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Social Structure And Cohesiveness Of GPS Tracked Wild Pigs In The Southeastern United States

Jack McIlraith, *The University of Western Ontario*

Supervisor: Long, Jed, *The University of Western Ontario*
: Wang, Jinfei, *The University of Western Ontario*

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Title:

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Abstract

The social structure of invasive wild pigs directly affects the risk of disease transmission and other harmful effects. Here, the social structure of wild pigs at four study sites in the United States was measured between individuals and within dyads over time to gain insight into contact heterogeneity and the cohesiveness of social groups using GPS tracking data. A data stream randomization test was used to identify pairwise social associations based on synchronous movement, and contact patterns within social pairs were measured over time. Wild pigs at all four study sites exhibited contact heterogeneity, but more moderate association rates were observed in social pairs as well. It was found that most social pairs had long interruptions in their associations over time characterized by less cohesive movement and space use. Therefore, periods of non-social behaviour and space use should be accounted for within wild pig social groups.

Keywords

GPS tracking, movement ecology, home range, dynamic interaction, contact rate, social network, wild pigs, *Sus scrofa*, invasive species

Summary for Lay Audience

Wild pigs are a widespread invasive species in the United States, responsible for $1.5 billion USD in damages to crops, livestock, wildlife and the environment every year. Female wild pigs live in packs and primarily interact with other pack members, but little is known about how much pack members interact with each other, or how interaction patterns between individuals in packs might change over time. Interactions between wild pigs affect the risk of disease transmission and other harmful damages, making the relationship between pack membership and patterns of interaction an important research topic. To study this relationship, GPS tracking collars were used to measure interactions between wild pigs at four study sites in the southeastern United States. First, packs of wild pigs were identified using the GPS tracking data by measuring how interactions depended on synchronized movement. Next, interactions between individuals belonging to the same pack were measured over time to look for patterns in how often pack members interacted or did not interact with each other. Multiple unique packs of wild pigs were found at all four study sites, but not all packs had the same amount of interaction between pack members. It was found that wild pig pack members went long periods without interacting with other pack members, indicating wild pig packs are not always together. The implications of these findings are that the amount of interaction that constitutes belonging to the same pack as another is not equal across all wild pig packs, and even though wild pigs live in packs, they can temporarily leave their pack. This is important knowledge for managing wild pigs because the splitting of packs could lead to disease transmission and other harmful behaviours. More generally, this research provides a more detailed understanding of wild pig pack structure and the relationship between pack members.

Co-Authorship Statement

Research collaborator Dr. Stephen Webb of Noble Research Institute, Ardmore, Oklahoma, United States provided the wild pig GPS tracking data from two of the four study sites: The Red River Ranch and Oswalt Road Ranch. Stephen Webb also provided all information related to the trapping, sedation and collaring of wild pigs described in the methods section of chapter two in this thesis.

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I would also like to thank my secondary supervisor Dr. Jinfei Wang, for her availability and guidance over the course of my degree program.

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List of Abbreviations

GPS – Global positioning system; part of the global satellite navigation system, consisting of a satellite receiver that records the location and time of the receiver on earth based on signals from a constellation of satellites.

SNA – Social network analysis; the theory and practice of representing people, animals or other objects and the relationships between them using mathematical graph theory.

PBSN – Proximity-based social network; a social network where the relationship between individuals in the network is spatially based, such as the distance between individuals, or spatial-temporal contact rate (a.k.a contact network).

BBUD – Brownian bridge utilization distribution; a probability density surface, usually a raster or grid, giving the relative likelihood of an object occurring at any location based on known occurrences such as GPS tracking points. Probability of occurrence between temporally ordered known occurrences is given by random motion between the two known locations (a Brownian bridge).

VI – Volume of intersection index; equal to the cell-by-cell sum of the minimum of two overlapping utilization distribution surfaces, providing a measure of the similarity of two utilization distributions between 0 (no overlap) and 1 (identical utilization distributions).

SRI – Simple ratio index; the association index used to quantify contact rates between GPS tracked moving objects.

RRR – Red River Ranch; one of Noble Research Institute's agricultural research ranches located in Love County, Oklahoma where wild pigs were captured and GPS tracked.

ORR – Oswalt Road Ranch; the second of Noble Research Institute's research ranches located in Love County, Oklahoma where wild pigs were captured and GPS tracked.

SRS – Savannah River Site; United States Department of Energy site in South Carolina. Wild pig GPS tracking data recorded at this site was retrieved online.

ABIR – Archbold Buck Island Ranch; research ranch in Florida. Wild pig GPS tracking data recorded at this site was retrieved online.

DI – Dynamic interaction index; a measure of the correlation between the direction and displacement of two moving objects, ranging from -1 (negative correlation) to 0 (random, no correlation) to 1 (positive correlation).

Chapter 1

1 Introduction

1.1 Background

1.1.1 GPS tracking methods in movement ecology

Space use is fundamental to understanding the behaviour of animals, such as the association between established areas of regular space use and day-to-day activities (Burt, 1943; Powell & Mitchell, 2012). This area frequented by an animal is called its home range, which is commonly represented as a two-dimensional area on a map delineating the geographic space required to satisfy ecological and behavioural needs of the animal (Fig. 1-1). The home range is a ubiquitous concept in the field of spatial ecology, which is broadly concerned with how landscape spatial heterogeneity and the distribution of organisms interact to shape ecological processes (Kareiva, 1994). Research themes in spatial ecology include the interplay of ecological processes across spatial scales (Leibold et al., 2004), spatial autocorrelation of ecological processes (Legendre, 1993), and possibly most prominently, ecological responses to habitat patchiness and anthropogenic effects, which has important implications in ecological conservation (Wiens, 1997).

