STOCHASTIC MODELS FOR INDIVIDUAL AND COLLECTIVE ANIMAL MOVEMENT

A Dissertation in
Statistics
by
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Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Doctor of Philosophy

August 2016
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Abstract

Several novel models for analyzing animal movement data are presented in this dissertation. The models are motivated by real world data sets consisting of guppy movement in an enclosed fish tank and ant movement within a four chambered nest. High temporal resolution allows the development of complex movement models. I first present a model that accounts for interactions between individuals in a novel way using point process interaction functions. A double Metropolis Hastings algorithm is developed for model inference due to intractable normalizing constants. Next, a novel method for spatially-varying individual movement rate is incorporated in a stochastic differential equation model for animal movement which allows for directional persistence and spatially-varying directional bias. This model is then enhanced to allow for latent behavioral states and a novel method is presented which accounts for behavioral interactions between individuals. Bayesian inference via Markov chain Monte Carlo algorithms is used to estimate model parameters.
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I would like to express my gratitude to my co-advisors Ephraim Hanks and Murali Haran. Their feedback over the past few years has been essential toward completing this work and their advice and career guidance has been indispensable. It has been a privilege working with each of them.

I would also like to thank my committee members John Fricks and David Hughes whose insights have greatly improved this dissertation. Additionally, I’d like to thank the members of the Hughes lab for their work collecting data and the helpful discussions we’ve had regarding the nature of ants. I’d also like to thank the faculty, staff, and students of the Department of Statistics for their collaboration, and for creating an excellent working community.

Finally, I would like to thank my family and friends for their support and encouragement over the years.
Chapter 1  |  Introduction

Statistical models for animal movement allow ecologists to answer important questions about animal behavior. Models can provide insight into animal migration, the impact of human activity and climate change, the spread of infectious disease, and a wide spectrum of additional ecological phenomena. Recent advances in technology have enabled researchers to collect vast amounts of data on animal locations, necessitating the development of more complex statistical models. First, motivation for studying animal movement will be discussed. Then, in Section 1.2, correlated random walk (CRW) models for animal movement will be introduced. Next, various models for animal movement will be discussed which account for spatial-variation, temporal-variation, and inter-animal dependence. In Section 1.6, the contributions of this dissertation will be presented and Section 1.7 will conclude the chapter with an outline for the remainder of the thesis.

1.1 Motivation

Animal movement models have been applied to a wide variety of species of animals in a broad spectrum of contexts. Statistical analysis of movement data has provided insight into multiple areas of ecological and biological interest. For example, studying migration patterns provides insight into animal conservation and can reveal the impact that human activity has on migration patterns. Several studies focus on the migratory behavior of birds (Guilford et al., 2011; Vardanis et al., 2011; Végvári et al., 2011) but many other species, such as marine vertebrates (Costa et al., 2012; Papastamatiou et al., 2013) have been considered.

One of the biggest current ecological concerns is global climate change. Climate
change may impact the behavior and movement of animal species, and using movement models to study such behavioral changes is important for animal conservation. For example, Rode et al. (2015) studied polar bear locations and found that polar bears’ habitats are changing to include more land based territory as sea ice shrinks. Human changes to the environment are also ecologically important. Northrup et al. (2015) concluded that oil and natural gas extraction from shale has altered the habitat of mule deer. The impact of changing environments have been studied in several other species, including elephants (Bohrer et al., 2014) and sea lions (Lowther et al., 2013).

Studying the movement patterns of animals is essential for understanding a multitude of other ecological issues. It can be used to study the habitat or home range of individuals or groups (Oksanen et al., 2015; Muelbert et al., 2013) and in the study of entire populations (Ivan et al., 2013; Vanak et al., 2013; Morales et al., 2010). Animal movement provides insight into species invasion dynamics (Tamburello and Côté, 2015) and the spread of disease (Wells et al., 2013) and provides useful information for the management of ecosystems (Block et al., 2011). Additionally, with the use of genetic data, long term population movement can be studied through landscape connectivity (Petkova et al., 2015; Bolliger et al., 2014; Hanks and Hooten, 2013).

In recent years, technological advances have facilitated the collection of an abundance of animal movement data. Examples of technological advances include tiny fluorescent probes used to track zooplankton (Lard et al., 2010), acoustic proximity receivers that can record social interactions of sharks (Guttridge et al., 2010), and low-power sensor network systems for tracking large numbers of bats (Dressler et al., 2016). Additionally, animal movement data is becoming more accessible through the use of online databases such as Movebank (Kranstauber et al., 2011). The combination of a recent explosion of easily-available animal tracking data and a multitude of relevant ecological issues provides a rich opportunity for the development of novel statistical methodologies to answer fascinating scientific questions.
1.2 Correlated Random Walk Models

Animal movement modeling is a rapidly growing area of research in statistics and animal ecology. Ecological researchers have historically been interested in the drivers of animal movement, which is evident by the fact that mathematical descriptions of animal movement have existed for hundreds of years (Hooten et al., 2014). Interest in statistical analysis of animal movement has exploded in recent years resulting in many novel movement models that can account for complex behaviors such as spatial variation in movement, temporal variation in movement, and collective movement. Much of this research has been built on the framework of the correlated random walk (Fagan and Calabrese, 2014).

An early discussion of modeling the location of a wandering beetle was given by Skellam (1951), which focuses on population level dispersion of organisms. Dunn and Gipson (1977) extends this idea by modeling animal movement as a diffusion process, where an animal’s current location in two-dimensions $z(t) = (z_x(t), z_y(t))$ is assumed to follow an Ornstein-Uhlenbeck process. This results in a Gaussian distribution for the location of an animal at time $(s + t)$ conditional on it’s location at an earlier time $s$

$$z(s + t) \sim N(\mu + e^{Bt}[z(s) - \mu], \Lambda - e^{Bt}\Lambda e^{B't})$$

where $\mu$ represents a location of attraction, $B$, represents autocorrelation through time, and $\Lambda$ relates to overall variability in location. This model can be used to generate predictive values and confidence intervals for future locations. Dunn and Gipson (1977) discuss several model drawbacks, including the assumption of time-homogenous behavior, and difficulties incorporating spatial constraints to movement.

An alternative formulation of the CRW for animal movement involves modeling turning angle $\theta_l$ and step length $l_l$ (Kareiva and Shigesada, 1983) between observations at time $t - 1$ and $t$. The model was based on the concept of a moving butterfly, with each observed location being a landing location of a wandering flight path. Directional persistence can be easily incorporated if the probability distribution of turning angles between two flights is centered at zero (Turchin, 1998). Further temporal dependence can be incorporated by modeling correlation.
in consecutive step lengths. Kareiva and Shigesada (1983) uses a summary statistic from this model, net displacement of an individual, to test if the animal’s movement follows a correlated random walk. If movement duration and stationary duration are recorded for the individual, the entire path of the animal can be recreated in both space and time.

The CRW model for animal movement data was expanded by Johnson et al. (2008a) to incorporate several improvements in a continuous-time correlated random walk (CTCRW) model. For simplicity, assume that an individual is moving in one dimension. The location at time \( t \) is denoted \( x(t) \), and the velocity at time \( t \) is denoted \( v(t) \). To model directional persistence in velocity, an Ornstein-Uhlenbeck process is used for the velocity term

\[
\frac{dv(t)}{dt} = \beta (\mu - v(t)) dt + \sigma dW_v(t) \tag{1.1}
\]

where \( \beta \) is the autocorrelation parameter, \( \mu \) represents directional drift and \( \sigma \) scales the Brownian motion \( W_v(t) \), thus controlling the level of variability in velocity. To obtain the location an additional noise process is added to the velocity term

\[
\frac{dx(t)}{dt} = v(t)dt + \kappa dW_x(t) \tag{1.2}
\]

where \( \kappa \) scales the additional noise generated by the Brownian motion process \( W_x(t) \), and can be set to 0 to get the physical interpretation of position as the integral of velocity

\[
x(t) = x(0) + \int_0^t v(s)ds.
\]

Solutions for equation (1.1) and (1.2) can be obtained with stochastic calculus, resulting in Gaussian distributions for both velocity and location terms. Additionally, flexible measurement error can be incorporated through a state-space framework. Note that lowercase letters are rarely used for random variables and processes. However, this notation is prominent throughout animal movement literature that uses stochastic differential equations. Therefore, we elect to use lower case notation for these random processes.

There are various benefits to the CTCRW model for animal movement. The ability to deal with non-uniform observations in time and utilize flexible models
for measurement error make this model useful in many scenarios. The state-space framework enables fast inference using the Kalman Filter (Petris et al., 2009). The model can be easily fit using the crawl package in R (Johnson, 2013). It has been used to study the behavior of many species including melon-headed whales (Herman and Durban, 2015), northern fur seals (Kuhn et al., 2014b) and migratory chinstrap and Adèlie penguins (Hinke et al., 2015).

### 1.3 Spatially-Varying Movement

Animal movement is often studied so that an animal’s interactions with their environment can be understood. This is important for application to conservation, planning of construction, the spread of animal populations and the impact of changes to the environment such as global warming. Thus, many methods have been proposed to model the spatially-varying environmental factors that impact animal movement.

Perhaps the earliest examples of spatially-varying studies of animal location data involve the study of animal home range. An animal’s home range can be defined as a region that contains a certain percentage (often 95%) of the space used by an animal (Fleming et al., 2015). Hayne (1949), for example uses data from repeated capture of an animal to determine the "center of activity" for the animal. Multiple early studies on the location of individuals, as summarized in Van Winkle (1975), utilize various statistical methods to study the spatially-varying space use of animals. Home range analyses have become more complex over the years with advances in statistical methods and the development of novel animal tracking technology. For example, Worton (1989) proposes adaptive smoothing for kernel density estimates for the utilization distribution of animal location data and Fleming et al. (2015) analyzes the movements of a Mongolian gazelle using an autocorrelated kernel density estimate to determine its home range.

Home range distributions by definition describe the locations of an animal at a random point in time. Thus, they inherently average the behavior of animals over time. Thus, to study animal movement over time alternative methods have been developed. One such method involves the use of potential functions to model spatial-variation in the direction of animal movement. Potential functions can be used to model spatially-varying directional drift which allows for regions of
attraction and repulsion. The potential function can be parametric, such as a function of environmental features, it can be a non-parametric spatial surface, or it can be a semi-parametric combination. In potential surface methods for movement, the mean velocity of an animal at a given location is in the direction of the gradient of the potential surface. In two dimensions, this results in expected velocities

\[
E(v_x(t)) = -\frac{dH(x(t), y(t))}{dx}
\]

\[
E(v_y(t)) = -\frac{dH(x(t), y(t))}{dy}
\]

where \(H(x, y)\) denotes the potential surface and \(v_x(t), v_y(t)\) represent the velocity of a particle in the x and y dimensions respectively. The movement of particles can be thought of as the movement of marbles on a topographical surface with peaks and valleys (Brillinger et al., 2001). The marble will, on average, tend to roll down the slope from the peaks to the valleys of the surface.

Potential functions were first used in Brillinger et al. (2001) to model animal movement by examining the long-run density of an animal’s locations using methods for kernel density estimation. Approximate inference for the potential surface movement models with negligible temporal dependence between observations is presented in Brillinger et al. (2002). Preisler et al. (2004) expands upon potential surface models by incorporating environmental covariates and accounting for seasonal movement patterns. Potential surface methods have been applied to study the impact of human activity, such as hiking and mountain biking, on the movement of elk (Preisler et al., 2013) and the movement of fishing vessels on the English channel (Gloaguen et al., 2015).

An animal’s movement is often restricted by its environment. Examples of this include man made barriers such as roads or fences, and natural barriers such as cliffs or the shores of a lake. Potential surfaces can be used to model these barriers through repulsion near the barriers via steep upward potential slopes (Brillinger, 2003). To test if physical environmental features are barriers to animal movement actual data can be compared to simulated movement paths. Shepard et al. (2008) uses this method and concludes that multiple species, such as the eastern box turtle, cross roads less frequently than they would by chance alone. Additionally, barriers can complicate inference when they are not accounted for in model specification.
Brost et al. (2015) propose a model to account for movement constraints and estimate resource selection functions. Resource selection refers to animals’ tendency to move toward locations with preferable features, or "resources". Resource selection functions have been developed to model these preferences. The general concept of the resource selection function compares the locations available to an animal, via availability distributions, to the locations an animal selects, via use distributions (Hooten et al., 2014). Numerous variations of resource selection function models have been proposed to study animal movement. Examples include models which allow for dynamic ecological environments (McLoughlin et al., 2010), variation among different individuals (Roshier et al., 2008), and statistical methods based on weighted distributions (Johnson et al., 2008b; Lele and Keim, 2006).

Numerous other general methods to test environmental impacts on animal movement have been used. For example, Crist et al. (1992) uses analysis of variance to compare the movement of beetles in different types of environment and Watkins and Rose (2013) evaluates the effectiveness of animal movement models to recapture true parameter values across changing environments using simulated data. Measuring the impact of the environment is increasingly important as human activity alters the landscape. Animals have evolved under certain environmental conditions, and sudden changes to the environment may result in non-optimal behavior in changing surroundings (Fahrig, 2007). Thus, developing spatially-varying movement models that incorporate environmental features is essential.

1.4 Temporally-Varying Movement

Improvements in technology have enabled researches to track the movements of animals over long time periods. Assuming that an animal’s behavior is constant during these long periods of observation is often inappropriate. For example, if an animal is observed for many years there may be a seasonal trend due to animal migration. Similarly, there may be periodic daily trends in animal movement caused by behavioral tendencies of feeding or sleeping at certain times of the day. In some circumstances, movement behavior at a given time may depend on other factors, such as internal state (i.e. hungry, tired), societal needs (i.e nest cleaning, foraging), or environmental factors (i.e. weather, nearby predators). Thus, more complex
statistical models are necessary to account for temporal variability in movement behavior.

One method of modeling temporal variation utilizes a set of discrete behavioral states corresponding to specific behavior. These discrete states may correspond to behaviors such as exploring, resting, or returning to a den. This type of behavior first appears in simulation studies by Worton (1995) that questioned the effect of assuming time-homogeneous movement behavior when an animal actually moved following two distinct distributions. Simulated data was generated from a movement process which alternated between two bivariate Ornstein-Uhlenbeck models (Dunn and Gipson, 1977). Inference on a single movement model was used and Worton (1995) conclude that in some cases behavioral switching can be ignored if the movement paths are sub-sampled by analyzing only times when the animal is likely to be in a certain state (i.e., active vs resting).

Hidden Markov models provide an efficient method for describing discrete unobserved states, such as animal behaviors, through time. Hidden Markov models are useful for modeling underlying latent processes which impact observations. Assume that data, such as an animal’s movement \((w_t = (\theta_t, l_t))\) is observed at times \(t \in \{1, ..., T\}\), and the animal is always in one of two states, resting or foraging. The state at each observation time \((s_t)\) is hidden, or unobserved. In the model the latent state at time \(t\), \(s_t\), is updated conditional on the state at the previous time point, \(s_{t-1}\), and the animal’s movement, \(w_t\) is a function of its state at the current time, \(s_t\). The dependence structure for this simple example is presented in Figure 1.1. Hidden Markov models are advantageous due to their relative simplicity, the efficiency of inference for model parameters and the estimation of latent states, and the availability of predictive distributions for future observations (Cappé et al., 2009).
Hidden Markov models have been frequently used to study animal movement. Blackwell (1997) expands upon previous work by considering a model that incorporates random switching between discrete behavioral states. This discrete behavioral process can either be latent, observed, or partially observed. Blackwell (1997) performs Bayesian inference using MCMC on a wood mouse data set, using states (resting, feeding, traveling) which follow a continuous time finite state Markov chain. Within each state, the movement is assumed to follow the bivariate Ornstein-Uhlenbeck location process (Dunn and Gipson, 1977). Morales et al. (2004) analyzes the movement of elk through different types of habitat using a similar model, but incorporate a correlated random walk model (Turchin, 1998) by modeling turning angle ($\theta_t$) and step length ($l_t$) rather than location. Morales et al. (2004) also discusses using environmental covariates to model the transition probability between states. An overview of animal movement with discrete behavioral states using hidden Markov models is presented by Langrock et al. (2012).

Several methods have been proposed to extend hidden Markov models for animal movement. For example, state switching models have been expanded to model measurement error (Jonsen et al., 2005). One drawback of the hidden Markov model is the geometric distribution for the amount of time spent in a state before switching. Semi-Markov processes (Langrock et al., 2012) allow for the specification of alternative dwell time distributions. Similarly, to relax the memoryless property of the dwell time, higher order Markov processes can be used (Langrock et al., 2012; McClintock et al., 2012). Bayesian methods for model selection such as reversible jump MCMC and model averaging have been incorporated (McClintock et al., 2012). Additional data is often available to inform the latent behavioral states. For example, Bestley et al. (2015) use dive behavior variables as covariates to infer the latent state of seals moving in 2-dimensions. Finally, to extend the model to allow for behavioral switches in continuous time in which the transition rate depends on location, exact simulation methods can be utilized to avoid approximation error for exact Bayesian inference (Blackwell et al., 2016).

Although behavioral switching models have become popular in animal movement modeling, it is important to examine their effectiveness at recovering true values. Using simulation studies and a real-world moose movement data set, Beyer et al. (2013) concludes that Bayesian state-space models are effective as long as the movement distributions in different behavioral states are not similar, and the
occurrence of a given state is not rare in the observed path. Joint estimation by combining individuals or using a hierarchical model improves inference, but large observation errors can make latent states indiscernible (Jonsen, 2016).

Several other methods have been proposed to deal with temporal variation in animal movement. Models have been developed which estimate the times of a random number of behavioral change points. At each of these change points, one or more of the movement model parameters are allowed to change, resulting in a random number of discrete behavioral states. These methods have been proposed in both a likelihood based framework by Gurarie et al. (2009), and in a Bayesian framework by Hanks et al. (2011) which uses cluster analysis to interpret the resulting parameter estimates.

One potential drawback of the models presented above for modeling temporal variation in animal movement is the discontinuous behavioral jumps between discrete states. Alternative methods have been proposed which allow for continuous behavioral switching. For example, Gaucherel (2011) uses wavelet analysis to model continuous shifts between different movement behaviors of albatross. Other models allow for continuous temporal variation by utilizing temporally-varying coefficients. Examples of this include Breed et al. (2012), which analyzes animal movement on a regular time grid by augmenting movement paths, and Hanks et al. (2015) which analyzes movement in continuous time and discrete space through transition rates between tangent cells of a spatial grid.

### 1.5 Group Movement

The models that have been discussed up to this point focus on individual animals, assuming that their movement is independent of other observed or unobserved neighbors. This assumption is unreasonable for many species, which often exhibit herding, flocking, territorial behavior, or other forms of between individual dependence. Therefore, it is important to consider the collective behavior of multiple individuals when studying animal movement. Although collective behavior can be extremely complex, incorporating simple interaction rules such as collision avoidance, group attraction, and neighbor alignment can result in realistic collective behavior (Sumpter, 2006). Various methods have been proposed to study group dependence in animal movement, including summary statistics, self-propelled
particle system simulations, and dynamic statistical models.

Many techniques that do not explicitly model movement can still provide insight into complex behavior. When locations of a group of interacting individuals are recorded, various statistics have been proposed to summarize the relationships between animals. Examples of these summary statistics include average nearest neighbor distance, group expanse (the largest distance between members of a group), group polarization (which measures the tendency of group members to face a common direction), group speed, and the number of stragglers (Viscido et al., 2005).

Summary statistics have been applied to several sets of movement data. Katz et al. (2011) analyze the movement of schooling fish by considering the average speeding and turning acceleration of individuals as a function of neighbor’s relative position. Correlations between the orientations of neighbors are used to study the alignment of individuals. Polansky and Wittemyer (2011) uses Fourier and wavelet approaches to analyze the relationship between the time series of step lengths of individuals. This method captures related movement, or synchrony, with respect to both circadian rhythms and correlated movement processes. It is used to study the relationship between movements of families and extended families of elephants. Bode et al. (2012b) separates social navigational, driven by relationships with neighboring fish, and non-social navigation, such as attraction to objects in the environment, by modeling the mean movement velocity as a linear combination of social and non-social factors.

Another approach used to model group movement dynamics involves self-propelled particle (SPP) systems. In these systems, particles are simulated to follow a specific set of rules, usually with random noise incorporated. These particles each represent an individual, and patterns generated from these SPP systems can be compared to real-life group movement. These systems can be altered by changing the movement rules, the underlying parameters, and the initial conditions to create a wide variety of types of collective movement including swarming and parallel movement (Couzin et al., 2002). An early example of this type of analysis, proposed in Vicsek et al. (1995), assumes each particle travels at a constant velocity and a random direction with mean value given by the average of the directions of all other particles within some radius \( r \).

The simulation based model of Vicsek et al. (1995) has been extended for several
new features. Rules have been added for attraction and repulsion by utilizing exponential functions that decay as the distance between particles increases (Levine et al., 2000). Similarly, Couzin et al. (2002) separates the repulsion, alignment, and attraction into three separate zones and incorporates blind spots so that simulated particles are not impacted by other particles directly behind them that animals would not be able to see. Other examples of SPP systems include Viscido et al. (2005), which studies the effect of population size and the number of interacting neighbors, Gautrais et al. (2008), which studies the effect of initial conditions of the particles, and Perna et al. (2014), which considers anisotropy due to the tendency of some species to prefer certain respective positions (i.e. slightly behind, to the side).

Several movement models that incorporate dependence between individuals and allow for inference on model parameters have been proposed. Mann (2011) uses Bayesian inference to infer parameter values in a movement model that assumes constant velocity and models dependence through a weighted combination of nearby individuals’ alignment and mass. Gautrais et al. (2012) expands upon this work by incorporating wall repulsion in the distribution of the turning angle. An alternative approach is proposed by Langrock et al. (2014) that utilizes separate movement processes, one for the group centroid, and one for each individual in the group. This method allows for flexible movement models that can incorporate different behaviors such as attraction to the group center and independent exploration. One drawback of this method is the difficulty in modeling multiple groups, or interaction between individuals outside of a herd, shoal or flock.

Alternatively, network methods have been used to model dependence in movement. Networks can be used to assess the spread of sudden movements (Rosenthal et al., 2015), or can be incorporated as a latent underlying structure that determines the relationship between individuals (Scharf et al., 2015). A general unifying framework for modeling movement that incorporates three features: individual movement, interactions with the environment, and interactions with other individuals’ locations at previous time points, is presented in Potts et al. (2014).

### 1.6 Summary of Contributions

This dissertation makes the following contributions
• A dynamic model for animal movement with point process interactions is proposed. This model provides a novel method for modeling animal movement with inter-animal dependence. It is presented in a flexible framework that can be adjusted for various different types of movement and interaction behaviors.

• A novel model for within-nest movements of ants is presented which accounts for directional persistence, spatially-varying directional bias, and spatially-varying overall movement rate. Stochastic differential equations are used to model animal movement with directional persistence. Potential and motility surfaces are embedded in the stochastic differential equations to account for spatial-variation.

• A novel method for dependence between individuals in animal movement is proposed which allows for interactions between the behaviors of individuals rather than dependence in the movement process itself. The dependence is modeled in transition probabilities between discrete behavioral states, allowing for heterogeneous behavior in time.

1.7 Dissertation Outline

Several models for animal movements are presented in the remaining Chapters. These models have been motivated by real-world data sets consisting of the movement of guppies within an enclosed tank and ants within a four chambered nest. Bayesian inference via Markov chain Monte Carlo is used for inference in all cases. Results provide insight into group movement, the use of space and the social structure of animal societies, all of which impact the spread of infectious disease through animal populations.

In Chapter 2 a novel model for animal interactions using point process interaction functions is presented. Inference in this model is complicated by intractable normalizing constants. An article based on this work has been published in the Journal of Agricultural, Biological, and Environmental Statistics (Russell et al., 2015). Next, in Chapter 3, a spatially-varying stochastic differential equation model for animal movement is developed. The model incorporates a novel spatial motility surface and captures the tendency of ants to travel at different speeds in different chambers of their nest. A manuscript based on this work has been submitted
for publication (Russell et al., 2016). In Chapter 4 the model from Chapter 3 is extended to allow for changing behaviors over time and behavioral interactions between individuals. This novel model allows for interactions between individuals through their behavioral decisions. This project is ongoing work with Ephraim Hanks, Murali Haran and David Hughes. Finally, Chapter 5 concludes with a summary and a discussion of future work.
Chapter 2  
Dynamic Models of Animal Movement with Spatial Point Process Interactions

In this chapter, I propose an approach to model interactions between individuals by augmenting a dynamic marginal movement model with a spatial point process interaction function within a weighted distribution framework. I develop a double Metropolis-Hastings algorithm to perform Bayesian inference and I illustrate my approach through the analysis of movement tracks of guppies (Poecilia reticulata).

2.1 Introduction

Movement models are important for studying animal behavior as they can reveal how animals use space and interact with the environment. Information on the movement patterns of animal species can play an important role in conservation, particularly for migratory species (Durban and Pitman, 2012). Interactions between animals can give insight into the structures of animal societies (Mersch et al., 2013). Many methods exist for modeling individual animal movement, including models that account for changing behaviors at different locations and times by utilizing Markovian switching models (Harris and Blackwell, 2013; Blackwell, 1997) and models that account for the animal’s preferences for covariates measured throughout the territory (Hooten et al., 2013; Johnson et al., 2013).

Animal species often exhibit herd or school behavior, and even those that do
not form groups have movement that depends on the behavior of other individuals. Langrock et al. (2014) incorporate dependence by assuming the animals in a herd move around a central point, such as a designated group leader or a latent central location. Codling and Bode (2014) propose a model that combines individual navigational behavior with the tendency to copy the behavior of other nearby individuals by taking a weighted average of the two behavioral mechanisms. This enables information sharing among neighbors. Perna et al. (2014) considers a model that encourages individuals to have a preferential structure. For example, an individual might tend to stay directly behind another, thus creating a leader-follower relationship. Sumpter (2006) gives a broad overview of animal movement, including computer simulation models which utilize self propelled particle (SPP) systems with specific movement rules to account for interaction. For example, Gautrais et al. (2008), describe three mechanisms driving group movement behavior: repulsion (or collision avoidance) at small scales, alignment at medium ranges, and attraction at longer distances. These mechanisms are modeled through velocity rules that depend on the location of neighbors within each of these distance ranges.

We propose a model that describes continuous-time dynamics of animal movement (Johnson et al., 2008a) while simultaneously allowing for current-location based interactions by modeling animal locations as a spatial interacting point process (Møller and Waagepetersen, 2004). Point process models allow interaction between point locations such as clustering and regularity, or repulsion, through the use of interaction functions. This provides a paradigm for different types of interactions between animals including collision avoidance, herding behavior, animals that break off into multiple smaller groups, and animals that interact with each other without moving in herds or schools. Our model allows for incorporation of several features, including

i. directional persistence in movement through a continuous-time correlated random walk,

ii. inter-animal behavior modeled using spatial point process interaction functions,

iii. observation error in animal locations.

Other models exist which incorporate one or more of these features; we propose a flexible framework for all three.
To illustrate our approach we analyze the guppy (Poecilia reticulata) movement data of Bode et al. (2012b) in which ten guppies are released in the lower right section of a fish tank, and are attracted to the top left by shelter in the form of shade and rocks. A realization of this experiment is shown in Figure 2.1(a) where the interaction between guppies is evident, as the guppies remain together in a shoal. To illustrate the need for statistical models incorporating between-animal dependence, Figure 2.1(b) shows a simulation from an independent movement model, as described in Section 2.2. In the simulation, the guppies tend to drift apart, so the model does not replicate the shoaling behavior. In Figure 2.1(c) we show a simulated realization from our proposed dynamic point process interaction (DPPI) model, described in Section 2.4. Each guppy’s marginal movement is modeled as a continuous-time correlated random walk which results in smooth paths similar to the observed guppy paths. Group movement is modeled using the attraction-repulsion interaction function of Goldstein et al. (2015). The simulated guppies in Figure 2.1(c) stay together in a group, similar to the observed guppies in Figure 2.1(a).

The rest of this paper is organized as follows. In Section 2.2, we introduce the general modeling framework, and give several examples of point process interaction functions useful for modeling group animal movement. In Section 2.3, we propose a Markov Chain Monte Carlo algorithm to sample from the posterior distributions of model parameters. We describe a double Metropolis-Hastings algorithm for
inference complicated by the intractable normalizing function that arises from our point process interaction approach to modeling group movement. In Section 2.4, we examine the performance of our approach by utilizing several simulated movement paths. Finally, in Section 2.5, we use our approach to analyze the guppy movement paths of Bode et al. (2012b).

2.2 Modeling Movement Dynamics with Interactions

In this section, we describe our proposed model, starting with a continuous-time stochastic model for the dynamics of individual guppy movement. Next, we aggregate the individual model to incorporate multiple individuals and describe our point process approach to modeling interactions. Finally, we compare our approach to existing approaches in the literature.

