in parameters or missing fixes. For example the function `wawotest` outputs a z-score and p-value that are used to quantify the amount of independence present between values in a vector (Calenge, 2006; Wald and Wolfowitz, 1943).

2.4.2 Linking movement and behavior: trajectory segmentation

Wildlife movement trajectories incorporate a mixture of movement patterns representing changes in an animal’s behavioral state as it moves through the surrounding environment. Although often useful to be able to link movement patterns to behavioral states, classifying unique patterns is
difficult. Movement trajectory segmentation is challenged by the noise of natural variation movement patterns (Nams, 2014), as well as the scale dependence of movement patterns. For instance, changes in movement patterns occurring at one space-time scale may be masked if represented at another scale (Fleming et al., 2014; Gurarie et al., 2009; Schick et al., 2008). These methods are often applied to both exploratory and explanatory research questions in wildlife movement. They can be used in an exploratory capacity to quantify changes in movement patterns (Gurarie et al., 2009; Sur et al., 2014), or in an explanatory capacity to link pattern changes back to changes in underlying processes (Barraquand and Benhamou, 2008).

Approaches that identify statistical change points in trajectories are useful when little is known about the ecological and biological processes operating in a given system. Approaches that define breaks based on consistency in a user defined movement parameter are advantageous, as homogeneous segments within a trajectory can be identified without prior assumptions as to the mechanisms driving variation in pattern (Buchin et al., 2010; Nams, 2014). In wildlife movement analysis, several approaches have been applied to identify consistent patterns in step length and turning angles at the step level including regression (Limñana et al., 2007), time series analysis (Madon and Hingrat, 2014), and change point analysis (Gurarie et al., 2009; Thiebault and Tremblay, 2013).

Two packages in R supported analysis tools for segmenting trajectories at natural break points: adehabitatLT, and bcpa (Table 2.3). In each case, data pre-processing involved transforming data into the same package specific object classes needed for quantifying movement patterns; however, the Lavielle functions required missing values to be removed from the trajectory (Calenge, 2011; Calenge, 2006), and performing behavioral change point analysis
with the bcpa package required movement parameters to be calculated as first step (Gurarie, 2013).

The Lavielle option supported by adehabitatLT is the more straightforward approach, as it applies a contrast function to minimize the difference between an observed trajectory and a theoretical model consisting of a user specified number of segments. The associated functions provided the option to characterize homogenous segments based on a constant mean value for a specified movement parameter, constant variance or a combination of both (Calenge, 2011). For example, if the user is interested in patterns of step length, the Lavielle method can be used to identify segments within a trajectory that have a constant mean step length, constant variance in step length, or constant mean/variance in step length.

The behavioral change point analysis method (bcpa) is more complex and provides a more in depth characterization of changes in movement pattern within a trajectory, as it incorporates autocorrelation in movement parameters into the analysis. Bcpa uses a likelihood-based approach to identify significant changes in movement parameter values, and has components that can be adjusted by the user to customize the sensitivity of the method (i.e., window size, and BIC constant). Change points can be defined as individual shifts in the mean, standard deviation or local autocorrelation, or as shifts in any combination of the three (Gurarie, 2013; Gurarie et al., 2009).

Both packages provided graphical and numerical summaries for the segments within the movement trajectories. The Lavielle function outputs segments as subset bursts of the original ltraj object used as the input for the analysis. These bursts, representing series of consistent patterns, can be transformed into data frames, and characterized using descriptive statistics. The graphical outputs summarize timing of change points throughout the trajectory as a function of
the parameter values, and also in terms of the trajectory itself by displaying the pathway as a series of segments (Figure 2.3). However, any characterization of the segments has to be performed by the user as a secondary step.

The output data frames for the bcpa analysis includes summary statistics of movement parameters by segment, as well as information on which model was used to define segments. Similar to Lavielle, the graphical outputs summarize the timing of change points throughout the trajectory as shifts in parameter values, and the pathway as a series of segments. Additionally, bcpa provides graphical representations of how movement parameters change from segment to segment. For example, one segment could be characterized with long meandering movements, followed by a segment of short directed movements. Output plots detailing the temporal scales of autocorrelation relative to mean and variance of the movement parameter throughout the trajectory can also be created to help contextualize the segments in terms of possible behavioral states (Gurarie, 2013).

2.4.3 Linking movement and behavior: trajectory modelling

Quantifying movement patterns using models requires a priori knowledge of the theoretical mechanisms governing movement associated with a behaviour of interest (Nams, 2014; Thiebault and Tremblay, 2013). Trajectory modelling approaches have the broadest range of use, being suitable for research questions in all three categories: exploratory, explanatory and predictive. For example, null models can be used to explore movement patterns in terms of process-based hypotheses by comparing observed movements to simulated trajectories (i.e., random walks, levy flights) (Codling et al., 2008; Kareiva and Shigesada, 1983; Root and Kareiva, 1984). Conversely, state-space models can be used to answer predictive questions around animal movement (Jonsen et al., 2005; Patterson et al., 2008).
Using models to quantify movement creates a statistically robust characterization of pattern that can be used to evaluate complex behavioural states and link movement parameters back to environment. However, increasing model complexity necessitates an increase in technical capabilities and computational power (Morales et al., 2004; Nams, 2014). Differing assumptions amongst movement models can result in different characterizations of the same data (Gurarie et al., 2015; Schick et al., 2008), and a mismatch between model assumptions and movement processes can lead to misleading results (Nams, 2014). Therefore, to effectively apply model based approaches, *a priori* knowledge of the underlying processes influencing movement is essential (Barraquand and Benhamou, 2008).

Three packages in R supported analysis tools for quantifying movement using models: *move*, *adehabitatLT*, and *crawl* (Table 2.4). The data processing required for these approaches was more in depth than the other two categories, as some degree of theoretical knowledge about the study system was required to appropriately apply the analysis options. The complexity of the required knowledge reflected the complexity of the analysis. For example, the corridor function in *move* required only proportional thresholds for speed and azimuth parameters to define probable corridor movements within a trajectory (Kranstauber et al., 2015); fitting a continuous-time correlated random walk with the *crawl* package, however, involved quantifying initial movement states or drift models with position, speed and error (Johnson, 2014). *Move* and *adehabitatLT* required the data to be formatted into their specific object classes, and *crawl* required a data frame with columns for coordinates, positional errors, and time.

Similar to the observations made by Gurarie et al. 2015, the analysis options available within the packages can be described in terms of the strength of the model assumptions, complexity of the outputs and explanatory capabilities. The corridor function offered in *move*,
has minimal assumptions and its explanatory power extends only to identifying segments within a trajectory that suggest corridor use behavior. First passage time (fpt) and residence time (RT), offered by adehabitatLT also have minimal assumptions, requiring only the radius for defining movement patterns within a trajectory (Calenge et al., 2015; Gurarie et al., 2015). These approaches have been used to explain the scales of foraging behavior using area restricted searches (Fauchald and Tveraa, 2003; McKenzie et al., 2009) and habitat use in patchy environments (Barraquand and Benhamou, 2008). Gueguen’s approach to trajectory segmentation using Markov models in adehabitatLT has a moderate level of assumptions that need to be met. These include independence between steps for the movement parameter being tested, and that the trajectory can be segmented based on a set of user-defined candidate models (Calenge, 2011; Calenge et al., 2015). While this method is not designed to identify a particular behavior, it does segment trajectories into homogeneous movement bouts that can then be contextualized using ancillary data to link movement pattern to behavior. It differs from bcpa and Lavielle segmentation, as it requires the definition of a priori Markovian models to identify the number and characteristics of homogeneous segments within a trajectory (Calenge, 2011). AdehabitatLT also provided functions for creating null models for analyzing wildlife movement including correlated random walks, Levy walks, and Ornstein-Uhlenbeck processes (Calenge, 2011; Calenge et al., 2015). Finally, the continuous-time correlated random walk (CTCRW) option supported by the crawl package has the strictest assumptions, but also provides the greatest explanatory capabilities including trajectory simulation, prediction and segmentation (Johnson et al., 2008; Johnson, 2013).

The output complexity from each of the packages mirrors the models’ assumptions and explanatory capabilities. For example, the corridor function offers the most straightforward
output options, producing a MoveBurst object with individual steps categorized as either corridor or non-corridor movements, and a trajectory plot with corridor movements indicated by colored points. Correspondingly, the more complex CTCRW analysis options output data frames of statistical summaries of model performance, estimated parameter values, predicted parameter values, plots of simulated trajectories and graphical summaries of estimated parameter values and associated confidence intervals. The exception to the rule is the Gueguen segmentation function with moderately strict assumptions, but straightforward outputs consisting of a graphical summary of any identified segments, plus a list object detailing the segmentation structure of the trajectory and ltraj objects for each segment (Figure 2.4).

