Animal Selection and Movement Analysis: Finding Missed Connections

by

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Abstract

In movement ecology, many methods currently exist for analyzing and estimating animal movement patterns and selection for habitat types. However, the accuracy of the estimates for quantifying animal movement and selection are difficult to determine, especially when data is missing. In the literature, there are many techniques for simulating animal movement and determining animal selection, yet they are rarely used in tandem and, instead, simpler methods are favoured. In this study, we use continuous-time animal movement to estimate selection in the presence of missing data. We first determine a model for continuous-time animal movement with influence of the environment on the selection of location as a small time-step limit of a step-selection process. Second, we propose an algorithm that uses the continuous-time model to fill in missing locations, and determines estimates for the movement and selection coefficients. The estimates are compared directly against existing methods for determining the selection coefficients. For data sets with extensive loss of information, the proposed algorithm could provide more accurate estimates for animal selection of environmental characteristics.

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Chapter 1

Introduction

Ecology is the study of processes affecting populations and individuals of organisms over space and time [8]. Two key features in ecology are the ability of an organism to move and the driving forces behind that movement. The study of movement ecology gives insight to the influences, mechanisms, and spatiotemporal patterns of animal movement as well as how these factors play into an animal's life processes and species dynamics [7], [52]. Movement ecology of individuals is prevalent in the study of animals, and composes approximately 8% of articles in ecology, evolution, behavioural science, and environmental science journals from 1997-2006, with an expectation to increase further [31]. Animal movement data, by itself, can help identify links between behaviour, landscape ecology and population dynamics [32], [35]. By quantifying habitat use, we can more easily assess biological requirements, the impact of environmental changes due to habitat loss and climate change, identify key habitat areas, and control the spread of invasive species or diseases [3], [52], [59].

The science of movement ecology has developed rapidly [31] and is expected to continue this increasing trend due to technological advancements [18], [22]. The use of radio-collars to track animal locations has been in use since the mid-late 1900s for study and has since revolutionized the ability of researchers to study wildlife [32]. Since then, location trackers are used extensively in the field. However they are still subject to variations in collection times, either due

to interference (such as from water, landscape, etc.) or to prescribed settings on the data collection. Marine animals are particularly difficult to track if they do not surface long enough for a signal to be established or because surfacing occurs infrequently [17]. These irregularities pose many issues for the analysis of the data, because variable-time intervals between collections can limit the inferences made. Telemetry also comes with inherent measurement error, both spatially and temporally [32]. Recent technology for collaring animals may have partially driven the shift from population level data collection to those for individual pathways [52]. The shift to telemetry devices attached to animals has heightened our ability to study animals in the wild with little to no human interference [18], [35].

How the study of animal movement can be practised, modelled, and interpreted is still an active area of research, and nowadays studies are often designed to answer questions regarding management and conservation of both the animals themselves and the surrounding environment [18]. The scale of habitat selection associated with the study of movement data generally falls under one of four categories: (1) first-order selection: the extent of the species distribution, (2) second-order selection: the home range of an individual or natural group of individuals, (3) third-order selection: sub-home range features, or (4) fourth-order selection: micro-movement and behaviour [32], [34]. Each scale can be adapted to answer questions about how an animal uses its environment. The movement itself can be important to an individual's fitness, and as a result effect the development of the species [52]. Movement studies are used to determine space-use and distributions of populations, and in, some cases, are adapted to learn more about reproductive events and processes [41]. They also identify the interplay between behaviour, landscape ecology, and population dynamics, which is critical to our understanding of ecological systems [32], [35], [49].

An animal's movement is known to be influenced by the environment [59], other individuals, food supplies [9], [32], physical limitations [50], memory [4],

[23], and "personality" [20]. Typically the environment is thought to influence the animal by a selection for, or against, specific environmental characteristics [5], [16]. Good quality habitat can slow movement and result in a more sinuous pathways. Alternatively, poor quality habitat may result in faster, more direct pathways [9], [10]. The physical ability for an animal to traverse a habitat type can also increase or decrease its movement speed and affect pathway conformation. While the specification of how different species use their ability to remember the environment is unclear, memory modelling [23] is a popular field in movement ecology and has been included in models to discern its effect on movement choices [4]. While individual "personality" is difficult to define, it may be that some individuals are better fit to certain environments due to personal characteristics [20]. These are but a few examples of the drivers behind animal movement, which can be identified using telemetry data.

Selection can be described empirically as "a behavioural process by which animals choose the most suitable locations in order to maximize fitness" [27], [53]. Translated into more statistical language, selection is the probability that an animal chooses a specific habitat type(s) over others when it is available and within range [40], and is mechanistically linked to animal movement [48]. If an animal uses a location more or less than suggested by stochastic movement, this would suggest selection [34]. In order to determine what is selected for, or alternatively against, researchers often make estimates from used and available location data [14], [33]. This process of selection can only be determined indirectly from the data [44], and there are many theoretical efforts to distinguish it from random movement [12], [55].

One of the best established methods for identifying an animal's selection is called resource selection. Resource selection analysis (RSA), and the related resource selection functions [43], connect an animal's movement patterns to the environmental drivers that they encounter [7], [39] and is a fundamental tool for discerning the effect of the environment on animal presence and movement [63]. This type of analysis can be used to answer questions about species

distributions and diversity, home ranges, to identify key habitat locations, and to manage solutions [43], [44], [62]. RSAs are also accommodating to practically any type of resource data, including categorical or scalar variables [16].

While RSA infers selection and movement characteristics, another perspective comes from models for realistic continuous-time behaviour [51], [59]. The spatiotemporal probability of animal occurrence is known as the utilization distribution (UD) [36]. RSA returns a probability of a location being selected by an animal, however a UD is here defined as the probability that an animal moves from a specific starting location to another location. The key difference between these concepts is that RSA relies on selection for spatial locations, whereas UDs are directly expressed in terms of the movement parameters. Continuous-time scale movement can be derived from the UD [65] as partial or stochastic differential equations that describe animal's pathway with specific movement and selection characteristics.

This thesis aim's to add to the field of movement analysis by (1) finding the equivalency between the utilization distribution and a stochastic differential equation of animal movement, (2) overviewing and comparing existing selection algorithms, and (3) developing a new algorithm for the analysis of telemetry data sets where some portions are missing that outputs estimates for the selection and movement parameters. Goal 1 is completed in Chapter 2, which focuses on the derivation of a continuous-time movement model with selection and the mathematics required for goals 2 and 3. Chapter 3 covers goals 2 and 3 by outlining the algorithms for resource selection analysis, step selection analysis, and integrated selection analysis, followed by our proposed new algorithm, missing point selection analysis. This proposed algorithm connects the two chapters by simulating a stochastic differential equation (continuous pathways) when steps are missing in the telemetry data. All four algorithms are compared together on exactly the same data to establish the effectiveness of each, as well investigate any draw backs. The presented novel algorithm allows for accurate estimations of movement and selection parameters, espe-

cially compared to the other algorithms when large amounts of data is missing from the animal location data set.

Chapter 2

A Model for Continuous Movement Behaviour with Selection

2.1 Introduction

While telemetry data is collected at discrete time intervals, it is reasonable to assume that movement, instead, occurs in continuous time, with animals constantly making movement decisions [32], however, it is unreasonable to expect data to be collected at this time scale, due to both limitations from technology and the amount of data that would be involved. Extrapolating to continuous time models from discrete data is then of great interest, with studies using these models to determine fine-scale space use [32]. We are interested in continuous time modelling because the transition from the general probability model for animal selection of a new location to continuous time movement can allow for more types of analysis, and can provide a more realistic depiction of the movement process.

Suppose one has telemetry data, or any kind of tracking data, for animals along with the landscape data for the region in which they reside, and one wishes to know the selection made by the individuals that were tracked. Several pieces of data are required for this analysis, including telemetry data from the animals and landscape information. In this thesis we focus on the relationship between the probability of selection and simulated animal move-

ment before directly analyzing the data. That is, the theory presented in this chapter will provide the groundwork for the proposed algorithm for selection analysis in chapter 3, specifically in section 3.10.

In order to maintain a level of consistency, all variables are described in Table 2.1, and their definitions do not change throughout the thesis. We consider both one spatial dimension and two spatial dimensions, so as to be thorough for possible applications. We do not consider three dimensional movement, such as fish movement in the ocean, or birds in the sky, because of the level of complexity required for the analysis as well as the concomitant increase in computation time. While the use of three dimensions is not the standard, it could be a possible in the future with further research.

First, suppose that the locations of the animal are known and given in the form of a vector of length $n + 1$, which describes the locations at times t_0, t_1, ... t_n. Thus, $\underline{X}$ is the vector of length $n + 1$ with entries $\underline{x}(t_i)$, which are the animal's individual locations. That is, $\underline{x}(t_i)$ is the known location of the animal at time t_i. For simplicity we will ignore the measurement error and assume that the reported locations are spatially accurate. In two dimensions, our data is in the form

$$\underline{x}(t_i) = \begin{pmatrix} x_1(t_i) \\ x_2(t_i) \end{pmatrix} \tag{2.1}$$

where $x_1(t_i)$ and $x_2(t_i)$ are the 2-dimensional coordinates at time t_i. Thus, each element of the vector $\underline{x}(t_i) \in \mathbb{R}^2$.

We define the probability that an animal chooses to move from $\underline{y}$ to $\underline{x}$, with probability density function, also known as the utilization distribution [32],

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2)w(\mathscr{F}(\underline{z}); \underline{\beta})d\underline{z}}, \tag{2.2}$$

where $K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)$ is the distribution of dispersal displacements that would be found in a spatially uniform environment, $\mathscr{F}(\underline{x})$ is the list of environmental covariates, $\underline{\beta}$ is the vector of selection coefficients for the covariates,

and $w(\mathscr{F}(\underline{x}); \underline{\beta})$ is the weighting function for the landscape covariates. In our model the weighting function shows habitat preference as a function of the finishing point of the move [62]. In our case we focus on the case where $K(\underline{x} - \underline{y}; \mu, \sigma^2)$ is a Gaussian. This choice is based on the normal distribution having an exponential form which is helpful for some of the algorithms in Chapter 3. The normal distribution also has the important property of being robust to the effect of time intervals on the probability distribution [60]. In other words, when the size of the time interval τ_i varies, a model for simple Brownian motion means that the probability distribution remains a normal distribution, albeit with a different variance This is shown in Appendix A.1, where a precise definition of robustness is also given.
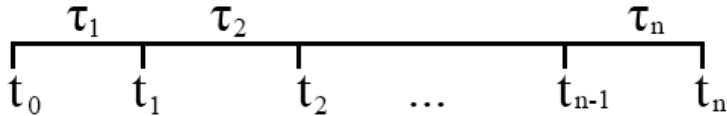
Figure 2.1: The structure of time steps (t_i) and time intervals (τ_i) for telemetry data. The τ_is need not be equal.

Time steps follow the structure shown in Figure 2.1, where t_i is the time step and τ_i is the interval between t_{i-1} and t_i. Telemetry data rarely is collected with identical time intervals between time steps, often due to data collection issues that result in missing points and consequently irregular time intervals [32]. In the case where have irregular time intervals, the mean and the variance for the dispersal kernel can change between time steps, so the step selection function can take the form

$$f(\underline{x}, \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i), \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i))w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i))w(\mathscr{F}(\underline{z}); \underline{\beta})d\underline{z}}. \quad (2.3)$$

This probability density function differs from equation 2.2 because the shape of the movement kernel depends on the amount of time the animal has to move. That is, the standard deviation will be bigger for longer time intervals.

We can rewrite K as

$$K(\underline{x} - \underline{y}; \underline{\mu}(\tau), \sigma^2(\tau)) = k(\underline{x}, \underline{y}; \tau_i, \underline{\theta}), \tag{2.4}$$

where

$$\underline{\theta} = \begin{pmatrix} \mu(\tau) \\ \sigma^2(\tau) \end{pmatrix}. \tag{2.5}$$

For the weighting function $w(\mathscr{F}(\underline{x}); \underline{\beta})$, we can use many different forms; however, we will focus on the two following forms: first the exponential form

$$w(\mathscr{F}(\underline{x}); \underline{\beta}) = \exp\left(\sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right), \tag{2.6}$$

and second the logistic form

$$w(\mathscr{F}(\underline{x}); \underline{\beta}) = \frac{\exp(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x}))}{1 + \exp(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})}. \tag{2.7}$$

In animal habitat selection studies, equation 2.6 is the more commonly used [3]. However, equation 2.7 provides the ability to determine probability of selection, rather than relative probability of selection [39], [62]. This difference is further elaborated on in section 3.4.1.

This chapter covers the derivation of a stochastic differential equation for animal movement with environmental influences from the utilization distribution, or master equation. In order to accomplish this goal, the Fokker-Planck equation, a partial differential equation, is established first from the master equation, or the utilization distribution. Once the Fokker-Planck equation is found, the stochastic differential equation can then be determined. We show the mathematics behind this process for both one dimension and two dimensions, as well as for both an exponential model and a logistic model for the probability of selection. Finally, we cover the simulation of the stochastic differential equation as a bridge between two known movement points with the added effect of habitat selection.

2.2 Underlying Unbiased Animal Movement

When the environment is uniform, we expect the animals to move, so that the direction and step length are not influenced by outside environments.

This externally unbiased animal movement model underlies movement with selection, and is thus key to the utilization distribution. As mentioned earlier, we assume that the externally unbiased movement kernel adheres to a normal distribution because the normal distribution has an useful exponential form as well as being robust to the effects of time intervals (see Appendix A.1). We generally assume a zero mean for the normal distribution, which means that there is no intrinsic bias in the movement towards a given location. The parameter that needs to be estimated for data for the unbiased movement is the variance of the step length. For the case with simple Brownian motion, this variance depends on the time interval available for animals to move. We can write the variance as:

$$\sigma_i^2 = \gamma \tau_i, \tag{2.8}$$

Where σ_i is the variance of the unbiased movement kernel for time interval i, and τ_i is the time interval. In Chapter 3, we outline how data is used to determine the fitted values for γ.

If we were to include bias into the movement kernel, the mean for the biased movement kernel would be given by

$$\underline{\mu}_i = \underline{m}\tau_i \tag{2.9}$$

where $\underline{\mu}_i$ is the mean for time interval i, and $\underline{m}$ is the velocity of the bias. However, we assume $\underline{m} = 0$, so the movement kernel does not show an intrinsic bias to any given direction.

2.3 Probability Density Functions for Movement

The introduction to this chapter poses the general model for animal movement for discrete time intervals τ_i, but what happens to movement patterns when $\tau_i \to 0$? We can use partial differential equations and stochastic differential equations to develop the model in this case. We use the master equation to begin, and then end with a stochastic differential equation model. We base

our analysis of the master equation on Moorcroft and Barnett [48]. To move to the continuous time framework, we consider the case where each τ_i has an identical value, τ, which is a small and constant and will approaches zero.

2.3.1 Fokker-Planck Derivation from a Master Equation (One Spatial Dimension)

We start with the master equation, a discrete-time equation describing the change in a probability density function for the location of an individual, and identify its connection with the Fokker-Planck equation, which is a partial differential equation describing the change in the probability density function in continuous time. The Fokker-Planck provides a necessary "middle-ground" for the the steps from a master equation for a probability density function for the location of the individual in discrete time to a stochastic differential equation for the movement path of the individual in continuous time. In one dimension, the domain is chosen to be the real line, $\Omega = (-\infty, \infty)$.

Consider the case where an individual is released with location given by probability density function $u_0(x)$ at time $t = 0$. For example, if the individual is released at $x = x_0$ at $t = 0$ then $u_0(x) = \delta(x - x_0)$ (point release). If we do not know exactly when the animal was released, we use a probability density function (pdf), $u_0(x)$. Note that

$$1 = \int_\Omega u_0(x)dxdy. \tag{2.10}$$

We would like to know the pdf for the individual for $t > 0$, $u(x, t)$. This is given by

$$u(x, t + \tau) = \int_\Omega f(x, y; \mu(\tau), \sigma^2(\tau), \underline{\beta})u(y, t)dy, \tag{2.11}$$

where f is given by equation 2.3. This is a special case of the Chapman-Kolmogorov equation [2].

We aim to derive a continuous time model by using an infinitesimal time step and Taylor series expansion approach. These two methods are combined

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by expanding the discrete-time equation 2.13 in a Taylor series and then approximating by removing higher order terms. In each time step τ, there is a change in the animal's spatial location. The step length and direction of movement are dependent only on the starting and ending locations, x and y, so we can write the displacement as $a = x - y$. This means the kernel (equation 2.2) can be rewritten as $f(x, y; \mu(\tau), \sigma^2(\tau), \underline{\beta}) = f_a(a, y; \mu(\tau), \sigma^2(\tau), \underline{\beta})$ because $f(x, y; \mu(\tau), \sigma^2(\tau), \underline{\beta})$ depends only on $x - y$ and y. Therefore, this results in

$$u(x, t + \tau) = \int_\Omega f_a(a, x - a; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x - a, t) da. \qquad (2.12)$$

We use a Taylor expansion to isolate specific terms for future steps, yielding

$$u(x, t + \tau) = \int_\Omega \left[f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x, t) \right. \qquad (2.13)$$

$$- a \frac{\partial}{\partial x} [f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x, t)] \qquad (2.14)$$

$$\left. + \frac{a^2}{2} \frac{\partial^2}{\partial x^2} [f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x, t)] + ... \right] da \qquad (2.15)$$

We know that $\int_\Omega f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x, t) da = u(x, t)$. Using this fact and dividing both sides by τ gives

$$\frac{u(x, t + \tau) - u(x, t)}{\tau} = - \frac{1}{\tau} \frac{\partial}{\partial x} \int_\Omega a f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x, t) da \qquad (2.16)$$

$$+ \frac{1}{2\tau} \frac{\partial^2}{\partial x^2} \int_\Omega a^2 f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) u(x, t) da + h.o.t. \qquad (2.17)$$

Taking the limit as $\tau \to 0$ yields

$$\frac{\partial u(x, t)}{\partial t} = - \frac{\partial}{\partial x} \left[\lim_{\tau \to 0} \frac{1}{\tau} \int_\Omega a f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) da \right] \qquad (2.18)$$

$$+ \frac{\partial^2}{\partial x^2} \left[\lim_{\tau \to 0} \frac{1}{2\tau} \int_\Omega a^2 f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) da \right] + h.o.t. \qquad (2.19)$$

Defining

$$c(x) = \lim_{\tau \to 0} \frac{1}{\tau} \int_\Omega a f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) da \qquad (2.20)$$

$$d(x) = \lim_{\tau \to 0} \frac{1}{2\tau} \int_\Omega a^2 f_a(a, x; \mu(\tau), \sigma^2(\tau), \underline{\beta}) da, \qquad (2.21)$$

to be the first and second infinitesimal moments of f_a yields the Fokker-Planck equation

$$\frac{\partial u(x,t)}{\partial t} = -\frac{\partial}{\partial x}[c(x)u(x,t)] + \frac{\partial^2}{\partial x^2}[d(x)u(x,t)]. \qquad (2.22)$$

Here we assume that the higher order terms approach zero as τ approaches zero [11].

We have taken the master equation for the probability that an animal moves to a location given a starting location to an partial differential equation, known as the Fokker-Planck equation, which describes the change in probability of selection over environment Ω in continuous-time. The connection between these two equations was found by using infinitesimal time step and a Taylor series expansion. After considering the two dimensional version of this connection and associated formulas for $c(x)$ and $d(x)$, the next step is to derive a stochastic differential equation from the Fokker-Planck equation (Section 2.4).

2.3.2 Fokker-Planck Derivation from a Master Equation (Two Spatial Dimensions)

Similar to Section 2.3.1, the goal of this section is to derive the Fokker-Planck equation from the master equation, but in this section we work in two dimensions rather than one dimension. A two dimensional space model is common in realistic animal movement studies, so it is important to provide the derivation in two dimensions. In two dimensions, the domain is $\Omega = (-\infty, \infty) \times (-\infty, \infty)$.

Let our space variable be $\underline{x} = (x_1, x_2)$. Then the master equation is

$$u(\underline{x}, t + \tau) = \int_\Omega f(\underline{x}, \underline{y}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) u(\underline{y}, t) d\underline{y}. \qquad (2.23)$$

Defining $\underline{a} = \underline{x} - \underline{y}$, which is the vector representing the move from $\underline{y}$ to $\underline{x}$, we can redefine $f(\underline{x}, \underline{y}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})$ as $f(\underline{x}, \underline{y}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) = f_{\underline{a}}(\underline{a}, \underline{x} -$

$\underline{a}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}$. The equation becomes

$$u(\underline{x}, t + \tau) = \int_\Omega f_{\underline{a}}(\underline{a}, \underline{x} - \underline{a}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) u(\underline{x} - \underline{a}, t) d\underline{a} \tag{2.24}$$

Expanding $u(\underline{x}, t + \tau)$, $u(\underline{x} - \underline{a}, t)$, and $f_{\underline{a}}(\underline{a}, \underline{x} - \underline{a}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})$ using the two-dimensional Taylor series, we obtain

$$u(\underline{x}, t + \tau) + \tau \frac{\partial}{\partial t} u(\underline{x}, t) = \int_\Omega \{ u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) \tag{2.25}$$

$$- a_1 \frac{\partial}{\partial x_1} [u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})] \tag{2.26}$$

$$- a_2 \frac{\partial}{\partial x_2} [u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})] \tag{2.27}$$

$$+ \frac{a_1^2}{2} \frac{\partial^2}{\partial x_1^2} [u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})] \tag{2.28}$$

$$+ \frac{a_1 a_2}{2} \frac{\partial^2}{\partial x_1 x_2} [u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})] \tag{2.29}$$

$$+ \frac{a_2 a_1}{2} \frac{\partial}{\partial x_2 x_1} [u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})] \tag{2.30}$$

$$+ \frac{a_2^2}{2} \frac{\partial^2}{\partial x_2^2} [u(\underline{x}, t) f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta})] + h.o.t. \} d\underline{a}, \tag{2.31}$$

where $\underline{a} = (a_1, a_2)^T$.

Dividing by τ, using the fact that $\int f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) u(\underline{x}, t) d\underline{a} = u(\underline{x}, t)$ to rearrange and taking the limit as $\tau \to 0$ gives the Fokker-Planck equation

$$\frac{\partial u}{\partial t} = - \nabla \cdot \left[\underline{c}(\underline{x}) u \right] + \frac{\partial^2 [d_{x_1 x_1}(\underline{x}) u]}{\partial x_1^2} + \frac{\partial^2 [d_{x_1 x_2}(\underline{x}) u]}{\partial x_1 x_2} \tag{2.32}$$

$$+ \frac{\partial^2 [d_{x_2 x_1}(\underline{x}) u]}{\partial x_2 x_1} + \frac{\partial^2 [d_{x_2 x_2}(\underline{x}) u]}{\partial x_2^2}, \tag{2.33}$$

where

$$\underline{c}(\underline{x}) = \lim_{\tau \to 0} \frac{1}{\tau} \int_\Omega \underline{a} f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) d\underline{a} \tag{2.34}$$

$$d_{x_1 x_1}(\underline{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int_\Omega a_1^2 f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) d\underline{a} \tag{2.35}$$

$$d_{x_1 x_2}(\underline{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int_\Omega a_1 a_2 f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) d\underline{a} \tag{2.36}$$

$$d_{x_2 x_1}(\underline{x}) = d_{x_1 x_2}(\underline{x}) \tag{2.37}$$

$$d_{x_2 x_2}(\underline{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int_\Omega a_2^2 f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) d\underline{a}. \tag{2.38}$$

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When the movement kernel K in equation 2.3 is isotropic (independent of direction), as is the case for normal kernel, it is possible to show that the cross diffusion terms become zero, and the remaining diffusion terms become $d_{x_1 x_1}(\underline{x}) = d_{x_2 x_2}(\underline{x}) = d(\underline{x})$, the details of which are shown in Appendices A.2 and A.3. In this, the Fokker-Planck equation can alternatively be expressed as

$$\frac{\partial}{\partial t} u(\underline{x}, t) + \nabla \cdot (\underline{c}(\underline{x}) u(\underline{x}, t)) = \nabla^2 (d(\underline{x}) u(\underline{x}, t)). \qquad (2.39)$$

This section showed the derivation of the Fokker-Planck equation from the master equation in two dimensions. Specifically, these steps identify the connection between the probability that an animal moves to a location, given a starting location, and the change in probability of an animal moving to a location over an environment Ω. We can then use the Fokker-Planck equation to derive a stochastic differential equation describing animal movement.

2.3.3 Derivation of Space Use Coefficients (One Spatial Dimension)

We require the space-use coefficients for the movements models to include the resource dependence in the movement. Following the work shown in Moorcroft and Barnett Appendix A [48], we derive the space-use coefficients for our model.

The utilization distribution is defined as

$$f(x, y; \mu(\tau_i), \sigma^2(\tau_i), \underline{\beta}) = \frac{K(x - y; \mu(\tau_i), \sigma^2(\tau_i)) w(\mathscr{F}(x); \underline{\beta})}{\int K(z - y; \mu(\tau_i), \sigma^2(\tau_i)) w(\mathscr{F}(x); \underline{\beta}) dz}, \qquad (2.40)$$

which includes movement and selection parameters. As before, letting $a = x - y$, which is the vector of displacement between steps, we can change from (x, y) coordinates to (a, y) coordinates by defining

$$f_a(a, y; \mu(\tau), \sigma^2(\tau), \underline{\beta}) = f(x, y; \mu(\tau), \sigma^2(\tau), \underline{\beta}). \qquad (2.41)$$

We now abbreviate notation for convenience and rewrite $f_a(a, y; \mu(\tau), \sigma^2(\tau), \underline{\beta}) = f_a(a, y; \tau)$, $w(\mathscr{F}, \underline{\beta}) = w(\mathscr{F})$, and $K(a; \mu(\tau), \sigma^2(\tau)) = K(a; \tau)$. This equation 2.41 becomes

$$f_a(a, y; \tau) = \frac{K(a; \tau)w(\mathscr{F}(y + a))}{\int K(a; \tau)w(\mathscr{F}(y + a'))da'}. \tag{2.42}$$

We note that we require $f_a(a, x; \tau)$ for the calculation of the advection (equation 2.22) and diffusion (equation 2.23) coefficients and so rewrite equation 2.42 as

$$f_a(a, x; \tau) = \frac{K(a; \tau)w(\mathscr{F}(x + a))}{\int K(a; \tau)w(\mathscr{F}(x + a'))da'}. \tag{2.43}$$

The pth moment of the distribution of displacement distances is

$$M_p(\tau) = \int a^p K(a; \tau)da. \tag{2.44}$$

The variance is $M_2 - M_1^2$, and so the variance equals the second moment if the mean $M_1 = 0$. $M_1 = 0$ when K is symmetric, which is one of our assumptions because $\mu = 0$. Also, since K is a probability density function, $M_0(\tau) = 1$. Under the above assumptions, Taylor expanding $w(\mathscr{F}(x + a'))$ yields the following expression for the denominator of equation 2.43,

$$\int K(a')w(\mathscr{F}(x + a'))da' = w(\mathscr{F}(x)) + \frac{w_{xx}(\mathscr{F}(x))}{2!}M_2(\tau) + \ldots \tag{2.45}$$

where $w_{xx}(\mathscr{F}(x)) = \frac{d^2 w(\mathscr{F}(x))}{dx^2}$. In the limit $\tau \to 0$, we only require the first two terms of equation 2.47. Using this expression for the denominator and inserting equation 2.47 into equation 2.34 yields

$$c(x) = \lim_{\tau \to 0} \frac{1}{\tau} \frac{w_x(\mathscr{F}(x))M_2(\tau) + \ldots}{w(\mathscr{F}(x)) + w_{xx}(\mathscr{F}(x))\frac{M_2(\tau)}{2!} + \ldots} \tag{2.46}$$

$$= \lim_{\tau \to 0} \frac{w_x(\mathscr{F}(x))M_2(\tau)}{w(\mathscr{F}(x))\tau} \tag{2.47}$$

$$= \frac{w_x(\mathscr{F}(x))}{w(\mathscr{F}(x))} \lim_{\tau \to 0} \frac{M_2(\tau)}{\tau} \tag{2.48}$$

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where $w_x = \frac{dw}{dx}$, etc. Similarly

$$d(x) = \lim_{\tau \to 0} \frac{1}{2\tau} \frac{w(\mathscr{F}(x))M_2(\tau) + w_{xx}(\mathscr{F}(x))M_4(\tau)/2! + ...}{w(\mathscr{F}(x)) + w_{xx}(\mathscr{F}(x))M_2(\tau)/2 + ...} \qquad (2.49)$$

$$= \lim_{\tau \to 0} \frac{M_2(\tau)}{2\tau} \qquad (2.50)$$

$$= d \text{ (constant)}. \qquad (2.51)$$

Here we make the standard assumption that the limit given in equations 2.50 and 2.52 exists and that higher order moments of the dispersal kernel go to zero faster than τ [11].

