

ABSTRACT

TRAUD, AMANDA LYNN. Animal Social Networks and Movement. (Under the direction of Dr. Alun Lloyd and Dr. Robert Dunn).

Studying animal social systems can provide valuable insight into the mechanisms behind animal population behaviors and inform scientists about the evolution of social structures in humans. We use social network analysis to discover whether animal networks are capable of serving as a suitable proxy for human contact networks. Finding this information has many ramifications for its use, including the spread of pathogens or being able to stop such spreading. To this end, we study the interactions of colonial animals, or animals that live in colonies such as prairie dogs (*Cynomys gunnisoni*) and ants (*Formica subsericea*).

In our study of prairie dog social networks, we examine how social network analysis techniques can be used to find important individuals and uncover the macro-structure. This then allows for the comparison of current prairie dog study techniques to social network analysis findings. We discover a high correlation between macro-structure found with social network analysis and current prairie dog social group classification. The social network techniques require far fewer data. Comparing macro-structure to prairie dog behavior, we discover no correlation thus groups of prairie dogs contain a mixture of behaviors. Key individuals are identified in each prairie dog social network. These key individuals have significant implications for disease spread and communication channels.

One way we study ant social structure is by examining how the ant queen's presence affects ant social networks. To ascertain whether the queen affects the structures of ant social networks, we compare networks with a queen to networks without, individual network

measures for queens to individual network measures for workers, individual network measures for workers in a network with a queen to those for workers in a network without a queen, and then compare the networks with and without queens to standard network models. While the queen is highly important to colony survival, the queen does not significantly affect global ant network structure. The queen is found to have a local network that is significantly different from that of workers. Like many human contact networks, both networks with queens and networks without are classified as Small-World networks, with networks with queens having a higher similarity to Small World networks than the networks without.

We also study ant social structure by examining how ant network structure changes over time, i.e. collecting and analyzing dynamic ant social networks. These data are also used to ascertain whether ants have preference to their associations, or friends. With this data, we create and present a method for finding the appropriate network observation window. We discover ants have preferred associations and that the accumulation of ant interactions approach a stable density.

As movement affects location and therefore affects the availability of individuals for interaction, we model ant movement. Ant trajectories are collected using the methods outlined in Appendix A and analyzed to produce movement models. Ant movement is highly complex: ants are discovered to have multiple ant step length categories, multiple states of movement, and different movement behavior based on individual location.

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Animal Social Networks and Movement

by
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A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Biomathematics

Raleigh, North Carolina

2017

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DEDICATION

This dissertation is dedicated to my wonderful family: my husband, my parents, my siblings, my in-laws, my Biomath family, my Cybraics family, and my cats.

BIOGRAPHY

Amanda Lynn Traud was born in Greenville, NC on December 13, 1984. After going to school in Washington, NC up to third grade, her mother pulled her and her brother out of school and homeschooled them both for the next five years due to the quality of education being received in public school. It was during this period of homeschooling that Amanda became interested in science. Amanda's father worked for ECU School of Medicine and opened her eyes to the possibilities of being a scientist. Homeschooling allowed Amanda a flexible schedule to visit museums, play outside at all hours, and read many many books. She participated in Girl Scouts and 4-H, and both programs allowed her to explore the sciences. Amanda started working towards the goal of becoming a marine biologist, attending marine ecology 4-H camp, but kept an open mind and also attended 4-H Electric Congress. During high school, Amanda was given the opportunity to participate in Summer Ventures, a science and math summer program for gifted rising juniors and seniors. During that summer, Amanda found that she both enjoyed the collection of samples from streams and the programming of computers to calculate descriptive statistics for her group's experiments. Amanda discovered she had a knack for math the next year, when she took Trigonometry at Fuquay Varina high school. Amanda also realized that year that marine biology might not be the right path for her when asked to dissect a shark in Marine ecology class. During her last years of high school, Amanda met her lifetime partner in crime, Ron Traud. After high school, Amanda pursued a bachelor's degree in Computer Science while working part time to pay her tuition. After taking Java, Amanda changed majors from Computer Science to Business to become an event planner, because she found she had a

knack for collecting data and logically organizing it. During her Business degree, she found while she was making good grades, she was most excited about attending her math classes. Amanda changed her major to applied mathematics after taking Calculus 2 for fun. Amanda transferred to UNC for her last two years of her degree and started doing undergraduate research with Dr. Peter J. Mucha on Facebook. Network science and the study of connections between individuals became Amanda's favorite tool in her toolbox. Amanda pursued her Masters in Applied Mathematics at UNC extending from Facebook studies to looking at networks of HIV transmission, neurons in *C. elegans* and creating new tools to visualize macro-structure in networks. After defending her masters in 2010, Amanda started her PhD at NC State University in Biomathematics under the direction of both Dr. Alun Lloyd in Mathematics and Dr. Robert Dunn in Biological Sciences. Amanda started a Data Scientist position at Data Tactics in Washington, DC in late August 2014. Amanda served as a Data Scientist on a government contract using network science to find anomalies in cyber data for 1.5 years. Amanda currently uses data science to create analytics to analyze cyber data as a Senior Data Scientist for Cybraics, Inc in Washington, DC.

ACKNOWLEDGMENTS

I am indebted to my advisors, Dr. Alun Lloyd and Dr. Rob Dunn, for putting up with my shenanigans, helping me grow as a scientist, and giving me invaluable advice for the past seven years. I am grateful to my committee members, Dr. Kenneth Pollock, Dr. Jules Silverman, and Dr. David Tarp, for giving wonderful advice and being patient with me. I also am grateful to so many others. To my husband, for listening to me rant and rave, listening to practice talks, reading my writing, and supporting me both emotionally and financially during this degree. To my mom, for listening to me, letting me call almost every day, and reading my work. To the Dunn Lab for listening to my practice talks, attending my presentations and workshops, going ant hunting, and editing my writing. To Carl Guiffre for helping me to get the tracking software off the ground. To Eleanor for teaching me to paint ants, and Dr. Silverman for letting me use his lab. To Jessica, Michael, Amy, Megan, Meagan, and Tim for reading and editing at the last minute. To Jessica, Jake, Michael, Kaska, Tim, Kelsey, and Greg for being there to talk over coding ideas with and problem solve. To Dr. Mike Carter, Dr. Meagan Kittle Autry, and all the members of the dissertation support group for their suggestions and support. To my undergraduate, Adrianna, for all the ant hunting and keeping help. To Dr. Peter J. Mucha for getting me excited about networks in the first place. To my dad for sparking my love of science. I am also grateful to the following for funding me: Statistical and Applied Mathematical Science Institute Complex Network Fellowship, NC State Mathematics Department and a NASA Biodiversity Grant (ROSES-NNX09AK22G)

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CHAPTER 1: Introduction

Background

Social network analysis (SNA), the study of individuals and their connections to each other, is a dynamic tool applicable to a variety of problems. In the recent years, it has had much advancement in both quantitative methods and study systems (Newman, 2003). The branch of mathematical study known as graph theory was established as early as 1736, and it is from this that the idea of SNA was born (Biggs, Lloyd, & Wilson, 1986). SNA was then further developed and perfected by sociologists and psychologists who used to study human interactions in the first half of the 20th century (Scott & Carrington, 2011). Since then, scientists have used SNA to study many human social networks and gleaned insights to a variety of questions otherwise unsolvable. While SNA was originally developed to study human social networks, recently these methods have been extended to investigate animal social systems (Krause, Lusseau, & James, 2009).

Studying animal social systems can provide valuable insight into the mechanisms behind animal population behaviors and inform scientists about the evolution of these social structures. Colonial animals, such as ants and prairie dogs, live in large populations and rely on specific structures of social interaction for survival as each social interaction allows one animal to transmit information and/or pathogens to another (Newman, 2003). Thus, understanding how these networks are structured and how they are affected by outside stimuli will take us one step closer toward understanding the patterns of information and pathogen transmission and how they affect these creatures' survival. We extend upon recent

SNA work by studying both the structure of a prairie dog social network and the effects of stimuli on ant social networks.

Motivations

Understanding animal social networks and how these networks respond to stimuli is imperative to understanding how social creatures survive and flourish. Studying colonial species is one of the best ways for understanding these social structures as colonial animals rely on these specific structures to transmit communications as well as prevent the transmission of disease. Studying animal social networks allows us to identify key individuals, define social groups, and add to the general understanding of social network structures (Wey, Blumstein, Shen, & Jordán, 2008).

Motivation for Chapter 2

Prairie dogs live in various sized colonies, and individuals within each colony are further separated into social groups. Prairie dogs transmit information in complex ways, which include both verbal (barking) and tactile (snuggling and greet kissing) modes of communication. Using social network analysis techniques, we can identify these social groups with far fewer data than used in current techniques. Prairie dogs also live in diverse habitats and adapt quickly to changes in their environment. Due to their altruistic nature, each prairie dog takes on a different task, like predator watching and food gathering, and works together with others in its social group to survive in these habitats. These behaviors are easily observable to a potential experimenter. We can use social network analysis techniques to confirm whether groups are made up of a single behavior or mixed behavior types. Prairie

dogs also contract diseases, such as bubonic plague. We can also use social network analysis techniques to identify key individuals that could drastically affect this spread.

Motivation for Chapters 3, 4, & 5

Formica subsericea also live in colonies, but in colonies of thousands of individuals. They interact with each other to communicate, pass food, and transfer pathogens. Ants have individuals already defined as important to survival, like queens (Holldobler & Wilson, 1990). We can use social network analysis techniques to discover whether social structures are affected by these key individuals and examine whether network measures of importance match with environmental importance. Studying the movement of these ants is important as location and availability of individuals to interact with directly affects interactions. Creating models for this movement allows for the synthetic creation of much larger networks.

Dissertation Outline

In Chapter 2, in order to study the social structure of three prairie dog colonies, we use SNA techniques to find macro-structure in the networks and compare this macro-structure to social group classification. Through social network analysis, it's also possible for us to distinguish key individuals. In Chapter 3, we examine the effects of queen presence on ant social networks to answer a couple of questions. Do network measures differ between workers and queens? What about the conditions of the network between workers, with and without a queen's presence? We also compare the networks to existing network models to better understand the network structure. In Chapter 4, we take the analysis to another level, studying the dynamics on ant networks over time. We examine the accumulation of ant

interactions and model the progression of network structure. We devise a method for finding the observation window that best captures the full network structure and test whether ants have “friends”. Finally, in Chapter 5, we study ant path data, fitting stochastic movement models to observed data. These models can then be used to study how movement is affected by interaction and to create larger ant interaction networks. Appendix A contains a method chapter on tracking social insect movements.

CHAPTER 2: Key players and hierarchical organization of prairie dog social networks

By Jennifer Verdolin; Amanda L Traud; Robert Dunn¹

Introduction

In the study of social animals, there is growing interest in complex emergent properties of group structure. Social network analysis (SNA) has been increasingly used to study the social dynamics of animal systems (Bergmiller, Schrch, & Hamilton, 2010; Brent, Lehmann, & Ramos-Fernández, 2011; D. Lusseau & Newman, 2004; David Lusseau, 2003; Newman, 2003). It is a unifying conceptual framework that can be applied comparatively across all social taxa—from microbes to humans. Social networks can help to identify features of organisms that are indiscernible (or even invisible) based on studies of individuals or behaviors alone (Darren P. Croft, Krause, & James, 2004; D. Lusseau & Newman, 2004). In other cases, there exists substantial intra-specific variation among networks based, in part, on group attributes, individual differences, and ecological factors (Bhadra, Jordan, Sumana, Deshpande, & Gadagkar, 2009; Faust & Skvoretz, 2002; Guimares Jr et al., 2007; Madden,

¹ **Note:** This chapter has been accepted for publication to *Ecological Complexity*. Jennifer Verdolin and Amanda Traud are co-first authors. Jennifer Verdolin, a post doc at Nescent, collected all prairie dog data. Amanda Traud used and created code in R for analyzing all networks with social network techniques. Jennifer Verdolin, Amanda Traud, and Rob Dunn share equally in the writing of this chapter. Rob Dunn advised and funded this project.

Drewe, Pearce, & Clutton-Brock, 2009). Furthermore, differences in social networks, whether among taxa or social groups, almost necessarily lead to differences in the spread of diseases, decision making strategies, information or, in some cases, food, through networks (Darren P. Croft et al., 2004; Drewe, Madden, & Pearce, 2009; Hamede, Bashford, McCallum, & Jones, 2009; A. Jacobs, Sueur, Deneubourg, & Petit, 2011; Kasper & Voelkl, 2009; Madden et al., 2009).

A key challenge with SNA is how to relate their results to the much larger literature on social interactions that relies on other approaches to distinguish social groups. Before social network analysis became popular, literally hundreds of studies considered the social interactions and social groups of organisms using approaches based on field observation and informal clustering. Our understanding of the social systems of most organisms rests on such traditional approaches. Can the results from these earlier studies be related to those of social network analysis? This question seems to have not been well-considered, particularly in the social mammals where research has tended to divide social groups into hierarchical categories, constructed out of the existence of interactions among individuals but also the nature of those interactions and whether they are negative, positive, reproductive, relate to food sharing, or have some other defining features. The advantages of SNA are frequently highlighted (Proulx, Proulx, & Blouin-Demers, 2013; Sueur, Jacobs, Amblard, Petit, & King, 2011; Wey et al., 2008), but whether SNA builds on, replaces or conflicts with other approaches is unclear.

Gunnison's prairie dogs, *Cynomys gunnisoni*, are large, diurnal, highly social ground squirrels whose range is limited to the grasslands of the Colorado Plateau (Hall, 1959). Gunnison's prairie dogs colonies contain a variable number of territories occupied by distinct social groups, whose sizes ranging from 3-14 individuals (Travis, Slobodchikoff, & Keim, 1995; J. L. Verdolin & Slobodchikoff, 2010) akin to small groups of social insects (e.g., *Temnothorax albipennis*: (Dornhaus & Franks, 2006)), primate groups (Chapman & Chapman, 2000), or hunter gatherer societies (Hamilton, Milne, Walker, Burger, & Brown, 2007). Traditionally, ecologists have distinguished prairie dog social groups using behavioral and spatial observations of known individuals over time (King, 1955; Slobodchikoff, 1984; Travis & Slobodchikoff, 1993; J. L. Verdolin, 2007), with a strong emphasis on negative interactions, where negative interactions among individuals imply those individuals are from different social groups (Slobodchikoff, 1984; Travis & Slobodchikoff, 1993; J. L. Verdolin, 2007). The designation of the size of groups and the identity of individuals within also often incorporates data on mating behavior, and behavioral time allocation (e.g., time spent being vigilant versus feeding), and groups are composed of one or more females, one or more males, and juveniles (Slobodchikoff, 1984; Travis & Slobodchikoff, 1993; Travis et al., 1995; J. L. Verdolin, 2007). The resulting identification of distinct social groups within a colony can be robust with regard to individual interactions, but tends to result in a categorical classification of groups, in which individuals either are or are not members of groups and any patterning in social structure above or below the standard social group is either not described or, if described, is in terms of the behavior of individual organisms and their histories. If a

network-based approach to exploring the social dynamics of Gunnison's prairie dog—or any other organism—produces social groupings similar to traditional methods, social network analysis can add to the insights of traditional approaches in several ways.

Comparing social network properties among groups may highlight subtle variation in social structure not readily observable or quantifiable by conventional behavioral studies (Faust & Skvoretz, 2002; Traud, Kelsic, Mucha, & Porter, 2011a; Wolf, Mawdsley, Trillmich, & James, 2007). If groups detected using traditional behavioral approaches and social network are similar, SNA has the advantage of requiring far fewer data, simply who is interacting with whom, not the nature of each interaction. Network analyses can also reveal emergent properties of social groups, including identifying individuals with central roles—such as the dolphin social brokers—and characterizing variability in group cohesion or hubs, individuals (Bezanson, Garber, Murphy, & Premo, 2008; D. P. Croft et al., 2005; D. Lusseau & Newman, 2004; David Lusseau, 2003) who are connected to an unusually high number of other organisms. SNA may provide a method for testing the hypothesis that individuals may group together based on similarities, differences, or random associations (Galef & Laland, 2005; Pedersen, Krieger, Vogel, Giraud, & Keller, 2006; Pepper, 2000; Reader & Biro, 2010; Rendell & Whitehead, 2001; Ross, 2001).

Here, we generated social network matrices using data on positive social interactions of Gunnison's prairie dogs (*Cynomys gunnisoni*). We then used community detection analysis to discern social groups from the networks and compared them to social groups identified by traditional behavioral approaches (Traud, Kelsic, Mucha, & Porter, 2011b). Next, we used

SNA to examine whether there were features of Gunnison prairie dog social behavior detectable only through SNA or behavioral studies alone. In addition, we tested whether, as in dolphins and other social organisms, individuals serve to connect social groups with no other connections (bridges) or disproportionately connect individuals within social groups (hubs) (D. P. Croft et al., 2005; Gero, Gordon, & Whitehead, 2013; Madden et al., 2009; Naug, 2008), and whether there were biological or environmental predictors of who was a bridge or a hub. Finally, we used the SNA method to compare the social network groups to traits of individual prairie dogs within each network to ask whether social groups differed in their behavioral traits.

Methods

Study area

A detailed description of live-trapping, handling, and marking methods are available in (J. L. Verdolin, 2007). A Scientific Collector's Permit (Arizona Game and Fish Permit no. SP742094) was obtained prior to trapping and all procedures were in compliance with Stony Brook University IACUC (IACUC no. 2009-1745, Stony Brook University). Individuals were trapped with veterinary supervision from mid-February (upon emergence from hibernation) through August at two colonies, Country Club (CC) (Figure 1) and Humane Society (HS), with two 1 ha-plots delineated per colony and separated by road. These distinct plots are referred to as CCI, CCII and HSI, HSII, respectively. For our purposes we consider these to be separate populations, as individuals from each plot within a colony did not co-mingle. AVID® identification microchips were implanted subdermally in all captured

animals for permanent identification. Individuals were also marked with black Lady Clairol® semi-permanent hair dye for visual identification. Data for the analyses presented here are based on data from March-August 2004 and reflects data collected from mutually exclusive social groups on HSI, HSII, and CCI.

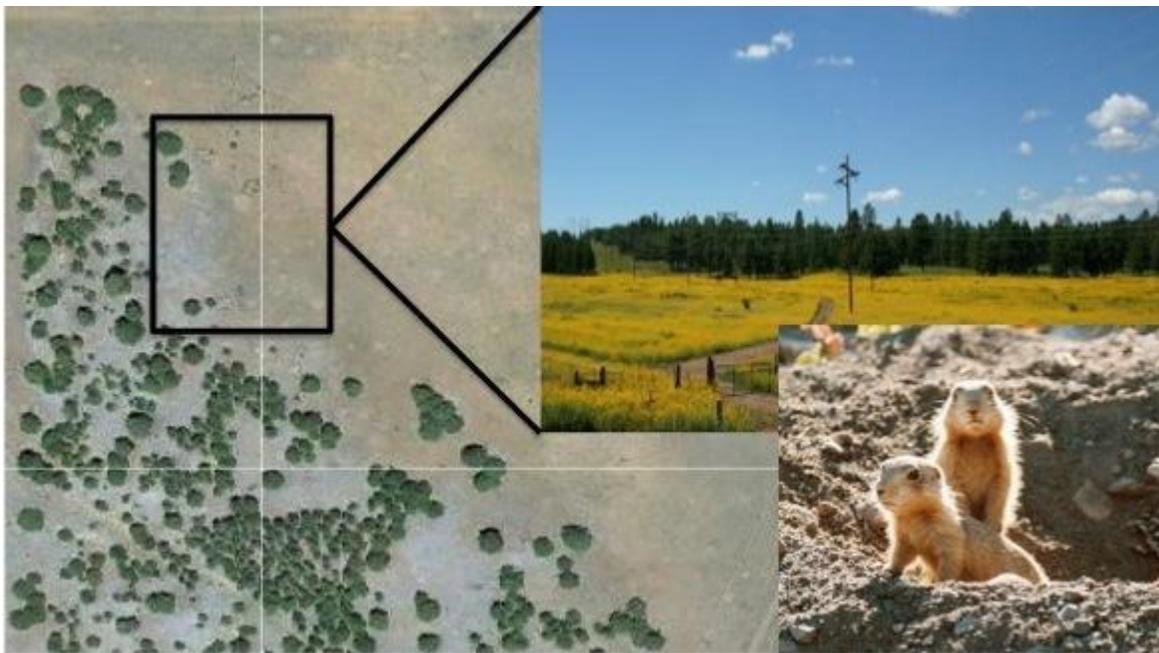


Figure : Map of one of the prairie dog colonies, Country Club I with inset of habitat photo and inset of prairie dog photo from the colony.

Data and Analysis

For each population, behavioral observations were made alternately in the morning from 0700-1000 and afternoon from 1500-1800, during the times when prairie dogs were most active (Longhurst, 1944). With the exception of days when trapping occurred, observations were made at least every other day at each plot from March 7-August 15, 2004, for a total of

396 hours of observation. Prairie dogs that consistently exhibited mutually tolerant behaviors with one another, such as greet-kisses and co-feeding, were assigned to the same social group (J. L. Verdolin, 2007).

Social group membership using traditional methods was determined on the basis of a dataset that included: 1) the home range overlap of individuals, 2) all occurrences of a mutually tolerant positive interactions such as greet-kissing and co-feeding (within 1 meter of each other), and 3) all occurrences of aggressive interactions, which was any interaction that resulted in fights or chases. Because aggressive interactions are infrequent (e.g., 0.016 events/hour among males), and rarely occur within a social group (N=5 in 396 hours of observation), aggressive interactions are typically used to determine who does *not* belong to the social group (J. L. Verdolin, 2007). This approach is similar to aggression trials used to discern, for example, the boundaries of ant colonies (Vásquez & Silverman, 2008) and followed common behavioral sampling approaches for social vertebrates (Altmann, 1974; Hinde, 1976).

To obtain data on the composition of social groups within each study population, behavioral observations included focal sampling, scan sampling and all occurrences sampling (Altmann, 1974). Focal samples were conducted for 5 min. During the focal sample, the location of the focal animal and all occurrences of social interactions were recorded. Four such focal samples were taken in sequence, then every 30 min a scan sample was used to record the location of each above ground animal within the study plot. Active individuals were chosen at random for observation, with the qualification that no individual was observed more than once

in a daily time block. During the observation period, each focal sample was recorded using a Sony Digital camcorder. Videos were later analyzed by JLV to extract data, with the behavior of the focal animal recorded every 5 seconds. We used vigilance, feeding, and moving behavior in our analyses. Vigilance behavior included both posting and scanning, where posting is a stationary bipedal alert posture and scanning is quadrupedal scanning of the environment with the head above a 90° angle (Jennifer L. Verdolin & Slobodchikoff, 2002). Feeding was defined as actively consuming a food item and moving was measured as movement from one location to another. The proportion of time that the focal animal spent engaged in each behavior was then calculated. In the case of multiple observations of the same individual, the average time spent in each behavior was calculated. In addition, we calculated trappability, which was the proportion of times an individual was trapped given the trapping period.

A total of 220 focal samples for 80 prairie dogs were collected. In addition, a total of 5, 5, and 4 social groups were identified using behavioral observations and spatial locations for populations HSI, HSII, and CCI, respectively. Given the low rate of agonistic interactions, we wanted to assess whether we could determine group membership using SNA solely on the basis of greet-kissing (positive interaction) among individuals. We did not include CCII in the analyses because an insufficient number of focal samples were made on prairie dogs in that colony to include them in the behavioral analysis. Two additional social groups on CCI were not included because they were primarily determined by spatial location and the number of interactions was insufficient for this analysis.