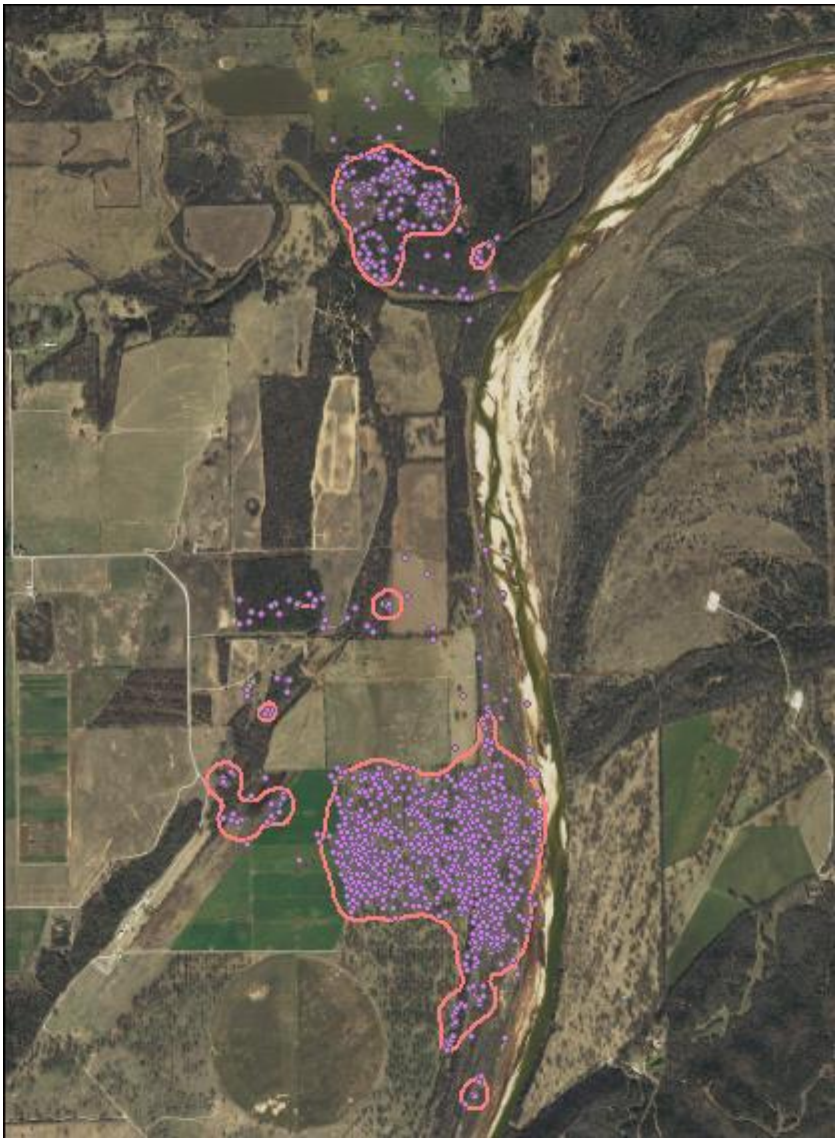

Figure 1-1: The home range of a wild pig (pink), estimated from its GPS tracking points (shown in purple). The home range represents the area of most concentrated space use, and is not meant to include exploratory ventures outside the most familiar and important areas to the animal that would not regularly be revisited (Burt, 1943; Powell & Mitchell, 2012).

To research spatial-ecological processes, the geographical extent of processes must be measured. Technological development has affected how animal space use is recorded and mapped, encouraging the development of new home range estimators (Fieberg & Kochanny, 2005; Laver & Kelly, 2008; Walter, Onorato, & Fischer, 2015) and in some cases rendering obsolete older methods (Kie et al., 2010). Therefore, it is the goal of researchers to take advantage of technological developments to refine methods used to estimate space use, and address meaningful ecological problems (Kie et al., 2010; Signer & Fieberg, 2021). One prominent example is the increasing use of global positioning systems (GPS) as a means of recording animal space use, and the development of more accurate (and ecologically informative) home range estimators that leverage the finer spatial resolution, reliability and temporal sequence of GPS tracking data (Fieberg & Kochanny, 2005; Walter et al., 2015).

Indeed, GPS tracking devices are an increasingly popular tool for measuring animal space use in ecological research due to the increased volume, resolution and reliability of tracking data, ability to track wide-ranging or hard to observe species, and opportunity to incorporate biological and environmental sensors (Cagnacci, Boitani, Powell, & Boyce, 2010; Tomkiewicz, Fuller, Kie, & Bates, 2010). Because of these attributes, in particular the higher volume and spatial-temporal resolution of tracking data, researchers come more close to measuring the continuous spatial-temporal reality of animal space use, and capturing the uneven space use of animals (Fieberg & Kochanny, 2005). These measurements and estimators of space use are less likely to overestimate the spatial extents of animals' ranges, and provide insight into the relative importance of different areas within an animal's total spatial extent (Laver & Kelly, 2008; Lichti & Swihart, 2011).

1.1.2 Movement and dynamic interaction

For some ecological questions, overall space use is less important than animal movement behaviour. To move away from descriptors of animal space use (such as some home range estimators), and gain insight into the underlying mechanisms driving space use, one must consider animal movement (e.g. how does an animal decide where to go, and how does this affect its overall space use?) (Kie et al., 2010; Moorcroft, Lewis, & Crabtree, 1999). Such questions are the domain of movement ecology, as sub-discipline of spatial ecology which is the study of the interplay of internal motivations and external factors affecting organismal movement across time scales (Nathan, 2008). Movement ecology is concerned with the biology of the animal in question that affects its motivation (why move? E.g. hunger), cognitive ability and decision making (where to move? E.g. sense of smell, knowledge of foraging areas), and biomechanical mechanisms of physically moving (how to move? E.g. galloping, short sprints, etc.) and environmental factors ultimately resulting in movement. For instance, Morelle et al. (2015) use these components of movement ecology to structure their review of the movement of wild pigs.