These new forms for $c(x)$ and $d(x)$ are used in a stochastic differential equation, derived below. Since the variance equals the second moment, we can substitute $\sigma^2 = \gamma\tau$ in for $M_2(\tau)$. Thus we retain the same movement parameters as the utilization distribution (equation 2.3). The selection parameters are included in $c(x)$ through $w_x(\mathscr{F}(x))/w(\mathscr{F}(x))$.

2.3.4 Derivation of Space Use Coefficients (Two Spatial Dimensions)

Similar to Section 2.3.3, we require the space-use coefficients in terms of the movement and selection parameters, but in two dimensions. The technique between these two sections is similar, but the detailed difference is important for final implementation.

The two dimensional utilization distribution is defined as

$$f(\underline{x}, \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i), \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i))w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i))w(\mathscr{F}(\underline{x}); \underline{\beta})d\underline{z}}, \qquad (2.52)$$

which includes movement and selection parameters. Letting $\underline{a} = \underline{x} - \underline{y}$ be the vector of distance travelled between steps, we can again change $(\underline{x}, \underline{y})$ to $(\underline{a}, \underline{y})$ by defining

$$f_{\underline{a}}(\underline{a}, \underline{y}; \mu(\tau(, \sigma^2(\tau), \underline{\beta}) = f(\underline{x}, \underline{y}; \mu(\tau), \sigma^2(\tau), \underline{\beta}). \qquad (2.53)$$

Using the abbreviated notation introduced in the previous section, we rewrite equation 2.52 as

$$f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) = \frac{K(\underline{a}; \tau)w(\mathscr{F}(\underline{x} + \underline{a}), \underline{\beta})}{\int K(\underline{a}; \tau)w(\mathscr{F}(\underline{x} + \underline{a}'), \underline{\beta})d\underline{a}'}. \tag{2.54}$$

The pth radial moment of the distribution of displacement kernel K is

$$M_p(\tau) = \int |\underline{a}|^p K(\underline{a}; \tau)d\underline{a}. \tag{2.55}$$

Again, the variance is $M_2 - M_1^2$, and so the variance equals the second moment if the mean $M_1 = 0$. $M_1 = 0$ when K is symmetric, and because K is a probability density function $M_0(\tau) = 1$. Under the above assumptions, Taylor expanding $w(\mathscr{F}(\underline{x} + \underline{a}'))$ yields the following expression for the denominator of equation 2.54,

$$\int K(\underline{a}')w(\mathscr{F}(\underline{x} + \underline{a}'))d\underline{a}' = w(\mathscr{F}(\underline{x})) + \frac{\nabla^2 w(\mathscr{F}(\underline{x}))}{2!}M_2(\tau) + \dots \tag{2.56}$$

In the limit $\tau \to 0$, only the first two terms of equation 2.56 remains. Using this expression for the denominator and inserting equation 2.58 into equation 2.34 yields

$$\underline{c}(\underline{x}) = \lim_{\tau \to 0} \frac{1}{\tau} \frac{\nabla w(\mathscr{F}(\underline{x}))\frac{M_2(\tau)}{2} + \dots}{w(\mathscr{F}(\underline{x})) + \nabla^2 w(\mathscr{F}(\underline{x}))\frac{M_2(\tau)}{2!} + \dots} \tag{2.57}$$

$$= \lim_{\tau \to 0} \frac{\nabla w(\mathscr{F}(\underline{x}))M_2(\tau)}{2w(\mathscr{F}(\underline{x}))\tau} \tag{2.58}$$

$$= \frac{\nabla w(\mathscr{F}(\underline{x}))}{w(\mathscr{F}(\underline{x}))} \lim_{\tau \to 0} \frac{M_2(\tau)}{2\tau}. \tag{2.59}$$

Similarly,

$$d(\underline{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \frac{w(\mathscr{F}(\underline{x}))\frac{M_2(\tau)}{2} + \dots}{w(\mathscr{F}(\underline{x})) + \nabla^2 w(\mathscr{F}(\underline{x}))\frac{M_2(\tau)}{2!} + \dots} \tag{2.60}$$

$$= \lim_{\tau \to 0} \frac{M_2(\tau)}{4\tau} \tag{2.61}$$

$$= d \text{ (constant)} \tag{2.62}$$

where $M_2(\tau)$ is the second moment of dispersal kernel. Here we again make the standard assumption that the limit given in equation 2.61 exists and that

higher order moments of the dispersal kernel go to zero faster than τ.

In this section we have defined the space-use coefficients for two dimensions. These space-use coefficients are described with the movement and selection parameters given in the utilization distribution, which will account for the connection between the utilization distribution and the related stochastic differential equation (SDE) model (see Section 2.4.2). In the following subsections we determine the exact form of the space-use coefficient given the weighting function and number of dimensions.

2.3.5 Exponential Weighting, One Dimension

In this section, we determine the $(1/w(x))(\partial w/\partial x)$ required for the space-use coefficient in Section 2.3.3. As described in Section 2.1, we first assume an exponential model for the probability of selection for environmental location (weighting model) in 1D given by equation 2.6. For the one-dimensional advection coefficient of equation 2.50, we require $(1/w(x))(\partial w/\partial x)$. The exponential weighting model given in equation 2.6 is

$$w(\mathscr{F}(x); \underline{\beta}) = \exp\left(\sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x) \right). \tag{2.63}$$

Differentiating equation 2.63 yields

$$\frac{dw}{dx} = \exp(\beta_1 \mathscr{F}_1(x) + \beta_2 \mathscr{F}_2(x) + ... + \beta_\eta \mathscr{F}_\eta(x))\left(\beta_1 \frac{d\mathscr{F}_1(x)}{dx} + \beta_2 \frac{d\mathscr{F}_2(x)}{dx} \right.$$
$$\left. + ... + \beta_\eta \frac{d\mathscr{F}_\eta(x)}{dx} \right). \tag{2.64}$$

Therefore

$$\frac{dw}{dx}\frac{1}{w} = \beta_1 \frac{d\mathscr{F}_1(x)}{dx} + \beta_2 \frac{d\mathscr{F}_2(x)}{dx} + ... + \beta_\eta \frac{d\mathscr{F}_\eta(x)}{dx}, \tag{2.65}$$

or equivalently

$$\frac{dw}{dx}\frac{1}{w} = \sum_{i=1}^{\eta} \beta_i \frac{d\mathscr{F}_i(x)}{dx}, \tag{2.66}$$

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and so

$$c(x) = 2d \sum_{i=1}^{\eta} \beta_j \frac{d\mathscr{F}_j(x)}{dx}. \tag{2.67}$$

The $(1/w(x))(\partial w/\partial x)$ term found in this section will later be used in the SDE model to influence the movement of the animal to include selection. The exponential model leads to a relatively simplistic form of the weighting derivative, as compared to the logistic weighting (Section 2.3.7).

2.3.6   Exponential Weighting, Two Dimensions

For the advection coefficient in two dimensions, we need $\nabla w(\underline{x})$ (equation 2.61). The exponential model in two dimensions is,

$$w(\mathscr{F}(\underline{x}); \underline{\beta}) = \exp\left(\sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right). \tag{2.68}$$

Using equation 2.68, we start by taking the gradient of w,

$$\nabla w = \left(\exp\left(\sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right) \left(\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_1}\right), \right.$$
$$\left. \exp\left(\sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right) \left(\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_2}\right)\right)^{\mathsf{T}}. \tag{2.69}$$

Thus we get

$$\frac{\nabla w}{w} = \left(\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_1}, \sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_2}\right)^{\mathsf{T}} \tag{2.70}$$

$$= \nabla \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x}), \tag{2.71}$$

and so

$$\underline{c}(\underline{x}) = 4d\nabla \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x}) \tag{2.72}$$

The gradient term $\nabla w(\underline{x})$ derived in this section will function as the influence of the environment on the animal's movement by included their selection for or against specific environmental covariates. The $\nabla w(\underline{x})$ found is similar

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to 1D in its ease of calculation and relative simplicity when compared to Section 2.3.8. This $\nabla w(\underline{x})$ is to be used in the case of an exponential model in a two dimensional space.

2.3.7 Logistic Weighting, One Dimension

The logistic weighting function (equation 2.7) for the probability of selection of a location is given by

$$w(\mathscr{F}(x);\underline{\beta}) = \frac{\exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x)\right)}{1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x)\right)}. \tag{2.73}$$

We require $(1/w(x))(\partial w/\partial x)$ of the logistic weighting in order to calculate the one-dimensional advection coefficient.

Differentiating equation 2.73 with respect to x yields

$$\frac{dw}{dx} = \frac{\exp(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x)) \sum \beta_j \frac{d\mathscr{F}_j(x)}{dx}}{(1 + \exp(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x)))^2}, \tag{2.74}$$

and therefore

$$\frac{dw}{dx}\frac{1}{w} = \frac{\sum_{j=1}^{\eta} \beta_j \frac{d\mathscr{F}_j(x)}{dx}}{1 + \exp(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x))}. \tag{2.75}$$

Thus,

$$c(x) = 2d\frac{\sum_{j=1}^{\eta} \beta_j \frac{d\mathscr{F}_j(x)}{dx}}{1 + \exp(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x))} \tag{2.76}$$

The $(1/w(x))(\partial w/\partial x)$ which is the weighting that will be used in the SDE below if a logistic model is chosen for an animal in a 1D environment. This term brings selection for (or against) environmental characteristics to the sde.

2.3.8 Logistic Weighting, Two Dimensions

The logistic weighting for the probability of selection of a location by an animal is given by

$$w(\mathscr{F}(x);\underline{\beta}) = \frac{\exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x)\right)}{1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(x)\right)}. \tag{2.77}$$

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We need $\nabla w(\underline{x})$ for the sde of animal movement with selection. The $\nabla w(\underline{x})$ term will function as the integration of selection for or against environmental characteristics by the animal.

Using equation 2.77, we start by taking the gradient of w,

$$\nabla w = \left(\frac{\exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)\left(\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_1}\right)}{\left(1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)\right)^2}, \right.$$

$$\left. \frac{\exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)\left(\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_2}\right)}{\left(1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)\right)^2} \right)^{\mathsf{T}}. \tag{2.78}$$

Thus we get

$$\frac{\nabla w}{w} = \left(\frac{\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_1}}{1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)}, \frac{\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_2}}{1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)} \right)^{\mathsf{T}}, \tag{2.79}$$

and so

$$\underline{c}(\underline{x}) = 4d \left(\frac{\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_1}}{1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)}, \frac{\sum_{j=1}^{\eta} \beta_j \frac{\partial \mathscr{F}_j(\underline{x})}{\partial x_2}}{1 + \exp\left(\beta_0 + \sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{x})\right)} \right)^{\mathsf{T}}. \tag{2.80}$$

We find here the equation for $\nabla w(\underline{x})$ given a logistic model for the probability of selection of a location by an animal. This $\nabla w(\underline{x})$ will also be used in the SDE under the assumption of a logistic model applied to a two dimensional environment and introduces selection in the SDE.

2.4 Deriving the Stochastic Differential Equation from the Partial Differential Equation

In the previous section, we determined the probability density function for the selection of a location given a starting location for an animal. Using the

master equation, we then derived the Fokker-Planck equation. Once the pdf has been determined, we can simulate movement of individuals following the fitted distribution.

In this section, we derive the stochastic differential equation from the partial differential equation. The stochastic differential equation allows for the simulation of animal movement pathways over continuous time. These simulations are accomplished by using stochastic differential equations to model the possible paths of a single individual. The stochasticity is incorporated in the animal's movement via a biased random walk process.

2.4.1 Stochastic Differential Equation, One Dimension

Once the connection between the utilization distribution and step selection equations is found, we now require the stochastic differential equation related to the step selection equation. We began with a probability density function for the probability that an animal move to a location given movement and selection parameters, $u(x, t)$. By way of contrast, the SDE provides a model for a track for an individual, which is $X(t)$. That is, we establish the connection between the utilization distribution and continuous time movement will be complete.

The Fokker-Planck equation, found in Section 2.3.1, was found to be in our case as

$$\frac{\partial u(x, t)}{\partial t} = -\frac{\partial}{\partial x}[c(x)u(x, t)] + \frac{\partial^2}{\partial x^2}[du(x, t)]. \tag{2.81}$$

This is also referred to as the forward Kolmogorov equation [2]. The forward Kolmogorov equation is related to an Ito stochastic differential equation (definition given by Allen [2]). Specifically, page 343 of this text shows the corresponding Ito SDE for the forward Kolmogorov equation. Translating our forward Kolmogorov equation to an SDE, we find the SDE is

$$dX(t) = c(X(t))dt + \sqrt{2d}dW(\tau), \tag{2.82}$$

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where $X(t), t \geq 0$ is a stochastic diffusion process, and $W(t), t \in [0, \infty)$ is a Wiener process (standard Brownian motion).

However for simulations of the SDE, we require the explicit definitions of the drift and diffusion terms. From Section 2.3.3, the drift was found to be

$$c(X(t)) = \frac{w_x(\mathscr{F}(x))}{w(\mathscr{F}(x))} \lim_{\tau \to 0} \frac{M_2(\tau)}{\tau}. \tag{2.83}$$

From Section 2.3.3, when the available distribution is symmetric, the second moment $(M_2(\tau))$ is equal to the variance of the available distribution. Our assumption that the second moment of the dispersal kernel K, $M_2(\tau)$ scales linearly with τ as τ approaches zero means that

$$c(X(t)) = \frac{w_x(\mathscr{F}(x))\gamma}{w(\mathscr{F}(x))}. \tag{2.84}$$

where γ is defined to be the rate at which the one-dimensional variance of the process grow with time so that the variance of the dispersal kernel is $\sigma^2(\tau) = M_2(\tau) = \gamma\tau$ as $\tau \to 0$.

Similarly, $d(x)$ defined in Section 2.3.3, equation 2.52 and 2.63, to be

$$d = \lim_{\tau \to 0} \frac{M_2(\tau)}{2\tau}. \tag{2.85}$$

Again since the second moment is equal to the variance of the available distribution, we can define $\beta(X(t))$ in equation 2.86 as

$$\sqrt{2d} = \sqrt{2\frac{M_2(\tau)}{2\tau}} \tag{2.86}$$

$$= \sqrt{2\frac{\gamma\tau}{2\tau}} \tag{2.87}$$

$$= \sqrt{\gamma}. \tag{2.88}$$

In this thesis, we consider the case where K is a Gaussian with zero mean and variance $\sigma^2(\tau) = \gamma\tau$ (one dimension) or $\sigma^2(\tau) = 2\gamma\tau$ (two dimensions), because both the x and y components of the variance grow with time at rate γ in two dimensions. In summary, SDE defined in this section follows the same movement and selection parameters as defined in the utilization distribution for one dimension. Animal movement in continuous time can then be simulated using that resulting SDE.

2.4.2 Stochastic Differential Equation, Two Dimensions

In most animal space-use studies, the biological questions of interest are in two dimensions rather than one. Therefore is it of interest to derive the stochastic differential equation from the utilization in two dimensions as well. The connection between utilization distribution and the step-selection function can be extended to find the SDE.

The Fokker-Planck equation in two dimensions, also known as the forward Kolmogorov equation, derived in Section 2.3.2 was found to be

$$\frac{\partial}{\partial t}u(\underline{x}, t) + \nabla \cdot (\underline{c}(\underline{x})u(\underline{x}, t)) = \nabla^2(du(\underline{x}, t)). \tag{2.89}$$

Using the connection between the forward Kolmogorov equation and the Ito stochastic differential equation (SDE) as defined by Allen [2] on page 417, yields the SDE

$$d\underline{X}(t) = \underline{c}(\underline{X}(t))dt + \sqrt{2d}d\underline{W}(\tau). \tag{2.90}$$

In equation 2.59, the drift term was found to be

$$\underline{c}(\underline{X}(t)) = \frac{\nabla w(\mathscr{F}(\underline{x}))}{w(\mathscr{F}(\underline{x}))} \lim_{\tau \to 0} \frac{M_2(\tau)}{2\tau}. \tag{2.91}$$

Yielding

$$\underline{c}(\underline{X}(t)) = \frac{\nabla w(\mathscr{F}(\underline{X}(t)))\gamma}{w(\mathscr{F}(\underline{X}(t)))}, \tag{2.92}$$

where $M_2(\tau) = 2\gamma\tau$ now scales the variance of the two-dimensional dispersal kernel as $\tau \to 0$. Using equation 2.61 yields

$$\sqrt{2d} = \sqrt{\gamma}. \tag{2.93}$$

We now have an two dimensional SDE with coefficients that depend on the movement and selection parameters. Note that the drift term $\underline{c}$ involves dispersal plus selection whereas the random motion term Ω involves only dispersal. This SDE can be used to simulate animal movement with influence of the environment. The desired utilization distribution thus influences the resulting SDE.

2.5 Numerical Solution of the SDE

In order to implement the SDE model found in Section 2.4.2, we require numerical methods that can find solutions to the equations in a given space. There are several methods for solving these types of equations, such as Euler, Milstein, and Itô-Taylor. However we use the Runge-Kutta method, specifically second order Runge-Kutta [30], because higher-order Runge-Kutta methods provide more accurate estimates. Runge-Kutta works by estimating the next step in the SDE given an initial value by finding the slope at a given point and looking forward a small amount in time. The slope is found through a Taylor expansion and uses one higher order term than first order Runge-Kutta (three terms of the Taylor series). This provides an estimate of the derivative of the equations without actually finding it.

There are two main ways we use the SDE to find solutions: (1) an initial value problem, which is to determine an $X(t)$ that satisfies equation 2.99 plus $X(0) = X_0$, and (2) a bridge problem, which is to determine an $X(t)$ that satisfies equation 2.99 plus $X(0) = X_0$ and $X(\tau) = X_\tau$. The initial value problem

gives simulated pathways with the given movement and selection parameters on a specified landscape. The only limiting factor in this case is the starting location, meaning that the final location is not pre-determined. On the other hand, the bridge solutions do have specific starting and ending points, but instead serve to understand what could have happened in between those points given specific movement and selection parameters. Equation 2.99 has an infinite number of solutions, and both ways (1) and (2) find those solutions.

Using the form of the SDE given in section 2.4.2, we simulate pathways using software in R. We use the Sim.DiffProc package by Arsalane Chouaib Guidoum and Kamal Boukhetala [30]. The "bridgesde2d" function takes a given SDE model and initialization parameters and outputs bridge pathways. The number of pathways can be adjusted, as well as the number of simulated points/time per bridge. We use the solver method 'rk2' which is the second order Runga-Kutta method. This function returns a discrete list of locations, x and y, which can then either be sampled from or used as a whole vector. Should any errors occur, such as a valid bridge simulation is not complete, it returns an error exception. Thus for repeated simulations, an error catcher must be used. An example pathway is given in Figure 2.2.

We apply the SDE model to a landscape with a single covariate called $\mathscr{F}(x)$. $\mathscr{F}(x)$ is a two-dimensional Gaussian centered at $(0,0)$ and a variance of σ_e. Given two known points, bridges can be simulated between those points as influenced by the environment (see Figure 2.2).

2.6   Discussion and Conclusion

The goal of this section was to establish the connection between the utilization distribution,

$$f(\underline{x}, \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i), \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i))w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}(\tau_i), \sigma^2(\tau_i))w(\mathscr{F}(\underline{z}); \underline{\beta})d\underline{z}}. \qquad (2.94)$$

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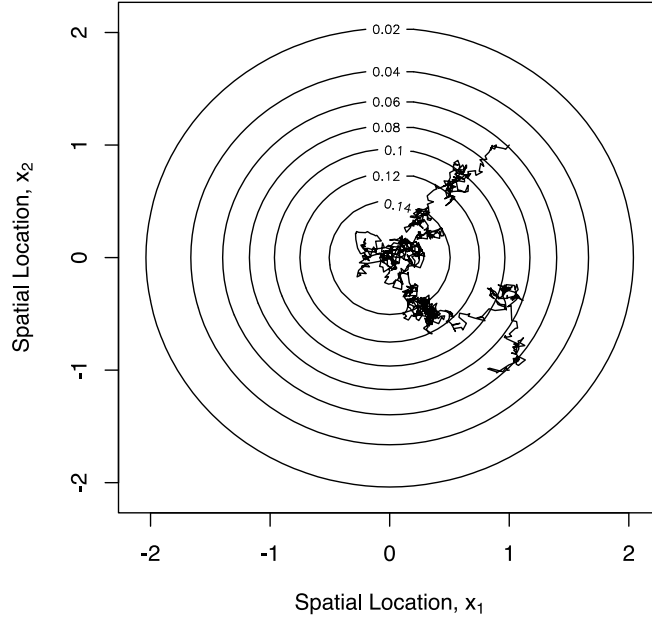
Figure 2.2: Simulation of a bridge between two known points with selection. The circular contour lines show the levels of the environmental covariate that is being selected for, with a normal distribution that is centered at (0,0) and a σ_e of 1 (identical to the distribution described in Section 3.2). The SDE bridge begins at (1,1) and ends at (1,-1) and follows the selection and movement parameters described in Table 3.1.

and a stochastic differential equation for animal movement

$$d\underline{X}(t) = \underline{c}(\underline{X}(t))dt + \sqrt{2d}d\underline{W}(\tau). \tag{2.95}$$

This was accomplished by first deriving the Fokker-Planck equation from the utilization distribution, then the SDE from the Fokker-Planck equation.

The derivations were shown for both one and two dimensions. Thus the resulting methods could be applied to a multitude of animal studies. The models could be extended to three dimensions and is an area in need of further development. We also included two forms of the selection weighting function; exponential and logistic. Exponential is the most common form of selection weighting functions. However we require the logistic weighting function for Chapter 3. An example of simulation was also shown, as the SDE can be used

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to find bridges between two known points.

This chapter showed the mathematics behind the connection between the utilization distribution and the SDE, which is extended in Chapter 3 by the application to data. The utilization distribution can be fit using resource selection analysis to find fitted movement and selection parameters, which means the SDE can be simulated with the estimated parameters. Thus, as we will demonstrate in the next chapter, it is possible to simulate animal pathways estimated from animal movement data.

Variable	Description	Size
$X(t)$	Stochastic process describing the location of the animal over $0 \leq t \leq T$	
$X_1(t)$	x_1 components of $X(t)$	
$X_2(t)$	x_2 components of $X(t)$	
$\underline{X}^U$	Entire set of used location pathway for one animal, $((X_1^U(0), X_2^U(0)), (X_1^U(t_1), X_2^U(t_1)), ..., (X_1^U(t_n), X_2^U(t_n)))^\intercal$	$n+1$
J	Total number of available steps	1
λ	Number of available steps created per used step	$1 \leq \lambda \leq J$
$\underline{X}^A$	Entire available set of locations for one animal pathway, $[(X_{11}^A(t_i), X_{21}^A(t_i)), (X_{12}^A(t_i), X_{22}^A(t_i)), ..., (X_{1J}^A(t_i), X_{2J}^A(t_i))]^\intercal$	$n+1$
$\underline{x}$	2 dimensional location, also ending location	2
$\underline{y}$	2 dimensional location, also starting location	2
t_i	Time at step i	1
τ_i	Time interval between steps $i-1$ and i	1
$x(t_i)$	Possible x-coordinate at time t_i in 1D	1
$x_1(t_i)$	Possible x_1-coordinate at time t_i in 2 dimensional	1
$x_2(t_i)$	Possible x_2-coordinate at time t_i in 2 dimensional	1
T	Time of last time step	1
$\underline{t}$	Vector of time steps	$n+1$
$\underline{\tau}$	Vector of time intervals	n
$\underline{\beta}$	Vector of covariate coefficients	k
$\mathscr{F}(\underline{x})$	Covariate value for location $\underline{x}$	1
$w(\mathscr{F}(\underline{x}), \underline{\beta})$	Weighting function	
$K(\underline{x} - \underline{y}; \mu, \sigma^2)$	Unbiased movement kernel	
$\underline{\psi}$	Movement kernel based on step length and turn angle, for iSSA	
$\underline{a}_i$	Distance between two points at time i, $|\underline{x_i} - \underline{y_i}|$	2
Ω	Landscape	$p \times q$

Table 2.1: All variables and their definitions. These remain consistent throughout the thesis.

Chapter 3

Connecting to Data: Informing Dispersal and Selection

3.1 Introduction

Resource selection models are used to determine the probability that an animal selects (or avoids) a specific location given it's environmental characteristics [40]. The statistical methods used for fitting these models have existed for a significant amount of time, but the novelty of the subject lies in the application and interpretation to animal ecology [32]. This type of analysis compares the characteristics of the environment in the locations the animal was found (used) to the environmental characteristics of locations where it could have moved (available). The product of the selection function and the availability function, when normalized, is proportional to the density function for space use [32].

Resource selection analysis (RSA), sometimes referred to via resource selection function (RSF) [43], is the most general method for determining selection. To analyze the RSA, most commonly a logistic regression is used for presence-only data, with randomly chosen available points to complete the data set [46]. An RSA can be associated with an exponential model as the probability of selection and be fit with a logistic regression to obtain unbiased estimates of the selection parameters [33], but it can also take other forms (e.g. probit, logit) [38]. RSAs typically estimate a relative probability of selection [62],

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which can go greater than 1.0, and thus resource selection probability analysis (RSPA) was developed to return a true probability of selection. RSAs predict specifically selection parameters only, and to incorporate movement step selection analysis (SSA) was introduced [24], [26], [63] and included step lengths and turning angles [55]. The next development in this area was to include the fitting of the movement parameters in the same model as the selection parameters using conditional regression, which is called integrated step selection analysis (iSSA) [8].