2.5 Discussion

Method development in movement ecology has led to a wide range of analysis techniques for examining questions about individual movement through to the distribution of entire populations (Morales et al., 2010; Schick et al., 2008; Smouse et al., 2010). Coupled with innovation in tracking technologies, researchers now have access to comprehensive movement datasets for many species (Cagnacci et al., 2010; Hebblewhite and Haydon, 2010). Though common methods for quantifying patterns have been thoroughly established, innovative methods for analyzing high resolution movement data will continue to be an active research area as there are many analytical tasks that are still challenging (Long and Nelson, 2013a). For instance, data-driven methods that can integrate movement trajectories and the physical environment are limited. As such, information from high frequency movement data is under-utilized, and formulating specific hypotheses about the ecological processes influencing wildlife movement patterns is difficult. The benefit of the R packages specifically designed for wildlife movement analysis is that they provide integrated toolboxes to perform exploratory analyses that can be used to formulate and
test more specific hypotheses, and direct the use of complex analytical approaches (Calenge et al., 2009). However, the capacity of R to carry out more complex analytical tasks is limited by the amount of virtual memory available to the program (Bivand et al., 2008).

Amongst the three Lagrangian movement themes, quantifying movement pattern was most comprehensively covered, which reflects the importance of describing steps in terms of linear and angular parameters. Steps are the most basic unit in wildlife movement analysis (Turchin, 1998), and as such, techniques for quantifying them have been a major topic of discussion through the movement ecology literature (e.g., Benhamou, 2004; Turchin, 1998; Turchin et al., 2013). Step length and turning angle have become the standard parameters for describing steps, as they have been consistently used in movement analysis to create a link between how animals move through the landscape, and processes driving their movement (e.g., Dyer et al., 2002; Root and Kareiva, 1984; Sawyer et al., 2009; Turchin, 1998). For example, Benhamou (1992) examined the interplay between step length and turning angle for a model predator switching between intensive and extensive search modes while looking for prey; whereas, Fryxell et al. (2008) explored changes in elk movement modes across a selection of spatial scales by examining the distributions of four movement parameters: daily movement rate, turning angle, step length and mean squared displacement.

Methods used for addressing exploratory research questions for movement analysis were well captured by all the R packages, with analytics available to calculate a wide range of descriptive parameters, independence between values, statistical change points within trajectories, and null model creation. The advantage of performing exploratory analyses in R are the outputs formats from the analyses were easily integrated into higher analysis functions aimed for research questions falling into the explanatory or predictive categories.
Although the analysis options for exploring animal movement patterns in R are impressive, there are still opportunities for methodological innovation. The relocation sampling rate of telemetry data, or granularity, is a key consideration in movement analysis because it is related to the degree of spatial and temporal autocorrelation present in the data. The biological importance of autocorrelation in wildlife movement data has been highlighted by many authors (e.g De Solla et al., 1999; Dray et al., 2010; Wittemyer et al., 2008). Autocorrelation is often seen as an obstacle in statistical analyses (Boyce et al., 2010); however, wildlife movement is inherently non-random, so consistent patterns can act as indicators for the scales at which unknown processes are operating (De Solla et al., 1999). As a result, quantifying autocorrelation in movement parameters can create a link between observed variation in pattern and the underlying processes responsible. Out of the selected packages, adehabitatLT and bcpa were the only two to take advantage of the autocorrelation present in movement datasets; AdehabitatLT provided tools to quantify autocorrelation (Calenge, 2011), while bcpa used it to detect changes in behavioural modes within a trajectory. However, in both cases only temporal autocorrelation in movement parameters was utilized (Calenge, 2011; Dray et al., 2010; Gurarie, 2013).

Another challenging aspect of movement analysis is within the existing analytics supported by R, there is limited capacity to integrate movement analysis with other ancillary data sets. For example, given the complexity of wildlife movement and biology, linking conditional movement analytics with environmental data will enable more complex and nuanced analysis. Integration of data sets seems especially relevant given the plethora of new sources of environmental mapping, being made available from remote sensing. As an example, STAARCH remote sensing products can be used to examine the effects of disturbance on the distribution of grizzly bear food resources (Gaulton et al., 2011; Hilker et al., 2009), and disturbance
characteristics can be derived from Landsat imagery and used to determine what disturbance attributes promote habitat selection, or feature avoidance by wildlife (Stewart et al., 2012a).

A key opportunity for movement methods research is to develop approaches to integrating wildlife and environmental data, but to succeed several difficulties must be addressed (Neumann et al., 2015). The lack of methods to quantify movement-environment interactions reflects the inherent conceptual and operational challenges of integrating two dissimilar data sources. Whereas, GPS tracking data are represented as discrete points in space and time, environmental variables derived from remote sensing imagery can have multiple representations. Environmental variables can be represented as a continuous surface for variables like topography (Fisher and Tate, 2006), a classified continuous surface for displaying land cover (Wulder et al., 2008), or a vector representing human disturbance features (Stewart et al., 2013). Integrating point based telemetry data with each representation of an environmental parameter creates unique challenges. Consider the example of how linear features affect wildlife movement, if roads are represented as vectors, movement and environment can be linked by calculating the distance between each step, or GPS location, and the nearest road. However, analysis accuracy can be impacted by the user’s definition of nearest and data resolution used to map anthropogenic features (Neumann et al., 2015). Linear features may be represented as a density surface; however, a number of subjective decisions about the area used for calculating density are required (Beyer et al., 2010).

Another fundamental and complex analytical challenge when linking wildlife movement patterns to the physical environment involves reconciling the disparate temporal and spatial scales between the two datasets. Movement trajectories are dynamic time series data that represent an individual’s change in position through time. High frequency sampling rates
correspond to an increase in dependence between observations and a more detailed representation of movement pattern; whereas, low sampling rates correspond to more independence between observations, and a more generalized representation of pattern (Dray et al., 2010; Long and Nelson, 2013a). For remotely sensed environmental data there is a tradeoff between spatial and temporal resolution. Neumann et al. (2015) classify remotely sensed data products into two categories: fine but infrequent (i.e., vegetation structure from LIDAR), and coarse but frequent (i.e., MODIS derived NDVI). Products that fall into the coarse but frequent category are still generally collected at longer temporal scales than most GPS tracking data. Whereas, they may be more temporally similar than products in the fine but infrequent category, there exists a mismatch in the spatial component. Fine but infrequent products, compare well spatially to the movement data; however, due to the longer revisititation times, variations in movement pattern are being contextualized using relatively static environmental conditions (Neumann et al., 2015). Several authors have identified the importance of matching the resolution of environmental variables to the research question being investigated, and suggest that questions around fine scale patterns are better addressed using fine but infrequent data, and broad scale movement patterns with coarse but infrequent data (Dodge et al., 2013; Johnson et al., 2002; Neumann et al., 2015). However, no work has been done to examine the optimal relationship between telemetry fix rate and environmental data resolution.

Although some analytical techniques have been developed to utilize spatial and temporal autocorrelation as an emergent property of wildlife movement data (Boyce et al., 2010; Dray et al., 2010), there remains an opportunity for the development of data driven methods that quantify movement patterns using the spatial autocorrelation in movement parameters. As anthropogenic activities continue to overlap into wildlife habitats, it is becoming increasingly important to
understand how wildlife movement patterns vary in response to human related landscape features like roads, pipelines, cut blocks, or well sites (Bourbonnais et al., 2013; Dyer et al., 2002; McKay et al., 2014; Roever et al., 2010; Stewart et al., 2012a). Quantifying spatial autocorrelation in movement parameters relative to these features will provide spatially explicit information about the distance at which wildlife perceive human activity and vary their movement patterns in response. An example, Kite et al. (in revision) propose a data-driven method, based in semivariogram modelling, to quantify the spatial scales at which wildlife movement patterns change in response to linear features. Using the variation in movement parameters relative to distance from feature, provides a representation of how similarity in movement patterns changes with proximity to specific landscape characteristics. Associated zones of influence can subsequently be defined as the spatial scales at which autocorrelation in movement pattern is the strongest relative to a particular feature (Kite et al. In revision). The resulting zones of influence provide spatially explicit information on how areas of human disturbance influence wildlife movement patterns, and can be used to inform future land use planning decisions and management initiatives aimed at minimizing the negative effects of infrastructure on wildlife populations.

Operationally, R is an effective tool for movement analysis as it provides users with an integrated platform that has the capability to perform a variety of exploratory analyses on movement datasets without having to switch software programs, or file formats. The ability of the package specific object classes used by move and adehabitatLT to handle trajectory data for multiple individuals demonstrated the convenience of performing movement analysis within the R programming platform. Both ltraj and MoveStack objects can be used to store, manage and analyze the trajectories for multiple individuals at the same time (Calenge et al., 2015;
Object classes that support multiple datasets eliminate the need for users to program loops and functions that iteratively apply analysis tools to individual datasets, thus streamlining project workflows and processing steps.

Combining differing data formats and projections is another important consideration when integrating remotely sensed imagery with GPS trajectory data (Dodge et al., 2013; Neumann et al., 2015). Transforming environmental and movement datasets into consistent formats and projections can constitute a major part of any analysis. R facilitates this process, as its flexibility allows for users to work with multiple data formats within the same software platform. However, R’s ability to simultaneously handle environmental and movement data is limited by the amount of virtual memory available to the program (Bivand et al., 2008).

Movebank, an online movement databases accessed through R using the move package, provides an alternative way of integrating movement and environmental datasets using the Env-DATA system. The Env-DATA system allows users to annotate trajectories with a suite of environmental variables stored in the database alongside movement data. It facilitates the process of reconciling data formats and projections as processing steps associated with transformation, resampling, and interpolation have been automated; thus allowing users to easily attribute movement trajectories with multiple environmental variables and indices all within the Movebank data portal (Dodge et al., 2013).