Let the unobserved states, consisting of the true locations and instantaneous velocities, of individuals \((1, \ldots, K)\) at a given time \(t_i\) be denoted by \(\mathbf{A}_{t_i} = (\alpha^{(1)}_{t_i}, \alpha^{(2)}_{t_i}, \ldots, \alpha^{(K)}_{t_i})^T\), and let \(\Theta\) denote our vector of parameters. We can write an aggregate group movement model by assuming independence and multiplying the marginal densities

\[
f(\mathbf{A}_{t_i} | \mathbf{A}_{t_{i-1}}, \Theta) = \prod_{k=1}^{K} f(\alpha^{(k)}_{t_i} | \alpha^{(k)}_{t_{i-1}}, \Theta)
\]

where \(f(\alpha^{(k)}_{t_i} | \alpha^{(k)}_{t_{i-1}}, \Theta)\) represents a marginal movement model. That is, the \(k^{th}\) individual’s state at time \(t_i\), \(\alpha^{(k)}_{t_i}\), is modeled conditional on that individual’s state at time \(t_{i-1}\), \(\alpha^{(k)}_{t_{i-1}}\), and the \(k\) individuals move independently of each other. To model movement interactions, we multiply the marginal model by an interaction function, which is a function of the pairwise distance between observations at time \(t_i\), yielding a joint distribution

\[
f(\mathbf{A}_{t_i} | \mathbf{A}_{t_{i-1}}, \Theta) = \frac{\prod_{k=1}^{K} f(\alpha^{(k)}_{t_i} | \alpha^{(k)}_{t_{i-1}}, \Theta) \prod_{j<k} \psi_{jk}(||\alpha^{(j)}_{t_i} - \alpha^{(k)}_{t_i}||; \Theta)}{c(\Theta)}
\]

where \(\psi_{jk}(||\alpha^{(j)}_{t_i} - \alpha^{(k)}_{t_i}||; \Theta)\) is the interaction function, which we take from methods in point process statistics. Note that \(c(\Theta)\) is an intractable normalizing function of \(\Theta\). This complicates computing as we will see later.
2.2.1 Marginal Movement Model

To develop a group movement model with interactions, we start with an existing movement model for an individual, the continuous time correlated random walk model (CTCRW) from Johnson et al. (2008a). The CTCRW model specifies an Ornstein-Uhlenbeck model for velocity, resulting in movement paths that show directional persistence, similar to that of the observed guppy movement paths in Figure 2.1(a). While not important for the guppy data, an additional advantage of the CTCRW model is that it allows for observations at non-uniform time points. The CTCRW model is flexible, and can easily be adjusted to account for complexities in a given data set. For example, Durban and Pitman (2012) use the CTCRW model to estimate the displacement velocities of killer whalers; Citta et al. (2013) use an adjusted version of the CTCRW model to analyze haul out behavior of Eastern Chukchi beluga whales and Kuhn et al. (2014a) use the CTCRW model to estimate locations of northern fur seals along foraging tracks. Additionally, Harris and Blackwell (2013) propose a framework that allows the behavioral state of an individual to switch between different states, including different CTCRW models.

Let $x(t)$ and $y(t)$ be the observed $x$ and $y$ locations of the animal at time $t$, $\mu^{(x)}(t)$ and $\mu^{(y)}(t)$ be the true unobserved $x$ and $y$ locations of the animal at time $t$, and $v^{(x)}(t)$ and $v^{(y)}(t)$ the instantaneous $x$ and $y$ directional velocities of the animal at time $t$. Let $s(t)$ be the observed location and $\alpha_t$ the unobserved state at time $t$, with

$$
\begin{align*}
\mathbf{s}_t &= \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}, \\
\mathbf{\alpha}_t &= \begin{pmatrix} \mu^{(x)}(t) \\ v^{(x)}(t) \\ \mu^{(y)}(t) \\ v^{(y)}(t) \end{pmatrix}.
\end{align*}
$$

We assume that $t \in \mathbb{R}^+$, and the locations $(x(t), y(t))$ belong to $\mathbb{R}^2$. The $x$ and $y$ elements are assumed to be independent, as a positive correlation between $x$ and $y$ velocities, for example, would indicate that the animal tends to move in a northeast or southwest direction.

To model directional persistence in movement, $v^{(x)}(t)$ and $v^{(y)}(t)$ are assumed to follow independent continuous-time Ornstein-Uhlenbeck processes. We first present
the CTCRW model for one-directional movement, focusing on the $x$ direction of Equation (2.1). Our development follows that of Johnson et al. (2008a).

Given a change in time $\Delta$, the $x$-directional velocity is given by

$$v^{(x)}(t + \Delta) = \gamma_1 + e^{-\beta \Delta} [v^{(x)}(t) - \gamma_1] + \xi_1(\Delta),$$

where $\xi_1(\Delta)$ is a normal random variable with mean 0 and variance $\sigma^2[1 - \exp(-2\beta\Delta)]/2\beta$. The location term $\mu^{(x)}(t + \Delta)$ is obtained by integrating the velocity equation

$$\mu^{(x)}(t + \Delta) = \mu^{(x)}(t) + \int_t^{t+\Delta} v^{(x)}(u)du.$$

Assuming we have $N$ observations at times $(t_1, ..., t_N)$, discretization of the continuous time model yields the distributions for the unobserved states,

$$\begin{pmatrix} \mu_{t_i}^{(x)} \\ v_{t_i}^{(x)} \end{pmatrix} \sim N \left( T_1(\beta, \Delta_i) \begin{pmatrix} \mu_{t_{i-1}}^{(x)} \\ v_{t_{i-1}}^{(x)} \end{pmatrix} + d_1(\gamma_1, \beta, \Delta_i), \sigma^2 V_1(\beta, \Delta_i) \right), i = 1, ..., N,$$

(2.2)

where $\Delta_i$ is the time change between observations $i - 1$ and $i$, $T_1(\beta, \Delta_i)$ accounts for the directional persistence,

$$T_1(\beta, \Delta_i) = \begin{pmatrix} 1 & \frac{1 - e^{-\beta \Delta_i}}{\beta} \\ 0 & e^{-\beta \Delta_i} \end{pmatrix},$$

direction $d_1(\gamma_1, \beta, \Delta_i)$ models directional drift,

$$d_1(\gamma_1, \beta, \Delta_i) = \gamma_1 \begin{pmatrix} \Delta_i & \frac{1 - e^{-\beta \Delta_i}}{\beta} \\ 1 - e^{-\beta \Delta_i} & \end{pmatrix},$$

and the variance matrix of Equation (2.2) is given by

$$V_1(\beta, \Delta_i) = \begin{pmatrix} v_1(\beta, \Delta_i) & v_3(\beta, \Delta_i) \\ v_3(\beta, \Delta_i) & v_2(\beta, \Delta_i) \end{pmatrix},$$
with

\[
v_1(\beta, \Delta_i) = \frac{\Delta_i - \frac{2}{\beta}(1 - e^{-\beta \Delta_i}) + \frac{1}{2\beta}(1 - e^{-2\beta \Delta_i})}{\beta^2},
\]

\[
v_2(\beta, \Delta_i) = \frac{1 - e^{-2\beta \Delta_i}}{2\beta},
\]

\[
v_3(\beta, \Delta_i) = \frac{1 - 2e^{-\beta \Delta_i} + e^{-2\beta \Delta_i}}{2\beta^2}.
\]

Finally, the observed position \(s_{t_i}^{(x)}\) of the animal is modeled as a Gaussian random variable centered at the true location \(\mu_{t_i}^{(x)}\)

\[
s_{t_i}^{(x)} \sim N(\mu_{t_i}^{(x)}, \sigma_E^2).
\]

To aggregate the x and y dimensional distributions into a 2-dimensional model, as given in Equation (2.1), the covariance terms between all x and y elements is set to 0. This yields the marginal model for the individual, with parameters \((\beta, \gamma_1, \gamma_2, \sigma^2, \sigma_E^2)\) and distributions

\[
s_{t_i} \sim N(Z\alpha_{t_i}, \sigma_E^2 I_2)
\]

\[
\alpha_{t_i} \sim N(T(\beta, \Delta_i)\alpha_{t_i-1} + d(\gamma_1, \gamma_2, \beta, \Delta_i), \sigma^2 V(\beta, \Delta_i)).
\]

where \(T = I_2 \otimes T_1(\beta, \Delta_i),\ d = [d_1(\gamma_1, \beta, \Delta_i)', d_1(\gamma_2, \beta, \Delta_i)']',\ V = I_2 \otimes V_1(\beta, \Delta_i),\) and \(Z = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}.\)

In the CTCRW model \(\beta\) controls the autocorrelation in velocity. Using this parametrization, small values of \(\beta\) imply a higher tendency to continue traveling with the same velocity over time. As \(\beta\) goes to infinity, if \(\frac{\gamma}{\beta}\) goes to a constant, the velocities become Brownian motion with drift \(\gamma = (\gamma_1, \gamma_1)\). The parameter \(\gamma_1\) describes the mean (drift) velocity in the \(x\) direction, and \(\gamma_2\) represents the mean (drift) velocity in the \(y\) direction. Finally, \(\sigma^2\) represents the variability in the random velocity, and \(\sigma_E^2\) represents the observation error variance. For details about the derivation of the model and examples using this model see Johnson et al.
2.2.2 Independent Group Movement Model

Assuming independent movement between individuals, this model can be easily extended to a group setting. For the remainder of the article we assume that the movement parameters \((\beta, \gamma_1, \gamma_2, \sigma^2, \sigma^2_E)\) are shared by all individuals.

Assume that we observe \(K \geq 1\) animals where every individual is observed at each time point \((t_1, t_2, ..., t_N)\). The observed locations are denoted by \(S_{t_i} = (s^{(1)}_{t_i}, s^{(2)}_{t_i}, ..., s^{(K)}_{t_i})^T\) for \(t_i \in t_1, t_2, ..., t_N\) and the unobserved states are denoted \(A_{t_i} = (\alpha^{(1)}_{t_i}, \alpha^{(2)}_{t_i}, ..., \alpha^{(K)}_{t_i})^T\). The joint distribution for the unobserved states may be expressed as

\[
g \left( A_{t_{1:N}} | \beta, \gamma_1, \gamma_2, \sigma^2 \right) = \prod_{i=1}^{N} \prod_{k=1}^{K} f(\alpha^{(k)}_{t_i} | \alpha^{(k)}_{t_{i-1}}, \beta, \gamma_1, \gamma_2, \sigma^2), \tag{2.5} \]

where \(f(\alpha^{(k)}_{t_i} | \alpha^{(k)}_{t_{i-1}}, \beta, \gamma_1, \gamma_2, \sigma^2)\) is the density of a normal random variable for the unobserved state for individual \(k\) at time \(t_i\), as defined in Equation (2.4). The joint distribution for the observed locations conditional on the unobserved states is therefore

\[
h \left( S_{t_{1:N}} | A_{t_{1:N}}, \sigma^2_E \right) = \prod_{i=1}^{N} \prod_{k=1}^{K} f(s^{(k)}_{t_i} | \alpha^{(k)}_{t_i}, \sigma^2_E), \tag{2.6} \]

where \(f(s^{(k)}_{t_i} | \alpha^{(k)}_{t_i}, \sigma^2_E)\) is the density of a normal random variable for the observation error for individual \(k\) at time \(t_i\), as defined in Equation (2.3).

2.2.3 Dynamic Point Process Interaction (DPPI) Model

If we assume independence between individuals, once two animals start to drift apart, there is no mechanism to draw the animals back towards each other. To model schooling or herd behavior, we propose an approach motivated by spatial point process models. Consider Equation (2.5), which gives the distribution of the unobserved states of a set of animals at the current time point conditional on the locations at the previous time point. To simplify notation, let \(\Theta_1 = (\beta, \gamma_1, \gamma_2, \sigma^2, \sigma^2_E)\) describe the parameters for the marginal movement model, and
let $\Theta_2$ describe the parameters for a spatial point process interaction function $\psi(\cdot)$. For each pair of locations at the current time point, we multiply the density by a point process interaction function $\psi_{jk}(||\alpha_{t_i}^{(j)} - \alpha_{t_i}^{(k)}||; \Theta_2)$ which depends only on the pairwise Euclidean distance between the current locations $||\alpha^{(j)} - \alpha^{(k)}|| = \sqrt{(\mu_x^{(j)} - \mu_x^{(k)})^2 + (\mu_y^{(j)} - \mu_y^{(k)})^2}$ and parameter $\Theta_2$. Hence we multiply Equation (2.5) by the product of our interaction functions

$$h(S_{t_1:N} | A_{t_1:N}, \sigma_E^2) g(A_{t_1:N} | \beta, \gamma_1, \gamma_2, \sigma^2) \psi(A_{t_1:N} | \Theta_2) c(\Theta_1, \Theta_2),$$

which takes values in $\mathbb{R}^+$. For two animals $i$ and $j$, if the value of $\psi_{jk}(||\alpha_{t_i}^{(j)} - \alpha_{t_i}^{(k)}||)$ is small, this discourages animals from moving to these locations at the same time.

The resulting model has joint density given by:

$$c(\Theta_1, \Theta_2) = \int h(S_{t_1:N} | A_{t_1:N}, \sigma_E^2) g(A_{t_1:N} | \beta, \gamma_1, \gamma_2, \sigma^2) \psi(A_{t_1:N} | \Theta_2) dA_{t_1:N}$$

The point process interaction function $\psi(A_{t_1:N} | \Theta_2)$ should be selected based on the assumed interaction behavior of the animals being studied. One of the simplest examples in the point process literature is the hardcore Strauss function (Møller and Waagepetersen, 2004), which can be used to incorporate collision avoidance, as it results in a repulsion zone which prevents points from being too close together. To incorporate attraction behavior, we could consider the very-soft-core interaction function, derived in (Ogata and Tanemura, 1984) which encourages clustering at small distances.
and behave independently when they are a large distance apart. An interaction function that captures this behavior is the attraction-repulsion interaction function found in Goldstein et al. (2015). This interaction function is given by:

$$
\psi(A_{t_1:N}, \theta_1, \theta_2, \theta_3, R) = \prod_{i=1}^{N} \prod_{k=2, j<k} \psi(||A_{t_i}^{(j)} - A_{t_i}^{(k)}||; \theta_1, \theta_2, \theta_3, R),
$$

with

$$
\psi(r; \theta_1, \theta_2, \theta_3, R) = \begin{cases} 
0 & \text{if } 0 \leq r \leq R \\
\psi_1(r) \equiv \theta_1 - \left(\frac{\sqrt{\theta_1}}{\theta_2 - R} (r - \theta_2)^2\right) & \text{if } R \leq r \leq r_1 \\
\psi_2(r) \equiv 1 + \frac{1}{(\theta_3(r - r_2))^2} & \text{if } 0 \geq r_1.
\end{cases} \tag{2.9}
$$

Using this parametrization, $\theta_1$ gives the peak height of the interaction function, $\theta_2$ gives the location of the peak, and $\theta_3$ controls the rate at which the function descends after the peak. The values $r_1$ and $r_2$ in Equation (2.9) are the unique real numbers that make $\psi(r)$ and $\frac{d}{dr} \psi(r)$ continuous, given by the solution to the differential equations

$$
\begin{cases} 
\psi_1(r_1) = \psi_2(r_1) \\
\frac{d\psi_1}{dr}(r_1) = \frac{d\psi_2}{dr}(r_1)
\end{cases}
$$

See Goldstein et al. (2015) for details. Examples of the interaction functions under different parameter settings are given in Figure 2.2.

### 2.2.4 Comparison with Existing Approaches

There have been several other models proposed to account for interaction behavior in animal movement. Let $A_{t_i}$ represent the true locations of each of the animals in the group at time $t_i$. Gautrais et al. (2008) utilize a model where the locations at the next time point $A_{t_i+1}$ are only dependent on neighbor’s locations at the current time point, so the interaction is a function of $A_{t_i}$. Since animals generally interact continuously over time we prefer a model that allows modeling of group behavior based on the joint distribution of the next location of the individuals in the group, resulting in an interaction which is a function of $A_{t_i+1}$. This results in a reasonable model, even if there are long time lags between the observations.
Figure 2.2: Behavior of Attraction-Repulsion Interaction Function

Examples of the attraction-repulsion interaction function from Goldstein et al. (2015).

a) Demonstrates the effect of changing the peak height parameter $\theta_1$.
b) Demonstrates the effect of changing the peak location parameter $\theta_2$.
c) Demonstrates the effect of changing the rate of descent parameter $\theta_3$.

Additionally, we consider direct estimation of model parameters, whereas Gautrais et al. (2008) utilize extensive simulations under different parametrizations followed by analysis of group summary statistics. Mann (2011) discuss Bayesian parameter estimation of a SPP system model, where the interaction term in the model is again assumed to depend only on the system state at the previous time point. However, the analysis is only accurate if the rate of observations matches the rate at which animals update their velocity, implicitly assuming that individuals update their velocities at discrete time points (McClintock et al., 2014).

Potts et al. (2014) propose a similar general framework that combines three different aspects of movement, individual movement, the effect of the environment and the interaction with previous behavior of the rest group, to model an individual's next location. Mann (2011) finds that parameter estimates can be biased if the time lag for the observations does not match the rate at which individuals update their velocities when only the previous locations are considered. Our model differs since our interaction behavior depends on the current joint locations of the group of individuals, rather than just the previous locations using point process interaction functions. Johnson et al. (2013) use spatio-temporal point process models to study resource selection, but they do not consider animal interactions.
2.3 Model Inference

Next, we describe a Metropolis-Hastings algorithm to perform Bayesian inference. We select priors for each of the parameters that reflect our limited prior information about the model parameters. For $\gamma_1$ and $\gamma_2$ we specify conjugate normal priors with zero mean and variance equal to $10^4$, $\pi(\gamma_1) \sim N(0, 10^4)$ and $\pi(\gamma_2) \sim N(0, 10^4)$. For the parameters that are restricted to be positive we specify truncated normal priors, denoted $\text{truncN}(\mu, \sigma^2, B_L)$, with lower bound given by $B_L$ and density proportional to

$$f(x|\mu, \sigma^2, B_L) \propto \exp\left(\frac{-(x - \mu)^2}{2\sigma^2}\right) I\{x > B_L\}$$

where $I$ is the indicator function. The priors chosen are given by $\beta \sim \text{truncN}(1, 10^4, 0)$, $\sigma^2 \sim \text{truncN}(1, 10^4, 0)$ and $\sigma^2_E \sim \text{truncN}(1, 10^4, 0)$. The parameter $R$ was fixed a priori to be the minimum distance between individuals across all time points.

We have additional interaction parameters $\theta_1$, $\theta_2$ and $\theta_3$. For $\theta_1$ and $\theta_2$ we use truncated normal priors; $\theta_1 \sim \text{truncN}(2, 10^4, 1)$ and $\theta_2 \sim \text{truncN}(\hat{R} + 1, 10^4, \hat{R})$. Finally, since the effect of $\theta_3$ on the interaction function is minimal for all $\theta_3$ greater than one (see Figure 2.2) we use a uniform prior on $(0, 1)$ for $\theta_3$.

Inference is straightforward when the point process interactions are not included in the model. For the independent group movement model discussed in Section 2.2, we use variable-at-a-time Metropolis-Hastings. At each iteration of our MCMC algorithm, we first update the unobserved states for each individual at each time point, $A_{t1:N}$, and then each of the model parameters $(\beta, \gamma_1, \gamma_2, \sigma^2, \sigma^2_E)$.

We assessed convergence by monitoring Monte Carlo standard errors using the batch means procedures, described in Jones et al. (2006) and Flegal et al. (2008), and by comparing kernel density estimates of the posterior of the first half of the chain and the second half of the chain.

Inference becomes more challenging when interactions are included in the model. Without the interaction function in the model, the normalizing constant does not depend on the parameters, so it can be ignored for Bayesian inference. However, the normalizing function in Equation (2.8) is a function of all of the model parameters $c(\Theta) = c(\Theta_1, \Theta_2)$. In the Metropolis-Hastings algorithm, using the model likelihood from Equation (2.8), and a proposal density $q(\cdot|\cdot)$ we have
acceptance probability:

$$\alpha = \min \left(1, \frac{p(\Theta') q(\Theta'|\Theta) h \left(S_{t_{1:N}} | A_{t_{1:N}}, \Theta' \right) g \left(A_{t_{1:N}} | \Theta' \right) \psi \left(A_{t_{1:N}} | \Theta' \right) c(\Theta)}{p(\Theta) q(\Theta'|\Theta) h \left(S_{t_{1:N}} | A_{t_{1:N}}, \Theta \right) g \left(A_{t_{1:N}} | \Theta \right) \psi \left(A_{t_{1:N}} | \Theta \right) c(\Theta')} \right).$$

Thus, since the normalizing functions do not cancel out we cannot use Metropolis-Hastings without accounting for them.

Many methods have been suggested to deal with this issue in the point process literature, however they are often computationally expensive. Besag (1974) proposed an estimation method using pseudo-likelihood which does not work well when there is strong interaction. Geyer and Thompson (1992) use importance sampling to estimate the normalizing constant, however this method only works if the parameter value used in the importance function is close to the maximum likelihood estimate of the parameter. Atchade et al. (2013) propose an MCMC algorithm for Bayesian inference. Møller and Waagepetersen (2004) gives an overview of several other estimation methods. Here we use the double Metropolis-Hastings (MH) algorithm (Liang, 2010). The algorithm uses a nested MH sampler so that the normalizing functions can be canceled out in the acceptance probability for the outer MH sampler as described below. This is an approximate version of the auxiliary variable M-H algorithm (Møller et al., 2006; Murray et al., 2012) but avoids perfect sampling (Propp and Wilson, 1996) which is not possible from our model.

In the DPPI model, the distribution involves a normalizing function as given in Equation (2.8). Let $p(\Theta)$ represent the prior distribution. The double MH algorithm (Liang, 2010) is

1. Generate a proposal $\Theta'$ from some proposal distribution $q(\Theta'|\Theta')$

2. Generate an auxiliary $Y = (A_{t_{1:N}}^*, S_{t_{1:N}}^*)$ from a kernel with stationary distribution

$$h \left(S_{t_{1:N}}^* | A_{t_{1:N}}^*, \Theta' \right) g \left(A_{t_{1:N}}^* | \Theta' \right) \psi \left(A_{t_{1:N}}^* | \Theta' \right) c(\Theta')$$

3. Accept $\Theta'$ with probability $\alpha = \min (1, R(\Theta, \Theta'))$, where $R(\Theta, \Theta')$ is given by

$$\frac{p(\Theta') q(\Theta'|\Theta) h \left(S_{t_{1:N}} | A_{t_{1:N}}, \Theta' \right) g \left(A_{t_{1:N}} | \Theta' \right) \psi \left(A_{t_{1:N}} | \Theta' \right) c(\Theta)}{p(\Theta) q(\Theta'|\Theta) h \left(S_{t_{1:N}} | A_{t_{1:N}}, \Theta \right) g \left(A_{t_{1:N}} | \Theta \right) \psi \left(A_{t_{1:N}} | \Theta \right) c(\Theta')} H \left(\Theta, \Theta', A_{t_{1:N}}^*, S_{t_{1:N}}^* \right)$$
and $H \left( \Theta, \Theta', A_{t_1:N}^*, S_{t_1:N}^* \right)$ is the ratio

$$H \left( \Theta, \Theta', A_{t_1:N}^*, S_{t_1:N}^* \right) = \frac{h \left( S_{t_1:N}^* | A_{t_1:N}^*, \Theta \right) g \left( A_{t_1:N}^* | \Theta \right) \psi \left( A_{t_1:N}^* | \Theta \right)}{h \left( S_{t_1:N}^* | A_{t_1:N}^*, \Theta' \right) g \left( A_{t_1:N}^* | \Theta' \right) \psi \left( A_{t_1:N}^* | \Theta' \right)}.$$ 

In our model, since none of the parameters can be easily separated from the integration over the unobserved states; the normalizing function is a function of all model parameters. Thus, we need to use the double Metropolis-Hastings algorithm for each parameter update. Therefore, for each parameter update, we simulate a realization of the unobserved states $A_{t_1:N}$ and observations $S_{t_1:N}$ from our model with the proposal parameters, and use this simulation $Y = (A_{t_1:N}^*, S_{t_1:N}^*)$ to estimate the ratio $H \left( \Theta, \Theta', A_{t_1:N}^*, S_{t_1:N}^* \right)$. Note that this estimate is only accurate if the value of $\Theta$ is similar to the value of $\Theta'$, so we elect to use variable at a time updates for all parameters, as opposed to block updates of $\Theta$.

Now we consider the DPPI model from Section 2.4 with the attraction-repulsion interaction function from Goldstein et al. (2015). In each iteration of our double Metropolis-Hastings algorithm we first update the unobserved states, $A_{t_1:N}$, using a four-dimensional block Metropolis-Hastings update, where the unobserved state of each fish $j$ at each time point $t_i$, $\alpha_{i,j}$ consisting of the true x and y locations and instantaneous velocities, is updated one at a time. Next, we update each each parameter $(\beta, \gamma_1, \gamma_2, \sigma_2^2, \sigma_E^2, \theta_1, \theta_2, \theta_3)$ one at a time using a double Metropolis-Hastings update. For each parameter, we generate an auxiliary variable $Y$ from the DPPI model using the current parameters in the MCMC chain and the proposed parameter to be updated. For parameters $(\beta, \gamma_1, \gamma_2, \sigma_2^2, \theta_1, \theta_2, \theta_3)$ the auxiliary variable is a simulated realization of the unobserved states $Y = A_{t_1:N}$ and for $\sigma_E^2$ the auxiliary variable also requires a simulated realization of the observations $Y = (A_{t_1:N}^*, S_{t_1:N}^*)$. Both of these auxiliary variables are generated using a Metropolis-Hastings algorithm.

The length of the nested MH sampler was determined by examining the distances between the simulated realizations of the observed locations $S_{t_1:N}$ as the length is increased. The length was doubled until the average distance between locations stabilized, resulting in a nested MH sampler of length 200. The double Metropolis-
Hastings step is time consuming, since it requires a nested Metropolis-Hastings sampler for each parameter at each MCMC step. Convergence was determined using the same methods as for the independent movement algorithm.

### 2.4 Application to Simulated Data

To test the performance of our double Metropolis-Hastings algorithm we generated simulated paths from our DPPI model and recovered the true parameters. We simulated three group movement paths with starting locations taken from the starting locations of the ten guppies in Figure 2.1(a). In all cases the CTCRW movement parameters \( \Theta_1 \) were set to the means of the posterior distributions from Section 5 (\( \beta = 0.15, \gamma_1 = -1.2, \gamma_2 = 1.5, \sigma^2 = 1.7, \sigma_E^2 = 0.4 \)). The interaction parameters \( \Theta_2 \) were chosen for three different scenarios. In scenario 1 (medium interaction), we used the posterior mean parameter values from Section 5 (\( \theta_1^{(1)} = 32, \theta_2^{(1)} = 33, \theta_3^{(1)} = 0.3 \)) to mimic the guppy movement. The parameters in scenario 2 were specified to encourage stronger interaction (\( \theta_1^{(2)} = 100, \theta_2^{(2)} = 20, \theta_3^{(2)} = 0.5 \)). The parameters in scenario 3 were specified to represent a weaker interaction (\( \theta_1^{(3)} = 10, \theta_2^{(3)} = 80, \theta_3^{(3)} = 0.5 \)). The interaction functions and simulated paths are plotted in Figure 2.3. The heights of the interaction functions show that the second set of parameters (Figure 2.3(b)) results in the strongest interaction, and the third set of parameters (Figure 2.3(c)) results in the weakest interaction. In the simulated movement paths, it is apparent that Figure 2.3(c) has less interaction, but it is difficult to compare the strength of attraction between Figures 2.3(a) and (b) from the plots of the movement paths alone.

We first estimated the parameters using the independent model that assumes that the fish moved independently, as in Section 2.2. The resulting parameter estimates and 95\% equi-tailed credible intervals, which are estimated from the 2.5\% and 97.5\% quantiles of the posterior distribution sample, are given in Table 2.1. Our credible intervals for \( \gamma_1, \gamma_2, \text{ and } \sigma_E^2 \) include the true parameters for all of the simulations. However, in the medium and strong attraction scenarios the credible intervals for \( \beta \) and \( \sigma^2 \) do not contain the truth. This indicates that assuming independence when there is actually interaction among the animals can result in biased parameter estimates.

Next, we used the correct DPPI model to analyze the simulated data. The
Figure 2.3: Simulated Data Under Different Settings

The attraction-repulsion point process interaction function for the (a) medium, (b) strong, and (c) weak simulated realizations of the model; and plots of the simulated paths for the (d) medium, (e) strong, and (f) weak interactions.