Even though RSAs are applied regularly to animal telemetry data, the issue of defining what is truly available to animals remains an open issue [8], [40], [44]. What is available to an animal can vary significantly between species, or in some cases amongst individuals. Available locations do not necessarily correlate with unused locations because an animal will not go to a location that it physically cannot access. Therefore not all unused location cannot be considered as available [16]. How available points are defined significantly affect the analysis outcome [34], by both the size and spatial extent of the available set [13], [15]. There is no definitive standard for defining the available set [53], and often it is chosen arbitrarily [3]. SSAs consider the movement limitations of the animals and use a distribution of step lengths and movement characteristics [6], [22]. However, even with the movement limitations, this assumes that the movement itself is not affected by the environment [7], which can lead to biased estimates for selection[24]. Integrated step selection analysis (iSSA) addresses this issue by using a conditional regression which then refits the movement parameters as affected by the environment [8].

Over the course of the use of resource selection models in science, the implementation of these models has been something of an enigma [32]. Not only are there multiple algorithms for fitting selection probability models, but there are also multiple ways to fit the models themselves [1], [64]. For example, the most common method for analyzing a RSA involves the fitting of a logistic model to binary data for used and available locations, but a Poisson regres-

sion may also be used to fit to count data on each cell which yields equivalent results [32]. Due to this lack of clarity, we outline multiple methods simultaneously so to retain a level of consistency for direct comparison. We use a logistic regression in all examples as it is the most widely used method.

The resource selection model being fitted in all described algorithms, also known as the utilization distribution [32], [36], is generally defined as

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2)w(\mathscr{F}(\underline{z}); \underline{\beta})d\underline{z}}, \tag{3.1}$$

which was introduced in equation 2.2 and is described in detail in Section 2.1. The two major parts that need to be fitted are the available distribution [40] $(K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2))$ and the environmental covariate selection weighting $(w(\mathscr{F}(\underline{x}); \underline{\beta}))$. These two components are typically determined separately; however they can be also estimated simultaneously (Sections 3.8 and 3.10). Both processes will be covered in detail below.

Missing data points within animal pathways sets are common and are often caused by the environment and technological failures [32]. These missing point pose a problem for analysis, as methods often required fixed time intervals. When points are missing, the time intervals are no longer consistent across the data set. RSA can be applied to data sets with missing points, however SSA and iSSA require fixed time intervals. Continuous methods, such as discrete-time and continuous-time movement models, similar to the one described in Chapter 1. But in regards to resource selection analysis, the proposed algorithm follows the same structure as RSA, SSA, and iSSA, yet is adaptable to cases with missing information.

In this chapter we first outline the necessary tools for resource selection models, followed by three existing algorithms to fit resource selection models and one novel algorithm. The necessary tools include the simulation of pathways, with pre-specified selection and movement parameters, and the maximum likelihood estimators used to determine initial estimates for the

movement parameters. The existing methods are resource selection analysis, step selection analysis, and integrated step selection analysis. The proposed algorithm is called missing point selection analysis. For all examples, we use simulated data that is repeated consistently for comparisons. The implementation of all algorithms is done in R, with detailed R code given in Appendix A.5 for each algorithm. Descriptions of the code are given in the following sections using equations and flow charts for generalization.

3.2   Simulated Pathways

For each example used in the analysis, we simulate pathways with known and consistent movement and selection parameters in order to see if the estimates match the actual parameters. Example pathways can be seen in Figures 3.1 and 3.2. The simulated pathways are influenced by the environment, with the simulated animal selecting for higher values of a single environmental covariate for our example. For illustrative purposes, only a single environmental covariate is used. However this is not a restriction of the method, which can be applied to models with multiple explanatory variables. The environmental covariate is modelled as a bivariate normal distribution, centered at the origin that is not affected by any bias (covariance is zero), and is therefore symmetric. The standard deviation of the environmental covariate value distribution is also preset and deterministic. A contour diagram of the environmental covariate can be seen in Figure 3.1.

The simulated pathways were first initialized with several parameters, including the mean of the environmental covariate, standard deviation of the environmental covariate, animal movement parameters ($\underline{\beta}$), and the animal's starting location, as described in Table 3.1. These are all constants set before simulating the pathway and are appointed by the user. The covariate is defined as

$$\mathscr{F}(\underline{x}) = \frac{1}{2\pi\sigma_e^2} \exp\left[-\frac{1}{2}\left(\frac{(x_1(t_i) - \mu_e^1)^2}{\sigma_e^2} + \frac{(x_2(t_i) - \mu_e^2)^2}{\sigma_e^2} \right) \right] \qquad (3.2)$$

with variance σ_e, and mean (μ_e^1, μ_e^2). This shape a symmetric, bivariate normal distribution. The random number seed is set to the same fixed value before each simulation to get the same realization of the stochastic process.

The generation of the pathway was completed using the package Sim.Diffproc [30] in R, which can be used to simulate a two-dimensional SDE. The SDE used is given in the form

$$d\underline{X}(t) = \underline{c}(\underline{X}(t), t)dt + \sqrt{2d}d\underline{W}(t) \tag{3.3}$$

where $\underline{c}(\underline{X}(t))$ is the advection/drift term, $\sqrt{2d}$ is the diffusion term, and $\underline{W}(t)$ is a Weiner process. This equation was derived in Section 2.4.2 in Chapter 2 (equation 2.90). Selection by the animal is introduced through β_{cov}, which is the selection for (or against) a specific habitat type, and the intercept value β_0. These two parameters determine the shape and magnitude of selection in the probability of selection model. The probability of selection model for our examples takes the shape of a logistic function, and is defined as

$$w(\mathscr{F}(\underline{x}); \underline{\beta}) = \frac{\exp(\beta_0 + \beta_{cov}\mathscr{F}(\underline{x}))}{1 + \exp(\beta_0 + \beta_{cov}\mathscr{F}(\underline{x}))}. \tag{3.4}$$

From Section 2.4.2, advection term is

$$\underline{c}(\underline{X}(t), t) = \gamma\beta_{cov}\frac{\nabla w(\mathscr{F}(\underline{x}); \underline{\beta})}{w(\mathscr{F}(\underline{x}); \underline{\beta})}. \tag{3.5}$$

Therefore the advection term is defined as the following given the environmental covariate in equation 3.2, with $\underline{x} = (x_1, x_2)$,

$$\underline{c}(\underline{X}(t), t) = \gamma\beta_{cov}\frac{\frac{1}{2\pi\sigma_e^2}\exp\left[-\frac{1}{2}\left(\frac{(x_1(t_i)-\mu_e^1)^2}{\sigma_e^2} + \frac{(x_2(t_i)-\mu_e^2)^2}{\sigma_e^2}\right)\right]\left(\frac{-x_1(t_i)}{\sigma_e^2}\right)}{1 + \exp\left(\beta_0 + \beta_{cov}\frac{1}{2\pi\sigma_e^2}\exp\left[-\frac{1}{2}\left(\frac{(x_1(t)-\mu_e^1)^2}{\sigma_e^2} + \frac{(x_2(t)-\mu_e^2)^2}{\sigma_e^2}\right)\right]\right)}. \tag{3.6}$$

As discussed in Section 2.4, the diffusion term yields

$$\sqrt{2d} = \sqrt{\gamma}. \tag{3.7}$$

The SDE includes the given selection of the animal to the environmental covariate, which can be seen in Figures 3.1 and 3.2, as it centers around the

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Parameter	Symbol	Value
Diffusion	$\sqrt{2d}$	1
Selection Intercept	β_0	-10
Selection Coefficient	β_{cov}	50
Starting location, x axis	$x_1(t_0)$	1
Starting location, y axis	$x_2(t_0)$	1
Environmental Covariate mean, x axis	μ_e^1	0
Environmental Covariate mean, y axis	μ_e^2	0
Environmental Covariate variance	σ_e	1

Table 3.1: The parameters for the SDE simulation for the generation of simulated animal pathways. These values are determined before simulation of the SDE by the user. These values result in a pathway with selection towards higher values of the environmental covariate, which peak at (0,0).

origin (vertex of the environmental covariate).

The pathways described in this section provide the data to be analyzed by the four algorithms in this Chapter. By simulating multiple pathways with the same selection and movement parameters we avoid any effects that the unique pathways have on the analysis and allow for the extrapolation of the parameters. By simulating pathways with known parameters we can assess estimation accuracy with ease, without confounding variables.

3.3   Available-Distribution Fitting

The available-distribution from the utilization-distribution describes the animal's movement when unaffected by the characteristics of the environment. Another way to interpret the available-distribution is the probability density function of a random walk given a starting location. In order to apply most of the selection algorithms described below, we must first have an estimate for the animal's movement without the influence of the environment on selection. We assume that the animals do not have an intrinsic directional bias and that the movement is isotropic, so the probability density function has zero mean and is symmetric and normal with variance $\sigma^2(\tau) = 2\gamma\tau$.

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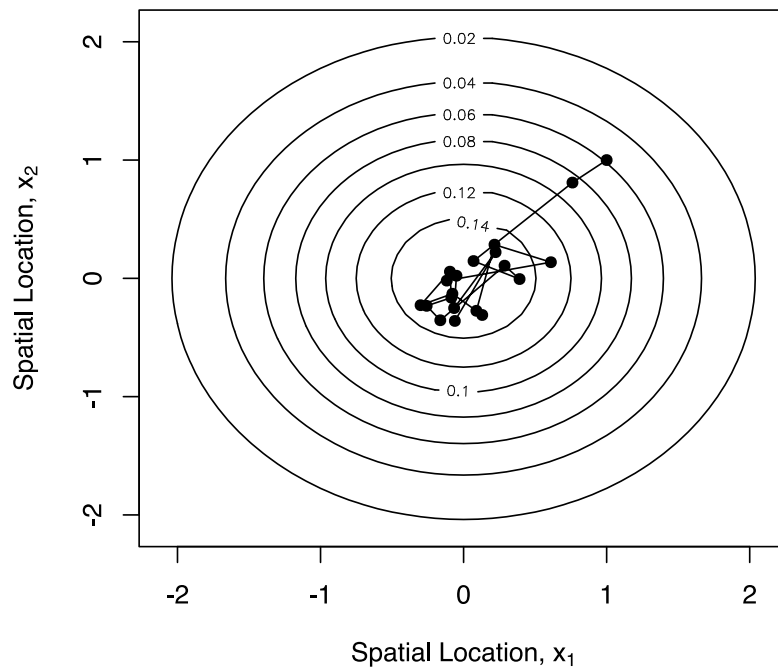
Figure 3.1: Contour lines for the environmental covariate used in all examples. The environmental covariate follows a two-dimensional normal distribution with no directional bias, and is centered at the origin and therefore the peak is at the origin. The environmental covariate has a variance of $\sigma_e = 1$ and a $\underline{\mu}_e$ of (0,0). An example pathway is shown for 20 time steps with selection and movement parameters matching those shown in Table 3.1.
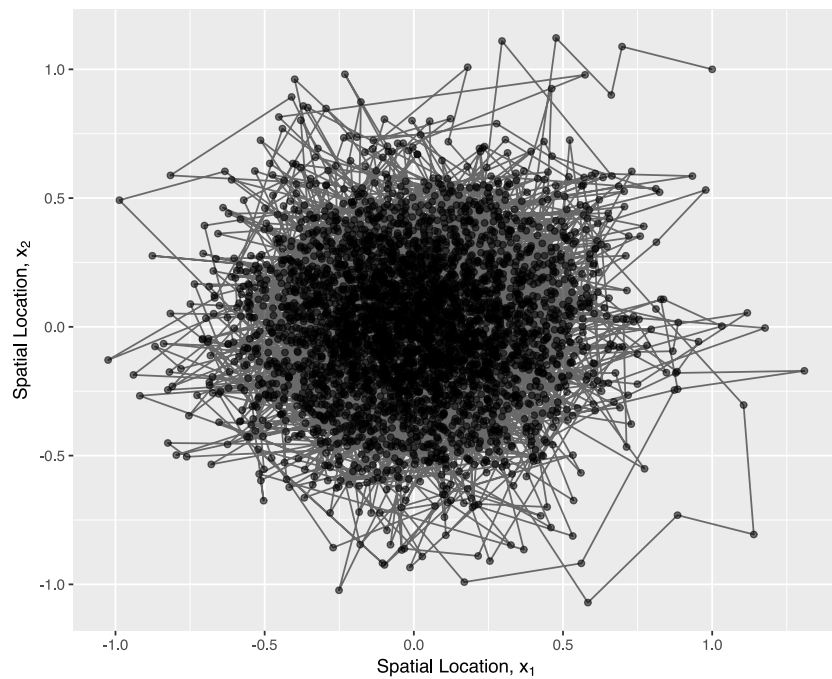
Figure 3.2: A simulated pathway with 2^{12} steps with parameters described in Table 3.1. The animal begins at (1,1) and has selection towards the origin, where the environmental covariate value is at its maximum. Note the tendency to move towards the origin due to positive selection for high environmental covariate values. The points have a transparency, so the darker the points, the more overlap in those locations. The τs for this simulation are all 0.1.

In order to apply these methods to pathways in one dimension, set x_2 in all equations to be zero. If the data has a fixed-time interval τ, set $\tau_j = \tau$.

In order to fit a normal distribution to the animal movement observed in telemetry data, we require an estimate for the distribution's γ value. Here we determine how to fit a bivariate normal distribution by finding the maximum likelihood estimator for γ, based on the location and time step data from animal pathways. We assume that the movement is isotropic, that is $\sigma_1 = \sigma_2$, where σ_1^2 is the variance in the x_1 direction and σ_2^2 is the variance in the x_2 direction. We assume that $\rho = 0$ for this bivariate normal, so the distribution is symmetric. An estimate for ρ could used to introduced as a directional bias (e.g. migrational behaviours) and would be of interest to future studies.

For the bivariate normal, we define the standard deviations as

$$\sigma_2 = \sqrt{\gamma\tau} = \sigma_1, \tag{3.8}$$

which means the variance will be the same in both spatial directions and therefore symmetric. The overall variance is given by $M_2(\tau) = \sigma^2 = \sigma_1^2 + \sigma_2^2 = 2\gamma\tau$ (see also equation A.13 with $\sigma_1^2 = m_{2,0}(\tau)$ and $\sigma_2^2 = m_{0,2}(\tau)$). The availability distribution is defined as the bivariate normal distribution, which is:

$$K(\underline{x} - \underline{y}; \mu, \gamma\tau) = \frac{1}{2\pi\gamma\tau} e^{-\frac{1}{2}\left(\frac{(x_1-y_1)^2}{\gamma\tau} + \frac{(x_2-y_2)^2}{\gamma\tau}\right)} \tag{3.9}$$

Given a series of independent steps from $(x_1(t_{i-1}), x_2(t_{i-1}))$ to $(x_1(t_i), x_2(t_i))$ with time steps $\tau_i = t_i - t_{i-1}$, $1 \leq i \leq n$. The likelihood of the data given in the model is defined as

$$
\begin{aligned}
L &= \prod_{j=1}^{n} \frac{1}{2\pi\gamma\tau_j} e^{-\frac{1}{2}\left(\frac{(x_1(t_j)-x_1(t_{j-1}))^2}{\gamma\tau_j} + \frac{(x_2(t_j)-x_2(t_{j-1}))^2}{\gamma\tau_j}\right)} \\
&= \frac{1}{(2\pi\gamma\tau_j)^n} e^{-\frac{1}{2}\sum_{j=1}^{n} \frac{(x_1(t_j)-x_1(t_{j-1}))^2}{\gamma\tau_j} + \frac{(x_2(t_j)-x_2(t_{j-1}))^2}{\gamma\tau_j}}.
\end{aligned}
\tag{3.10}
$$

Taking the log transform yields

$$l = - n \ln(2\pi\gamma) + \ln(\sum_{j=1}^{n} \frac{1}{\tau_j})$$
$$- \frac{1}{2\gamma} \sum_{j=1}^{n} \frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j}, \tag{3.11}$$

where $l = \log(L)$.

We assume that $\mu = 0$ and taking the derivative of the log likelihood in terms of γ, which gives us

$$\frac{\partial l}{\partial \gamma} = -n\gamma^{-1} - \frac{1}{2}\gamma^{-2} \sum_{j=1}^{n} \frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j} \tag{3.12}$$

Now solving for γ to get the MLE $\hat{\gamma}^2$,

$$0 = -n\gamma^{-1} + \frac{1}{2}\gamma^{-2} \sum_{j=1}^{n} \frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j} \tag{3.13}$$

$$\tag{3.14}$$

Solving for γ yields

$$\hat{\gamma} = \frac{1}{2n} \sum_{j=1}^{n} \frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j}. \tag{3.15}$$

In order to show that this is indeed a maximum, we use the second derivative test, which yields

$$\frac{\partial^2 l}{\partial \gamma^2} = n\gamma^{-2} - \gamma^{-3} \sum_{j=1}^{n} \frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j} \tag{3.16}$$

$$= -\gamma^{-1}(-n\gamma^{-1} + \frac{1}{2}\gamma^{-2} \sum_{j=1}^{n} (x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2$$
$$+ \frac{1}{2}\gamma^{-2} \sum_{j=1}^{n} \frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j}. \tag{3.17}$$

Evaluating at $\hat{\gamma}$ yields

$$\frac{\partial^2 l}{\partial \gamma^2}\Big|_{\gamma=\hat{\gamma}} = -\hat{\gamma}^{-1}\left(-n\hat{\gamma}^{-1} + \frac{1}{2}\hat{\gamma}^{-2}\sum_{j=1}^{n}\frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j}\right)$$

$$- \frac{1}{2}\hat{\gamma}^{-3}\sum_{j=1}^{n}\frac{(x_1(t_j) - x_1(t_{j-1}))^2 + (x_2(t_j) - x_2(t_{j-1}))^2}{\tau_j}$$

$$< 0$$

$$(3.18)$$

Note that the first term on the right hand side of this equation equals zero due to equation 3.13. Because 3.18 is always less than 0, we have a maximum.

Using a maximum likelihood estimator, we can determine a $\hat{\gamma}$ value, which gives the largest possible value for l. In this section, the $\hat{\gamma}$ is a constant value.

3.4   Resource Selection Analysis Overview

The method of resource selection analysis (RSA) [43], first introduced by Manly [42], attempts to determine if selection for habitat types is exhibited by animals through the use of spatio-temporal data [3]. Selection is identified by comparing the ratio of locations known to be used by the animal to locations that were available to the animal [40]. That is, the use and availability are treated as non-negative functions that affect the density of use by individuals [32]. RSAs are routinely used by ecologists to estimate habitat selection using telemetry data [13], [38], [62], with the relative ease of implementation being a key attraction to the method [53].

The probability of selection is found through a generalised linear model, meaning the selection is translated as an intercept value β_0 and β_j coefficients associated with each tested environmental parameter. The vector of $\underline{\beta}$ values can be found in multiple ways [32]. The first method and most common method, is to apply a logistic regression to the binary presence/absence values. The second most common method is to count the number of times the animal is in each cell and then fit a Poisson model. Both of these methods produce

comparable $\underline{\beta}$ values [32]. Other methods of analysis do exist, but are much less common in ecology, so we focus on the first, and simplest, method.

The main idea of using a logistic regression to fit the probability of selection is to treat the observed (used) locations and the not selected (available) locations as binary data (b), with 1 representing the used locations and 0 representing the available locations [32]. This binary data is then set as the responding variable. The explanatory variables are the environmental characteristics, that can be either categorical or scalar, for the corresponding used and available locations. RSA assumes that the observed locations of the animal are independent and identically distributed random variables. By using the logistic regression, the model is $b \sim \text{Bern}(p)$ where $\text{logit}(p) = \beta_0 + x_i \underline{\beta}$ for $i = 1, ..., n+1$ total binary observations. The code required to fit such a model only requires a single line in R, which is part of the attraction for the use of this type of analysis [32], which resulted in more common use compared fitting the model directly using maximum likelihood estimators. The comparison of used points to available points has been shown to give comparable estimates for the likelihood function [38].

3.4.1 Relative Probability of Selection versus Probability of Selection

After a logistic regression has been applied for the resource selection analysis, the researcher can apply the results to obtain either a relative probability (not restricted to being less than 1.0) or a true probability for the probability that an animal chooses a specific location [39]. The most common method is the relative probability of selection of a location by an animal, which is given by

$$P_{relative} = w(\mathscr{F}(\underline{x}); \underline{\beta}) = \exp \sum_{i=1}^{n} \beta_i \mathscr{F}(X_i), \qquad (3.19)$$

where $P_{relative}$ is the relative probability of selection, n is the number of environmental covariates, β_i is the fitted coefficient, and $\mathscr{F}(X_i)$ is the environ-

mental covariate value at location X_i. The exponential model has no upper bound, therefore the values of selection must be compared to each other to be meaningful and for the relative level of selection to be determined. Typically the p-values in this case are important to conclusions from the model, that is the exponential model is better at determining which environmental covariates are significant rather than the exact effect of the environmental covariate.

It is also important to note that β_0 value is meaningless in this case, meaning it is non-identifiable. Using the $P_{relative}$ in the utilization distribution,

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2)w(\mathscr{F}(\underline{z}); \underline{\beta})d\underline{z}} \tag{3.20}$$

$$= \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)\exp(\beta_0 + \sum_{i=1}^{n}\beta_i\mathscr{F}(\underline{x}))}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2)\exp(\beta_0 + \sum_{i=1}^{n}\beta_i\mathscr{F}(\underline{z}))d\underline{z}} \tag{3.21}$$

$$= \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)\exp(\beta_0)(\sum_{i=1}^{n}\beta_i\mathscr{F}(\underline{x}))}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2)\exp(\beta_0)\exp(\sum_{i=1}^{n}\beta_i\mathscr{F}(\underline{z}))d\underline{z}} \tag{3.22}$$

$$= \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)\exp(\sum_{i=1}^{n}\beta_i\mathscr{F}(\underline{x}))}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2)\exp(\sum_{i=1}^{n}\beta_i\mathscr{F}(\underline{z}))d\underline{z}} \tag{3.23}$$

we can see that β_0 cannot be calculated because it cancels from terms in the numerator and denominator, and thus have no effect on the probability of selection.

By way of contrast, the logistic model gives a true probability; that is the integral over the landscape will equal to 1. The model is given by

$$P = w(\mathscr{F}(\underline{x}); \underline{\beta}) = \frac{\exp(\beta_0 + \sum_{i=1}^{n}\beta_i\mathscr{F}(X_i))}{1 + \exp(\beta_0 + \sum_{i=1}^{n}\beta_i\mathscr{F}(X_i))}, \tag{3.24}$$

where P is the probability of selection. This model does give and estimate for β_0, meaning we have a "base" level estimate in addition to the effect of each of the environmental covariates. The advantage of using the logistic model over the exponential model is clear through the true probability instead of the relative probability, though the advantage of having a β_0 should not be overlooked. It is not much more difficult to implement the logistic model compared to the exponential. The exponential model is the most common because of

tradition and perceived ease of implementation, despite it's shortcomings [32]. We will use the logistic model for the remainder of this Chapter for consistent comparison across all four algorithms, as a β_0 estimate is required for the proposed algorithm in Section 3.10.

3.5 Resource Selection Analysis Methods

We apply the RSA algorithm directly to simulated animal pathway data in this section. First we outline the specific steps used in this example, which are shown in Figure 3.3. A total of three steps, Sections 3.5.1 to 3.5.3, are applied to simulated animals pathways generated using the methods and parameters given in Section 3.2. Results from the applied RSA are given in Section 3.5.4.

3.5.1 Step 1: Determine Used Points

This step is to assign the numerical values for presence, that is the used points. Under a new column, named 'presence/absence', a '1' is assigned for each data point collected. RSA requires that the length of time between location measurements to be sufficiently long enough to be considered independent identical random variables indicating where the animal is found in space. Should that assumption be violated for the individual being analyzed, a subset of that data should then be taken such that the assumption is reasonable. For each 'used' point, we also require the environmental covariates for that location. A separate column with the environmental covariates that corresponds with the 'presence/absence' column and contains the values (categorical or scalar) of those environmental characteristics is then determined.

3.5.2 Step 2: Generate Available Points

As previously mentioned, there are several options to simulate the available points for RSA. There is very little consensus on the method to use, mostly because availability can highly vary between species and even individuals. Two methods are to use the estimated home range or to determine a range around each point that is determine, somewhat arbitrarily, an acceptable distance [3].
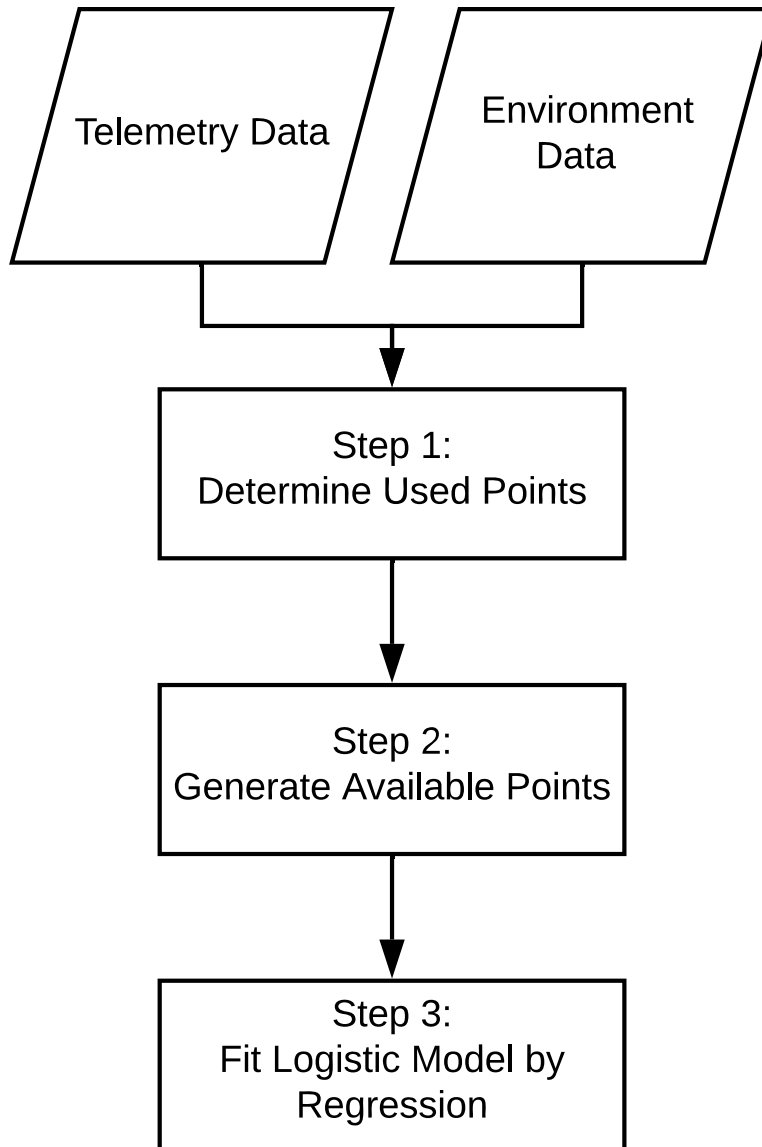
Figure 3.3: The steps for RSA used in this section for analysis of the pathways described in Section 3.2. There are two set of inputted data, telemetry data of the animal locations, and environment data of the values of relevant environmental covariates in corresponding spatial locations to the telemetry data.