AdehabitatLT proved to be the most valuable package for wildlife movement analysis. Unlike the other packages, it supported analytical tools in all three approach themes. In the case of quantifying pattern and trajectory modelling, it provided multiple analysis options accommodating a wide range of research questions. The ltraj object class and burst structure facilitated the analysis and management of movement data for multiple individuals.
simultaneously. Additionally, the functionality of adehabitatLT is built around the ltraj object class, so movement data only need to be formatted once to be used as inputs across the majority of functions. AdehabitatLT has with excellent documentation in the form of a reference manual, vignette, and several peer reviewed publications (e.g., Calenge, 2011a; Dray et al., 2010). This reference material, in combination with a wide user base, amounts to easily assessable user resources.

2.6 Conclusion

Advances in both tracking and remote sensing technologies are supplying wildlife researchers with extensive datasets to address relevant research questions around animal movement in heterogeneous landscapes. It is important to have methods that quantify autocorrelation in movement data to establish the relationship between wildlife movement and the physical environment. R is a popular tool for analyzing movement, but currently lacks applications for linking high density telemetry datasets with remotely sensed environmental variables. I suggested that data driven methods, that take advantage of autocorrelation movement parameters, provide a possible approach for linking wildlife movement parameters to underlying environmental and ecological processes. As adehabitatLT provided the greatest functionality for wildlife movement analysis, any future method development should be implemented within their ltraj object class framework creating an easily accessible, integrated toolbox for wildlife movement analysis.

References


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From fine-scale foraging to home ranges: a semivariance approach to identifying movement

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Johnson, D.S., 2013. crawl: Fit continuous-time correlated random walk models to animal movement data.


Table 2.1 Summary of selected R packages

<table>
<thead>
<tr>
<th>Package</th>
<th>Description</th>
<th>Source</th>
<th>Last Updated</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>adehabitatLT</td>
<td>Functions for managing, cleaning, exploring, analyzing, and visualizing animal telemetry data. Additional functions for simulating trajectories with different movement models.</td>
<td><a href="http://cran.r-project.org/web/packages/adehabitatLT/index.html">http://cran.r-project.org/web/packages/adehabitatLT/index.html</a></td>
<td>2015-03-29</td>
<td>Clement Calenge, contributions from Stephane Dray and Manuela Royer</td>
</tr>
<tr>
<td>bcpa</td>
<td>Functions to perform and visualize behavioural change point analysis (bcpa) on animal telemetry datasets</td>
<td><a href="http://cran.r-project.org/web/packages/bcpa/index.html">http://cran.r-project.org/web/packages/bcpa/index.html</a></td>
<td>2014-11-02</td>
<td>Eliezer Gurarie</td>
</tr>
<tr>
<td>trajectories</td>
<td>Functions for managing, cleaning, exploring, and visualizing animal telemetry data</td>
<td><a href="http://cran.r-project.org/web/packages/trajectories/index.html">http://cran.r-project.org/web/packages/trajectories/index.html</a></td>
<td>2015-04-25</td>
<td>Edzer Pebesma, Benedict Klaus</td>
</tr>
<tr>
<td>trip</td>
<td>Functions for managing, cleaning, exploring, and visualizing animal telemetry data</td>
<td><a href="http://cran.r-project.org/web/packages/trip/index.html">http://cran.r-project.org/web/packages/trip/index.html</a></td>
<td>2014-11-05</td>
<td>Michael D. Sumner, Sebastian Luque</td>
</tr>
<tr>
<td>crawl</td>
<td>Functions for analysing, simulating, and visualizing animal telemetry data with Continuous time random walk models (CTCRW).</td>
<td><a href="http://cran.r-project.org/web/packages/crawl/index.html">http://cran.r-project.org/web/packages/crawl/index.html</a></td>
<td>2013-07-26</td>
<td>Devin S. Johnson</td>
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</table>
Table 2.2 Review of packages supporting functions for quantifying pattern

<table>
<thead>
<tr>
<th>Package</th>
<th>Data pre-processing</th>
<th>Analysis Options</th>
<th>Outputs</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>adehabitatLT</td>
<td>• Convert to ltraj object: x/y coordinate pairs + time formatted as POSIX object</td>
<td>• Calculates step length, x-displacement, y-displacement, relative and absolute turning angles, Mean squared displacement, time lag</td>
<td>• Graphical descriptions of changes in movement metrics through time • Distribution of movement metrics • Correlogram • Test statistics for quantifying the independence of movement metrics</td>
<td>Calenge, 2011; Calenge et al., 2009; Djaković et al., 2014; Dray et al., 2010</td>
</tr>
<tr>
<td>Move</td>
<td>• Convert to move object: x/y coordinate pairs + time formatted as POSIX object + projection (requires coordinates in lat/long)</td>
<td>• Calculates step length, step direction, speed, relative turning angle, time lag</td>
<td>• Vectors of calculated movement metrics • Summary statistics of movement metrics</td>
<td>Kranstauber and Smolla, 2014</td>
</tr>
<tr>
<td>bcpa</td>
<td>• Convert to track object: x/y coordinate pairs + time formatted as POSIX object</td>
<td>• Calculates step length, speed, relative and absolute turning angles, time lag</td>
<td>• Vectors of calculated movement metrics</td>
<td>Gurarie, 2013</td>
</tr>
<tr>
<td>trajectories</td>
<td>• Convert to Track object: based on STIDF-class in spacetime package, x/y coordinate pairs + time formatted as POSIX object + projection</td>
<td>• Calculates step length, time lag, speed, direction</td>
<td>• Vectors of calculated movement metrics</td>
<td>Pebesma, 2012</td>
</tr>
<tr>
<td>trip</td>
<td>• Convert to trip object: x/y coordinate pairs in spdf + time formatted as POSIX object + individual identifier</td>
<td>• Calculates step length and turning angle</td>
<td>• Vectors of calculated movement metrics</td>
<td>Soanes et al., 2014</td>
</tr>
</tbody>
</table>
### Table 2.3 Review of packages supporting functions for linking movement to behaviour: trajectory segmentation

<table>
<thead>
<tr>
<th>Package</th>
<th>Data-preprocessing</th>
<th>Analysis Options</th>
<th>Outputs</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>adehabitatLT</td>
<td>• Convert to ltraj object or data frame of time ordered parameter values &lt;br&gt;• Remove missing values</td>
<td>• Lavielle method for trajectory segmentation</td>
<td>• Graphical plot of break points in movement parameter &lt;br&gt;• Plot of segmented trajectory &lt;br&gt;• Graphical plot of contrast function values for determining optimal number of segments &lt;br&gt;• Data frame of contrast function values for different numbers of segments used to select optimal number &lt;br&gt;• Vector of break point values or ltraj object with segments divided into bursts</td>
<td>Barraquand and Benhamou, 2008; Gurarie et al., 2015; Le Corre et al., 2014; Sommerfeld et al., 2013</td>
</tr>
<tr>
<td>bcpa</td>
<td>• Use GetVT() to calculate movement parameters from track object</td>
<td>• Behavioural change point analysis for single or multiple change points</td>
<td>• Model summaries with BIC values &lt;br&gt;• Graphical summaries change points &lt;br&gt;• Data frame summarizing change points and segment characteristics &lt;br&gt;• Data frame summarizing results of WindowSweep() including information on proposed breaks &lt;br&gt;• Graphical summaries of data normality to assess assumptions &lt;br&gt;• Phase plot that shows different segments along a trajectory in relation to movement parameter characteristics</td>
<td>Garstang et al., 2014; Gurarie et al., 2015, 2009; Zhang et al., 2015</td>
</tr>
</tbody>
</table>
Table 2.4 Review of packages supporting functions for linking movement to behaviour: trajectory modelling