Movement is also important in comparing animal space use; for instance, comparing the home ranges of two animals cannot determine if the animals ever actually met, regardless of the similarity of their space use. Using GPS tracking, animal movement can be measured in terms of the spatial location and temporal sequence of GPS recordings (fixes) (Long & Nelson, 2013b). The temporal component of GPS tracking data also allows researchers to quantify the interdependency of animals' movement, called dynamic interaction (Long & Nelson, 2013a; Long, Nelson, Webb, & Gee, 2014). Measuring dynamic interaction centres on identifying (Laube, Imfeld, & Weibel, 2005; Laube, Kreveld, & Imfeld, 2005) and quantifying (Long et al., 2014; Miller, 2015) the occurrence of related movement to gain insight into animal behaviours, such as attraction between individuals (Cole, 1949).

1.1.3 Social structure

Animals form social groups based on kinship (Hamilton, 1964), mutually beneficial behaviour, social hierarchy (Clutton-Brock, 2009), or a variety of other reasons. Social grouping cause animals to associate with preferred individuals more than non-selected individuals. The uneven association patterns in social animal populations characteristic of group forming stand in contrast to structures where individuals mix homogenously, such as the ideal gas model (Bansal, Grenfell, & Meyers, 2007; Dougherty, Seidel, Carlson, Spiegel, & Getz, 2018). Social groups in animal populations and space use and movement are closely related and the former can influence the latter (Bode, Wood, & Franks, 2011). Accordingly, measuring and understanding the relationships between animal sociality and movement has become a popular lens to gain insight into animal behaviours (Wey, Blumstein, Shen, & Jordán, 2008).

Broadly, social structure can be thought of as individuals in a population tied together by interactions, which constitute relationships, which constitute the overall structure (Hinde, 1976) (Fig. 1-2). Therefore, the term social structure refers to the overall patterning of relationships between all individuals when used in this thesis, while the terms relationship, association, interaction, or contact refers to the tie between specific individuals (e.g. a pair of individuals) within the population, akin to 'relationship' in Fig. 1-2. Mathematical graph theory, a framework for describing relationships between associated objects, is commonly used to model and investigate animal social structure in social network analysis (SNA). The uneven association patterns characteristic of animal social structure are represented well by social networks, where the measurement of interactions between individual animals can be used to quantify their relationship, the patterning of which across different dyads of individuals in the population describes the overall structure (Borgatti & Halgin, 2011; Farine & Whitehead, 2015) (Fig. 1-2). Animal social networks are used to describe the overall social structure and roles/positions of individuals within it, but social networks can also be used as a proxy for other ecological processes that are affected by the heterogeneity of associations in an animal population, such as disease transmission (Craft, 2015a; M. J. Silk et al., 2017, 2019). The quantitative structure of social networks also makes SNA suitable for statistical hypothesis testing to identify non-random structures and factors affecting the underlying interactions (Croft, Madden, Franks, & James, 2011; Farine & Whitehead, 2015; Spiegel, Leu, Sih, & Bull, 2016).

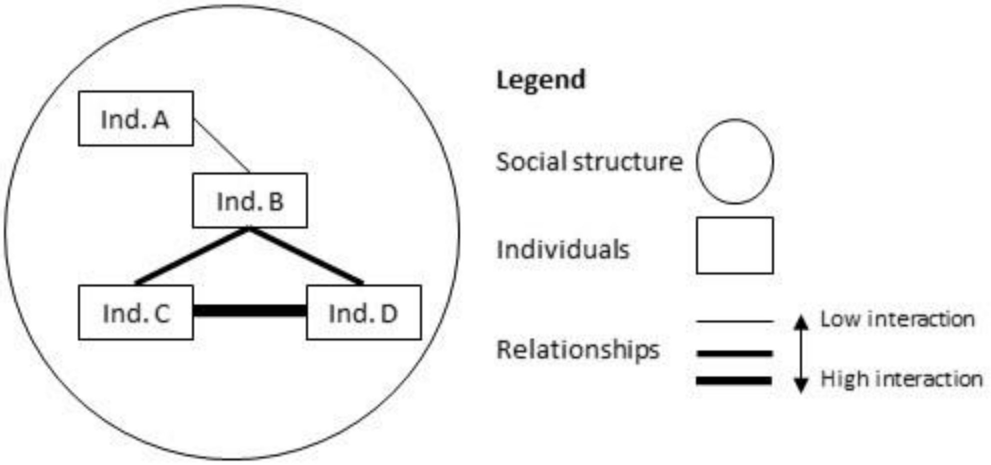

Figure 1-2: A social network diagram of a simple social structure, consisting of four individuals (Ind. A, Ind. B, Ind. C and Ind. D) tied together by relationships, which are composed of interactions varying in quantify or strength. Relationships in social networks can be measured by the interrelatedness of the movement of individuals using GPS tracking, which often mirrors real social structure due to contact heterogeneity and the uneven association patterns between individuals in a socially structured population. Social network analysis can provide insight into the overall social structure of an animal population, and the relative positions and roles of individuals within it, such as the observation that individual B has the most connections, or that individuals C and D are the most strongly associated.

The uneven association patterns of social animals are usually manifested spatially in a process called contact heterogeneity, where individuals are more often in close spatial proximity to their socially associated counterparts, and further apart from non-associated individuals (Bansal et al., 2007; Craft, 2015a; Krause, Lusseau, & James, 2009). GPS tracking is suitable for measuring spatial associations and contact heterogeneity, which can be used as the measurement of relationships, defining social structure (providing the measure of spatial association reflects the spatial patterning of social groups [Farine, 2015]). Various measures of dynamic interaction, such as proximity analysis (a measure of the distance between individuals over time) can be used to quantify spatial associations in the social network, representing interactions and associations between animals (Long et al., 2014; Whitehead, 1997). Therefore, GPS tracking and dynamic interaction are suitable methods for describing and analyzing animal social structures and behaviours (Sih, Hanser, & McHugh, 2009; Wey et al., 2008), and spatial-ecological processes affected by animal social structure (Chen & Lanzas, 2016; Craft, 2015a). Some examples of journal articles involving SNA, GPS tracking, dynamic interaction and spatial associations are presented in table 1-1.