We consider three different methods for generating available points: (I) minimum convex hull (Figure 3.4), (II) circles centered around each individual point (Figure 3.5) with a radius of the maximum step length, and (III) a circle centered at the origin with a radius of 1.4 (Figure 3.6). The radius is chosen as two standard deviations for the known movement parameter ($\gamma = 1$) for five time steps ($\tau = .5$). Two standard deviations, $2\sqrt{\gamma\tau} = 1.4$, were chosen as to encompass approximately 95% of the possible locations that the animal would move under the null hypothesis that there is no habitat selection.

For the first method, we use a home range estimate of a minimum convex hull. The available points are chosen uniformly from the convex hull. The second method draws available points uniformly from a circle with a radius of the maximum step length. The final method find a circle of radius 2σ, where $\sigma^2 = \gamma\tau$ and $\gamma = 1$, is to uniformly draw available points, centered at the radius which is the same location of the peak of the covariate. σ is found using the MLE outlined in Section 3.3.

Any available simulated points are assigned a '0' under the 'presence/absence' column created in step 1. The corresponding covariate values is then found for the new available locations.

3.5.3 Step 3: Fit Logistic Model by Regression

The next step is to fit the effect of the environmental covariates to the presence/absence of the animal via. logistic regression using the column 'presence/absence' as the responding variable and the environmental covariates as the explanatory variable. This type of regression may also include mixed effects, random effects, offsets, etc. when appropriate. The model fits the log-odds, l, given by

$$\log \frac{P}{1 - P} = \beta_0 + \sum_{i=1}^{\eta} \beta_i \mathscr{F}(X_i) \tag{3.25}$$

where p is the probability that the presence/absence equals 1, β_0 for the intercept, and β_i is the environmental covariate i coefficient, and $\mathscr{F}(X_i)$ is the envi-

46
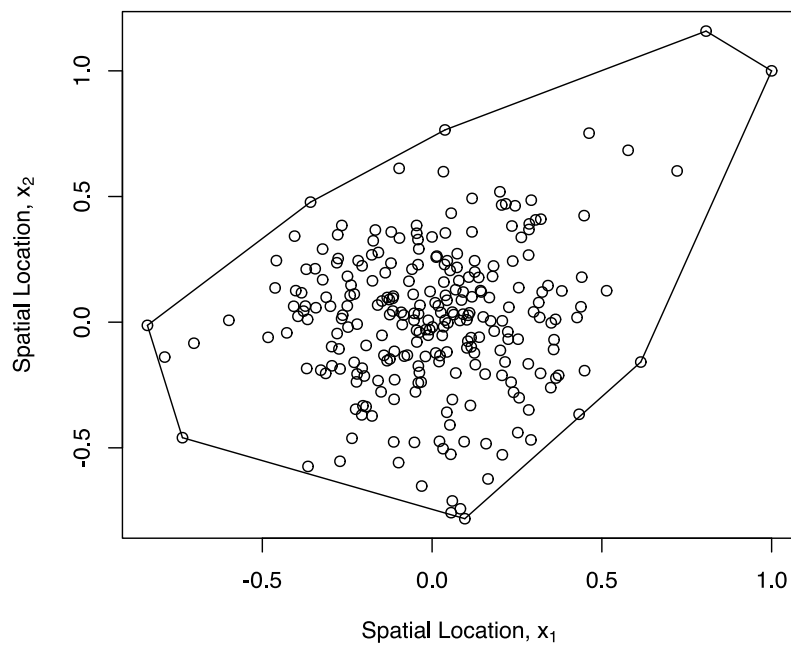
Figure 3.4: The convex hull around the used points of an an example animal pathway. All used points are within the boundary, which is treated as a pseudo home-range. In our examples, any available points are selected from within the convex hull.
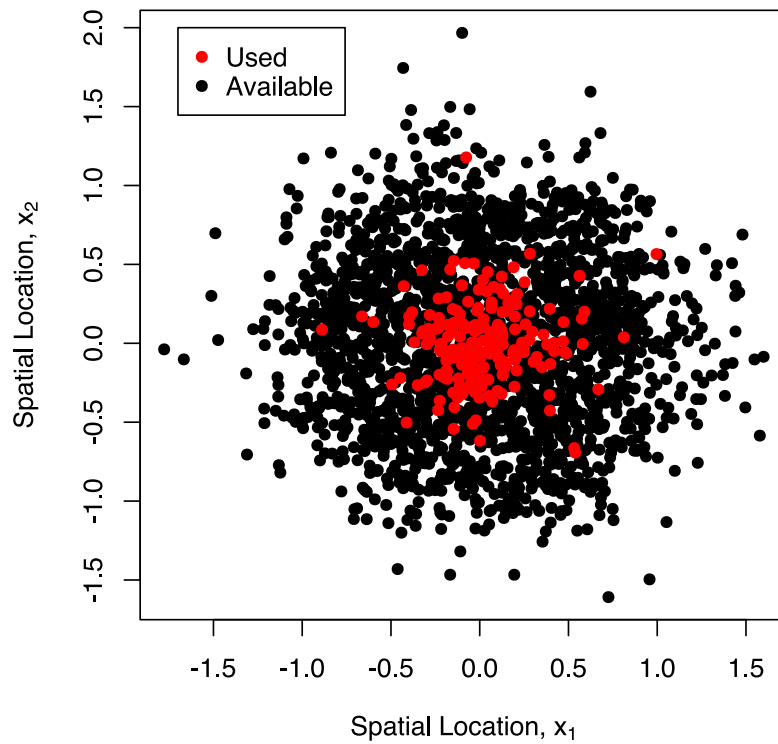
Figure 3.5: The available points generated for RSA II. In this case, circles with a radius of the maximum step length are drawn around each used point and the available points are selected from within that circle.
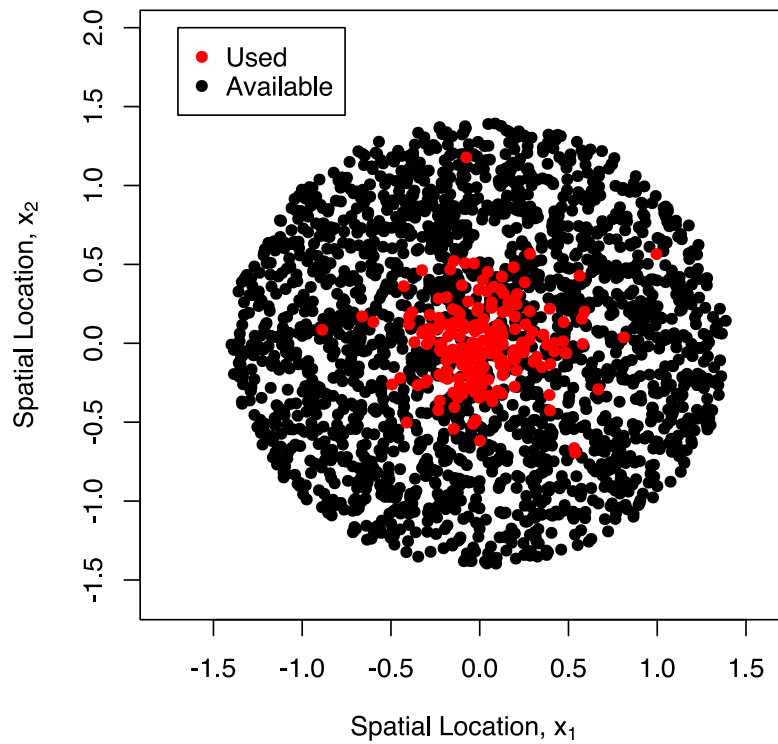
Figure 3.6: The available points generated for RSA III. In this case, a circle centered at the origin of radius 4.47 is used to select the available points. The available points are randomly selected uniformly from the circle.

ronmental covariate value at location X_i. Equation 3.26 comes from equation 3.25. This method uses a linearization of the model called the logit transform, and then fits the now linear data and is the standard approach for generalized linear models.

In our examples, we use $\eta = 1$. Once the $\underline{\beta}$ coefficients, here just β_0 and $\beta_1 = \beta_{cov}$, have been estimated, we can input them back into the probability of selection model, for example

$$w(\mathscr{F}(\underline{x}); \underline{\beta}) = \frac{\exp \beta_0 + \sum_{i=1}^{n} \beta_i \mathscr{F}(Xi)}{1 + \exp \beta_0 + \sum_{i=1}^{n} \beta_i \mathscr{F}(Xi)} \tag{3.26}$$

to determine the probability that an animal uses a specific location $(\underline{X_i})$. This model, in conjunction with the newly fitted $\underline{\beta}$ values, can also be applied to an entire landscape to show probability of selection over the entire map. The resulting map of probabilities of selection are then open to interpretation depending the the study purpose and species.

3.5.4   Example Results

We ran multiple simulations of the pathways given in Section 3.2 and analyzed them using the RSA methods outlined above and in Figure 3.3. For defining the available points, we use all three methods, a convex polygon on the used pathways points, circles around each point, and a circle centered at the origin. The results were run on different pathways, however all were initialized under the same conditions and had the same selection parameters.

Pathways are originally 2^{10} points, but in order to assume independence, every other point in the pathway was removed, changing the time interval from 0.1 to 0.5, thus the pathways are 205 steps. 10 available points are generated for each used point. The pathways are simulated and analyzed 300 times, and results are shown as sampling distributions in Figure 3.7.

RSA I, II, and III all provide fairly similar estimates for the selection parameters. All three under-estimated the β_0 and over-estimated the β_{cov}. In

Method	Parameters	Variance	Bias	MSE
RSA I	β_0	1.1248	-4.7647	23.824
	β_{cov}	52.783	25.956	726.3
RSA II	β_0	1.2373	-4.4247	20.812
	β_{cov}	61.132	39.003	1582.1
RSA III	β_0	1.0435	-4.8828	24.882
	β_{cov}	49.643	45.547	2124

Table 3.2: A comparison of the mean squared error (MSE), bias, and variance of the parameter estimates for RSA I, II, and III on the exact same data. The total path length was 2^{10} steps with 10 available points per used. The true value for γ is 1, β_0 is -10, and β_{cov} is 50.

Table 3.2, the lowest MSE for β_0 is RSA II and the lowest MSE for β_{cov} is RSA I. This makes it more difficult to determine which method is the most accurate. All three methods have fairly similar variance and bias as well.

3.6 Step Selection Analysis Overview

The term 'step selection analysis', first coined by Fortin et al [26], was introduced as an alternative to RSA. For RSA, it is assumed that the animal locations are independent and identically distributed random variables, which requires either the data to be sub-sampled or sufficiently long time intervals, which is intrinsically difficult to determine what is appropriate for each species/individual. SSA, however, assumes that the steps taken can be described by a Markov process, possibly depending also on the previous step taken. Therefore it does not assume that the locations are independent [54]. This difference means that there is a change in the way the available points are generated, and the available points are now limited by a estimated movement distribution describing the animal's possible next location. That is, the available points are now influenced by physically reasonable location as determined by the data points themselves. SSA is quite popular and well used [62], but development in the theory and the definition of the formal differences between SSA and RSA took quite some time [54].
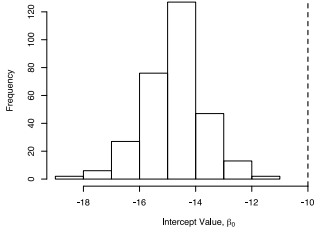
(a) RSA I, β_0 Estimate
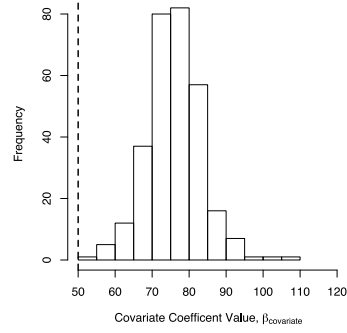
(b) RSA I, β_{cov} Estimate
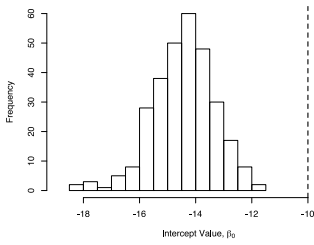
(c) RSA II, β_0 Estimate
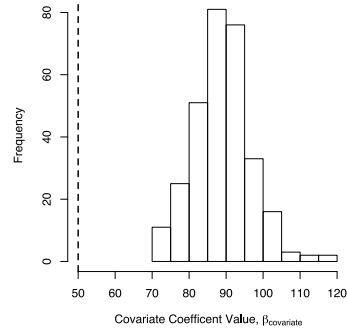
(d) RSA II, β_{cov} Estimate
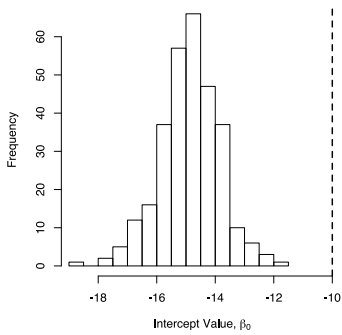
(e) RSA III, β_0 Estimate
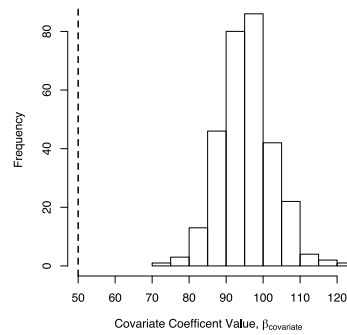
(f) RSA III, β_{cov} Estimate

Figure 3.7: The sampling distributions of the parameter estimates for RSA I (minimum convex hull), RSA II (circle for each point), and RSA III (circle centered at origin). Each RSA method was applied to 300 unique pathways of length 2^{10} points and a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed vertical lines.

SSA defines the availability distribution using empirical step lengths associated with the telemetry data [32]. The available points used are selected randomly using the fitted availability distribution centered at each step in the animal pathway. We proceed as we did with RSA by comparing the used points to the available points. Currently, there are two methods to fit the probability of selection model for an SSA, which are effectively equivalent [38]. Both methods require the used and available points to be determined first, but the inference step differs. We cover both of these methods, and highlight the difference between the two in the section below.

3.6.1 First Method: Define Likelihood and Maximize

With this method we write a direct expression for the likelihood associated with observing $\underline{X}$ given the model and parameters $(m, \gamma, \underline{\beta})$. We then maximize the likelihood. This method assumes that each step is independent. The probability of observing the data given the model and parameters is thus

$$L = \Pi_{i=0}^{n-1} f(\underline{X}_{i+1}^{U}, \underline{X}_{i}^{U}; \gamma, \tau, \underline{\beta}). \tag{3.27}$$

where f is given by equation 2.2.

3.6.2 Second Method: Monte-Carlo Approximation

This method uses logistic regression to fit the $\underline{\beta}$ values to the data plus the simulated points, rather than fitting the likelihood function directly to the data. The full process that we implement is shown in Figure 3.9. The first step is to estimate the dispersal parameters μ (or $\underline{\mu}$) and σ^2 for the available distribution (Section 3.3). This is achieved by fitting the available distribution function $K(\underline{a}; \underline{\mu}, \sigma^2)$ to the observed displacements are: $\underline{a}_{1i} = \underline{x}_{1i} - \underline{y}_{1i}$ and $\underline{a}_{2i} = \underline{x}_{2i} - \underline{y}_{2i}$. This fit can be achieved using the method of maximum likelihood. However, as discussed in the next section, the displacements $\underline{a}_i$ are influenced by the weighting function w according to the utilization distribution

$$f_{\underline{a}}(\underline{a}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) \propto K(\underline{a}; \underline{\mu}, \sigma^2) w(\mathscr{F}(\underline{a} + \underline{y}); \underline{\beta}). \tag{3.28}$$
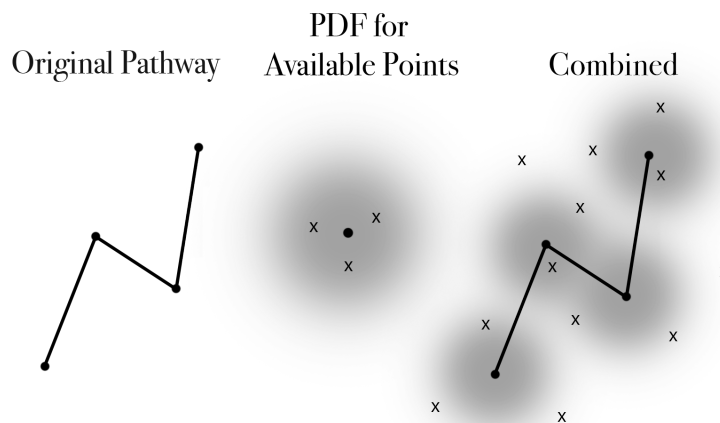
Figure 3.8: The original animal pathway is shown on the left with the black points being the used locations. The middle image is the probability density function for the probability that an animal moves to a location. The x's represent the generated available points, with three available points per used point. On the far right multiple PDFs and available points are shown.

Once K is fitted, this function is used to generate "available" data points for each $\underline{X}_i^U$. These points indicate how the animal would have moved in the absence of habitat preference (Figure 3.8). Several absence points are generated for each presence point. It is assumed that the available distribution is fitted for the dispersal parameters of the data and movement is not affected by the habitat preference $w(\mathscr{F}(\underline{x}); \underline{\beta})$.

The logistic regression requires two possible dependent variable values, often 0 or 1. In the case of step selection analysis, 0 represents a point that is available and 1 represents a point that was selected.

The logistic function itself is defined be equation 3.25. The regression finds the $\underline{\beta}$ values that then maximize the probability of the known presences/absences. The $\underline{\beta}$ values are found using optimization methods, such as

Nelder-Mead, on the likelihood function which is given by

$$L(\underline{\beta}|\underline{X}^U) = \Pi_{i=1}^n (1 + \exp[-\sum_{j=1}^{\eta} \beta_j \mathscr{F}_j(\underline{X}_i^U)])^{-1}. \qquad (3.29)$$

Note that the available distribution is determined before the likelihood model in both cases. In either cause, the fitted $K(\underline{x}-\underline{y}; \mu, \sigma^2)$ function will be used to determine the probability density function from which we generate the available steps.

3.6.3 Marginalization of the Spatial Influence ($\underline{y}$)

During SSA, the available distribution and the weighting function are fitted separately. Thus our utilization distribution

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) = \frac{K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2) w(\mathscr{F}(\underline{x}); \underline{\beta})}{\int K(\underline{z} - \underline{y}; \underline{\mu}, \sigma^2) w(\mathscr{F}(\underline{z}); \underline{\beta}) d\underline{z}} \qquad (3.30)$$

is fitted in separate parts and ignores the interaction between selection and movement. We show here the effect of this separation and the implications for the estimation of the utilization distribution.

Given a distribution of starting locations described by probability density function $g(\underline{y})$, the expected step length distribution becomes

$$\int_\Omega f_{\underline{a}}(\underline{a}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) g(\underline{y}) d\underline{y} \propto K(\underline{a}; \underline{\mu}, \sigma^2) \int_\Omega w(\mathscr{F}(\underline{a} + \underline{y}; \underline{\beta})) g(\underline{y}) d\underline{y} \qquad (3.31)$$

(see equation 3.28) and thus does not, in general, equal $K(\underline{a}; \underline{\mu}, \sigma^2)$. However standard SSA assumes that K provides a sufficiently close approximation, which, as we will show, is not always the case. The need for such an approximation is side-stepped in Section 3.8 where integrated step selection analysis (iSSA) is introduced.

3.7 Step Selection Analysis Methods

In this section we apply SSA to simulated animal pathways that follow the structure described in Section 3.2 to estimate the movement and selection
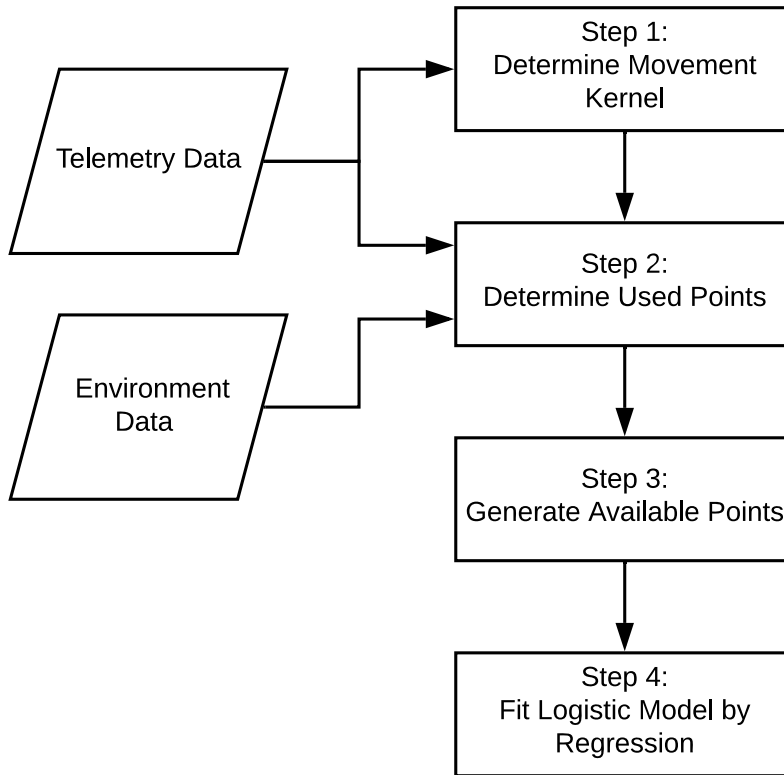
Figure 3.9: The steps followed in the SSA that is implemented for the examples in this section. There are four steps, that end in estimates for β_0, β_{cov}, and γ. There are two sets of inputted data, telemetry data of the animal's known locations, and the environmental characteristics of the desired environmental covariates associated with those locations.

parameters. SSA is comprised of four steps, described in Sections 3.7.1 to 3.7.4, with results from our example given in Section 3.7.5. All SSA steps are shown in Figure 3.9.

3.7.1 Step 1: Determine Movement Kernel

The movement kernel K is fit using the animal movement steps and maximum likelihood. The exact method is given in Section 3.3 with equations 3.10 through 3.15. This equation fits a two-dimensional normal distribution and finds γ. Slower animals have a smaller γ, while faster animals have a larger γ. While the available distribution follows a normal distribution in this example, this shape is not the only option, for example gamma and exponential

distributions are also options [8]. The distribution is the one most appropriate for the specific individuals/species analyzed because it has the property of robustness (Appendix A.1). The movement kernel is typically the same for every used point and requires a fixed-time interval in order to choose available points consistently and logically. This step gives the distribution of points available to the animal at each time step.

3.7.2   Step 2: Determine Used Points

Similar to RSA, the used points come from the animal pathway, and are assigned a value of '1' in a new column here called 'presence/absence', however here are assumed dependent. The environmental covariate values of the associated locations are also assigned in this step.

3.7.3   Step 3: Generate Available Points

Using the fitted available distribution (Step 1), the available points are generated randomly from the fitted distribution using the γ estimate from step 1. The number of points generated is determined by the user (see Section 3.12). Each available point is assigned a '0' under the 'presence/absence' column with the corresponding environmental covariate values in other columns.

3.7.4   Step 4: Fit Logistic Model for Selection by Regression

For the logistic regression, the response variable is the 'presence/absence' column and the explanatory variables are the desired environmental covariates. Again a logistic model is used to determine the probability of selection because the logistic model gives a true probability of selection. The details here are identical to Section 3.5.3 as the major difference between RSA and SSA lies in the determination of the available locations.

3.7.5   Example Results

The code for the steps described above was applied to simulated pathways that follow the conditions described in Section 3.2. 300 pathways were simu-

lated for each pathway length (n). Each pathway analyzed is initialized with the same parameter values. The pathways are 2^{10} steps long and 10 available points are generated for each used point. The β_0 and β_{cov} estimates around determined during step 4 (Section 3.7.4) using a logistic regression, however the γ estimates are found using MLEs when the available distribution was fitted in step 1 (Section 3.7.1).

The sampling distributions of the parameter estimates are shown in Figure 3.10. The true value is shown by a vertical dashed line. SSA over-estimated β_0 and under-estimated β_{cov}, but both of the distributions have a small overlap with the true value. The γ estimate, however, is not close to the true value, consistently underestimating the value seemingly on average by 25%. This bias in the γ estimate is likely due to the exclusion of the influence of the environment on the movement parameter.

3.8   Integrated Step Selection Analysis Overview

Integrated step selection analysis (iSSA) was introduced to address limitations of SSA, specifically issues with the fitting of the movement kernel [8]. The iSSA method has many similar aspects to SSA; however it also fits the step length during the regression. This estimation is accomplished by first assuming a movement model, generating available points, then fitting a logistic model using a conditional regression, which also refits the movement parameters.

Similar to SSA, iSSA assumes the steps are dependent, that is the location of the previous location affects the subsequent location. To avoid the marginalization discussed in Section 3.6.3 found in SSA, the available distribution and selection term are estimated simultaneously. The utilization term of the available distribution and selection term can be expressed as

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) \propto K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2) w(\mathscr{F}(\underline{x}); \underline{\beta}). \qquad (3.32)$$
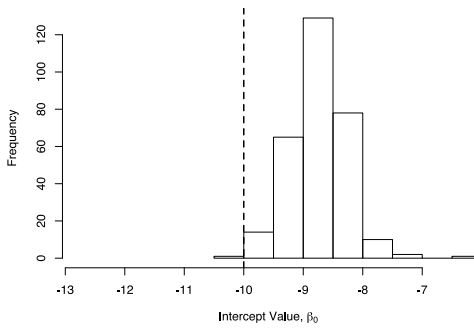
(a) SSA β_0 Estimate
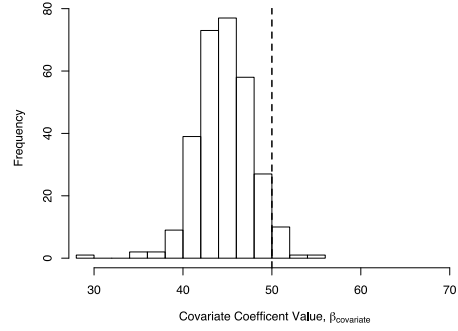
(b) SSA β_{cov} Estimate
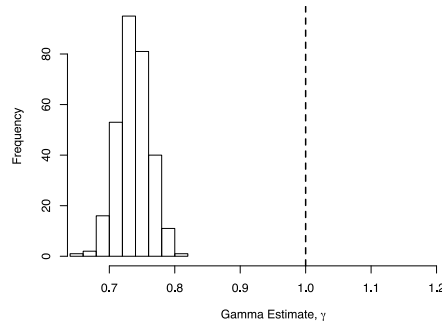
(c) SSA γ Estimate

Figure 3.10: The sampling distributions of the parameter estimates for SSA. SSA was applied to 300 unique pathways of length 2^{10} points and a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed vertical lines. The β_{cov} estimate overlaps with the actual value, which means it is a relatively accurate estimate. However, the estimate for β_0 was consistently above the true value and γ was consistently below the true value.