Table 2.1: Simulated Model Assuming Independent Movement

<table>
<thead>
<tr>
<th>Interaction Strength</th>
<th>$\beta = 0.15$</th>
<th>$\gamma_1 = -1.2$</th>
<th>$\gamma_2 = 1.5$</th>
<th>$\sigma^2 = 1.7$</th>
<th>$\sigma_E^2 = 0.4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium</td>
<td>.184</td>
<td>-1.25</td>
<td>1.64</td>
<td>1.94</td>
<td>.389</td>
</tr>
<tr>
<td></td>
<td>(.15, .21)</td>
<td>(-1.57, -0.91)</td>
<td>(1.33, 1.98)</td>
<td>(1.76, 2.12)</td>
<td>(.36, .41)</td>
</tr>
<tr>
<td>Strong</td>
<td>.210</td>
<td>-1.11</td>
<td>1.30</td>
<td>1.92</td>
<td>.385</td>
</tr>
<tr>
<td></td>
<td>(.18, .23)</td>
<td>(-1.40, -0.83)</td>
<td>(1.02, 1.59)</td>
<td>(1.72, 2.11)</td>
<td>(.35, .41)</td>
</tr>
<tr>
<td>Weak</td>
<td>.146</td>
<td>-1.40</td>
<td>1.53</td>
<td>1.75</td>
<td>.392</td>
</tr>
<tr>
<td></td>
<td>(.12, .16)</td>
<td>(-1.78, -1.00)</td>
<td>(1.13, 1.93)</td>
<td>(1.61, 1.93)</td>
<td>(.36, .42)</td>
</tr>
</tbody>
</table>

Posterior means and 95% equi-tailed credible intervals estimated using a variable at a time Metropolis-Hastings algorithm assuming there is no interaction between individuals on the data simulated from a DPPI model with medium $(\theta_1^{(1)} = 32, \theta_2^{(1)} = 33, \theta_3^{(1)} = 0.3)$, strong $(\theta_1^{(2)} = 100, \theta_2^{(2)} = 20, \theta_3^{(2)} = 0.5)$, and weak $(\theta_1^{(3)} = 10, \theta_2^{(3)} = 80, \theta_3^{(3)} = 0.5)$ interaction settings.
Table 2.2: Simulated Model Including Interactions

<table>
<thead>
<tr>
<th>Interaction Strength</th>
<th>$\beta = 0.15$</th>
<th>$\gamma_1 = -1.2$</th>
<th>$\gamma_2 = 1.5$</th>
<th>$\sigma^2 = 1.7$</th>
<th>$\sigma_F^2 = 0.4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium</td>
<td>.161</td>
<td>-1.25</td>
<td>1.64</td>
<td>1.72</td>
<td>.404</td>
</tr>
<tr>
<td></td>
<td>(.13,.18)</td>
<td>(-1.58, -0.90)</td>
<td>(1.30,2.01)</td>
<td>(1.57,1.86)</td>
<td>(.37,.43)</td>
</tr>
<tr>
<td>Strong</td>
<td>.161</td>
<td>-1.11</td>
<td>1.32</td>
<td>1.51</td>
<td>.413</td>
</tr>
<tr>
<td></td>
<td>(.13,.18)</td>
<td>(-1.45, -0.79)</td>
<td>(1.00,1.64)</td>
<td>(1.38,1.68)</td>
<td>(.38,.44)</td>
</tr>
<tr>
<td>Weak</td>
<td>.144</td>
<td>-1.40</td>
<td>1.53</td>
<td>1.74</td>
<td>.391</td>
</tr>
<tr>
<td></td>
<td>(.12,.16)</td>
<td>(-1.82, -1.01)</td>
<td>(1.12,1.92)</td>
<td>(1.59,1.91)</td>
<td>(.36,.42)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Interaction Strength</th>
<th>$\theta_1 = (32,100,10)$</th>
<th>$\theta_2 = (33,20,80)$</th>
<th>$\theta_3 = (0.3,0.3,0.5)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium</td>
<td>37.5</td>
<td>33.7</td>
<td>.408</td>
</tr>
<tr>
<td></td>
<td>(18.1,74.4)</td>
<td>(29.6,39.1)</td>
<td>(.050,.954)</td>
</tr>
<tr>
<td>Strong</td>
<td>66.9</td>
<td>19.4</td>
<td>.614</td>
</tr>
<tr>
<td></td>
<td>(31.0,134.2)</td>
<td>(16.6,21.5)</td>
<td>(.073,.983)</td>
</tr>
<tr>
<td>Weak</td>
<td>12.4</td>
<td>78.7</td>
<td>.359</td>
</tr>
<tr>
<td></td>
<td>(4.0,33.3)</td>
<td>(20.2,114.4)</td>
<td>(.011,.947)</td>
</tr>
</tbody>
</table>

Posterior means and 95% equi-tailed credible intervals estimated using the double Metropolis-Hastings algorithm on the data simulated from a DPPI model with medium, strong, and weak interaction settings.

results are given in Table 2.2. From Table 2.2, we can see that our algorithm accurately recovers the movement parameters $\Theta_1$ with the exception of $\sigma^2$ which falls just outside the 95% credible interval in the strong attraction scenario. In Table 2.2, we are also successful in recovering $\theta_1$ and $\theta_2$, but there is greater uncertainty in these parameter estimates than in the movement parameters. Although the simulated paths looked similar in Figure 2.3, we are able to distinguish between the medium attraction and the strong attraction scenarios. However the width of the credible interval increases as attraction increases, indicating it is harder to differentiate between levels of attraction as the peak of our attraction-repulsion interaction function increases. For $\theta_3$, the posterior is very similar to the prior distribution, a uniform distribution on $(0,1)$, which indicates that there is not enough information in the simulated data to infer the parameter. To test the effect that having an incorrect estimate for $\theta_3$ would have on the other parameter estimates, the double Metropolis-Hastings algorithm was rerun fixing $\theta_3$ at several different values. The resulting posterior distributions for the other parameters remained consistent with our previous results, so the lack of identifiability of $\theta_3$
does not invalidate our estimates for the other parameters.

2.5 Guppy Data

To illustrate our approach, we analyze the guppy shoal data set of Bode et al. (2012b), available online (Bode et al., 2012a), where the individuals show a tendency to interact, as evident by the shoaling behavior in Figure 2.1(a). Gravel and shade were added in one corner of the tank to attract the guppies, and a group of ten guppies is released in the opposite corner. The full trajectories are observed for the guppies from the time they begin moving towards the destination until the first guppy reaches the target. One realization of the experiment is plotted in Figure 2.1(a). The experiment was repeated several times, but we focus our analysis on a single realization of the experiment. Bode et al. (2012b) calculated a summary statistic based on angles of direction to estimate the social interactions of a group. A permutation test, which randomly assigned group membership of guppies to artificial experimental trials, found that the social interaction summary statistic was larger in actual groups than in artificially permutated groups in all but 75 out of 10,000 permutations. Bode et al. (2012b) concluded that the guppies do interact socially. Using our approach, we are able to directly infer parameter values that reflect this interaction between fish.

We first performed inference using the independent movement model from Section 2.2. Next we used our double Metropolis-Hastings algorithm to estimate the parameters for the DPPI model described in Section 2.3. The results are presented in Table 2.3. The means of the posterior distributions for the parameters $\gamma_1$, $\gamma_2$, and $\sigma_E^2$ are almost identical for the independent and the interaction models. However, the estimates for $\beta$ and $\sigma^2$ differ slightly. Our results from the simulation study imply that the independent model estimates could be inaccurate, since the fish interact with each other socially (Bode et al., 2012b). The results for the movement model parameters $\Theta_1$ indicate that there is autocorrelation in the observations over time, the fish tend to move toward the shelter in the upper left corner, and there is appreciable measurement error.

To compare the independent model and the DPPI model, we analyze the distribution of pairwise distances from simulated realizations of the two models. In point process statistics, Ripley’s K function, which is described in Møller and
Table 2.3: Guppy Data Set

<table>
<thead>
<tr>
<th>Model</th>
<th>$\beta$</th>
<th>$\gamma_1$</th>
<th>$\gamma_2$</th>
<th>$\sigma^2$</th>
<th>$\sigma_E^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Indep.</td>
<td>.159</td>
<td>-1.18</td>
<td>1.51</td>
<td>1.88</td>
<td>0.384</td>
</tr>
<tr>
<td></td>
<td>(.13, .18)</td>
<td>(-1.56, -0.80)</td>
<td>(1.14, 1.89)</td>
<td>(1.71, 2.04)</td>
<td>(0.35, 0.41)</td>
</tr>
<tr>
<td>Interact</td>
<td>.145</td>
<td>-1.17</td>
<td>1.51</td>
<td>1.75</td>
<td>0.395</td>
</tr>
<tr>
<td></td>
<td>(.12, .16)</td>
<td>(-1.58, -0.77)</td>
<td>(1.12, 1.89)</td>
<td>(1.60, 1.95)</td>
<td>(0.36, 0.42)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model</th>
<th>$\theta_1$</th>
<th>$\theta_2$</th>
<th>$\theta_3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interact</td>
<td>32.0</td>
<td>32.9</td>
<td>0.304</td>
</tr>
<tr>
<td></td>
<td>(15.1, 58.2)</td>
<td>(23.4, 44.4)</td>
<td>(0.019, 0.921)</td>
</tr>
</tbody>
</table>

Posterior means and 95% equi-tailed credible intervals for the guppy data of Bode et al. (2012b) assuming no interaction and attraction-repulsion point process interactions, estimated using variable at a time Metropolis-Hastings and the double Metropolis-Hastings algorithm respectively.

Waagepetersen (2004), can be used to analyze the attraction or repulsion between points. The K function, however, requires an estimate for the intensity of the point process, which does not exist in our model since each point has a unique distribution. Instead, we consider the number of pairs of points that lie within a distance of $d$ of each other, a monotone function which starts at 0 and ends at the total number of pairs of points in the process, defined by

$$K^*(d) = \sum_{i=1}^{N} \sum_{k=2}^{K} \sum_{j<k} I\{||\alpha_{ti}^{(j)} - \alpha_{ti}^{(k)}|| < d\}$$

where $I$ represents the indicator function. Larger values of the function indicate that there are more pairs of points within that distance of each other; for example larger values of $K^*(d)$ for small values of $d$ indicate that there is more attraction between points at small scales. To test if our fitted model is capturing the interaction between guppies, we simulate 100 movement paths using draws from the posterior densities of the parameters from the independent movement model and from the DPPI model. We calculate $K^*(d)$ for each of the simulated paths, and create 95% pointwise envelopes for the K-functions in the two simulation settings by taking the 2.5% and 97.5% quantiles. The $K^*(d)$ function is then calculated for the data and is compared to the envelopes. The result is plotted in Figure 2.4. The $K^*(d)$ function for the guppy data is above the envelope for the independent movement model at
Estimates of the $K^*(d)$ function for the data compared to 95% Equi-tailed confidence intervals calculated from simulated paths using parameters drawn from the posterior distributions of (a) the CTCRW model assuming no interactions; and (b) The DPPI model with the attraction-repulsion interaction function.

small distances, indicating that there is more attraction between individuals not present in the independent group movement model. When we use the fitted DPPI model with an attraction-repulsion interaction function, the envelope includes the $K^*(d)$ function for the guppy data at all distances, indicating that the inclusion of the interaction function improves the performance of the model.

2.6 Discussion

The movement model with point process interactions we have developed allows us to study group movement of individuals by considering location-based interactions directly. Our double Metropolis-Hastings algorithm for Bayesian inference allows us to accurately estimate parameters. We analyze the movement tracks of a shoal of guppies, which was previously studied using permutation tests and summary statistics in Bode et al. (2012b), and find that the DPPI model captures the observed pairwise interactions between guppies. We are able to generate paths with similar distributions of pointwise distances between individuals using our model, and show that an independent model fails to do so. We have shown that ignoring interactions leads to unrealistic group movement paths and inaccuracies.
in parameter estimates. One drawback of our model is that the simulated paths appear less smooth than the actual paths in the data. This could be due to the large turn that the guppies take, which is apparent in Figure 2.1(a). This in turn may inflate the variance of the velocity in our model, causing the fish to change direction more frequently. Including a time-varying drift term in our CTCRW model might better capture the observed movement behavior, but we are still able to capture the social interactions using our model.

This model could be extended in several ways. Analyses of group movement mechanics have focused on three main features: collision avoidance at small scales, alignment at medium scales, and attraction at larger scales (Gautrais et al., 2008). Our model as presented in Section 2.3 does not explicitly account for the alignment behavior. One method to account for the alignment is to model correlation between the velocities of different individuals as a function of their pairwise distance at the previous time step. For example, the correlation between two velocities could be modeled as the function

$$\exp \left( -\frac{||\alpha_{tk-1}^{(i)} - \alpha_{tk-1}^{(j)}||}{\phi} \right)$$

where the parameter $\phi \in \mathbb{R}^+$ measures the rate at which the correlation decreases as the distance between the animals increases. A larger value of $\phi$ indicates that the correlation drops off more slowly. Katz et al. (2011), however, find that the alignment is automatically induced by the attraction and repulsion behavior, indicating that this might not be necessary to add to the model.

**Acknowledgements**

This research is supported by the NSF grant EEID 1414296.
Chapter 3  
A Spatially-Varying Stochastic Differential Equation Model for Animal Movement

In this chapter I propose a stochastic differential equation framework for modeling animal movement. Within this framework I model spatially-varying movement rates and spatially-varying directional bias through novel semi-parametric motility and potential surfaces, respectively. Directional persistence is modeled as in Chapter 2. I use this model to study the movements of ants within a four-chambered nest. This model differs from the DPPI model I developed in Chapter 2 in that it allows for flexible individual movement driven by the local environment. However the model does not incorporate dependence between individuals. In Chapter 4 I will model dependence in movement through discrete interacting behavioral states.

3.1 Introduction

Studying the movement of animals allows scientists to address fundamental questions in ecology and epidemiology. It can be used to understand how animals are impacted by their environment; for example Gibert et al. (2016) studied the impact of temperature on animal movement to understand potential impacts of climate change and Watkins and Rose (2013) studied the impact of novel environments on small fish in a simulation-based analysis. Animal movement can give insight into the impact of external stimuli, as studied by Dodge et al. (2013) and Thiebault and
Tremblay (2013). Further, animal movement is important in understanding the collective behavior of animal societies (Watkins and Rose, 2013). Understanding these factors can benefit animal conservation (Killeen et al., 2014) and can increase understanding of the impact of migration on disease dynamics (Altizer et al., 2011).

Improvements in technology have allowed scientists to observe animal movement at a fine temporal resolution over long periods of time (Toledo et al., 2014). This fine scale observation enables researchers to observe more complete individual paths, revealing the animal’s behavioral patterns in more detail and allowing for the fitting of more complex statistical models (Avgar et al., 2015; Bestley et al., 2015). Since animal movement data inherently consist of observations through time, it is intuitive to describe movement using differential equations which are often used to describe dynamic systems. As any deterministic differential equation is unlikely to capture the movement of a single animal, we propose a stochastic differential equation (SDE) approach to modeling animal movement. Similar approaches based on stochastic differential equations have been utilized several times to model animal movement (Blackwell, 1997; Preisler et al., 2004; Johnson et al., 2008a; Preisler et al., 2013).

In this article, we will focus on the analysis of the movement of ants in a four chambered nest. Ants provide an ideal system for studying animal movement, as an entire population (colony) can be observed and tracked (Mersch et al., 2013), something rarely possible outside of laboratory systems. For this same reason, ants provide an ideal system for studying the spread of information or infectious disease in societies. Despite the fact that they live in close proximity to one another, researchers have hypothesized a ‘collective immunity’ where collective behavior helps to prevent the spread of disease (Quevillon et al., 2015; Cremer et al., 2007). Proposed mechanisms which result in this ‘collective immunity’ include the spatial and social segregation of ants in the nest which minimizes the number of foraging ants which come into contact with the queen. Ant behavior, however, can be challenging to model due to this social and spatial segregation within the nests (Quevillon et al., 2015). In this paper, we propose a novel spatially-varying SDE model to capture ant movement behavior within the nest. Analysis of the ant movement indicates a tendency to move more quickly in the central chambers of the nest with ants utilizing the central chambers primarily as corridors for commuting. Simulation of new ants entering the nest highlights that the time needed to pass
through sections of the nest varies based on spatial location.

Johnson et al. (2008a) use a continuous time correlated random walk model based on integrated Brownian motion to model directional persistence in movement. However Johnson et al. (2008a) do not consider the case in which the behavior of an animal is dependent on its position. Quevillon et al. (2015) analyze the movement of ants in a nest using the continuous time discrete space Markov chain model of Hanks et al. (2015). Their results reveal spatially-varying movement behavior near the queen.

Brillinger et al. (2002) and Preisler et al. (2004) propose an SDE based model for movement on a potential surface which captures directional bias in movement patterns across space. These potential surface methods allow for flexible modeling of directional bias in movement, but cannot easily model variation in the absolute speed of movement when there is no directional bias. This is important in ant systems, as ant nests typically contain "corridors" which connect important chambers in the nest. Ant movement through these corridors shows high velocity and directional persistence (correlated movement), but directional bias is not consistent across observations, as some ants are moving in one direction while other ants are moving in the other. Existing models allow for directional persistence or spatially-varying directional bias. We propose an SDE approach to model movement behavior with all three features: (1) correlated movement patterns, (2) directional bias through a potential surface and (3) spatial variation in movement rates through the inclusion of a novel spatially-varying motility surface.

The remainder of the paper is organized as follows. In Section 3.2, we introduce the carpenter ant system in detail. Next, in Section 3.3 we discuss our proposed model for the ant movement data which incorporates autocorrelation, spatially-varying directional bias, and spatially-varying absolute movement rate using potential and motility surfaces respectively. In Section 3.4 we describe a discrete approximation of the model and our Bayesian inferential approach. The results of the application of our approach to ant movement data are presented in Section 3.6. We conclude in Section 3.7 with a discussion and potential directions for future work.
3.2 Carpenter Ant Movement

We begin with a description of the ant movement data and describe an exploratory data analysis that motivates our modeling approach. We analyze the movement of the ants in a custom-constructed nest. We used the common black carpenter ant *Camponotus pennsylvanicus* which nests in wood in temperate forests in the Eastern USA. We collected colonies between May and June 2015. The ants were placed in a nest structure consisting of four distinct chambers. Each chamber is divided into two sections by an internal barrier, creating a small passageway 12mm across between the upper and lower halves of the chamber. Each of the four chambers measures 65mm by 40mm resulting in a total nest size of 65mm by 160mm. Each doorway between chambers is 6mm across. There is an exit from the nest in chamber IV, leading to an area with food and water. The queen resides primarily in chamber I, far from the nest exit.

A plot containing three examples of individual ant movement paths in the nest is given in Figure 3.1. The nest exit is marked with an "X" below chamber IV in each plot. The movement paths indicate that ant behavior is different within different chambers of the nest, with faster, more directed movement happening in chambers II and III. This type of spatially-varying behavior would be difficult to capture using the potential surface SDE approach (e.g. Brillinger et al. (2002) and Preisler et al. (2004)) as the ants move at a faster rate in some regions of the nest than in others, but do not show consistent directional bias.
The data consist of the 2-dimensional location coordinates \((x_{t_i,j}, y_{t_i,j})\), a time index \(t_i\), and a unique ant identifier \(j\) for each of 32 ants for one hour at 1-second intervals. One camera was positioned over each chamber of the nest. Ants were filmed under infrared lighting with GoPro Hero3 and Hero3+ cameras with modified infrared filters (RageCams, Sparta, MI) to simulate natural lighting conditions. Each ant was individually tagged with a unique identifier allowing a human observer to record their position. Observations were recorded at every second by clicking on the location of the ant using a custom software package. Locations were recorded for the entire hour for all ants that enter chamber IV at any time during observation. The dimensions of the nest were recorded by clicking on predetermined corners in the nest at the beginning of the observation period. These observations can then be aggregated to generate movement paths across the four chambers.

Several challenges arise in combining the data from the four cameras. At some time-points (0.02% of observations) an ant is positioned at the door between two chambers and is observed by two cameras in two chambers at the same time. This could be due to different segments of the ants being visible in different chambers at the same time-point. Further complications arise when the ants are not observed for a span of time. This can happen when the ant has exited the nest structure (5.46% of observations) or when the ant is situated in chamber doorways (1.08% of observations). When the ant has exited the nest structure no cameras capture its movement. In what follows, we assume that when the ant re-enters the nest its movement is independent from prior in-nest movements. If the ant is between chambers and not visible on any camera, the ant’s locations are linearly interpolated from the observations before and after the ant is in the entryway. A summary of the classes of the observations used for aggregating the data are presented in Table 3.1.

To explore the spatial movement behavior of the ants kernel density estimates are utilized. A two-dimensional kernel density estimate is applied to the \(x\) and \(y\) coordinates of all ants aggregated through time in Figure 3.2a(a). To study the impact of location on velocity, the empirical speeds of each ant at each time point are calculated and segregated into four groups, one for each nest chamber, based on the ant’s observed location at each respective time point. Separate kernel density estimates are applied to empirical speed of the ants in each of the four chambers and plotted in Figure 3.2b. From Figure 3.2a, we can see that the ants
Table 3.1: Ant Data Cleaning

<table>
<thead>
<tr>
<th>Code</th>
<th>Meaning</th>
<th>Count</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Ant Outside of Nest</td>
<td>6173</td>
<td>5.46</td>
</tr>
<tr>
<td>1</td>
<td>Ant Observed in Chamber I</td>
<td>8985</td>
<td>7.95</td>
</tr>
<tr>
<td>10</td>
<td>Ant Observed in Chamber II</td>
<td>729</td>
<td>0.65</td>
</tr>
<tr>
<td>100</td>
<td>Ant Observed in Chamber III</td>
<td>524</td>
<td>0.46</td>
</tr>
<tr>
<td>1000</td>
<td>Ant Observed in Chamber IV</td>
<td>95315</td>
<td>84.38</td>
</tr>
<tr>
<td>5.5</td>
<td>Ant Between Chambers I &amp; II</td>
<td>856</td>
<td>0.76</td>
</tr>
<tr>
<td>55</td>
<td>Ant Between Chambers II &amp; III</td>
<td>161</td>
<td>0.14</td>
</tr>
<tr>
<td>550</td>
<td>Ant Between Chambers III &amp; IV</td>
<td>190</td>
<td>0.17</td>
</tr>
<tr>
<td>1050</td>
<td>Ant in nest Doorway</td>
<td>8</td>
<td>0.01</td>
</tr>
<tr>
<td>110</td>
<td>Ant Observed in both Chambers II &amp; III</td>
<td>11</td>
<td>0.01</td>
</tr>
<tr>
<td>1100</td>
<td>Ant Observed in both Chambers III &amp; IV</td>
<td>8</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Observation counts and percentage for ant data.

spend most of their time in chamber IV, and figure 3.2b indicates that the average speeds in chambers I and IV tend to be less than the average speeds in chambers II and III. These exploratory results indicate that both the directional bias and the absolute ant velocity may vary spatially and suggest that the center chambers are primarily used for higher velocity transit. To explore the temporal autocorrelation in movement, an autoregressive model of order 1 was fit to the empirical velocities of a randomly selected ant. The resulting estimated autoregressive parameter, 0.81 (standard error 0.015) indicates the need to model directional persistence. Our exploratory data analysis suggests that an appropriate model for these data should therefore include temporal autocorrelation, spatially-varying directional bias, and a spatially-varying movement rate. We develop a model which allows for this type of behavior in the Section 3.3.

### 3.3 Spatially-Varying SDE Model

In this Section, we propose an SDE model for animal movement that captures

1. directional persistence via a continuous time correlated random walk (CTCRW),
2. spatial variation in directional bias through a potential surface,
3. spatial variation in overall movement rate using a motility surface.
These three features have not been jointly utilized in any previous models. In previous work, potential surfaces have been used ignoring temporal autocorrelation (Preisler et al., 2004; Brillinger et al., 2012). We extend these methods by modeling directional persistence through a CTCRW, and expand the model to allow for variability in movement rate. This model will be used to analyze within-nest ant movement, where at time $t$, an individual’s location at time $t$ is denoted $(x(t), y(t))$ and its velocity is denoted $(v_x(t), v_y(t))$. We will begin by describing the movement of one individual, and in Section 3.4, we will generalize for multiple independent ants.

### 3.3.1 Continuous Time Correlated Random Walk

Animal movement is often autocorrelated through time, resulting in smooth movement paths. The CTCRW model presented by Johnson et al. (2008a) provides one method for modeling dependence through time. The CTCRW model specifies an Ohrstein-Uhlenbeck (O-U) process on an animal’s velocity with directional drift $\mu$. The O-U process is defined as a stochastic process that is stationary (the joint density remains the same for uniform shifts in time), Gaussian, Markovian and has continuous paths (Klebaner et al., 2005). Alternatively, the O-U process can be derived using linear stochastic differential equations (Gardiner, 1986).
We consider a process that describes the movement of a particle in two dimensions. The movement in each dimension is assumed to follow an independent CTCRW. This is a reasonable assumption for animal movement since positive correlation in the x-dimension and y-dimension would result in bias toward movement in the North-East or South-West directions. The CTCRW model to describe the velocities $v_x(t), v_y(t)$ and the locations $x(t), y(t)$ is defined as

$$\begin{align*}
    dv_x(t) &= \beta (\mu_x - v_x(t)) \, dt + \sigma dW_v(t), \\
    dv_y(t) &= \beta (\mu_y - v_y(t)) \, dt + \sigma dW_v(t), \\
    dx(t) &= v_x(t) \, dt + \kappa dW_x(t), \\
    dy(t) &= v_y(t) \, dt + \kappa dW_y(t).
\end{align*}$$

In the velocity equations, $\mu_x$ represents the mean drift in the x direction, $\mu_y$ represents the mean drift in the y direction, $\beta$ controls the autocorrelation in movement, $\sigma$ is related to the variability in velocity, and $W_v(t)$ represents independent Brownian motion processes with unit variance. In the equation for location, $\kappa$ is related to the additional variability in location (i.e. measurement error) and $W_{x}(t), W_{y}(t)$ are again Brownian motion with unit variance. The case where $\kappa = 0$ gives intuition on the position of the object over time

$$x_t = x_0 + \int_0^t v_x(s) \, ds. \tag{3.1}$$

The CTCRW process results in a model where the conditional mean of the discretized velocity is a weighted average of the previous velocity and the directional drift term $\mu$. Examples of the use of this model include Baylis et al. (2015), which analyzes the decline in population of southern sea lions, Northrup et al. (2015), which studies the impact of habitat loss on the movement of mule deer, and Rode et al. (2015), which analyzes the movement of polar bears in reaction to the decrease in sea ice habitat. The CTCRW model, however, assumes that the movement behavior is homogeneous in space. This assumption can be relaxed by allowing the drift term for the individual’s velocity to be a function of the individual’s location $(x(t), y(t))$. Doing so unifies the CTCRW model with the potential function models of Brillinger et al. (2002) and Preisler et al. (2004).
3.3.2 Potential Surface

Potential surfaces are described in relation to animal movement modeling by Brillinger et al. (2002) and Preisler et al. (2013). There are several examples of analyses using potential surfaces in movement modeling, including Preisler et al. (2004), which studies the influence of roads on the movement of elk, and Brillinger et al. (2012), which analyzes the movement of elk in a fenced in experimental forest. In a potential function approach, the individuals, or ants in our case, are considered to be moving around on a surface with regions of attraction and repulsion.

First consider a potential surface, $H(x, y)$, that is only a function of the current two-dimensional location of the object $(x, y)$. This function can be thought of as a topological surface where objects are drawn to lower regions similar to a marble moving on a curved surface. The directional tendency of movement is therefore down the slope of the surface, or equivalently in the direction of the negative gradient of the potential surface. Using this analogy, if temporal autocorrelation is ignored, the expectations of the $x$ and $y$ components of velocity, denoted $v_x(t)$ and $v_y(t)$ respectively, of an individual can each be calculated by taking the negative of the $x$ and $y$ derivatives of $H(x, y)$ respectively:

$$E(v_x(t)) = -\frac{dH(x(t), y(t))}{dx}$$
$$E(v_y(t)) = -\frac{dH(x(t), y(t))}{dy}$$

Note that temporal autocorrelation is not incorporated in these mean movement equations, and therefore they do not result in realistic animal movement behavior. To construct a model that incorporates both temporal autocorrelation and a potential surface, directional bias in movement is incorporated in the CTCRW model from Section 3.3.1 by defining the mean drift $\mu$ as the negative gradient of $H(x, y)$. The result is a system of stochastic differential equations for correlated velocity with spatially-varying movement bias defined by the potential surface $H(x, y)$

$$dv_x(t) = \beta \left(-\frac{dH(x(t), y(t))}{dx} - v_x(t)\right) dt + \sigma dW_{v_x}(t)$$
$$dv_y(t) = \beta \left(-\frac{dH(x(t), y(t))}{dy} - v_y(t)\right) dt + \sigma dW_{v_y}(t)$$

(3.2)
In previous work (e.g. Brillinger et al. (2002) and Preisler et al. (2004)), only the over-damped case is considered, where $\beta \rightarrow \infty$. This simplifies estimation of the potential surface, but fails to model the temporal autocorrelation which is normally present in animal movement. The SDE model for velocity (3.2) jointly models directional bias through the potential function $H(x, y)$ and temporal autocorrelation through the finite autoregressive parameter $\beta$.