Table 1-1: A selection of journal articles where dynamic interaction was measured in GPS tracking data for the purpose of analyzing social relationships. Each article measures the spatial proximity of individuals over time, a simple measure of dynamic interaction, to quantify relationships between individuals in a social network.

Authors	Animal researched	Spatial data collection tool	Measure of spatial association	Ecological question
Spiegel et al., 2016	Sleepy lizards (*Tiliqua rugosa*)	GPS tracking units	Proximity analysis	Are spatial associations driven by social movement behaviour?
Peignier et al., 2019	Caribou (*Rangifer tarandus*)	GPS tracking collars	Proximity analysis	Are social associations affected by attraction or resources?
Jones et al., 2020	Australasian gannets (*Morus serrator*)	GPS tracking collars	Proximity analysis and other dynamic interaction metrics	Are social associations affected by changes in behavioural state?
McClanahan, Rosell, & Mayer, 2020	Eurasian beaver (*Castor fiber*)	GPS tracking units	Proximity analysis	How spatially cohesive are beaver social pairs?

1.1.4 Wild pig ecology, impacts and management

Wild pigs (*Sus scrofa*) are a widely distributed pest/invasive species in their native Eurasia and in North America and Australia (Barrios-Garcia & Ballari, 2012). Wild pigs in Eurasia refer to the Eurasian wild boar, while invasive wild pigs is an umbrella term for Eurasian wild boar, escaped domesticated pigs and hybrids of the two in their non-native range (Keiter, Mayer, & Beasley, 2016). Wild pigs were introduced in North America for agriculture and sport hunting, and populations were established in the wild through escaped livestock or deliberate introductions for hunting (Graves, 1984; Giovanna Massei, Roy, & Bunting, 2011; Mayer & Brisbin, 1991). Since their introduction, wild pig populations have increased and spread across North America (Bevins, Pedersen, Lutman, Gidlewski, & Deliberto, 2014; Gipson, Hlavachick, & Berger, 1998). Large established wild pig populations are responsible for significant damages to crops, livestock, wildlife and natural environments in the order of $1.5 billion USD annually (Barrios-Garcia & Ballari, 2012; Pimental, 2007).

Female wild pigs are a social animal, occurring in groups of one to several breeding age females and their young, while males are usually solitary (Graves, 1984). A particular concern with wild pigs are their potential to transmit disease to livestock, other wildlife, and humans (Barrios-Garcia & Ballari, 2012). It is increasingly recognized that the spatial and social heterogeneity of animal populations affects disease transmission (Bansal et al., 2007; Craft, 2015a; Dougherty et al., 2018; M. J. Silk et al., 2017, 2019). This has motivated research on the density and social structure of wild pigs (Pepin et al., 2016; Podgórski, Apollonio, & Keuling, 2018), which affects the dynamics of disease transmission (Cowled & Garner, 2008). Further, wild pig social and spatial associations have been used in predictive models of disease transmission (Pepin, Golnar, & Podgórski, 2021; Yang et al., 2021). However, the social structure and dynamics of wild pigs remains an important research topic as some aspects remain unclear, such as the cohesiveness or independence of wild pigs belonging to the same sounder, as well as factors affecting group dynamics such as the fission of large groups, or dispersal from the natal group (Beasley, Ditchkoff, Mayer, Smith, & Vercauteren, 2018). Such wild pig social dynamics have the potential to affect disease transmission, population density, range expansion, and other harmful effects.

A number of methods have been employed by stakeholders to manage wild pig populations, usually seeking to prevent or remove established populations (Campbell & Long, 2009; Centner & Shuman, 2015; Giovanna Massei et al., 2011). Common methods of removal are usually lethal, and include hunting, trapping, poisoning, or non-lethal methods such as fertility control. Preventative measures include fencing, diversionary feeding, and others (Giovanna Massei et al., 2011). The unique behavioural and movement ecology of wild pigs also directly impacts the success of management strategies. The challenges of wild pig management posed by their unique behavioural and movement ecology are reviewed by Keiter & Beasley (2017), and include their flexible and fast reproductive biology, intelligence and cathemerality that allows them to resist and respond to hunting pressure, avoid recapture in traps, and repopulate/reinvade managed areas. Management is also complicated by human conflicts, such as ethical concerns, stakeholder interest, and self-sabotage due to the value of wild pigs as a sport hunting game species (Bevins et al., 2014; Giovanna Massei et al., 2011). Knowledge of wild pig sociality is leveraged to increase the success of management actions, such as the 'Judas pig' hunting method, and developing species specific trapping strategies (Gaskamp, Gee, Campbell, Silvy, & Webb, 2021). In the Judas pig method, one female is captured, attached with a GPS tracking collar and released, allowing it to rejoin a group. The group is then located and removed, with the exception of one female, and the process is repeated, providing an effective method for removal of lingering or low density populations (Giovanna Massei et al., 2011). Finally, the successfulness of wild pig management actions can also be affected by unintended consequences and responses by wild pig populations, such as altered spatial or movement behaviour (Bastille-Rousseau et al., 2021; Fischer et al., 2016) or increased reproductive activity (Hanson et al., 2009).

1.2 Research Questions and Objectives

GPS tracking can provide detailed movement data suitable for measuring dynamic interaction and relationships between animals, providing insight into animal social structure, dynamics, and behaviour. Sociality is an important factor in the spatial ecology, movement, harmful impacts and management of wild pigs, making it a topic in need of further research. Specifically, Beasley et al. (2018) and Keiter et al. (2017) advocate for research that describes within-group social dynamics of wild pigs to improve knowledge of wild pig ecology and inform their management. Guided by these research topics, this thesis seeks to address the questions:

1) How heterogeneous are wild pig spatial and social associations between individuals and within associated pairs over time?

2) How can individuals be assigned to groups based on spatial associations measured from GPS tracking data?