We detected and analyzed social networks using a community detection approach. Although, SNA has been used recently for a variety of social organisms, its application has focused primarily on individual measurements or full network measurements. When SNA methods are used to find intermediate (within network) structure in the full networks, these methods are referred to as community detection (Leu, Bashford, Kappeler, & Bull, 2010; D. Lusseau & Newman, 2004; David Lusseau, 2003; Maryanski, 1987). The use of community detection techniques in the analysis of social networks has recently gained traction (Porter, Onnela, & Mucha, 2009). Often network structure is not obvious by simply looking at a list of interactions, or a resulting graph of interactions. Community detection permits a researcher to identify social groups by discerning which individuals in the network have more connections to the other individuals within the group than to individuals outside the group.

We used the number of greet kisses recorded over a period of six months, which is to say we considered a subset of the data available from field observations of these prairie dogs, excluding all behavioral observations except for data on who greet-kissed with whom and how often (see above). Although a fine-scale temporal (e.g., monthly) analysis of social network structure would have been desirable, the frequency of positive interactions was too sparse to permit this approach. Based on these data, we created a matrix for each site where all individuals are listed on both the horizontal and vertical axes and each entry in the matrix became the integer corresponding to the number of interactions between each pair of prairie dogs. Then, the matrix was fed into R, and using the `igraph` library we detected social

network communities using multilevel community detection (Blondel, Guillaume, Lambiotte, & Lefebvre, 2008). This algorithm is a modularity-maximizing algorithm. Modularity is a measure of number of ties within a group minus the expected number of ties within that group given the network. This process works in two steps, which are then iterated, where each prairie dog is first placed into its own community and each community's neighbors are then checked to see if merging two communities results in a gain in modularity. The second step of this algorithm is to treat each community as an individual prairie dog, summing ties within the community to make a weighted self-loop and then summing ties between communities to make weighted ties. The first step is then repeated with this new network. This process is iterated until no gains in modularity can be made. The resulting set of communities then has optimal modularity.

In many studies, once communities are identified through SNA, traits of individuals are then compared to those communities to test for non-randomness among communities. For example, Traud et al. (2011) tested for communities in the Caltech 2005 Facebook network. The traits of users were then compared within and among communities where it was found that users are most likely to be in groups of friends by House, or dormitory (Traud et al., 2011b). We took advantage of this approach to test whether social network communities predicted traditional behavioral groups. To compare these two sets of classifications, we first calculated the Rand similarity coefficient in Equation 1 for the pair of classifications (Rand, 1971).

$$r = \frac{w_{00} + w_{11}}{M}$$

where, M was the total number of pairs of prairie dogs in the colony, $\frac{n(n-1)}{2}$, n being the total number of prairie dogs in the colony we were testing, w_{00} was the number of pairs of prairie dogs, where both prairie dogs were in different communities and in different social groups, w_{11} was the number of pairs of prairie dogs where both prairie dogs were in the same community and both prairie dogs were in the same social group.

We then compared the Rand coefficient to the distribution of possible Rand coefficients using randomization tests (Edgington & Onghena, 2007). This allowed us to empirically calculate the p-value corresponding to the degree of matching between communities and social groups (Edgington & Onghena, 2007) (Table 1).

Table 1: The number of identified traditional behavioral social groups was fewer than the number of Social network communities based on SNA; most social groups include > 1 communities (see Figure 1). P-values are based on the Rand similarity coefficient

Colony	# Traditional behavioral groups	# Social network communities	P-value
CCI	4*	8**	P<0.001
HSI	5	5	P<0.001
HSII	5	6	P<0.001

Due to the slightly biased nature of the distribution of Rand coefficients for these small networks, we used randomization tests as opposed to z-scores, which assume a normal distribution of Rand coefficients. P-values were calculated empirically using Monte Carlo simulations. To find the p-values for each Rand statistic, we iterated n (10,000) times, randomizing the communities and calculating the Rand statistic for the random communities paired with the actual social groups. We then calculated the number of times (r) that we got a Rand statistic larger than the Rand statistic for the actual social network communities and the

social groups. The approximate p-value is then calculated as $(r+1)/(n+1)$ (North, Curtis, & Sham, 2002).

To test for differences in behavioral traits among the communities we used the proportion of time an individual spent being vigilant (e.g., posting, scanning), feeding, moving (Loughry, 1992; Jennifer L. Verdolin & Slobodchikoff, 2002), and trappability. We separated the different behavior and trappability scores for each behavior into categorical variables from the quartiles for that behavior. We compared communities to prairie dog behavioral traits using Rand Similarity coefficients and randomization tests in the same manner as described above, see also (Traud et al., 2011b).

We present a description of degree centrality and betweenness centrality for the communities and identify key individuals that act as hubs (individuals who disproportionately connect individuals within social groups) and/or bridges (individuals who serve to connect social groups with no other connections). Both degree centrality and betweenness centrality are measures of the importance of an individual in a given network (Opsahl, Agneessens, & Skvoretz, 2010). Degree centrality is the number of interactions each individual participates in and we used it to classify hubs, or individuals with a significantly higher degree centrality than the rest of the network they were a part of. Prairie dogs with a significantly higher degree centrality were classified as hubs. Individuals with a degree centrality outside the range of 95% of the degree centralities of the network were regarded as hubs. Betweenness centrality is a measure of the number of paths that are required to pass through a prairie dog to get from one prairie dog to all other prairie dogs in the network and

uncovers individuals that act as bridges between communities that would otherwise be unconnected. We measured betweenness centrality to quantify whether or not a prairie dog acts as a bridge between networks. Prairie dogs with a significantly higher betweenness centrality than the rest of the prairie dogs in the network were considered bridges. We calculated significance for betweenness centrality similarly to that of degree centrality: individuals with a betweenness centrality outside the range of 95% of the betweenness centralities for that network are classified as bridges. We tested whether hubs and bridges occurred more than expected at random by simulating random networks with the same number of prairie dogs and the same number of interactions and then calculating the number of hubs and bridges for this distribution of networks. We then calculated the p-value for the empirical number of hubs or bridges. For these p-values, we used a similar process to the one described above for the p-values associated with Rand coefficients, only we used a random network each iteration instead of the randomized communities. Lastly, we tested whether degree centrality and betweenness centrality were correlated with age, sex, and group size using a generalized linear model (GLM) in JMP Pro 10 ® (Dryad doi: to be added).

Results

Network analysis resulted in three different weighted networks, where each connection between a pair of prairie dogs was weighted by the number of interactions between the prairie dogs in that pair (Figure 1). Overall, CCI, HSI, and HSII, consisted of 46, 32, and 47 prairie dogs respectively, and had average contacts of 4, 3.56, and 3.57 per prairie dog respectively.

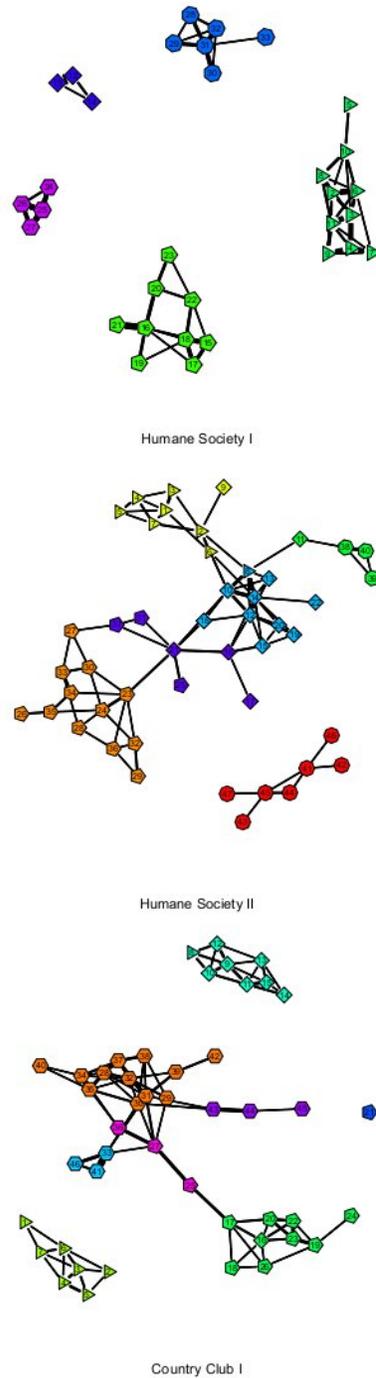


Figure 1: Interaction networks for the three prairie dog colonies analyzed in this study. Shapes indicate the social group and colors indicate the community. Thickness of lines between shapes indicate number of interactions between prairie dog pairs (Colors indicate groups based on network analysis, shapes indicate groups based on traditional behavioral approaches, color and shape groups are similar indicating a good match between social network communities and traditional behavioral groups (numbers identify specific individuals)).

For each of the three colonies, the Rand coefficient similarity values for community and group assignments were significantly different than random ($P < 0.001$), indicating agreement between social groups identified using SNA and those identified using traditional methods. However, with the exception of HSI, SNA detected additional social groups thereby uncovering subgroups (Table 1).

When testing for similarities in behavioral traits across social groups derived from SNA, we found general differences in behavioral traits among social groups within each of the plots. The Rand similarity coefficient suggested that, in both CCI and HSI, individuals within social groups were more similar to each other in the proportion of time spent feeding, however only HSI was significant ($P = 0.01$). No other behavioral trait showed significant non-random assortment among communities, although HSII indicated a trend for the proportion of time spent being vigilant (Table 2).

*Table 2. P-values for the comparison of social network communities to the observed prairie dog behavioral traits where *= $P < 0.1$ and **= $P < 0.05$*

Network	Trappability	Vigilance	Feeding	Moving
CCI	0.20	0.77	0.09*	0.14
HSI	0.17	0.18	0.01**	0.91
HSII	0.62	0.08*	0.95	0.19

Across all three plots, we identified key individuals that acted as hubs within the network and individuals that were bridges between groups. In CC1, individuals 30, 31, and 32 were quantified as hubs (having a significantly higher degree centrality than the rest of their network), with the numbers of contacts for these individuals being 9, 9, and 8

respectively compared to the average of 4 (± 1.96 SD). On HS1, only one hub was present, individual 11, with 7 contacts compared to the network average of 3.56 (± 1.63 SD). Lastly, HS2 had 3 hubs, individuals 10, 12, and 14, with contacts numbering 8, 9, and 10 respectively compared to a network average of 3.57(± 2.12 SD). CCI had significantly more hubs than expected at random (CCI: $P=0.05$) while HSII and HSI did not (HSII: $P=0.07$; HSI: $P=0.39$).

Another important characteristic found in these networks was the existence of bridges. In CC1, prairie dogs 17, 25, 27, and 30 were identified as bridges (Figure 2). The average betweenness centrality for this network is 29.37 (± 51.57 SD), while the betweenness centralities for these prairie dogs are 168, 180, 194.8 and 171.5 respectively. HSI had only one bridge, prairie dog 16. The average betweenness was 3.63 (± 5.29 SD), while this individual's betweenness was 21.8. Similarly, on HS2, individuals 10 and 21 were bridges, with values of 242.6 and 381.5 respectively, while the average betweenness for the network was 52.92(± 76.45 SD). Simulation results revealed that CCI had significantly more individuals that were bridges than expected by random chance alone (CCI: $P=0.009$). In contrast, the number of bridges on HSI and HSII was not significantly different from random (HSI: $P=0.14$; HSII: $P=0.64$).

We found that age, sex, group size, and age*sex interaction were not significant predictors of degree centrality (GLM: whole model: $R^2=0.04$, $F_{4, 120}=1.21$, $P=0.31$) or normalized betweenness centrality (GLM: whole model: $R^2=0.03$, $F_{4, 120}=0.89$, $P=0.47$). Although there was no clear pattern of relationships between any of these variables and who

was a hub (degree centrality) or bridge (betweenness centrality) there was variation among individuals across colonies (Figure 3a,b). Interestingly, of the 7 identified hubs, 4 were female and 3 were male. In contrast, all 7 individuals identified as bridges were female.

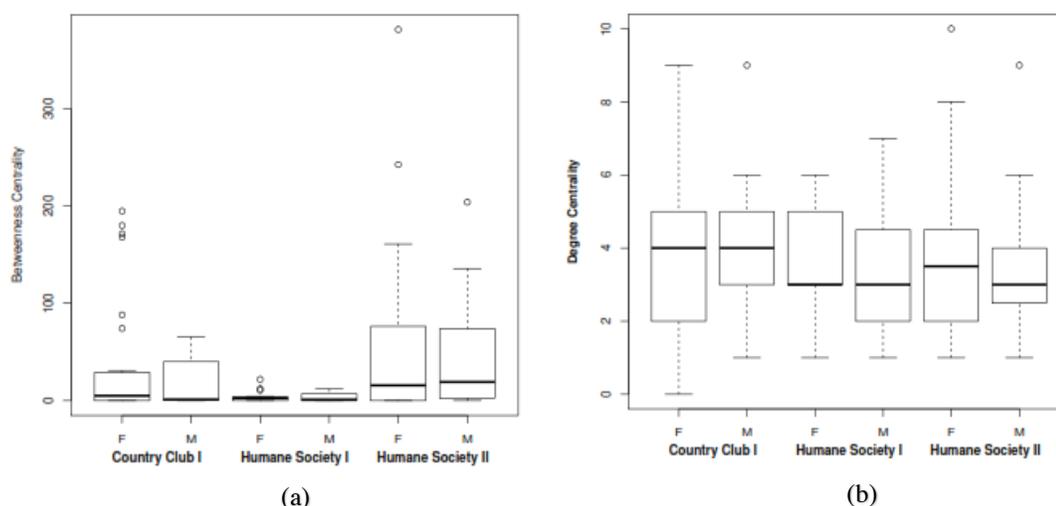


Figure 2(a) Betweenness centrality quartiles for all colonies separated by both colony and sex. The betweenness centrality plots show very low variability between quartiles of betweenness centrality values for each sex within each colony. CCI had four female outliers matching the number of bridges in this network, HSI had three female outliers, only one of these is classified as a bridge, and HSII had two female outliers and one male outlier, only the two females were considered bridges. (b) Degree centrality quartiles for all colonies separated by colony and then by sex. The degree centrality box plots show a high variability in degree centrality values. In CCI, three individuals were classified as hubs, but only the male one was an outlier. In HSI, none of the prairie dogs are outliers, even though one was classified as a hub, and in HSII two of the three classified hubs are outliers, one male and one female.

Discussion and conclusions

We found that the majority of the prairie dogs were placed in social network communities that were consistent with their traditional behavioral social group placement (see Figure 1). More importantly, the Social Network Analysis (SNA) approach also recovered additional structure within those groups; previously undetected cliques within social groups. Within

network-based social groups, individuals were subdivided into smaller subunits of prairie dogs that mostly interact with each other in ways apparent only when using SNA.

Prairie dog social networks also showed variation within and among populations in both colonies. For example, HSI social network communities lacked subgroups, suggesting that social groups were more cohesive in this location. Differences in environmental conditions and selective pressures impacting organisms often lead to social patterns that are conditional on the circumstances experienced by a given population at any point in time (Gadagkar, 2001; Jacoby, Busawon, & Sims, 2010; Jetz & Rubenstein, 2011; Lehmann & Dunbar, 2009; J. L. Verdolin, 2007). We suspect that variation in ecological and historical processes, coupled with group specific social dynamics may contribute to the diversity we see in social networks across prairie dogs colonies. In addition, although individuals within social groups were not, on average, more closely related to each other than individuals between social groups (J. L. Verdolin & Slobodchikoff, 2009), some individuals within social groups were related. Community detection may be picking up on these details and suggests many directions for further study. This implies that prairie dog social groups within colonies act as societies with distinct membership.

In addition to detecting subgroups, SNA also detected interactions among social groups, which in some cases were very complex (Figure 1). These interactions were hidden in traditional analyses that simply categorically considered prairie dogs as either in or not in groups. Behavioral and social variability in this species has traditionally been under-emphasized in the search for simplistic universal categorical descriptions and ignores the social complexity and variability that is likely driven largely by environmental differences

(Hoogland, Cully, Rayor, & Fitzgerald, 2012). In reality, while some social groups really are discreet groups in which information (and pathogens) move in a relatively closed system, other groups are more connected such that both pathogens and information may be more likely to be moving readily both within and among what would be regarded as traditional social groups. However, some of these bridges may be temporary in nature. For example, on CCI individuals 25 and 25 were identified as bridges, but were actually transitioning from one social group to another. Without detailed behavioral observations documenting social group transfer SNA might not detect that some bridges are short-lived.

In Gunnison's prairie dogs, the origin of social groups remains somewhat mysterious. Current research provides convincing evidence that many social systems, including that of Gunnison's prairie dogs, display significant sensitivity to resource availability and distribution (Botero & Rubenstein, 2012; Jetz & Rubenstein, 2011; Schradin et al., 2012; J. L. Verdolin & Slobodchikoff, 2009). While some individuals in social groups are typically related, the variability in social structure and dispersal patterns documented in this species (Pizzimenti, 1975, 1981; Robinson, 1989; Slobodchikoff, 1984; Travis & Slobodchikoff, 1993; Travis et al., 1995; J. L. Verdolin, 2007) may explain differences in the average relatedness among individuals, with some populations having social groups composed primarily of nonkin (J. L. Verdolin & Slobodchikoff, 2009). Thus, kinship within social groups may actually be an artifact of sociality in this species, not the cause. One additional hypothesis that has emerged to explain social grouping patterns is that within colonies individuals that share social traits tend to group together (one might also imagine the

opposite, that individuals whose social traits are complimentary group). Do shared behavioral traits explain social group formation and networks in prairie dogs? To address this question, we compared the social network groups within colonies to the observed prairie dog behavioral traits. We document variation in a suite of behavioral traits (e.g., vigilance, feeding) among groups and across colonies. However, with only one colony (HSI) showing significant assortment of individuals within groups for feeding, it seems unlikely that behavioral similarities and/or differences among individuals are strong enough to drive social group formation and network patterns in prairie dogs. Rather, the variation across social networks in behavioral traits may be a function of idiosyncratic differences among colonies. Alternatively, differences in personality, along a bold-shy axis, may contribute to network attributes (Darren P. Croft et al., 2009), and is an important direction for future inquiry in this system.

We also detected non-random variation among individual in their connectedness (degree). In a subset of social groups/communities in each population, some individual prairie dogs were more well-connected than would be expected by chance, so-called hub individuals. For others, their betweenness centrality significantly greater than expected, and these individuals act as bridges between networks. Central individuals (hubs) play a critical role in maintaining group cohesiveness and their removal can sometimes alter group dynamics substantially (Flack, de Waal, & Krakauer, 2005; Kanngiesser, Sueur, Riedl, Grossmann, & Call, 2011; Manno, 2008). In some species, males and females differ in their role in social networks, particularly with regard to their likelihood of being hubs or bridges.

For example, in meerkats, the dominant female will act aggressively towards a subset of females, while other subordinate females are involved in initiating fewer aggressive acts (Madden et al., 2009). Similarly, in many female bonded primates, dominant females have disproportionately higher degree centrality than subordinates (Lehmann & Dunbar, 2009; Ramos-Fernandez, Boyer, Aureli, & Vick, 2009). Network attributes of individuals in Gunnison's prairie dogs do not, however, appear to be determined primarily by sex. The lack of dominance hierarchies in both male and female Gunnison's prairie dogs (J. L. Verdolin, 2007), may explain why sex and age were not significant predictors of degree centrality.

As in dolphins (D. Lusseau & Newman, 2004; David Lusseau, 2007) and primates (Lehmann, Andrews, & Dunbar, 2010), some individuals acted as bridges across communities, yet age and sex were not significantly statistically correlated with betweenness centrality. Interestingly, however, these individuals were all female, suggesting that in Gunnison's prairie dogs it is females who connect different social groups, even though the individuals who serve as hubs within social groups can be both female and male. As pointed out earlier two of the females identified as bridges actually were dispersing to neighboring groups. In Gunnison's prairie dogs both males and females disperse, but males tend to disperse between populations while females disperse within populations (Robinson, 1989). This difference in dispersal patterns may explain why all the bridges were females and also suggests that some females may act as temporary bridges while others are permanent one. What is unclear is why these individuals are more connected and what factors influence the stability of bridges in these populations. Unlike in other species, where network centrality

measures are correlated with group size (Drewe et al., 2009; Lehmann & Dunbar, 2009; Wittig et al., 2008), there was no relationship between degree and betweenness centrality measures and group size in our populations.

Here, we demonstrate considerable variation in the structure of prairie dog social groups. Previous observational and experimental work has linked this variability to ecological factors (Pizzimenti, 1975; Slobodchikoff, 1984; Travis & Slobodchikoff, 1993; Travis et al., 1995; J. L. Verdolin, 2007; J. L. Verdolin & Slobodchikoff, 2009). The results of this study suggest that fine-scale network interactions may be a consequence of the particular set of individuals that comprise a given social group. While age, sex, group size, did not significantly predict key individuals within networks, the presence of individuals that act as hubs or bridges highlights the potential importance of some individuals to act as strategic players in prairie dog social dynamics. Statistically, these connected individuals almost certainly have a disproportionate effect on the movement of information, food, and disease through the network, but using traditional approaches their uniqueness was invisible. It would be interesting to investigate whether the removal of such individuals substantially alters the social network properties of a given group. We also detected similarities in behavioral traits within social network communities, although the traits varied among colonies. While grouping may have non-random features, the rules that govern such non-randomness are far from clear. In the future it would be interesting to explore what role individual variation in personality (e.g., behavioral syndromes) plays in social network structure. Is there an optimum distribution of personality types? Are there fitness differences

among social networks depending on the particular types of individuals that make up a given social group? Our results show that SNA analysis can be used in lieu of traditional behavioral observation methods. Not only does SNA detect statistically similar group structure, but also identifies important sub-structuring not readily apparent. More importantly, the structure of social networks can be determined on relatively short time-scales, such that they are adapted to the immediate internal and external needs of the group (Bhadra et al., 2009). However, one potential drawback to using SNA to the exclusion of more detailed behavioral observations is the potential to misidentify dispersing individuals as bridges. More generally, our work suggests that at least in this system, and we suspect others, social network approaches can build upon rather than compete with more traditional approaches of identifying and studying social groups.

Acknowledgements

JLV was supported by NESCent (EF-0905606). ALT was supported by the Statistical and Applied Mathematical Science Institute Complex Network Fellowship, NC State Mathematics Department and a NASA Biodiversity Grant (ROSES-NNX09AK22G). RRD was supported by a US DOE PER award (DE-FG02-08ER64510), a NASA Biodiversity Grant (ROSES-NNX09AK22G) and an NSF Career grant (0953390). For assistance in the field many thanks to Dr. David Washabau, Bill and Theresa Emig, Carolyn Parker, Perry Crompton, Kristen Hoss, and Jessica Hagan. Fieldwork for this study was supported by grants from the American Museum of Natural History, Sigma Xi and the American Society of Mammalogists. Microchip donations were made by Schlering-Plough and sunflower seeds

were provided by Western Organics, Inc. For use of tomahawk traps we thank Norris Dodd. Lastly, we thank the City of Flagstaff, Arizona Game and Fish Department and the Arizona State Land Trust Department for all necessary permits to conduct this research. For comments that greatly improved the manuscript we thank Dr. Alun Lloyd and Ronald Traud Jr.