This utilization distribution is expressed as

$$f(\underline{x}, \underline{y}; \underline{0}, \sigma^2, \underline{\beta}) \propto \exp[b_1 l^2 + \beta_0 + \beta_1 \mathscr{F}(\underline{x}) + ... + \beta_n \mathscr{F}(\underline{x})] \qquad (3.33)$$

where $l = |\underline{x} - \underline{y}| = |\underline{a}|$ is the step length, and b_1 is the movement coefficient arising from the normal dispersal kernel equation 3.9 so $b_1 = 1/\sigma^2$.

A more general form of the iSSA which includes the possibility of gamma and log-normal distributed distributed movement kernels [8] takes the form

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) \propto \exp[b_1 l^{b_2} + b_3 \ln l + b_4 l + \beta_0 + \beta_1 \mathscr{F}(\underline{x}) + ... + \beta_n \mathscr{F}(\underline{x})] \quad (3.34)$$

iSSA uses a conditional logistic regression rather than a logistic regression to account for the effect of the environment on movement [8]. The conditional logistic regression model takes the form

$$\log \frac{P}{1 - P} = \alpha_1 + \alpha_2 z_2 + ...\alpha_s z_s + \beta_1 x_1 + ... + \beta_n x_n \qquad (3.35)$$

where α are conditions for the data set, z is a binary indicator for each strata, and s is the number of conditions [61]. The conditional logistic regression estimates both the βs and the αs. Thus, the odds ratio for each covariate can be found that are adjusted for the conditions. The intercept in conditional logistic regression is unidentifiable, and cannot be estimated through the regression.

3.8.1 Estimating β_0

Conditional logistic regressions do not provide and estimate for an intercept because the intercept is unidentifiable. We require an intercept for the weighting function portion of the utilization distribution because a β_0 is required for the logistic weighting. As a way to still retain an intercept estimate, we use two regression, first a conditional logistic regression with the explanatory variables step lengths and the environmental covariate values, and second a logistic regression with an offset that matches the fitted β values from the

first regression.

If our weighting is

$$w(\mathscr{F}(\underline{x}), \underline{\beta}) = \frac{\exp[\beta_0 + \beta_1\mathscr{F}(\underline{x}) + ... + \beta_n\mathscr{F}(\underline{x})]}{1 + \exp[\beta_0 + \beta_1\mathscr{F}(\underline{x}) + ... + \beta_n\mathscr{F}(\underline{x})]} \qquad (3.36)$$

then let

$$c_1 = \frac{\exp(\beta_0 + \sum_{i=1}^{n} \beta_i\mathscr{F}(\underline{x}))}{1 + \exp(\beta_0 + \sum_{i=1}^{n} \beta_i\mathscr{F}(\underline{x}))}. \qquad (3.37)$$

Simplifying,

$$c_1(1 + \exp(\beta_0 + \sum_{i=1}^{n} \beta_i\mathscr{F}(\underline{x}))) = \exp(\beta_0 + \sum_{i=1}^{n} \beta_i\mathscr{F}(\underline{x})) \qquad (3.38)$$

Thus,

$$c_1 = \exp(\beta_0 + \sum_{i=1}^{n} \beta_i\mathscr{F}(\underline{x}))(1 - c_1), \qquad (3.39)$$

and so

$$\exp(\beta_0 + \sum_{i=1}^{n} \beta_i\mathscr{F}(\underline{x})) = \frac{c_1}{1 - c_1} = c_2. \qquad (3.40)$$

Therefore c_2 is the form we input in the conditional regression, and from this calculate $c_1 = \frac{c_2}{(1+c_2)}$. Note that we square the step lengths before input into the conditional regression in equation (3.38).

3.9 Integrated Step Selection Analysis Methods

The five steps of iSSA used are described in Sections 3.9.1 to 3.9.5 and are visually depicted in Figure 3.11. The results from iSSA are given in Section 3.9.6.

All the examples in this section do not include an additional turning angle in the model for simplicity and consistency amongst our examples. The steps used for these example analyses are outlined in Figure 3.11 in a flow chart.
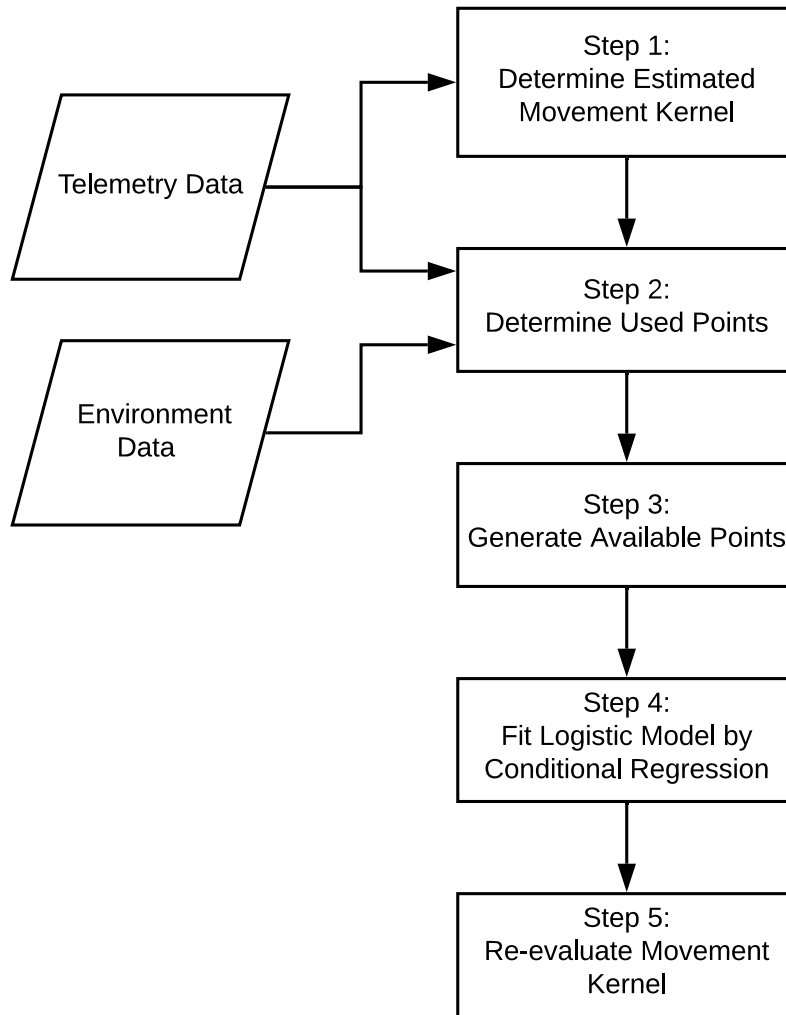
Figure 3.11: The steps followed in the iSSA that is implemented for the examples in this section. There are five steps, that end in estimates for β_0, β_{cov}, and γ. There are two sets of inputted data, telemetry data of the animal's known locations, and the environmental characteristics of the desired environmental covariates associated with those locations.

3.9.1 Step 1: Determine Estimated Movement Kernel

The iSSA method requires an initial estimate of the movement parameters. These are needed for the movement kernel which is used to give "available" points. Therefore, the first fit of the movement parameters, using MLEs, uses the same method as SSA. However with iSSA this movement parameter is only an initial estimate which is used to locate "available" points, and is then subsequently refit to include the effect of selection. The iSSA method requires that step length must be able to be written as an exponential function (see equation 3.39).

Once the shape is decided upon, MLEs can be used to fit the distribution to the data. We focus on the half-normal distribution for our example. The fitting for the MLEs is the same as Section 3.7.1, except we need the step lengths for the conditional regression. A 'strata' column, which is an identification number connecting corresponding used and available points, is also required. The strata number will eventually associate the used points to the corresponding available points. The strata column for the used points will just go from 1 to the number of points, so each point has its own identification number. That is, each used point has a strata identification number that corresponds to the same strata number for the available points generated for that used point. The strata values are required in the conditional regression to match the conditions between the corresponding used and available points.

3.9.2 Step 2: Determine Used Points

As with SSA, a new data set named 'presence/absence' is created which will contain a 1 corresponding to each used point and a 0 for each available point once generated. The used points will also have the corresponding environmental covariate values. iSSA requires fixed time intervals [8], thus any points that violate this assumption must be removed.

3.9.3 Step 3: Generate Available Points

Available points are simulated from the fitted distribution in step 1, using the fitted step length and possibly turning angle. Once simulated, the available points are given a value of '0' under the 'presence/absence' column. For iSSA, a strata value is required that corresponds to the used point that was the center of the available point, that is they will have the same strata number.

3.9.4 Step 4: Fit Logistic Model for Selection by Conditional Regression

The conditional logistic regression is run with the 'presence/absence' column as the responding variable, the environmental covariate columns and the movement parameters as the explanatory variables, and the 'Strata' column as the strata. Due to the use of a conditional logistic regression, no β_0 value is returned. Since the movement parameters and selection parameters are fit at the same time, the fitted term from the utilization distribution here defined as

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) \propto K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2) w(\mathscr{F}(\underline{x}); \underline{\beta}) \tag{3.41}$$

where $K(\underline{x} - \underline{y}; \underline{\mu}, \sigma^2)$ is the available distribution and $w(\mathscr{F}(\underline{x}); \underline{\beta})$ is the selection term. The general model for $f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta})$ is

$$f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta}) \propto \exp[b_1 l^{b_2} + b_3 \ln l + b_4 l + \beta_0 + \beta_1 \mathscr{F}(X) + ... + \beta_n \mathscr{F}(X)] \tag{3.42}$$

where $f(\underline{x}, \underline{y}; \underline{\mu}, \sigma^2, \underline{\beta})$ is the utilization distribution, l is the step length, and b_1 through b_4 are the movement coefficients. The significance and values of the movement coefficients determine the shape of the movement distribution. The possible movement distributions can be adjusted by choosing which movement coefficients to include. In this case, half normal distribution is assumed, thus $b_3 = b_4 = 0$ and $b_2 = 2$. The model for the half-normal distribution is

$$f(\underline{x}, \underline{y}; \underline{0}, \sigma^2, \underline{\beta}) \propto \exp[b_1 l^2 + \beta_1 \mathscr{F}(X) + ... + \beta_n \mathscr{F}(X)]. \tag{3.43}$$

where $b_1 = 1/\sigma^2$.

3.9.5 Step 5: Re-evaluate Movement Kernel

In order to determine the new estimate for γ, the relationship between the original γ estimate, called $\hat{\gamma}$, and selection needs to be identified. The utilization function, given by

$$f(\underline{x}, \underline{y}; \underline{0}, \sigma^2, \underline{\beta}) = \frac{\exp\left[-\frac{l^2}{2\hat{\gamma}} + b_1 l^2\right] \exp[\beta_0 + \beta_1 \mathscr{F}_1(x) + ... + \beta_n \mathscr{F}_n(x)]}{\int \exp\left[-\frac{l_1^2}{2\hat{\gamma}} + b_1 l_1^2\right] \exp[\beta_0 + \beta_1 \mathscr{F}(z) + ... + \beta_n \mathscr{F}_n(z)] dz} \tag{3.44}$$

where b_1 is the coefficient for the step length $l = |\underline{x} - \underline{y}|$, $\hat{\gamma}$ is the initial γ estimate, and the denominator step length of $l_1 = |\underline{z} - \underline{y}|$. The model that is fitted for the conditional logistic regression is

$$f(\underline{x}, \underline{y}; \underline{0}, \sigma^2, \underline{\beta}) = \frac{\exp\left(-\frac{l^2}{2\gamma\tau}\right) \exp(\beta_0 + \beta_1 \mathscr{F}_1(\underline{x}) + ... + \beta_n \mathscr{F}_n(\underline{x}))}{\int_\Omega \exp\left(-\frac{l_1^2}{2\gamma\tau}\right) \exp(\beta_0 + \beta_1 \mathscr{F}_1(\underline{z}) + ... + \beta_n \mathscr{F}_n(\underline{z})) d\underline{z}}. \tag{3.45}$$

Comparing the two, cancel the $\underline{\beta}$ expressions to get

$$\exp\left(-\frac{l^2}{2\gamma\tau}\right) = \exp\left(-\frac{l^2}{2\hat{\gamma}\tau} + b_1 l^2\right) \tag{3.46}$$

which simplifies to

$$\frac{1}{2\gamma\tau} = \frac{1}{2\hat{\gamma}\tau} - b_1. \tag{3.47}$$

b_γ is the fitted value of gamma from the original movement kernel fitting, that is it's the original estimate for gamma. Letting

$$b_l = \frac{1}{2\gamma\tau} = \frac{1}{2\hat{\gamma}\tau} - b_1 \tag{3.48}$$

then the $\underline{l}$ value fitted from the conditional regression for the step length describes the change in the new γ estimate from the original γ estimate. So finally, the new gamma estimate is

$$\gamma = \frac{1}{2b_l\tau}. \tag{3.49}$$

3.9.6   Example Results

The code for the steps described above was applied to simulated pathways that follow the conditions described in Section 3.2. 300 unique pathways were simulated with time step 0.1 and with 2^{10} steps. 10 available points are generated for each used point. In iSSA, the γ values are determined twice, once to generate available points and second to get final estimates of the movement parameters using a conditional regression. However, the selection parameters, β_0 and β_{cov}, are determined once in the conditional regression. Thus, the movement parameter estimates account for the effect of the selection bias.

The sampling distributions for the parameter estimates are shown in Figure 3.12. The true values for the parameters are shown by a vertical dashed line. iSSA under-estimated the β_0 value and over-estimated the β_{cov}, which is the direct opposite of SSA. However the γ estimate overlaps with the true value and seemingly has little bias. Thus iSSA gives a more accurate estimate for γ as compared to SSA, but also affects the estimates for the selection parameters.

3.10   Missing Point Step Selection Analysis Overview

Missing point step selection analysis (MPSA) is our proposed algorithm for dealing with iSSA problems with missing data. The main idea is to simulate points in cases where a point may be missing on the animals pathway. The missing point(s) may be due to collection errors or changes in data collection times. These missing points can be problematic for SSA and iSSA because when a missing point occurs we also must remove the points after the missing time from analysis and then restart the analysis when sampling of the pathway resumes. With our proposed algorithm, no data would be removed, and instead it would be generated in these missing spaces by simulating movement. The simulated steps are generated using an SDE bridge with selection. The selection is determine by a preliminary run of iSSA to find the $\underline{\beta}$ values and a
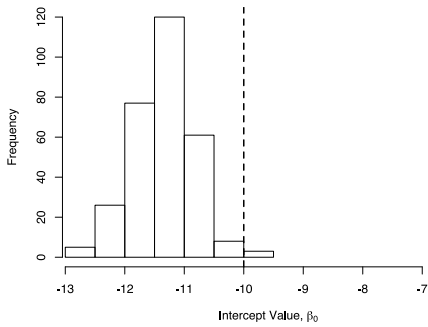
(a) iSSA β_0 Estimate
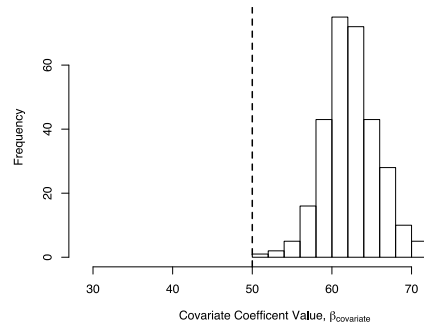
(b) iSSA β_{cov} Estimate
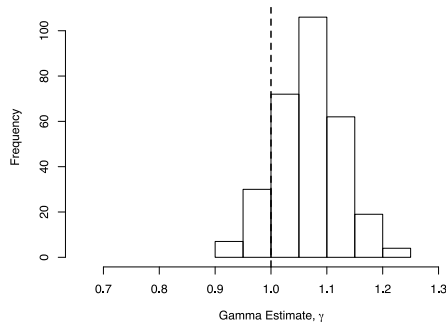
(c) iSSA γ Estimate

Figure 3.12: The sampling distributions of the parameter estimates for iSSA. iSSA was applied to 300 unique pathways of length 2^{10} points and a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed vertical lines. The γ and β_0 estimate distributions overlap with the true value, and give fairly accurate estimation. β_{cov}, however, is being over estimated.

new γ estimate.

We propose this algorithm as a way to handle data with missing points. SSA and iSSA require fixed time intervals, so the proposed algorithm adapts to variable time intervals but also follows the same structure as that used in SSA and iSSA. The key difference between MPSA and existing methods is the generation of pseudo-used points, which are points estimated to be used by the animal when it is not possible to collect data. Using the SDE bridges described in Chapter 1, we simulated pathways between known points to find a possible location the animal may have visited during the missing points. The SDE includes selection, thus the pathways are biased based on the environmental characteristics available.

3.11 Missing Point Selection Analysis Methods

MPSA is described in Section 3.2. Steps 1 to 5 are described in Sections 3.11.1 to 3.11.5 and are shown in Figure 3.13. Results for MPSA are given in Section 3.11.6.

3.11.1 Step 1: Run iSSA, Ignoring Missing Points

iSSA is run on the pathway, ignoring the points after any missing step due to the time step being larger than the fixed time interval. That is, any points that have a time-step longer than the collected time are not included as pathway steps in only this part of MPSA. iSSA requires a fixed time interval [8] and so they must be removed from the analysis. These points after the missing point are returned to the pathway after this step. The initial iSSA is to get estimates for the $\underline{\beta}$ values and γ value. The available points generated from the iSSA are discarded, but the full original pathway is reused. SSA can also be used in this step instead of iSSA, however a new γ estimate will not be found. Note, a logistic weighting is used for selection in this example.
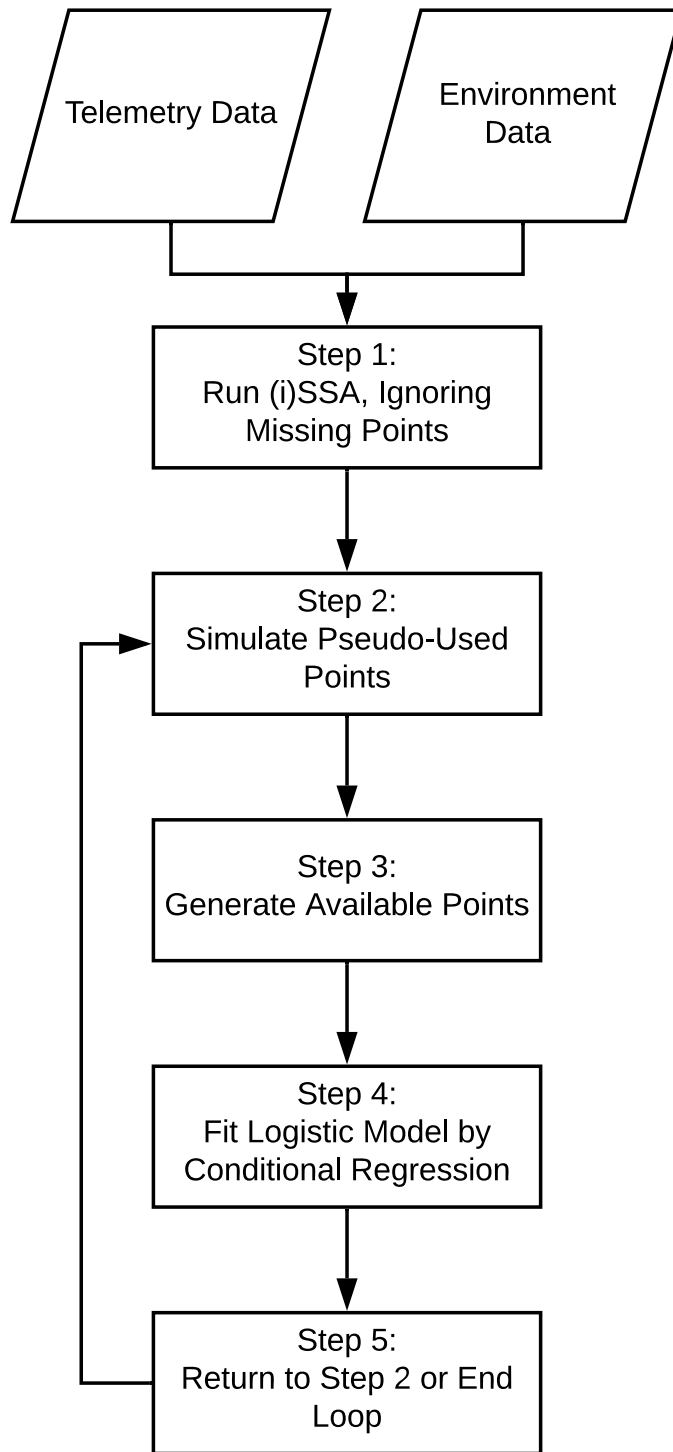
Figure 3.13: The steps followed by MPSA that is implemented for the examples in this section. There are five steps, that end with estimates for β_0, β_{cov}, and γ. There are two sets of inputted data, telemetry data of the animal's known locations, and the environmental characteristics of the desired environmental covariates associated with those locations.

3.11.2 Step 2: Simulate Pseudo-Used Points

For each time step that is missing a point, a SDE bridge is simulated and sample the bridge pathway at the missing time step. The SDE solver used is from the 'Sim.Diffproc'. The pseudo used points is labelled as a '1' under the 'presence/absence' column, allow with all pathway used points. The environmental covariate values are then found for both the used and pseudo-used points.

3.11.3 Step 3: Generate Available Points

Similar to the previous methods, available points are simulated for every used and pseudo-used point. The only variation now is the fitted γ from the iSSA in step 1 is now used to determine the movement kernel that the available point are chosen from. Each available point is assigned a '0' in the 'presence/absence' column, and the strata values and environmental covariates values are also assigned for each point.

3.11.4 Step 4: Fit Logistic Model by Conditional Regression

If iSSA was used to initialize the $\underline{\beta}$ values, a conditional regression is also used in this step. However if an SSA was used, a logistic regression is utilized. The 'presence/absence' column is the responding variable, and the environmental covariate and movement parameters are the explanatory variables. The new γ estimate is also determined from the β_l.

3.11.5 Step 5: Return to Step 2 or End Loop

Steps 2 through 5 can be repeated until the $\underline{\beta}$ values converge, or alternatively the algorithm can be stopped after the first round. For this example, steps 2 through 5 are repeated until the change in the β_{cov} is sufficiently small, here less than 3. 3 was chosen as the threshold somewhat arbitrarily, as it was small, 16.7% of the true value, yet big enough to not drastically increase computation time. The results appeared to be fairly robust to this choice,

however the sensitivity will likely vary per study.

3.11.6 Missing Point SSA Results

The code for the steps described above was applied to simulated pathways that follow the conditions described in Section 3.2. The pathways simulated have a total of 2^{10} steps each, with the missing points removed randomly with a uniform distribution. All simulations also have 10 available points per used point and the simulations end when the β_{cov} change is less than 3. There are two simulation structures: (i) missing 10% to 80% of the points and (ii) only 70% missing. For structure (i), 10 pathways are repeated for each missing percent (10% to 80%) with results shown in Figures 3.14 to 3.16. Structure (ii) repeats 300 pathways with 70% missing with results in Figures 3.17 to 3.19.

Structure (i) results are shown as box and whisker plots of the estimates for each selection and movement parameter. The true value is shown by a horizontal dashed line. As the number of missing points increase, the variation increases for SSA and iSSA. However the changes in MPSA is minimal, indicating that MPSA is more resilient to missing data. Accuracy of the estimates depends on the parameter, overall though iSSA consistently overlaps with the true value most.

Structure (i) results are presented as sampling distributions for each estimated parameter. The true value is shown by a vertical dashed line. Similar to structure (i), iSSA has the most accurate results in terms of the most overlap with the true value. SSA consistently does not estimate γ well, while iSSA and MPSA appear to provide similar γ estimates that are relatively accurate. Given large amount of missing data, MPSA can provide suitable estimates as compared to iSSA and SSA.
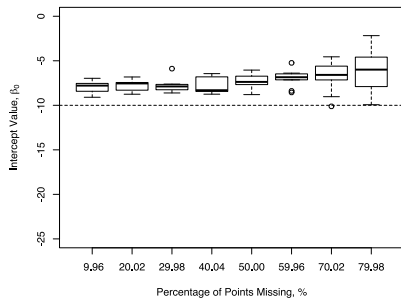
(a) Step Selection Analysis
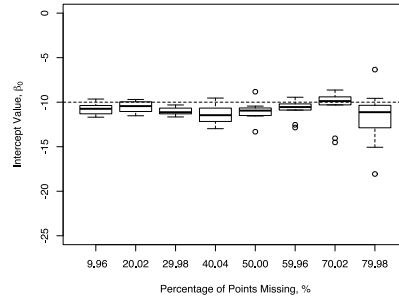
(b) Integrated Step Selection Analysis
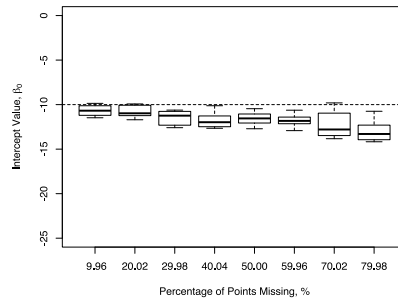
(c) Missing Point Step Selection Analysis

Figure 3.14: The β_0 estimates for all four algorithms. All algorithms were applied to 10 unique pathways for each percent of missing data points. The pathways were 2^{10} points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed horizontal lines.
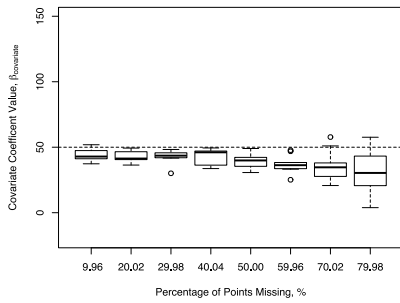
(a) Step Selection Analysis
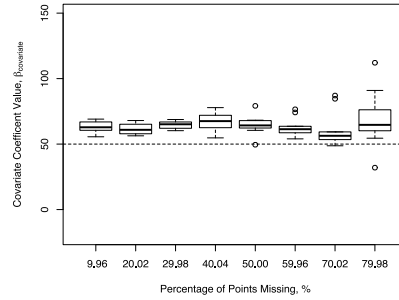
(b) Integrated Step Selection Analysis
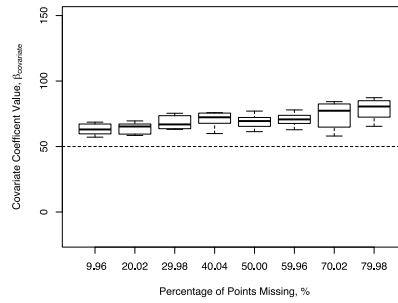
(c) Missing Point Selection Analysis

Figure 3.15: The β_{cov} estimates for all four algorithms. All algorithms were applied to 10 unique pathways for each percent of missing data points. The pathways were 2^{10} points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed horizontal lines.