We model the potential surface using B-spline basis functions (De Boor, 1978). Parametric models of the potential surface are also possible (Quevillon et al., 2015; Hanks et al., 2015) but our goal in this analysis is to flexibly model spatially-varying behavior within the nest. We thus assume the potential surface is given by

$$H(x, y) = \sum_{k,l} \gamma_{kl} \phi^{(M)}_k(x) \psi^{(M)}_l(y)$$

(3.3)

where $\phi^{(M)}_k(x)$ and $\psi^{(M)}_l(y)$ are B-spline basis functions of order $M$, with $K$ basis functions in the $x$-direction and $L$ basis functions in the $y$-direction so that $k \in \{1, \ldots, K\}$ and $l \in \{1, \ldots, L\}$. We chose to set $M = 4$ so that the potential surface $H(x, y)$ has two continuous derivatives. As a result, the gradient of the potential surface (3.3) also has a continuous derivative, meaning it is relatively smooth. The potential surface $H(x, y)$ only impacts movement through its gradient. Thus only contrasts of the B-spline coefficients $\{\gamma_{kl}\}$ are identifiable and we elect to subject them to the constraint $\sum_{k,l} \gamma_{kl} = 0$. Rather than using tuning to select the number of knots directly, the number of basis functions is set to a large number, 560, selected to keep the scale in the dimensions approximately equal ($K=16$, $L=35$) and the surface is smoothed (Eilers and Marx, 1996) by using a normal prior on the coefficients with mean 0. The smoothing priors act similar to penalization techniques in a maximum likelihood setting. Details of this prior will be given in Section 3.4.

The movement of the ants in our analysis is restricted by the locations of the walls in the ant chambers (Figure 3.1). Various models that account for restricted animal movement have been proposed (Brillinger, 2003; Brost et al., 2015). In this case, we restrict ant movement near walls by augmenting the spatially smooth potential function (3.3) with an additive exponential potential $R(x, y)$

$$R(x, y, r, r_1) = \exp\{-r_1(x - r^x_1)\} + \exp\{r_1(x - r^x_1)\} +$$

45
\[ \exp\{-r_1(y - r_{yl})\} + \exp\{r_1(y - r_{yu})\} \]

where \( r = (r^x_u, r^x_l, r^y_u, r^y_l) \); \( r^x_u \) and \( r^x_l \) represent the upper and lower wall boundaries in the x-dimension; and \( r^y_u \) and \( r^y_l \) represent the upper and lower wall boundaries in the y-dimension. The parameter \( r_1 \) controls the rate of decay of the wall repulsion function. Other formulations for this basis are possible, but estimation using more flexible wall basis functions may require observations with a higher temporal frequency near the boundaries. The combined potential surface we consider is

\[ H(x, y) = \sum_{k,l} \gamma_{kl} \phi_k^{(M)}(x) \psi_l^{(M)}(y) + R(x, y, r, r_1). \] (3.4)

### 3.3.3 Motility Surface

In previous studies of the movement of ants in a nest, researchers have found that ants tend to move at different speeds in different areas of their nest (Quevillon et al., 2015). To incorporate this behavior in our SDE model, we propose a novel spatially varying motility surface \( M(x(t), y(t)) \) which scales the overall rate of movement in different parts of the nest. The motility surface scales the absolute movement rate in different spatial locations, allowing for flexible modeling of animal movement in which velocities can depend on the individual’s environment. This results in the following stochastic differential equation model, where the location equation from the CTCRW model of Johnson et al. (2008a) in each dimension has been adjusted to account for the spatially-varying motility

\[
\begin{align*}
\frac{dx(t)}{dt} &= M(x(t), y(t))v_x(t)dt + \kappa dW_x(t) \\
\frac{dy(t)}{dt} &= M(x(t), y(t))v_y(t)dt + \kappa dW_y(t).
\end{align*}
\] (3.5)

When \( \kappa = 0 \), we get the physical interpretation of velocity scaled by the motility surface \( x(t) = \int_0^t M(x(s), y(s))v_x(s)ds \), and when \( M(x, y) = 1 \), we get back (3.1).

For an example of movement behavior induced by the motility surface, consider a habitat separated into two distinct regions, one in which ants move fast, and another in which ants move more slowly. If \( M(\cdot) = 2 \) in the fast region, and \( M(\cdot) = 1 \) in the slow region, the ants will move approximately twice as fast in the fast region as they will in the slow region. Equations (3.2) and (3.5) together define a continuous time 2-dimensional stochastic movement process. Note that the \( v_x \)
and \( v_y \) can no longer be interpreted directly as velocity, but instead are a scaled version of the animal’s movement rate; at \((x(t), y(t))\) the animal’s mean movement rate vector ignoring autocorrelation is \((M(x, y) \cdot v_x(t), M(x, y) \cdot v_y(t))\).

For the motility surface \( M(x(t), y(t)) \), we again utilize smoothed B-spline basis functions.

\[
M(x, y) = \sum_{q,r} \alpha_{qr} c_q^{(P)}(x) \xi_r^{(P)}(y)
\]

(3.6)

where \( c_q^{(N)}(x) \) and \( \xi_r^{(N)}(y) \) are b-spline basis functions of order \( P \), with \( Q \) basis functions in the \( x \)-direction and \( R \) basis functions in the \( y \)-direction so that \( q \in \{1, ..., Q\} \) and \( r \in \{1, ..., R\} \). We set \( P = 4 \), \( Q = K \), and \( R = L \) so that the motility surface and the potential surface share the same basis functions.

### 3.3.4 Identifiability

Without imposing constraints, the model defined by equations (3.2) and (3.5) is not identifiable. First, the potential surface \( H(x, y) \) only enters the model through its gradient. Therefore adding some constant \( c_1 \) to the surface results in an equivalent model \((H^*(x, y) = H(x, y) + c_1)\). As discussed in Section 3.3.2, the constant \( c_1 \) is fixed to 0 by constraining the sum of the basis coefficients \( \{\gamma_{kl}\} \) to equal 0.

Second, the motility surface and velocity terms are only identifiable to a multiplicative constant \( c_2 \). Multiplying the motility surface by \( c_2 \) and the velocities by \( \frac{1}{c_2} \) yields an equivalent model

\[
\frac{1}{c_2} dv_x(t) = \beta \left( -\frac{1}{c_2} \frac{dH(x(t), y(t))}{dx} - \frac{1}{c_2} v_x(t) \right) dt + \frac{1}{c_2} \sigma dW_v(t)
\]

\[
\frac{1}{c_2} dv_y(t) = \beta \left( -\frac{1}{c_2} \frac{dH(x(t), y(t))}{dy} - \frac{1}{c_2} v_y(t) \right) dt + \frac{1}{c_2} \sigma dW_v(t)
\]

\[
dx(t) = c_2 M(x(t), y(t)) \frac{1}{c_2} v_x(t) dt + \kappa dW_x(t)
\]

\[
dy(t) = c_2 M(x(t), y(t)) \frac{1}{c_2} v_y(t) dt + \kappa dW_y(t).
\]

(3.7)

To obtain identifiability, the model is constrained by setting \( c_2 = \sigma^2 \), or equivalently, fixing \( \sigma^2 = 1 \).
3.4 Inference

It is impossible to analytically solve the non-linear SDEs given by Equations (3.2) and (3.5) so instead we consider approximate solutions using the Euler-Maruyama method (Kloeden and Platen, 1992) which is based on a first order Taylor expansion. We approximate the continuous time process (3.2) and (3.5) at a set of observed (or simulated) discrete-times $t_i, i = 1, 2, \ldots N_{sim}$, where $N_{sim}$ is the number of points on the path to simulate. Higher order discrete time approximations could be used to improve accuracy, and these higher order methods may be interesting directions for future research, both in the context of simulation and inference. Higher order approximations are not necessary in this case due to the high temporal frequency of discrete observations, every second for the ants. The Euler-Maruyama method results in the following discrete approximations for Equations (3.2) and (3.5)

\[
\begin{align*}
v_{x,t,i+1} &= v_{x,t,i} + \beta \left( -\nabla H (x_{t_i}, y_{t_i}) - v_{x,t_i} \right) \Delta t + \sigma \epsilon_{2x} \\
v_{y,t,i+1} &= v_{y,t,i} + \beta \left( -\nabla H (x_{t_i}, y_{t_i}) - v_{y,t_i} \right) \Delta t + \sigma \epsilon_{2y} \\
x_{t,i+1} &= x_{t_i} + M(x_{t_i}, y_{t_i}) v_{x,t_i} \Delta t + \kappa \epsilon_{1x} \\
y_{t,i+1} &= y_{t_i} + M(x_{t_i}, y_{t_i}) v_{y,t_i} \Delta t + \kappa \epsilon_{1y}
\end{align*}
\]

where $\Delta t$ is the time step of the discretized solver and $\epsilon_{1x}, \epsilon_{1y}, \epsilon_{2x}, \epsilon_{2y}$ are independent Gaussian random variables with mean 0 and variance $\Delta t$. These discrete Euler-Maruyama approximations will be used for inference, similar to Wikle and Hooten (2010). A 2-dimensional simulation generated using the Euler-Maruyama method is presented in Section 3.5 to illustrate the range of behavior possible under our SDE model.

We use Bayesian inference to estimate the model parameters. The Euler method approximations of the SDEs are used to provide an approximation for the likelihood function in the posterior distribution. Markov chain Monte Carlo is used to draw samples from this approximate posterior distribution. Vague priors are used for the location variability parameter $\kappa^2 \sim \text{Gamma}(0.001, 0.001)$, and for the autocorrelation parameter $f_{\beta} (\beta) \propto \exp \left( -\frac{(\beta - 1)^2}{20000} \right) I(\beta > 0)$, a normal distribution truncated to be positive. For identifiability $\sigma^2$ is fixed at 1. To induce spatial smoothness in the potential and motility surfaces, a proper CAR covariance structure (Banerjee et al., 2014, Chapter 3) is used for the coefficients of both of the
B-spline expansions in (3.9) and (3.6). Thus, for the potential surface coefficients, the prior selected is:

$$\gamma \sim N \left(0, (\tau_\gamma (D - \rho_\gamma Q))^{-1}\right)$$

Where $D_{jj} \equiv$ \{number of neighbors of j\}; $D_{ij} = 0$ if $i \neq j$; $(Q)_{jj} = 0$ and $Q_{ij} = I(i, j \text{ are neighbors})$. For the smoothness parameter we use the prior $\rho_\gamma \sim \text{Uniform}(0.1, 0.99)$. The parameter $\tau_\gamma$ is a tuning parameter that determines the scale of the potential surface. The prior distribution for $\tau_\gamma$ is set to be an exponential distribution $\tau_\gamma \sim \exp(\mu_\alpha)$ so that the observed data will inform the level of tuning, and the distribution of the potential surface will scale with the level of the motility surface through $\mu_\alpha$. As discussed in Section 3.3.4, only contrasts of the B-spline coefficients $\{\gamma_{kl}\}$ are identifiable, so we utilize the constraint $\sum_{k,l} \gamma_{kl} = 0$.

This is done through a linear transformation of a set of unconstrained basis function coefficients $\tilde{\gamma}$ (Gelfand et al., 2010, Chapter 12)

$$\gamma = \tilde{\gamma} - \Sigma 1^t \left(1\Sigma 1^t\right)^{-1} (1\tilde{\gamma} - 0)$$

where $\Sigma$ represents the covariance matrix of the unconstrained coefficients.

Similarly, the coefficients of the B-spline basis functions for the motility surface were assigned a CAR prior

$$\alpha \sim N \left(\mu_\alpha 1, \mu_\alpha^2 (\tau_\alpha (D - \rho_\alpha Q))^{-1}\right).$$

For the motility surface the prior for the smoothing parameter is again set to $\rho_\alpha \sim \text{Uniform}(0.1, 0.99)$. For identifiability, as discussed in Section 3.3.4, the tuning parameter $\tau_\alpha$ is set to 9 so that 99.8% of the prior mass is positive. Alternatively, a truncated normal distribution could be used as a prior to restrict the motility surface coefficients to be positive. Doing so is difficult however, as simulating from a multivariate truncated normal distribution is computationally burdensome in this case. The parameter $\mu_\alpha$ adds flexibility to the model as it scales the motility surface. The inclusion of $\mu_\alpha$ allows for approximating $c_2$ in Equation (3.7), and therefore, it can be used to approximate $\sigma_2$ if the identifiability constant ($c_2$) in Equation (3.7) had instead been fixed at 1. Additionally, $\mu_\alpha$ alters the tuning such that the smoothing of variability by the multivariate Gaussian prior in the motility
surface coefficients is less in regions of greater relative motility. A Gaussian prior is used for the scaling parameter \( \mu_\alpha \sim N(1, 1) \). A logNormal distribution is used for the prior on the wall parameter \( r_1 \sim \log\text{Norm}(10, 1) \). Full-conditional distributions are available for most parameters in the model, and are presented in Section 3.8.3.

Block-update MCMC is used to estimate the posterior distributions. When available, the updates are drawn from full-conditional distributions (a Gibbs sampler). The coefficients of the potential and motility surfaces, \( \gamma \) and \( \alpha \), are each updated as a separate block. A total of \( 10^5 \) samples are drawn from the posterior distribution and convergence of the Markov chains is determined by monitoring Monte Carlo standard errors using the batch means procedures (Jones et al., 2006; Flegal et al., 2008). The initial 20000 values of the chain are discarded as burn in, as the initial estimates for the potential surface and motility surface are difficult to select, resulting in inaccurate parameter estimates at the beginning of the chain. Multiple chains with different starting values were run to ensure estimates are robust across initial values.

Inference is computationally taxing, as it takes approximately 6 days to generate \( 10^5 \) samples from the posterior distribution using one core of a PC with code written in R. The computing time scales at a linear rate with increases in observations. Bayesian implementation allows for straightforward estimation of tuning parameters for the smoothness of our B-spline surfaces, and avoids the additional difficulties of selecting the number of basis functions using other methods such as generalized cross validation. Improving the computational efficiency of inference is an important direction for future work, especially due to the availability of data sets with more individuals and observation over longer time periods.

### 3.5 Application to Simulated Data

To illustrate the range of behavior possible under our SDE model we generated a 2-dimensional simulation using the Euler-Maruyama method described in Section 3.4. For simplicity, a quadratic well with a center at the origin is used for the potential surface \( H(x, y) = x^2 + y^2 \). For the motility surface, the upper right
quadrant is set to 0.25 and the remainder of the support is set to 1.

\[ M(x, y) = \begin{cases} 
0.25 & x > 0, y > 0 \\
1 & x < 0 \text{ or } y < 0 
\end{cases} \quad (3.10) \]

The potential surface and the motility surface are plotted in Figure 3.3 (a) and (b) respectively.

The model parameters were set to the following values: \((\beta = 1.5 , \sigma^2 = 1 , \kappa^2 = 0.01, m_1 = 0)\). A total of 6000 observations were simulated for five individuals, with observations made every 0.1 units of time. The first 2000 locations of the simulated data for one of the individuals is plotted in Figure 3.3(c). In the simulation, the animal tends to move around a central point of attraction at the
Table 3.2: Simulated Data

<table>
<thead>
<tr>
<th>Parameter</th>
<th>truth</th>
<th>posterior mean</th>
<th>credible interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>1.5</td>
<td>1.496</td>
<td>(1.406, 1.587)</td>
</tr>
<tr>
<td>$\kappa^2$</td>
<td>0.01</td>
<td>0.0109</td>
<td>(0.0106, 0.0112)</td>
</tr>
</tbody>
</table>

origin. The path is somewhat smooth due to the directional persistence included in the model. The histograms plotted in Figure 3.3(d) indicate the animal moves at a slower speed in the first quadrant, consistent with the specification of the motility surface. This simulated movement path demonstrates that our model allows for spatially varying movement rate as well as directional persistence and directional bias. This is necessary for the ants, whose movement rate depends on spatial location, as illustrated in Figure 3.2 (b). Previous models allow for directional persistence or spatially-varying directional bias, whereas our model is flexible enough to combine these directional traits with spatially-varying absolute movement rate and allow for different movement behavior in different chambers of the nest.

To gain a better understanding of our model, inference is performed on the simulated data example. The posterior sample means and 95% credible intervals for several parameters are presented in Table 3.2. The resulting posterior means and credible intervals indicate that we are able to recover the true values (when true values exist).

Estimates of the potential surface and motility surface are plotted in Figure 3.4 (a) and (b) respectively. These surfaces are constructed by taking the mean of each coefficient in the joint posterior distribution. As evident in Figure 3.4 (a), the estimated posterior surface captures the tendency to draw particles back to the origin. The height of the potential surface is arbitrary, since the potential surface only impacts movement through its gradient, and therefore the height is inestimable. The resulting posterior mean motility surface plotted in Figure 3.4 (b) matches the truth well, as it captures the shape and height of the surface accurately in areas where simulated data is observed.
Figure 3.4: Posterior Mean Surface Estimates for the Simulated Data Example.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>posterior mean</th>
<th>credible interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>0.872</td>
<td>(0.866, 0.877)</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>0.00133</td>
<td>(0.00131, 0.00134)</td>
</tr>
<tr>
<td>$r_1$</td>
<td>0.078</td>
<td>(0.044, 0.114)</td>
</tr>
</tbody>
</table>

### 3.6 Results

Posterior sample means and 95% credible intervals for the model parameters are presented in Table 3.3. There is significant autocorrelation in the ant’s velocity as the credible interval for $\beta$ does not include 1, but the autocorrelation is not strong. This is reasonable for ant movement, as the ant paths are not smooth since the ants tend to change direction suddenly inside the nest. The estimate for $\kappa$ is small, which indicates that there is not much additional location variability after conditioning on latent velocity. Our estimate for $r_1$ indicates that there is a repulsion behavior from the wall, but the size of the effect is relatively small.

Estimates of the posterior mean potential surface and motility surface are constructed by taking the point-wise sample mean of each coefficient, and plotting the resulting surfaces over a fine grid. The potential surface, plotted in Figure 3.5 (a), reveals a tendency to move away from the walls on the left and right sides of
the nest, particularly in the center chambers (II and III). This is consistent with ants that turn as they approach the walls while traveling between chambers.

The motility surface, plotted in Figure 3.5 (c), reveals a tendency to move faster in the center of the nest, in chambers II and III. This suggests that this area is mainly used by the ants for commuting between chambers. Additionally, there is low relative motility in each of the doorways between chambers. The combined gradient field plotted in Figure 3.5 (b) reveals both the tendency to move away from walls, and the tendency to move faster in the central chambers.

The 95% point-wise credible intervals for the motility surface estimated from the ant movement observations are plotted in Figure 3.6. The upper limits in most regions in chambers I and IV are below the lower limits in parts of chambers II and III, indicating that the difference in movement rates in the different areas of the nest are statistically significant. Additionally, the regions with low relative motility in the doorways are apparent, particularly in the doorway connecting the chambers I and II and in the doorway connecting chambers II and III. This might be due to the data imputation procedure described in Section 3.2, or it could reveal a tendency to move slower in the doorways between these chambers. A simpler model for animal movement would not be able to capture this variation, nor would it model the statistically significant autocorrelation presented in Table 3.3.

The spread of nutrients, pathogens, and other agents is important to the health of a community of ants, as well as other group living organisms, including humans. The spread of such agents is closely related to the movement of ants in the nest. To study the impact of the spatially-varying movement behavior of ants, we simulated
the spread of 100 ants, each starting at the exit doorway located at the bottom left corner of chamber IV (Figure 3.1). The parameters for the forward simulation were set to the mean values from the posterior distributions. Simulated movements were truncated to prevent ants from traveling through walls. To estimate the time it would take for an agent to spread to different regions of the nest, the nest was split into 8 sections, two in each chamber. This was done by dividing each of the 4 chambers into two halves along the wall across the middle of the nest. The resulting sections have been designated Ia, Ib, ... , IVa, IVb from top to bottom, so that IVa and IVb represent the top and bottom halves of chamber IV respectively. Using this notation, the nest exit is located in the bottom left corner of section IVb. The first entry time of each of the 100 simulated ants into each of these segments was recorded. Boxplots of the results are shown in Figure 3.7.

In Figure 3.7 (a), the total time in hours until entry into the designated region is plotted. The average time it takes to reach the top half of Chamber I, the farthest section from the next exit, is approximately 24 hours. As expected, the time to enter each of the chambers increases as you move up in the nest from chamber IVb through Ia. This is due to the fact that all ants are simulated to start at the nest doorway in chamber IVb. In Figure 3.7 (b), the time from entry in the previous region until entry into the designated region is plotted. This gives an impression of the amount of time it would take an agent to spread through each region of the
nest. The simulation results indicate that on average, agents spread much more slowly through chambers I and IV than through chambers II and III. For example, on average it takes about 2.5 hours from entry into the lower half of chamber IV until entry into the top of chamber III, and about 14 hours on average to pass from the top of chamber I to the bottom of chamber I, making these the two regions that takes the longest to pass through. It only takes about 1 hour on average to pass from entry into the top half of chamber III until entry into the bottom half of chamber III. This is mainly due to the corridors of fast movement in the middle area of the nest captured by the motility surface in our model. The existence of a separate slower moving region at the entrance of the nest (chamber IV) thus may act to delay the rate at which an ant carrying an agent could spread deeper into the nest. To gain a better understanding of the rate at which resources move through the nest, several model assumptions could be adjusted. Using a hierarchical model to allow for variability in individual movement behavior, for example, may better reflect the behavior of the individual ants. Additionally, time varying behavior is evident in the videos of ant movement. Incorporating this temporally varying behavior via latent discrete states (Langrock et al., 2012) would impact the rate of spread. Further expanding the simulation to allow the agent to spread between interacting ants would also provide a more realistic model. Further research is needed to gain a better understanding of the relationship between animal movement...
behavior and resource spread dynamics.

3.7 Discussion

The novel SDE based model we have developed allows for autocorrelated movement and flexible spatially-varying directional bias and velocity. Ant movement observed every second within a nest for an hour is investigated, and the transit behavior of ants between different chambers is captured. The motility surface impacts the rate at which ants spread through the nest, as evident by the simulated movement of 100 ants presented in Section 3.6. Modeling this is important, as the spatially-varying rate of movement has important implications for the spread of resources, pathogens, and pesticides within the nest.

This model is flexible, allowing for temporal autocorrelation and movement which is dependent on an animal’s environment. The environmental dependency can be based on covariates, such as resources in the area, it can be nonparametric, using a variety of basis functions, or it can be a semi-parametric structure combining both environmental features and the additional spatially-varying behavior. This is important, as it is often impossible to observe all environmental covariates when analyzing animal movement over large areas. Thus this model provides a flexible framework to model movement to help understand a variety of processes. Examples include resource selection, impacts of environmental changes, and the spread of agents, such as pathogens or nutrients through animal societies.

Some parts of the model are only identifiable up to a multiplicative constant. Therefore, interpretation of the estimated surfaces should be limited on the scale of the motility and potential surfaces. Further, computation becomes more burdensome as the number of basis functions and observations increase. Thus, more efficient methods for inference would be necessary to estimate surfaces with high resolution features, such as walls or fences, in very large regions. The model requires a high temporal rate of observation of animal locations due to the Euler-Maruyama approximation to the SDEs. To correct this issue, when data are sparse in time, locations between observations can be imputed from the model, however this may become computationally taxing since the motility and potential surface estimates require using B-spline basis representation for these imputed observations. Updating the basis representation of these imputed locations at every iteration in a
Metropolis-Hastings algorithm is often slow. Alternatively, higher order approximations to the SDEs can be used which may provide more accurate numerical approximations of the underlying SDE model (3.2) and (3.5).

In future work, temporally varying behavior will be considered. A state-space model with distinct potential surfaces and movement parameters in different states could be utilized, however these states may be difficult to identify if the behavior in different states is similar (Beyer et al., 2013). This could also allow for the interaction of ants through combining a latent interaction network model (Scharf et al., 2015) with potential surfaces consisting of directed movement toward specific neighboring ants.

Acknowledgements

This research is supported by the NSF grant EEID 1414296.

3.8 Supplementary Material

Several additional materials are presented in this section. First, an efficient method for approximate inference of a partial model without the motility surface is discussed. Next, the full model is specified. Finally, full conditional distributions are presented.

3.8.1 B-Spline Lasso Regression to estimate Potential Functions

The B-spline potential surface, in the absence of autocorrelation and with the motility surface fixed everywhere at 1, can be estimated using penalized B-spline regression. Although these assumptions are not often met in real-world movement data, efficient inference can indicate whether or not it is necessary to model spatially-varying directional drift.

Assume we have data consisting of \( x \) and \( y \) locations for individuals \( j \in \{1, \ldots, J\} \) at times \( t \in \{1, \ldots, T_j\} \) (Note: assume \( t \) takes this format to simplify notation) given by \((x_t^{(j)}, y_t^{(j)})\). We assume that the data comes from a potential function of the form.

\[
(x_t^{(j)}, y_t^{(j)}) = H(x, y)
\]
Taking the gradient, we get \( \nabla \left( x_t^{(j)}, y_t^{(j)} \right) = \nabla H(x, y) \) yielding two equations

\[
\nabla x_t^{(j)} = \frac{dH(x, y)}{dx}, \quad \nabla y_t^{(j)} = \frac{dH(x, y)}{dy}
\]

We estimate the derivative of the \( x \) and \( y \) locations using discrete velocity approximations:

\[
\nabla x_t^{(j)} \approx \frac{x_{t+1}^{(j)} - x_t^{(j)}}{\nabla t} := v_{x_t}^{(j)}
\]

\[
\nabla y_t^{(j)} \approx \frac{y_{t+1}^{(j)} - y_t^{(j)}}{\nabla t} := v_{y_t}^{(j)}
\]

We estimate the potential surface using the equation

\[
H(x, y) = \sum_{k,l} \beta_{kl} \phi_k(x) \psi_l(y)
\]

where \( \phi_k(x) \) and \( \psi_l(y) \) are b-spline basis functions with \( k \in \{1,...,K\} \) and \( l \in \{1,...,L\} \). Note that \( K \) and \( L \) are determined by the respective degree and number of knots. If we take the derivative of these functions, we get the equations

\[
\frac{dH(x, y)}{dx} = \sum_{k,l} \beta_{kl} \phi_k'(x) \psi_l(y)
\]

\[
\frac{dH(x, y)}{dy} = \sum_{k,l} \beta_{kl} \phi_k(x) \psi_l'(y)
\]

We can estimate the coefficients using linear regression:

\[
v_{x_t}^{(j)} = \sum_{k,l} \beta_{kl} \phi_k'(x_t^{(j)}) \psi_l(x_t^{(j)}) + \epsilon_{x_t}^{(j)}
\]

\[
v_{y_t}^{(j)} = \sum_{k,l} \beta_{kl} \phi_k(x_t^{(j)}) \psi_l'(y_t^{(j)}) + \epsilon_{y_t}^{(j)}
\]

where \( \epsilon_{x_t}^{(j)} \sim N(0, \sigma^2) \) and \( \epsilon_{y_t}^{(j)} \sim N(0, \sigma^2) \) are all assumed independent.

To aggregate the model we construct \( v \) and \( X \) by stacking \( v_x \) and \( v_y \) terms and use a Lasso penalization on the coefficients to get the equation:

\[
(v - X\beta)^T (v - X\beta) + \lambda ||\beta||_1
\]

Note that \( \lambda \) can be estimated using cross validation.
3.8.2 Model Formulation

In this Section, the full model developed in Section 3.3 will be presented. First, the conditional distributions for the locations and velocities are defined. Next, the prior distributions for the model are specified.