<table>
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<tr>
<th>Package</th>
<th>Data pre-processing</th>
<th>Analysis Options</th>
<th>Outputs</th>
<th>References</th>
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<tbody>
<tr>
<td>move</td>
<td>• Convert to move object</td>
<td>• Corridor identification</td>
<td>• Plot of trajectory with corridor movements identified</td>
<td>Kranstauber and Smolla, 2014; LaPoint et al., 2013</td>
</tr>
<tr>
<td></td>
<td>• Corridor identification</td>
<td></td>
<td>• MoveBurst object with a data frame storing values used to identify corridor segments. Burst values identify corridor and non-corridor segments</td>
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<tr>
<td>adehabitatLT</td>
<td>• Convert to ltraj object or data frame of time ordered parameter values</td>
<td>• Gueguen method for trajectory segmentation, first passage time, residence time</td>
<td>• Graphical plot of break points</td>
<td>Calenge, 2011; Eftestøl et al., 2013; Richard et al., 2013; Thiebault and Tremblay, 2013</td>
</tr>
<tr>
<td></td>
<td>• Remove missing values</td>
<td>• Functions for simulating Brownian motion, correlated random walk, levy walk, Ornstein-Uhlenbeck process</td>
<td>• Plots of simulated trajectories</td>
<td></td>
</tr>
<tr>
<td></td>
<td>• Graphical outputs of modelled trajectory and predicted movements</td>
<td></td>
<td>• Ltraj objects of simulated trajectories</td>
<td></td>
</tr>
<tr>
<td></td>
<td>• Summaries of model fit</td>
<td></td>
<td>• Values for mean an variance of first passage time</td>
<td></td>
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<td></td>
<td>• Predicted parameter values for unsampled locations</td>
<td></td>
<td>• Ltraj objects with bursts corresponding to residence time movement segments</td>
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<tr>
<td>crawl</td>
<td>• Data frame with time, x/y coordinates (Latitude, Longitude), X location error, Y location error</td>
<td>• Functions for fitting continuous-time correlated random walk models</td>
<td>• Graphical outputs of modelled trajectory and predicted movements</td>
<td>Johnson, 2013, 2014</td>
</tr>
<tr>
<td></td>
<td>• Values for initial state, drift processes</td>
<td>• Functions for predicting movement at unsampled locations</td>
<td>• Summaries of model fit</td>
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<td></td>
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<td>• List of parameter maximum likelihood estimates</td>
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<td></td>
<td></td>
<td></td>
<td>• Predicted parameter values for unsampled locations</td>
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<td></td>
<td></td>
<td></td>
<td>• Graphical summaries of parameter maximum likelihood estimates with confidence interval</td>
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</tbody>
</table>
Figure 2.1. Flow chart of inclusion criteria for selected R packages
Figure 2.2. Selection of outputs for analysis options available for quantifying movement pattern in the adehabitatLT package. Panels A and B are plots of step length and turning angle distributions for a trajectory, respectively; Panel C is the output plot for the acfdist.ltraj function. Time lags with significance autocorrelation in step lengths are shown as white circles, whereas black squares represent lags with no significant autocorrelation. The grey area represents 95% confidence interval for significance (Clément Calenge et al., 2015); Panel D is a plot output produced by the plotltr function showing the change in step lengths through time.
Figure 2.3. Outputs for Lavielle method of segmentation in adehabitatLT. Top figure shows how the step length time series is broken up into segments with a similar mean value, with red lines indicating breakpoints. The bottom figure displays the same segments, but in terms of their location along the trajectory. Blue triangles represent the beginning of a segment, whereas, red triangles represent the end.
Figure 2.4. Gueguen method of segmentation supported in adehabitatLT. Top panel shows segments characterized by homogenous step lengths, with segments indicated by the red/green/blue horizontal lines. Bottom panel shows segments in terms of their position within the trajectory.
3.0 A spatial autocorrelation-based approach to analyzing wildlife movement patterns in disturbed landscapes: Linking grizzly bear (*Ursus arctos*) near-road movement to survival

3.1 Abstract

Advances in GPS telemetry and remote sensing technologies provide researchers with abundant data that can be used to investigate detailed questions about how disturbance can affect wildlife populations. Existing methods for linking wildlife movement to remotely sensed landscape data generally rely on the application of subjectively derived distance thresholds to represent proximity (i.e., near or far) relative to disturbance, thereby limiting the scope of research questions and insight gained. I develop an alternative method based in semivariogram modelling that quantifies the spatial autocorrelation in movement characteristics as a function of distance to disturbance features. My approach uses movement data to identify spatially explicit ‘zones of influence’. I illustrate the benefits of this with grizzly bear (*Ursus arctos*) movement data and specifically examine how mortality is linked to near road movements. The semivariogram-based method demonstrated consistent in step length (i.e., zones of influence) ranging from 35 m - 90 m from roads but varied by age, sex, and season. Given this pattern, my data suggest a minimum vegetation buffer of 90 m to serve as screening cover along roadsides to improve survival in this ecosystem. More broadly, my generalizable method can identify definitive zones of influence around human disturbance features in any wildlife system, thereby, providing managers with data-driven insight reducing impacts on wildlife in multi-use landscapes.

3.2 Introduction

Understanding how animals move through their environment and the consequences such movement has on survival and reproduction is increasingly important, given ever expanding industrial and recreational activity in landscapes (Buij et al., 2007; Gibeau et al., 2002; Laberee
et al., 2014; Laliberte and Ripple, 2004; Polfus et al., 2011). Some consequences of human activity are direct, like the fragmentation of habitat and wildlife populations through the establishment of infrastructure (Coffin, 2007; Dyer et al., 2002; Fahrig and Rytwinski, 2009; Forman and Alexander, 1998; Proctor et al., 2012). Others are indirect, caused by avoidance behaviours (Ciarniello et al., 2007; Dyer et al., 2002; Northrup et al., 2012; Polfus et al., 2011; Whittington et al., 2005). These behavioral modifications can be subtle, and might require extensive and detailed datasets to detect.

GPS radio tracking techniques have led to an exponential increase in availability of wildlife movement data. Researchers have demonstrated how movement patterns quantified with metrics can be associated with specific behavioural states and the physiology of individual animals (Gurarie et al., 2009; Martin et al., 2012; Nathan et al., 2008; Schick et al., 2008). For example, step length and turning angle, can be linked to a variety of behaviours like foraging, hunting, resting, and dispersal (Fleming et al., 2014; Fortin et al., 2005; Gurarie et al., 2009; Schick et al., 2008; Turchin, 1998). Fleming et al. (2014) used semivariance in velocity to identify different behaviours exhibited by Mongolian gazelles across a range of spatial and temporal scales that were linked to a suite of environmental and physiological influences. In a northern fur seal (Callorhinus ursinus) system, Gurarie et al. (2009) used significant changes in not only the mean and variance, but also autocorrelation of movement data (persistence and turning angle) to demonstrate how animal behaviour can be influenced by environmental and physiological factors.

Remote sensing data are proliferating and leading to new spatial-temporal detail in environmental mapping. Combining high resolution remotely sensed and telemetry data opens up new possibilities for investigating the relationships between wildlife movement patterns, and
ecological processes occurring in a heterogeneous landscape (Cagnacci et al., 2010).

Specifically, researchers now have the opportunity to develop more nuanced hypotheses about the effects of human disturbance on patterns of habitat selection, movement and distribution of wildlife populations. For instance, a key question we can now ask is how the physical environment influences animal movement at fine scales and, with it, mortality and survival.

Several analytical approaches have been used to investigate wildlife-disturbance interactions including step selection functions (Thurfjell et al., 2014), resource selection functions (Houle et al., 2009), Brownian bridges (Sawyer et al., 2009) and utilization distributions (Montgomery et al., 2012). While all of these methods are an effective means of incorporating the effects of human disturbance on movement probability, their focus is on quantifying response in terms of habitat use or selection, rather than changes in movement pattern.

New methods that draw on identifying autocorrelation in movement data can yield new insights into how animals respond to landscapes features, such as human disturbance. Typically, when wildlife movement and habitat selection patterns are quantified in relation to disturbance features, researchers define proximity, or nearness to feature, using a subjective distance threshold. These are referred to as zones of influence within which wildlife behaviour and distribution are assumed to be affected (Gibeau, 1998; Johnson et al., 2005). Generally, distances used to delineate zones of influence range between 50m-3000m in ungulates (e.g., Dyer et al., 2001; Laurian et al., 2008). 500m is commonly applied in the case of grizzly bears (Ursus arctos) (e.g., Berland et al., 2008; Boyce and Waller, 2003; Hood and Parker, 2001). Using subjective thresholds to define proximity can be misleading however, as variation in movement patterns can be obscured when averaged over distances that do not reflect the spatial scale of movement processes. For instance, fine scale movement patterns associated with foraging
behaviours along roadsides could be masked by a threshold applied at a larger spatial scale; foraging movements would be incorporated into a broader group of movements potentially hiding their distinctive signature. Examining spatial autocorrelation in movement can tease apart behavioural modes that occur on different scales to resolve this potential problem.

My goal is to demonstrate a new approach for quantifying wildlife movement patterns relative to road features based on assessing spatial autocorrelation in movement. Specifically, my semivariogram modelling method uses movement data to define zones of influence, thereby obviating subjective distance thresholds to define proximity or response. I illustrate the utility of the semivariogram-based method in the context of quantifying how grizzly bear mortality relates to near road movements in west-central Alberta, Canada. Grizzly bear movement near roads is a particularly important wildlife-landscape interaction to understand as road networks are essential for the development and operation of resource extraction industries (Boulanger and Stenhouse, 2014). However, establishing road networks through undeveloped landscape areas have a number important of ramifications for bear populations (Boulanger and Stenhouse, 2014). Roads facilitate human access to isolated areas of the landscape, which can adversely affect bear populations by increasing the chances of animal-vehicle collisions, and human-bear encounters ending in animal mortality (Benn and Herrero, 2002; McLellan and Shackleton, 1988; Nielsen et al., 2004b; Roever et al., 2008a). Building on the principles of spatial analysis and semivariogram modelling I introduced a quantitative technique for characterizing distances at which bears respond to roads, based on the spatial autocorrelation or similarity in movement metrics. I then reveal how bear mortality can be predicted by variation among individuals in near-road movement characteristics.
3.3 Materials and Methods

3.3.1 Semivariogram-based method for quantifying movement patterns in relation to linear features

I modified a general spatial analysis approach, the semivariogram, to quantify movement patterns relative to physical landscape features. Semivariograms are used to describe spatial dependence structure in a dataset by plotting the squared difference in attribute values between pairs of locations as a function of the distance that separates them (Cressie, 1993). To facilitate interpretation, distance is broken up into a series of lags resulting in a summary of the variance between pairs of values across a range of discrete spatial scales. The spatial dependence pattern can be approximated using a mathematical function fitted to the mean semivariance values for each distance lag. From the shape of fitted semivariogram model, an array of properties can estimated and used to quantify the spatial scales at which autocorrelation occurs. The range is a key the property of semivariograms, as it indicates the distance beyond which there is no spatial dependence among locations (O’Sullivan and Unwin, 2010). While semivariogram modelling is customarily used to inform the weighting values for kriging interpolation, recently it has been applied to wildlife movement data to identify distinct movement patterns associated with shifts in behaviour occurring at varying spatial temporal scales along an animal’s movement pathway (Fleming et al., 2014).