(a) Step Selection Analysis

(b) Integrated Step Selection Analysis

(c) Missing Point Selection Analysis

Figure 3.16: The γ estimates for all four algorithms. All algorithms were applied to 10 unique pathways for each percent of missing data points. The pathways were 2^{10} points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed horizontal lines.

(a) Step Selection Analysis

(b) Integrated Step Selection Analysis

(c) Missing Point Step Selection Analysis

Figure 3.17: The sampling distributions of the β_0 estimates for all four algorithms. All algorithms were applied to 300 unique pathways with 70% missing. The pathways were 2^{10} points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed vertical lines.
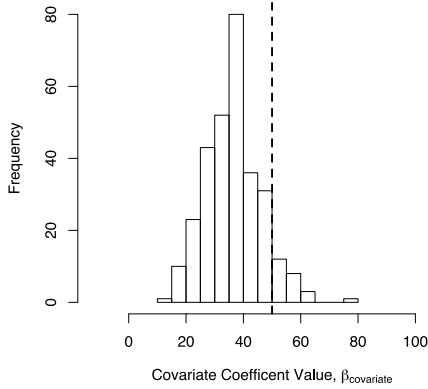
(a) Step Selection Analysis
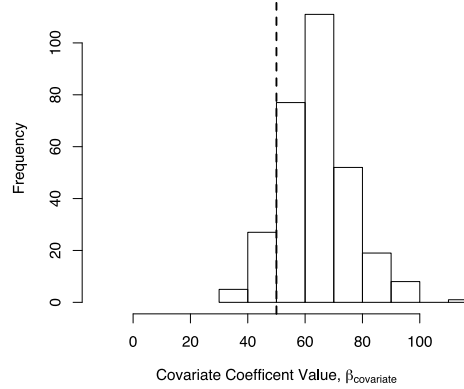
(b) Integrated Step Selection Analysis
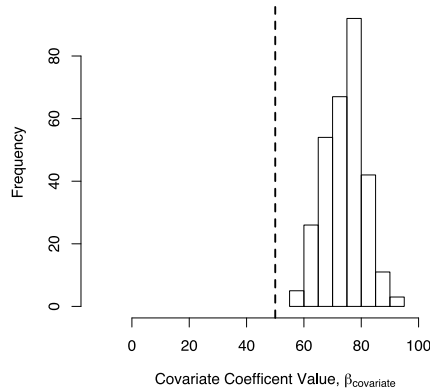
(c) Missing Point Selection Analysis

Figure 3.18: The sampling distributions of the β_{cov} estimates for all four algorithms. All algorithms were applied to 300 unique pathways with 70% missing. The pathways were 2^{10} points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed vertical lines.
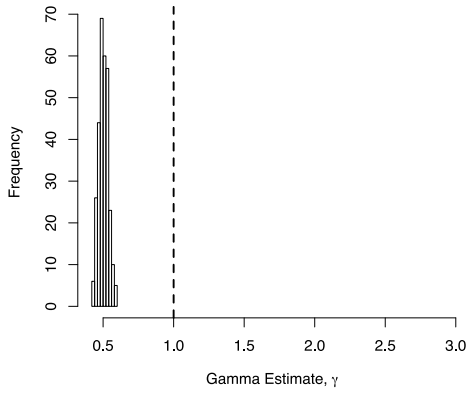
(a) Step Selection Analysis
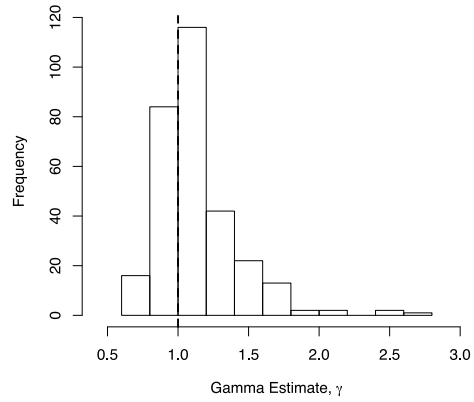
(b) Integrated Step Selection Analysis
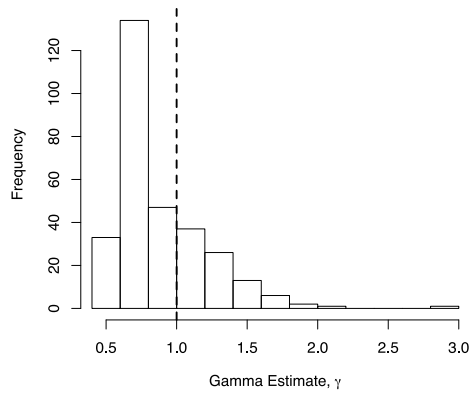
(c) Missing Point Selection Analysis

Figure 3.19: The sampling distributions of the γ estimates for all four algorithms. All algorithms were applied to 300 unique pathways with 70% missing. The pathways were 2^{10} points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed vertical lines.

Method	Parameters	Variance	Bias	MSE
SSA	β_0	2.0094	2.4222	7.8698
	β_{cov}	91.946	-13.565	275.66
	γ	0.0011043	-0.49702	0.24813
iSSA	β_0	3.2547	-1.7028	6.1435
	β_{cov}	143.05	14.188	343.87
	γ	0.079231	0.13211	0.096419
MPSA	β_0	1.0868	-2.9928	10.04
	β_{cov}	47.813	23.977	622.56
	γ	0.01522	-0.11265	0.11756

Table 3.3: A comparison of the mean squared error (MSE), mean, median, and variance of the parameter estimates for RSA, SSA, iSSA, MPSA on the exact same data. The total path length was 2^{10} steps and 70% of the data was randomly removed. RSA does not provide an estimate for γ, however all provide estimates of β_0 and β_{cov}. The true value for γ is 1, β_0 is -10, and β_{cov} is 50.

3.12 Effect of the Number of Generated Available Points

Similar to the definition of available locations, there is very little guidance to determining the number of available points that are generated [53]. Sensitivity analysis may be used as a guide to determine the sample size [43], and other studies have suggested to use of at least 10 000 total locations [1], [38], [39]. We compared the effect on all four algorithms of two different sample sizes; five available points per used point and ten available points per used point. All pathways tested were of a length of 2^{10} points and were not missing any steps (fixed-time interval). Therefore, for five available points per used point, there was a total of 5120 available points, and for forty available points were used point there was a total of 10240 available points. Pathways were simulated under the settings described in Section 3.2. A total of 300 pathways were simulated and all four algorithms were applied to the same pathways.

Table 3.4 shows the results of all four algorithms. We measure accuracy

using mean squared error, which is defined as

$$\text{MSE}(\hat{\beta}) = \text{VAR}(\hat{\beta}) + \text{BIAS}^2(\hat{\beta}, \beta) \tag{3.50}$$

where $\hat{\beta}$ is the coefficient being measured (either $\hat{\beta}_0$ or $\hat{\beta}_{cov}$) and β is the true value. Our results show that most results have a lower MSE with more available points. The only exceptions are β_0 for iSSA and MPSA which both have lower MSE with less available points.

Algorithm	Parameter	Mean Squared Error	
		5 Available Points	10 Available Points
SSA	β_0	12.081	7.8698
	β_{cov}	287.52	275.66
	γ	0.2502	0.24813
iSSA	β_0	4.7999	6.1435
	β_{cov}	370.64	343.87
	γ	0.15088	0.096419
MPSA	β_0	6.564	10.04
	β_{cov}	641.13	622.56
	γ	1.4356	0.11756

Table 3.4: The mean squared error for the movement and selection parameters estimated by all four algorithms when five available points are generated per one used point versus ten available points are generated per one used point. In most cases, the MSE is reduced when more available points are used, meaning more accurate results. 70% of the data was missing for all simulations.

3.13   Pathway Length

The pathway examples for the above sections all have a length of 2^{10}, so we now use a pathway of length 2^7 to determine the effectiveness of each algorithm with that length. Almost all other parameters were kept consistent, with $\beta_0 = -10$, $\beta_{cov} = 50$, $\gamma = 1$, $\tau = 0.1$, and 10 available points per used point. For Table A.1, 50% of the points were missing versus the 70% of the previous sections, because of convergence issues with too few points.

Figures A.1 through A.3 show that as the percentage of missing points increases, the variance of the estimates for both SSA and iSSA increases rapidly,

yet MPSA's variance stays smaller. This result is also shown in Table A.1 when comparing the variance for β_0 and β_{cov}. Thus, MPSA outperforms iSSA when the pathways are relatively short or missing a large amount of data.

3.14 Discussion and Conclusion

Using the model found in Chapter 1, we designed a novel algorithm that simulates data when there are missing points in telemetry data. The simulated data comes from pathways that include selection bias for the environment and creates bridges between two known points. The missing points are then determined and selected from along those pathways. The data is then fit to a logistic model using a logistic regression for the selection and movement parameters. The process is repeated until the change in estimates is sufficiently small.

In order to determine the relative effectiveness of the new algorithm, we compared it directly to existing methods and highlight the advantages and disadvantages of each. These result are summarized in Table 3.5. MPSA is more complicated than existing methods, and thus should be used only when the data set is missing large amounts of information. The method used should be carefully considered based on each individual study, specifically does the ecological limitations make sense for that type of analysis.

The method used to generate available points can significantly affect the results. For example, the difference between RSA I, RSA II, and RSA III demonstrate the difference in the respective sampling distributions. The number of available points can also affect the results, using the current standard of at least 10 000 points gave more accurate results in the presented example. Here we only consider a single covariate, however most studies can have several different environmental covariates. It is unclear how this would affect the estimates, and needs more investigation to determine its impact.

Our example is restricted to only two selection parameters and one movement parameter, being step length. Multiple environmental covariates may be used, as well as mixed effect models that incorporate random effect. It is also possible to include turning angles into the movement parameters, which is typically matched with a von Mises distribution [8], [54].

The assumptions and limitations of each algorithm are compared in Table 3.5. Depending on reasonable assumptions for the data collected, the most appropriate algorithms can be determined. SSA, iSSA, and MPSA have similar assumptions, but vary among the limitations. The major limitation for MPSA is that it has not been proven to converge.

Using MSE as a measure for accuracy, we compared SSA, iSSA and MPSA in Table 3.3. For β_0, iSSA was the most accurate, for β_{cov} SSA was the most accurate, and for γ iSSA was the most accurate. However, MPSA has the lowest variance for both β_0 and γ.

Algorithm	Assumptions	Limitations
RSA	- Steps are independent. - Available sampling	- Requires large time intervals or data to be a subset.
SSA	- Steps described by Markov process. - Available distribution shape. - Movement parameters are not affected by selection.	- Marginalizes y. - Requires fixed-time intervals, otherwise multiple points are discarded.
iSSA	- Steps described by Markov process. - Available distribution shape.	- Requires perfect fixed time intervals, otherwise multiple points are discarded.
MPSA	- Steps described by Markov process. - Available distribution shape.	- Not proven to converge. - Only works for missing points, not variable time intervals.

Table 3.5: An overview of the assumptions and limitations of each of the four implemented algorithms. Each algorithm has pros and cons, which should be considered before use to determine which is the most appropriate for the potential studies.

Chapter 4

Conclusion

4.1 Discussion

In this study, we first establish the connection between the probability density function for the next step of an animal, given a starting location and movement/selection parameters, also known as the utilization distribution, and a stochastic differential equation describing continuous-time movement. The stochastic differential equation was then applied to missing point selection analysis. However it is not limited only to this inferential method, and could be useful for other studies. For instance, numerical simulations of the animal's movement over continuous time could be applied by itself to studies interested in animal distribution or reactions in new/changed environments. It would be practical to know the effect of the environment on animal pathways rather than only selection.

Chapter 2 focused on establishing the connection between the utilization distribution and a stochastic differential equation model with environmental selection. This goal was accomplished by first determining the master equation, then the forward Fokker-Plank equation, and finally the SDE. The SDE can be used to simulate pathways of animal movement with the same movement and selection parameters as an established utilization distribution. One of the key applications for Chapter 3 was the simulation of bridges using the SDE between two known points.

In Chapter 3 we covered two key topics, the direct comparison of different selection algorithms on the same data with known movement and selection parameters, and the introduction of the novel algorithm called missing point selection analysis. We found that accounting for the effect of selection on movement and the amount of missing steps can both significantly affect the accuracy of the estimates. MPSA reduced the error for all parameter estimates as compared to iSSA, however did not have the lowest MSE due to some bias.

Missing points in data are common and create issues for analysis assumptions, often resulting in the discarding of data [32]. These missing points may be caused to specific environmental characteristics (e.g. forest with a thick canopy) which can result in biased estimates during selection studies [3]. If the missing data is correlated to the value of the covariate, it is possible that that simulating bridges in these missing points could help adjust for this bias. MPSA is a solution to the selection bias and should be considered especially in cases when large amount of data are missing and habitat interference is suspected. For the examples given, the initial estimate of the parameters comes from running iSSA in step 1 of MPSA. However, this step could be replaced with informed estimates of the selection parameter determined by the researcher.

Given the advantages, disadvantages, assumptions, and limitations of the methods, the key question becomes: "What algorithm should I use for my data?" The resource selection models are affected by the issues highlighted above; therefore choosing an appropriate algorithm can be tedious [53]. If movement parameters are considered to be imperative to the model, SSA, iSSA, or MPSA are clear choices. If not, then the collected locations must be considered independent, that is no correlation between known locations, for RSA to be applicable. RSA and SSA are relatively simple algorithms with fewer steps involved than iSSA and MPSA, which is an attractive feature. Due to our results showing that MPSA gives similar parameter estimates when little data is missing, it is more practical to use SSA or iSSA in this case. Should

missing points be a major concern for the data set, MPSA is a compelling choice. The weighting model used, either exponential or logistic, will result in a relative use of probability or a true probability respectively [33], [37], [39]. The true probability found using a logistic weighting allows for easier interpretation of the results and fits the data better [39], which is strong argument for its use over an exponential model. The combination of algorithm and weighting model chosen should be well justified and answer the hypotheses posed in each unique study.

4.2   Future Directions

The models outlined in this thesis can be applied to a multitude of data sets and conditions, however there is still room for advancement, such as the inclusion of the effect of memory and "personality" on selection and movement. Certain "personality" characteristics and traits may be more beneficial for individuals, for example a nervous disposition versus a bold disposition [20]. "Personalities" are increasingly no longer being associated with exclusively humans, which opens opportunities for their study in the context of movement ecology. Related to "personality" is memory, which is unique to individuals and based on previous experiences [23]. How an individual learns and remembers it's environment are increasingly being considered in movement studies [4], [21], [45], [47].

In all of the examples provided, we defined the environmental characteristics determining an animal's movement step as the values that were assigned to the endpoint of the step [25], [29], [58]. However the environmental characteristics could follow other definitions as well, such as the average of the continuous variables along the step [25], the proportion of habitats along the step [25], extreme values of continuous variable along the step [25], selected intervals along the step [19], or buffer zones of the covariate around the steps or endpoints [19], [56], [62]. Typically, these assume that the step between

two known points follow a straight line because of ease of implementation. The SDE bridges with selection described in Chapter 2 provides an alternative method for selecting covariate values used by the animal, for example by averaging the covariate values over the bridge. All of the described methods for determining covariate values impact the selection estimates and should be carefully considered as another way to introduce bias into the estimates.

Existing continuous-time methods could also be merged with our results for account for specific components not addressed here. One existing model is an Ornstein–Uhlenbeck (OU) model that accounts for the effect of long distance attraction and the effect of memory of the landscape, such as the model introduced by Wang et al. [63]. Alternatively, this same model uses an RSA to determine selection coefficients and MPSA could be used in the place of the RSA. Another key aspect of the study that introduced the OU model is the application to discrete or patch landscapes, and provides an approach to modeling movement on a patch landscape which could be used to make MPSA more versatile, as it currently requires derivatives of the environmental covariates. Smoothing methods such as kriging could also be used on the discrete or patch landscapes during MPSA to also create a continuous landscape. Existing studies could then be merged with those described here to create even more powerful and versatile movement and selection models.

The models presented in this thesis also assume that habitat selection is constant for the individual and is not influenced by any outside factors other than the environmental characteristics. Environmental characteristics that are temporally dynamic are not considered in our examples, and are rarely considered at all [7]. Constant habitat characteristic are uncommon, and temporal changes are likely to have dramatic effect on animal distributions and selection [3]. Currently no analytical methods exist for analyzing temporally dynamic environments and is an open issue that has no existing analytical solution [32].

The effect of the temporal and spatial landscape single scale on the data

collected was not addressed in our examples. However animal movement and selection is often scale dependent [28], [57]. The scale on which data is collected needs to be carefully considered as movement patterns may be discernible at only certain temporal and spatial scales [7], and should be guided by current literature on the species being studied. Sensitivity analysis in regards to scale could also help determine the impact on a specific study and may lead to an appropriate decision.

Population level selection is rarely considered, instead with the focus being on individuals that represent a subset of the population [7]. Interactions within a population may affect the movement choices through both herding and avoidance behaviours. Correlated movements may also be time-dependent, for example during breeding season. It is unclear how well individuals can be used to extrapolate behaviours to the population, and requires future work.

Finally, turning angles were not used in this study, and could be used to determine a bias for specific directions by the animal. Because turning angles may be influenced by missing steps, they were not considered here, however they can still hold key information for movement characteristics. Temporal and spatial scale, population level selection, and turning angles are of important consideration for future studies using the methods outlined and should not be overlooked.

4.3   Conclusion

Movement ecology studies are increasingly prolific amongst ecology studies [31], and therefore the number of analysis techniques have also increased. The relatively quick uptake of selection studies has resulted in confusion and mystery surrounding the techniques and their application due to a large variation in methods and their descriptions [32]. By carefully choosing the models, inferences on environmental impacts on animal movement can be formed.

Understanding environmental impacts, especially in rapidly changing environmental conditions, is paramount for species conservation and management. By increasing our understanding and tool set, scientists are better prepared to answer such big-picture questions about the future of the world's high-risk species. Our additions to this field can be taken and used to approach new and old ecological problems alike to determine their optimal solutions.

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Appendix A

Background Material

A.1 Robustness

Here we refer to robustness as the quality of a movement model not to be affected by the time intervals over which data are collected. In other words, a dispersal kernel fit to data collected at time intervals of length τ would still have the same functional form if fit to data collected as some other time interval, say 2τ, but, of course, with different parameters. Formally, robustness was defined by [60] as:

Definition Let $n \in \mathbb{N}$ be finite and $p_{t-\tau,t}(\underline{x}|\underline{y}, \underline{\theta})$ be the transition density for the probability of moving from location $\underline{y}$ to $\underline{x}$ between times $t - \tau$ and t. A movement model of the above type is *robust of degree n* if there exists an injective function $g_n : \Theta \to \Theta$ such that

$$p_{t-n\tau,t}(\underline{x}|\underline{y}, \underline{\theta}) = p_{t-\tau,t}(\underline{x}|\underline{y}, g_n(\underline{\theta})) \text{ for all } t \in T \text{ and } \underline{x}, \underline{y} \in \mathbb{R}^2 \qquad (\text{A.1})$$

In our case, we assume that animals have an underlying movement distribution (without selection) of a Gaussian, as described by

$$G(\underline{x}_i|\sigma^2, \underline{\mu}) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{1}{2}\frac{(x_i-\mu)^2}{\sigma^2}}. \qquad (\text{A.2})$$

Suppose we sample at irregular intervals for $\underline{x}_0, ..., \underline{x}_n$ at intervals $t_0, ..., t_n$. However, $\Delta t_1, t_0 \neq \Delta t_1, t_2$. Let $\sigma = \sigma(\tau_i)$.

Distribution at time t_1: $G(\underline{x}; \sigma^2(\tau_1), \underline{\mu})$

Distribution at time t_2: $G(\underline{x}; \sigma^2(\tau_2), \underline{\mu})$

Given that an individual starts at $\underline{x}_1$ at t_1, the distribution to find $\underline{x}_2$ should be $G(\underline{x}_2 - \underline{x}_1, \sigma(t_2 - t_1), \mu)$.

$t_0 \to t_1 \to t_2$ has the same distribution as $t_0 \to t_2$. That is, observation doesn't affect distribution. To do $t_0 \to t_2$, use a convolution. $K(\underline{x})$, $K_2(\underline{x})$ on real time.

$$
\begin{aligned}
K_1 * K_2 &= \int K_2(\underline{x} - \underline{y}) K_1(\underline{y}) d\underline{y} \\
&= \int K_2(\underline{x}_2 - \underline{x}_1) K_1(\underline{x}_1) d\underline{x}_1
\end{aligned}
\tag{A.3}
$$

Now taking Gaussians:

$$
G_1 * G_2
$$
$$
G_1 = G(\underline{x}_1; \sigma_1^2, \mu_1) \tag{A.4}
$$
$$
G_2 = G(\underline{x}_2; \sigma_2^2, \mu_2)
$$

then

$$
G_1 * G_2 = G(\underline{x}; \sigma_1^2 + \sigma_2^2; \mu_1 + \mu_2) \tag{A.5}
$$

In our case, $\mu = 0$. We require the following Markovian property:

$$
G(\underline{x}_2, \sigma^2(\tau_2), 0) = \int G(\underline{x}_2 - \underline{x}_1, \sigma^2(\tau_2 - \tau_1), 0) G(\underline{x}_1, \sigma^2(\tau_1), 0) d\underline{x}_1 \tag{A.6}
$$

then we know we can use

$$
= G(\underline{x}_2, \sigma^2(\tau_1) + \sigma^2(\tau_2 - \tau_1), 0) \tag{A.7}
$$

We need $\sigma^2(\tau_2) = \sigma^2(\tau_1) + \sigma^2(\tau_2 - \tau_1)$. However

$$
\begin{aligned}
\gamma^2 \tau_2^2 &= \gamma^2 \tau_1^2 + \gamma^2 (\tau_2 - \tau_1)^2 \\
\gamma^2 \tau_2^2 &= \gamma^2 \tau_1^2 + \gamma^2 \tau_2^2 - 2\gamma^2 \tau_1 \tau_2 + \gamma^2 \tau_1^2 \\
0 &= 2\gamma^2 \tau_1^2 - 2\gamma^2 \tau_1 \tau_2
\end{aligned}
\tag{A.8}
$$

$$
2d\tau_2 = 2d\tau_1 + 2d(\tau_2 - \tau_1) \tag{A.9}
$$

$\sigma(\tau) = \sqrt{\gamma \tau}$ would have property of robustness.

A.2   Moments of $K(\underline{a}; \tau)$

Let p and q be rational numbers and $\Omega = (-\infty, \infty) \times (-\infty, \infty)$. Define the moments of $K(\underline{a}; \tau)$ to be

$$m_{p,q}(\tau) = \int_\Omega a_1^p a_2^q K(\underline{a}; \tau) d\underline{a} \tag{A.10}$$

and the radial symmetric moments of $K(\underline{a}; \tau)$ to be

$$M_p(\tau) = \int_\Omega |\underline{a}|^p k(\underline{a}; \tau) d\underline{a}. \tag{A.11}$$

The second radially symmetric moment of K is

$$M_2(\tau) = \int_\Omega (a_1^2 + a_2^2) K(\underline{a}; \tau) d\underline{a} \tag{A.12}$$

$$= m_{2,0}(\tau) + m_{0,2}(\tau). \tag{A.13}$$

The diffusion scaling assumption posits that

$$\lim_{\tau \to 0} \frac{M_2(\tau)}{4\tau} = d \neq 0 \tag{A.14}$$

and

$$\lim_{\tau \to 0} \frac{m_{p,q}(\tau)}{4\tau} = 0 \tag{A.15}$$

for $p + q > 2$. Thus higher order moments become negligible as $\tau \to 0$ [11].

We make the further assumption that $K(\underline{a}; \tau)$ is a radically symmetric function. That is:

$$K(\underline{a}; \tau) = \hat{K}(|\underline{a}|; \tau). \tag{A.16}$$

This means that $K(\underline{a}; \tau)$ is an even function of a_1 (for any fixed a_2) and $K(\underline{a}; \tau)$ is an even function of a_2 (for any fixed a_1). Hence, $m_{p,q}(\tau) = 0$ for p odd and $m_{p,q}(\tau) = 0$ for q odd.

A.3 Calculation of Advection and Diffusion Coefficients in 2 Dimensions

We now calculate the 2-dimensional advection and diffusion coefficients as given by equations 2.36-2.40 where

$$f_{\underline{a}}(\underline{a}, \underline{x}; \underline{\mu}(\tau), \sigma^2(\tau), \underline{\beta}) = \frac{K(\underline{a}; \tau)w(\mathscr{F}(\underline{x} + \underline{a}), \underline{\beta})}{\int K(\underline{a}; \tau)w(\mathscr{F}(\underline{x} + \underline{a}'), \underline{\beta})d\underline{a}'} \tag{A.17}$$

as given in equation 2.56. We use a Taylor expansion of w with respect to $\underline{a}$ when computing the coefficients.

Note that

$$\frac{\partial}{\partial x_i}w(\mathscr{F}(\underline{x})) = w'(\mathscr{F}(\underline{x}))\frac{\partial \mathscr{F}}{\partial x_i} \qquad i = 1, 2 \tag{A.18}$$

and

$$\frac{\partial^2}{\partial x_i \partial x_j}w(\mathscr{F}(\underline{x})) = w''(\mathscr{F}(\underline{x}))\frac{\partial \mathscr{F}}{\partial x_i}\frac{\partial \mathscr{F}}{\partial x_j} + w'(\mathscr{F}(\underline{x}))\frac{\partial^2 \mathscr{F}}{\partial x_i \partial x_j} \qquad i, j = 1, 2 \tag{A.19}$$

In what follows, it is assumed that w and its derivatives are calculated at $\mathscr{F}(\underline{x})$, e.g. $w = w(\mathscr{F}(\underline{x}))$, $\frac{\partial w}{\partial x_i} = \frac{\partial}{\partial x_i}w(\mathscr{F}(\underline{x}))$ and so forth.