CHAPTER 3: Testing Queen Presence on *Formica Subsericea* Social Networks

Introduction

Many studies analyze the social structure of animals using social networks, particularly the hierarchies within animal social networks. Network studies of animal social network hierarchies have studied, for example, the rank of individual crayfish in crayfish social networks (Goessmann, Hemelrijk, & Huber, 2000); the identification of leaders and followers in pigeon social networks (Nagy, Ákos, Biro, & Vicsek, 2010); the ranks of individual rhesus macaques in a rhesus macaque society (Fushing, McAssey, Beisner, & McCowan, 2011); and the hidden leaders in human inter-organizational social networks (Leblebici & Whetten, 1984). Perhaps the systems in which social network hierarchies are best studied and most permanently established are those of the societies of social insects, such as ants, bees, wasps, and termites (Choe & Crespi, 1997). In ant, bee, and wasp social networks, a single queen may exert dominance over hundreds of other individuals (or in a few cases, such as with army ants, over millions of other individuals). In some social insects, this dominance takes the form of physical interactions (e.g., (Penick, Brent, Dolezal, & Liebig, 2014)). More often, queens repress the reproduction of workers through chemical communication. Yet, few studies have explored the effect that queens have on social network structure. Here, we explore the interorganizational influence on social network structure exerted by queens in one social insect species, the ant *Formica subsericea*.

A challenge in studying the influence of particular individuals in human social networks is that removing individuals from human social networks (or experimenting on

human social networks more generally) raises many serious ethical concerns (Kramer et al. 2014). Experiments on insect social networks, on the other hand, suffer from fewer ethical concerns. But apart from serving as useful experimental models for biological networks, insect social networks are interesting intrinsically. Among insects, one finds tens of thousands of unique societies (Jandt et al., 2014). During the more than hundred million years of evolution of insect societies, natural selection likely has favored a balance of certain behaviors, which may affect social network structure. For example, natural selection may have resulted in social networks that balance the relative advantages of communicating food and information rapidly while simultaneously mitigating the spread of pathogens. Given the clear internal organization present within many insect societies (e.g., division of labor, demography), key individuals might have a disproportionate effect on social network structure. The disproportionate effect may be because those key individuals need to stay better connected or, conversely, because of the costs of connectedness for such individuals. For instance, in paper wasp societies, newly established queens have highly central (eventually perfectly central) positions, while older queens may be less central, or even leave the main component of the network (Bhadra et al., 2009). The central positions of new queens ensure rapid and efficient communication to the other individuals in the network. We might speculate that the less central position of older queens minimizes their threat from pathogens, though without a better understanding of the generality of the pattern seen in these queens, any such speculation is premature.

Like with paper wasps, termites, and other social insects, ant colonies include reproductive individuals (queens and drones) and non-reproductive individuals (Gordon, 1999; Lach, Parr, & Abbott, 2010). In the “classic” ant colony, the queen ant is the only reproductive female and suppresses the reproductive capacities of the workers. She also, to varying extents, triggers other behavioral changes within the colony (Brunner, Kroiss, & Heinze, 2009; Helanterä & Sundström, 2007; Holldobler & Wilson, 1990; Monnin, Ratnieks, Jones, & Beard, 2002; Sousa-Souto & Souza, 2006). Given this queen-centric internal colony organization, Jeanson (2012) predicted that removal of the queen (or queens) would have a disproportionate effect on the structure of the colony’s social network compared to the removal of any other individual. Jeanson’s prediction is in line with what one might expect from Bharda et al.’s (2009) work on young wasps, in which the wasp queen was better connected than other individuals (and hence her absence more likely to be of consequence). Jeanson (2012) tested this hypothesis with the behaviorally primitive trapjaw ant species *Odontomachus hastatus*. Specifically, Jeanson predicted that the number of interactions and other centrality measures would be significantly higher for the queen than for the workers. Jeanson also predicted that the overall network structure would change significantly when the queen was removed (Jeanson, 2012). In testing his hypotheses, Jeanson studied over a time period of approximately four weeks proximity networks—networks created by connecting two individuals who come within a certain distance of each other. Jeanson found that while the queen had significantly more interactions than workers, her removal did not significantly change the network structure (Jeanson, 2012).

In this study, we, like Jeanson, investigate whether significant differences exist between groups of ants including a queen and groups of ants not including a queen. However, the ant species we study, *Formica subsericea*, is one in which the behavioral and morphological differences between workers and queens are extreme. In the species studied in Jeanson (2012), queens and workers are very similar morphologically, and workers retain some reproductive ability. A *F. subsericea* queen, in contrast, is twice as large as the workers and has extremely high fecundity, and *F. subsericea* workers are completely unable to reproduce (Choe & Crespi, 1997). With *F. subsericea*, we considered antennation networks—networks created by connecting two individuals who antennate with each other. Antennation is the act of two individuals coming face-to-face and rubbing antennae (McCabe, Farina, & Josens, 2006). While many different things can be communicated through antennation (and the associated trophallaxis that often goes along with it), antennation nonetheless demonstrates a physical connection between individuals through which information, pathogens, and food can pass.

F. subsericea ants live in nest structures composed of chambers connected by tunnels (similar to other *Formica* species), (e.g. (Mikheyev & Tschinkel, 2004)). For our experimental unit, we focused on simulating chambers in as much as actual nests include both chambers with queens (the minority) and those without. In field colonies, chambers also vary in ant density, so we also varied the ant density in our experimental chambers. We observed *F. subsericea* social networks by recording, over a period of 4.5 minutes, all antennation interactions between ants in ant groups of three different sizes, wherein each

group size was studied with and without a queen. The experimental design is a factorial design with two treatments, one with two levels (queen/no queen) and the other with three (ant density). Within this experimental framework, we considered the network attributes of individuals of different types, and the attributes of the entire networks themselves. In considering individuals, we compared the network statistics of queens, workers in a queen's presence, and workers outside of a queen's presence in chambers of different sizes. In considering whole networks, we considered the network structure of chambers with and without queens (hereinafter "queenright" and "queenless," respectively) in chambers of different ant densities using network statistics to discover whether queens affected the entire network structure. Finally, we compared the networks to two known network models to ascertain how the network structure of the ant networks compared to other social networks.

Methods

Data Collection

The observed ants of the species *F. subsericea* were collected from a lab colony including over five thousand workers, which were as many as could be collected from the nest site. The lab colony was kept in a large, rectangular plastic box like those used for storage (hereinafter, the "colony box"). The bottom of the colony box was lined with porous plaster to keep the humidity in the box high, and the top edges of the colony box was lined with Fluon® (Bioquip Products, Rancho Dominguez, CA) to prevent ant escape (Chen, 2007). Fluon® is a fluoropolymer resin that prevents the ants from climbing out because the ants are unable to obtain a foothold on the surfaces coated with Fluon®. To mitigate age and

location effects, a random sample of workers was collected from the colony box. Then, each ant was numbered by gluing a paper number onto the ant abdomen using non-toxic acrylic white paint (FolkArt, PLAID®, Indicator, GA). For each trial, 11, 20, or 39 individuals were chosen randomly from the pool of the 60 numbered ants to mitigate size effects (larger ants tended to receive larger numbers because more digits would fit on a larger gaster) and put into the prepared observation container.

The observation container was an eight ounce plastic circular container (Ziploc®, SC Johnson, Racine, WI) with all vertical edges lined in Fluon® (Chen, 2007). Larger numbers of ants were not tested due to the observation container size. For example, if more than 39 ants were placed in the observation container, antennation events were hard to distinguish from mere proximity. Ants were placed in the observation container and allowed to acclimate to the new environment for a period of 20 minutes. An acclimation period was provided so that antennation events were not a result of panicked ants and instead more accurately reflected normal social interaction. Time trials indicated ant behavior in the observation container mimicked ant behavior in the colony box after a 20 minute acclimation period.

After the acclimation period, ants were observed for 4.5 minutes, and the participants in each antennation event were carefully recorded in real time. During the recording process, an observer watched the ants and called out the participants in the antennation events and a recorder transcribed the participants. After each observation, ants were placed back into the

colony box such that each random draw of ants for an observation was random with replacement.

For the queenless observations, five queenless groups of each size were created and observed for 4.5 minutes each, resulting in a total of 15 queenless groups. Four queenright groups of each size were also created and observed, resulting in a total of twelve queenright groups. In the queenright groups, one of the workers was replaced with a queen. Fewer queenright networks were collected due to the number of queens available. The colony was collected in early spring and had four queens, potentially getting ready to bud off into three more colonies like many other *Formica* species (Holldobler & Wilson, 1990). Each queen was used once per group size. The list of ant pairs' antennation events was used to create a weighted network for each sample, where connections between ant individuals were weighted by the number of interactions that occurred between that specific pair.

Individual and Network Measures

We compared queenright networks and queenless networks using three individual measures (number of interactions, shortest path length, betweenness) and five network level measures (average number of interactions, number of bridges, number of hubs, largest clique size, and clustering coefficient). The number of interactions, path length, and betweenness were calculated for each ant in each network (Opsahl et al., 2010). The per ant number of interactions provides a metric of how interactive each individual ant was. We calculated average shortest path length for each ant by finding the average number of hops over interactions required for each ant to communicate information to all other ants in the network

neglecting infinite path lengths (Opsahl et al., 2010). The calculation of shortest paths takes weighting into account by giving interactions with a higher weight a shorter length. Ants that interacted more were more likely to pass information along, but interacting with the most connected ants also had a similar effect. As in Opsahl et al. (2010), we measured an individual's betweenness as the number of shortest paths that passed through the ant divided by the total number of shortest paths (Opsahl et al., 2010). Using ANOVA, we compared the effect of group size and individual type (Queens or Workers) on number of interactions, path length, and betweenness. Using multiple Welch t-tests (Welch, 1947), we compared for each respective group size, the number of interactions, path length, and betweenness of workers with a queen present to workers without a queen present using a t-test. We used the Bonferroni correction to mitigate the p-value multiplicity caused by multiple t-tests (Bonferroni, 1936).

In addition to calculating number of interactions, path length, and betweenness for each individual, we also calculated the average number of interactions, average path length, average betweenness, number of bridges, number of hubs, largest clique size, and clustering coefficient, for each network. The average number of interactions for each network provides a measure of how social each ant group was. Average path length is a measure of a network's efficiency, or how quickly a phenomena can spread through a network. A network's average betweenness gives a measure of the network's information processing capability (Gulyas, Horváth, Cséri, Szakolczy, & Kampis, 2010).

We regarded individuals as bridges if they had a betweenness score greater than two standard deviations above the mean betweenness of their particular network (Girvan & Newman, 2002; Pinney & Westhead, 2006; J. Verdolin, Traud, & Dunn, 2014). The number of bridges in a network is used as a measure of how modular a network is. In our study, some ants were more connected to each other than to the rest of the respective network. As in chapter 2, we characterized as hubs those individuals who had a number of interactions greater than two standard deviations above the mean number of interactions for the respective network. Hubs facilitate the rapid spread of information (Waters & Fewell, 2012), food (Girvan & Newman, 2002), and/or disease (Kurvers et al., 2013). The existence of hubs and bridges in a network is indicative of a heterogeneous distribution of interactions, which is characterized by most individuals having few interactions and few individuals having many interactions.

A clique is a complete sub-network, or a group of ants in which each ant is connected to each other ant (VanderWaal, Wang, McCowan, Fushing, & Isbell, 2013). In other words, a clique of size three makes a triangle shape in the network. The clustering coefficient is the number of cliques of size three in a network divided by the number of paths of length two (Opsahl & Panzarasa 2009). The clustering coefficient gives a measure of how many ants antennate with “friends of their friends.” All of the network measures were calculated using functions in the igraph library in R (Csardi & Nepusz 2006; R Core Team 2014).

Other Statistical Methods Used

Ward's Method

Ward's method, also known as Ward's minimum variance method, is a hierarchical grouping procedure (J. H. Ward Jr., 1963). Here, we used Ward's method to formally split the set of networks in our study into two groups as a function of their network measures. In Ward's method, the within-group variance of input variables is used to group items, creating multidimensional ellipsoids where each dimension's diameter is the variance of one variable. Ward's method minimizes the multidimensional volume of the ellipsoids for the number of groups decided on by the researcher. The procedure begins with every item in its own group; then, at each iteration, a pair of groups is selected for merging. The pair of groups selected to be merged is the pair that leads to the least increase in within-group variance over all dimensions. Iteration continues until the total number of groups is equal to a number previously chosen by the researcher. Here, we used Ward's method to split the collection of networks into two groups using the number of hubs, number of bridges, and largest clique size simultaneously to distinguish whether queen status significantly changed these network measures. These three are network-level measures that were found to be uncorrelated with each other. Ward's method was implemented using the **hclust** command in R (R Core Team, 2014).

Rand Coefficient

The Rand similarity coefficient was used to compare the Ward's Method grouping to queen classification in order to show whether queen presence significantly affected network structure (Traud et al., 2011b). The Rand similarity coefficient is a statistic used to compare

two groupings of the same data (Rand, 1971). The formula for the Rand similarity coefficient is $(w_{00}+w_{11})/M$, where w_{00} is the number of pairs of networks in which the two networks in each pair are in different Ward's Method groups and also have different queen presence values; w_{11} is the number of pairs of networks in which the two networks in each pair are in the same Ward's Method grouping and also have the same queen presence value; and M is the total number of pairs of networks. The Rand coefficient was also implemented in R (R Core Team, 2014).

Comparing Queenright to Queenless Networks

To compare the queenright and queenless networks, ANOVA, partitioning, and similarity coefficients were used. ANOVA was used to test whether network size and queen status had significant effects on each of the network measures: betweenness, path length, clustering, and average number of interactions. ANOVA takes advantage of the factorial design of this study (Quinn & Keough, 2002). We use ANOVA to test whether network size and queen status has a significant effect on network measures. Of the seven network measures, betweenness, path length, clustering, and average number of interactions do not violate the assumptions for ANOVA: normality and homogeneity of variance.

To use partitioning, networks of different sizes were analyzed separately. Ward's Method, as described above, was used to split the sets of networks into two groups. The groups obtained from Ward's Method were compared to their queenright/queenless

classification using the Rand similarity coefficient, computing the p-value of the match using a posthoc distribution (Traud, Mucha, & Porter, 2012; J. H. Ward Jr., 1963).

Comparing Networks to Models

All the networks were compared to networks created using two known graph models, the Erdos-Renyi random graph and the Watts-Strogatz Small-World graph (Erdős & Rényi, 1959; Watts & Strogatz, 1998). The Erdos-Renyi random graph model assumes each pair of individuals is, independently, equally likely to interact and thus is characterized by two parameters: N and p . N is the number of individuals in the network, in this case the number of ants, and p is the probability that two individuals will interact (Erdős & Rényi, 1959). The Erdos-Renyi model characteristically has an average path length that is very short and a low clustering coefficient. The Erdos-Renyi graph model is compared to the ant networks by producing 1000 Erdos-Renyi graphs with the same number of individuals and the same average number of interactions as each collected network. The other network statistics for the empirical data were compared to the matching Erdos-Renyi model network statistics, and statistical significance was calculated using this ad-hoc distribution of networks.

The Watts-Strogatz Small-World model refers to a network model that is a cross between a regular lattice and an Erdos-Renyi random graph (Newman, 2003). A regular lattice (a network where all individuals have exactly k connections) has high clustering and long path lengths, while the Erdos-Renyi random graph has short path lengths and low clustering (Newman, 2003). The Small-World model is described by a large clustering coefficient and a short average path length. Path length in a Small-World network is slightly

larger than or equal to that of corresponding Erdos-Renyi random graphs, but the clustering coefficient of the Small World network is much larger than the corresponding Erdos-Renyi model (Watts & Strogatz, 1998). To classify a network as Small-World, we calculate the Small-World-ness. To measure whether the Small-World model fits a given network, the Small-World-ness property of the network is tested. The Small-World property is tested by calculating the “Small-World-ness” in the manner described by Humphries and Gurney (Humphries & Gurney, 2008). The Small-World-ness is described by the following formula:

$$S = \frac{\gamma}{\lambda}$$

where γ is the ratio of each empirical network’s clustering coefficient to the matching Erdos-Renyi random network’s clustering coefficient, and λ is the ratio of each empirical network’s unweighted path length to the matching Erdos-Renyi random network’s path length. If $S < 1$, then the network is considered Small-World.

A chi-squared test is used to test whether this Small-World property is correlated with queen status. To test whether the Small-World property is randomly distributed among networks, we created 1000 Erdos-Renyi networks for each observed network and calculated the Small-World-ness value for each of these networks. The fraction of Erdos-Renyi networks for each network size and queen classification that is classified as Small-World is compared to the fraction of observed networks of the corresponding size and classification that are classified as Small-World.

Results

Comparing Ant Individuals

To test whether queens and workers differ in their network characteristics we calculated the number of interactions, betweenness, and path length for each individual ant in all networks. The results of the ANOVA are shown in Table 3. Approximate 95% confidence intervals, based on the t-distribution, for the means of these individual measures are shown in Table 4.

Table 3: ANOVA results for the effects of Individual Type (Worker/Queen), Group Size(11,20,39) and the interaction of Individual Type and Group Size on number of interactions, betweenness, and path length. Significant results are bolded. Group size has a significant affect on these network statistics, but not Individual Type or the interaction of Individual Type and Group Size.

	Sum of Squares	Degrees of Freedom	F – value	Pr(>F)
Individual Type	535	1	1.431	0.23
Group Size	6819	2	9.123	0.0001
Individual Type*Group Size	449	2	0.6	0.55

*Table 4: 95% confidence intervals about the mean of numbers of interactions, betweenness, and path length. Workers (W) compared to queens (Q). *For queens in 39 ant networks and 20 ant networks, the betweenness for all queens was zero because queens were either isolates or had only one connection. Worker sample size for each interval is represented by WSS. Queens sample sizes are all 4.*

	Interactions	Betweenness	Path Length
11 Ants (WSS=95)	W: (1.67,2.41) Q: (0.727,3.774)	W: (1.59,3.58) Q: (-3.768,12.768)	W: (1.353,1.748) Q: (1.553,2.272)
20 Ants (WSS=176)	W: (1.23,1.76) Q: (-0.046,1.546)	W: (3.19,5.95) Q: (0)*	W: (1.391,1.730) Q: (-0.999,4.395)
39 Ants (WSS=348)	W: (1.33,1.71) Q: (-0.546,1.046)	W: (8.24,12.99) Q: (0)*	W: (1.705,2.018) Q: (-1.773,3.398)

Generally speaking, queens tended to be less social and less central than were workers, but Individual Type did not have a significant effect on number of interactions, path length and betweenness as shown in Table 3. Group size, however, did have a significant effect on number of interactions, path length and betweenness. For the networks with 11 individuals, path length was longer for queens than for workers (Table 4 & Table 5). For the networks containing 20 or 39 individuals, both the number of interactions and the betweenness values were significantly lower (mean = 0.75, 0 for 20 ant networks interactions and betweenness, respectively, and mean = 0.25, 0 for 39 ant networks interactions and betweenness, respectively) for queens than for all workers (mean = 1.49, 4.57 for 20 ant networks interactions and betweenness, respectively, and mean = 1.52, 10.62 for 39 ant networks interactions and betweenness, respectively), as shown in Figure 3. The number of interactions and the betweenness values were also significantly smaller for queens than for workers without a queen present for networks with 20 and 39 individuals. Queenright and queenless workers are significantly different in all measures in 20 ant networks, and significantly different in number of interactions in 39 ant networks. Due to the low values of betweenness and interactions for queens, queens are not classified as hubs or bridges.

Table 5: Comparing Queens and Workers. Using a two-sample t test, number of interactions, betweenness and path length are compared between queens and queenless workers, between queenright workers and queenless workers, and between queens and all workers. The table below lists the corrected p-values for each test and degrees of freedom; p-values less than 0.05 are considered significant (i.e. the two groups are significantly different from each other) and are emphasized. In eleven ant networks, none of the comparisons exhibit significant results. Queens differ significantly from all workers in the twenty ant and thirty-nine ant network groups in both betweenness and number of interactions. Degrees of freedom are adjusted for unequal variances.

	Queens vs. Queenless Workers (intp, betp, pathp)(df)	Queenright Workers vs. Queenless Workers (intp, betp, pathp)(df)	Queens vs. All Workers (intp, betp, pathp)(df)
11 Ants	(.96, .57, .29) (5,4,23)	(.23, .59, .31) (92, 92, 87)	(.69, .52, .08)(4,3,13)
20 Ants	(.29, <.001, .53) (6,99,3)	(<.001, .03, .007)(147,125,158)	(.047, <.001, .69)(5,175,3)
39 Ants	(.015, <.001, .43) (5,194,3)	(.02, .45, .17)(300,340,323)	(.009, <.001, .38)(4,346,3)

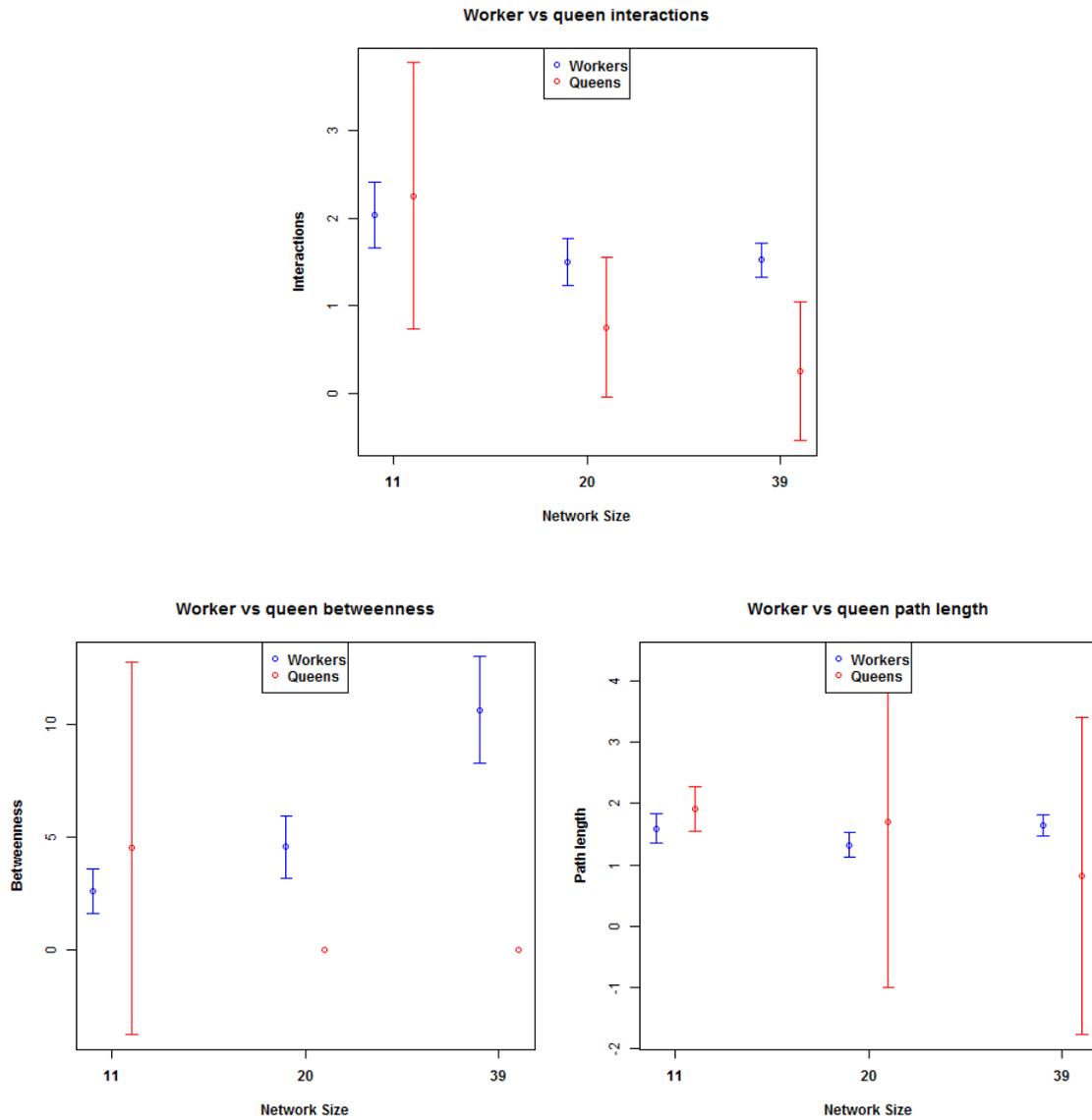


Figure 3: Comparing Workers to Queens. These plots compare the three individual measures (interactions, betweenness, and path length) for queens to all workers. Error bars exhibit the 95% confidence interval of the mean for each measure. Betweenness scores and number of interactions are significantly larger for workers than for queens in both 20 ant networks and 39 ant networks

Comparing Queenright to Queenless Networks

To test whether the presence of a queen has a significant impact on the network structure within chambers, we first compare the network measures (average betweenness, clustering, average path length, and average number of interactions) for queenless networks to the same measures for queenright networks using a two factor ANOVA design, with number of individuals in a chamber and queen presence as independent variables. Average path length varied as a function of network size, but no network features varied as a function of queen presence (Table 3).