3) Does the cohesiveness of associated pairs vary based on the attributes of the paired individuals?

In response to these questions, it is the objective of this thesis to:

1) Quantify the strength of association and identify social associations between wild pigs using GPS tracking data

2) Measure and compare spatial associations within pairs over time, and between pairs by sex and age of paired individuals

The findings of analyses into these questions should improve upon how social structure in wild pigs (and other socially structured animals) can be measured and identified in GPS tracking data, and provide a better understanding of what group belonging actually means in terms of the spatial relationships between wild pigs.

1.3 Thesis Structure

This thesis is an integrated article style, composed of four chapters: an introduction, two stand-alone analysis chapters and a conclusion. The introduction (chapter one) provides a general literature background on key research topics, research questions and objectives, and outlines the structure of the thesis. The research questions and objectives are addressed in the two analysis chapters (chapters two and three), which are composed in the general style of a manuscript, consisting of introduction, methods, results and discussion sections. Chapter two focuses on the first and second research question and the first research objective: quantifying spatial associations between wild pigs and identifying social wild pig pairs using GPS tracking data. Chapter three further addresses the first and second research questions with more data from additional studies, and addresses the third research question and the second research objective: measuring and comparing the cohesiveness of wild pig social pairs over time and between pairs by individual sex, age and strength of association. Chapters two and three are written as stand-alone articles, though chapter three includes and expands upon some of the results from chapter two with additional data and analysis. The conclusion (chapter four) addresses the research questions and objectives presented in chapter one with reference to the results of the analysis chapters. A final discussion is included concerning directions for future work in chapter four.

1.4 Research Area and Design

Wild pigs are well established and widespread in the southeastern United States, and damages and management actions are widespread as a result (Bevins et al., 2014; Centner & Shuman, 2015; Mayer & Brisbin, 1991). Wild pig GPS tracking data from four different study sites with established wild pig populations in the southeastern United States are analyzed in chapters two and three. In Chapter two, GPS tracking data of 29 wild pigs from one study area was analyzed, provided by research collaborator Stephen Webb of Noble Research Institute (NRI), Ardmore, Oklahoma. Chapter three also analyzes this data, in addition to another NRI study site, as well as openly available wild pig GPS tracking data published by Yang et al. (2021). The two NRI study sites are two nearby but separate research farms in Oklahoma, while the data retrieved from Yang et al. (2021) includes a research ranch in Florida, and a United States Department of Energy research area in South Carolina (Fig. 1-3). The movement of 104 unique GPS tracked wild pigs from all four study sites was analyzed in chapter three.

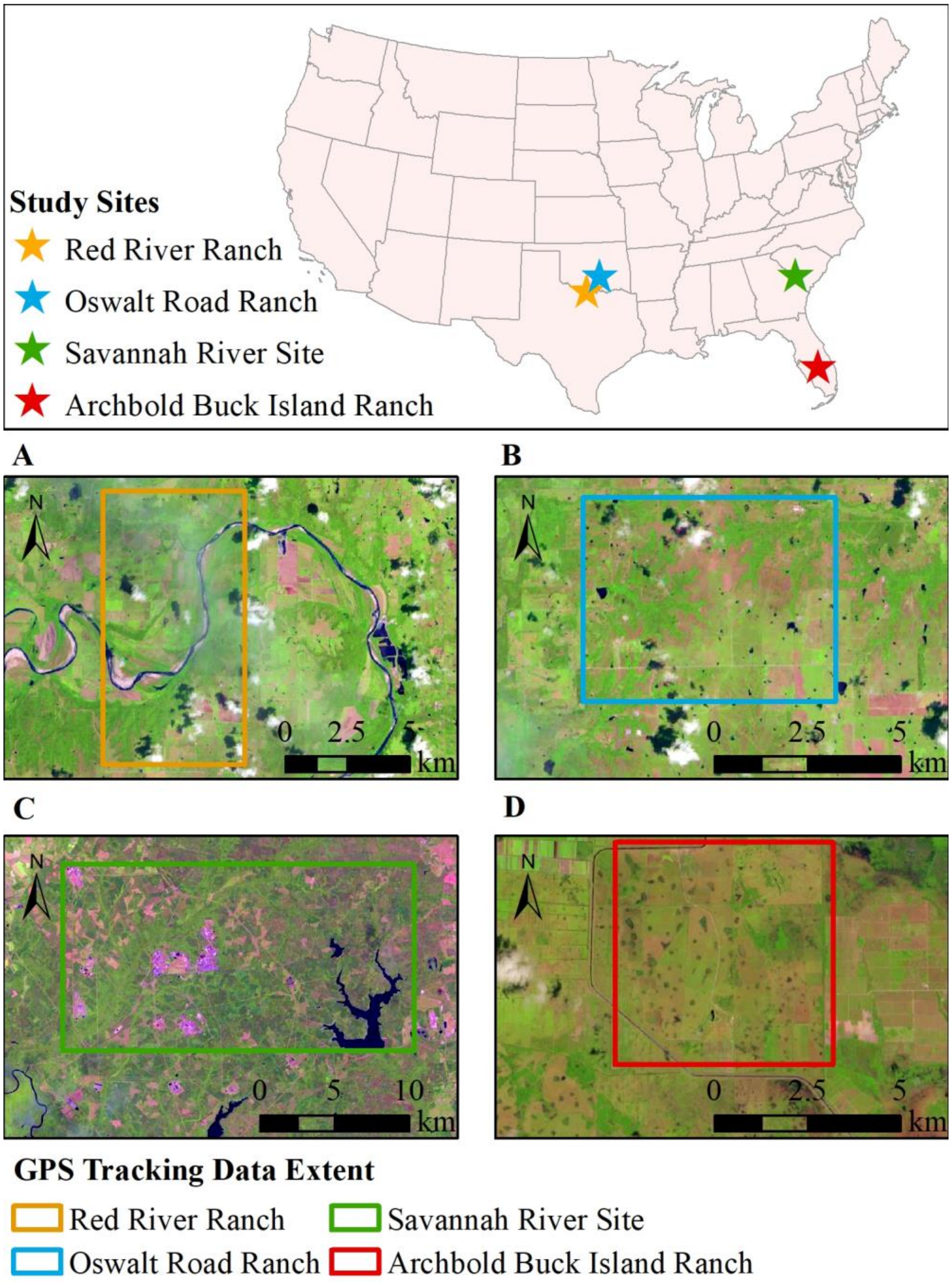

Figure 1-3: Study sites, including Red River Ranch (A), Oswalt Road Ranch (B), Savannah River Site (C) and Archbold Buck Island Ranch (D).