To prepare, we calculate the moments of $K(\underline{a}; \tau)w(\mathscr{F}(\underline{x} + \underline{a}))$. The zeroth moment is given by

$$\int_\Omega K(\underline{a}; \tau)w(\mathscr{F}(\underline{x} + \underline{a}))d\underline{a} = \int_\Omega K(\underline{a}; \tau)\left[w + a_1\frac{\partial w}{\partial x_1} + a_2\frac{\partial w}{\partial x_2}\right.$$
$$\left. + \frac{a_1^2}{2}\frac{\partial^2 w}{\partial x_1^2} + a_1 a_2\frac{\partial^2 w}{\partial x_1 \partial x_2} + \frac{a_2^2}{2}\frac{\partial^2 w}{\partial x_2^2} + \text{h.o.t.}\right] \tag{A.20}$$

$$= w \int_{\Omega} K(\underline{a}; \tau)) d\underline{a} + \frac{\partial^2 w}{\partial x_1^2} \int_{\Omega} \frac{a_1^2}{2} K(\underline{a}; \tau) d\underline{a} + \frac{\partial^2 w}{\partial x_2^2} \int_{\Omega} \frac{a_2^2}{2} K(\underline{a}; \tau) d\underline{a} + \text{h.o.t.}$$

$$\text{(A.21)}$$

$$= w + \frac{\partial^2 w}{\partial x_1^2} \frac{m_{2,0}(\tau)}{2} + \frac{\partial^2 w}{\partial x_2^2} \frac{m_{0,2}(\tau)}{2} + \text{h.o.t.} \tag{A.22}$$

$$= w + \left(\frac{\partial^2 w}{\partial x_1^2} + \frac{\partial^2 w}{\partial x_2^2} \right) \frac{M_2(\tau)}{4} + \text{h.o.t.} \tag{A.23}$$

$$= w + \nabla \frac{M_2(\tau)}{4} + \text{h.o.t.} \tag{A.24}$$

Moment with respect to a_i:

$$\int_{\Omega} a_1 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a} = \int_{\Omega} a_1 K(\underline{a}; \tau) \left[w + a_1 \frac{\partial w}{\partial x_1} + a_2 \frac{\partial w}{\partial x_2} \right.$$
$$\left. + \frac{a_1^2}{2} \frac{\partial^2 w}{\partial x_1^2} + a_1 a_2 \frac{\partial^2 w}{\partial x_1 \partial x_2} + \frac{a_2^2}{2} \frac{a_2^2}{2} \frac{\partial^2 w}{\partial x_2^2} + \text{h.o.t.} \right]$$

$$\text{(A.25)}$$

$$= \frac{\partial w}{\partial x_1} \int_{\Omega} a_1^2 K(\underline{a}; \tau) d\underline{a} + \text{h.o.t.} \tag{A.26}$$

$$= \frac{\partial w}{\partial x_1} m_{2,0}(\tau) + \text{h.o.t.} \tag{A.27}$$

$$= \frac{\partial w}{\partial x_1} \frac{M_2(\tau)}{2} + \text{h.o.t.} \tag{A.28}$$

Similarly
$$\int_{\Omega} a_2 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a} = \frac{\partial w}{\partial x_2} \frac{M_2(\tau)}{2} + \text{h.o.t.} \tag{A.29}$$

Moment with respect to a_i^2

$$\int_{\Omega} a_1^2 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a} = w \int_{\Omega} a_1^2 K(\underline{a}; \tau) d\underline{a} + \text{h.o.t.} \tag{A.30}$$

$$= w \frac{M_2(\tau)}{2} + \text{h.o.t.} \tag{A.31}$$

Similarly
$$\int_{\Omega} a_2^2 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a} = w \frac{M_2(\tau)}{2} + \text{h.o.t.} \tag{A.32}$$

We also require

$$\int_{\Omega} a_1 a_2 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a} = w \int_{\Omega} a_1 a_2 K(\underline{a}; \tau) d\underline{a} + \text{h.o.t.} \tag{A.33}$$

$$= \text{h.o.t.} \tag{A.34}$$

We use these results to eliminate the coefficients 2.36-2.40. So

$$\underline{c} = \lim_{\tau \to 0} \frac{1}{\tau} \frac{\int_\Omega \underline{a} K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a}}{\int_\Omega K(\underline{a}'; \tau) w(\mathscr{F}(\underline{x} + \underline{a}')) d\underline{a}'} \tag{A.35}$$

$$= \lim_{\tau \to 0} \frac{1}{\tau} \frac{\nabla w \frac{M_2(\tau)}{2} + \text{h.o.t.}}{w + \nabla^2 w \frac{M_2(\tau)}{4} + \text{h.o.t.}} \tag{A.36}$$

$$= \frac{1}{w} \nabla w \lim_{\tau \to 0} \frac{M_2(\tau)}{2\tau} \tag{A.37}$$

$$= \frac{2d}{w} \nabla w \tag{A.38}$$

and

$$d_{x_1 x_1} = \lim_{\tau \to 0} \frac{1}{2\tau} \frac{\int_\Omega a_1^2 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a}}{\int_\Omega K(\underline{a}'; \tau) w(\mathscr{F}(\underline{x} + \underline{a}')) d\underline{a}'} \tag{A.39}$$

$$= \lim_{\tau \to 0} \frac{1}{2\tau} \frac{w \frac{M_2(\tau)}{2} + \text{h.o.t.}}{w + \nabla^2 \cdot w \frac{M_2(\tau)}{4} + \text{h.o.t.}} \tag{A.40}$$

$$= \lim_{\tau \to 0} \frac{M_2(\tau)}{4\tau} + \text{h.o.t.} \tag{A.41}$$

$$= d. \tag{A.42}$$

Similarly,

$$d_{x_2 x_2} = d \tag{A.43}$$

$$d_{x_1 x_2} = \lim_{\tau \to 0} \frac{1}{2\tau} \frac{\int_\Omega a_1 a_2 K(\underline{a}; \tau) w(\mathscr{F}(\underline{x} + \underline{a})) d\underline{a}}{\int_\Omega K(\underline{a}'; \tau) w(\mathscr{F}(\underline{x} + \underline{a}')) d\underline{a}'} \tag{A.44}$$

$$= \lim_{\tau \to 0} \frac{\text{h.o.t.}}{w + \nabla^2 \cdot w \frac{M_2(\tau)}{4} + \text{h.o.t.}} \tag{A.45}$$

$$= 0 \tag{A.46}$$

Also note that, by symmetry,

$$m_{2,0}(\tau) = m_{0,2}(\tau) = \frac{M_2(\tau)}{2}. \tag{A.47}$$

Since we consider isotropic diffusion,

$$M_2(\tau) = m_{2,0}(\tau) + m_{0,2}(\tau) \tag{A.48}$$

$$= 2d\tau + 2d\tau \tag{A.49}$$

$$= 4d\tau \tag{A.50}$$

where d is the diffusion coefficient.

Method	Parameters	Variance	Bias	MSE
SSA	β_0	6.0276	2.0317	10.135
	β_{cov}	268.92	-10.646	381.36
	γ	0.0082043	-0.35818	0.13647
iSSA	β_0	9.9107	-2.2948	15.144
	β_{cov}	428.9	18.528	770.75
	γ	18.855	0.67987	19.255
MPSA	β_0	4.3294	-2.4403	10.27
	β_{cov}	198.27	20.884	633.77
	γ	13.258	0.3727	13.352

Table A.1: A comparison of the mean squared error (MSE), mean, median, and variance of the parameter estimates for RSA, SSA, iSSA, MPSA on the exact same data. The total path length was 2^7 steps and 50% of the data was randomly removed. RSA does not provide an estimate for γ, however all provide estimates of β_0 and β_{cov}. The true value for γ is 1, β_0 is -10, and β_{cov} is 50.

A.4   Pathway Length Results

The results for shorter pathways with 2^7 steps and 50% missing. The remaining parameters are consistent with the other simulations, which are $\beta_{cov} = 50$, $\beta_0 = 0$, $\gamma = 1$, 10 available points per used, and a threshold of 3.

A.5   R Code for Algorithms

A.5.1   Numerical Solution of the SDE Code

The numerical solution, described in Section 2.5, can be applied to the simulation of bridges between two known points. This results in a pathway that uses the selection given by the user to traverse between the starting and ending locations. The code to creat a single bridge is given below.

```
library(Sim.DiffProc)
set.seed(237) #set.seed(237)
cmu1 <- 0  # Covariate x1 mean
cmu2 <- 0 # Covariate x2 mean
csig <- 1 # covariate standard deviation
beta0 <- -10 # Selection intercept coefficient
beta1 <- 50 # Selection coefficient
D4 <- 1 # 4*Diffusion
xstart <- -1 # x1 starting location
```
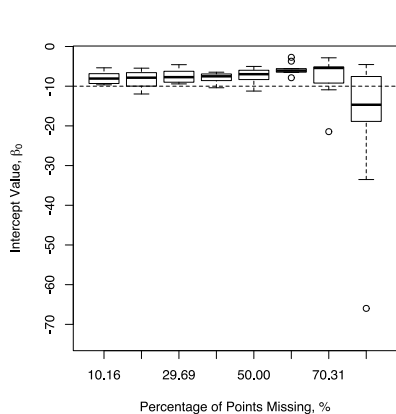
(a) Step Selection Analysis
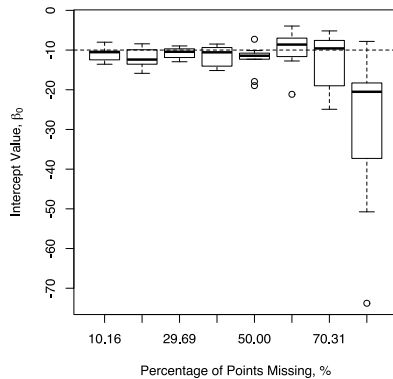
(b) Integrated Step Selection Analysis
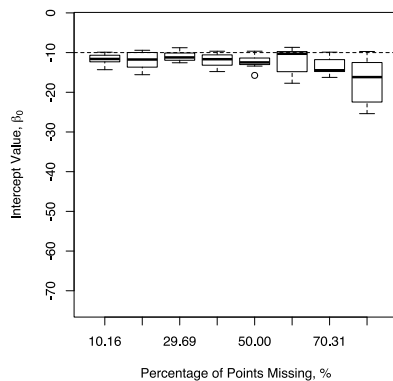
(c) Missing Point Step Selection Analysis

Figure A.1: The β_0 estimates for all four algorithms. All algorithms were applied to 10 unique pathways for each percent of missing data points. The pathways were 2^7 points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed horizontal lines.
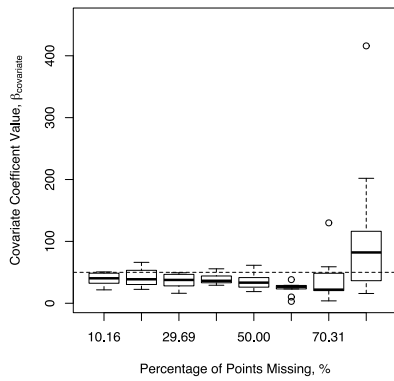
(a) Step Selection Analysis
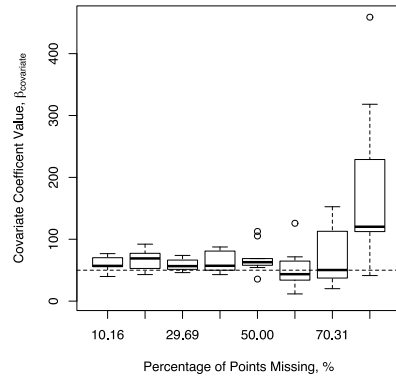
(b) Integrated Step Selection Analysis
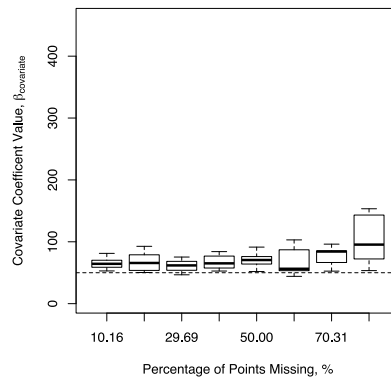
(c) Missing Point Selection Analysis

Figure A.2: The β_{cov} estimates for all four algorithms. All algorithms were applied to 10 unique pathways for each percent of missing data points. The pathways were 2^7 points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed horizontal lines.

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(a) Step Selection Analysis

(b) Integrated Step Selection Analysis

(c) Missing Point Selection Analysis

Figure A.3: The γ estimates for all four algorithms. All algorithms were applied to 10 unique pathways for each percent of missing data points. The pathways were 2^7 points and had a time step of 0.1. All pathways were simulated under the same movement and selection parameters ($\gamma = 1$, $\beta_0 = -10$ and $\beta_{cov} = 50$), shown by the dashed horizontal lines.

```
ystart <- 1 # x2 starting location
xend <- 1
yend <- 1

fx <- expression((D4*beta1*normal.2D(x=x,y=y,sig=csig)*
(-x/(csig^2)))/(1+exp(beta0 +
beta1*normal.2D(x=x,y=y,sig=csig))),
(D4*beta1*normal.2D(x=x,y=y,sig=csig)*(-y/csig^2))
/(1+exp(beta0 + beta1*normal.2D(x=x,y=y,sig=csig))))
gx <- expression(sqrt(D4),sqrt(D4)) # SDE Diffusion
res <- bridgesde2d(drift=fx,diffusion=gx,Dt=0.005,M=500)
res
summary(res)
```

A.5.2 Pathway Simulation: Code

The pathways simulated for all examples, and described in Section 3.2, uses the R code described in this section. The R code for the initialization is as follows:

```
set.seed(237)
cmu1 <- 0   #covariate x1 mean
cmu2 <- 0 #covariate x2 mean
csig <- 1 #covariate standard deviation
beta0 <- -10 #animal movement beta_0
beta1 <- 50 #animal movement beta_1 for covariate
D4 <- 1 #4*Diffusion
scale <- 2^0 #number of points per step
Npoints <- 2^16 #number of steps
Time <- 1000 #end time
xstart <- 1 #starting x1
ystart <- 1 #starting x2
availc <- 10 #number of available per used
```

The code for the SDE simulation is shown below:

```
fx <- expression((D4*beta1*normal.2D(x=x,y=y,sig=csig)*
(-x/(csig^2)))/(1+exp(beta0 + beta1*normal.2D(x=x,y=y,
sig=csig))),(D4*beta1*normal.2D(x=x,y=y,sig=csig)*(-y/csig^2))/
(1+exp(beta0 + beta1*normal.2D(x=x,y=y,sig=csig))))
gx <- expression(sqrt(D4),sqrt(D4)) # SDE Diffusion

mod2d <- snssde2d(drift=fx,diffusion=gx,x0=c(xstart,ystart),
M=1,T=Time,N=Npoints*scale)
```

```
track1 <- xstart
track2 <- ystart
for (i in 2:(Npoints+1)){
  track1[i] <- mod2d$X[scale*(i-1)+1]
  track2[i] <- mod2d$Y[scale*(i-1)+1]
}
rtime <- rep(Time/Npoints,(length(track1)-1))
totTime <- 0
repsTime <- length(rtime)+1
for (i in 2:repsTime){
  totTime[i] <- totTime[i-1]+rtime[i-1]
}
p1 = qplot(track1,track2,xlim=c(min(track1),max(track1)),
ylim=c(min(track2),max(track2))) + geom_path()
print(p1)
```

A.5.3   Resource Selection Analysis: Step 2 Code

Step 2 of RSA (Section 3.5.2) finds the convex hull of the known animal
pathway and samples available points from within that hull. The code is:

```
### RSA I ###### STEP 2 #########################
rsamat <- cbind(track1rsa,track2rsa)
# Creating a Matrix for convex hull
ch <- convex_hull(rsamat) # Convex Hull
ch1 <- cbind(ch$rescoords[,1],ch$rescoords[,2])
# Two dimensional matix of vertices
rsaav <- runif_in_polygon(Npoints*availc, ch1,
center="centroid")# Samples available points from convex hull
rsaavx1 <- rsaav[,1] # X1 locations of availables
rsaavx2 <- rsaav[,2] # X2 location of availables
rsatotx1 <- c(track1rsa,rsaavx1)
# X1 locations of available and used
rsatotx2 <- c(track2rsa,rsaavx2)
# X2 locations of available and used
rsaCOV <- 0 # Reset value
for(i in 1:length(rsatotx1)){
# For loop to find covariate values
    rsaCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
    *((rsatotx1[i]-cmu1)^2+(rsatotx2[i]-cmu2)^2))
    #finding covariate values
}
RSAAVAILABLE <- rep(0,length(rsaavx1))
# Setting available as 0
RSAUSED <- rep(1,length(track1rsa)) # Setting available as 1
RSAPRES <- c(RSAUSED,RSAAVAILABLE) # Presence/absence column
RSAdata <- data.frame(RSAPRES,rsaCOV) # RSA data frame
```

```
### RSA II ###### STEP 2 #########################
radiusrsa <- max(distance)
rsaiix1 <- 0
rsaiix2 <- 0
rsacount <- 1
for(l in 1:length(track1rsa)){
    xorigin <- track1rsa[l]
    yorigin <- track2rsa[l]
    trsa <- 2*pi*rand(availc,1);
    rrsa <- radiusrsa*sqrt(rand(availc,1));
    xrsa <- xorigin + rrsa*cos(trsa);
    yrsa <- yorigin + rrsa*sin(trsa);
    for(u in 1:availc){
        rsaiix1[rsacount] <- xrsa[u]
        rsaiix2[rsacount] <- yrsa[u]
        rsacount <- rsacount + 1
    }
}
rsaiitotx1 <- c(track1rsa,rsaiix1)
# X1 locations of available and used
rsaiitotx2 <- c(track2rsa,rsaiix2)
# X2 locations of available and used
rsaiiCOV <- 0 # Reset value
for(i in 1:length(rsaiitotx1)){
# For loop to find covariate values
    rsaiiCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
    *((rsaiitotx1[i]-cmu1)^2+(rsaiitotx2[i]-cmu2)^2))
    #finding covariate values
}
RSAIIAVAILABLE <- rep(0,length(rsaiix1))
# Setting available as 0
RSAIIUSED <- rep(1,length(track1rsa))
# Setting available as 1
RSAIIPRES <- c(RSAIIUSED,RSAIIAVAILABLE)
# Presence/absence column
RSAIIdata <- data.frame(RSAIIPRES,rsaiiCOV)
# RSA data frame
### RSA III ###### STEP 2 #########################
radiusiiirsa <- 1.4
rsaiiix1 <- 0
rsaiiix2 <- 0
rsacount <- 1
for(l in 1:length(track1rsa)){
    xorigin <- 0
    yorigin <- 0
    trsa <- 2*pi*rand(availc,1);
```

```
     rrsa <- radiusiiirsa*sqrt(rand(availc,1));
     xrsa <- xorigin + rrsa*cos(trsa);
     yrsa <- yorigin + rrsa*sin(trsa);
     for(u in 1:availc){
         rsaiiix1[rsacount] <- xrsa[u]
         rsaiiix2[rsacount] <- yrsa[u]
         rsacount <- rsacount + 1
     }
}
rsaiiitotx1 <- c(track1rsa,rsaiiix1)
# X1 locations of available and used
rsaiiitotx2 <- c(track2rsa,rsaiiix2)
# X2 locations of available and used
rsaiiiCOV <- 0 # Reset value
for(i in 1:length(rsaiiitotx1)){
# For loop to find covariate values
     rsaiiiCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
     *((rsaiiitotx1[i]-cmu1)^2+(rsaiiitotx2[i]-cmu2)^2))
     #finding covariate values
}
RSAIIIAVAILABLE <- rep(0,length(rsaiiix1))
# Setting available as 0
RSAIIIUSED <- rep(1,length(track1rsa))
# Setting available as 1
RSAIIIPRES <- c(RSAIIIUSED,RSAIIIAVAILABLE)
# Presence/absence column
RSAIIIdata <- data.frame(RSAIIIPRES,rsaiiiCOV)
# RSA data frame
```

A.5.4   Resource Selection Analysis: Step 3 Code

Step 3 of RSA (Section 3.5.3) fits a logistic model using a logistic regression to the presence/absence data. The one line of code is:

```
## RSA I ###### STEP 3 ########################
modelrsa <- glm(RSAPRES~rsaCOV,family=binomial(link=logit),
data = RSAdata) # RSA log regression
data$rsaB0[count] <- modelrsa$coefficients[1] # RSA Intercept
data$rsaB1[count] <- modelrsa$coefficients[2]
# RSA Coefficient for covariate
### RSA II ###### STEP 3 #######################
modelrsaii <- glm(RSAIIPRES~rsaiiCOV,family=
binomial(link=logit),data = RSAIIdata)
# RSA log regression
data$rsaiiB0[count] <- modelrsaii$coefficients[1]
# RSA Intercept
data$rsaiiB1[count] <- modelrsaii$coefficients[2]
```

```
# RSA Coefficient for covariate
### RSA III ###### STEP 3 #######################
modelrsaiii <- glm(RSAIIIPRES~rsaiiiCOV,family=binomial(link=
logit), data = RSAIIIdata) # RSA log regression
data$rsaiiiB0[count] <- modelrsaiii$coefficients[1]
# RSA Intercept
data$rsaiiiB1[count] <- modelrsaiii$coefficients[2]
# RSA Coefficient for covariate
##############################################
```

A.5.5 Step Selection Analysis: Step 1 Code

Step 1 of SSA (Section 3.7.1) uses MLEs to determine the σ or γ value of the unbiased movement kernel. The code for finding the σ value is as follows:

```
fit.var2D <- function(x1,x2,tau){
  n <- length(x1) #needs to match length(x2)
  #the average is the location of the starting spot
  gam <- 0
  for (i in 2:n){
    gam <- gam + ((x1[i]-x1[i-1])^2 + (x2[i]-x2[i-1])^2)
    /tau[i-1]
  }
  gam <- (1/(2*(n-1)))*gam
  gam
}
```

A.5.6 Step Selection Analysis: Step 3 Code

Step 3 of SSA (Section 3.7.3) generates the available points for the analysis using the movement kernel fitted from step 1. The function to simulate available points is:

```
det.avail2D <- function(x1,x2,gam,tau,c=5){
  #c is the number of available points per used points
  n <- length(x1)
  av1 <- 0
  av2 <- 0
  r<-1
  for (i in 1:(n-1)){
    for(j in 1:c){
      std <- sqrt(gam*tau)
      #std <- gam*tau
      av1[r] <- rnorm(1,mean = x1[i], sd = std)
      av2[r] <- rnorm(1,mean = x2[i], sd = std)
```

```
      r <- r + 1
    }
  }
  av <- data.frame(av1,av2)
  av
}
```

A.5.7 Step Selection Analysis: Step 4 Code

Step 4 of SSA (Section 3.7.4) fits a logistic model to the presence/absence data using a logistic regression. The code for our examples only includes one explanatory variable. The line for fitting the model is:

```
glm(presence~covariate1,family=binomial(link=logit))
```

A.5.8 Integrated Step Selection Analysis: Step 1 Code

Step 1 of iSSA (Section 3.9.1) fits the unbiased movement kernel using MLEs. This fitting returns a γ value. The R code is:

```
## MLE #########
gam <- fit.var2D(track1,track2,rtime)

## FIND STEP LENGTHS ##########
distance <- 0
for (i in 1:(length(track1)-1)){
  distance[i] <- sqrt((track1[i] - track1[i+1])^2
  + (track2[i]- track2[i+1])^2)
}

## STRATA #################
stratau <- c(1:(length(track1)-1))
```

A.5.9 Integrated Step Selection Analysis: Step 2 Code

Step 2 of iSSA (Section 3.9.2) finds the covariate values for the used points in the animal pathway in our examples. The code is:

```
usedX1 <- c(track1)
usedX2 <- c(track2)
USED <- rep(1,length(usedX1))
uCOV <- 0
for (i in 1:length(USED)){
  uCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))*
```

```
    ((usedX1[i]-cmu1)^2+(usedX2[i]-cmu2)^2))
}
USED <- USED[2:length(USED)]
uCOV <- uCOV[2:length(uCOV)]
```

A.5.10   Integrated Step Selection Analysis: Step 3 Code

Step 3 of iSSA (Section 3.9.3) generates the available points using the γ fitted in Step 1. It also finds the covariate values for the locations of the available points. The code is:

```
## STEP 3 ##################
availc <- 10
avail <- det.avail2D(x1=track1,x2=track2,gam=gam,tau=rtime,
c=availc)
ax1 <- avail[,1]
ax2 <- avail[,2]
distance_avail <- 0
countavail <- 1
for (i in 1:(length(track1)-1)){
  for(j in 1:availc){
    distance_avail[countavail] <- sqrt((track1[i]
    - ax1[countavail])^2+ (track2[i] - ax2[countavail])^2)
    countavail <- countavail + 1
  }
}
strataa <- rep(1:(length(track1)-1), each=availc)
totx1 <- c(track1,avail[,1])
totx2 <- c(track2,avail[,2])
availX1 <- ax1
availX2 <- ax2
timesa <- rep(rtime,each=availc)

## Finding the covariate values ########
AVAILABLE <- rep(0,length(availX1))
aCOV <- 0
for (i in 1:length(AVAILABLE)){
  aCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
  *((availX1[i]-cmu1)^2+(availX2[i]-cmu2)^2))
}

## Connecting the columns ###########
presence <- c(USED,AVAILABLE)
covariate1 <- c(uCOV,aCOV)
steplength <- c(distance,distance_avail)
strata <- c(stratau,strataa)
```

```
times <- c(rtime, timesa)
```

A.5.11 Integrated Step Selection Analysis: Step 4 Code

Step 4 of iSSA (Section 3.9.4) applies a conditional regression to fit a logistic model with the responding variable of presence/absence and explanatory variables of the covariate values and step length squared. The code is:

```
clogit(presence ~ covariate1 + steplength2 +
strata(strata))
```

Finding β_0:

```
#To find B_1
model1a <- clogit(presence ~ covariate1/(1-covariate1)
+ steplength + strata(strata))
#To find b_0
modelia <- glm(presence ~ 1 + offset(model1a$coefficients[1]*
covariate1), family = binomial(link = logit))
```

A.5.12 Missing Point Selection Analysis: Step 2 Code

Step 2 of MPSA (Section 3.11.2) simulates the SDE with the new fitted β_0 and β_{cov} values from step 1. SDE bridges are simulated in every instance where a point is missing. The code is:

```
b0 <- intercept
beta <- beta_c
ubpx1 <- 0
ubpx2 <- 0
count <- 1
for (i in 1:length(rtime)){
  if (rtime[i]>0.1){
    points <- rtime[i]/0.1
    mod <- SDE2D(y1=track1[i],rp=100,y2=track2[i],
    x1=track1[i+1],x2=track2[i+1],cmu1=cmu1,cmu2=cmu2,csig=csig,
    beta0=b0,beta1=beta,D4=gam, t0 = totTime[i],
    t1 = totTime[i+1])
    np <- ncol(mod$X)
    l <- nrow(mod$X)
    for (i in 1:(points-1)){
      spot <- round(l * (i/points))
      randp <- sample(1:np,1,TRUE)
      ubpx1[count] <- mod$X[spot,randp]
      ubpx2[count] <- mod$Y[spot,randp]
```

```
      count <- count + 1
    }
  }
}
```

A.5.13 Missing Point Selection Analysis: Step 3 Code

Step 3 of MPSA (Section 3.11.3 generates available points using the new γ value fitted in step 1. The code is:

```
avail <- det.avail2D(x1=usedX1,x2=usedX2,gam=gam,
tau=rtime,c=3)
ax1 <- avail[,1]
ax2 <- avail[,2]
availX1 <- ax1
availX2 <- ax2
AVAILABLE <- rep(0,length(availX1))
aCOV <- 0
for (i in 1:length(AVAILABLE)){
  aCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
  *((availX1[i]-cmu1)^2+(availX2[i]-cmu2)^2))
}
presence <- c(USED,AVAILABLE)
covariate1 <- c(uCOV,aCOV)
```