To detect spatial autocorrelation in movement patterns in relation to linear features, I adapted the conventional semivariogram to compare the variance in movement characteristics as a function of distance to linear feature, rather than as a function of the distance between locations (Figure 1). Using the variation in movement indices relative to distance from feature, provides a representation of how similarity in movement patterns changes with proximity to specific
landscape features. My assumption is that if movement patterns are similar at a certain distance from a specified feature, that feature is likely influencing movement. However, if movement patterns are variable relative to the feature at a certain distance, then the feature is no longer having an influence on behaviour. The variability of movement pattern within each distance lag are summarized at that distance using the coefficient of variation (CV). Low CV values represent homogeneity in movement pattern, and high values represent heterogeneity.

I fit mathematical functions to the movement characteristic semivariograms using non-linear least squares to quantify the scales at which spatial autocorrelation is present (Figure 1). Similar to conventional semivariograms, the shape of the function approximates the spatial dependence structure present, and can be used to determine the range of spatial dependency (Cressie, 1993). I evaluated the performance of the curves (i.e. models) using Akaike Information Criterion (AIC), and model selection is based on the lowest AIC scores.

Within the context of my semivariogram-based method, the range represents the spatial scale at which autocorrelation in a movement pattern is the strongest relative to a particular linear feature (Figure 1). In other words, the range of spatial dependence corresponds to the zone of influence around a linear feature where wildlife are responding to that feature’s presence as evidenced by consistent movement characteristics. The range is determined by the cumulative sum of differences between the slope value for a given lag, and the average slope value across all lags. The maximum cumulative sum value is selected to delineate the zone of influence because it identifies the distance at which the trend in CV changes from increasing to constant random.
3.3.2 Application to data: Mortality in relation to near-road movements

The Kakwa and Yellowhead regions of west-central Alberta are located in the eastern foothills of the Rocky Mountains. They consist of multi-use landscape supporting both recreational and extensive resource-extraction activities. Although resource extraction industries (e.g. oil & gas, forestry, mining) have been active in the area since the 1950s, they have intensified over the last two decades (Laberee et al., 2014; White et al., 2011). Fire-suppression has reduced the occurrence of natural openings in the landscape, so disturbance has become the largest driver of landscape change in the area (Stewart et al., 2012b) (Figure 2).

I obtained movement data for grizzly bears from 2001 to 2013 as GPS collar locations collected by the Foothills Research Institute Grizzly Bear Project. Bears were captured and collared through the use of leg snaring, aerial darting and culvert traps following the accepted protocols set out by the Canadian Council of Animal Care for the safe handling of bears (Animal Use Protocol Number 20010016). Captured bears were fitted with one of three different collar types: Tellus/Followit GPS collars, ATS GPS, or Televit GPS collars. Followit GPS satellite collars were used from 2011-2013. The Tellus/Followit collars were programmed to record locations every hour, while the Televit and ATS collars recorded locations every four hours (Graham and Stenhouse, 2006) (Table 1). Telemetry points with positional dilution of precision values (PDOP) greater than ten were removed to reduce positional accuracy errors. A PDOP limit of ten was selected for this project as D’Eon and Delpart (2005) found that it effectively removed outliers created by positional accuracy errors while minimizing data reduction, thus avoiding the introduction of systematic bias into the analysis through the removal of large numbers of locations.
Grizzly bear movement data were divided according to season, and demographic profiles (Table 1). Seasons were defined based on the breeding season: breeding (Den emergence-July 15), and non-breeding (July 16-September 30) (Benn and Herrero, 2002; Chruszcz et al., 2003; Gibeau et al., 2002; Stenhouse et al., 2005). Movement data within the seasonal categories were then partitioned by bear sex and age, resulting in four datasets per season: adult female, adult male, sub-adult female, sub-adult male. Bears were considered to be sub-adults if they were less than 5 years old.

I chose to illustrate the utility of my semivariogram-based method in the context of grizzly bear movement patterns in relation to roads, as the impacts of roads on grizzly bear mortality, habitat selection, and behavior have been well documented (Benn and Herrero, 2002; Northrup et al., 2012; Roever et al., 2008a). I applied my semivariogram-based method to identify seasonally specific zones of influence, meaning the areas in which a bear’s movements are impacted by the presence of a road, by grizzly bear age and sex. The resulting zones of influence were used to partition GPS data, and movement in and out of these zones were correlated to collared bear survival and mortality with near-road movements.

Movement patterns were assessed using step length. Step length was calculated as the Euclidean distance between successive locations using the R package adehabitatLT, and log transformed to approximate a normal distribution (Calenge, 2011a). Step length was selected to characterize movement pattern because it is often used to link movement to behaviour (e.g., Beyer et al. 2013; Eftestøl et al. 2013; Turchin 1998). For instance, long step lengths in grizzly bears have been associated with travelling or searching, whereas short step lengths have been associated with foraging or resting (Blanchard and Knight 1991, Roever et al. 2010, Graham and Stenhouse 2014). Variation in movement patterns were calculated for five meter distance lags up to a
maximum of 1000m from roads. Only lags with 15 or more samples were used to ensure a representative characterization of movement at that distance.

When calculating distance to the nearest road feature, the telemetry data and road features were linked by year to ensure that the calculated distances reflected the physical landscape as accurately as possible. The yearly road network datasets were created from the Alberta Environment and Sustainable Development base features dataset, and were updated by digitizing high spatial resolution SPOT imagery (5 m resolution) and air photos.

To examine the relationship between near-road movements and grizzly bear mortality, the identified zones of influence were applied to compare movement patterns between bears that were killed (n = 8 bears) those that survived through the foraging season (i.e., breeding and non-breeding periods combined; n = 28 bears)(Table 1). The leading cause of death was illegal kills (n = 5), followed by bear-human conflict kill (n = 1). Two bears died of unknown causes, however, I suspect their deaths were also human-related. The distribution of step lengths near roads and the timing of near road movements were compared between groups to examine whether variation in near-road movement might relate to mortality. Sub-adult females were omitted from this analysis due to the lack of data in human-related mortality. The sample size for killed adult males during the non-breeding season was also too small to be included (n = 1 bear) (Table 1).

I used a similar approach to examine whether variation in step length existed between bears that survived and those that were killed. To evaluate the distribution of step lengths near roads, proximity was again determined using the zones of influence. Box-plots for each age/sex class were constructed for step lengths close to roads, and the distributions compared using a Mann-Whitney U test.
Finally, I also examined the potential relationship between timing of near-road movements and mortality. I first assigned each GPS location a time of day category (Day, Night, and Twilight). Time of day was determined using a method developed by the Foothills Research Institute Grizzly Bear Project based on sunset/sunrise tables from the National Research Council of Canada (Government of Canada, 2014). Locations were defined as twilight, if sunrise or sunset occurred within their four hour interval. The amount of time spent near roads by time of day was determined by summing the number of locations that occurred within the zone of influence for each of the three categories. The resulting count data were then organized into a 3 x 2 contingency table with columns indicating mortality (Survived vs. Killed) and rows indicating time of day (Day vs. Night vs. Twilight). The counts were compared using a Chi-squared test for independence with the null hypothesis that mortality is independent of time spent nears roads across time of day categories.

3.4 Results

Semivariograms indicated that the association between movement patterns and proximity to roads varied by season, age, and sex (Table 2). For adult and sub-adult females, the spatial scale of response was finer, with dominant spatial autocorrelation at short distances, during the non-breeding season (35m and 25m respectively) than during the breeding season (90m and 80m respectively). In contrast, adult and sub-adult males demonstrated a consistent response to roads between the seasons, with the zone of influence for males remaining constant at 55 m, and decreasing slightly by five meters for sub-adult males (from 75 m to 70 m) (Table 2).

Using the zone of influence to define nearness to roads, significant differences in step lengths related to mortality for adult females, and sub-adult males were observed (Figure 3). During both seasons, females that were killed displayed significantly longer step lengths near roads than bears.
who survived. For example, the median step length during the breeding season for killed bears was 886 m, while only 477 m for survivor bears (P = 0.00). The difference between the groups was more pronounced during the non-breeding season with median step lengths of 1547 m, and 500 m respectively (P = 0.00). Sub-adult males likewise showed similar differences between groups but only during the non-breeding season with killed bears having longer median step lengths (1666 m vs. 818 m, P = 0.00)(Table 3, Figure 3). No significant difference in step lengths related to mortality were observed for adult males, although step lengths for killed bears was shorter as compared to bears who survived (1088 m vs. 2031 m, P = 0.10)(Table 3, Figure 3).