Assume we have observations for the locations of \( N_a \) ants \((x_{i,j}, y_{i,j})\) and unobserved "quasi-velocities" \((v_{i,j}^{(x)}, v_{i,j}^{(y)})\) at equally spaced times \( i \in \{1, \ldots, N_t\} \) for individuals \( j \in \{1, \ldots, N_a\} \) and \( \Delta = t_{i+1} - t_i \). The Euler-Maruyama approximation to the stochastic differential equations (3.2) and (3.5) gives the following conditional distributions for location and velocity.

\[
[v_{i+1,j}^{(x)} | v_{i,j}^{(x)}, x_{i,j}, y_{i,j}, \beta, \sigma, H(\cdot)] \sim N(v_{i,j}^{(x)} + \beta(-\frac{dH(x_{i,j}, y_{i,j})}{dx} - v_{i,j}^{(x)})\Delta, \Delta \sigma^2)
\]

\[
[v_{i+1,j}^{(y)} | v_{i,j}^{(y)}, x_{i,j}, y_{i,j}, \beta, \sigma, H(\cdot)] \sim N(v_{i,j}^{(y)} + \beta(-\frac{dH(x_{i,j}, y_{i,j})}{dy} - v_{i,j}^{(y)})\Delta, \Delta \sigma^2)
\]

\[
[x_{i+1,j} | v_{i,j}^{(x)}, x_{i,j}, y_{i,j}, \kappa, m(\cdot)] \sim N(x_{i,j} + M(x_{i,j}, y_{i,j})v_{i,j}^{(x)}\Delta, \Delta \kappa^2)
\]

\[
[y_{i+1,j} | v_{i,j}^{(y)}, x_{i,j}, y_{i,j}, \kappa, m(\cdot)] \sim N(y_{i,j} + M(x_{i,j}, y_{i,j})v_{i,j}^{(y)}\Delta, \Delta \kappa^2).
\]

Here, \( H(x_{i,j}, y_{i,j}) = \sum_{k,l}^{N_H} \gamma_{kl} \Psi_{kl}(x_{i,j}, y_{i,j}) + R(x_{i,j}, y_{i,j}, r, r_1) \) is the potential surface, \( \Psi_{kl}(x_{i,j}, y_{i,j}) \) are B-spline basis functions, \( N_H \) is the number of B-spline basis functions used for the potential surface, \( R(x_{i,j}, y_{i,j}, r, r_1) = \exp(-r_1(x_{i,j} - r_1^x)) + \exp(r_1(x_{i,j} - r_1^x)) + \exp(-r_1(x_{i,j} - r_1^y)) + \exp(r_1(x_{i,j} - r_1^y)) \), \( r_1 \) represents the rate of decay of the wall repulsion, \( r = (r_u^x, r_u^y, r_l^x, r_l^y) \), \( r_u^x \) and \( r_u^y \) represent the upper and lower wall boundaries in the x-dimension, \( r_l^x \) and \( r_l^y \) represent the upper and lower wall boundaries in the y-dimension, \( M(x_{i,j}, y_{i,j}) = \sum_{k,l}^{N_M} \alpha_{kl} \Phi_{kl}(x_{i,j}, y_{i,j}) \) is the motility surface, \( \Phi_{kl}(x_{i,j}, y_{i,j}) \) are B-spline basis functions, \( N_M \) is the number of B-spline basis functions used for the motility surface, \( \beta \) represents the autocorrelation parameter, \( \sigma \) represents the variability in the "quasi-velocity" term, \( \kappa \) represents the variability in the location term.

Prior distributions for the model are presented in Table 3.4. In the Gaussian prior for the B-spline surface coefficients, a proper conditional autoregressive covariance structure is used to induce spatial smoothing. Thus, we define \( (Q)_{kk} = 0 \), \( (Q)_{kl} = I(k, l \text{ are neighbors}) \), \( (D)_{kk} = \# \text{ neighbors of k} \), and \( (D)_{kl} = 0 \) if \( k \neq l \).
Table 3.4: Prior Distributions

<table>
<thead>
<tr>
<th>$v_{1,j}(x)$</th>
<th>$N(0, \tau^2_{v_1})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$v_{1,j}(y)$</td>
<td>$N(0, \tau^2_{v_1})$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>$\propto \exp\left(\frac{-(\beta - \mu_{\beta})^2}{\sigma^2_{\beta}}\right) I(\beta &gt; 0)$</td>
</tr>
<tr>
<td>$\sigma^2_{\gamma}$</td>
<td>$1$</td>
</tr>
<tr>
<td>$\kappa^2$</td>
<td>$IG(\alpha_{\kappa}; \beta_{\kappa})$</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>$N\left(0, (\tau_{\gamma} (D - \rho_{\gamma} Q))^{-1}\right)$</td>
</tr>
<tr>
<td>$\tau_{\gamma}$</td>
<td>$\text{Exp}(\mu^2_{\alpha})$</td>
</tr>
<tr>
<td>$\rho_{\gamma}$</td>
<td>Uniform($l_{\rho_{\gamma}}, u_{\rho_{\gamma}}$)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>$N\left(\mu_{\alpha} 1, \mu^2_{\alpha} (\tau_{\alpha} (D - \rho_{\alpha} Q))^{-1}\right)$</td>
</tr>
<tr>
<td>$\mu_{\alpha}$</td>
<td>$N(\mu_{\mu}, \sigma^2_{\mu})$</td>
</tr>
<tr>
<td>$\tau_{\alpha}$</td>
<td>$9$</td>
</tr>
<tr>
<td>$\rho_{\alpha}$</td>
<td>Uniform($l_{\rho_{\alpha}}, u_{\rho_{\alpha}}$)</td>
</tr>
<tr>
<td>$\tau_1$</td>
<td>$\log\text{Norm}(\mu_{\tau_1}, \sigma^2_{\tau_1})$</td>
</tr>
</tbody>
</table>

3.8.3 Full Conditional Distributions

In this Section the full conditional distributions for the spatially-varying stochastic differential equation model defined in Section 3.3 are presented.

1. $|\beta| \sim N_{+}\left(\sum_{j=1}^{N_a} a_j + \frac{1}{2\sigma^2} \left(\sum_{j=1}^{N_a} b_j + \mu_{\beta}\right)^{-1}, \left(\sum_{j=1}^{N_a} b_j + \mu_{\beta}\right)^{-1}\right) [0, \infty]$

   $$a_j = \frac{\Delta}{2\sigma^2} \sum_{i=1}^{N_t} \left(-\frac{d}{dx} H(x_{i,j}, y_{i,j}) - v_{i,j}^{(x)}\right)^2 + \frac{\Delta}{2\sigma^2} \sum_{i=1}^{N_t} \left(-\frac{d}{dy} H(x_{i,j}, y_{i,j}) - v_{i,j}^{(y)}\right)^2$$

   $$b_j = \frac{1}{2\sigma^2} \sum_{i=1}^{N_t} \left(-\frac{d}{dx} H(x_{i,j}, y_{i,j}) - v_{i,j}^{(x)}\right) \left(v_{i+1,j}^{(x)} - v_{i,j}^{(x)}\right) + \frac{1}{2\sigma^2} \sum_{i=1}^{N_t} \left(-\frac{d}{dy} H(x_{i,j}, y_{i,j}) - v_{i,j}^{(y)}\right) \left(v_{i+1,j}^{(y)} - v_{i,j}^{(y)}\right)$$

2. $\kappa^2 \sim IG(\alpha_{\kappa} + N_t * N_a - 1, \sum_{j=1}^{N_a} a_j + \beta_{\kappa})$
\( a_j = \frac{1}{2\Delta} \sum_{i=1}^{N_t} \left( x_{i+1,j} - x_{i,j} - M(x_{i,j}, y_{i,j})v_{i,j}(x)\Delta \right)^2 + \frac{1}{2\Delta} \sum_{i=1}^{N_t} \left( y_{i+1,j} - y_{i,j} - M(x_{i,j}, y_{i,j})v_{i,j}(y)\Delta \right)^2 \)

3. \( v_{1,j}^{(x)} \sim N(a_{1,j}^{-1}b_{1,j}, a_{1,j}^{-1}) \) for \( j \in \{1, ..., N_a\} \)

\[
 a_{1,j} = \frac{\Delta}{\kappa^2} (M(x_{1,j}, y_{1,j}))^2 + \frac{\beta \Delta - 1}{\Delta \sigma^2} + 1 \frac{1}{\tau_{v_1}^2} 
\]

\[
 b_{1,j} = \frac{1}{\kappa^2} M(x_{1,j}, y_{1,j}) (x_{2,j} - x_{1,j}) - \frac{\beta \Delta - 1}{\Delta \sigma^2} \left( v_{2,j}^{(x)} + \beta \Delta \frac{d}{dx} H(x_{1,j}, y_{1,j}) \right) 
\]

4. \( v_{i,j}^{(x)} \sim N(a_{i,j}^{-1}(b_{i,j}), a_{i,j}^{-1}) \) for \( i \in \{2, ..., N_t - 1\}, j \in \{1, ..., N_a\} \)

\[
 a_{i,j} = \frac{\Delta}{\kappa^2} (M(x_{i,j}, y_{i,j}))^2 + \frac{\beta \Delta - 1}{\Delta \sigma^2} + 1 \frac{1}{\Delta \sigma^2} 
\]

\[
 b_{i,j} = \frac{1}{\kappa^2} M(x_{i,j}, y_{i,j}) (x_{i+1,j} - x_{i,j}) - \frac{\beta \Delta - 1}{\Delta \sigma^2} \left( v_{i+1,j}^{(x)} + \beta \Delta \frac{d}{dx} H(x_{i,j}, y_{i,j}) \right) 
\]

\[
 + \frac{1}{\Delta \sigma^2} \left( v_{i-1,j}^{(x)} + \beta \Delta \left( \frac{d}{dx} H(x_{i-1,j}, y_{i-1,j}) - v_{i-1,j}^{(x)} \right) \right) 
\]

5. \( v_{N_t,j}^{(x)} \sim N(a^{-1}b_{N_t,j}, a^{-1}) \) for \( j \in \{1, ..., N_a\} \)

\[
 a = \frac{1}{\Delta \sigma^2} 
\]

\[
 b_{N_t,j} = \frac{1}{\Delta \sigma^2} \left( v_{N_t-1,j}^{(x)} + \beta \Delta \left( \frac{d}{dx} H(x_{N_t-1,j}, y_{N_t-1,j}) - v_{N_t-1,j}^{(x)} \right) \right) 
\]
6. \( \gamma | \cdot \sim N(\cdot, \cdot) \) with mean \((\sum_{j=1}^{N_a} a_{i,j} + \tau_\gamma (D - \rho_\gamma Q))^{-1} (\sum_{j=1}^{N_a} b_{i,j}) \) and variance 
\((\sum_{j=1}^{N_a} a_{i,j} + \tau_\gamma (D - \rho_\gamma Q))^{-1} \)

\[
a_{i,j} = \frac{\beta^2 \Delta}{\sigma^2} \sum_{i=1}^{N_t-1} \Phi_x'(x_{i,j}, y_{i,j}) \Phi_x(x_{i,j}, y_{i,j}) + \\
\frac{\beta^2 \Delta}{\sigma^2} \sum_{i=1}^{N_t-1} \Phi_y'(x_{i,j}, y_{i,j}) \Phi_y(x_{i,j}, y_{i,j})
\]

\[
b_{i,j} = \frac{\beta}{\sigma^2} \sum_{i=1}^{N_t-1} \Phi_x'(x_{i,j}, y_{i,j}) \left( v_{i+1,j}^{(x)} - v_{i,j}^{(x)} + \beta \Delta \left( v_{i,j}^{(x)} + \frac{d}{dx}R(x_{i,j}, y_{i,j}) \right) \right) + \\
\frac{\beta}{\sigma^2} \sum_{i=1}^{N_t-1} \Phi_y'(x_{i,j}, y_{i,j}) \left( v_{i+1,j}^{(y)} - v_{i,j}^{(y)} + \beta \Delta \left( v_{i,j}^{(y)} + \frac{d}{dy}R(x_{i,j}, y_{i,j}) \right) \right)
\]

Where \( \Phi_x(x_{i,j}, y_{i,j}) \) and \( \Phi_y(x_{i,j}, y_{i,j}) \) are the derivatives of the B-spline Basis functions \( \Phi(x_{i,j}, y_{i,j}) \) with respect to \( x \) and \( y \).

7. \( \alpha | \cdot \sim N(\cdot, \cdot) \) with mean \((\sum_{j=1}^{N_a} a_{i,j} + \frac{\tau_\alpha}{\mu_\alpha} (D - \rho_\alpha Q))^{-1} (\sum_{j=1}^{N_a} b_{i,j} + \frac{\tau_\alpha}{\mu_\alpha} (D - \rho_\alpha Q)) \) and variance \((\sum_{j=1}^{N_a} a_{i,j} + \frac{\tau_\alpha}{\mu_\alpha} (D - \rho_\alpha Q))^{-1} \)

\[
a_{i,j} = \frac{\Delta}{\kappa^2} \sum_{i=1}^{N_t-1} (v_{i+1,j}^{(x)} - v_{i,j}^{(x)})^2 \Phi_x'(x_{i,j}, y_{i,j}) \Phi_x(x_{i,j}, y_{i,j}) + \\
\frac{\Delta}{\kappa^2} \sum_{i=1}^{N_t-1} (v_{i+1,j}^{(y)} - v_{i,j}^{(y)})^2 \Phi_y'(x_{i,j}, y_{i,j}) \Phi_y(x_{i,j}, y_{i,j})
\]

\[
b_{i,j} = \frac{1}{\kappa^2} \sum_{i=1}^{N_t-1} \Phi_x'(x_{i,j}, y_{i,j}) v_{i,j}^{(x)} (x_{i+1,j} - x_{i,j}) + \\
\frac{1}{\kappa^2} \sum_{i=1}^{N_t-1} \Phi_y'(x_{i,j}, y_{i,j}) v_{i,j}^{(y)} (y_{i+1,j} - y_{i,j})
\]

8. \( \tau_\gamma^2 | \cdot \sim IG(\frac{1}{2} N_H * N_M + \alpha_{\tau_\gamma}, \frac{1}{2} \gamma' (D - \rho_\gamma Q) \gamma + \beta_{\tau_\gamma}) \)
3.8.4 Analysis of the Euler-Maruyama Approximation Error

The Euler-Maruyama method discussed in Section 3.4 only provides an accurate approximation of the continuous time process when the temporal increments of the discrete time approximation are sufficiently small. Determination of an acceptable temporal resolution depends on the underlying problem. Various simulations should be used to gain an understanding of the impact of the discrete approximation (Kloeden and Platen, 1992). In this Section, to gain a better understanding of the impact of the discrete time approximation, we apply our algorithm for Bayesian inference to simulated data sets under a variety of temporal resolutions. Data is simulated from a model with parameters \( \beta = 0.8, \sigma^2 = 1, \kappa^2 = 0.0001 \) and surfaces \( H(x, y) = 0.05x^2 + 0.05y^2, \ M(x, y) = [1 - 0.25(|x| + |y|)]^+ \) with \( \Delta = 0.1 \) for 10 individuals. The surfaces are plotted in Figure 3.8. Simulated data 'observations' for each individual are dropped so that the impact of the temporal resolution of observation can be studied. For example, if every other observation is dropped, this is equivalent to a discrete time approximation with \( \Delta = 0.2 \). The length of the total observation time is adjusted so that under each scenario, the total number of observations remains the same (\( N_t = 5000 \)).

Results for the relevant model parameters are presented in Table 3.5. The temporal dependence in the model is described by the product \( \beta \Delta \). A value of \( \beta \Delta = 1 \) indicates independent movement and the autocorrelation increases as...
### Table 3.5: Computational Efficiency and Surface Resolution

<table>
<thead>
<tr>
<th>$\Delta$</th>
<th>$\beta \Delta$</th>
<th>95% CI for $\beta \Delta$</th>
<th>$\kappa^2 \Delta$</th>
<th>95% CI for $\kappa^2 \Delta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.080</td>
<td>(0.077, 0.084)</td>
<td>0.00018</td>
<td>(0.00017, 0.00019)</td>
</tr>
<tr>
<td>0.2</td>
<td>0.125</td>
<td>(0.121, 0.129)</td>
<td>0.00027</td>
<td>(0.00024, 0.00030)</td>
</tr>
<tr>
<td>0.5</td>
<td>0.216</td>
<td>(0.210, 0.222)</td>
<td>0.0028</td>
<td>(0.0027, 0.0029)</td>
</tr>
<tr>
<td>1</td>
<td>0.490</td>
<td>(0.483, 0.496)</td>
<td>0.0047</td>
<td>(0.0042, 0.0051)</td>
</tr>
<tr>
<td>3</td>
<td>1.122</td>
<td>(1.110, 1.134)</td>
<td>0.034</td>
<td>(0.032, 0.036)</td>
</tr>
<tr>
<td>5</td>
<td>1.503</td>
<td>(1.485, 1.530)</td>
<td>0.051</td>
<td>(0.047, 0.055)</td>
</tr>
<tr>
<td>50</td>
<td>2.329</td>
<td>(2.297, 2.353)</td>
<td>0.437</td>
<td>(0.401, 0.459)</td>
</tr>
</tbody>
</table>

$\beta \Delta \to 0$. The autocorrelation parameter estimate reveals that we are able to capture the true value of $\beta$ when there is no temporal thinning. As the simulated data is thinned the parameter estimates indicate that as the temporal resolution of observation becomes coarser the dependence between observations is biased towards independence. If the time lag between observations is large enough, the value of $\beta \Delta$ exceeds 1, indicating negative correlation in velocity through time. This is closely related to the incorrect scaling of the surfaces, and is discussed further after the surface results are presented. The estimate for variability in location $\kappa^2$ also increases as the temporal resolution increases.

Estimates for the gradient fields are calculated by taking the point-wise mean of each basis function coefficient as the estimated value and plotting the surface over a fine grid. Results for the potential and motility surfaces in several cases, $\Delta = 0.1$ (keeping every simulated observation), $\Delta = 5$ (keeping every 50th simulated observation) and $\Delta = 50$ (keeping every 500th simulated observation) are plotted in Figure 3.9. The results indicate that the change in temporal resolution causes difficulties in estimating the scale of the surfaces. This is related to the incorrect estimate for $\beta \Delta$ described above. Due to identifiability, as discussed in Section 3.3.4, the value of $\sigma^2$ has been fixed at one. The velocity equation approximation (in one dimension) is therefore

$$v_{t+1}^x = v_t^x + \beta \left( -\nabla H(x_t, y_t) - v_t^x \right) \Delta + \epsilon_x$$

where $\epsilon_x$ is an independent Gaussian random variable with mean 0 and variance $\Delta$. Thus, the variability in velocity increases with larger values of $\Delta$. This is intuitive.
for small values of \( \Delta \), as the variability in velocity is likely to increase as the time between observations increases. However, as the temporal resolution becomes more coarse, the velocity approximations lose their meaning. For example, if \( \Delta = 5 \), the variability in velocity indicates that speeds greater than 5 units per observation are reasonable. However, the space use of any individual is limited to the area near the origin by the quadratic well potential surface, such that the maximum distance in the \( x \)-dimension between any two points in a simulated individual’s observed path is less than 5. Hence, at a fine temporal resolution the latent velocities increase to unrealistic values.

The unrealistic estimates of the latent velocities \( (v_x^t) \) result in small estimates for the motility surface (the scale of the surface is underestimated to reduce the movement rate to a realistic value) larger estimates in the gradient for the potential surface (the scale of the surface is overestimated to induce directional bias in the inflated velocities) and incorrect estimates for \( \beta * \Delta \) (which determines the weights between the potential surface and the previous velocity in the distribution for the current velocity) driven by the incorrect scaling of the velocities and the potential surface.

The inability to recover the scale of the surfaces is reflected in Figure 3.8. However, the shape of both estimated surfaces remains accurate when \( \Delta = 5 \), as we are able to capture the tendency of individuals to be drawn to the origin via the potential well, and to move faster while near the origin via the motility surface in the simulated data example with the coarsest temporal resolution. If the scale of observation is increased further (\( \Delta = 50 \)) the estimated potential surface still retains the shape of a quadratic well but the features of the motility surface disappear. This is intuitive since estimates of differences in movement rate are unreliable when a simulated particle’s velocity is averaged over longer periods of time, however directional bias is still reflected in the space-use of an individual at arbitrary time scales.

Overall, Table 3.5 indicates that the estimates for model parameters gradually break down as the temporal resolution increases, however Figure 3.9 indicates we are still able to estimate the shape of the potential surface that determines spatial-variation of directional bias in movement behavior when only infrequent observations are available.
Figure 3.9: Estimated Surfaces for the Thinned Simulated Data Examples.
Chapter 4  
A Model for Collective Movement with Interacting Behavioral States

In this chapter the spatially-varying movement model presented in Chapter 3 is extended to incorporate temporally inhomogeneous behavior and interactions between individuals. I propose a novel behavioral interaction structure that incorporates dependence through discrete interacting behavioral states by including functions of the latent behaviors of nearby individuals as regression covariates for state transition probabilities. The model is applied to ant movement within a four-chambered nest.

4.1 Introduction

Statistical models for animal movement can provide insight into the movement tendencies of individuals and the drivers of movement, such as the local environment or the location of nearby resources. The collective behavior of groups of animals can provide additional insight into the social structures of communities of animals (Vicsek and Zafeiris, 2012). When individuals in a society, such as ants in a colony, perform different tasks at different times, studying these behavioral tendencies across different individuals can provide insight into the allocation of work among group members (Seely, 1995; Franks et al., 1990). In general, animal movement is often dependent on the movement of other nearby individuals (Vicsek and Zafeiris,
Ignoring this inter-animal dependence in statistical models could generate misleading results (Langrock et al., 2014). Examples of dependent behaviors include the 'trafalgar effect,' named after the flag signals used between ships at the Battle of Trafalgar, where information can spread through a group of individuals allowing them to flee at a faster rate than an individual can move (Treherne and Foster, 1981), and the concept of quorum decision making, where animals' collective movement decisions are based on a minimum number of animals deciding to flee (Ward et al., 2008). This improves survival through information sharing, but prevents inefficient excessive flight behavior by ignoring the sometimes erratic behavior of single individuals. Collective movement decisions have also been studied in humans. For example Milgram et al. (1969) discovered that the probability that humans who are passing by on a sidewalk will stop to look up at an imaginary point increases with the number of nearby individuals who are stopped on the sidewalk looking at the imaginary point.

The most common method for accounting for behavioral changes in animal movement modeling involves assigning discrete behavioral states to each distinct behavior. Blackwell (1997) provides an early example of this, analyzing wood mouse movement with latent behavioral states, such as traveling, resting, or feeding. Morales et al. (2004) utilizes a hidden Markov model to study the movements of elk via latent behavioral states and correlated random walk movement models, and discusses the idea of environmental covariates that impact the transition probabilities between latent states. Langrock et al. (2012) provides an overview of hidden Markov models for animal movement with latent behavioral states and proposes several extensions, including semi-Markov processes, as well as higher order Markov processes.

Several methods have been proposed for modeling dependence in animal movement. One common method involves modeling animals as self-propelled particles, each of which follows specific movement rules. Vicsek et al. (1995) proposes a simple method for incorporating dependence in movement direction by modeling the mean movement of each individual as an average of the directions of all other nearby individuals. This method produces alignment between individuals. Complexity can been added to this model through various extensions. For example, ranges of attraction and repulsion have been incorporated (Couzin et al., 2002).
and anisotropy in the dependence between neighbors has been modeled (Perna et al., 2014). Alternative collective movement models have utilized a group centroid, for example a weighted average of all members’ location, and discrete behavioral switching between correlated random walks with or without attraction to this centroid (Langrock et al., 2014). Alternatively, Scharf et al. (2015) estimates a latent dynamic network which represents relationships between moving individuals. However, none of these approaches to modeling collective behavior are well-suited to modeling ant movement inside the nest (see Chapter 3, Section 3.2). In the nest, ants do not move in a herd, matching speed and direction with nearby neighbors. Rather, ants often start or stop moving because of interactions (e.g. antennation) with other nearby ants.

In this chapter, we propose a novel approach that models dependent movement behavior using latent interacting behavioral states. We assume that there are a finite set of discrete behavioral states that describe the movement of an individual. Functions of the latent behavioral states of other nearby individuals are included as regression covariates in the latent state transition probabilities, and can capture a variety of behavioral interactions. For example, the number of nearby neighbors in a moving state can be used as a covariate to model the behavior of an animal that becomes agitated by nearby activity. Existing approaches focus on joint modeling of position (Russell et al., 2015) and/or direction (Mann, 2011; Vicsek et al., 1995) of animals when they are moving. The approach we develop here is complementary to these existing models as we develop a joint model for collective transitioning between discrete behavioral modes.

In our previous model, we assumed that each ant was independent of all others and that each ant’s behavior is the same throughout the hour of observation (see Chapter 3, Section 3.3). In reality, the ants exhibit multiple behaviors as evident by the fact that many of the ants remained stationary for long periods of time during observation. Therefore, we will define discrete behavioral states in ant movement that include an active state and a resting state, and we will model the transitions between states dependant on the number of nearby active and resting individuals. While the ants are in an active state, we will model directional persistence, spatially-varying directional bias, and spatially-varying movement rate using the spatially-varying stochastic differential equation model for animal movement developed in Chapter 3, Section 3.3.
The rest of this chapter is organized as follows. In Section 4.2 we explore the ant movement data and select covariates for behavioral transition probabilities. Next, in Sections 4.3 and 4.4, we describe the model and discuss a Bayesian approach to inference. We present an application to simulated data in Section 4.5. We discuss results for the ant movement analysis in Section 4.6. We conclude in Section 4.7 with a summary the model and a discussion of future work.

### 4.2 Carpenter Ant Data

The data set that we analyze here using our model with behavioral interactions consists of the movement of carpenter ants *Camponotus pennsylvanicus* from the Hughes laboratory (see Chapter 3, Section 3.2). Ant colonies have evolved various mechanisms to improve colony survival over time. For example, various studies have discussed a "collective immunity" that has developed in ant societies (Quevillon *et al.*, 2015; Cremer *et al.*, 2007). Studying the collective behavior of ants can therefore provide insights that may be useful for preventing the spread of disease in other species. Additionally, ants provide a rare opportunity to observe an entire community of individuals through time, which is often impossible in other communities of organisms. Observing entire communities is essential for understanding the role interactions play in movement behaviors.

Our data consist of the locations of ants in their nest over the course of two hours. The data is recorded using four cameras, one covering each of four chambers. The locations of the ants are recorded every second for the entire two hours using a custom software package. The resulting data set consists of 2-dimensional location coordinates \((x_{t,j}, y_{t,j})\), a time index \(t\), and a unique ant identifier \(j\). Analyzing the data for all 72 of the ants for the entire 2 hour period is computationally taxing so for this analysis we will only consider ants in two of the chambers during the first hour of observation. Chambers I and II (see Chapter 3, Section 3.2) have been selected since the queen remains in Chamber I during the entire observation period. The queen is the central ant in the colony. By focusing our analysis on movement near the queen, we can gain insights into behavior in this critical subset of space in the nest. Sample paths for two of the ants are presented in Figure 4.1. The nest exit is not included in the plot; instead the chamber entrance at the bottom left of the sample plots represents the passageway between Chambers II and III. For
The spatially-varying SDE model developed in Chapter 3 assumes homogenous movement behavior through time (see Section 3.3). In this chapter, we will consider the ants’ behavior and utilize the spatially-varying SDE model to analyze movement only at times when they are active. Thus, to explore the data and motivate our model, we first separate the ant location observations into separate categories by classifying each ant at each time point as either moving or non-moving. To do so, empirical speeds for each ant are calculated at each observed time. If the empirical speed is greater than some cutoff, here chosen to be 0.02 mm (an average ant is between 7mm and 12mm long (Spicer Rice, 2013)), the ant is deemed to be moving, otherwise it is classified as non-moving. First, we will provide an exploratory analysis of the data, and next, we will analyze the transitions between pre-categorized moving and non-moving states to determine which covariates are likely to be important for ant behavioral state transitions. In Section 4.3 we will propose a model in which the behavioral states are not known a priori and are estimated from the data. Here, we explore the data by assuming the states are known.

Conditional on the fact the we have classified the observations as moving, we perform a kernel density estimate to approximate the spatial distribution of the moving ants averaged over time. This estimate is plotted in Figure 4.2a. We perform 1-dimensional kernel density estimates for the empirical speeds of the ants separately in each of the chambers, plotted in Figure 4.2b. These plots reveal the need to model spatially-varying directional drift and spatially-varying movement rate. Additionally an autoregressive model of order 1 is fit to the observations of
moving ants, resulting in an estimated autoregressive parameter of 0.52 (standard error 0.005). This indicates that the model for movement while the ants are assumed to be in an 'active' state should incorporate autocorrelation. These exploratory results parallel those found in Chapter 3.

To gain a better understanding of which factors impact transition between moving and non-moving states, the preliminary classifications discussed above are modeled as a 2-state Markov chain with transition probabilities modeled using binary probit regression. Potential covariates that may impact transition probabilities are considered, such as ant location (discretized to chamber), the number of moving ants within some radius, the number of stopped ants within some radius, and whether or not the queen is within some radius. A variety of radii are used to assess the importance of these possible covariates within a binary probit regression framework. Two separate regressions are run, one using all of the moving observations, where the response is taken to be the next state (moving or non-moving), and the second using all non-moving observations similarly. In each case the probability of a behavioral transition is modeled (i.e. moving to non-moving for case 1, non-moving to moving for case 2) as a linear combination of the possible covariates with an inverse Gaussian cumulative distribution function link (the probit link).
The results from the probit regression on transitions when in the moving state (case 1) are presented in Table 4.1. Positive values indicate positive correlation between the covariate and the probability of transition from a moving state to a non-moving state. The parameter estimates for location covariates ($\eta_{M1}$ through $\eta_{M3}$) indicate that an ant is most likely to stop moving in chamber 1. The parameter estimates for covariates for behavioral interactions ($\eta_{M4}$ through $\eta_{M11}$) reveal that an ant is less likely to stop moving when there are other moving ants nearby and more likely to stop when there are non-moving ants nearby. Finally, the parameter estimates for covariates for behavioral interaction with the queen ($\eta_{M12}$ through $\eta_{M14}$) indicate that an ant is less likely to stop moving if the queen is nearby. All of these results are conditioned on our a priori classification of each ant into a moving or non-moving state at each time point. In Section 4.6 we will allow for these states to be unknown and estimated. The pre-specified states can substantially change if the cutoff value for movement is altered. Estimating these latent states using our model in Section 4.3 avoids the necessity of selecting a cutoff value a priori.