A.5.14 Missing Point Selection Analysis: Step 4 Code

Step 4 of MPSA (Section 3.11.4 fits a logistic model using a conditional regression. The responding variable is the presence/absence and the explanatory variables are the environmental covariates and the step length squared. The code is:

```
model1a <- clogit(presence ~ covariate1/(1-covariate1) +
steplength2 + strata(strata))
# Conditional logistic regression

modelia <- glm(presence ~ 1 +
offset(model1a$coefficients[1]*covariate1),
family = binomial(link = logit))
# Regression for intercept values

bl <- 1/(2*gamorg*timeinterval)-
model1a$coefficients[2]
# Gamma calculation intermediate step
gamma <- abs(1/(2*bl*timeinterval)) # New gamma value
```

A.5.15   All Algorithm Functions

The file for the functions required for all of the algorithms is called 'MPSA-Functions.R'. While not all functions are necessary for every algorithm, this files consolidates all the necessary functions for running all of the algorithms at the same time. The code is as follows:

```R
############################################################
############## FUNCTIONS FOR ALL ALGORITHMS ##############
############################################################

#----------------------------------------------------
## PACKAGE DOWNLOADS
#----------------------------------------------------
#Plotting package
library(ggplot2)
#SDE Packages
library(Sim.DiffProc)
library(knitr)
library(MASS)
knitr::opts_chunk$set(comment="",prompt=TRUE,
fig.show='hold', warning=FALSE, message=FALSE)
options(prompt="R>␣",scipen=16,digits=5,warning=FALSE,
message=FALSE, width = 70)
library(survival)
library(geometry)
library(uniformly)
#Bivariate normal random calculation
rbvn<-function (n, mu1, s1, mu2, s2, rho)
{
  X1 <- rnorm(n, mu1, s1)
  X2 <- rnorm(n, mu2 + (s2/s1) * rho *
                (X1 - mu1), sqrt((1 - rho^2)*s2^2))
  cbind(X1, X2)
}


############----------------------------------------
## ALGORITHM FUNCTIONS
############----------------------------------------
#----------------------------------------------------
## TWO DIMENSIONAL NORMAL
#----------------------------------------------------
normal.2D <- function(x,y,sig){ #assumes mu is zero
  (1/(2*pi*sig^2))*exp((-1/2)*(((x^2)/sig^2)+((y^2)
  /sig^2)))
}
```

```r
#----------------------------------------------------
## DETERMINE MOVEMENT KERNEL
#----------------------------------------------------
#First step, 1D
#Fitting sigma^2 based on the x coordinates in 1D
fit.var.1D <- function(x1, tau){
  n <- length(x1)
  #the average is the location of the starting spot
  gam <- 0
  for(j in 2:n){
    gam <- gam + ((x1[j]-x1[j-1])^2)/tau[j-1]
  }
  (gam <- (1/n)*gam)
}


#First step, 2D
#Fitting sigma^2 based on the x1 and x2 coordinates in 2D
fit.var2D <- function(x1,x2,tau){
  n <- length(x1) #needs to match length(x2)
  #the average is the location of the starting spot
  gam <- 0
  for (i in 2:n){
    gam <- gam + ((x1[i]-x1[i-1])^2 + (x2[i]-x2[i-1])^2)
    /tau[i-1]
  }
  gam <- (1/(2*(n-1)))*gam
  gam
}
#----------------------------------------------------
## DETERMINE AVAILABLE POINTS
#----------------------------------------------------
#Second step, 1D
#Determine available locations
det.avail1D <- function(x1,gam,tau,c=5){
  #c is the number of available points per used points
  av <- 0
  r <- 1
  n <- length(x1)
  for (i in 2:n){
    for(j in 1:c){
      std <- gam*tau[i-1]
      av[r] <- rnorm(1,mean = x1[i], sd = std)
      r <- r + 1
    }
  }
  av
}
```

```r
#Second step, 2D
#Determine available locations
det.avail2D <- function(x1,x2,gam,tau,c=5){
  #c is the number of available points per used points
  n <- length(x1)
  av1 <- 0
  av2 <- 0
  r<-1
  for (i in 1:(n-1)){
    for(j in 1:c){
      std <- sqrt(gam*tau)
      #std <- gam*tau
      av1[r] <- rnorm(1,mean = x1[i], sd = std)
      av2[r] <- rnorm(1,mean = x2[i], sd = std)
      r <- r + 1
    }
  }
  av <- data.frame(av1,av2)
  av
}


#-----------------------------------------------------
## RUN SDE PATHS FOR USED POINTS
#-----------------------------------------------------
#1D SDE pathway, y= start, x=end, rp = repetitions

SDE1D <- function(y1,x1,rp=100,cmu1 = 0, cmu2 = 0,
beta1 = -100,D4 = 1){
  fx <- expression(D4*beta1*(-x/(csig^2)))
  gx <- expression(D4)
  leng <- 0
  while (leng < 1){
    modx <- tryCatch(bridgesde1d(drift=f,diffusion=g
    ,x0=y1,y=x1,M=rp,method="milstein"),
    error=function(e) return(0))
    leng <- tryCatch(ncol(modx$X),error=function(e) return(0))
    if (is.null(leng)){
      leng <- 0
    }
  }
  modx
}
#2D SDE pathway
SDE2D <- function(y1,y2,x1,x2,rp=100,cmu1 =0, cmu2 = 0,
csig = 7,beta0 = 0, beta1 = 100, D4 = 1,t0,t1){
  fx <- expression(D4*beta1*(1/(2*pi*csig^2))*exp((-1/2)
```

```
*((( x ^2)/ csig ^2)+(( y ^2)/ csig ^2)))*( - x /( csig ^2))/(1
+exp( beta0 + beta1 *(1/(2* pi * csig ^2))* exp (( -1/2)*((( x ^2)
/ csig ^2)+(( y ^2)/ csig ^2))))) ,D4* beta1 *(1/(2* pi * csig ^2))
*exp (( -1/2)*((( x ^2)/ csig ^2)+(( y ^2)/ csig ^2)))*( - y
/ csig ^2)/(1+ exp( beta0 + beta1 *(1/(2* pi * csig ^2))
*exp (( -1/2)*((( x ^2)/ csig ^2)+(( y ^2)/ csig ^2))))))
gx <- expression(sqrt(D4),sqrt(D4)) # SDE Diffusion

leng <- 0
count <- 0
while (leng < 1){
  mod2 <- tryCatch(bridgesde2d(drift=fx,diffusion=gx,
  x0=c(y1,y2),y=c(x1,x2),M=rp,type="str",method="rk1",
  t0=t0, T=t1),
  error=function(e)
  return(0) )
  leng <- tryCatch(ncol(mod2$X),error=function(e) return(0))
  if (is.null(leng)){
    leng <- 0
  }
  count <- count+1
  print(count)
}
mod2
}
# 1D Selects random points along random pathways
#mod=model,n=points per pathway,
#p=number of pathways to select from
selectUsed1D.sde <- function(mod,n=1,p=1){
  l <- nrow(mod$X)
  np <- ncol(mod$X)
  pts <- 0
  for (i in 1:p){
    randp <- sample(1:np,1,TRUE)
    randx <- runif(n,0,l-0.000000000000000000001)
    pts <- c(pts,mod$X[randx,randp])
  }
  points <- pts[2:length(pts)]
}
# 2D Selects random points along random pathways
#mod=model,n=points per pathway,
#p=number of pathways to select from
selectUsed2D.sde <- function(mod,n=1,p=1){
  l <- nrow(mod$X)
  np <- ncol(mod$X)
  ptsx1 <- 0
  ptsx2 <- 0
```

```
  for (i in 1:p){
    randp <- sample(1:np,1,TRUE)
    randx <- runif(n,0,l-0.000000000000000000001)
    ptsx1 <- c(ptsx1,mod$X[randx,randp])
    ptsx2 <- c(ptsx2,mod$Y[randx,randp])
  }
  pointsx1 <- ptsx1[2:length(ptsx1)]
  pointsx2 <- ptsx2[2:length(ptsx2)]
  points <- data.frame(ptsx1,ptsx2)
  points
}
```

A.5.16   All Algorithms Examples

The file containing the code for the testing of all algorithms on the same data is called 'MPSALoop.R'. This code repeats the analyses on the same data for a user specified number of loops. The code is as follows:

```
#----------------------------------------
# SOURCE FILE WITH FUNCTIONS
#----------------------------------------
source("MPSAFunctions.R")
# Functions required for missing point algorithm
set.seed(237) #set.seed(237)
start <- 7 # starting k value for repeats
end <- 7 # ending k value for repeats
rmax <- 300 # Number of times each sim settings repeated
rmin <- length(c(start:end)) # Number of repeats
delta <- 10
# The minimum required difference between betas to end sim
timeintervalvec <- rep(NA,rmin*rmax)
# Vector for time intervals
gammavec <- rep(NA,rmin*rmax)
# Vector for inputted gamma
gammaestvec <- rep(NA,rmin*rmax)
# Vector for gamma from kernel fit
mp1gammaestvec <- rep(NA,rmin*rmax)
# Vector for missing point gamma fit (final)
sssteplength <- rep(NA,rmin*rmax)
# Vector for step lengths
issaB1 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_covariate
issaB0 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_0
issaBL <- rep(NA,rmin*rmax)
# Vector for iSSA beta_steplength
```

```r
mpsa1B1 <- rep(NA,rmin*rmax)
# Vector for missing point beta_covariate
mpsa1B0 <- rep(NA,rmin*rmax)
# Vector for missing point beta_0
mpsa1BL <- rep(NA,rmin*rmax)
# Vector for missing point beta_steplength
ssaB1 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_covariate
ssaB0 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_0
rsaB1 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_covariate
rsaB0 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_0
rsaiiB1 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_covariate
rsaiiB0 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_0
rsaiiiB1 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_covariate
rsaiiiB0 <- rep(NA,rmin*rmax)
# Vector for iSSA beta_0
whilec <- rep(NA,rmin*rmax)
# Vector for number of rounds in missing point
x <- rep(NA,rmax) # Vector for percent missing
count <- 1 # Counter for simulation number
data <- data.frame(timeintervalvec,gammavec,
gammaestvec,mp1gammaestvec,sssteplength,issaB0,issaB1,
issaBL,mpsa1B0,mpsa1B1,mpsa1BL,ssaB0,ssaB1,
rsaB0,rsaB1,rsaiiB0,rsaiiB1,rsaiiiB0,rsaiiiB1,
x,whilec) # Data frame for final collection
for ( s in 1:rmax){ # Repeat for each percent
  for( k in start:end ){
  # Repeating for multiple simulations of each setting

    #-----------------------------------------
    # PATHWAY INITIALIZATION
    #-----------------------------------------
    cmu1 <- 0  # Covariate x1 mean
    cmu2 <- 0 # Covariate x2 mean
    csig <- 1 # covariate standard deviation
    beta0 <- -10 # Selection intercept coefficent
    beta1 <- 50 # Selection coefficent
    D4 <- 1 # 4*Diffusion
    scale <- 2^8 # Number of points per reported points
    Npoints <- 2^10 # Total number of steps
    Time <- Npoints*0.1 # End Time
```

```r
timeinterval <- Time/Npoints
# The regular time interval
data$timeintervalvec[count] <- timeinterval
# Saving the time interval
xstart <- 1 # x1 starting location
ystart <- 1 # x2 starting location
availc <- 10 # Available points per used point
nummiss <- round(((k*10)/100)*Npoints)
# Number of missing points
#nummiss <- round(0.8*Npoints)
countw <- 0 # Counter for while loop reset
difference <- 999
# value for the difference between beta estimates
errortest <- 0
errortest2 <- 0
#-------------------------------------
# PATHWAY SIMULATION
#-------------------------------------
fx <- expression((D4*beta1*normal.2D(x=x,y=y,sig=csig)
*(-x/(csig^2)))/(1+exp(beta0 + beta1*normal.2D(x=x,y=y,
sig=csig))),(D4*beta1*normal.2D(x=x,y=y,sig=csig)*(-y
/csig^2))/(1+exp(beta0 + beta1*normal.2D(x=x,y=y,
sig=csig))))
#SDE Drift
gx <- expression(sqrt(D4),sqrt(D4)) # SDE Diffusion

mod2d <- snssde2d(drift=fx,diffusion=gx,x0=c(xstart,
ystart),M=1,T=Time,N=Npoints*scale,method="rk2")
#SDE Pathway simulation
track1 <- xstart # First x1 point on pathway
track2 <- ystart # First x2 point on pathway
for (i in 2:(Npoints+1)){
# Determines the rest of the pathway removing the scale
  track1[i] <- mod2d$X[scale*(i-1)+1] # x1 location
  track2[i] <- mod2d$Y[scale*(i-1)+1] # x2 location
}
rtime <- rep(Time/Npoints,(length(track1)-1))
# Vector of time intervals

toDelete <- seq(1,length(track1),1)
toDelete1 <- seq(5,length(track1),5)
toDelete <- toDelete[-toDelete1]
track1rsa <-  track1[-toDelete]
track2rsa <-  track2[-toDelete]
#-------------------------------------
# DETERMINE MISSING POINTS
#-------------------------------------
```

```r
missing <- sample(2:(length(track1)-1), nummiss,
replace=F)
# The points that are removed and missing
missing <- sort(missing)
# sorts the missing points for the next loop
track1 <- track1[-missing] # Removes missing x1 points
track2 <- track2[-missing] # Removes missing x2 points
counter <- 0 #counter keeps track time intervals removed
for( i in 1:length(missing)){
# Loop to calculate new time intervals
  rtime[missing[i]-1-counter] <- rtime[missing[i]-1
  -counter] + rtime[missing[i]-counter]
  # add missing time to next time
  rtime <- rtime[-(missing[i]-counter)]
  # Remove missing points
  counter <- counter + 1 # Increase index counter
}
totTime <- 0 # Reset Total time vector
repsTime <- length(rtime)+1
# variable for number of repeats
for (i in 2:repsTime){
# Ignores first time interval,
#repeats for each new time interval
  totTime[i] <- totTime[i-1]+rtime[i-1]
  # Cumulative sum of time intervals
}
rtimeorg <- rtime
#saves the original time intervals

#-------------------------------------
# STEP 1: DETERMINE MOVEMENT KERNEL
#-------------------------------------
gam <- fit.var2D(track1,track2,rtime)
# Fit the movement kernel to find gamma
gamorg <- gam # saves the original fit
data$gammavec[count] <- gam # save fit for plotting

#-------------------------------------
# STEP 2: DETERMINE USED POINTS
#-------------------------------------
usedX1 <- c(track1) # set used points, x1
usedX2 <- c(track2) # set used points, x2
USED <- rep(1,length(usedX1)) # used points are set 1
uCOV <- 0 # Reset used covariate values
for (i in 1:length(USED)){
# For each used location, find the covariate
  uCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
```

```
  *((usedX1[i]-cmu1)^2+(usedX2[i]-cmu2)^2))
  #determines covariate values of used points
}
USED <- USED[2:length(USED)]
#removes starting location from analysis
uCOV <- uCOV[2:length(uCOV)]
#removes starting location from analysis

## FIND STEP LENGTHS ##########
distance <- 0 # Resets distance vector
for (i in 1:(length(track1)-1)){
# For each viable step, find step length
  distance[i] <- sqrt((track1[i] - track1[i+1])^2
  + (track2[i] - track2[i+1])^2)
  #determines step lengths for used steps
}

## STRATA #################
stratau <- c(1:(length(track1)-1))
# Strata values for each used point

#--------------------------------------
# STEP 3: SIMULATE AVAILABLE POINTS
#--------------------------------------
avail <- det.avail2D(x1=track1,x2=track2,gam=gam,
tau=timeinterval,c=availc)
# Simulate available points for each used point
ax1 <- avail[,1] # set x1 available location
ax2 <- avail[,2] # set x2 available location
distance_avail <- 0 # Reset distance vector
countavail <- 1 # Counter for index
for (i in 1:(length(track1)-1)){
# Find the step length for each available point
  for(j in 1:availc){
  # Find the amount of available points required
    distance_avail[countavail] <- sqrt((track1[i]
    - ax1[countavail])^2 + (track2[i]
    - ax2[countavail])^2)
    # step lengths for available points
    countavail <- countavail + 1 # Increase index counter
  }
}
strataa <- rep(1:(length(track1)-1), each=availc)
# Strata values for the available points
availX1 <- ax1 # x1 available points
availX2 <- ax2 # x2 available points
```

```
timesa <- rep(rtime,each=availc)
# time intervals for available points

AVAILABLE <- rep(0,length(availX1))
# each available point gets a 0
aCOV <- 0
for (i in 1:length(AVAILABLE)){
# Find the covariate values for each available location
  aCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
  *((availX1[i]-cmu1)^2+(availX2[i]-cmu2)^2))
  # calculate covariate values for each available point
}
presence <- c(USED,AVAILABLE)
# The presence/absence binary value
covariate1 <- c(uCOV,aCOV) # Covariate values
steplength <- c(distance,distance_avail) # Step lengths
strata <- c(stratau,strataa) # Strata values
times <- c(rtime, timesa) # Time intervals
steplength2 <- steplength^2 # Step length squared

#--------------------------------------
# REMOVE POINTS WITH TIMEINTERVAL > STANDARD,
# iSSA CAN'T HANDLE THE EXTRA TIME
#--------------------------------------
presence <- presence[times==timeinterval]
# save only points with time interval equal to set time
# interval, presence/absence
covariate1 <- covariate1[times==timeinterval]
# save only points with time interval equal to set time
# interval, covariate values
steplength <- steplength[times==timeinterval]
# save only points with time interval equal to set time
# interval, steplengths
strata <- strata[times==timeinterval]
# save only points with time interval equal to set time
# interval, strata values
steplength2 <- steplength2[times==timeinterval]
# save only points with time interval equal to set time
# interval, step lengths squared
times <- times[times==timeinterval]
# save only points with time interval equal to set time
# interval, time intervals

#--------------------------------------
# STEP 4: RUN CONDITIONAL LOGISTIC REGRESSION
#--------------------------------------
model1a <- clogit(presence ~ covariate1/(1-covariate1)
```

```r
+ steplength2 + strata(strata))
# model for covariate
data$issaB1[count] <- model1a$coefficients[1]
# Save beta for covariate

modelia <- glm(presence ~ 1
+ offset(model1a$coefficients[1]
*covariate1), family = binomial(link = logit))
# Model for intercept
data$issaB0[count] <- modelia$coefficients[1]
# Save beta for intercept

#### SSA COMPARISON ######################
model <- glm(presence~covariate1,
family=binomial(link=logit))
# SSA log regression
data$ssaB0[count] <- model$coefficients[1]
# SSA Intercept
data$ssaB1[count] <- model$coefficients[2]
# SSA Coefficeint for covariate
##########################################
#--------------------------------------
# STEP 5: RE-EVALUATE MOVEMENT KERNEL
#--------------------------------------
bl <- 1/(2*gamorg*timeinterval)-model1a$coefficients[2]
# calculate the "beta" for step length
gamma <- abs(1/(2*bl*timeinterval))
# new estimated gamma value
data$gammaestvec[count] <- gamma
# save estimated gamma value

ss <- sum(steplength2)/length(steplength2)/2
# step length squared
data$sssteplength[count] <- ss
# save step length squared

while(difference > delta | errortest != 0
| errortest2 != 0 ){
# while difference between the betas is greater than delta,
#repeat missing point step
  countw <- countw + 1
  # Increase missing point round counter

  #--------------------------------------
  # STEP 6: DETERMINE BRIDGE POINTS
  #--------------------------------------
  b0 <- modelia$coefficients[1]
```

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```r
# Set the new beta values for the intercept
beta <- model1a$coefficients[1]
# Set the new beta values for the covariate
gam <- gamma # Set the new gamma value
ubpx1 <- 0 # Reset bridge point vector for x1
ubpx2 <- 0 # Reset bridge point vector for x2
countc <- 2
# Counter for used and pseudo-used vector index
countu <- 2 # Counter for used vector index
usedtempx1 <- track1[1] # Sets first used point, x1
usedtempx2 <- track2[1] # Sets first used point, x2
for (i in 1:length(rtimeorg)){
# For each time interval,
#find the used or pseduo-used point
  if (rtime[i]>(timeinterval)){
  # If a point is missing, find a pseudo-used point
    points <- rtimeorg[i]/(timeinterval)
    # Number of pseudo-used points required
    mod <- SDE2D(y1=track1[i],rp=50,y2=track2[i],
    x1=track1[i+1],x2=track2[i+1],cmu1=cmu1,
    cmu2=cmu2,csig=csig,beta0=b0,beta1=beta,
    D4=gam, t0 = totTime[i], t1 = totTime[i+1])
    # Bridge simulation
    np <- ncol(mod$X) # Number of successful bridges
    l <- nrow(mod$X)
    # Number of location steps within the bridges
    for (i in 1:(points-1)){
    # For each required missing point
      spot <- round(l * (i/points))
      # Find the times where the points are needed
      randp <- sample(1:np,1,TRUE)
      # Randomly choose a succesful bridge to sample from
      usedtempx1[countc] <- mod$X[spot,randp]
      # Save pseudo-used x1
      usedtempx2[countc] <- mod$Y[spot,randp]
      # Save pseudo-used x2
      countc <- countc + 1
      # Increase used/pseudo-used counter
    }
    usedtempx1[countc] <- track1[countu] # Save used x1
    usedtempx2[countc] <- track2[countu] # Save used x2
    countc <- countc +1
    # Increase used/pseduo-used counter
    countu <- countu +1 # Increase used counter
  }else{
  # If there are no missing points, get original pathway
    usedtempx1[countc] <- track1[countu] # Save used x1
```

```r
    usedtempx2[countc] <- track2[countu] # Save used x2
    countc <- countc + 1 # Increase used/pseudo-used x1
    countu <- countu + 1 # Increase used counter
  }
}


#------------------------------------
# STEP 7: DETERMINE USED POINTS
#------------------------------------
usedX1 <- usedtempx1
# Set used points to the ordered used/pseudo-used, x1
usedX2 <- usedtempx2
# Set used points to the ordered used/pseudo-used, x2
rtime <- rep((timeinterval),(length(usedX1)-1))
# Set time intervals to be all the same and regular

USED <- rep(1,length(usedX1))
# Set 1 for each used for presence/absence column
uCOV <- 0 # Reset used covariate values
for (i in 1:length(USED)){
# For each used point, find the covariate values
  uCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
  *((usedX1[i]-cmu1)^2+(usedX2[i]-cmu2)^2))
  # Calculate the covariate values
}
USED <- USED[2:length(USED)]
# Remove first point
uCOV <- uCOV[2:length(uCOV)]
# Remove first point

## FIND STEP LENGTHS ##########
distance <- 0 # Reset distance vector
for (i in 1:(length(usedX1)-1)){
# For each used/pseudo-used point,
#find the step length
  distance[i] <- sqrt((track1[i] - track1[i+1])^2
  + (track2[i]- track2[i+1])^2)
  # Calculation of step length
}

## STRATA #################
stratau <- c(1:(length(usedX1)-1))
# Assign strata values


#------------------------------------
# STEP 8: DETERMINE AVAILABLE POINTS
#------------------------------------
```

```r
avail <- det.avail2D(x1=usedX1,x2=usedX2,gam=gam,
tau=rtime,c=availc)
# Determine available points for each used/pseudo-used
ax1 <- avail[,1] # Available x1 locations
ax2 <- avail[,2] # Available x2 locations
distance_avail <- 0 # Reset distance vector
countavail <- 1 # Counter for relevant step lengths
for (i in 1:(length(usedX1)-1)){
# For each viable point, find the step length
  for(j in 1:availc){
    # Repeat for the number of available points made
      distance_avail[countavail] <- sqrt((usedX1[i]
      - ax1[countavail])^2 + (usedX2[i]
      - ax2[countavail])^2)
      # Calculation for step length
      countavail <- countavail + 1
      # Increase counter for available points index
  }
}
strataa <- rep(1:(length(usedX1)-1), each=availc)
# Strata values for each available point
totx1 <- c(usedX1,avail[,1])
# All used and available, x1
totx2 <- c(usedX2,avail[,2])
# All used and available, x2
availX1 <- ax1 # Available points, x1
availX2 <- ax2 # Available points, x2

timesa <- rep(rtime,each=availc)
# Intervals for the available points

AVAILABLE <- rep(0,length(availX1))
# 0 for each available point in the presence/absence
aCOV <- 0 # Reset available covariate vector
for (i in 1:length(AVAILABLE)){
# For each available point, the covariate values
  aCOV[i] <- (1/(2*pi*csig^2))*exp((-1/(2*csig^2))
  *((availX1[i]-cmu1)^2+(availX2[i]
  -cmu2)^2))
  # Calculation of covariate values
}

presence <- c(USED,AVAILABLE)
# The presence/absence binary value
covariate1 <- c(uCOV,aCOV) # Covariate vector
steplength <- c(distance,distance_avail)
# Step length vector
```

```r
    strata <- c(stratau, strataa) # Strata vector
    times <- c(rtime, timesa) # Time interval vector
    steplength2 <- steplength^2
    # Step lengths squared vector

    #---------------------------------------
    # STEP 9: RUN MODELS
    #---------------------------------------
    model1aold <- model1a
    modeliaold <- modelia
    model1a <- tryCatch(clogit(presence ~ covariate1
    /(1-covariate1) + steplength2 + strata(strata)),
    error=function(w) return(model1a))
    # Conditional logistic regression
    modelia <- tryCatch(glm(presence ~ 1
    + offset(model1a$coefficients[1]*covariate1),
    family = binomial(link = logit)), error=function(w)
    return(model1a))
    # Regression for intercept values
    if(model1aold$coefficients[1]==
    model1a$coefficients[1] & model1aold$coefficients[2]==
    model1a$coefficients[2]){
      errortest <- 1
    }
    if(modeliaold$coefficients[1]==
    modelia$coefficients[1]){
      errortest2 <- 1
    }
    bl <- 1/(2*gamorg*timeinterval)-model1a$coefficients[2]
    # Gamma calculation intermediate step
    gamma <- abs(1/(2*bl*timeinterval)) # New gamma value

    difference <- abs(beta - model1a$coefficients[1])
    # Difference between previous beta_covariate
    #value and new beta_covariate value
}

data$mpsa1B1[count] <- model1a$coefficients[1]
# Save the beta_covariate value
data$mpsa1B0[count] <- modelia$coefficients[1]
# Save the beta_0 value
data$mp1gammaestvec[count] <- gamma
# Save the gamma estimate
data$whilec[count] <- countw
# Save the number of rounds completed
data$x[count] <- nummiss
# Save the number of missing points
```

```
      count <- count + 1
      # Increase counter for the number of sims index
      print("Good")
      # Print "good" for each succesful run as a check
      print(count)
      # Print the simulation number as a check
  }
}
```