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Chapter 2

2 A test for identifying wild pig social associations with GPS tracking data

2.1 Introduction

Wild pigs (*Sus scrofa*) are escaped domesticated swine, Eurasian boar or hybrids of the two introduced to North America for agriculture and sport hunting (Keiter et al., 2016; Mayer & Brisbin, 1991). Due to their generalist ecology and deliberate introductions to new ranges, wild pigs have been a very successful invader in North America and have spread prolifically (Bevins et al., 2014; Delgado-Acevedo, Zamorano, Deyoung, & Campbell, 2021; Morelle et al., 2015). Female wild pigs (sows) occur in socially organized groups (sounders), comprised of one to several breeding age sows and their young, while males are mostly solitary except during breeding periods (Graves, 1984). Much of the regular activity and movement of sows is tied to group behaviours such as co-parenting, scrounger-producer foraging, learning from conspecifics, territoriality and more (Graves, 1984; Janeau, Cargnelutti, Cousse, Hewison, & Spitz, 1995; Kay et al., 2017; Morelle et al., 2015). Sounders are both socially and spatially distinct, as individuals spend most of their time in the presence of other group members and are much less likely to come in contact with non-group members (Podgórski, Lusseau, Scandura, Sönnichsen, & Jędrzejewska, 2014). Accordingly, the social behaviour, space use and movement of wild pigs are closely related.

Wild pigs are responsible for significant damages to habitat, wildlife, agriculture and livestock through destructive rooting, trampling and wallowing behaviour, predation, competition and disease transmission (Barrios-Garcia & Ballari, 2012). These harmful effects, along with their previous success and spread warrant significant management efforts to prevent their range expansion and remove established populations (Massei, Roy, & Bunting, 2011). The relationship between social structure and space use in wild pigs is directly related to their harmful effects and has contributed to their success and range expansion. For instance, the social structure of wild pigs influences the likelihood of contacts between individuals, which affects the risk of disease transmission (Pepin et al., 2016, 2021; Podgórski et al., 2018, 2014). Further, wild pig social structure and movement behaviours can directly affect management efforts, as wild pigs have been found to change their spatial behaviour, re-invade areas subjected to population removal, and learn from conspecifics in response to management efforts (Bastille-Rousseau et al., 2021; Fischer et al., 2016; Hanson et al., 2009; Massei et al., 2011). Because of the relatedness of their movement, sociality and harmful effects, wild pig movement is an important consideration in their management (Morelle et al., 2015).

The development of GPS tracking provides more opportunity for researchers to reliably compare and measure how animal movement is directly influenced by other individuals (termed dynamic interaction; Long & Nelson, 2013; Long, Nelson, Webb, & Gee, 2014). Proximity-based social networks (PBSN) are social networks where the strength of associations (edge weight) between individuals (nodes) is based on dynamic interaction rates between individuals (e.g. river otters *Lontra canadensis*: Gorman, Erb, McMillan, & Martin, 2006; caribou *Rangifer tarandus*: Peignier et al., 2019; tent-making bats *Artibus watsoni*: Chaverri, Gamba-Rios, & Kunz, 2007). While social networks can describe group structure and specific individuals' positioning within the network (Farine & Whitehead, 2015; Wey et al., 2008), they require further testing to identify any underlying patterns, such as preferential associations between individuals (Croft et al., 2011; Farine & Whitehead, 2015; Kemp & Manly, 1997). To test hypotheses in social networks, randomized networks can be generated by swapping network attributes (e.g. node identities, edge weights, group membership) across the network in a series of permutations, and the observed network can be compared for differences in network structure (e.g. sex based differences in bottlenose dolphin associations: Smolker, Richards, Connor, & Pepper, 1992). Though non-random associations can be detected, this type of test fails to identify the causes of spatial associations between individuals, as animal movement and associations can be influenced by a variety of environmental and social factors (Muller, Cantor, Cuthill, & Harris, 2018; Peignier et al., 2019).

To separate the influence of multiple factors that could affect observed dynamic interaction in a social network, the network null model needs to retain some conditions that also cause associations to occur in addition to those of interest in the alternate hypothesis. To achieve this, some structure in the telemetry data stream can be preserved in the null model to retain parts of the social-environmental context that influences animal movement. By randomizing data (i.e. creating new data, called pre-network randomization: Farine, 2017; or data stream randomization: Spiegel, Leu, Sih, & Bull, 2016) rather than randomizing network attributes, one can incorporate desired spatial-temporal or attribute constraints on possible associations, providing null model social networks where edge weights are not completely random and retain some context from the observed data. This is especially important in telemetry-based social networks as completely random null models can easily violate the constraints of space and time on individual movement, causing hypothesis testing error (Farine, 2017). This allows social network research using GPS tracking to go beyond describing observed social networks and patterns, and test for the effects of different movement influences (Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015; Spiegel et al., 2016).