Table 6: Looking at size and queen status effects, we analyzed betweenness, clustering, path length, and the average number of interactions using ANOVA. These are the p-values obtained from each test.

	Network Size (df=2)	Queen Status (df=1)	Network Size x Queen Status (df=2)
Betweenness	0.695002	0.75351	0.57268
Clustering	0.64796	0.53735	0.23640
Path Lengths	<0.001	0.85	0.82
Average Number of Interactions	0.09	0.41357	0.615.32

Comparing Networks to Network Models

We compared each of the networks to a set of one thousand Erdos-Renyi random graphs with the same number of nodes and the same probability of connection using clustering

coefficient, path length, number of hubs, and number of bridges: see Figure 2. The clustering coefficients for the observed networks (regardless of the presence of a queen) were significantly higher than the clustering coefficients for the simulated networks ($p < .05$). Other network measures were not found to be significantly different for Erdos-Renyi networks. Most networks were found to include both hubs and bridges indicating the existence of a heterogeneous degree distribution, though not significantly more than their Erdos-Renyi distribution.

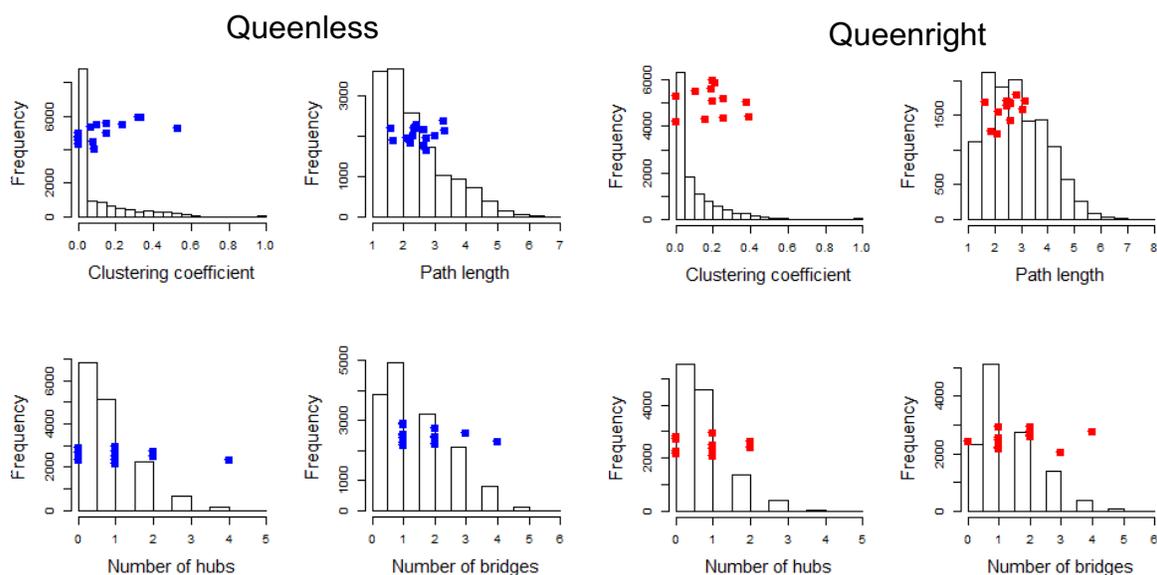


Figure 4: Network measures for all the Queenless/Queenright networks compared to distributions of network measures of Erdos-Renyi random graphs of the same size and average number of interactions. Observed networks are displayed as dots above each distribution. Left half: All Queenless networks compared to their Erdos-Renyi counterparts, the clustering coefficients for the empirical networks are larger than the average clustering coefficient for their Erdos-Renyi counterparts. Right half: All Queenright networks compared to their Erdos-Renyi counterparts, the clustering coefficients for the Queenright networks were also larger than the average clustering coefficient for their Erdos-Renyi counterparts.

To understand whether these networks might show more similarity to Small-World networks than Erdos-Renyi networks, Small-World-ness was calculated for each network using the corresponding set of Erdos-Renyi networks. A value greater than one indicated that the network displayed the Small-World property: see Figure 5. Generally speaking, the more ants in a chamber, the greater the Small-World-ness of their network, independent of the presence or absence of a queen (Figure 3, Table 7). Both classifications of 20 ant networks and 39 ant networks had significantly more Small-World networks than would be expected for same-sized Erdos Renyi networks.

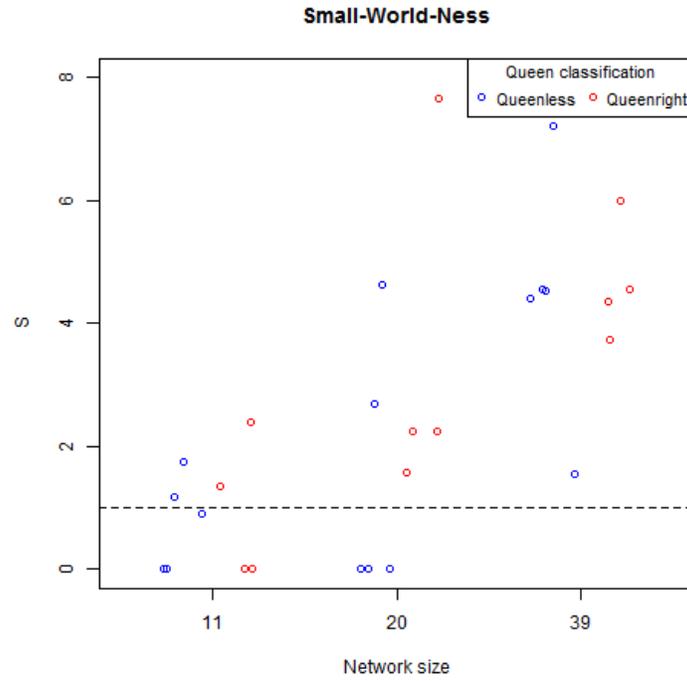


Figure 5: Small-World-ness values for the *Queenless* (blue on the left) and *Queenright* (red on the right) networks. Most of the networks have S values larger than 1 (dashed line), implying that these networks have the Small-World property. The few networks that do not have this property are in one of the two smaller groups.

Table 7: Chi-Square p -values: For each network size and classification, a chi-square test was performed testing whether the fraction of networks classified as Small-World is larger than the fraction expected at random. The *Queenright* classification of 20 ant networks and both classifications of 39 ant networks had significantly larger fractions of Small-World networks than expected at random.

	Queenless	Queenright
11 ants	0.99	0.341
20 ants	0.13	0.016
39 ants	<0.001	0.025

We used a chi-square test to test whether the number of Queenright networks that are Small-World was significantly different from the number of Queenless networks that were Small-World both by size and in aggregate. As illustrated in Table 7, the largest size networks of both classifications have a significantly higher fraction of networks classified as Small-World, and the smallest networks do not have a significantly higher fraction classified as Small-World in either group, but in the 20 ant networks the queenright networks have a significantly higher fraction classified as Small-World and the queenless networks do not. In aggregate, we obtained a p-value of 0.02(df=1); therefore, we reject the null hypothesis meaning that the fraction of Queenright networks classified as Small-World is significantly larger than the fraction of Queenless networks classified so.

Discussion

In our study, queens and workers of the ant species *F. subsericea* differed in their position in the social networks of their colonies. Queens interacted with fewer individuals than workers and were significantly less likely to bridge together groups than workers. These findings contrast with those of Jeanson, who found that *Odontomachus hastus* queens had significantly more interactions than workers, to the extent that queens were regarded as social hubs (Jeanson, 2012). A possible explanation for the discrepancy in our results is the

types of networks collected in each study. In our study, antennation networks were collected for small random groups of ants over 4.5 minutes, while Jeanson (2012) collected proximity networks for full colonies over 4 weeks. This finding suggests network collection techniques may significantly affect results.

Ant networks generally have interaction distributions that are heterogeneous, meaning most individuals have few interactions while a few have many (Blonder & Dornhaus, 2011; Pinter-Wollman, Wollman, Guetz, Holmes, & Gordon, 2011; Waters & Fewell, 2012). When few individuals have significantly more interactions than the rest of the network, these individuals are classified as hubs. We did not find *F. subsericea* queens to be hubs, unlike in Jeanson et al (2012, which found *Odontomachus hastus* queens to be hubs. But the distributions of interactions for the *F. subsericea* networks were found to be heterogeneous, indicated by the existence of hubs and bridges in most networks. This finding is consistent with Pinter-Wollman et al (Pinter-Wollman et al., 2011) Blonder et al (2011), and Waters et al (2012). This finding is also consistent with the interaction distributions found in many other species, including dolphins, pigeons, and humans (D. Lusseau & Newman, 2004; Nagy et al., 2010; Yang, Jiang, Wang, Wang, & Fang, 2012).

A-priori we predict that the presence and absence of queens in *F. subsericea* networks would affect network structure. If such an effect is present in insect societies at all, we would expect to see it in colonies like those of *F. subsericea* in which the behaviors and role of queens are very different from those of workers. Yet, just as in Jeanson (2012), queenright and queenless networks did not differ in terms of hubs, bridges, and largest clique

size. The only distinction between queenright and queenless networks in this study was that the fraction of queenright networks found to be Small-World was significantly larger than the fraction of queenless networks found to be Small-World. Since Small-World networks are found to be more efficient (Amaral, Scala, Barthélemy, & Stanley, 2000), the queen's presence in a given network may make it slightly more efficient. In our findings, the queen has few interactions and does not bridge groups, implying the network would be robust to her removal (Callaway, Newman, Strogatz, & Watts, 2000), therefore the workers may organize themselves slightly differently in the presence of a queen. Iyer et al (2013) found that removal of the individuals having the most interactions changes the network structure more than the removal of individuals having fewer interactions. The removal of the individuals with the most interactions leaves the network vulnerable, i.e. susceptible to invasion by outside individuals due to the loss (Iyer, Killingback, Sundaram, & Wang, 2013). If the queen does not participate in the most interactions, her removal will not leave the network vulnerable. This may be a safety mechanism for both the colony and the queen.

Like many other species' networks, including human sexual networks (Amaral et al., 2000; Watts & Strogatz, 1998) and neuronal networks (Latora & Marchiori, 2001; Watts & Strogatz, 1998), most of the networks in this study fit the Small-World network model. The fraction of networks that were classified as Small-World increased as the network size increased, and the Small-World-ness for all network types in this study increased as network size increased. Small-World-ness gives a measure of how quickly information will permeate the network (Latora & Marchiori, 2001). Due to the increase in Small-World-ness, the ant

networks in this study are more efficient at information spread as the number of ants in the network is increased.

As eusocial organisms, ants in the *Formicidae* family have engaged in social networks for approximately 100 million years (P. S. Ward, 2007). Over long evolutionary time scales, ants have had the time to adapt their social networks to potentially form ideal social networks. Ants can thus inform the development of social networks in other species, including humans. An ideal network would optimize the rate of information flow and limit the transfer of parasites to important individuals (Newman, 2003). Should an ideal network structure exist in one situation, one can explore to see whether that network is observed in other social networks. Due to the Small-World property and the individual measures of the queens, the social networks exhibited by the ants in this study are close to ideal and information can spread rapidly through the network to the workers (however not to the queen). Moreover, due to her lack of interactions, the queen is protected from parasite transfer.

There are multiple limitations to this study. We studied a single species of ants, all collected in the same location. Both species and environmental factors may affect the social structures collected. *Formica subsericea* live in colonies with thousands of individuals, thus groups of 39 are small compared to the size of groups found in nature and the group sizes may affect social structure as well. As with any lab study, lab conditions could also affect the data collected. Finally, the data collection relied on human observation.

CHAPTER 4: Dynamic *Formica subsericea* Social Networks

Introduction

Research in the field of social networks have found, perhaps not surprisingly, that the structure of social networks influences the movement of food, information and disease through them. However, for practical reasons these networks tend to be a set of observations from a single time window, be it long or short (Newman, 2003). It is possible that the network structure can differ greatly from these networks observed in a single time window in ways that impact many features of their dynamics. For example, if interactions in networks accumulate with no specified structure through time, more and more individuals will be connected until all individuals have the chance to be exposed to whatever comes with interactions (Bignami-Van Assche, 2005; Blonder, Wey, Dornhaus, James, & Sih, 2012; Christakis & Fowler, 2013; Jeanson, 2012), be it a deadly pathogen or necessary food. However, if interaction networks approach a stable structure after a certain amount of time, finding the right observation window is extremely important for both capturing the stable network structure and making the most of limited researcher time (Kossinets & Watts, 2006; Pinter-Wollman et al., 2013; Waters & Fewell, 2012). The few recent studies of social networks through time suggest that this appropriate observation window depends on the percentage of individuals connected in the network (Waters & Fewell, 2012) or the progression of average individual measures to limiting values (Kossinets & Watts, 2006). In this study, I report a novel method for identifying the appropriate time windows for data collection for use in network models. This approach will increase our ability to properly describe networks and simulate dynamics on them across a broad range of applications.

Ants provide an ideal study system for assessing social network models and the role of temporal dynamics on network structure. Ants live in large social communities making them an ideal candidate for social network study. Although little is known about how their social interactions change over time, ant social systems are easily observable, even in laboratory settings (Blonder & Dornhaus, 2011; Blonder et al., 2012; Charbonneau, Blonder, & Dornhaus, 2013; Pinter-Wollman et al., 2013, 2011; Waters & Fewell, 2012). Different species of ants and social insects more generally are best suited to addressing different questions with regard to social networks, since ant species vary in colony size from a dozen individuals to millions and in social structure from those in which interactions are mediated by physical dominance (Penick et al., 2014) to those in which most communication is chemical (Brunner et al., 2009). Our model species, *Formica subsericea*, lives in colonies with over 10,000 individuals (Helanterä & Sundström, 2007) and communicates through chemical pheromones, tropholaxis (oral food sharing) and antennation, which is when two ants face each other and rub antennae (Jackson & Ratnieks, 2006; McCabe et al., 2006). Our focus, in terms of the study of networks of these ants is on antennation in as much as it is readily observable and represents one important network type in these ants. Information is communicated during antennation and the proximity of ants during antennation also allows the transfer of parasites and other host dependent taxa (Blonder & Dornhaus, 2011; Waters & Fewell, 2012).

In this study, we observed episodes of antennation in order to construct social networks over an hour. We compared the accumulated set of antennations for each group of

ants to sets of random antennations to find pairs of ants that prefer each other's company, or ants that have friends. We also studied how the accumulation of antennations and network structure progress over time. We report the results of studying antennation patterns and network structure. In addition, the methods undertaken in this study represent a new procedure for finding an observation time window that captures the full network structure.

Methods

Data Collection

The observed ants, which were all of the species *Formica subsericea*, were collected from two distinct lab colonies with more than five thousand workers each. The lab colonies were kept in rectangular plastic boxes (66 qt. volume) (of the type usually used for storage). The bottoms of the boxes were lined with porous plaster to keep the humidity in the boxes high, and the top edges of the boxes were lined with Fluon® (Bioquip Products, Rancho Dominguez, CA) to prevent ant escape (Chen, 2007). A Fluon® coating keeps ants from climbing out by not allowing them to grip the areas coated in Fluon® (Chen, 2007). To create each experimental sample, a random sample of 60 workers was collected from one of the lab colony boxes, labelled, and sampled for the group put into the observation container. Sampling twice serves to prevent location bias, and ant size bias. To mark each ant, a small dot of Shiny Wicker White non-toxic acrylic paint (FolkArt, PLAID®, Indicator, GA) purchased at a local craft store, acrylic paint (as in (Hagler & Jackson, 2001)) was placed on the gaster of each ant using the flat end of a cylindrical pointed toothpick. A paper number was then put in the wet paint, using the paint as glue. From the group of 60 labelled workers,

a random sample of 11 or 20 individuals was chosen randomly to prevent ant size bias and put into the prepared observation container, which was a 48 ounce cylindrical plastic container (Gladware®, Clorox Company, Oakland, CA) that has a 16.51cm bottom diameter with all vertical edges lined in Fluon®. Ants not chosen were cleaned and returned to the lab colony. The bottom of this container was lined with black felt for both contrast and to allow the ants to walk normally.

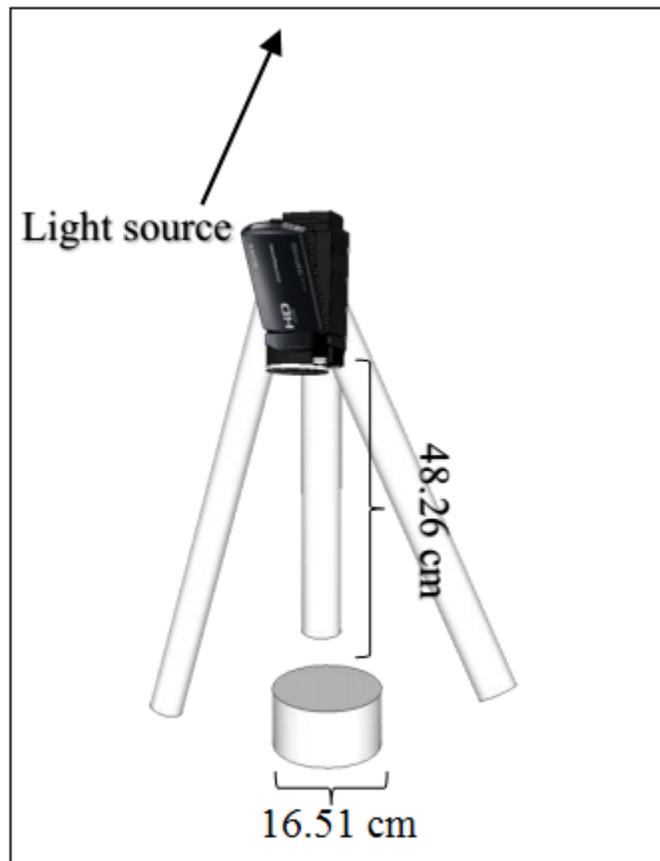


Figure 6: Experimental setup: The camera was placed on a tripod 48.26 cm above the top edge of the observation container which had a diameter of 16.51 cm. A light source was hung above the camera to prevent shadow and glare in recordings.

The ants in each container were video recorded for 60 minutes. Videos were observed at half speed, and the participants in each antennation event were recorded along with time stamp. An antennation event was defined as when two ants faced each other and rubbed antennae for more than one second (Jackson & Ratnieks, 2006). Ants were then placed in vials of ethanol for future study. Three one hour videos were collected for each group size. The list of antennation events and participants was used to create 12 five minute weighted networks for each sample. The weights in each network were the number of interactions that occurred between specific pairs of ants during the five minute period. One aggregated network was created for each sample at each of 12 time steps, the first five minutes of interactions, first 10 minutes of interactions, first 15 minutes of interactions, and so on.

Edge Accumulation

To study the accumulation of interactions, or aggregation of edges, in *F. subsericea* antennation networks, we calculated the density for each network aggregate where density is the number of unique connections divided by the number of possible unique connections (Wasserman, 1994). We then examined the change in density over time. The density for all samples appeared to approach a limiting value as longer time windows were observed. To find this limiting value for each ant group, we fit an exponential model, in Equation 1, to each one hour sample's density progression due to the rapid initial growth in each of the densities using the command `nls` in **R** (R Core Team, 2014). If ants do not have friends, the expectation would be that the limiting density would be one (i.e., all possible interactions observed) and if ants do have friends the stable density would be less than one.

$$C(t) = \alpha + \beta e^{-\gamma t} \quad (1)$$

We also calculated the number of hubs and number of bridges for each of these network aggregates. A hub is an individual with a number of interactions that is more than two standard deviations away from the mean for the network (Newman, 2003). A bridge is an individual who brings together through interaction two groups who would not have been previously connected (Pinney & Westhead, 2006). A bridge is calculated by finding individuals with betweenness values greater than two standard deviations away from the mean betweenness for the network. Betweenness is a measure of the number of paths that need to pass through an individual to get to the rest of the network (Pinney & Westhead, 2006). Betweenness and number of interactions are calculated using the **igraph** package in **R** (Csardi & Nepusz, 2006; R Core Team, 2014). The number of bridges and the number of hubs did not progress towards a limiting value.

Friendship

For accumulated networks to be stable through time, the same pairs of individuals must interact persistently. If individuals continually interact with new individuals, accumulated networks will ultimately fill in, even if the features of a network at any particular time point (density, hubs, or bridges) are similar to each other in another time point. In the network literature, individuals who persistently interact with each other are referred to as “friends” and the relationships are designated “friendships” (S. M. A. Z. Jacobs, Mason, & Clauset, 2013). To understand whether friendships influenced accumulative ant networks, we calculated the friendship levels of ants where ant friendship is defined as the occurrence of a number of interactions between a pair of ants that is significantly higher than expected given

random interactions among individuals (at empirical frequencies of interaction). To make these comparisons, we first created an empty network with the correct number of ants, and then randomly added interactions between pairs of ants until the total number of interactions matched the total number of interactions in the one hour aggregate. We created a distribution of 10,000 of these random networks and compared the number of interactions in the observed one hour aggregate for each pair of ants to the distribution of interactions for that pair of ants using the **igraph** package in **R** (Csardi & Nepusz, 2006; R Core Team, 2014). We used this distribution to calculate the probability of getting a number of interactions for that pair of ants larger than the number observed in the one hour aggregate. If this probability was sufficiently small (i.e. observing this number of repeated interactions, or higher, was unlikely under the assumption of random interaction) then the two ants were determined to be friends. Given that a large number of ant pairs were examined (more so for the larger network size), we made a Bonferroni-type correction when determining the friendship probability threshold (0.024 for 11 ants and 0.009 for 20 ants) (Bonferroni, 1936).

Results

Edge Accumulation

The network density for each network aggregate approaches a limiting value for almost all replicates. To find the density limiting value, we fit a model to each network aggregate's density matching the form in Equation 1. Only one model was a poor fit for the data, the model for the second twenty ant network aggregate. We show the fitted values for α , β , and γ

in Table 1. A linear model was also fit to the network density for each network aggregate, but residuals indicated linear models were a poor model choice.

Table 1: Exponential models fit to density data. The standard error for each estimated coefficient is in parentheses. Only the model for 20b has fit coefficients that are not significantly different from zero for the data. The density for each network aggregate is approaching the α value. All models except the model for 20b required very few iterations to reach a model with a convergence tolerance of less than 0.000005.

Network	α	B	γ
11a	0.309*** (0.01)	-0.245*** (0.02)	0.047*** (0.01)
11b	0.368*** (0.03)	-0.303*** (0.03)	0.022** (0.01)
11c	0.248*** (0.04)	-0.221*** (0.03)	0.025* (0.01)
20a	0.303*** (0.01)	-0.283*** (0.01)	0.037*** (0.003)
20b	0.915 (0.71)	-0.861 (0.71)	0.004 (0.004)
20c	0.336*** (0.04)	-0.325*** (0.03)	0.018*** (0.003)
All Data Model	0.311*** (0.06)	-0.268*** (0.05)	0.025* (0.01)

Of these fitted values, the α value tells us how dense each network is likely to become through time. Again, if these networks were random, α would always equal one. For the models that have a significant fit, the α value ranges from 0.248 to 0.368. The ants are far from random in terms of their interactions with other ants. Using all the data, we created an average model because the average density over time for the two network sizes were extremely close. The α value for this model is 0.311; on average the networks are approaching 31% connected (Figure 1). Neither the fraction of hubs nor the fraction of bridges seem to approach a limiting value (Figure 2). If the betweenness and interaction distributions for all networks were approaching normal distributions, each network would approach having one or no hubs or bridges, or network fractions of 0.091 for 11 ants and 0.05

for 20 ants. If networks were approaching a density of one, hubs and bridges would disappear altogether.