How near-road movements influenced mortality depended on time of day, but patterns differed among demographic groups. Patterns were most pronounced for adult and sub-adult males during the breeding season and adult females during the non-breeding season. During the breeding season, adult and sub-adult male bears that were killed spent more time moving around roads during the day than expected (Observed vs. Expected: Adult Males 34% vs. 26%, Chi squared = 6.40, P = 0.04; Sub-adult Males 43% vs. 30%, Chi squared = 13.31, P = 0.00), and bears who survived spent more time moving around roads at night than expected (Observed vs. Expected: Adult Males 51% vs. 41%, Chi squared = 6.40, P = 0.04; Sub-adult Males 46% vs. 38%, Chi squared = 13.31, P = 0.00) (Figure 4). In contrast, for adult females, I observed that mortality appeared to be independent of time spent moving nears roads across time of day categories (Chi squared = 3.25, P = 0.20). Conversely, in the non-breeding season, female bears that were killed spent more time moving around roads during the day than expected (Observed vs. Expected: 49% vs. 27%, Chi squared = 11.90, P = 0.00), and bears who survived spent more time moving around roads at night than expected (Observed vs. Expected: 35% vs. 32%, Chi squared = 13.31, P = 0.00) (Figure 4); while, sub-adult males demonstrated no significant
relationship between mortality and the timing of near road movements (Chi squared = 1.23, P = 0.54)

3.5 Discussion

Using a semivariogram-based method for quantifying wildlife movement patterns in relation to disturbance features, I quantified different spatial scales at which roads influenced grizzly bear step lengths. Movement patterns result from unmeasurable environmental and biological processes that are the expression of behaviours affecting survival and reproduction. The spatial patterns observed from telemetry data represent these cryptic spatial processes. Consistent patterns indicate processes are not random, and provide evidence for developing hypotheses about the biological and ecological processes influencing wildlife movement. When movement patterns are structurally different relative to landscape features I can refine my hypotheses. For instance, Dickson et al. (2005) observed that cougar movement rates varied with vegetation type and hunting/travelling movement pathways were consistently associated with less rugged terrain like valley bottoms or gentle slopes. Insight into the spatial-temporal variation in cougar movement patterns relative to topography and vegetation type could be used to improve hypotheses regarding the effect of anthropogenic disturbance on cougar populations, and to parameterize more complex movement models (Dickson et al., 2005).

My semivariogram-based method improves upon the use of subjective thresholds by using a pattern based approach to identify the spatial scales at which animal movement is influenced by a particular feature. Pattern approaches use changes in movement pattern to infer changes in the underlying processes influencing an animal’s movement (Getis and Boots, 1978). Specifically, by quantifying autocorrelation in patterns relative to feature proximity, I are able to identify spatially explicit, local zones of influence by species and feature type. Wildlife management is
operationalized at the landscape level (e.g., Sawyer et al., 2009), so analytical methods for
determining situationally specific zones of influence can be used to support land-use planning
decisions aimed at mitigating the effects of anthropogenic features on wildlife populations. Data-
driven approaches, such as the semivariogram-based method, can facilitate the decision making
process since they allow data to speak for themselves resulting in a localized measure of
variation in movement pattern that can be visualized as a map (Hebblewhite and Haydon, 2010).
Local methods for identifying variation in movement patterns are valuable, as changes in pattern
across space or between individuals can be easily conceptualized in context of biological or
environmental processes (Long and Nelson, 2013a). For example, in the context of grizzly bear
movement patterns, my semivariogram-based method revealed that individual bears varied in
how they moved around roads according to their age and sex, and the time of year. All of the
semivariogram-derived zones of influence were narrower than the standard 500 m, emphasizing
the limitations of representing proximity as a subjectively selected threshold: individual variation
can be masked, and threshold selection acts as a determinant of pattern rather than vice-versa.
With these spatially and temporally localized results, variation in movement patterns can be
contextualized with other environmental factors like terrain, food availability, or disturbance
density to further examine the relationship between grizzly bears, and the presence of roads
(Nelson and Boots, 2008; Nelson et al., 2009).

Habitats in proximity to roads can act as primary sinks or ecological traps for grizzly bears as
they represent high-risk, high-quality habitats (Bourbonnais et al., 2013; Ciarniello et al., 2007;
Nielsen et al., 2006); however, despite this trade-off for individuals and populations, information
about the distances or spatial scales at which bears’ behaviour is impacted by roads is still
limited. In earlier work, mortality was evaluated in relation to both landscape characteristics and
anthropogenic landscape features either by examining where the mortalities occurred, or by predicting probability of bear occurrence using resource selection functions (McLellan et al. 1999, Benn and Herrero 2002, Nielsen et al. 2004b, Nielsen et al. 2010). While each study emphasized the link between mortality risk and human access, the relationship between movement characteristics and mortality were not considered. Chruszcz et al. (2003), Roever et al. (2010), Graham et al. (2010), and Northrup et al. (2012) took a more movement orientated approach to describe the relationship between grizzly bears and human access by examining the spatial temporal patterns of near-road movements. In these studies, authors discussed their results in terms of behavioural responses to roads and mortality risk; however, the link between near-road movement patterns and mortality or survival was not quantitatively established.

By applying my semivariogram-based method I were able to quantify how the influence around roads varied by season, bear reproductive status, and bear sex. I showed objectively that the timing of near-road movements and step length are useful metrics for linking movement to grizzly bear mortality and survival. Noting significant differences for both metrics in relation to mortality, my approach illustrates that the inclusion of these metrics in mortality analyses could provide additional means of evaluating the response of grizzly bear populations to continuing road development. Interactions with roads are particularly fine scaled, especially during the non-breeding season when the presence of berries along roadsides and in cut blocks has been associated with increased patterns of habitat selection around roads across all age/sex classes (Nielsen et al. 2004a, Roever et al. 2008b, Stewart et al. 2013).

I observed that the timing of near road movements was linked to grizzly bear survival and mortality. During both seasons, females who survived spent more time moving near roads at night than expected, while females who were killed performed the majority of their near-road
movements during the day. However, this trend was far more pronounced during the non-breeding season. Adult and sub-adult males showed a similar trend, however, this trend was only observed during the breeding season. For bears, it is likely less risky to move near roads during times of low human use (night), than during peak hours as the chances of encountering humans are much lower. However, bears that are more behaviourally-inclined to accept risk, are less wary around humans, or who are under stress may be less risk adverse and willing to move along roadsides during the day (Bourbonnais et al., 2013; Mattson et al., 1992). Roever et al. (2010) suggested bears make use of roads at night as travel corridors between cut blocks containing berries to avoid the high traffic volumes present on roads during the day.

Applying the semivariogram derived zones of influence highlighted the difference in the variation in step length with mortality when bears were interacting with roadside habitats. Roever et al. (2010) noted longer step lengths near roads and suggested it was in response to reducing the amount of time spent in risky near-road areas. While Graham et al. (2012) and Chruszcz et al. (2003), both noted age/sex differences in time spent near roads and suggested that it could lead to unequal mortality risk amongst demographic groups. Accordingly, both these and many authors suggest restricting human access into bear habitats through seasonal road closures under these conditions to reduce human-related mortality risk (Graham et al., 2010; Nielsen et al., 2004b; Northrup et al., 2012; Roever et al., 2010). I observed larger median step lengths for both adult females and sub-adult males that were killed, suggesting that bears vulnerable to human-related mortality are moving along roadsides and are covering greater distances looking for either carrion or vegetation; thus increasing their chances of human interaction. I identified the coarsest scale of response by grizzly bears to roads was 90 m. Accordingly, I can recommend that a minimum vegetation buffer of 90 m is required to provide sufficient cover along roadsides.
to improve grizzly bear survival in west-central Alberta. My zone of influence approach supports the previous recommendations with new detail, highlighting the variation in spatial-temporal patterns of near-road movements and providing information about when specific demographic groups of bears are more likely to be active in risky roadside habitats.

3.6 Conclusion

Our semivariogram–based method provided an alternative means of defining proximity, one based on the spatial scales at which consistency in movement patterns is observed in relation to anthropogenic disturbance features. It emphasizes the spatial-temporal variation in movement patterns using a pattern-based approach to define proximity, thus supporting the development of more complex ecological questions regarding animal movement. The identified zones of influence can be used to facilitate the integration of telemetry and landscape data by refining parameters in step selection or resource selection functions, or by guiding a more in depth analysis of the processes influencing animal behaviour relative to specific features.