Separating the influence of various factors that can affect wild pig dynamic interaction would provide better understanding of the relationship between movement, space use and social behaviour in wild pigs, as well as the risk of disease transmission (Beasley et al., 2018; Morelle et al., 2015). For instance, though sociality heavily influences wild pig movement and associations, factors such as resource distribution, landscape topography, weather and population density also influence wild pig movement and dynamic interaction (Castillo-Contreras et al., 2018; Johann et al., 2020; G. Massei, Genov, Staines, & Gorman, 1997; Pepin et al., 2016; Thurfjell et al., 2009). The influence of sociality on wild pig spatial associations can be identified through data stream randomization tests of a PBSN, where the effects of environmental and spatial-temporal constraints on movement are preserved in the null model. This can be achieved by temporally desynchronizing each individual in the data stream but preserving their movement tracks within themselves so that regular space use is preserved, but any synchronous movement behaviours are interrupted (Spiegel et al., 2016). Dynamic interaction in the randomized data stream between individuals will then be the effect of overall space use, so differences in the amount of dynamic interaction in the observed data will depend on synchronous movement. Here, GPS tracking data of wild pigs is used to measure a PBSN and develop a null model to identify how social movement behaviour affects observed dynamic interaction between individuals. Using these methods it is expected that wild pig social groups will be detected in the GPS tracking data, where the observed association rates between social group members will be greater than association rates that could be expected under random associations caused by regular space use. Separating the influences of various factors influencing wild pig dynamic interaction in a social network will provide a better understanding of how sociality affects wild pig space use and social relationships.

2.2 Methods

2.2.1 Study area

Wild pigs have repeatedly been introduced in the Southern United states for agriculture and sport hunting, resulting in a well-established range that includes the study area in Oklahoma, United States (Mayer & Brisbin, 1991). Wild pigs were captured by the Noble Research Institute (NRI) at their research ranch in Love County, Oklahoma, the Red River Ranch (RRR). RRR is a 1316 hectare agricultural research and demonstration farm with a large pecan orchard (150 hectares) and cattle pasture. RRR is located on the northern banks of the Red River, opposite small forested bluffs to the south, while smaller water systems such as the Walnut Bayou exit into the Red River nearby (Fig. 2-1). The mixed agricultural, forested and riparian areas in and around RRR provide a variety of potential habitat, food and water sources for wild pigs (Boyer, Fairbanks, Rohla, & Webb, 2020).

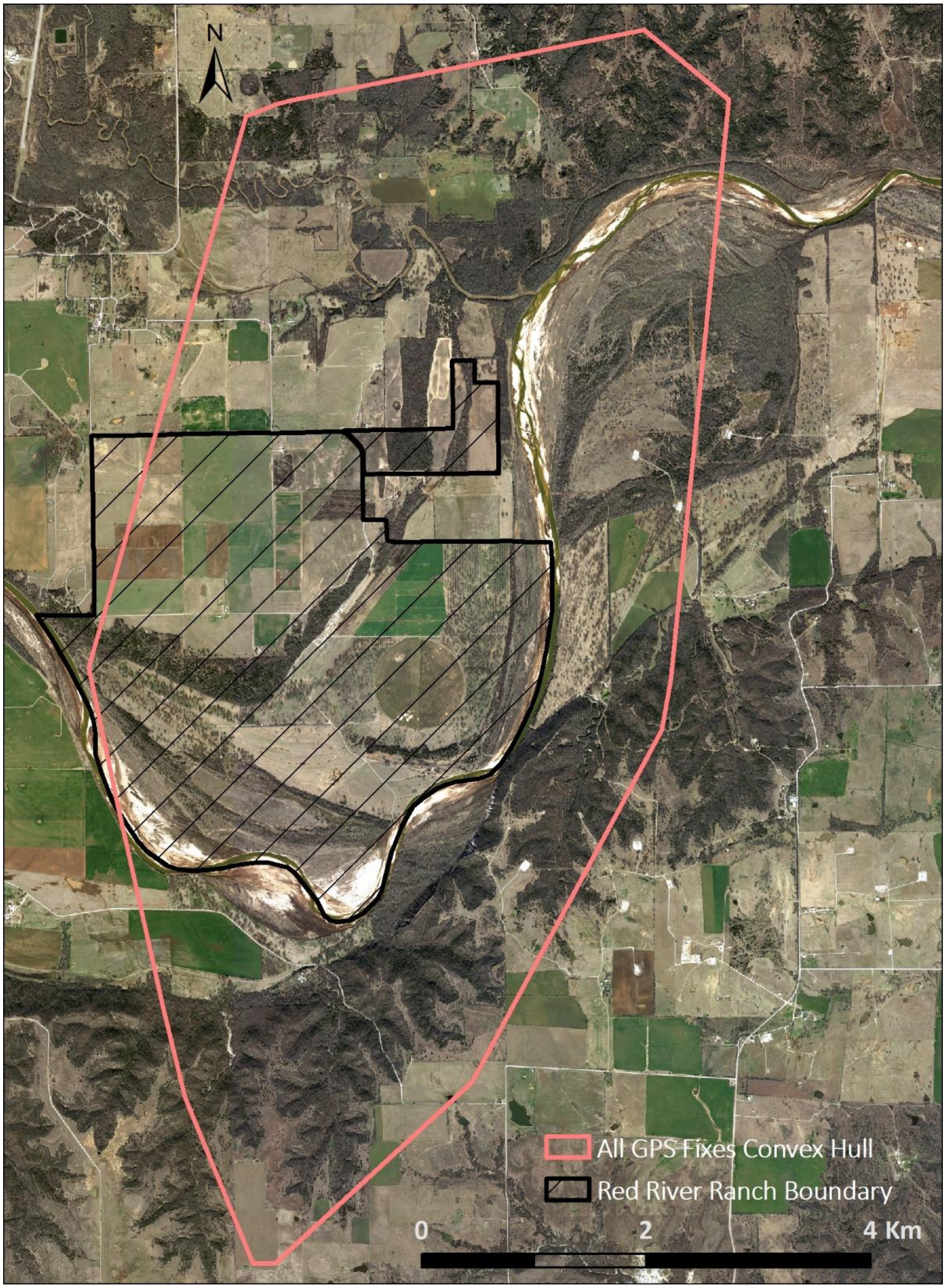


Figure 2-1: Aerial imagery of Noble Research Institute’s Red River Ranch and surrounding area, and the extent of all 2016 and 2017 GPS tracking points.