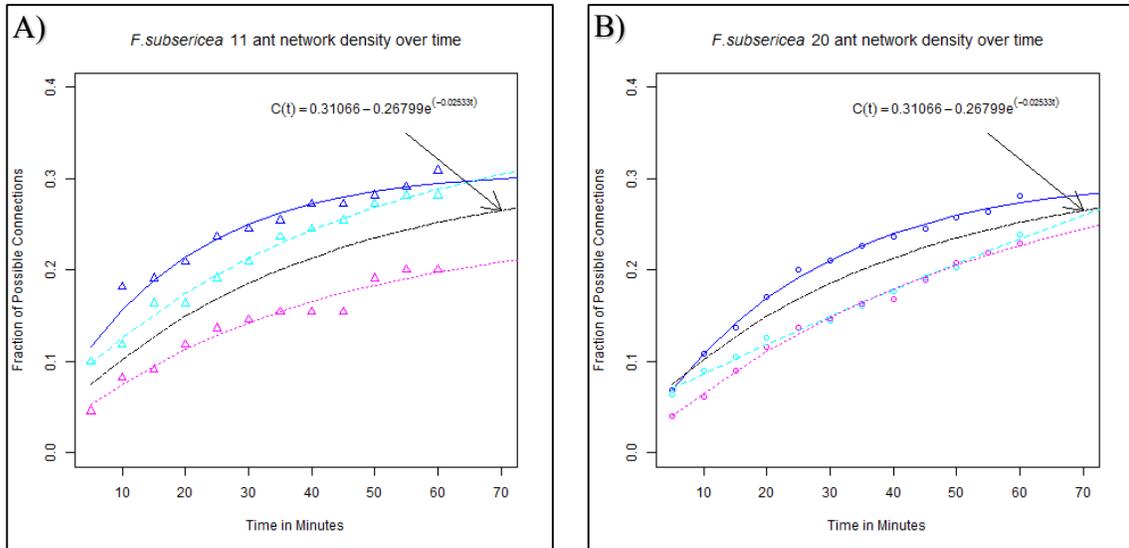


Figure 7: Network Density: A) Network density of 11 ant network aggregates, triangles represent data and lines represent the model. B) Network density of 20 ant network aggregates, circles data and lines represent best fit models. The black line in both panels is the best fit model for all data.

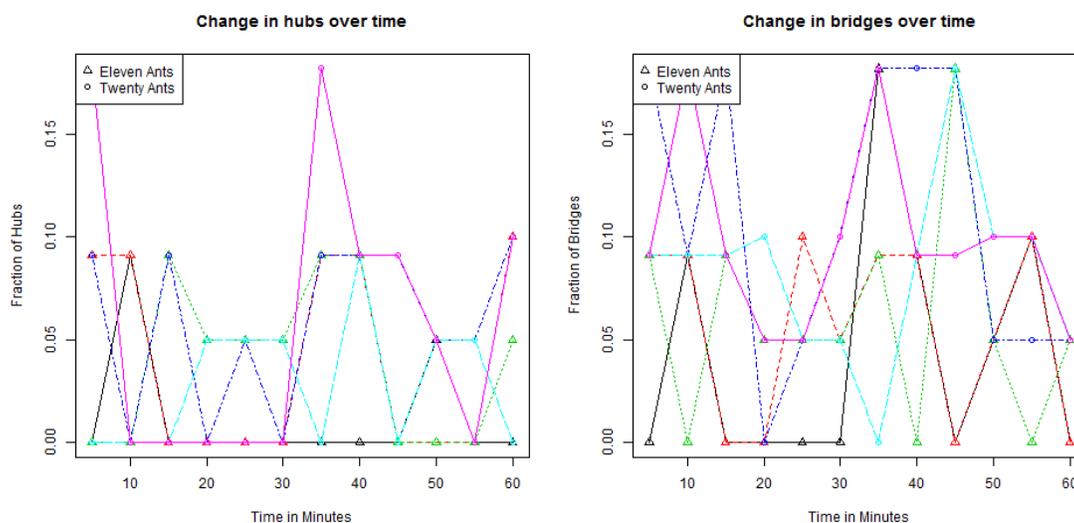


Figure 8: Hubs and Bridges over Time: The fraction of hubs and the fraction of bridges are not approaching a limiting value. If the betweenness and interaction distributions for all networks were approaching normal distributions, each network would approach having one or no hubs or bridges, or fractions of 0.091 for 11 ants and 0.05 for 20 ants.

Friendship

The number of friendships varied among ant networks. However, in each one hour aggregate network, at least two pairs of ants were found to prefer each other's company more than would be expected with a random network. All one-hour aggregates are shown in Figure 3. In Figure 3 [Ref386818310](#), each one hour aggregate network is shown with edges that have significantly larger weights highlighted in red. Each network had at least two edges with a significantly higher weight than expected at random. For example, in a), ant two and ant five participate in two of these friendships, though they are not friends with each other. As might be expected, not all ants that have a high number of interactions participate in friendships, and conversely not all ants that have low numbers of interactions are excluded from

friendships. There were five, two, seven, six, seven, and ten pairs of ants that are friends in networks a-f respectively.

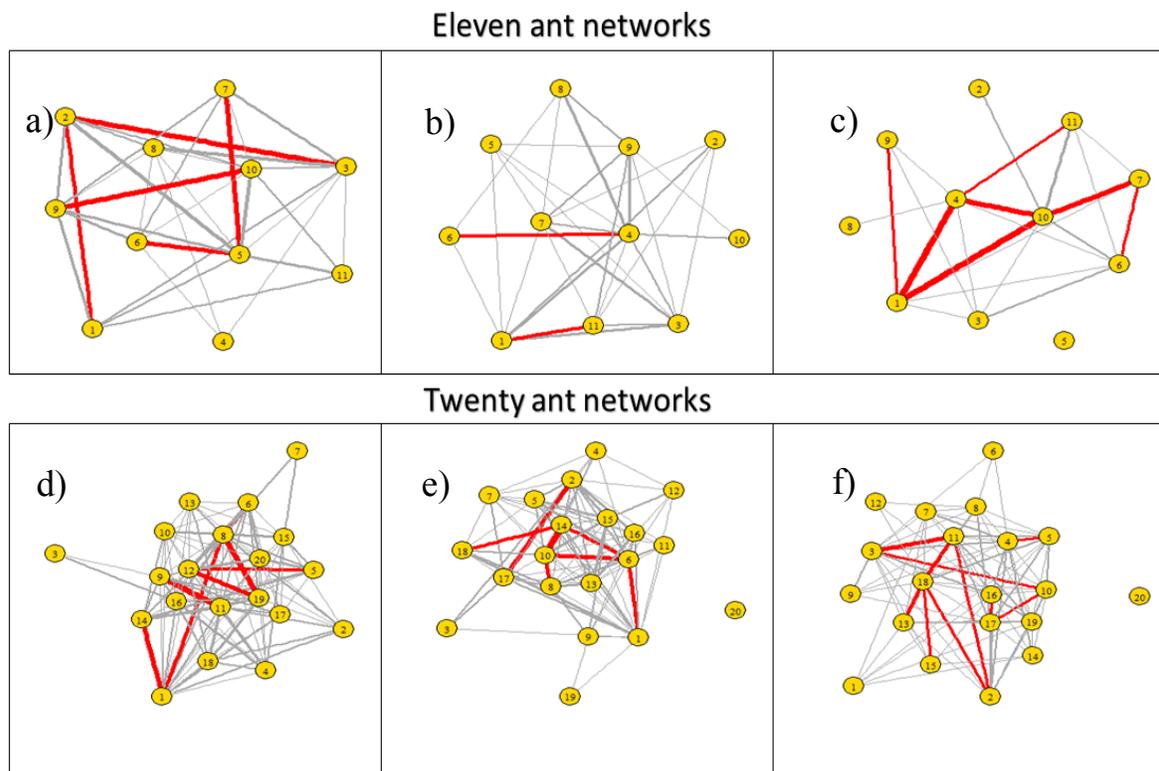


Figure 9: One Hour Aggregate Networks. For each aggregate, the edges with significantly higher weights than expected at random are highlighted in red. Each network had at least two edges with significantly higher weights than expected..

Discussion

Most network studies to date have been focused on a single time window (Krause et al., 2009; Newman, 2003; Pinter-Wollman et al., 2013), with little understanding of the role of temporal dynamics in the structure and stability of social networks. In this study, we used the accumulation of interactions over time to examine network structure stability. We found

evidence that ant networks approach a stable density of interactions, which in turn, points to a technique for finding that stable density.

In this study, ant individuals interacted repeatedly with the same individuals, leading us to the conclusion that ants have friends. While ant interactions are a spatially mediated process, i.e. ants have to be close to interact, ants were observed to traverse the entire observation arena many times during the one hour of observation, which would lead to a well-mixed network if ants simply interacted with individuals in close proximity. Ant workers may all look the same, but they behave differently, whether as a function of their genetic background, experiences or personalities (Jandt et al., 2014; Kralj-Fišer & Schuett, 2014). These differences may lead to better compatibility between certain pairs of ants, i.e. friendships. Other non-human animals have also been shown to have friends: elephants, giraffes, bats, dolphins, and primates (Kerth, Perony, & Schweitzer, 2011; D. Lusseau & Newman, 2004; VanderWaal et al., 2013) though we believe this to be the first report of friendship in insects. Elephants, giraffes, bats, dolphins, and primates have been shown to retain relationships with certain individuals even through group fusion and fission. Though the ants in this study are not forcibly separated like the elephants, bats, and dolphins, ants are given enough space to refrain from any interaction and still demonstrate clear companion choices.

Instead of continually encountering and interacting with new ants in the observation arena, ants interact with the same individuals over and over. These relationships lead to a stable network structure, most recognizable by its density (the actual interactions/all possible

interactions). If each individual were interacting at random, eventually all possible interactions would be evident in the network, revealing a network density of one. Such networks are common and have been observed, for example, in human networks (Bhat & Abulaish, 2013) and even another ant species (Jeanson, 2012). These networks with density one are most often proximity networks, or networks in which the connections between individuals are approximated by how close two individuals come to each other. Ant individuals in our study were observed to traverse the entire observation arena many times during observation. Yet, only a third of the possible interactions occurred in our experiment. The network density for other animals approaches other values over time as shown in Figure 10, e.g. elephant interaction network density approaches a value of three quarters after the elephants were observed for over 20 months (de Silva, Ranjeewa, & Kryazhimskiy, 2011) and bottlenose dolphin networks approach a density of .04 after being observed for 6 years (D. Lusseau & Newman, 2004).

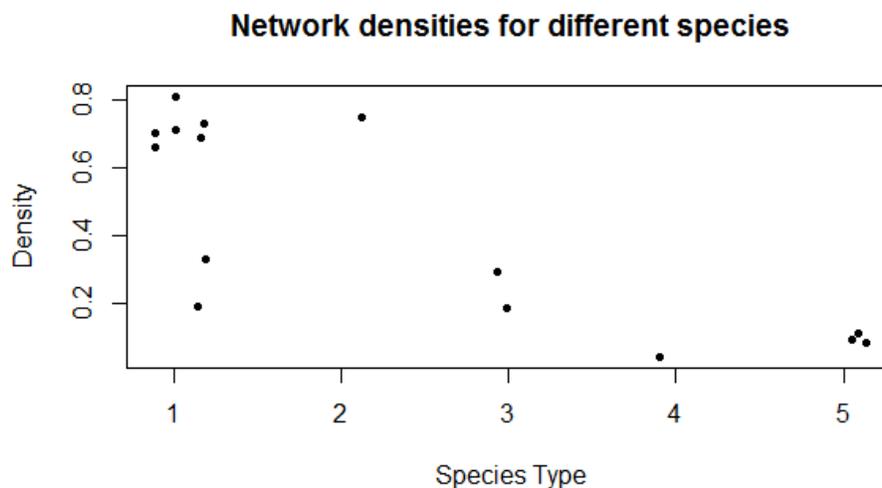


Figure 10: Network Densities for Many Species. Network densities for *Temnothorax regulatus* (1), *Elephas maximus* (2), *Pogonomyrmex barbatus* (3), *Tursiops spp.* (4), and *Cynomys gunnisoni* (5). (Blonder & Dornhaus, 2011; de Silva et al., 2011; D. Lusseau & Newman, 2004; Pinter-Wollman et al., 2011; J. Verdolin et al., 2014)

Other ant studies that used antennation interactions found the network density for observation windows of 5 minutes (Pinter-Wollman et al., 2011) to be approximately .24 and 30 minutes (Blonder & Dornhaus, 2011) to be approximately .6, both less than one (Blonder & Dornhaus, 2011; Pinter-Wollman et al., 2011). This finding suggests that perhaps network density approaches different values for different species, different experimental setups, and different ways of measuring the network, therefore the appropriate observation window needs to be tested for each combination.

We suggest using network density to obtain the appropriate observation window for a species. To find the appropriate observation window for species x, a longitudinal interaction assay, like the one implemented in this study, should be undertaken and the participants, and time stamps, for each interaction should be recorded. The progression of structural

characteristics of the network (e.g. density) should be examined. The progression of structural characteristics can inform the researcher of the amount of time needed to observe interactions to capture the full network structure and can point to a limiting value for these characteristics. Network structure dictates the movement of information and pathogens, and capturing the full network structure is important for making predictions of this spread (Bignami-Van Assche, 2005; Christakis & Fowler, 2013; Kossinets & Watts, 2006).

There are many limitations to this study. We studied a single species of ants, all collected in the same location. Both species and environment may affect the social structures collected. *Formica subsericea* live in colonies with thousands of individuals, thus groups of 11 and 20 are small compared to the size of groups found in nature and these group sizes may affect social structure as well. As with any lab study, lab conditions could also affect the data collected. Finally, the data collection relied on human observation of video recordings.

CHAPTER 5: Modeling *Formica subsericea* Movement

Introduction

Many studies explore movement data; however, recent studies focus on using location data to create proxies for interaction networks such as cell phone location networks for humans (Oloritun, Madan, Pentland, & Khayal, 2013), RFID location networks for ants (Jeanson, 2012), and GPS collar location networks for cows (Boyland, James, Mlynski, Madden, & Croft, 2013). While the ability to collect large sets of location data has become more pronounced as technology has advanced, collecting this data for all individuals in a certain population can still be very costly (Thomas, Holland, & Minot, 2011). One way to mitigate this cost is to use location data for a small sample of individuals to create mathematical models of movement (Fronhofer, Hovestadt, & Poethke, 2013). We can then use these movement models along with interaction rules to create interaction networks of varying sizes (Blonder & Dornhaus, 2011).

Determining movement patterns is especially important for species that live in large populations, like ants. The movement of many individuals can influence the spread of information, populations, and pathogens (Avagar, Mosser, Brown, & Fryxell, 2013). Crist and Macmahon (1991) gathered individual movement data for harvester ant foragers (*Pogonomyrmex occidentalis*) and fit a correlated random walk (CRW) model (Turchin, 1998) to two different movement behaviors, namely, running and searching (Crist & MacMahon, 1991). CRW models (Turchin, 1998) are frequently used to model movement because they assume directional persistence (Fronhofer et al., 2013), i.e. individuals are most

likely to move from one time step to the next with slight variation in direction, but high variability in turning angle. The model for forager searching was reported to fit the data well, but the model for forager running was not a good match, implying that while a CRW model might be a good model for forager searching, a different model type would be better for describing forager running movement data (Crist & MacMahon, 1991).

Movement models have been created for other insects as well. Like the harvester ant foragers, cockroach (*Blattella germanica*) and butterfly (*Proclissiana eunomia*) movement also exhibited two components. For butterflies, a CRW model fit movement between resource patches well; however, within each resource patch, individuals exhibited random walk behavior, i.e. individual direction has high variability (Schtickzelle, Joiris, Van Dyck, & Baguette, 2007). Jeanson and colleagues found that a CRW model described the cockroach movement data (collected in bounded arenas) within the interior of the arena, but another model needed to be used to describe the movement at the boundary: the cockroaches spent more time near the arena boundary than in the interior of the arena, thus exhibiting wall-following behavior (Jeanson et al., 2003).

Ants have also been shown to exhibit wall-following behavior (Pratt, Brooks, & Franks, 2001). *Leptothorax albipennis* workers were found to use walls for navigation and would keep the wall at a constant retinal position (Pratt et al., 2001). *Leptothorax niger* workers have been shown to choose paths with walls (Dussutour, Deneubourg, & Fourcassie, 2005). Workers were given the choice of two paths, one with a wall and one without, and workers chose the path with a wall significantly more often than the path without.

We propose the movement of our ants would be best modeled by splitting the movement into two components: interior and peripheral movement. In field and lab observations, *F. subsericea* path directionality was observed to be highly persistent away from boundaries; we, therefore, suggest a CRW model captures the dynamics of ant movement in the interior of the arena (Fronhofer et al., 2013; Klotz, 1987). *F. subsericea* also exhibited wall following behavior, and thus we use a second model type that exhibits wall-following behavior for the peripheral section of the container. We collect individual movement data for *F. subsericea* individuals in a bounded arena and fit a two stage model to this collected data. We reveal differences in ant movement based on environmental and individual characteristics for these ants.

Methods

Study Species

F. subsericea, also known as the field ant, is one of the United States' largest and most common species of ant (Rice & Dunn, 2014). This species is abundant on the east coast of the US and ranges from southern Maine to northern Florida. These ants build large shallow mounds in open areas or fields as their name suggests. This species' defining characteristics are black bodies with stripes of gold hairs on their abdomens, and a thorax that has two humps as shown in Figure 11. Each individual is approximately .5cm from abdomen to head with approximately .1cm antennae. The individuals in this study were from two lab

colonies collected in Raleigh, NC in May of 2013. Two workers are depicted in Figure 11.

F. subsericea workers are not known to be polymorphic species (Rice & Dunn, 2014).



Figure 11: Two *F. subsericea* workers, photo by Benoit Guenard, part of the Dunn Lab Group.

Data Collection

Ant individuals were marked using the methods outlined in Appendix A and placed in an 8-ounce cylindrical plastic container (Ziploc®, SC Johnson, Racine, WI) with a 3.82 cm radius. Each container was prepared by gluing black felt to the circular bottom of the inside and coating the vertical inner sides of the container with Fluon® (Bioquip Products, Rancho

Dominguez, CA). The felt ensured that ants were able to walk normally across the bottom of the container and that there was high contrast between ant markings and the container. The Fluon® coating ensured that ants could not climb the container sides. Fluon® has been used with many different ant species to prevent escape (Chen, 2007). This container size and these preparation methods are known to work well with the video analysis techniques we chose for ant observations (See Appendix A).

Video analysis was conducted to extract ant movement data from each video using the methods in Appendix A. Only six individual ants from two different colonies were recorded, for 6300 frames at 24 frames per second (i.e. 4.375 minutes), due to the observer time needed to collect data from each video. Ants were recorded from directly above the container as depicted in Figure 12 (left). We used image analysis techniques in ImageJ paired with the AntTrackLib library in R to retrieve ant movement data from the video recordings using methods described in Appendix A (R Core Team, 2014; Schneider, Rasband, & Eliceiri, 2012). Figure 12 depicts the observation setup and a single ant trail in this data set.

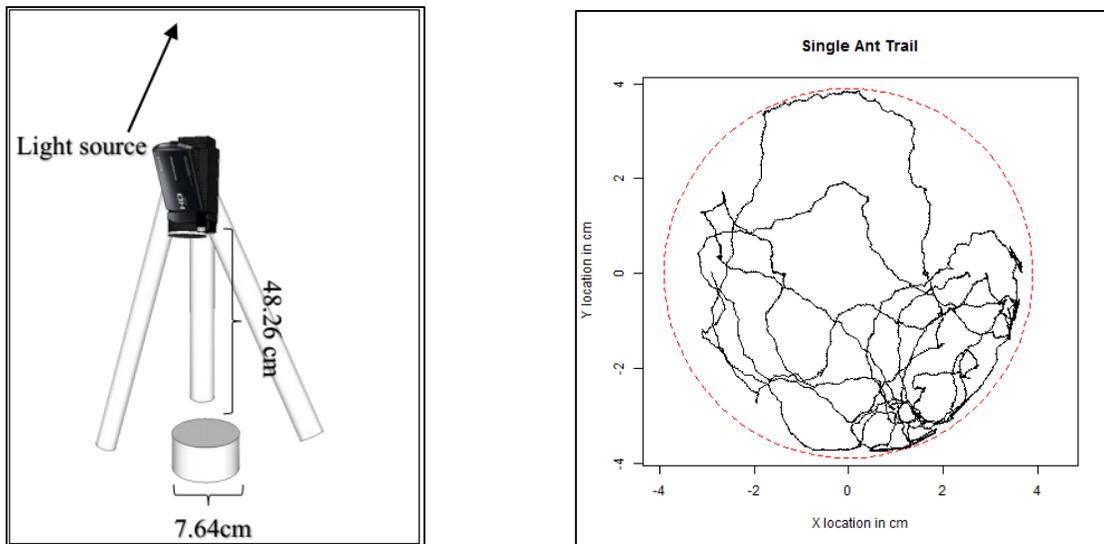


Figure 12: Experimental setup and data collected. Left: Observation setup. A camera on a tripod is placed directly 48.26cm above the observation container which is 7.64cm in diameter. Right: Trail data was collected for each ant over 4.375 minutes. The black line is the track a single ant walked. The center of the container is located at (0,0). The red circle indicates the container edge.

Modeling Approach

Data Analysis

Prior to fitting a movement model to the movement data, the data were thoroughly analyzed. From observation and data analysis, ant individuals did not move continually but each ant had multiple periods of movement followed by periods of inactivity; hence, the trails were divided into moving and still states. Even when an ant individual was observed to be unmoving, the camera and setup were vibrated by airflow, thus the distance between time steps was not zero for an unmoving individual. To mitigate the camera and setup movement, the still state definition was found by video-recording a non-moving ant using the same methods, tracking its positions, and calculating the maximum distance between consecutive tracked points for this still ant. This maximum distance was used as the cutoff for minimum

distance moved between time steps. If an ant did not move this minimum distance or greater between two time steps, the ant was classified as being in the still state for the first of the two time steps. In this study, we input the progression of observed states for each empirical ant trail into the model.

After separating out moving and still states, ant individuals were found to have multiple speeds or step lengths. Aggregating many step length distributions for individuals with varying behaviors can result in a “fat-tailed” distribution and can lead to choosing a step length distribution for the model that produces a significantly lower mean squared displacement (Petrovskii, Mashanova, & Jansen, 2011). Within this data set, three of the six ants moved with significantly larger average step lengths per frame than the remaining ants as shown in Figure 13. The step lengths were compared using a t-test, performed in R (R Core Team, 2014), obtaining a very small p-value ($p < .001$), showing that there were two significantly different average step lengths. Due to only two significantly different step length ranges, ant step length is split into two categories for this model, fast and slow.