Understanding the complex relationship between anthropogenic disturbance, movement patterns, and survival is crucial for implementing effective management strategies for minimizing the negative impacts of human activity on wildlife populations. In the context of grizzly bear movement patterns relative to roads, some management strategies may include retaining or creating the appropriate width and placement of vegetation buffers to increase concealment cover along roadways, or the correct timing and location of seasonal road closures is directly supported by the spatially explicit zones of influence derived from my semivariogram-based method. My semi-variogram method provides a data-driven approach for quantifying variation in pattern improving my ability to ask and answer questions regarding the spatial scales at which animals are perceiving specific disturbance features, and altering their movement patterns in response.
The spatially localized results can capture a variety of responses by wildlife to human related disturbance, and can be used to inform management policies required for a balance to occur between human use of wildlife habitats and the long term survival of wildlife species.

References


Table 3.1. Summary of grizzly bear telemetry datasets for linking mortality and near-road movement. Values in brackets indicate the total sample size for each group. Data were re-sampled to 4-hour intervals.

<table>
<thead>
<tr>
<th>Survival Status</th>
<th>Pre-berry</th>
<th>Berry</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Adult female</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survived</td>
<td>8 unique bears, 12 datasets (1,990)</td>
<td>8 unique bears, 12 datasets (2,555)</td>
</tr>
<tr>
<td>Killed</td>
<td>4 unique bears, 4 datasets (854)</td>
<td>3 unique bears, 3 datasets (377)</td>
</tr>
<tr>
<td><strong>Adult Male</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survived</td>
<td>3 unique bears, 6 datasets (708)</td>
<td>3 unique bears, 6 datasets (708)</td>
</tr>
<tr>
<td>Killed</td>
<td>2 unique bears, 2 datasets (367)</td>
<td>1 unique bear, 1 dataset (447)</td>
</tr>
<tr>
<td><strong>Sub-adult Male</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survived</td>
<td>3 unique bears, 5 datasets (575)</td>
<td>3 unique bears, 5 datasets (1093)</td>
</tr>
<tr>
<td>Killed</td>
<td>3 unique bears, 3 datasets (274)</td>
<td>2 unique bears, 2 datasets (397)</td>
</tr>
</tbody>
</table>
Table 3.2. Summary of zone of influence distances identified by the variogram-based method by season, and bear age/sex group.

<table>
<thead>
<tr>
<th>Season</th>
<th>Age, Sex</th>
<th>Range</th>
<th>Function</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult Female</td>
<td>90 meters</td>
<td>$Y \sim a + b/X^{0.5}$</td>
<td>-871.82</td>
</tr>
<tr>
<td></td>
<td>Sub-adult Female</td>
<td>80 meters</td>
<td>$Y \sim a + b/X^{0.5}$</td>
<td>-540.69</td>
</tr>
<tr>
<td></td>
<td>Adult Male</td>
<td>55 meters</td>
<td>$Y \sim a + b/X$</td>
<td>-656.31</td>
</tr>
<tr>
<td></td>
<td>Sub-adult Male</td>
<td>75 meters</td>
<td>$Y \sim a + b/X^{0.5}$</td>
<td>-519.67</td>
</tr>
<tr>
<td>Berry</td>
<td>Adult Female</td>
<td>35 meters</td>
<td>$Y \sim a + b/X^{1.5}$</td>
<td>-785.38</td>
</tr>
<tr>
<td></td>
<td>Sub-adult Female</td>
<td>25 meters</td>
<td>$Y \sim a + b/X^2$</td>
<td>-618.26</td>
</tr>
<tr>
<td></td>
<td>Adult Male</td>
<td>55 meters</td>
<td>$Y \sim a + b/X$</td>
<td>-678.72</td>
</tr>
<tr>
<td></td>
<td>Sub-adult Male</td>
<td>70 meters</td>
<td>$Y \sim a + b/\log X$</td>
<td>-654.41</td>
</tr>
</tbody>
</table>
Table 3.3. Comparison of median step lengths in meters by age/sex group for pre-berry and berry seasons using both methods for defining proximity. Significance (*) was determined using a two-sided Mann-Whitney U test at P=0.05.

<table>
<thead>
<tr>
<th>Age, Sex</th>
<th>ZOI</th>
<th>P-value</th>
<th>Mortality</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pre-Berry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Female</td>
<td>90 meters</td>
<td>0.002*</td>
<td>Survived: 477.41</td>
<td>103</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 886.27</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>500 meters</td>
<td>0.002*</td>
<td>Survived: 261.20</td>
<td>402</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 591.62</td>
<td>167</td>
</tr>
<tr>
<td>Adult Male</td>
<td>55 meters</td>
<td>0.101</td>
<td>Survived: 2031.87</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 1088.00</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>500 meters</td>
<td>0.389</td>
<td>Survived: 555.83</td>
<td>139</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 843.74</td>
<td>72</td>
</tr>
<tr>
<td>Sub-adult Male</td>
<td>75 meters</td>
<td>0.270</td>
<td>Survived: 826.32</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 1537.00</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>500 meters</td>
<td>0.886</td>
<td>Survived: 730.27</td>
<td>132</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 633.80</td>
<td>78</td>
</tr>
<tr>
<td><strong>Berry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Female</td>
<td>35 meters</td>
<td>0.003*</td>
<td>Survived: 500.51</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 1547.08</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>500 meters</td>
<td>0.000*</td>
<td>Survived: 270.77</td>
<td>548</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 1261.37</td>
<td>91</td>
</tr>
<tr>
<td>Sub-adult Male</td>
<td>70 meters</td>
<td>0.004*</td>
<td>Survived: 818.73</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 1666.00</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>500 meters</td>
<td>0.000*</td>
<td>Survived: 556.71</td>
<td>213</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Killed: 1303.00</td>
<td>80</td>
</tr>
</tbody>
</table>
Figure 3.1. Illustration of variogram based method. (Top) Distribution of a particular movement characteristic by distance lag relative to disturbance feature. Trends in pattern are hard to distinguish using boxplots, so the movement characteristics in each lag are summarized to a single value using the coefficient of variation. (Bottom left) A mathematical function is fit to the variogram to approximate the spatial dependence structure. (Bottom right) Range is determined using the cumulative sum differences to the mean. The maximum cumulative sum value is selected as the range distance.
Figure 3.2. Kakwa and Yellowhead study areas in west-central Alberta, Canada displaying the distribution of GPS bear locations, and the combined extent of the road network for 2005-2013.
Figure 3.3. Flow chart detailing the analysis approach for determining the zone of influence associated with roads for grizzly bear age/sex group by season. The width of the age/sex/season specific zones of influence were identified from the range calculated from the variograms. The variograms were built from the coefficient of variance in step lengths for five meter intervals ranging from 5 to 1000 meters from roads.
Figure 3.4. Comparison of step lengths near roads in relation to mortality for the pre-berry and berry seasons. Proximity to roads was determined using variogram-based method (Females: 90 meters pre-berry, 35 meters berry, Males: 55 meters pre-berry, Sub-adult male: 75 meters pre-berry, 70 meters berry), and using the standard 500 meters. Significance (*) was determined using a two-sided Mann-Whitney U test at P=0.05
Figure 3.4 Proportion of time spent near roads in relation to mortality and time of day for the breeding and non-breeding seasons. Proximity to roads was determined using semi variogram-based method (Females: 90 meters breeding, 35 meters non-breeding, Males: 55 meters breeding, Sub-adult males: 75 meters breeding, 70 meters non-breeding. Significance (*) was determined using a Chi-squared test at $P=0.05$. 
4.0 CONCLUSION

4.1 Discussion and Conclusions

Owing to the availability of high resolution wildlife movement and environmental datasets, the potential for more detailed investigations around wildlife movement-environment interactions has been highlighted several times (e.g., Breed et al., 2012; Cagnacci et al., 2010; Dodge et al., 2013; Fryxell et al., 2008; Neumann et al., 2015). Accessible methods for integrating the two data sources have lagged behind technological advances, resulting in untapped data potential and research question limitations in wildlife movement analysis (Breed et al., 2012). While a variety of methods have been used to relate wildlife movement to landscape features (e.g. Brownian bridges, step selection functions, resource selection functions, utilization distributions), these methods quantify movement in terms of habitat selection, rather than variation in movement parameters (Horne et al., 2007; Stafford et al., 2006; Thurfjell et al., 2014). Methods that do quantify movement using descriptive parameters often apply subjective thresholds to define proximity to feature, possibly limiting the relevancy of their results (Berland et al., 2008; Dyer et al., 2002; Laurian et al., 2008).

Developing analytical approaches for linking movement patterns to the physical environment has become increasingly important, as human activities are continuing to expand into wildlife habitats (Gibeau et al., 2002; Laberee et al., 2014; Polfus et al., 2011). Methods for quantifying wildlife movement patterns relative to disturbance features are particularly desirable, as spatially explicit information on wildlife responses to disturbance can be used to direct management strategies in multi-use landscapes. For example, considerable research has examined the effect road features on patterns of habitat selection (Roever, 2006; Stewart et al., 2013), mortality (Benn and Herrero, 2002; Nielsen et al., 2004b), and behavior (Beyer et al.,
2013; Laurian et al., 2008); however, there remains a gap in my knowledge regarding the spatial scales at which these interactions are occurring, and how movements at these given distances affect survival.