The corresponding results from the probit regression when in the non-moving state are presented in Table 4.2. Positive coefficients indicate an increased proba-
Table 4.2: EDA for Behavioral State Transitions of Non-Moving Observations

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>p-value</th>
<th>notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\eta_{N_0}$</td>
<td>-2.101</td>
<td>$&lt;2e-16^*$</td>
<td>baseline probability of stopping</td>
</tr>
<tr>
<td>$\eta_{N_1}$</td>
<td>0.474</td>
<td>4e-05*</td>
<td>bottom of chamber II</td>
</tr>
<tr>
<td>$\eta_{N_2}$</td>
<td>0.328</td>
<td>7e-07*</td>
<td>top of chamber I</td>
</tr>
<tr>
<td>$\eta_{N_3}$</td>
<td>0.443</td>
<td>2e-11*</td>
<td>bottom of chamber I</td>
</tr>
<tr>
<td>$\eta_{N_4}$</td>
<td>0.578</td>
<td>$&lt;2e-16^*$</td>
<td>moving ants in radius of 2mm</td>
</tr>
<tr>
<td>$\eta_{N_5}$</td>
<td>0.004</td>
<td>0.891</td>
<td>moving ants in radius of 4mm</td>
</tr>
<tr>
<td>$\eta_{N_6}$</td>
<td>0.241</td>
<td>$&lt;2e-16^*$</td>
<td>moving ants in radius of 8mm</td>
</tr>
<tr>
<td>$\eta_{N_7}$</td>
<td>0.178</td>
<td>$&lt;2e-16^*$</td>
<td>moving ants in radius of 12mm</td>
</tr>
<tr>
<td>$\eta_{N_8}$</td>
<td>-0.084</td>
<td>0.001*</td>
<td>stopped ants in radius of 2mm</td>
</tr>
<tr>
<td>$\eta_{N_9}$</td>
<td>-0.118</td>
<td>4e-14*</td>
<td>stopped ants in radius of 4mm</td>
</tr>
<tr>
<td>$\eta_{N_{10}}$</td>
<td>-0.009</td>
<td>0.253</td>
<td>stopped ants in radius of 8mm</td>
</tr>
<tr>
<td>$\eta_{N_{11}}$</td>
<td>-0.030</td>
<td>1e-11*</td>
<td>stopped ants in radius of 12mm</td>
</tr>
<tr>
<td>$\eta_{N_{12}}$</td>
<td>-1.099</td>
<td>2e-05*</td>
<td>queen in radius of 4mm</td>
</tr>
<tr>
<td>$\eta_{N_{13}}$</td>
<td>-0.167</td>
<td>9e-06*</td>
<td>queen in radius of 8mm</td>
</tr>
<tr>
<td>$\eta_{N_{14}}$</td>
<td>0.025</td>
<td>0.362</td>
<td>queen in radius of 12mm</td>
</tr>
</tbody>
</table>

bility for non-moving ants to start moving. The parameter estimates for location covariates ($\eta_{N_1}$ through $\eta_{N_3}$) indicate that an ant is more likely to start outside of the top of chamber II. The parameter estimates for covariates for behavioral interactions ($\eta_{N_4}$ through $\eta_{N_{11}}$) reveal that an ant is more likely to start moving when there are other moving ants nearby and less likely to start when there are non-moving ants nearby. Finally, ants near the queen are less likely to start moving ($\eta_{N_{12}}$), but this effect disappears as the radius of interaction increases ($\eta_{N_{13}}$ and $\eta_{N_{14}}$).

Based on the results of the two exploratory probit regressions, all four factors (location, moving neighbors, non-moving neighbors, and the location of the queen) may impact the behavioral transition probabilities. This highlights the social behavioral dependence that exists in ant movement behavior. Hence, to properly analyze this movement data we propose a novel model that accounts for discrete behavioral states which depend on spatial location and interaction between individuals, as well as modeling directional persistence, spatially-varying directional bias, and spatially-varying absolute movement rate while the ants are in an active state.
4.3 Model for Movement with Interacting Behavioral States

In this section, the model for movement and state transitions will be described. The ants are assumed to transition between three discrete states, moving ‘M’ non-moving ‘N’ and out of chambers ‘O’. The third state, ‘O’, is essentially a nuisance state as we are not interested in behavior outside of the relevant chambers. The state ‘O’ is also completely observed, when an ant is not located in the chambers at a given time it is always in this state. Following our model developed in Chapter 3, let \((x_{t,j}, y_{t,j})\) denote the observed location at time \(t\) of ant \(j\), \((v_{x,t,j}^m, v_{y,t,j}^m)\) denote the latent x and y directional velocities at time \(t\) of ant \(j\), and let \(s_{t,j}\) denote the latent behavioral state at time \(t\) of ant \(j\). Assume that a total of \(J\) ants are each observed at \(T\) times.

4.3.1 Model Summary

We will first describe the movement model for the locations and velocities conditional on the behavioral states, and then describe the model for the interacting latent behavioral states of each ant. For ease of notation, we define the vector \(u_{t,j} = (x_{t,j}, y_{t,j}, v_{x,t,j}^m, v_{y,t,j}^m)\) to be the movement state, consisting of the locations and latent velocities, of individual \(j\) at time \(t\). The distribution of the movement vector of ant \(j\) at time \(t\), denoted \(g(u_{t,j}|s_{t-1,j}, u_{t-1,j})\), is dependent on the behavioral state and the movement vector at the previous time point. The distribution for the behavioral state \((s_{t,j} \in \{M, N, O\})\) of ant \(j\) at time \(t\), denoted \(h(s_{t,j}|s_{t-1,1:J}, u_{t-1,1:J}, u_{t,j})\), is dependent on the state and movement vectors of all individuals at the previous time point, and also the movement vector at the current time point. The dependence on the current movement vector \(u_{t,j}\) is necessary so that the individual’s behavioral state can instantly change to 'out of chambers' upon leaving the study area. Thus, the joint distribution for all \(J\) ants at all \(T\) observation times is

\[
f(u_{1:T,1:J}, s_{1:T,1:J}) = \prod_{t=1}^{T} \prod_{j=1}^{J} h(s_{t,j}|s_{t-1,1:J}, u_{t-1,1:J}, u_{t,j}) g(u_{t,j}|s_{t-1,j}, u_{t-1,j}). \tag{4.1}
\]

The conditional distributions \(g(u_{t,j}|s_{t-1,j}, u_{t-1,j})\) and \(h(s_{t,j}|s_{t-1,1:J}, u_{t-1,1:J}, u_{t,j})\) are specified in Sections 4.3.2 and 4.3.3 respectively.
4.3.2 State-Dependent Movement Models

In this section, the distribution of movement behavior, which consists of locations \((x_{t,j}, y_{t,j})\) and velocities \((v^x_{t,j}, v^y_{t,j})\), will be defined, conditioned on an individual’s discrete behavioral state ('N', 'M', 'O').

4.3.2.1 Ant Behavior When Moving

When the ants are moving, we would like to utilize a flexible movement model that incorporates directional persistence, spatially-varying directional bias, and spatially-varying overall movement rate. Hence, we will model the ants’ locations and velocities using the Euler-Maruyama approximation to the spatially-varying stochastic differential equation model developed in Chapter 3, Section 3.3.

\[
\begin{align*}
[x_{t,j}|s_{t-1,j} = 'M'] & \sim N(x_{t-1,j} + M(x_{t-1,j}, y_{t-1,j})v^{(x)}_{t-1,j} \Delta, \Delta \kappa^2_M) \\
[y_{t,j}|s_{t-1,j} = 'M'] & \sim N(y_{t-1,j} + M(x_{t-1,j}, y_{t-1,j})v^{(y)}_{t-1,j} \Delta, \Delta \kappa^2_M) \\
v^{(x)}_{t,j}|s_{t-1,j} = 'M' & \sim N(v^{(x)}_{t-1,j} + \beta(-\frac{dH(x_{t-1,j}, y_{t-1,j})}{dx} - v^{(x)}_{t-1,j}) \Delta, \Delta \sigma^2_M) \\
v^{(y)}_{t,j}|s_{t-1,j} = 'M' & \sim N(v^{(y)}_{t-1,j} + \beta(-\frac{dH(x_{t-1,j}, y_{t-1,j})}{dx} - v^{(y)}_{t-1,j}) \Delta, \Delta \sigma^2_M).
\end{align*}
\]

Here \(\Delta\) represents the time step between observations. The potential surface \(H(\cdot, \cdot)\), which controls the spatially-varying directional bias, is modeled as a linear combination of B-spline basis functions with a wall repulsion effect added. The motility surface \(M(\cdot, \cdot)\), which controls the spatially-varying directional bias, is similarly modeled with B-spline basis functions. For further details, see Section 3.3.

4.3.2.2 Ant Behavior When Not Moving

While the ant is in a non-moving state, we assume the only variability in movement comes from observation error. Thus, the distribution of an ant’s location is Gaussian with mean centered on the ant’s location at the most recent observation time, and a relatively small variance which may be pre-specified. Similarly, the latent velocity
is assumed to be centered at zero with very small variance

\[
\begin{align*}
[x_{t,j} | s_{t-1,j} = 'N'] &\sim N(x_{t-1,j}, \kappa_N^2) \\
[y_{t,j} | s_{t-1,j} = 'N'] &\sim N(y_{t-1,j}, \kappa_N^2) \\
[v_{t,j}^{(x)} | s_{t-1,j} = 'N'] &\sim N(0, \sigma_N^2) \\
[v_{t,j}^{(y)} | s_{t-1,j} = 'N'] &\sim N(0, \sigma_N^2).
\end{align*}
\]  

(4.3)

Note that the velocity does not enter the location observation so estimating \( \sigma_N^2 \) becomes difficult. Taking the limit of the velocity distribution as \( \sigma_N^2 \) approaches 0 results in fixing the latent velocity at 0 while non-moving. We have elected not to fix velocity at 0 when ants are in the non-moving state since doing so would complicate inference (fixing the velocity at one value would make the latent state completely deterministic conditional on the latent velocity). Instead we propose fixing \( \sigma_N^2 \) at a value small enough that any movement is negligible.

### 4.3.2.3 Ant Behavior When Out of Chambers

When the ant is out of the two relevant chambers, there is no observed location, and the velocity is therefore meaningless to our model. The only time the distribution of location and speed is relevant in this state is upon nest reentry. The reentry locations and velocities are therefore assumed to be Gaussian

\[
\begin{align*}
[x_{t,j} | s_{t-1,j} = 'O'] &\sim N(\mu_{xO}, \kappa_{xO}^2) \\
[y_{t,j} | s_{t-1,j} = 'O'] &\sim N(\mu_{yO}, \kappa_{yO}^2) \\
[v_{t,j}^{(x)} | s_{t-1,j} = 'O'] &\sim N(\mu_{vx}, \kappa_{vx}^2) \\
[v_{t,j}^{(y)} | s_{t-1,j} = 'O'] &\sim N(\mu_{vy}, \kappa_{vy}^2)
\end{align*}
\]  

(4.4)

where \( \mu_{xO} \) and \( \mu_{yO} \) represent the mean for the first observed location coordinates upon reentry, \( \kappa_{xO}^2, \kappa_{yO}^2 \) represent the variability in these observed locations, \( \mu_{vx} \) and \( \mu_{vy} \) represent the mean latent velocities in the \( x \) and \( y \) dimensions respectively, and \( \kappa_{vx}^2, \kappa_{vy}^2 \) represent the variability in these latent velocities. We will estimate all of these parameters from the data.
4.3.3 Modeling Transitions between Latent Behavioral States

To simplify modeling of the behavioral states, the ants are only allowed to transition between behaviors at observation times. Since we observe the locations of the ants every second, the effect of this simplifying assumption is minor. Thus, at each observed time point, each ant will transition to some new behavioral state with some probability. When the ant is out of the nest, we model the probability of reentry \( p_{OM} = P(s_{t,j} = M|s_{t-1,j} = O) \) directly. Intuitively, the ant is only allowed to transition to the moving state upon reentry since the ant must have moved into the nest, so \( p_{ON} = 0 \) and \( p_{OO} = 1 - p_{OM} \).

While in the nest, the transitions to state ‘O’ (out of chambers) are modeled through the movement behavior; if an ant’s location moves outside the study area, the state automatically switches to to "out of chambers". Assuming the ant remains in the nest, and based on the exploratory data analysis presented in Section 4.2, we will model probabilities of switching between moving and non-moving states as a function of the ant’s location, the behavior of nearby ants, and the proximity of the queen. Therefore, the latent behavioral states will be modeled using probit regression, with covariates corresponding to these factors

\[
P(s_{t,j} = M|s_{t-1,j} = N) = g^{-1}(Z_{t-1,j}' \eta_N) \tag{4.5}
\]
\[
P(s_{t,j} = N|s_{t-1,j} = M) = g^{-1}(Z_{t-1,j}' \eta_M). \tag{4.6}
\]

Here \( Z_{t-1,j} \) is a vector of the relevant covariates for ant \( j \) at time \( t \), and \( \eta_N \) and \( \eta_M \) are regression coefficients for the probit regressions in the non-moving and moving transition models. Note that the transition is dependent on the current location to determine if an individual is outside the area of observation, whereas the transition probability covariates are dependent on the movement at the previous time point \( (t-1) \). The probit model framework allows for flexible modeling of inter-animal dependence based on various potential drivers such as behavior of nearest neighbor, distance to nearest neighbor behaving a certain way, or the number of ants within some radius with a certain behavior. This allows a framework for testing or comparing behavioral hypotheses about the cause of switches in behavior.
4.3.4 A Joint Model for State Dependent Movement and Collective State Transitions

In this section, the full model is specified. The likelihood of a sequence of movement vectors $\mathbf{u}_{t;1\cdot J}$ is defined by equation (4.1) in combination with the equations presented in Sections 4.3.2 and 4.3.3. To calculate the joint likelihood, $g(\mathbf{u}_{t,j}|s_{t-1,j}, \mathbf{u}_{t-1,j})$, for the movement state of individual $j$ at time $t$ we assume conditional independence in the the $x$ and $y$ dimensions, as commonly done in animal movement models (Johnson et al., 2008a), since correlations in the $x$ and $y$ dimensions can result in directed movement. For example, a positive correlation in the $x$ and $y$ directions would generate a tendency for individuals to move in a Northeast or Southwest direction. The resulting model, introduced above, yields a multivariate Gaussian movement distributions for ant $j$ at time $t$ conditioned on the previous movement and the latent state, with mean determined by the spatial surfaces, the behavior at the previous time, the latent behavioral state and several other model parameters. Thus, the likelihoods for the distributions defined in Section 4.3.2 conditionally on being in a moving behavioral state

$$[x_{t,j}|s_{t-1,j} = 'M'] \sim N(x_{t-1,j} + M(x_{t-1,j}, y_{t-1,j})v^{(x)}_{t-1,j} \Delta, \Delta \kappa^2_M)$$

$$[y_{t,j}|s_{t-1,j} = 'M'] \sim N(y_{t-1,j} + M(x_{t-1,j}, y_{t-1,j})v^{(y)}_{t-1,j} \Delta, \Delta \kappa^2_M)$$

$$[v^{(x)}_{t,j}|s_{t-1,j} = 'M'] \sim N(v^{(x)}_{t-1,j} + \beta(-\frac{dH(x_{t-1,j}, y_{t-1,j})}{dx} - v^{(y)}_{t-1,j}) \Delta, \Delta \sigma^2_M)$$

$$[v^{(y)}_{t,j}|s_{t-1,j} = 'M'] \sim N(v^{(y)}_{t-1,j} + \beta(-\frac{dH(x_{t-1,j}, y_{t-1,j})}{dx} - v^{(y)}_{t-1,j}) \Delta, \Delta \sigma^2_M),$$

in a non-moving behavioral state

$$[x_{t,j}|s_{t-1,j} = 'N'] \sim N(x_{t-1,j}, \kappa^2_N)$$

$$[y_{t,j}|s_{t-1,j} = 'N'] \sim N(y_{t-1,j}, \kappa^2_N)$$

$$[v^{(x)}_{t,j}|s_{t-1,j} = 'N'] \sim N(0, \sigma^2_N)$$

$$[v^{(y)}_{t,j}|s_{t-1,j} = 'N'] \sim N(0, \sigma^2_N),$$
or outside of the studied chambers

\[
\begin{align*}
[x_{t,j}|s_{t-1,j} = 'O'] &\sim N(\mu_{xO}, \kappa_{xO}^2) \\
[y_{t,j}|s_{t-1,j} = 'O'] &\sim N(\mu_{yO}, \kappa_{yO}^2) \\
[v_{x_{t,j}}^{(x)}|s_{t-1,j} = 'O'] &\sim N(\mu_{vx}, \kappa_{vx}^2) \\
[v_{y_{t,j}}^{(y)}|s_{t-1,j} = 'O'] &\sim N(\mu_{vy}, \kappa_{vy}^2),
\end{align*}
\]

are multiplied together to yield the joint likelihood of the 4-dimensional movement state, \( \mathbf{u}_{t,j} = (x_{t,j}, y_{t,j}, v_{x_{t,j}}^{(x)}, v_{y_{t,j}}^{(y)}) \), for one individual \( j \) at one time \( t \) conditional on its previous behavioral state \( (s_{t-1,j}) \) and its previous movement state \( (\mathbf{u}_{t-1,j}) \).

As in Section 3.3.2, the potential surface, \( H(x,y) \), is specified as the linear combination of 2-dimensional B-spline basis functions with a wall repulsion function added

\[
H(x,y) = \sum_{k,l} \gamma_{kl} \phi_k^{(M)}(x)\psi_l^{(M)}(y) + R(x,y,r,r_1). \tag{4.7}
\]

Here, \( \phi_k^{(M)}(x) \) and \( \psi_l^{(M)}(y) \) are B-spline basis functions of order \( M \), with \( K \) basis functions in the \( x \)-direction and \( L \) basis functions in the \( y \)-direction. A large number of knots is used for the B-spline basis functions. The coefficients are smoothed using a multivariate Gaussian prior with mean vector \( \mathbf{0} \) and spatial smoothness is induced in the potential surface through a conditional autoregressive spatial prior covariance structure. The prior distribution for the B-spline coefficients of the estimated potential surface is therefore

\[
\gamma \sim N \left( \mathbf{0}, (\tau_\gamma (\mathbf{D} - \rho_\gamma \mathbf{Q}))^{-1} \right)
\]

where \( (\mathbf{D})_{jj} = \) \{number of neighbors of \( j \)\}; \( (\mathbf{D})_{ij} = 0 \) if \( i \neq j \); \( (\mathbf{Q})_{jj} = 0 \) and \( Q_{ij} = I(i,j \text{ are neighbors}) \); and \( \tau_\gamma \) and \( \rho_\gamma \) are hyperparameters that control the level of the spatial smoothing.

The wall repulsion function in Equation (4.7) is defined as

\[
R(x,y,r,r_1) = \exp\{-r_1(x - r_1^-)\} + \exp\{r_1(x - r_1^+\}) + \\
\exp\{-r_1(y - r_1^y)\} + \exp\{r_1(y - r_1^y_\gamma)\}
\]

where \( r = (r_1^x, r_1^y, r_1^x_\gamma, r_1^y_\gamma) \); \( r_1^x \) and \( r_1^y \) represent the upper and lower wall boundaries.
in the x-dimension; and \( r_u^y \) and \( r_l^y \) represent the upper and lower wall boundaries in the y-dimension. The parameter \( r_1 \) controls the rate of decay of the wall repulsion function.

The motility surface \( M(x, y) \), similar to the potential surface, is modeled using a linear combination of B-spline basis functions

\[
M(x, y) = \sum_{q,r} \alpha_{qr} \zeta_q^P(x) \xi_r^P(y),
\]

where \( \zeta_q^N(x) \) and \( \xi_r^N(y) \) are b-spline basis functions of order \( P \), with \( Q \) basis functions in the \( x \)-direction and \( R \) basis functions in the \( y \)-direction. A Gaussian prior is used for spatial smoothing

\[
\alpha \sim N \left( \mu_\alpha 1, \mu_\alpha^2 \left( 9 \left( D - \rho_\alpha Q \right) \right)^{-1} \right),
\]

where \( \mu_\alpha \) scales the overall level of the motility surface and \( \rho_\alpha \) is related to the level of spatial smoothing. To prevent estimated surfaces with large regions of negative motility, the precision of the covariance matrix is set to 9 so that 99.8% of the prior mass is positive.

The distribution of the behavioral state of individual \( j \) at time \( t \), denoted \( h(s_{t,j} | s_{t-1,1:j}, u_{t-1,1:j}, u_{t,j}) \), is defined in Section 4.3.3. First, we consider ants that are not observed in the study area that we assume are located outside the chambers of interest. These individuals either return and enter the nest in a moving state with probability \( p_{OM} \) or remain outside the nest with probability \( 1 - p_{OM} \).

Otherwise, if individual \( j \) is observed in the study area at time \( t - 1 \), it can leave the study area or remain in the chambers of interest. If the ant leaves the area and its updated location \( (x_{t,j}, y_{t,j}) \) is no longer within the nest, the behavioral state will transition to the ‘Out of chambers’ behavioral state \( (s_{j,t} = O) \). If the ant remains in the nest, the probability mass function for the behavioral state transition probability, denoted \( h(s_{t,j} | s_{t-1,1:j}, u_{t-1,1:j}, u_{t,j}) \), is determined by the probabilities

\[
\begin{align*}
P(s_{t,j} = N | s_{t-1,j} = M) &= g^{-1}(Z_{t-1,j}^t \eta_M) \\
P(s_{t,j} = M | s_{t-1,j} = M) &= 1 - g^{-1}(Z_{t-1,j}^t \eta_M) \\
P(s_{t,j} = O | s_{t-1,j} = M) &= 0
\end{align*}
\]

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if the ant is in a moving state at time $t - 1$, or

$$
P(s_{t,j} = N|s_{t-1,j} = N) = 1 - g^{-1}(Z'_{t-1,j} \eta_N)
$$

$$
P(s_{t,j} = M|s_{t-1,j} = N) = g^{-1}(Z'_{t-1,j} \eta_N)
$$

$$
P(s_{t,j} = O|s_{t-1,j} = N) = 0
$$

if the ant is in a non-moving state at time $t - 1$. In either case we need to estimate some of the behavioral state transitional probability covariates ($Z_{t-1,j}$). The covariates ($Z_{t-1,j}$) can depend on the latent states ($s_{t-1,1:J}$) and observed locations ($x_{t-1,1:J}, y_{t-1,1:J}$) of all ants at the previous time point. For example, one possible covariate is the number of moving ants within 12mm

$$
z_{t-1,j} = \sum_{k \neq j} I(s_{t-1,k} = M, \sqrt{(x_{t-1,j} - x_{t-1,k})^2 + (y_{t-1,j} - y_{t-1,k})^2} < 12\text{mm}
$$

where $I(\cdot)$ represents the indicator function. Since the behavioral state of the other ants ($s_{t-1,k}$) is unobserved, the covariate ($z_{t-1,j}$ in this case) is latent and must be estimated. Here, for computational efficiency the covariates were selected to be the same for the non-moving and moving states, but defining different covariates for different behavioral states is possible. Bringing everything back together, the joint likelihood for all $J$ ants at all $T$ observation times is

$$
f(u_{1:T,1:J}, s_{1:T,1:J}) = \prod_{t=1}^{T} \prod_{j=1}^{J} h(s_{t,j}|s_{t-1,1:J}, u_{t-1,1:J}, u_{t,j}) g(u_{t,j}|s_{t-1,j}, u_{t-1,j}).
$$

A summary of all the model parameters is presented in table 4.3. Prior distributions for all parameters are given in Section 4.4, Table 4.4.

### 4.4 Bayesian Inference via MCMC

Bayesian inference via Markov chain Monte Carlo is used to estimate the model parameters. Prior distributions are presented in Table 4.4. The prior distributions used for the movement model are similar to those used for the spatially-varying SDE movement model (see Chapter 3, Section 3.4). To update the transition probability coefficients, the auxiliary variable method of Albert and Chib (1993) is used in which, conditional on the latent states, the auxiliary variables $w_{t,j}$ are
Table 4.3: Description of Model Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>autocorrelation parameter while in state $M$</td>
</tr>
<tr>
<td>$\kappa_M^2$</td>
<td>variability in $x$ and $y$ while in state $M$</td>
</tr>
<tr>
<td>$\sigma_M^2$</td>
<td>variability in velocity while in state $M$</td>
</tr>
<tr>
<td>$H(\cdot, \cdot)$</td>
<td>potential surface while in state $M$</td>
</tr>
<tr>
<td>$M(\cdot, \cdot)$</td>
<td>motility surface while in state $M$</td>
</tr>
<tr>
<td>$\kappa_N^2$</td>
<td>variability in $x$ and $y$ while in state $N$</td>
</tr>
<tr>
<td>$\sigma_N^2$</td>
<td>variability in velocity while in state $N$</td>
</tr>
<tr>
<td>$\mu_{xO}$</td>
<td>mean $x$-location on entering nest from $O$</td>
</tr>
<tr>
<td>$\mu_{yO}$</td>
<td>mean $y$-location on entering nest from $O$</td>
</tr>
<tr>
<td>$\kappa_{xO}^2$</td>
<td>variability in $x$-location on entering nest from $O$</td>
</tr>
<tr>
<td>$\kappa_{yO}^2$</td>
<td>variability in $y$-location on entering nest from $O$</td>
</tr>
<tr>
<td>$\mu_{vO}$</td>
<td>mean $x$-velocity on entering nest from $O$</td>
</tr>
<tr>
<td>$\mu_{vO}$</td>
<td>mean $y$-velocity on entering nest from $O$</td>
</tr>
<tr>
<td>$\sigma_{vO}^2$</td>
<td>variability in $x$-velocity on entering nest from $O$</td>
</tr>
<tr>
<td>$\sigma_{vO}^2$</td>
<td>variability in $y$-velocity on entering nest from $O$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Behavioral State Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\eta_M$</td>
</tr>
<tr>
<td>$\eta_N$</td>
</tr>
<tr>
<td>$p_{OM}$</td>
</tr>
</tbody>
</table>

Defined for the moving observations such that

$$w_{t,j} = Z_{t-1,j}^T \eta_M + \epsilon_{t,j}$$

Where $\epsilon_{t,j} \simiid N(0, 1)$, and the latent states are completely determined by the sign of $w_{t,j}$ with

$$s_{t,j} = \begin{cases} 
1 & w_{t,j} \geq 0 \\
0 & w_{t,j} < 0.
\end{cases}$$

Where $1$ represents a behavior transition (i.e. non-moving to moving; or moving to non-moving) and $0$ indicates the individual’s behavioral state remains the same (i.e. non-moving to non-moving; or moving to moving). The introduction of the auxiliary variables ($w_{t,j}$) allows for conjugate full-conditional updates of the regression coefficients $\eta_N$ and $\eta_M$ (Albert and Chib, 1993).
### Table 4.4: Prior Distributions

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>$N_+(1, 10^4)$</td>
</tr>
<tr>
<td>$\kappa_M^2$</td>
<td>1 (fixed for identifiability)</td>
</tr>
<tr>
<td>$\sigma_M^2$</td>
<td>$IG(10^{-3}, 10^{-3})$</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>$N \left( 0, (\tau_\gamma (D - \rho_\gamma Q))^{-1} \right)$</td>
</tr>
<tr>
<td>$\tau_\gamma$</td>
<td>$Exp(\mu_\alpha^2)$</td>
</tr>
<tr>
<td>$\rho_\gamma$</td>
<td>Uniform(0.001, 0.999)</td>
</tr>
<tr>
<td>$r_1$</td>
<td>logNorm(1, 10)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>$N \left( \mu_\alpha 1, \mu_\alpha^2 (9(D - \rho_\alpha Q))^{-1} \right)$</td>
</tr>
<tr>
<td>$\mu_\alpha$</td>
<td>$N_+(1, 10)$</td>
</tr>
<tr>
<td>$\rho_\alpha$</td>
<td>Uniform(0.001, 0.999)</td>
</tr>
<tr>
<td>$\kappa_N^2$</td>
<td>$IG(10^{-2}, 10^{-2})$</td>
</tr>
<tr>
<td>$\sigma_N^2$</td>
<td>$10^{-4}$ (fixed for identifiability)</td>
</tr>
<tr>
<td>$\mu_{xO}$</td>
<td>$N(0, 1)$</td>
</tr>
<tr>
<td>$\mu_{yO}$</td>
<td>$N(0, 1)$</td>
</tr>
<tr>
<td>$\kappa_{xO}^2$</td>
<td>$IG(10^{-2}, 10^{-2})$</td>
</tr>
<tr>
<td>$\kappa_{yO}^2$</td>
<td>$IG(10^{-2}, 10^{-2})$</td>
</tr>
<tr>
<td>$\mu_x$</td>
<td>$N(0, 1)$</td>
</tr>
<tr>
<td>$\mu_y$</td>
<td>$N(0, 1)$</td>
</tr>
<tr>
<td>$\sigma_x^2$</td>
<td>$IG(10^{-2}, 10^{-2})$</td>
</tr>
<tr>
<td>$\sigma_y^2$</td>
<td>$IG(10^{-2}, 10^{-2})$</td>
</tr>
</tbody>
</table>

### Behavioral State Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\eta_M$</td>
<td>$N(0, 10^0 I)$</td>
</tr>
<tr>
<td>$\eta_N$</td>
<td>$N(0, 10^0 I)$</td>
</tr>
<tr>
<td>$\rho_{OM}$</td>
<td>Beta$(10^{-3}, 10^{-3})$</td>
</tr>
</tbody>
</table>

Updating the latent states, $s_{t,j}$, is complicated by the dependence structure of the model, as evident in a 1-dimensional simplification pictured in Figure 4.3. All of the arrows connected to the latent state, $s_{t,j}$, in Figure 4.3 represent distributions which factor into the full conditional for $s_{t,j}$. The resulting full conditional distribution is Bernoulli with success probability depending on the individual’s own behavior and
social interactions with neighbors. At time $t$ for individual $j$

$$
[s_{t,j}] \propto [x_{t+1,j}|s_{t,j}, x_{t,j}, v_{t,j}^{x}, \theta_1][y_{t+1,j}|s_{t,j}, y_{t,j}, v_{t,j}^{y}, \theta_1]
$$

$$
[v_{t+1,j}^{x}|s_{t,j}, x_{t,j}, v_{t,j}^{x}, \theta_1][v_{t+1,j}^{y}|s_{t,j}, x_{t,j}, v_{t,j}^{y}, \theta_1]
$$

$$
[s_{t+1,j}|s_{t,1:J}, x_{t+1,j}, y_{t+1,j}, x_{t,1:J}, y_{t,1:J}, \theta_2]
$$

$$
[s_{t,j}|s_{t-1,1:J}, x_{t,j}, y_{t,j}, x_{t-1,1:J}, y_{t-1,1:J}, \theta_2]
$$

$$
\prod_{k \neq j} [s_{t+1,k}|s_{t,1:J}, x_{t+1,k}, y_{t+1,k}, x_{t,1:J}, y_{t,1:J}, \theta_2].
$$

(4.8)

Here, $\theta_1 = (\beta, \kappa_M^2, \sigma_M^2, \gamma, \alpha, \kappa_N^2, \sigma_N^2, \mu_x, \mu_y, \mu_\mu, \mu_\sigma, \sigma_\mu, \sigma_\sigma)$ represents the movement state parameters, and $\theta_2 = (\eta_M, \eta_N, \rho_{OM})$ represents the behavioral state parameters. In Equation 4.8, the distributions $[x_{t+1,j}|s_{t,j}, x_{t,j}, v_{t,j}^{x}, \theta_1]$ and $[y_{t+1,j}|s_{t,j}, y_{t,j}, v_{t,j}^{y}, \theta_1]$ represent the $x$ and $y$ locations for individual $j$ at the next time point; $[v_{t+1,j}^{x}|s_{t,j}, x_{t,j}, v_{t,j}^{x}, \theta_1]$ and $[v_{t+1,j}^{y}|s_{t,j}, x_{t,j}, v_{t,j}^{y}, \theta_1]$ represent the distributions of the $x$ and $y$ velocities for individual $j$ locations at the next time point; $[s_{t+1,j}|s_{t,1:J}, x_{t+1,j}, y_{t+1,j}, x_{t,1:J}, y_{t,1:J}, \theta_2]$ represents the distribution of the latent behavioral state at the next time point; $[s_{t,j}|s_{t-1,1:J}, x_{t,j}, y_{t,j}, x_{t-1,1:J}, y_{t-1,1:J}, \theta_2]$ represents the distribution of the latent behavioral state at the current time; and $[s_{t+1,k}|s_{t,1:J}, x_{t+1,k}, y_{t+1,k}, x_{t,1:J}, y_{t,1:J}, \theta_2]$ represents the distribution of the latent state of each other individual ($k \neq j$) at the next observation time.