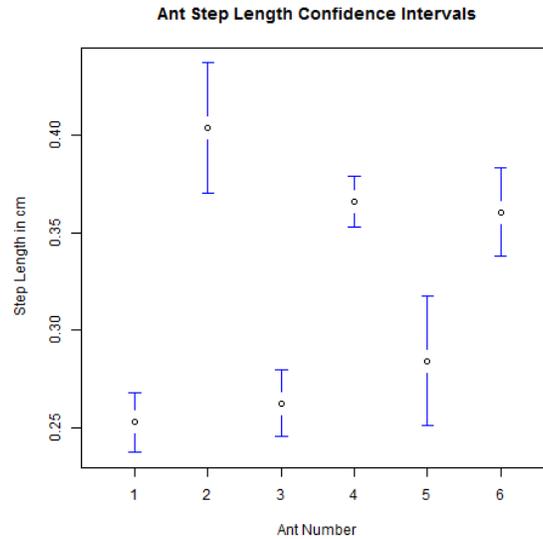


Figure 13: 95% confidence intervals around the mean step length for each ant measured in cm. Each ant's id number is listed on the x-axis

Model Dependent Data Analysis

In a correlated random walk, direction angle has low variability and high correlation but turning angles are assumed to have no significant serial autocorrelations (Turchin, 1998). To eliminate some significant serial autocorrelations in turning angles in the raw data, the data were resampled at a coarser level as is standard practice (Jeanson et al., 2003; Turchin, 1998). This new level was determined by iterating over coarser and coarser levels of the data and using a Box-Pierce test (Box & Pierce, 1970) which was conducted in the R programming language (R Core Team, 2014). A Box-Pierce test identifies serial autocorrelations for various numbers of lags and produces a p-value for the significance of the autocorrelations (Box & Pierce, 1970). The resample level chosen was the level that produced a p-value greater than .05 in the Box-Pierce test. It was found that taking every

seventh frame eliminates significant autocorrelations between turning angles for this data set changing the number of frames for each sample from 6300 to 900 or approximately 3.43 frames per second.

If ants were indifferent to all parts of the container, we would expect ants to follow a random walk. If ants followed a random walk, ant position frequency, or the occupation distribution, would increase linearly with distance from the center of the container due to the area of an annulus of the observation container at radius r and of width δr is approximately $2\pi * r * \delta r$ up to a point between the boundary and the center as shown in dependent on the boundary condition.

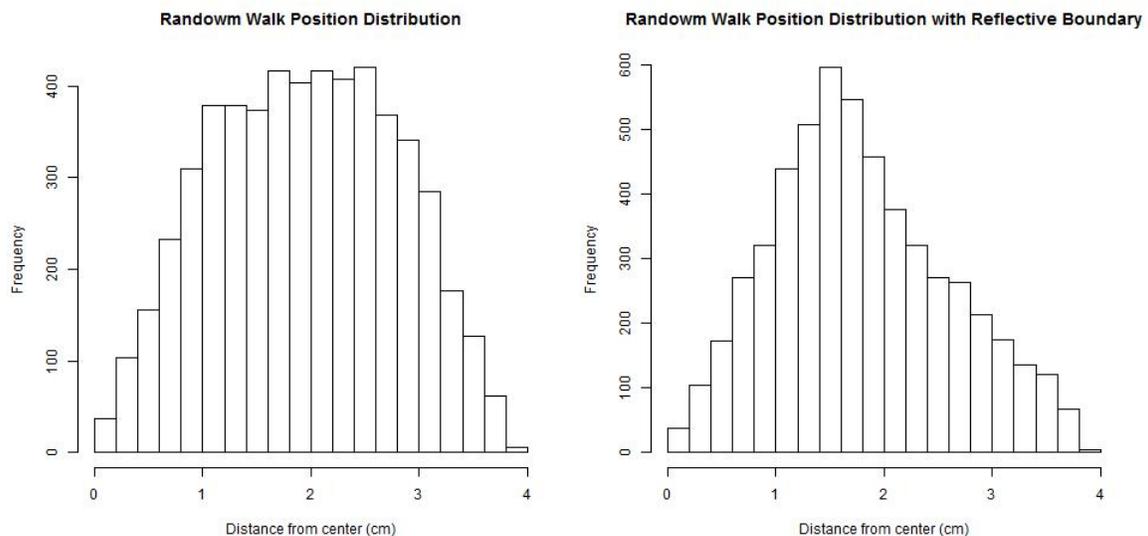


Figure 14: Left: Distribution of ant positions relative to the circle center given ants move with a random walk that is bounded in a container with radius of 3.82cm and ants are placed in a random position in the container upon exiting the boundary. Step size is same as average for all ants in this analysis, .32cm. Positions exhibit linear frequency up to ~ 1.91 cm and then the frequency decreases linearly as ants approach the edge. Right: Distribution of ant positions relative to the circle center given ants move with a random walk that is bounded in a container with radius of 3.82cm and ants are reflected off the boundary. Step size is same as average for all ants in this analysis, .32cm. Positions exhibit linear frequency up to ~ 3.5 cm. If random walk was boundless, linear relationship would continue infinitely.

For the empirical data, a linear relationship seems to apply up to 2.3 cm from the container center with a much smaller rate than either of the random walk models, and then observed ants spent a larger percentage of their time within 1.52 cm of the edge of the observation container than expected per this linear relationship or either random walk model (as shown in the left half of Figure 15). We chose to segregate ant trail data into two sections because of the occupation distribution: peripheral (the area contained within 1.52 cm of the edge of the observation container) and interior (the remaining portion of the observation container).

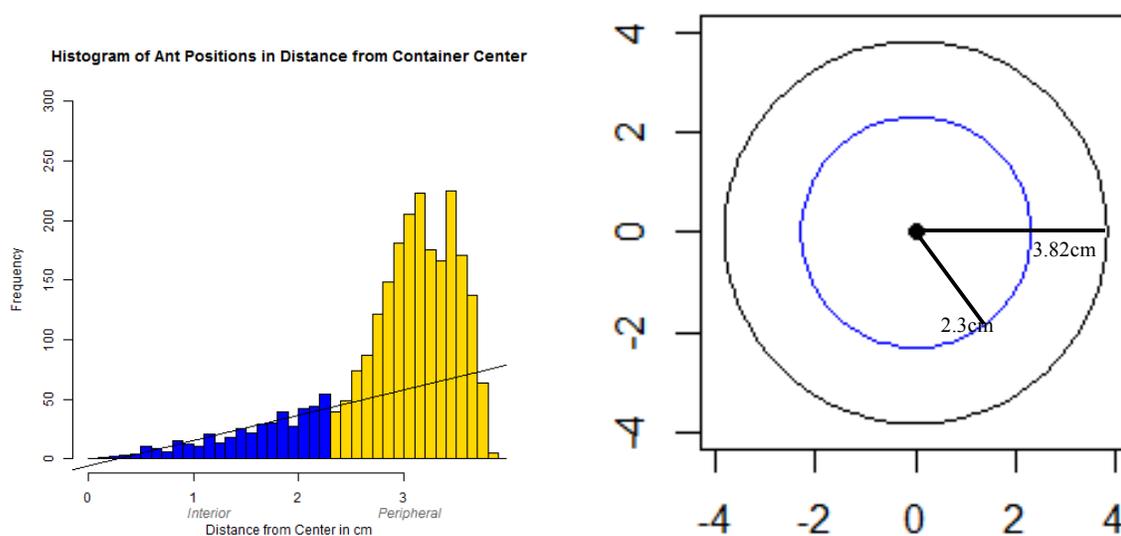


Figure 15: Empirical Occupation Distribution and diagram of container bottom. Left: Occupation distribution shows the frequency of ant positions at different distances from the center of the observation container. Blue represents the interior area and yellow represents the peripheral area. The solid line illustrates the expected relationship between occupation and distance from center for a correlated random walk. Right: Observation arena is a circle with a radius of 3.82 cm. The blue circle represents the divide between interior and peripheral areas of the container.

This splitting produced 38 interior trail sections and 42 peripheral (edge) trail sections.

Interior trail sections and peripheral trail sections were analyzed separately. Figure 16 shows examples of both an interior trail section and an edge trail section.

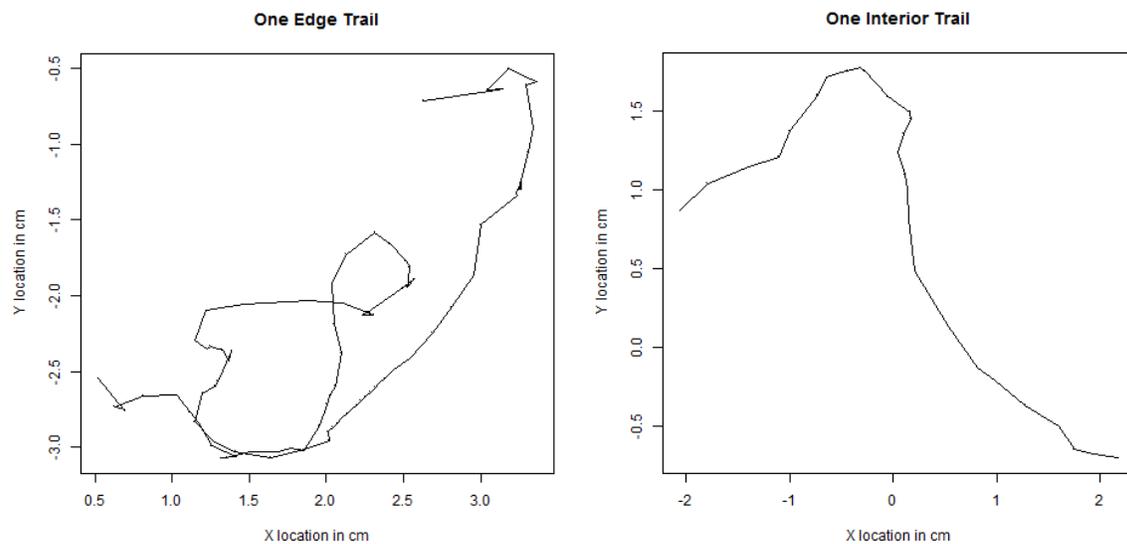


Figure 16: Example of one interior trail section and one edge trail section from the empirical data. The container has a radius of 3.82cm with the center at (0,0).

Model Description

Interior Model

At each time step in the interior movement model, each moving ant is given a new turning angle and step length from distributions dependent on the speed category of the individual ant. The new position for the ant is calculated given the previous direction angle and position. The progression of still states and moving states for each model ant are taken directly from empirical ant trails. A program flow chart for this portion of the model is

depicted in Figure 17.

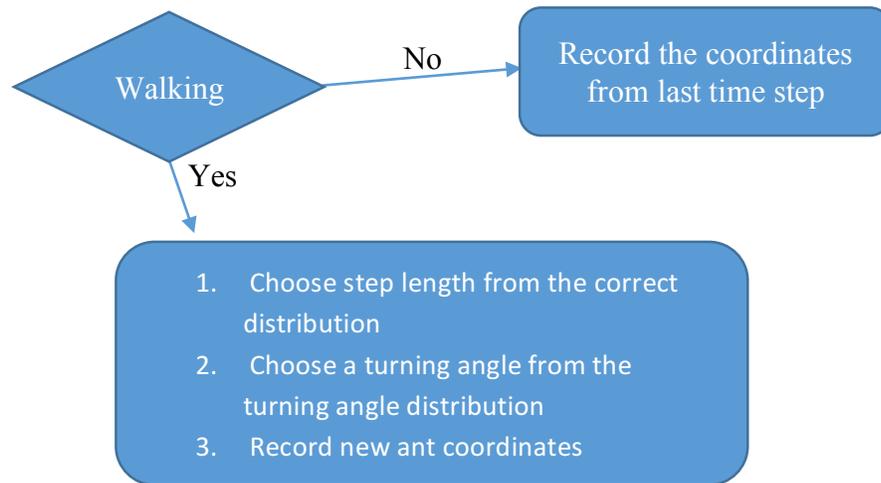


Figure 17: Interior Model Flow chart. At each time step, this process is run for each ant within the interior section of the container.

Prior to fitting distributions to the turning angle data for the interior model, synthetic data were used to validate that the model includes all relevant characteristics. The simplest way to model movement would be use the empirically observed distributions for both turning angle and step size, but due to the autocorrelations in the step size distributions, we need to preserve more of the structure. Surrogate data creation is a method for creating a synthetic data set from an empirical data set, maintaining a chosen set of statistics—in our case, the mean, standard deviation, and the complete autocorrelation spectrum (Theiler, Galdrikian, Longtin, Eubank, & Farmer, 1991). To keep the complete autocorrelation spectrum consistent with the empirical data set, the Fourier transform of the data was taken and the phases were randomized. The synthetic data were synthesized using the *surrogate* function

in the **tseries** package in R (R Core Team, 2014; Trapletti & Hornik, 2013), and allowed for testing the model framework without the added possibility of fitting error. Surrogate data creation was used for both the step size distributions and the turning angle distributions separately. Due to the lack of autocorrelations in turning angles, surrogate data creation for these distributions equates to using the empirical turning angle distribution.

The interior model framework was verified by comparing distance travelled by model ants and distance travelled by observed ants (Turchin, 1998). Model verification ensures code is running correctly and parameters are calculated correctly. Distance travelled is defined to be a cumulative sum of the step lengths over time for each individual. Distance travelled for the model ants would not match the observed trail data if the positions or step sizes were incorrectly calculated. Distance travelled was calculated for both the model ants and the observed ants, and the mean distance travelled for model ants and the mean distance travelled by observed ants were compared both graphically and with a t-test at each time step. The model framework was validated by comparing mean squared displacement between the model ants and the observed ants (Turchin, 1998). Model validation ensures that the model is producing results comparable to the empirical data. Mean squared displacement is a measure of how far an ant travels over time in a single trail, or squared distance from starting point, giving a measure of how appropriate the model framework is for this data. Mean squared displacement progresses differently given the underlying model, e. g. for an uncorrelated unbounded random walk mean squared displacement would increase linearly with time (Turchin, 1998). The mean squared displacement was calculated using code written

in R and then the mean squared displacement for the data set was compared to the mean squared displacement of the model ants. This comparison is done using a t-test for each time step. Because of the boundary of the arena, using the mean squared displacement is not a good validation method for the trails along the boundary, therefore for the peripheral sections, the model was validated using the occupation distribution.

Once the interior model framework was verified and validated, the synthetic datasets for the turning angle distributions were replaced with distributions. Turning angles are measured in radians and wrapped distributions have support $[-\pi, \pi)$, so wrapped distributions are a good choice for the turning angle distributions.

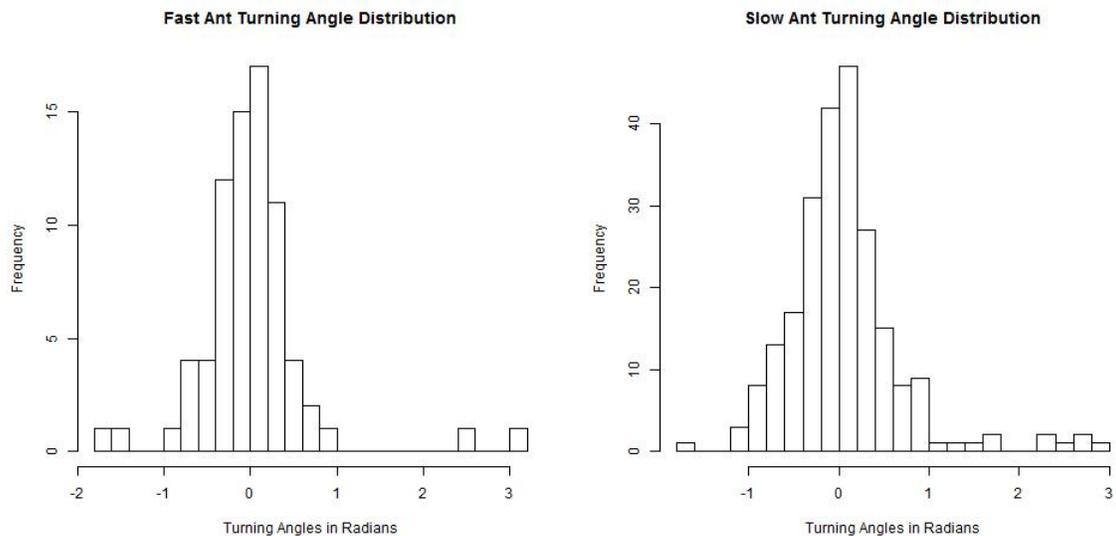


Figure 18: Ant turning angle distributions. Left: The observed turning angle distribution for fast ants. Right: The observed turning angle distribution for slow ants.

Ants were classified into fast and slow, therefore the turning angle distributions were made separately for the two classifications. Both ant turning angle distributions are shown in

Figure 18. Due to the location and scale parameters of the turning distributions (Figure 7), a wrapped Cauchy distribution (WCD) was fit to each distribution using the *wr pcauchy.ml* function in the **CircStats** package in R, which uses maximum likelihood methods to numerically find estimates for the location and scale parameters using the turning angle data (Jammalamadaka & Sengupta, 2001; Kent & Tyler, 1988; Lund & Agostinelli, 2012; R Core Team, 2014). The new turning angle at time step $n+1$ is defined as:

$$\varphi_{n+1} = \varepsilon_{n+1} \quad (1)$$

where

$$\varepsilon_{n+1} \sim WCD(a, b) \quad (2)$$

where a *WCD* is the wrapped Cauchy distribution. Due to the use of the CRW model for interior movement, the location parameter (a) for this *WCD* is assumed to be zero.

The interior model was then verified with the new turning angle distributions comparing distance travelled for observed ants to distance travelled for model ants using a t-test on the model and the data at each time point. The interior model was validated with the new distributions for turning angles, while keeping surrogate data for step lengths due to autocorrelations, by comparing mean squared displacement for model ants and observed ants using a t-test at each time step.

Peripheral Model

For the peripheral trail sections, ants no longer exhibited the behavior indicative of a

correlated random walk, thus a different type of movement model was used, a biased random walk. A biased random walk is a random walk where directions are chosen from a non-uniform distribution. The peripheral trails were split into sections based on distance from center of arena, section 1 (2.3, γ cm), section 2 (γ cm, ρ cm), and section 3 (ρ cm, 3.82cm). Between 2.3cm and γ , ants were observed to move towards the edge of the arena. Once ants crossed the threshold of 2.3cm from the center of the arena, model ants were then given an angle at each time step chosen from a wrapped Cauchy distribution with parameters α_1 and β .

$$\theta_1 \sim WCD(\alpha_1, \beta) \quad (2)$$

Beyond this second boundary, ants exhibited wall-following behavior. Once ants crossed that second threshold, γ , they were then given an angle at each time step chosen from a distribution from a wrapped Cauchy distribution with parameters α_2 and β .

$$\theta_2 \sim WCD(\alpha_2, \beta) \quad (3)$$

If ants crossed a third boundary, ρ , they were given an angle chosen from a wrapped Cauchy distribution with parameters α_3 and β .

$$\theta_3 \sim WCD(\alpha_3, \beta) \quad (4)$$

All of the angle distributions in the peripheral model were wrapped Cauchy distributions due to their shape and support. All step sizes were chosen from the empirical step length distribution for each ant, which were created using the same surrogate data methods described above due to the correlations in those distributions. The amount of time spent in the peripheral section of the container before exiting, or the peripheral time window, is well described by an exponential distribution. The amount of time, τ , that an ant spends in the

peripheral section is therefore chosen from an exponential distribution with mean λ , which was found using the peripheral time window values from the data.

Once the peripheral time window value taken from this distribution is reached, ants return to the interior section of the container.

The peripheral model is illustrated in Figure 19.

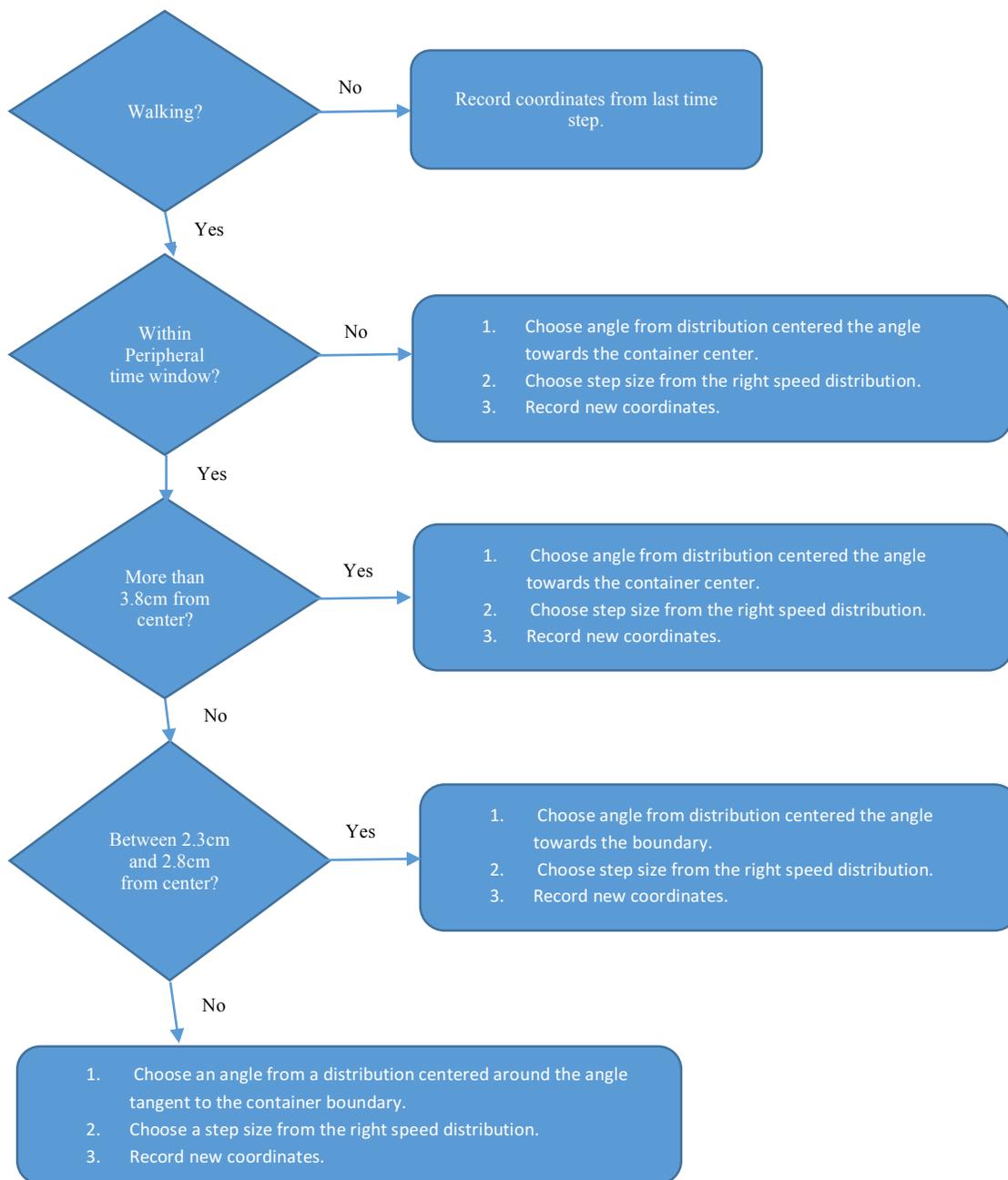


Figure 19: Peripheral Model Flow Chart: Flow chart of the decisions made in the peripheral model. First check whether the ant is in the walking state, then whether the ant is within the peripheral time window, then the location of the ant. The next movement is then chosen accordingly.

The peripheral model was validated with the new distributions for turning angles by comparing occupation distributions as in Figure 15. To compare the occupation distribution of the data to the occupation distribution of the model, we used a Kolmogorov-Smirnoff (KS) test. The null hypothesis for the KS test is that two data sets come from the same distribution. To compare the peripheral occupation distribution, we look for a distribution when compared to the data that produces a p-value larger than .05. When the p-value is greater than .05, the two distributions are not from two significantly different distributions.