The goal of this research was to develop a data-driven approach for quantifying grizzly bear movement patterns relative to roads, and to examine the link between near-road movement patterns and survival. To meet the research goal, two objectives were addressed: 1) a review of existing tools for conducting movement analysis was performed to highlight any existing methodological opportunities and limitations associated with relating movement to landscape features; and 2) a data-driven approach to quantify the spatial scales of wildlife movement response to linear features was developed and applied to quantify how grizzly bear near-road movements affect mortality and survival.

In Chapter 2, I reviewed R packages for wildlife movement analysis, with the specific aim of identifying opportunities and challenges in quantifying wildlife movement-environment interactions. R packages specifically designed for wildlife movement are useful in that they provide integrated toolboxes to perform exploratory analyses. Exploratory analyses are an important step in wildlife movement analysis, as they can be used to formulate more specific questions about the processes influencing movement. R’s strongest analytical capabilities were related to approaches for quantifying pattern. AdehabitatLT offered the widest variety of parameters, as well as, options for quantifying dependence structures within the trajectory, and graphical representations of parameter changes through time. However, despite R’s strengths, there were no analytical options to integrate movement analysis with other ancillary datasets. A key opportunity for movement methods research is to develop approaches that integrate wildlife movement and environmental data; however, the analytical and technical challenges of
integrating two disparate data types must be first be resolved. I suggest data-driven approaches, which take advantage of autocorrelation inherent in high resolution telemetry datasets, as a possible approach for overcoming these challenges. Patterns of spatial autocorrelation in movement parameters, such as step length, can be quantified to create a direct link between wildlife movement and landscape features.

In Chapter 3, I presented a new data-driven method, based on semivariogram modelling, for quantifying wildlife movement patterns relative to linear features. Methods for linking wildlife movement to remotely sensed landscape data are in short supply, with some approaches relying on subjective distance thresholds to define proximity to feature (Berland et al., 2008; Boyce and Waller, 2003; Dyer et al., 2001; Laurian et al., 2008). The method quantifies the spatial autocorrelation in movement parameters, as a function of distance to disturbance features, to create spatially explicit ‘zones of influence.’ The method is based on the assumption that when movement patterns are homogeneous at a given distance relative to a disturbance feature, that feature’s presence is likely influencing wildlife movement. Conversely, if movement patterns are heterogeneous at a given distance, that feature is no longer having an effect. I used my data-driven method to quantify the spatial autocorrelation in grizzly bear step lengths, as a function of distance to roads, to identify the spatial scales at which movement patterns demonstrated persistence. I observed consistent movement patterns ranging from 35 meters-90 meters from roads depending on bear age, sex, and season. Adult females demonstrated both the coarsest and finest scales of response to roads among the four demographic groups. During the breeding season, adult female step lengths were consistent up to 90m from roads, however, the distance narrowed considerably to 35m during the non-breeding season. As females have been observed to select for roadside habitats more than males (Boulanger and Stenhouse, 2014; Graham et al.,
identifying zones of influence particular to females provides managers with specific information for reducing the impacts of human-related mortality on grizzly bear populations. Using this information, more informed land-use decisions regarding seasonal road closures, or a minimum width of 90 meters for vegetation buffers along roadsides can be recommended to ensure the health of grizzly bear populations in multi-use landscapes.

Based on the zones of influence defined using the semivariogram based method, I also examined near-road movement patterns in terms of bear mortality and survival. In general, I observed that bears that were killed exhibited riskier near-road movements than bears who survived. For example, bears who were killed moved more frequently around roads during the day than expected, and had longer median step lengths. Longer step lengths near roads suggest that bears are more vulnerable to human-related mortality when covering greater distances in roadside habitats due to an increased chance of human interaction. Their chances of mortality are further compounded, if their near-road movements occur during daylight hours, as human activity is at its peak during the day (Graham et al., 2010; Roever et al., 2010). Bourbonnais et al. (2013) suggest that food-rich roadsides may make bears more willing to move through risky habitats in order to secure resources, and habituation may cause bears to be less-wary and inclined to move along roads during the day. Accordingly, evaluating how near-road movements influence mortality and survival can lend support to management initiatives, like seasonal road closures, by highlighting when specific demographic groups are more likely to be active along roadways.

4.2 Research Contributions

The first major contribution of this research is an overview of the strengths and weaknesses of conducting wildlife movement analysis using the R statistical platform,
specifically when investigating movement-environment interactions. The wide range of R packages available can involve long hours of searching for the most suitable analytical tool. Combing through R package reference manuals and documentation can be an overwhelming task, as they are often written from a methods-based perspective. For applied researchers, a guide that outlines the analytical capabilities of each package would facilitate a more efficient selection of the appropriate tool without having to decipher every methodological detail. I provide a brief overview of tools according to three common analytical approaches: quantifying movement pattern, linking movement to process and behaviour via trajectory segmentation, and linking movement to process and behaviour using models.

The review also contributes to the discussion around the methodological and technical challenges of linking wildlife movement data to environmental variables. I propose that data driven methods, like the semivariogram-based approach, could offer an analytically intuitive method of overcoming these challenges. Data-driven methods utilize spatial and temporal autocorrelation in movement parameters to create links between movement patterns and underlying movement processes. Applying data driven approaches reduces the number of subjective decisions within analysis workflows, generating more pertinent relationships between wildlife movement and environmental conditions.

The third major contribution of this research was the development of a data-driven method for quantifying wildlife movement patterns in relation to linear features. Quantifying the spatial scale of response by wildlife to disturbance, without the use of subjective thresholds, is a significant contribution to the fields of wildlife conservation and management, ecology and biology, and emphasized the utility of pattern based –approaches in wildlife movement analysis. Using subjective thresholds can limit the relevancy of an analysis, as variation in movement
patterns can be masked when movements are averaged over distances that do match the spatial scales of underlying processes (Benn and Herrero, 2002; Berland et al., 2008; Hood and Parker, 2001). The semivariogram-based method addresses these limitations by supplying a spatially explicit measure for movement pattern variation based on consistency in movement parameters as a function of distance to feature. Quantifying consistency in movement pattern relative to landscape feature exploits the autocorrelation present in high density telemetry datasets, and allows the data to “speak for themselves” creating a direct link between wildlife movement and the movement processes associated with anthropogenic landscape change.

The final major contribution of this research is a quantitative assessment of how near-road movement patterns are linked to mortality and survival. Although the effects of roads on grizzly bear habitat selection, mortality, and behavior are well documented, there remains a gap in our knowledge regarding the spatial scales at which these interactions are occurring, and how movements at these given distances affect survival. I was able to show that grizzly bear responses to roads varied by demographic group and season, and in each case, the scale of response was narrower than the previously suggested 250m or 500m thresholds. Building on these zones of influence, I was able to link the timing and step-lengths of near-road movements to grizzly bear survival and mortality. The results of my analysis contributed new insights into the spatial-temporal relationships between near-road movement patterns and their impact on survivorship. Understanding the complex relationship between roads, movement patterns, and survival is crucial for implementing effective management strategies. My results can be used to support previous suggestions around seasonal road closures (Boulanger and Stenhouse, 2014; Graham et al., 2010; Northrup et al., 2012; Roever et al., 2010), and suggest that a minimum
90m vegetation buffer along roadways could be implemented to minimize the negative impacts of roads on grizzly bear populations.

4.3 Research Opportunities

The methods and findings in this thesis present many new insights in wildlife movement analysis that could be used to formulate more complex research questions around animal movement in disturbed landscapes. High density movement datasets have been collected for a range of species including wolves (Latham et al., 2011), ungulates (Dettki et al., 2004; Dussault et al., 2007), and cougars (Dickson et al., 2005). The construction of road networks through undeveloped landscape areas affects all wildlife species; as such, it would be interesting to apply my semivariogram-based method to quantify the zones of influence around road features for multiple species occupying the same geographical area. The semivariogram-based method uses universal movement parameters, like step length, to quantify movement; therefore, zones of influence would be easily and directly comparable across species to implement more comprehensive land use decisions, and management strategies.

Although my results for grizzly bear zones of influence varied by demographic group and season, it would be interesting to evaluate zones of influence in terms of fluctuations in vehicle traffic. Roever et al. (2008) and Northrup et al. (2012) both demonstrated that vehicle traffic impacts patterns of grizzly bear movement and habitat selection. Building on their results, zones of influence could be created for high volume and low volume roadways, to assess the variation in movement response in terms of traffic load. Understanding the relationship between wildlife movements and road characteristics, could be used to inform wildlife initiatives focused on highways or popular recreation destinations that experience more traffic than industrial road networks.
From an analytical perspective, it would be interesting to create a multivariate version of the semivariogram-based method. Currently, zones of influence are quantified using spatial autocorrelation in only one parameter, step length. The addition of an angular parameter, like turning angle, would permit the delineation of response based around more complex patterns of movement. Including a parameter that could be used to quantify the direction of movement relative to roads would also be useful, as it may create spatially explicit zones of influence that could be classified in terms of attraction or aversion.

The granularity of movement data affects the distribution of step lengths and turning angles observed within a trajectory. Since movement parameters are dependent on the time elapsed between fixes, it would be informative to test how zones of influence calculated using the semivariogram based-method varied with sampling interval. Understanding how patterns of spatial and temporal autocorrelation in movement parameters change in response to sampling would help researchers select a fix rate appropriate for their research goals when deploying tracking devices for data collection.