Due to the behavioral interactions in state transition distributions the transition probability calculation increases in complexity as the number of observed individuals increases. This results in a computational burden in updating the latent states which is exacerbated by the fact that the transition probability covariates, which depend on the latent states, must be updated within each iteration of the MCMC algorithm.

To improve computational efficiency, block updates are used for several parameters. Within each iteration of the Markov chain, the following steps are taken.

1. Update $\kappa_N^2$, $\beta$, and $\kappa_M^2$ via variable at-a-time Gibbs sampling.
2. Update the potential surface B-spline coefficients $\gamma$ via block Gibbs sampling.
3. Update $\tau_\gamma$ via Gibbs sampling.
4. Update $\rho_\gamma$ via Metropolis-Hastings.
5. Update the motility surface B-spline coefficients $\alpha$ via block Gibbs sampling.

6. Update $\mu_\alpha$ and $\rho_\alpha$ via variable at-a-time Metropolis-Hastings.

7. Update $\mu_{x_0}$, $\mu_{y_0}$, $\kappa_{x_0}^2$, $\kappa_{y_0}^2$, $\mu_v$, $\nu_v$, $\sigma_{v_x}^2$, and $\sigma_{v_y}^2$ via variable at-a-time Gibbs sampling.

8. For each individual ($j \in \{1 : J\}$):
   
   i. Update the initial behavioral state $(s_{j,1})$ via Gibbs sampling.
   
   ii. Update the even behavioral states $\{s_{j,t} : t = 2n, n = 1, 2, \ldots, \frac{T-2}{2}\}$ via block Gibbs sampling.
iii. Update the odd behavioral states \( \{s_{j,t} : t = 2n - 1, n = 1, 2, ... \frac{T}{2} \} \) via block Gibbs sampling.

iv. Update the final behavioral state \((s_{j,T})\) via Gibbs sampling.

v. Update the transition probability covariates \( \{Z_{t-1,j} : t = n, n = 2, 3, ..., T\} \).

9. Update the transition probability covariates \((\eta_M, \text{ and } \eta_N)\) via block Gibbs sampling using the auxiliary variable method (Albert and Chib, 1993).

10. Update \(p_{OM}\) via Gibbs sampling

11. For each individual \((j \in \{1 : J\})\):

   i. Update the initial \(x\) velocity \((v_{j,1}^x)\) via Gibbs sampling.

   ii. Update the even \(x\) velocities \((\{v_{j,t}^x : t = 2n, n = 1, 2, ... \frac{T-2}{2}\})\) via block Gibbs sampling.

   iii. Update the odd \(x\) velocities \((\{v_{j,t}^x : t = 2n - 1, n = 1, 2, ... \frac{T}{2}\})\) via block Gibbs sampling.

   iv. Update the final \(x\) velocity \((v_{j,T}^x)\) via Gibbs sampling.

   v. Update the initial \(y\) velocity \((v_{j,1}^y)\) via Gibbs sampling.

   vi. Update the even \(y\) velocities \((\{v_{j,t}^y : t = 2n, n = 1, 2, ... \frac{T-2}{2}\})\) via block Gibbs sampling.

   vii. Update the odd \(y\) velocities \((\{v_{j,t}^y : t = 2n - 1, n = 1, 2, ... \frac{T}{2}\})\) via block Gibbs sampling.

   viii. Update the final \(y\) velocity \((v_{j,T}^y)\) via Gibbs sampling.

Initial values for the coefficients \(\eta_N\) and \(\eta_M\) were set to the estimates from a probit regression, similar to the exploratory analysis in Section 4.2. The MCMC sampler was run for 50,000 iterations. Updating the posterior states is computationally taxing as it takes approximately 14 days to generate the entire Markov chain for the carpenter ant movement data. If the latent states are not estimated, and instead they are fixed a priori as in Section 4.2, the behavioral state parameters and the movement parameters can be estimated separately and the total time for computation is reduced to about three days.
4.5 Application to Simulated Data

To gain a better understanding of our proposed model, a simulated data example is generated. While in the moving behavioral state, the simulated particles are drawn to the origin using a quadratic well for the potential surface to model the directional drift \( H(x, y) = x^2 + y^2 \). While moving, the motility surface is given by \( M(x, y) = 2.4 - 0.5(|x| + |y|) \) which results in slower movement as the distance from the origin increases. The particles were transitioned to the 'out of area' behavioral state if they left the square with boundaries given by the lines at \( x = \pm 1, y = \pm 1 \). Plots for these surfaces are presented in Figure 4.4. Ten moving particles are simulated with random starting locations for 5000 observations with an arbitrary time step of \( \Delta = 0.1 \). The reentry parameters are set so that the particle will reenter at the origin moving in a south-east direction \( (\mu_{xO} = 0, \mu_{yO} = 0, \kappa_{xO}^2 = 0.01, \kappa_{yO}^2 = 0.01, \mu_v = 0.25, \mu_{vy} = -0.25, \sigma_{vx}^2 = 0.02, \sigma_{vy}^2 = 0.02) \). The remaining movement parameters are set to the following values: \( (\beta = 2.5, \kappa_M^2 = 10^{-4}, \sigma_M^2 = 1, \kappa_N^2 = 10^{-6}, \sigma_N^2 = 10^{-6}) \).

To mimic the covariates we will be using for the ants, covariates are included in the transition probabilities for the moving and non-moving behavioral states which incorporate the location \( (\eta_{M1}, \eta_{N1}) \), the behavior of nearby individuals \( (\eta_{N2}) \), and the behavior near one specific individual regardless of its behavioral state \( (\eta_{M2}, \eta_{N2}) \).
Table 4.5: Description of Model Parameters for the Behavioral Transition Probabilities in the Simulated Data Example

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\eta_{M_0}$</td>
<td>-2</td>
<td>baseline probability of stopping</td>
</tr>
<tr>
<td>$\eta_{M_1}$</td>
<td>0.75</td>
<td>more likely to stop in Quadrant I</td>
</tr>
<tr>
<td>$\eta_{M_2}$</td>
<td>-1</td>
<td>less likely to stop if particle 10 is within 0.2mm</td>
</tr>
<tr>
<td>$\eta_{N_0}$</td>
<td>-2</td>
<td>baseline probability of starting to move</td>
</tr>
<tr>
<td>$\eta_{N_1}$</td>
<td>0.75</td>
<td>more likely to start in Quadrant I</td>
</tr>
<tr>
<td>$\eta_{N_2}$</td>
<td>0.25</td>
<td>more likely to start if moving neighbor within 0.2mm</td>
</tr>
<tr>
<td>$\eta_{N_3}$</td>
<td>0.5</td>
<td>more likely to start if particle 10 is within 0.2mm</td>
</tr>
<tr>
<td>$POM$</td>
<td>0.01</td>
<td>probability of re-entry</td>
</tr>
</tbody>
</table>

$\eta_{N_3}$). Specific descriptions of the transition probability parameters are presented in Table 4.5.

Using the method discussed in Section 4.4, we test our ability to recover the parameters in our model. The results show that we are able to successfully recover all parameters. Estimates for the surfaces are constructed by separately taking the mean of each B-spline coefficient and plotting the resulting surface over a fine grid. The resulting surfaces plotted in Figure 4.5 reveal that we can successfully recover the size and shape of both the potential and motility surfaces. Posterior mean parameter estimates and 95% credible intervals for the movement parameters are given in Table 4.6. In general, we are successful in capturing the truth using only the location data of the simulated particles. Some of the movement parameter estimates have a minor bias, as the credible intervals do not cover the truth for some of the parameters in Table 4.6. However the differences are minor in all such cases and they do not have an impact on the parameter’s interpretations.

We are also able to estimate the true latent behavioral states and the regression coefficients governing transitions between states. Examining individual draws from the posterior distributions of the latent states reveals that we are able to recover greater than 99.9% of the true states for all ten of the simulated particles. Estimates of these latent states tend to be accurate because we are able to directly observe one of the states, "out of region", the distributions of an individual’s movement in the moving and non-moving behavioral states are very distinct, and observation error in this system is negligible. Simulation studies of animal movement models have found that latent states are easy to recover when this is the case (Beyer et al., 2013).
Table 4.6: Inference for Parameters of the Movement Models in the Simulated Data Example

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Truth</th>
<th>Estimate</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>2.5</td>
<td>2.38</td>
<td>(2.302, 2.449)</td>
</tr>
<tr>
<td>$\kappa^2_M$</td>
<td>1e-04</td>
<td>2.1e-03</td>
<td>(1.8e-03, 2.5e-03)</td>
</tr>
<tr>
<td>$\kappa^2_N$</td>
<td>1e-06</td>
<td>1.1e-06</td>
<td>(1.06e-06, 1.09e-06)</td>
</tr>
<tr>
<td>$\mu_xO$</td>
<td>0</td>
<td>0.027</td>
<td>(0.004, 0.050)</td>
</tr>
<tr>
<td>$\mu_yO$</td>
<td>0</td>
<td>-0.011</td>
<td>(-0.035, 0.012)</td>
</tr>
<tr>
<td>$\kappa^2_xO$</td>
<td>0.01</td>
<td>0.011</td>
<td>(0.008, 0.015)</td>
</tr>
<tr>
<td>$\kappa^2_yO$</td>
<td>0.01</td>
<td>0.011</td>
<td>(0.008, 0.015)</td>
</tr>
<tr>
<td>$\mu_{v_x}$</td>
<td>0.25</td>
<td>0.24</td>
<td>(0.202, 0.273)</td>
</tr>
<tr>
<td>$\mu_{v_y}$</td>
<td>-0.25</td>
<td>-0.27</td>
<td>(-0.298, -0.235)</td>
</tr>
<tr>
<td>$\sigma^2_{v_x}$</td>
<td>0.02</td>
<td>0.022</td>
<td>(0.015, 0.031)</td>
</tr>
<tr>
<td>$\sigma^2_{v_y}$</td>
<td>0.02</td>
<td>0.016</td>
<td>(0.011, 0.023)</td>
</tr>
</tbody>
</table>

Posterior mean parameter estimates and 95% credible intervals for the behavioral transition parameters are given in Table 4.7. The resulting estimates are accurate for all behavioral parameters as the 95% credible intervals include the truth for every parameter in Table 4.7. This suggests that the minor bias in the estimates of some movement parameters evident in Table 4.6 does not have a significant impact in interpreting the type of behaviors of individuals in the simulated colony.
Table 4.7: Inference for Parameters of the Behavioral Transition Probabilities in
the Simulated Data Example

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Truth</th>
<th>Estimate</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>η_{M0}</td>
<td>-2</td>
<td>-1.96</td>
<td>(-2.007, -1.915)</td>
</tr>
<tr>
<td>η_{M1}</td>
<td>0.75</td>
<td>0.71</td>
<td>(0.648, 0.780)</td>
</tr>
<tr>
<td>η_{M2}</td>
<td>-1</td>
<td>-1.17</td>
<td>(-1.418, -0.956)</td>
</tr>
<tr>
<td>η_{N0}</td>
<td>-2</td>
<td>-1.96</td>
<td>(-2.004, -1.918)</td>
</tr>
<tr>
<td>η_{N1}</td>
<td>0.75</td>
<td>0.71</td>
<td>(0.605, 0.806)</td>
</tr>
<tr>
<td>η_{N2}</td>
<td>0.25</td>
<td>0.21</td>
<td>(0.175, 0.252)</td>
</tr>
<tr>
<td>η_{N3}</td>
<td>0.5</td>
<td>0.63</td>
<td>(0.499, 0.759)</td>
</tr>
<tr>
<td>p_{OM}</td>
<td>0.01</td>
<td>0.009</td>
<td>(0.007, 0.011)</td>
</tr>
</tbody>
</table>

4.6 Carpenter Ant Movement Results

In this Section, we present preliminary results for the movement of carpenter ants. Section 4.6.1 contains a discussion of the results for the movement behavior. We present the estimates for latent behavioral states (s_{j,t}) and the relevant transition probability parameters in Section 4.6.2.

4.6.1 Results for Movement Behavior in Different Behavioral States

While the ants are in a non-moving state, the only estimated parameter, κ_{N}^{2}, controls the variability in location. The posterior mean for the location variability, 5.74 * 10^{-5}, indicates that this state consists of only negligible shifts in location. The 95% credible interval for κ_{N}^{2} is calculated from the 2.5% and 97.5% quartiles, yielding (4.38 * 10^{-5}, 7.22 * 10^{-5}), confirming that only small relocations can occur in this state.

If an ant re-enters the study area from the "out of chamber" state, we estimate parameters that determine its initial location and speed. Posterior mean estimates and credible intervals for these reentry parameters are presented in Table 4.8. The estimates for mean reentry location, μ_{xO} = 0.176 and μ_{yO} = 0.225, capture the obvious tendency to enter the nest at the doorway which is centered at (0.15, 0). Intuitively, the mean posterior velocities are both positive, μ_{vx} = 1.737 and μ_{vy} = 0.642, since the ants are moving away from the doorway. These latent
Table 4.8: Results for Parameters of the Re-Entry Behavior of Ants

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>95% CI</th>
<th>notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_xO$</td>
<td>0.176</td>
<td>(0.064, 0.290)</td>
<td>re-entry x-location mean</td>
</tr>
<tr>
<td>$\mu_yO$</td>
<td>0.225</td>
<td>(0.113, 0.338)</td>
<td>re-entry y-location mean</td>
</tr>
<tr>
<td>$\kappa^2_xO$</td>
<td>0.055</td>
<td>(0.025, 0.115)</td>
<td>re-entry x-location variance</td>
</tr>
<tr>
<td>$\kappa^2_yO$</td>
<td>0.055</td>
<td>(0.025, 0.113)</td>
<td>re-entry y-location variance</td>
</tr>
<tr>
<td>$\mu_vx$</td>
<td>1.737</td>
<td>(1.061, 2.376)</td>
<td>re-entry x-velocity mean</td>
</tr>
<tr>
<td>$\mu_vy$</td>
<td>0.642</td>
<td>(0.353, 0.938)</td>
<td>re-entry y-velocity mean</td>
</tr>
<tr>
<td>$\sigma^2_vx$</td>
<td>1.676</td>
<td>(0.728, 3.564)</td>
<td>re-entry x-velocity variance</td>
</tr>
<tr>
<td>$\sigma^2_vy$</td>
<td>0.311</td>
<td>(0.126, 0.691)</td>
<td>re-entry y-velocity variance</td>
</tr>
</tbody>
</table>

Figure 4.6: Ant Posterior Mean Surfaces

velocities are scaled by the motility surface $M(\cdot, \cdot)$, so the magnitude of these velocities can not be directly interpreted as the overall rate of movement away from the doorway.

While an ant is in a moving state, the location and velocity are updated via the spatially-varying stochastic differential equation model (see Chapter 3, Section 3.3). Estimates for the potential surface $H(\cdot, \cdot)$ and motility surface $M(\cdot, \cdot)$ are calculated pointwise using the posterior mean of each B-spline coefficient and plotting the estimated surface over a fine grid. Contour maps of the resulting B-spline estimates for the surfaces along with a vector gradient map are plotted in Figure 4.6. The potential surface estimate in Figure 4.6(a) reveals a tendency to move away from the outer walls towards the center of the nest or to change direction when moving toward a nearby wall. The potential surface also indicates directed movement away from the passageways between different sections of the nest. These areas may be
Table 4.9: Results for Parameters of the Movement Behavior of Ants

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>95% CI</th>
<th>notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta$</td>
<td>0.2465</td>
<td>(0.1736, 0.3101)</td>
<td>autocorrelation</td>
</tr>
<tr>
<td>$\kappa_M$</td>
<td>0.0012</td>
<td>(0.0010, 0.00013)</td>
<td>moving location variance</td>
</tr>
<tr>
<td>$r_1$</td>
<td>0.1751</td>
<td>(0.0573, 0.3156)</td>
<td>wall repulsion scaling</td>
</tr>
</tbody>
</table>

avoided so that individuals do not block the passage of other ants through the nest. The motility surface estimate plotted in Figure 4.6(c) reveals a slower movement rate in the top chamber relative to the bottom chamber. This indicates that the lower chamber is used for higher-speed transit and slower movement characterizes the top chamber where the queen is located. The gradient map plotted in 4.6(b) combines the effects of the potential surface and the motility surface, highlighting directed movement away from outer walls and slower movement in the top chamber.

Posterior means and 95% credible intervals for the remaining parameters of the movement state model are given in Table 4.9. The results indicate the existence of significant temporal autocorrelation, since the credible interval for $\beta$ does not include 1. The directional persistence is stronger $\beta = 0.2465$ when the non-moving observations are not included (see Chapter 3, Section 3.4 where we found $\beta = 0.872$ assuming homogeneous behavior in time). Additionally, there is a small wall repulsion effect $r_1 = 0.1751$ captured by the model.

4.6.2 Results for Latent Behavioral States and Transition Probabilities

Estimates for the latent states are calculated by taking the most frequent state for each ant at each time point drawn from the posterior distribution (the posterior mode). To examine aggregate behavior over time, the proportion of ants in each behavioral state at each time is calculated. On average, approximately 8% of ants that enter the two relevant chambers during observation are active at any given time. The results for the moving state and the "out of chambers" state are plotted in Figure 4.7 in black and red respectively. The proportion of moving ants indicate that there may be slight "pulses" of behavior followed by periods of relative inactivity. There is no obvious relationship between the proportion of ants outside the chambers and the proportion of ants moving.
Figure 4.7: Proportion of Estimated Behaviors in the Nest Over Time.

Posterior means and 95% credible intervals for the behavioral state transition parameters are calculated in Table 4.10. In each case, the probability of transition to a new behavioral state is modeled, so that positive values indicate a greater likelihood of a behavioral state transition (i.e., non-moving to moving; or moving to non-moving.) For example, if a non-moving ant is located in chamber I it is slightly less likely to start moving ($\eta_{N_1} = -0.29$), and if a moving ant is located in chamber I it is much more likely to stop ($\eta_{M_1} = 0.95$). This agrees with the finding in Section 4.6.1 that the bottom chamber (Chamber II) is primarily used for transit. The estimates for behavioral interaction coefficients in the model indicate that stationary ants are more likely to start moving when there are other moving ants nearby ($\eta_{N_2} = 0.30$), and less likely to start moving if they have non-moving neighbors ($\eta_{N_3} = -0.07$). Moving ants, on the other hand, are more likely to stop moving when there are many nearby ants in either behavioral state ($\eta_{M_2} = 0.07$, $\eta_{M_3} = 0.15$). Regardless of their current state, ants are less likely to change their behavior when the queen is nearby ($\eta_{N_4} = -1.19$, $\eta_{M_4} = -1.39$). Finally, the queen is more likely to switch behaviors than other ants ($\eta_{N_5} = 0.94$, $\eta_{M_5} = 1.91$), indicating a tendency for the queen to make frequent small movements.
Table 4.10: Results for Parameters of the Behavioral State Transitions of Ants

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>95% CI</th>
<th>notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\eta_{N_0}$</td>
<td>-1.54</td>
<td>(-1.69,-1.43)</td>
<td>baseline probability of starting located in chamber I</td>
</tr>
<tr>
<td>$\eta_{N_1}$</td>
<td>-0.29</td>
<td>(-0.42,-0.10)</td>
<td>moving ants in radius of 12mm</td>
</tr>
<tr>
<td>$\eta_{N_2}$</td>
<td>0.30</td>
<td>(0.25,0.34)</td>
<td>stopped ants in radius of 4mm</td>
</tr>
<tr>
<td>$\eta_{N_3}$</td>
<td>-0.07</td>
<td>(-0.11,-0.05)</td>
<td>queen in radius of 4mm is the Queen</td>
</tr>
<tr>
<td>$\eta_{N_4}$</td>
<td>-1.19</td>
<td>(-2.10,-0.60)</td>
<td></td>
</tr>
<tr>
<td>$\eta_{N_5}$</td>
<td>0.94</td>
<td>(0.37,1.87)</td>
<td></td>
</tr>
<tr>
<td>$\eta_{M_0}$</td>
<td>-0.77</td>
<td>(-0.96,-0.61)</td>
<td>baseline probability of stopping located in chamber I</td>
</tr>
<tr>
<td>$\eta_{M_1}$</td>
<td>0.95</td>
<td>(0.79,1.14)</td>
<td>moving ants in radius of 12mm</td>
</tr>
<tr>
<td>$\eta_{M_2}$</td>
<td>0.07</td>
<td>(0.03,0.11)</td>
<td>stopped ants in radius of 4mm</td>
</tr>
<tr>
<td>$\eta_{M_3}$</td>
<td>0.15</td>
<td>(0.09,0.21)</td>
<td>queen in radius of 4mm is the Queen</td>
</tr>
<tr>
<td>$\eta_{M_4}$</td>
<td>-1.39</td>
<td>(-3.65,-0.22)</td>
<td></td>
</tr>
<tr>
<td>$\eta_{M_5}$</td>
<td>1.91</td>
<td>(0.70,4.18)</td>
<td></td>
</tr>
<tr>
<td>$\text{POM}$</td>
<td>0.0008</td>
<td>(0.0004,0.0012)</td>
<td>probability of re-entry</td>
</tr>
</tbody>
</table>

4.7 Discussion

In this chapter we have presented a model that captures heterogeneous movement behavior in time driven by social and spatial mechanisms. Collective movement behavior is modeled through dependence in the transition probabilities between behavioral states on the behavior of nearby individuals. These interactions are efficiently modeled and estimated using covariates in a nested generalized linear model. This provides a novel method for modeling dependence in collective animal movement. Most existing methods model dependence in animal locations or velocities rather than animal behavioral states. Thus, this work compliments existing models for collective movement, which focus on modeling movement when all animals are in a similar behavioral state.

This novel methodology is applicable to a wide range of applied problems (Treherne and Foster, 1981; Ward et al., 2008; Milgram et al., 1969). Complex animal movement patterns can be modeled by combining this behavioral structure with existing movement models such as the spatially-varying SDE movement model (see Chapter 3). The resulting combined model accounts for all of the following factors:

1. changes in behavior over time
2. dependence between individuals
3. spatially-varying behavioral tendencies
4. directional persistence
5. spatially-varying directional drift
6. spatially-varying absolute movement rate

The proposed model has been used to analyze the location data of carpenter ants within two chambers of a four chambered nest. Bayesian inference via Markov chain Monte Carlo reveals complex behavioral interactions between individuals. For example, non-moving ants tend to copy the behavior of other nearby ants, and moving ants are more likely to stop whenever other ants are nearby regardless of their behavioral state. Additionally, all ants in the nest are less likely to change their behavior when they are within 4mm of the queen.

In our analysis we have assumed that the number of behavioral states and a general description (‘N’, ‘M’, ‘O’) is known. In future work, model selection could be used to select the number of states (Fox et al., 2011). For example, ants often stop moving to antennate or engage in trophallaxis with other nearby ants. This may constitute a different behavioral state than ants who are merely dormant and not engaged in social interaction, even though the observed movement is similar (little or no movement when dormant or when in trophallaxis). A combination of potential functions based on particle interactions (Brillinger et al., 2001), which impose a gradient directed towards other specific particles, with a latent network depending on movement (Scharf et al., 2015), which can estimate dynamic interactions, would be well suited for modeling this interacting state.

Here an exploratory analysis was utilized to select important covariates for behavioral transitions and the related radii of dependence. Instead, variable selection methods such as the Bayesian Lasso (Park and Casella, 2008) could be used to select covariates and the radii of behavioral dependence between individuals could be estimated directly in the model.

Within our framework, the behavioral state of an animal is only allowed to change at discrete times of observation. This is reasonable here since the temporal resolution of observation can be arbitrarily fine due to the video tracking technique used to record data. In other scenarios a model which allows behavioral switching in continuous time would be preferable (Blackwell et al., 2016). Inference on a
continuous time model would be computationally burdensome in our case due to
the large number of observations. Improving the computational efficiency through
parallel computing or other methods is important to future work so that all 72 ants
in all four chambers of the nest can be analyzed for the entire two hour observation
period.

Acknowledgements

This research is supported by the NSF grant EEID 1414296.

4.8 Supplementary Material: Full Conditional Distributions

In this Section the full conditional distributions for the model defined in Section
4.3 are presented.