Results

Interior Model

The maximum distance a still ant was tracked to move was 0.034cm. For each interior trail, each time step was classified into a moving state if the ant moved more than 0.034cm and a still state if the ant moved .034cm or less. The moving state and still state classifications for each ant were utilized in the model. Ants spent an average of 30.43% of the time recorded in the still state.

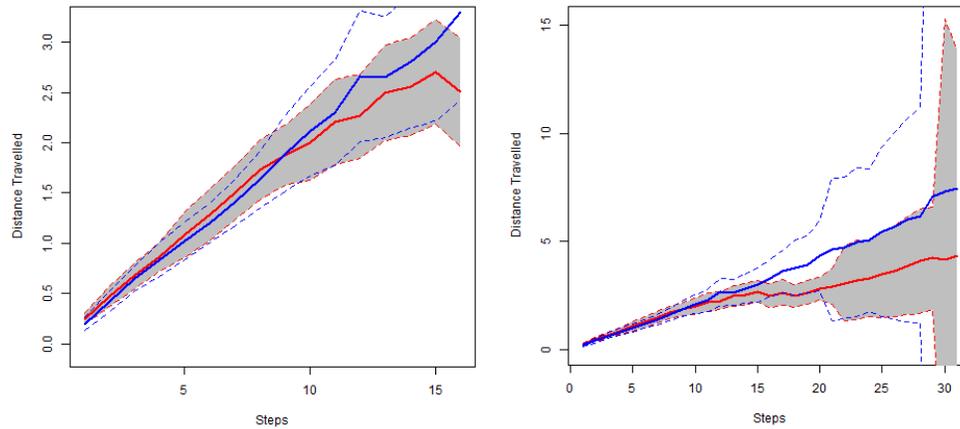


Figure 20: Distance Travelled. Left: Distance travelled compared over 15 steps for both the model framework (blue) and the observed data (red). Right: Distance Travelled compared over 30 steps for both the model framework (blue) and the observed interior trail data (red). The gray envelope around the empirical distance travelled is the 95% confidence interval around the mean of the empirical data. The 95% confidence interval around the mean for the model is represented with blue dashed lines.

Interior Model

To verify this model framework for interior trails, synthetic data sets were first used in lieu of turning angle and step length distributions. This distance travelled is shown in Figure 20.

The distance travelled for the model is not significantly different from the distance travelled for the observed data for any time steps.

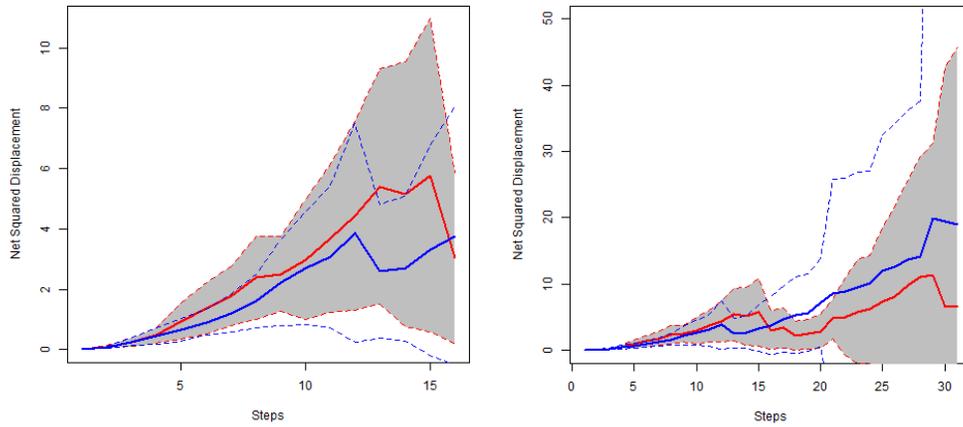


Figure 21: Net Squared Displacement for Model Framework. Left: Net Squared Displacement compared between the model framework (blue) and the observed data (red) for 15 steps. Right: Net Squared Displacement compared between the model framework (blue) and the observed data (red) for 30 steps. The gray envelope around the empirical net squared displacement is the 95% confidence interval around the mean of the empirical data. The 95% confidence interval for the model is represented with blue dashed lines.

The net squared displacement for the model compared to the observed data is shown in Figure 21. Along with the visual comparison, t-tests were performed from which p-values of greater than .05 for every time step were obtained, meaning the model mean squared displacement and the observed ant mean squared displacement were not significantly different for any time steps.

After using synthetic data to verify and validate the model framework for the interior sections, the synthetic data sets for the turning angle distributions for fast and slow ants were exchanged with fit turning angle distributions.

For fast ants, the turning angle distribution parameters were found to be 0 for the location

and 0.799 for the concentration parameters (Jammalamadaka & Sengupta, 2001). Equations 5 and 6 define the new turning angle choice for fast ants.

$$\varphi_n = \varepsilon_n \quad (5)$$

where

$$\varepsilon_n \sim WCD(0, 0.7987052). \quad (6)$$

The fitted fast ant turning angle distribution shape is similar to the turning angle distribution shape in the observed ants as shown in Figure 22.

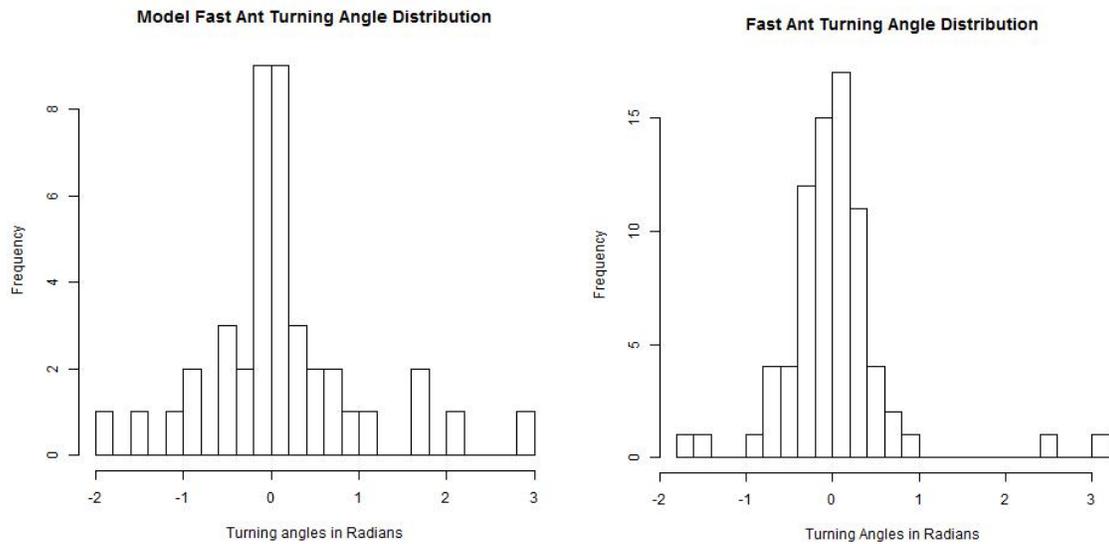


Figure 22: Comparing Fast Ant Turning Angle Distributions: Left: Model fast ant turning angle distribution. Right: Observed fast ant turning angle distribution.

For the slow ant turning angle distribution, the fitted parameters were found to be location

parameter 0 and concentration parameter 0.7695. Figure 23 depicts the comparison between the fitted slow ant turning angle distribution and the observed slow ant turning angles.

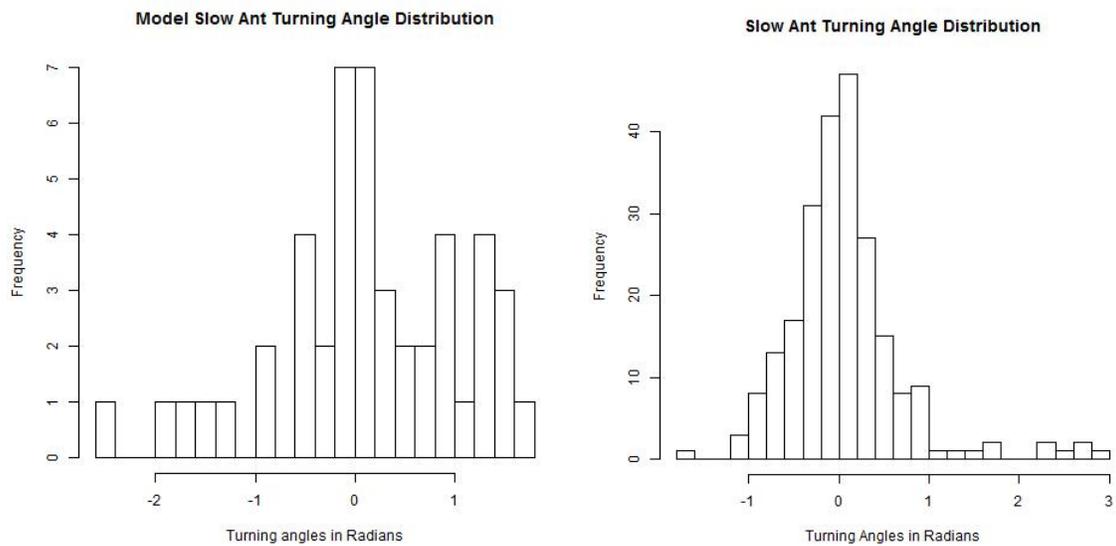


Figure 23: Comparing Slow Ant Turning Angles distributions. Left: Model slow ant turning angle distribution. Right: Observed slow ant turning angle distribution.

As with the model using synthetic data, the model with the fit distributions are validated in Figure 24 and verified in Figure 25 respectively using distance travelled and net squared displacement. A t-test is used to test whether the model and the data are significantly different from each other in mean squared displacement at each time step; the model and data are not significantly different from each other.

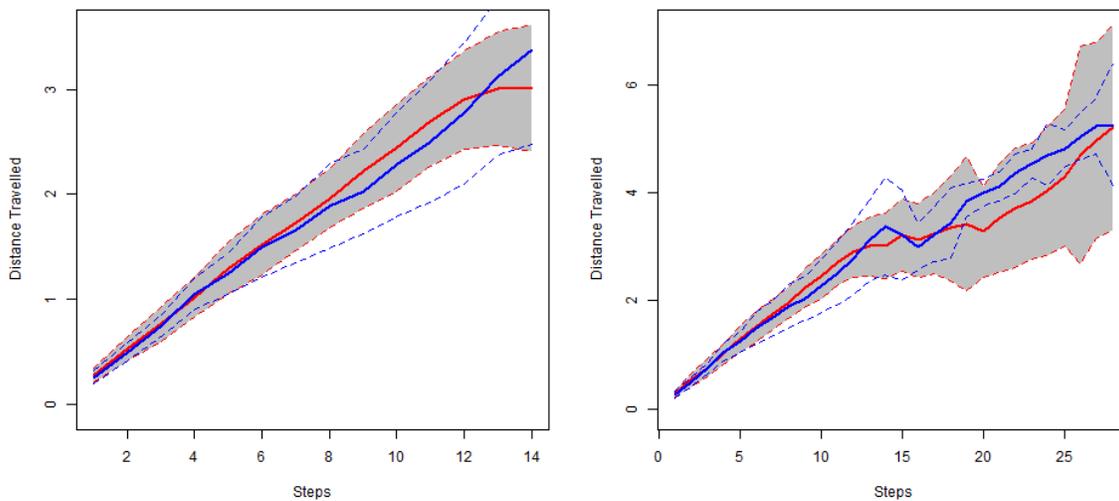


Figure 24: Distance Travelled. Left: Distance travelled for fitted model (blue) compared to observed data (red) for 15 steps. Right: Distance Travelled for fitted model (blue) compared to the observed data (red) for 30 steps.

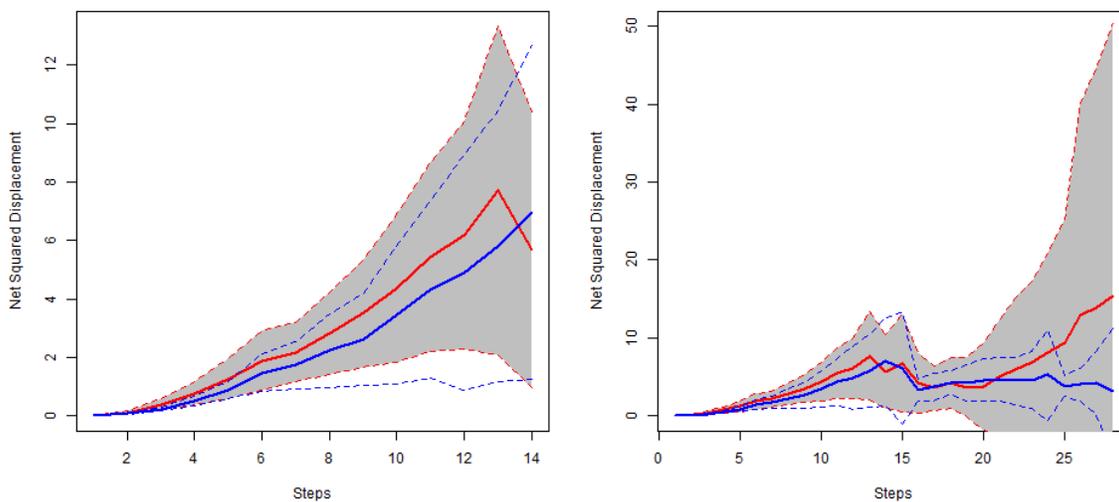


Figure 25: Net Squared Displacement. Left: Comparing fitted model (blue) Net Squared Displacement to observed data (red) Net Squared Displacement for 15 steps. Right: Comparing fitted model (blue) Net Squared Displacement to observed data (red) Net Squared Displacement for 30 steps.

Peripheral Model

To fit a model to the peripheral behavior, the periphery is split into three distinct areas: the area between 2.3cm and γ cm from the container center, the area between γ cm and ρ cm from the container center, and the area between ρ cm and 3.82cm (the boundary) from the container center. In each of these sections, ants are given an angle from a different wrapped Cauchy distribution with location parameters $\alpha_1, \alpha_2, \alpha_3$ respectively and concentration β . To define these parameters, we studied the occupation distribution between 2.3cm and 3.82cm from the container center. We then split this section of the distribution into the three distinct areas of the periphery. Observed ant behavior suggested ant individuals were attracted to a section of the container near the wall, so α_1 was chosen to be the angle towards the closest point on the container boundary with respect to an ant's current position. Wall-following behavior was observed when ants were closer to the container boundary; therefore we propose α_2 to be the angle tangent to the closest point on container boundary to an ant's current position. We find $\rho = 3.82$ cm and α_3 to be the angle towards the container center due to the occupation distribution shape observed and observed ant behavior. We then use the KS test to test whether parameter values for γ and β for create an occupation distribution fit for the section of the occupation distribution between 2.3cm and 3.82cm. We find that for $\gamma = 2.8115$ and $\beta = 0.758$, we obtain an average p-value of .18, meaning that the occupation distribution for the data and the occupation distribution for the model with these parameters are not significantly different from one another.

The last step in fitting this model is connecting the peripheral and interior models. Once an ant that begins in the interior reaches a distance of 2.3cm from the container center, the peripheral model is used to decide future movements. However, model constraints would imply that ants would then stay in the periphery for the rest of the simulation, which would not match observed behavior. To compensate, once ants reach the periphery, a time limit, τ , is drawn from an exponential distribution with $\lambda = 144.74$, the average number of time steps spent in the periphery from the observed data. Once that time limit is reached, ants return to the interior section of the container. The model occupation distribution and the actual occupation distribution are shown in Figure 26.

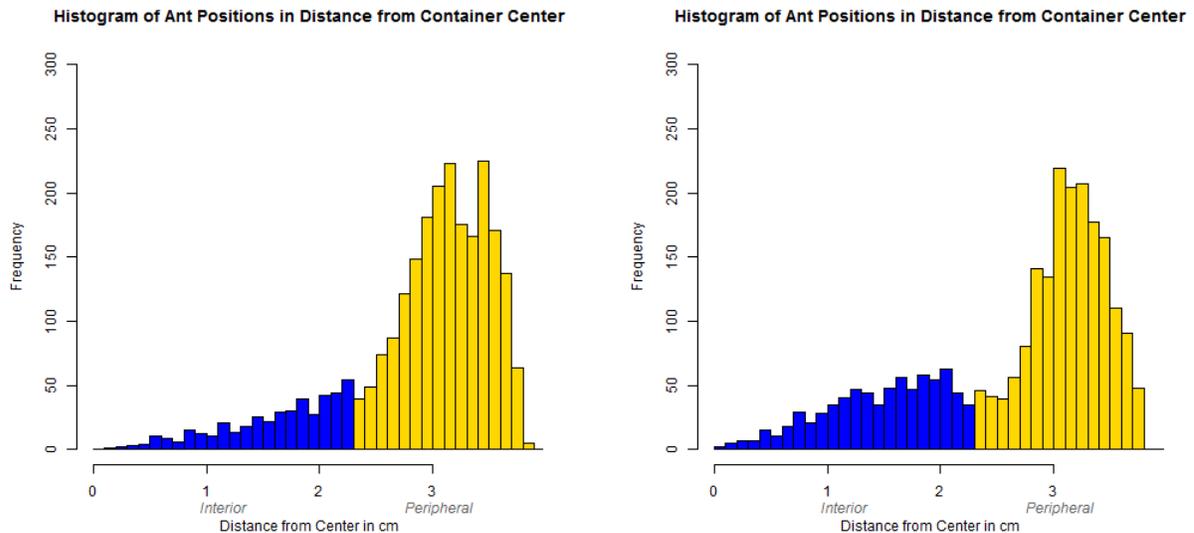


Figure 26: Observed occupation distribution (Left) compared to Model occupation distribution (Right). The interior occupation distribution is in blue and the peripheral occupation distribution is in yellow.

The KS test indicates that they do not come from two significantly different distributions.

An observed trail and a model trail are shown in Figure 27.

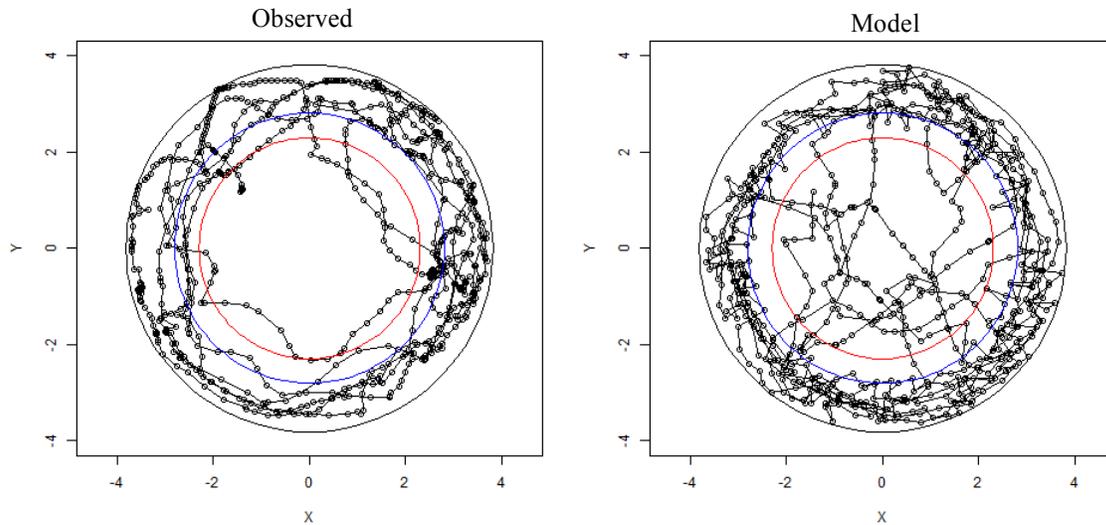


Figure 27: Observed ant trail (Left) compared to Model ant trail (Right). The large black circle represents the container boundary, the red circle divides the interior and the periphery, and the blue circle indicates γ . Small black circles indicate ant positions, while lines indicate paths.

Both observed and model ants spent a large amount of time near but not touching the container boundary. Both trails show wall-following behavior when ants reach the area between the red circle and the blue circle.

Discussion

Edge effects

The edge of the container is affecting ant behavior, which is why we were unable to fit the same framework as was used for the interior trail sections. The edge behavior was fit using a combination of three models, one of which was wall-following. The behavior of *Leptothorax albipennis* and *L. niger*, two other ant species, are known to be affected by walls (Dussutour et al., 2005; Pratt et al., 2001). Wall-following behavior has been shown to be both a foraging behavior and a defensive maneuver (Dussutour et al., 2005). This wall-following

behavior is also exhibited in other insects like cockroaches and fruit flies (Jeanson et al., 2003; Soibam et al., 2012). Perhaps this behavior can be generalized to all insects.

Fast Ants versus Slow Ants

Half of the ants in this study were found to walk significantly faster than the rest of the ants.

We expect that with larger sample sizes the number of distinct ant speeds might increase.

Ant speed could point to different ant personalities. Measures of activity in other social insects have been used to distinguish personalities (Jandt et al., 2014). Two significantly different speeds in the ants in this study, points to two different personality types. It is very possible that these personalities will have a significant effect on their social networks. These different personalities may lead to differences in network statistics. Other insects have also been tested for personality: aphids, crickets, roaches, and flies (Jandt et al., 2014; Kralj-Fišer & Schuett, 2014). Personality is not limited to primates as previously suspected.

Interior Model Implications

Edges may not be important in *F. subsericea* searching and foraging behaviors in natural settings because of the lack of boundaries that individuals come across in the field. Because *F. subsericea* nests are built in large open areas, individuals do not often come in contact with insurmountable boundaries. The interior model may be the only model necessary to model outside the nest, or searching and foraging behavior in this species. Additionally, MacMahon and Crist (1991) found that a CRW model was a good fit for *Pogonomyrmex* (Harvester ant) searching behavior (Crist & MacMahon, 1991). Searching behavior in other ant species may also be well described with a CRW model. Other insect species' movements

follow a CRW model when boundaries are not detected by the insect, including cockroaches, and butterflies (Jeanson et al., 2003; Schtickzelle et al., 2007; Turchin, 1998). Edges are more important when looking at inside the nest behaviors.

Future Work

Synthetic Data Replacement

Synthetic data for turning angle distributions was replaced with fitted distributions, but synthetic data was used for step length distributions due to the high number of significant lags in the autocorrelation spectrum. One possible way to mitigate the significant lags would be to adjust the CRW to take in change in step length. Ant states (moving and still) were inserted into the model directly from the observed data. Future work would require replacing the state data with a model predicting ant movement states.

Network Creation

This study focused on creating a movement model to better understand ant movement and its role in ant contact networks. Creating a movement model for an individual ant was just one small step in the overarching goal of creating ant interaction networks. To continue towards this goal, the effect of interactions between ants (if there are any) on movement would have to be studied. Additionally, if interaction affects movement, interaction rules would need to be gleaned from observed ant social networks. We could then use these rules and the movement models to create networks.

Need for Further Data Collection

In this study, we collected movement data for six ant individuals in a small circular

container. For these six individuals, we found two distinct movement speeds, we expect with more data we might find more distinct movement speeds. We expect in different shaped containers the peripheral model would have to be adjusted and the boundaries between models will change as well. We also expect in different sized containers these boundaries between models will change.

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APPENDICES

Appendix A: Open Source Automated Insect Tracking

Carl Giuffre, Amanda L. Traud, Alun Lloyd, Robert R. Dunn²

Introduction

There has been recent interest in the study of the movement and interactions of social insects (Blonder & Dornhaus, 2011; Jeanson, 2012a; Pinter-Wollman, Wollman, Guetz, Holmes, & Gordon, 2011). Insect social systems and networks are often analogized to those of humans (Moffett, 2012). Social insects are easily experimentally manipulated but actually documenting the movement of individual insects has long been a challenge (Pinter-Wollman et al., 2011). In this light, we sought to develop an automated method of tracking members of insect societies—be they ants, bees, wasps, termites or other taxa—and their interactions.

² **Note:** Amanda Traud helped with experimental setup, data acquisition, wrote three of the five .R files used to communicate between programs, and gathered all .R files into a library for public consumption. Carl Guiffre helped with experimental setup, did most of the data acquisition, wrote two of the five .R files for communicating between software and wrote the Java macro to automate MOSAIC. Alun Lloyd advised this project and helped write this paper. Robert Dunn advised and supported this project and helped write this paper.

There are currently many different techniques of tracking insect movement, each of which has its own strengths and weaknesses. These techniques can be generally categorized as visual techniques, electronic sensing, and image analysis techniques. Visual techniques range from tracing an individual insect's path on paper to marking landing sites of a flying insect with flags and can be augmented with insect marking, night vision paraphernalia, and GPS recorders (Bell, 1991; Hulbert & French, 2001; Lingren et al., 1995; Rempel & Rodgers, 1997; Wiens, Chr, Van Horne, & Ims, 1993; Zalucki, Kitching, Abel, & Pearson, 1980). These techniques can be used both in the lab and in the field but are restricted to tracking either one insect or one group of insects per observer (Chapman et al., 2002). Electronic sensing techniques include acoustic sensing, RFID, X-rays, actographs, servospheres, and instrumented habitats. Acoustic sensing, actographs, and X-ray techniques are used to detect the location of populations of insects, but cannot detect individual movement (BUCHAN & MORETON, 1981; Harrison, Gardner, Tollner, & Kinard, 1993; Knoppien, van der Pers, Jan NC, & van Delden, 2000; Mankin, Shuman, & Coffelt, 1997; Renou, Berthier, Desbarats, Van der Pers, & Guerrero, 1999; Shuman, Weaver, & Mankin, 1997; Weaver, Shuman, & Mankin, 1997). RFID, optical sensors, instrumented habitats, and servospheres detect individual movements. RFID tags are restricted to larger insects, including a few large ant species. Optical sensors can only detect the presence of an insect but not which individual. Instrumented habitats are restricted by the number of readers and orientation of insects. A servosphere can only track the movement of one insect at a time (Bell, 1991; Jeanson, 2012b; KRAMER, 1976; Sasaki, 1989; Waddington, Esch, & Burns,

1996). Video analysis can be done both in the lab and in the field with the only restriction being the size of the field of vision (David, Kennedy, & Ludlow, 1983; Riley, 1994; Vickers & Baker, 1997; Willis, David, Murlis, & Cardé, 1994). Analyzing video visually, the standard approach, can take up a great deal of time, but individual trails can be analyzed at a very fine scale (Chapman et al., 2002). Computer-based video analysis can take up less observer time, but software allowing automated approaches is not readily available including software created for in-house use (Blonder & Dornhaus, 2011; Dell et al., ; Pinter-Wollman et al., 2011), particularly in an open source framework.

We develop an image analysis framework that combines the advantages of visual analysis and image analysis into one approach. Our approach meshes both visual and software tracking to simultaneously achieve the time-savings of automated tracking and the ability to correct computer errors. We combine a suite of existing tools that together allow tracking of social insects. This approach gives researchers the ability to perform automated tracking themselves in a manner that is both free and accessible to anyone with a digital camcorder or webcam. Some aspects of our experimental design are specific to the study species *Formica subsericea*, but in principle these techniques could be applied across a wide array of social organisms.

Experimental Setup

Here we focus on the ant species, *Formica subsericea*, a mound-nesting ant species common in eastern North America. Ants of the species *F. subsericea* are a useful model organism for

exploring automated tracking methods because they are relatively large and dark-bodied (to maximize contrast), maximizing the ability of automatic detection. Twenty *F. subsericea* workers and a queen, a subset of a lab colony gathered from Yates Mill Park, Raleigh, NC, USA, were marked with a small dot of Shiny Wicker White non-toxic acrylic paint (FolkArt™) purchased at a local craft store, acrylic paint widely used to mark individuals in entomology (Hagler & Jackson, 2001). The dot of paint was placed on the abdomen of each ant using the flat end of a cylindrical pointed toothpick. A circular plastic 236-mL container, with a bottom area of 47 cm² (Ziploc™), was prepared by coating the inside of the vertical sides of the container with red dyed Fluon® and then hot-glueing black felt to the inside of the bottom of the container. Fluon® prevents the ants from climbing the walls of the container, and was an integral part of our experimental setup (Chen, 2007). By coloring the Fluon® red and using black felt we prevented undesirable, reflective glare off the surface of the container. The red dyed Fluon® prevents glare because the arena is illuminated with only red light. In addition, the black felt helps create contrast with the white paint, by blending in with the coloration of the ants' bodies.

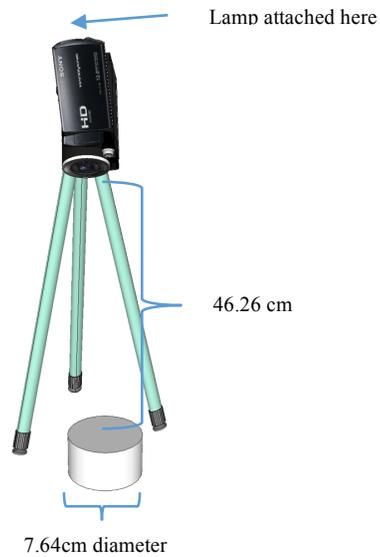


Figure 28: Setup of camera and container, lamp was clamped above the camera.

We prepared the room by blocking out all but one light source, an 8.5” clamp lamp (Intertek). In the lamp we placed a red 25 lumens CFL light bulb (Ecobulb™ Partybulb) and hung the lamp above the container. We recorded the ant movements using a Canon EOS 7d camera with a Macro 100x lens, set at a temporal resolution of 60 frames per second. This camera was placed on a tripod and mounted directly above the arena, with the camera lens pointing directly down as shown in Figure 28. We then placed the twenty workers and queen in the container and let them acclimate to their new environment for 20 minutes to prevent recording external vibrations and recording fast movements due to ant anxiety. After the acclimation period, we recorded the ant movements for 11 minutes, including one minute of buffer time to allow the camera lens to settle from vibrations caused by human interaction. The 11-minute window of time allowed us to ensure that we would have 10 minutes of trackable data, our goal for this experiment.

Software

To be able to track insects through video, we brought together two different plugins in ImageJ using R. R is an open source mathematical programming language and statistical computing environment (Team, 2014), commonly used by biologists (Beckerman, 2012), which embraces our accessibility goal for the automated tracking process. To bring together these two plugins, we created a library in R called AntTrackLib. This library contains functions for reformatting files, cleaning artifacts from the data, and analyzing the data in R. ImageJ (Schneider, Rasband, & Eliceiri, 2012) is an open-source digital image processing suite. Since it is open-source, the suite can be customized to accomplish specific tasks by anyone with the ability to read and modify computer code. Such customization is commonly implemented by the use of Java plug-ins and macros, many of which are available on the ImageJ website (Schneider et al., 2012). MOSAIC (Sbalzarini & Koumoutsakos, 2005) and MTrackJ (Meijering, Dzyubachyk, Smal, & van Cappellen, 2009) are the two plug-ins that we used. MOSAIC is a plug-in that will automatically track multiple circles with the same radius across a landscape for a set number of frames. Each frame must be formatted into an 8-bit grayscale TIFF file for MOSAIC to work, using the video conversion software like Video Mach, regardless of the original video formatting.

MOSAIC has a graphical user interface that allows a user to input three parameters, radius, cutoff, and percentile. These three parameters have to be fine-tuned by the user to detect the highest percentage of individuals and the least amount of noise. The number of frames MOSAIC can preallocate for tracking depends on system RAM, on a laptop with 4gb of RAM, 300 frames can be preallocated. Since our videos are substantially longer than 300

frames, a simple Java macro was written to run commands in ImageJ. This way, the process could automate through all sets of 300 frames contained in one video. The trail data generated by MOSAIC inherits both error generated by the tracking algorithm and noise created by environmental factors, such as glare. MOSAIC can also introduce errors in which two trails are linked from two different individuals, artifacts in the video are identified as individuals, and trails are missing coordinates for some individuals, requiring the need for editing capabilities. The trail data generated by MOSAIC last for a maximum of 300 frames for each individual, therefore the trails must be stitched together to track each individual through an entire video.

Because MOSAIC does not allow editing of trail data, we use another ImageJ plugin to manually edit. MTrackJ is a manual tracking ImageJ plug-in with no automated component. MTrackJ allows a user to import trail data or a set of images and edit trail data or create trail data by manually clicking on the object the user wishes to track. Both MOSAIC and MTrackJ save the trail data to text files, unfortunately MOSAIC formatted text files are incompatible with MTrackJ formatted text files and cannot be imported without modification. MOSAIC files were formatted to open into MTrackJ using code written in R contained in the AntTrackLib library. MTrackJ is then used to stitch trails together and split trails for two unique individuals. The method described above is illustrated in the flow chart in Figure 29 and Figure 30. We use code written in R contained in the AntTrackLib library to deal with missing frames (where certain individuals were not detected) and artifacts in the video identified as individuals (where we have not eliminated glare).

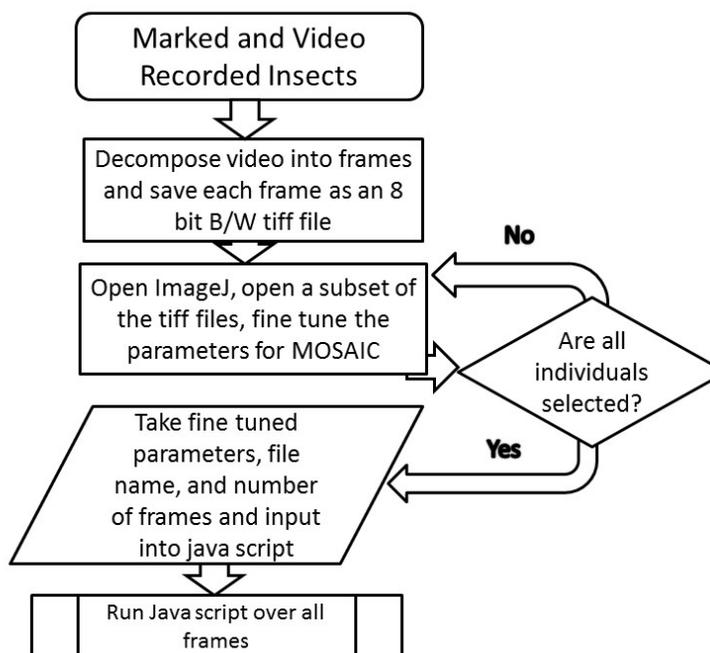


Figure 29: Flow Chart part 1: The process of tracking the movement of individuals going from a video of marked individuals to a Java script that runs MOSAIC to automatically track individuals in each chunk of TIFF files. From this flow chart, proceed to flow chart part 2 in Figure 30.

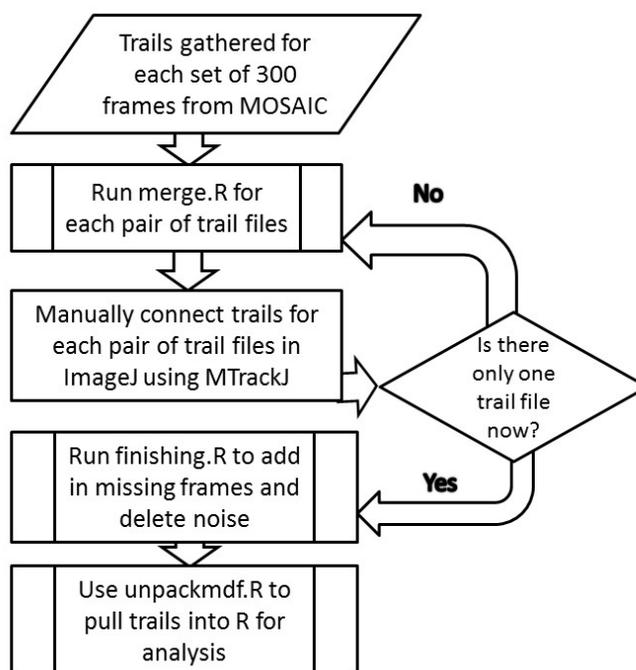


Figure 30: Flow Chart part 2: The process of tracking the movement of individuals going from trails gathered from MOSAIC to the unpacked data in R.

Applying Software to Data

To use our software suite, we first converted the video footage to TIFF files, using the video conversion software Video Mach. The converted footage is then analyzed using MOSAIC. We then used an R library we created, AntTrackLib, to convert files, get coordinates for trails that are missing frames, delete artifacts, and renumber trails after artifacts were deleted. To provide coordinates for trails' missing frames, we simply fit a line to the points in the trail around the missing frames and took the missing coordinates from that line. To merge two or more MOSAIC files, we needed to renumber trails so as not to write over previously gathered data, using renumber.R and merge.R. We then manually edited and connected broken trails using MTrackJ. Manual editing and merging of files can happen as needed. We

finally used an R function, `finishing.R`, to delete artifacts, renumber the final set of trails, and add in any further missing frames through linearization. In Figure 31, we show the time lapse of trails for one 10 minute video as well as a screenshot from the video these trails were taken from. We can use another R function, `unpackmdf.R`, in the library to import the data in to R and plot the data as seen in Figure 31. For a more detailed description and tutorial on using this software, as well as to download the software, please visit our website.

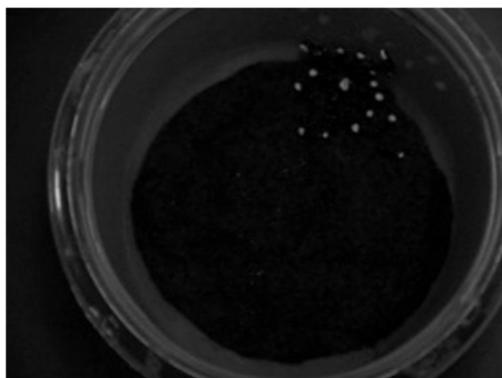
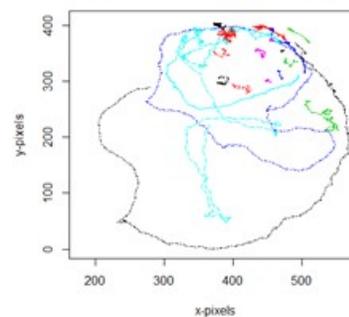
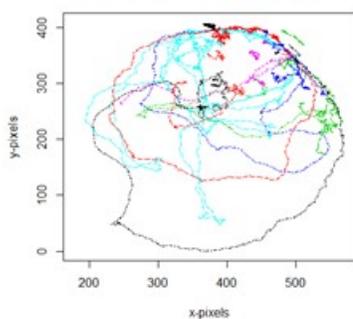
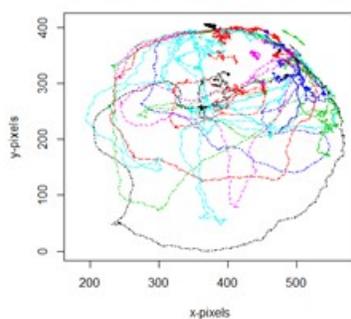
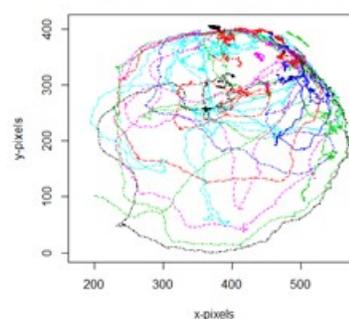
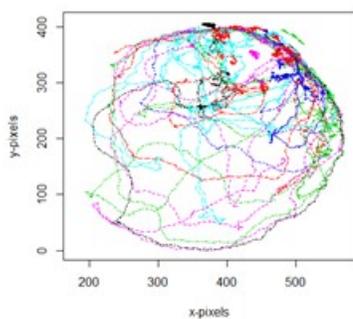
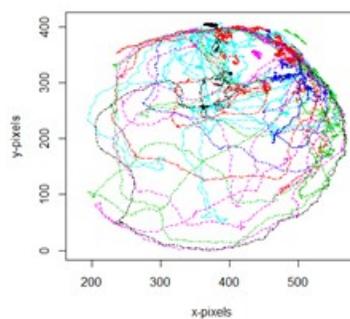
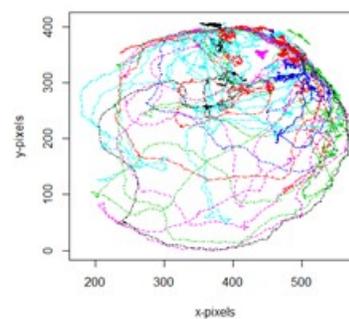
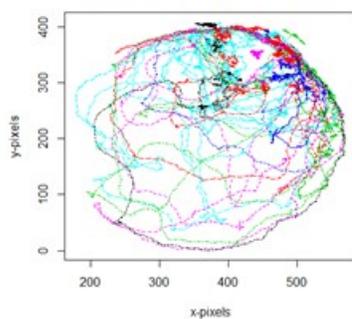
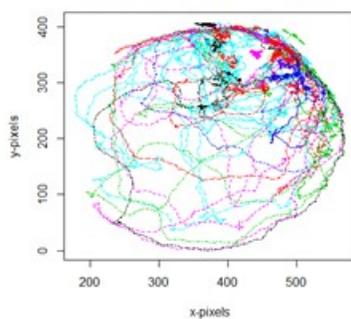
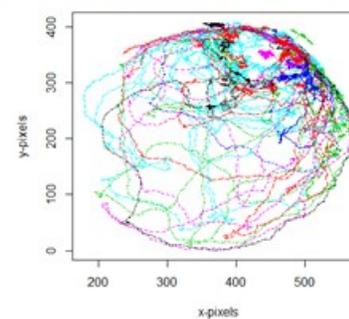
20 *Formica subsericea* trails over 1 minute20 *Formica subsericea* trails over 2 minutes20 *Formica subsericea* trails over 3 minutes20 *Formica subsericea* trails over 4 minutes20 *Formica subsericea* trails over 5 minutes20 *Formica subsericea* trails over 6 minutes20 *Formica subsericea* trails over 7 minutes20 *Formica subsericea* trails over 8 minutes20 *Formica subsericea* trails over 9 minutes20 *Formica subsericea* trails over 10 minutes

Figure 31: Top Left: Screenshot from video. Bottom: Ant trails constructed from the ten minute ant video, each frame represents the trails up to that minute, i.e. frame one shows the trails up to minute one.

Conclusions/Limitations

There are two major roadblocks in digital image processing which exist due to technological capabilities. Since one goal of the method outlined in this paper is tracking insects without expensive equipment, all tracking was performed on personal computers and laptops. One of the challenges to this approach is the ceiling on the number of frames MOSAIC will allocate and process at one time. At a grayscale TIFF resolution of 640 x 480 pixels, an upper limit of approximately 300 frames could be buffered at one time on a system with 4 gigabytes of RAM (on machines with 16gb of RAM, we hit an upper limit of 1000 frames), as indicated in the above section. Second, conversion of video footage to TIFF files is incredibly demanding for file storage. A single ten minute video, when converted to TIFF at the previously stated frame-rate and pixel resolution, needs approximately 9.89 gigabytes of available storage. While we convert chunks of the video into TIFF files, all TIFF files are needed to track individuals through the entire video. Physical storage acts as an upper bound because while it can be upgraded, using automated tracking on footage recorded over the span of days could become financially expensive. That being said, preliminary analysis of the data indicates a conversion rate of 60 fps may be higher than necessary to capture the movement behavior (Turchin, 1998). The authors suspect a conversion rate of 20 fps will be adequate for analysis for this species, which would substantially lower storage requirements. However, an exploration of the required conversion rate is left for future work.

Overall, *F. subsericea* proved an excellent model organism for this study, due to their size and their inability to climb Fluon-coated walls. Problems occurred with tracking the organism when the orientation of individuals' abdomens shifted away from the camera. This happened when ants cleaned their abdomens or gained footing to climb the Fluon.

Unfortunately, *F. subsericea* can climb over one another, which results in failure of the tracking software, since it cannot distinguish one individual circle passing beneath another. In other words, MOSAIC links the trails of two different individuals. These instances of data loss all suggest some level of manual editing is required to procure a meaningful data set for these insects, if the researcher is interested in differentiating between individuals.

Manual editing of trails can be quite labor-intensive. Since MOSAIC only accepts a single, integer radius value measured in pixels, small variations in how the abdomens were dotted can cause substantial issues with tracking if the camera lens is incorrectly positioned relative to the organism. We estimate approximately 45 labor hours were devoted to refining a ten minute video that tracked 21 individuals. This estimate will be significantly lower at a lower conversion rate. Much of the manual editing is due to the 300-frame buffer limitation (which can be mitigated with a higher amount of RAM), which forces us to manually merge trails from one set of 300 frames to the next 300 frames. If the scientist is not concerned with visually verifying individuals, a script could be written in R to merge the trails in two chunks of frames based on the locations of individuals at the beginning and end of each chunk. A high performance computer would eliminate the need to verify track mergers manually if the number of frames that can be processed in one set is comparable to the number of total

frames. Despite this labor intensity, the amount, quality, and timeliness of data gathered is exceptional when compared to previous studies (Pinter-Wollman et al., 2011). To collect the trail of one individual manually with MTrackJ, it takes one click per frame. At a rate of two clicks per second, for a 10 minute video with 60 frames per second, manual tracking would take five researcher hours for each individual. For 21 individuals, 105 researcher hours would be required just for manually tracking. This estimate assumes perfect detection by the scientist and does not include trail editing, and importing trail data into another program for analysis. As mentioned above, our method took approximately 45 labor hours, which included trail cleaning and importing data into R for analysis.

Next Steps

By automating the process of data acquisition, we hope to tease apart important components of social behavior quickly. The data we have gathered using the methods described in this paper can be used in multiple ways. One approach we will take is modelling ant movements by parameterizing a correlated random walk. We also plan to spatio-temporally characterize interactions between individuals to generate complete networks. We hypothesize these networks will fundamentally change under various stressors, such as pathogens, pesticides, and parasites.

Since we wanted this method to work under various laboratory conditions, we used the cheapest resources available, including light, paint, arena construction, and camera equipment. It is not necessary to use an expensive observation setup in order to obtain meaningful data. Different shades and types of paint (such as luminescent paint) may provide a better contrast, allowing more accurate tracking of individuals, and less manual editing.

Control over lighting conditions can get quite costly, however such control may be used to simulate daytime versus nighttime behaviors in organisms. A larger container would allow for more individuals, and custom arenas could be designed to simulate different foraging or territorial behaviors. The type of camera used to film the experiment determines the duration, quality, and resolution of our footage. The camera used can be easily improved, however this particular aspect of the experiment can accrue cost quite quickly. We believe that the most important factors for this method are the camera resolution, the amount of RAM in the computer, and the amount of storage. Without the camera resolution, the markings may not be able to be detected, without the RAM, the size of the chunks that can be analyzed can increase the number of research hours to a prohibitive amount, and without the physical memory the TIFF files cannot be stored.

Acknowledgements

Amanda Traud was supported by the Statistical and Applied Mathematical Science Institute Complex Network Fellowship, NC State Mathematics Department and a NASA Biodiversity Grant (ROSES-NNX09AK22G). Carl Guiffre was supported by the NC State Mathematics Department. Rob Dunn was supported by a US DOE PER award (DE-FG02-08ER64510), a NASA Biodiversity Grant (ROSES-NNX09AK22G) and an NSF Career grant (0953390). Many thanks go to Dr. Jules Silverman for use of his lab's camera, Adrianna Cardinal-De Casas for help in specimen gathering, and Eleanor Spicer for input on ant labeling.

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