1. latent x velocity \( v^{(x)}_{t,j} \) \( \sim N \left( m_v c_v^{-1}, c_v^{-1} \right) \)

\[
m_v = \frac{I(b)[v^{(x)}_{t-1,j} + \beta \left( \frac{dH(x_{t-1,j}, y_{t-1,j})}{dx} - v^{(x)}_{t-1,j} \right) \Delta]}{\Delta \sigma^2_M} + \frac{I(c)\mu_{v_x}}{\sigma^2_O} + \frac{I(d)\mu_{v_1}}{\sigma^2_{v_1}} + \frac{I(e)[(1 - \beta \Delta)(v^{(x)}_{t+1,j} + \beta \frac{dH(x_{t+1,j}, y_{t+1,j})}{dx} \Delta)]}{\Delta \sigma^2_M} + \frac{I(e)[M(x_{t,j}, y_{t,j})\Delta(x_{t+1,j} - x_{t,j})]}{\Delta \kappa^2_M}
\]

\[
c_v = \frac{I(a)}{\sigma^2_N} + \frac{I(b)}{\Delta \sigma^2_M} + \frac{I(c)}{\sigma^2_O} + \frac{I(d)}{\sigma^2_{v_1}} + \frac{I(e)(1 - \beta \Delta)^2}{\Delta \sigma^2_M} + \frac{I(e)(M(x_{t,j}, y_{t,j})\Delta)^2}{\Delta \kappa^2_M}
\]

where

- a : \( s_{t,j} = N \) and \( t \neq 1 \)
- b : \( s_{t,j} = M \) and \( t \neq 1 \)
- c : \( s_{t,j} = O \) and \( t \neq 1 \)
- d : \( t = 1 \)
• $e : s_{t,j} = M$ and $t \neq T$

2. latent y velocity $v^{(y)}_{t,j} | \cdot$ (similar to y)

3. latent state $s_{t,j} | \cdot \sim$ Multinomial with probability determined by the distributions of

(a) The next x location $x_{t+1,j}$ conditional on the current state $s_{t,j}$.
(b) The next y location $y_{t+1,j}$ conditional on the current state $s_{t,j}$.
(c) The next x velocity $v^{(x)}_{t+1,j}$ conditional on the current state $s_{t,j}$.
(d) The next y velocity $v^{(y)}_{t+1,j}$ conditional on the current state $s_{t,j}$.
(e) The current state $s_{t,j}$ conditional on the previous state $s_{t-1,j}$.
(f) The next state $s_{t+1,j}$ conditional on the current state $s_{t,j}$.
(g) The next state of all other individuals $s_{t+1,-j}$ conditional on the current state $s_{t,j}$.

4. auxiliary variable $w_{t,j} | \cdot \sim N_+ \left( (Z(\cdot)'\eta_N, 1) \right)$ if $s_{t,j} = N, s_{t+1,j} = M$

5. auxiliary variable $w_{t,j} | \cdot \sim N_- \left( (Z(\cdot)'\eta_N, 1) \right)$ if $s_{t,j} = N, s_{t+1,j} = N$

6. auxiliary variable $w_{t,j} | \cdot \sim N_+ \left( (Z(\cdot)'\eta_M, 1) \right)$ if $s_{t,j} = M, s_{t+1,j} = N$

7. auxiliary variable $w_{t,j} | \cdot \sim N_- \left( (Z(\cdot)'\eta_M, 1) \right)$ if $s_{t,j} = M, s_{t+1,j} = M$

8. $\beta | \cdot \sim N_+ \left( \left( \sum_{a=1}^{N_a} a_j + \frac{1}{2\sigma^2} \left( \sum_{j=1}^{J} b_j + \mu_\beta \right) \right)^{-1}, \left( \sum_{j=1}^{J} b_j + \mu_\beta \right)^{-1} \right)$

$$a_j = \frac{\Delta}{2\sigma^2} \sum_{\{t \in 1:T | s_{t,i} = M\}} \left( -\frac{d}{dx} H(x_{t,j}, y_{t,j}) - v_{t,j}^{(x)} \right)^2 +$$

$$b_j = \frac{1}{2\sigma^2} \sum_{\{t \in 1:T | s_{t,i} = M\}} \left( -\frac{d}{dx} H(x_{t,j}, y_{t,j}) - v_{t,j}^{(x)} \right) \left( v_{t+1,j}^{(x)} - v_{t,j}^{(x)} \right) +$$

$$\frac{1}{2\sigma^2} \sum_{\{t \in 1:T | s_{t,i} = M\}} \left( -\frac{d}{dy} H(x_{t,j}, y_{t,j}) - v_{t,j}^{(y)} \right) \left( v_{t+1,j}^{(y)} - v_{t,j}^{(y)} \right)$$

99
9. \( \sigma^2_M \mid = 1 \) (fixed for identifiability)

10. \( \kappa^2_M \mid \sim IG (\alpha_{\kappa_M} + \sum_{j=1}^{N_a} a_j, \beta_{\kappa_M} + \sum_{j=1}^{N_a} b_j) \)

\[
a_j = \sum_{\{t \in 1: T\}} I(s_{t,j} = M)
\]

\[
b_j = \frac{1}{2\Delta} \sum_{\{t \in 1: T\mid s_{t,j} = M\}} \left( x_{t+1,j} - x_{t,j} - M(x_{t,j}, y_{t,j})v^{(x)}_t \Delta \right)^2 + \frac{1}{2\Delta} \sum_{\{t \in 1: T\mid s_{t,j} = M\}} \left( y_{t+1,j} - y_{t,j} - M(x_{t,j}, y_{t,j})v^{(y)}_t \Delta \right)^2
\]

11. \( \gamma \mid \sim N \left( (\sum_{j=1}^{N_a} a_j + \tau_\gamma (D - \rho_\gamma Q))^{-1} \sum_{j=1}^{N_a} b_j, (\sum_{j=1}^{N_a} a_j + \tau_\gamma (D - \rho_\gamma Q))^{-1} \right) \)

\[
a_j = \frac{\beta^2 \Delta}{\sigma^2} \sum_{\{t \in 1: T\mid s_{t,j} = M\}} \Phi'_x(x_{t,j}, y_{t,j}) \Phi_x(x_{t,j}, y_{t,j}) + \frac{\beta^2 \Delta}{\sigma^2} \sum_{\{t \in 1: T\mid s_{t,j} = M\}} \Phi'_y(x_{t,j}, y_{t,j}) \Phi_y(x_{t,j}, y_{t,j})
\]

\[
b_j = \frac{1}{2\Delta} \sum_{\{t \in 1: T\mid s_{t,j} = M\}} \Phi'_x(x_{t,j}, y_{t,j}) \left( v^{(x)}_{t+1,j} - v^{(x)}_{t,j} + \beta \Delta \left( v^{(x)}_{t,j} + \frac{d}{dx} R(x_{t,j}, y_{t,j}) \right) \right) + \frac{1}{2\Delta} \sum_{\{t \in 1: T\mid s_{t,j} = M\}} \Phi'_y(x_{t,j}, y_{t,j}) \left( v^{(y)}_{t+1,j} - v^{(y)}_{t,j} + \beta \Delta \left( v^{(y)}_{t,j} + \frac{d}{dy} R(x_{t,j}, y_{t,j}) \right) \right)
\]

12. \( r_1 \mid \) (Metropolis-Hastings Update)

13. \( \tau_\gamma \mid \sim IG \left( \frac{1}{2} N_H \ast N_M + \alpha_{\tau_\gamma}, \frac{1}{2} \gamma' (D - \rho_\gamma Q) \gamma + \beta_{\tau_\gamma} \right) \)

14. \( \rho_\gamma \mid \) (Metropolis-Hastings Update)

15. \( \alpha \mid \sim N \left( (a + \frac{9}{\mu_\alpha}(D - \rho_\alpha Q))^{-1} (b + \frac{9}{\mu_\alpha}(D - \rho_\alpha Q)), (a + \frac{9}{\mu_\alpha}(D - \rho_\alpha Q))^{-1} \right) \)
\[ a = \frac{1}{\kappa^2} \sum_{j=1}^{N_a} \sum_{\{t \in T \mid s_{j,t} = M\}} (v_{t,j}^{(x)})^2 \Phi_x(x_{t,j}, y_{t,j}) \Phi_x(x_{t,j}, y_{t,j}) + \]

\[ \frac{\Delta}{\kappa^2} \sum_{j=1}^{N_a} \sum_{\{t \in T \mid s_{j,t} = M\}} (v_{t,j}^{(y)})^2 \Phi_y(x_{t,j}, y_{t,j}) \Phi_y(x_{t,j}, y_{t,j}) \]

\[ b = \frac{\Delta}{\kappa^2} \sum_{j=1}^{N_a} \sum_{\{t \in T \mid s_{j,t} = M\}} \Phi_x'(x_{t,j}, y_{t,j}) v_{t,j}^{(x)} (x_{t+1,j} - x_{t,j}) + \]

\[ \frac{\Delta}{\kappa^2} \sum_{j=1}^{N_a} \sum_{\{t \in T \mid s_{j,t} = M\}} \Phi_y'(x_{t,j}, y_{t,j}) v_{t,j}^{(y)} (y_{t+1,j} - y_{t,j}) \]

16. \( \mu_{a_{| \cdot}} \): (Metropolis-Hastings Update)

17. \( \rho_{a_{| \cdot}} \): (Metropolis-Hastings Update)

18. \( \sigma_N^2 \): \( = 10^{-4} \) (fixed for identifiability)

19. \( \kappa_N^2 \): \( \sim IG \left( \alpha_{\kappa_N} + \sum_{j=1}^{N_a} a_j, \beta_{\kappa_N} + \sum_{j=1}^{N_a} b_j \right) \]

\[ a_j = \sum_{\{t \in T\}} I(s_{t,j} = N) \]

\[ b_j = \frac{1}{2} \sum_{\{t \in T \mid s_{j,t} = N\}} (x_{t+1,j} - x_{t,j})^2 + \frac{1}{2} \sum_{\{t \in T \mid s_{j,t} = N\}} (y_{t+1,j} - y_{t,j})^2 \]

20. \( \mu_{x_O_{| \cdot}} \): \( \sim N \left( \frac{1}{\sigma_x^2} (a)(\frac{b}{2\sigma_x^2} - \frac{1}{2\kappa_N})^{-1}, (\frac{b}{2\sigma_x^2} - \frac{1}{2\kappa_N})^{-1} \right) \]

\[ a = \sum_{j=1}^{N_a} \sum_{\{t \in T \mid s_{j,t-1} = O, s_{j,t} = M\}} x_{t,j} \]
\[ b = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T\}} I(s_{j,t-1} = O, s_{j,t} = M) \]

21. \( \mu_{yO} | \sim N \left( \frac{1}{\sigma_y^2} (a) \left( \frac{b}{2\sigma_y^2} - \frac{1}{2\kappa_y^2} \right)^{-1}, \left( \frac{b}{2\sigma_y^2} - \frac{1}{2\kappa_y^2} \right)^{-1} \right) \)

\[ a = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T \mid s_{j,t-1} = O, s_{j,t} = M\}} y_{t,j} \]

\[ b = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T\}} I(s_{j,t-1} = O, s_{j,t} = M) \]

22. \( \kappa_{xO}^2 | \sim IG \left( \alpha_{\kappa_x} + b, \beta_{\kappa_x} + \frac{1}{2} a \right) \)

\[ a = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T \mid s_{j,t-1} = O, s_{j,t} = M\}} x_{t,j}^2 \]

\[ b = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T\}} I(s_{j,t-1} = O, s_{j,t} = M) \]

23. \( \kappa_{yO}^2 | \sim IG \left( \alpha_{\kappa_y} + b, \beta_{\kappa_y} + \frac{1}{2} a \right) \)

\[ a = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T \mid s_{j,t-1} = O, s_{j,t} = M\}} y_{t,j}^2 \]

\[ b = \sum_{j=1}^{N_a} \sum_{\{t \in 1:T\}} I(s_{j,t-1} = O, s_{j,t} = M) \]

24. \( \mu_{zv} | \sim N \left( \frac{1}{\sigma_{zv}^2} (a) \left( \frac{b}{2\sigma_{zv}^2} - \frac{1}{2\kappa_{zv}^2} \right)^{-1}, \left( \frac{b}{2\sigma_{zv}^2} - \frac{1}{2\kappa_{zv}^2} \right)^{-1} \right) \)
\begin{align*}
a &= \sum_{j=1}^{N_a} \sum_{\{t \in T : s_{j,t-1}=O, s_{j,t}=M\}} v_{t,j}^{(x)} \\
b &= \sum_{j=1}^{N_a} \sum_{\{t \in T\}} I(s_{j,t-1} = O, s_{j,t} = M)
\end{align*}

25. $\mu_{v_y} \sim N \left( \frac{1}{\sigma_{v_y}} (a) \left( \frac{b}{2\sigma_{v_y}^2} - \frac{1}{2\kappa_{v_y}} \right)^{-1}, \left( \frac{b}{2\sigma_{v_y}^2} - \frac{1}{2\kappa_{v_y}} \right)^{-1} \right)$

\begin{align*}
a &= \sum_{j=1}^{N_a} \sum_{\{t \in T : s_{j,t-1}=O, s_{j,t}=M\}} v_{t,j}^{(y)} \\
b &= \sum_{j=1}^{N_a} \sum_{\{t \in T\}} I(s_{j,t-1} = O, s_{j,t} = M)
\end{align*}

26. $\sigma_{v_y}^2 \mid \cdot \sim IG \left( \alpha_{\sigma_y} + b, \beta_{\sigma_y} + \frac{1}{2} a \right)$

\begin{align*}
a &= \sum_{j=1}^{N_a} \sum_{\{t \in T : s_{j,t-1}=O, s_{j,t}=M\}} \left( v_{t,j}^{(x)} \right)^2 \\
b &= \sum_{j=1}^{N_a} \sum_{\{t \in T\}} I(s_{j,t-1} = O, s_{j,t} = M)
\end{align*}

27. $\sigma_{v_y}^2 \mid \cdot \sim IG \left( \alpha_{\sigma_y} + b, \beta_{\sigma_y} + \frac{1}{2} a \right)$

\begin{align*}
a &= \sum_{j=1}^{N_a} \sum_{\{t \in T : s_{j,t-1}=O, s_{j,t}=M\}} \left( v_{t,j}^{(y)} \right)^2 \\
b &= \sum_{j=1}^{N_a} \sum_{\{t \in T\}} I(s_{j,t-1} = O, s_{j,t} = M)
\end{align*}
\[ b = \sum_{j=1}^{N_{a}} \sum_{t \in \{1:T\}} I(s_{j,t-1} = O, s_{j,t} = M) \]

28. \( \eta_{N} \mid \sim N(b^{-1}a, b^{-1}) \)

\[ a = (\sigma_{\eta_{N}}^{2})^{-1} \mu_{\eta_{N}} + Z_{N}(\cdot)'W_{N}(\cdot) \]

\[ b = (\sigma_{\eta_{N}}^{2})^{-1} + Z_{N}(\cdot)'Z_{N}(\cdot) \]

29. \( \eta_{M} \mid \sim N(b^{-1}a, b^{-1}) \)

\[ a = (\sigma_{\eta_{M}}^{2})^{-1} \mu_{\eta_{M}} + Z_{M}(\cdot)'W_{M}(\cdot) \]

\[ b = (\sigma_{\eta_{M}}^{2})^{-1} + Z_{M}(\cdot)'Z_{M}(\cdot) \]

30. \( p_{OM} \mid \sim \text{Beta}(\alpha_{P_{OM}} + a, \beta_{P_{OM}} + b) \)

\[ a = \sum_{j=1}^{N_{a}} \sum_{t=1}^{T-1} I(s_{t+1,j} = M, s_{t,j} = O) \]

\[ b = \sum_{j=1}^{N_{a}} \sum_{t=1}^{T-1} I(s_{t+1,j} = O, s_{t,j} = O) \]
Chapter 5 | Discussion and Future Work

In this chapter, I will summarize my dissertation and propose potential directions for future work.

5.1 Summary and Contributions

In my dissertation several novel models for animal movement are proposed. The models are motivated by the movement of guppies in an enclosed tank and ants in a four chambered nest. They incorporate between-animal dependence, spatial variation in movement, temporal variation in movement, and behavioral interactions. A Bayesian framework for inference is used in all cases. The use of a Bayesian framework enables the avoidance of high-dimensional integration that would need to be dealt with in a maximum likelihood setting. Bayesian methods result in straightforward estimates of variability in parameters and surfaces through posterior credible intervals. Further, models can be easily compared using the Bayes factor, including non-nested models.

In Chapter 2 a novel model for animal movement that uses point process interaction functions is presented. The model also accounts for measurement error and directional persistence. The attraction-repulsion interaction function of Goldstein et al. (2015) is used to model small-scale repulsion, or collision avoidance, and intermediate range attraction. A double Metropolis–Hastings algorithm is developed for inference due to intractable normalizing constants which allows for direct estimation of interaction parameters. Movement data from a shoal of guppies is analyzed and the pairwise interactions between the guppies is captured and recreated via simulation.
The within-nest movement of ants is studied in Chapter 3. Existing models for animal movement allow for directional persistence or spatially-varying directional bias, however, ant nests contain corridors of transit which result in fast local movement that cannot be modeled as directional bias since ants travel back and forth in opposite directions through these corridors. A novel spatially-varying stochastic differential equation model is proposed which captures directional persistence, spatially-varying directional bias, and spatially-varying overall movement rate via a motility surface. The motility surface is able to capture the higher relative motility in the chambers of the nest used for transit. Additionally, simulated trajectories from the fitted model provide insight into the rate of spread of agents through the nest.

In Chapter 4, the spatially-varying stochastic differential equation model is expanded to allow for temporal variation in movement behavior and behavioral interactions between nearby ants. Temporal variation is modeled via discrete latent states which allow for resting and active behavior. Dependence in the behavior of nearby individuals is modeled using covariates for the state transition probabilities that depend on the location and latent behavioral states of other ants. Results for the carpenter ant data reveal a variety of behavioral interactions. For example, moving ants tend to copy the latent behaviors of other nearby individuals and all ants have a decreased probability of switching behavior near the queen. The latent behavioral interaction framework allows the inclusion of complex movement models while the ants are in certain behavioral states. We use the model presented in Chapter 3 to capture the spatially-varying behavior of ants while they are active.

5.2 Plans for Future Research

In this Section, potential directions for future research will be discussed.

5.2.1 Improving Computational Efficiency

One of the primary weaknesses of the proposed models involves the computational burden of inference. As technology improves, observations of a larger number of animals at a finer time scale and over longer periods of time will result in larger and larger data sets. As such, computational efficiency in animal movement
modeling will become increasingly important. Therefore, developing computational algorithms for more efficient inference is essential. One method that holds potential to improve computational efficiency, particularly for the dynamic model with point process interactions, involves particle based methods (Andrieu et al., 2010). Particle MCMC methods often allow for efficient estimation of ratios of normalizing constants (Del Moral et al., 2006). However, the use of these methods for the DPPI model is not straightforward as the exact marginal distribution for the latent states of an individual is not available in closed form. Particle MCMC methods could also be used to improve the computational efficiency of the models presented in Chapters 3 and 4. Such methods may improve the convergence rate of the Markov chains, as high-dimensional proposal distributions can be used to update correlated variables (Andrieu et al., 2010).

The computational complexity of the models presented in Chapters 3 and 4 is driven by the large number of latent variables (velocities $v_{i,j}^{(x)}$, $v_{i,j}^{(y)}$ and states $s_{i,j}$). If the latent speeds and the latent states were known a priori, the computational time needed for inference would be significantly reduced. To explore this concept, the order of the number of floating point operations for one iteration of an MCMC algorithm with respect to number of observed individuals ($J$), the number of observations of each individual ($T$), and the total number of basis functions for the surfaces ($B$), is presented in Table 5.1.

<table>
<thead>
<tr>
<th>Number of Knots</th>
<th>$O$(number of operations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimate States and Estimate Velocities</td>
<td>$J^2T^2 + JT^2B + JT^2B^2 + B^3$</td>
</tr>
<tr>
<td>Estimate States and Fix Velocities</td>
<td>$J^2T^2 + JT^2B^2 + B^3$</td>
</tr>
<tr>
<td>Fix States and Estimate Velocities</td>
<td>$JT^2B + JT^2B^2 + B^3$</td>
</tr>
<tr>
<td>Fix States and Fix Velocities</td>
<td>$JT^2B^2 + B^3$</td>
</tr>
</tbody>
</table>

The order of complexity of the MCMC algorithms presented in Table 5.1 reveals that the computational burden grows the fastest with the number of basis functions used for the surfaces $O(B^3)$. This may cause issues if there are complex spatial surfaces that contain high-resolution features such as the boundaries in the environment. Through the use of semi-parametric spatial surfaces, as in Chapters 3 and 4, known environmental features can be incorporated directly in the model to avoid the additional computational complexity caused by using large numbers
Table 5.2: Computational Efficiency and Surface Resolution

<table>
<thead>
<tr>
<th>Knots</th>
<th>Number of Basis Functions ($B$)</th>
<th>Time (Hours)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 x 6</td>
<td>81</td>
<td>1.60</td>
</tr>
<tr>
<td>12 x 12</td>
<td>225</td>
<td>1.77</td>
</tr>
<tr>
<td>18 x 18</td>
<td>441</td>
<td>3.06</td>
</tr>
<tr>
<td>24 x 24</td>
<td>729</td>
<td>7.74</td>
</tr>
</tbody>
</table>

of basis functions.

To highlight the impact of the basis function specification for surface estimation, model parameters are estimated for a simulated data set keeping all values constant except the number of basis functions used to estimate the surface, $B$. The time needed to perform 5000 iterations of an MCMC algorithm using one core for computation is presented in table 5.2. The results indicate that increasing the number of basis functions does not impact the computational complexity when the number is kept fairly small. However, increasing the number of knots used past a certain point can cause a computational burden. Thus, selection of the number of basis functions to utilize involves a trade-off between computational complexity and the desired resolution of the estimated spatial surface and should be carefully considered on a case by case basis.

If the number of basis functions is set to a relatively small value, the complexity in estimating all latent variables is on the order of the product of the square of the number of observed individuals with the square of the number of observation times. This is driven by the pairwise interactions between the ants. If the latent states are known, the complexity can be decreased. The computational complexity can be further reduced to be linear with respect to both the number of ant and the number of observations if the latent states and the latent velocities are fixed.

Estimating the latent variables also impacts the convergence of the Markov chain. Thus, to determine the overall impact of estimating latent variables on inference we consider the effective sample size under several scenarios. Effective sample size approximates the number of independent draws that are obtained from a posterior distribution (Lenth, 2001). Thus, we generate simulated data examples and perform inference in order to test the impact that estimating latent states and velocities has on the required computation time. The number of basis functions, and the number of individuals have been fixed ($B = 225, J = 10$). As the number
of observations $T$ is increased, the total time taken to generate 5,000 posterior draws, and the effective samples generated per second are plotted in Figure 5.1. The results indicate that estimating the latent states and velocities clearly increases the time needed for inference. The plotted values of the time needed for computation indicate that estimating the latent states is more burdensome than estimating the latent velocities as the number of observations increases. However, calculation of the effective sample size per second indicates the opposite, as estimating the latent velocity actually has more of a detrimental impact on the overall computational complexity for inference. Overall, the computational burden of inference should be considered on a case by case basis, as it is problem specific.

Table 5.1 and Figure 5.1 together indicate computational efficiency of inference for the models presented in Chapters 3 and 4 can be improved by approximating the latent states and velocities. For example, estimating the latent behavioral state a priori via empirical velocities and fixing the latent states at these estimated values would provide significant improvements in computational efficiency. Fixing these behaviors, however, requires selection of a specific rule for assigning states. Developing an effective method to estimate these states a priori would reduce the computational burden. Fixing the behavioral states would also remove the need to update latent transition covariates. This would facilitate the use of parallel computing (Grama, 2003) to update each observed individual on a separate processor.
5.2.2 Potential Model Extensions

The ant movement experiment provides a rich set of data to study novel movement models and answer scientific questions regarding social structure and disease dynamics. In ant colonies, individuals interact with each other in several ways. Ants share food via trophallaxis, they clean foreign residue from other ants, and they use antennation to signal other members of the colony. These interactions can be difficult to differentiate from ants that are simply resting near each other in a certain region. In future work, I would like to develop a model that accounts for these types of interactions between ants. This behavior may be captured by a model which incorporates additional discrete behavioral states for interactions. These interactions are partially observed in the data, as trophallaxis between individuals in the nest has been recorded. Dynamic interaction networks (Scharf et al., 2015) could be used for transitions between behavioral states. While interacting, potential surfaces for interacting particles will be used to model attraction to specific ants.

Potential surfaces have been used to simulate interactions in self-propelled particle systems (Levine et al., 2000). Flocking behavior is generated in simulated examples by utilizing functional correlation, attraction and repulsion. The ants observed in the colony do not flock or herd, however they interact during trophallaxis (Gracia et al., 2014). I will develop attraction and repulsion potential surfaces that generalize those used in the simulation study of Levine et al. (2000) to account for social interactions between ants. Additionally, Levine et al. (2000) are only interested in simulation, while we will model interaction behavior and use observed ant movement to estimate interaction parameters.

To model interactions using potential surfaces, the potential surface of each ant, denoted $U_j$, must be distinct. Levine et al. (2000) suggests two different types of interaction functions, the first results in exponential decay of the interaction force,

$$U_j(x_{t,1:j}, y_{t,1:j}) = \sum_{j \neq k} C \exp(-d_{jk}/L)$$

where $d_{jk}$ represents the Euclidean distance from ant $j$ to ant $k$ (to avoid intractable normalizing constants and facilitate inference, ant $j$’s location is approximated by its previous location), $C$ controls the strength of the interaction, and $L$ controls the range of the interaction. As $d_{jk}$ approaches 0, the height of the interaction
surface grows, and the negative gradient pushes the ants apart. This generates
a repulsion effect. As \( d_{jk} \) increases, the height of the interaction surface value
shrinks at a decreasing rate, indicating a repulsion that diminishes with the distance
between individuals. An alternative formulation for an interaction function for two
interacting ants, \( j \) and \( k \), which has a 'hardcore' range is

\[
U_j(x_{t,jk}, y_{t,jk}) = \begin{cases} 
C_{hc}(d_{jk} - L_{hc})^5 & \text{if } d_{jk} \leq L_{hc} \\
0 & \text{if } d_{jk} > L_{hc}
\end{cases}
\]

where \( C_{hc} \) controls the strength of the interaction, and \( L_{hc} \) controls the range of the
attraction. The power is set to 5 as an example, but other values can be used. If
the distance between two ants is always greater than \( L_{hc} \), they move independently.

To account for both repulsion at small scales, and attraction at intermediate
scales, two different interaction functions can be combined. For demonstration, we
will use the exponential decay repulsion surface for both. The resulting interaction
surface is

\[
U_j(x_{t,1:J}, y_{t,1:J}) = \sum_{k \neq j} C_r \exp(-d_{jk}/l_r) - \sum_{k \neq j} C_a \exp(-d_{jk}/l_a)
\]

where \( C_r \) and \( L_r \) control the strength and range of repulsion, respectively; and \( C_a \) and \( L_a \) control the strength and range of attraction, respectively. We require
\( L_a > L_r \), so that the range of repulsion is smaller than the range of attraction.
Combining this attraction-repulsion surface with the spatially-varying potential
surface presented in Section 3.3.2 yields an aggregate spatially-varying potential
function with interactions

\[
H^*_j(x_{t,1:J}, y_{t,1:J}) = H(x_{t,j}, y_{t,j}) + U_j(x_{t,1:J}, y_{t,1:J}).
\]

An example of these functions is given in Figure 5.2. The object being interacted
with is at \( x = 0.5 \), denoted by a black circle. The spatially varying potential
surface, \( H(x_{t,j}, y_{t,j}) \), chosen here to be a quadratic potential centered at 0, the
interaction surface, \( U_j(x_{t,1:J}, y_{t,1:J}) \), which uses exponential decay for attraction
and repulsion, and the combination, \( H^*_j(x_{t,1:J}, y_{t,1:J}) \), are plotted. Incorporating
the motility surface, presented in Section 3.3.3, and the regression framework for
interacting behavioral states, presented in Section 4.3.2, with spatially-varying and
An example of a spatial potential surface $H(x, y)$, an interaction surface $U(x, y)$, where the interaction is with an object located at $x = 0.5$ denoted by a black dot, and the combined potential surface for another un-plotted ant $H^*(x, y)$.

interacting potential surfaces will result in a flexible model that captures many features of complex animal movement patterns including the movements of ants within a nest.

The applications studied in this dissertation are all laboratory experiments in which the temporal rate of observation is frequent. Many experiments that track the movements of animals in nature, however, observe animal locations less often. To analyze such movement data, locations are often imputed to fill in temporal gaps. The most commonly used method for imputation is the Brownian bridge model for animal movement (Horne et al., 2007). Brownian bridges, however, fail to capture directional persistence. Developing novel imputation methods, such as an Ornstein-Uhlenbeck bridge (Chen and Georgiou, 2016), for animal movement that are better suited for imputing locations and accounting for temporal autocorrelation would be beneficial. Bayesian methods for model comparison, model diagnostics, and methods for incorporating covariance in multi-dimensional credible regions can be expanded upon and applied to each of the proposed models. Other directions for
future research include variable selection for covariates in the transition probabilities between latent behavioral states, modeling behavioral transitions in continuous time, and developing methods for inference that are accessible to applied researchers.
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Manuscripts

• Russell, J., Hanks, E., Haran, M., Hughes, D. "A spatially-varying stochastic differential equation model for animal movement" *in review*
• Gracia, E.S., de Bekker, C., Russell, J., Manlove, K., Hanks, E., Hughes, D.P. "Within the fortress: a specialized parasite of ants is not evicted." *BioRxiv*, 1-13. *in preparation*