2.2.2 Data collection

Wild pigs were captured using BoarBuster^{TM} (W-W Manufacturing, Thomas, OK, USA) suspended drop enclosures, designed to capture entire sounders of wild pigs by remote operation (Gaskamp et al., 2021). Trapping procedures were designed to selectively trap at least two adult sows per sounder to be attached with GPS tracking collars, while minimizing other individuals trapped in order to maintain sounder cohesion and movement patterns, as all non-collared wild pigs trapped must be euthanized under the Oklahoma Wild Pigs Control Act (O.S. § 6-601). Captured wild pigs were immobilized using a Telazol® (Zoetis Inc., Kalamazoo, Michigan, USA) and Xylazine (MWI, Boise, Idaho, USA) mixture (2.2 mg/kg Xylazine and 4.4 mg/kg Telazol®) injection and fitted with GPS tracking collars (Vectronics Vertex Lite; Vectronics Aerospace GmbH, Berlin, Germany). GPS receiver accuracy for this model is published online by the manufacturer, and the mean accuracy for this model is 8 – 15 metres, with a finer expected accuracy for most fixes (Vectronics Aerospace GmbH, 2017). All non-target animals were euthanized. The GPS collars recorded locational coordinates and time (fixes) every 30 minutes for up to 78 days in the autumn of 2016 (n = 16) and 2017 (n = 13). A total of 98759 fixes were collected with an individual average of 72.8 days (min = 30, max = 78), where the average number of fixes-per-individual was 3406 ± 442, with an average fix success rate of 99.1% ± 2.4%. Trapping individuals in the same trap was considered a preliminary indication of sounder membership for the purpose of comparing and validating data stream randomization test results. From trapping, ten unique sounder pairs were identified across both study years while the remaining nine individuals were presumed to belong to their own unique sounders, for a total of 19 expected unique sounders (S. Webb, *unpublished data*, Appendix A). Sounders with a collared individual were tracked or recaptured using trapping and removed from the population at the conclusion of each study season. All wild pig trapping and handling and marking followed the American Society of Mammologists approved guidelines (Sikes, 2016).

2.2.3 Home ranges

To get a measure of the distance between individuals and spatial overlap of wild pigs of the study area, the home ranges and core areas of each individual were estimated.

Brownian bridge utilization distributions (BBUD) were constructed from the GPS tracking data, and the 95% volume contour was taken to represent the home range, and the 50% volume contour was taken to represent core areas (Horne, Garton, Krone, & Lewis, 2007). Brownian motion variance was estimated from the GPS tracking data using a maximum likelihood function as described by Horne et al. (2007), where motion variance is estimated by finding the optimum value that predicts intermediate GPS tracking fixes when a Brownian bridge is constructed between the fixes adjacent to the intermediate. The GPS telemetry error is assumed to be < 30 metres, which is more conservative than the expected < 15 metres accuracy for most fixes specified by the manufacturer.

Measures of spatial overlap were computed based on the joint space use of individuals. Individual BBUDs provide more informative measures of space use sharing between individuals than simple geometric home range overlap (e.g. area of overlap), as the relative likelihood of occurrence of each individual can be combined through various operations to produce a joint relative likelihood of occurrence surface (Fieberg & Kochanny, 2005). This preserves the heterogeneity of space use within each individual's home range when estimating two individuals' spatial overlap. Three measures of spatial overlap were performed: First, home range centroids were calculated to get a measure of the distance between home ranges and gauge the effect of distance between individuals on contact rates. Home range centroids were the geometric centroid of 95% volume contour utilization distributions. Next, home range and core area overlap was measured using the volume of intersection (VI) index, equal to the sum of the cell-by-cell minimum value of the two BBUDs:

$$\mathrm{VI} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \min\left[\widehat{\mathrm{UD}}_1(x,y), \widehat{\mathrm{UD}}_2(x,y)\right] dxdy \qquad [1]$$

Therefore, VI = 1 when two BBUDs are identical, and VI = 0 when no overlap occurs (Fieberg & Kochanny, 2005). As home ranges are 95% and core areas 50% of the volume of BBUDs, identical home ranges and core areas would have a VI of 0.95 or 0.5 respectively.

2.2.4 Spatial-temporal contacts

A common measure of dynamic interaction used in wildlife telemetry research are contact rates, where a contact between individuals is defined as the co-occurrence of individuals within a certain temporal and spatial threshold. Choosing time and distances to define contacts should reflect the ecological phenomenon of interest, which in this case is group membership. Therefore, to determine suitable contact parameters, a frequency distribution of all simultaneous (recorded within 15 minutes) GPS tracking fixes was measured. Based on capturing multiple individuals in the same trap, it is expected that some of the individuals in the data set would belong to the same sounder, and will therefore be spatially distinct from other individuals belonging to different sounders. As a result, a peak in the frequency distribution of distances between simultaneous fixes should occur at a low distance, where individuals are in the same sounder and regularly in close spatial proximity to group members, while other peaks should occur at greater distances, representing between-sounder spatial proximity. The lowest natural break in this frequency distribution should represent the upper limit of within-sounder proximity of group members. The first significant natural break in the distribution of distance between fixes occurs at 618 metres, though the proportion of distances increases as distance approaches zero metres (Fig. 2-2). To further explore the expected within-sounder distances between individuals, the same procedure was performed for only individuals captured at the same time (Fig. 2-3). The finer resolution shows a significant peak of fixes within 100 metres that increases towards 0 metres distance. Therefore, for the purposes of creating a PBSN modelling wild pig social structure, 100 metres was used as a contact distance threshold for measuring dynamic interaction in a social network of wild pigs. A 100 metre contact distance is more conservative than previous similar studies on wild pigs social structure (Iacolina, Scandura, Bongi, & Apollonio, 2009; Podgórski et al., 2014).

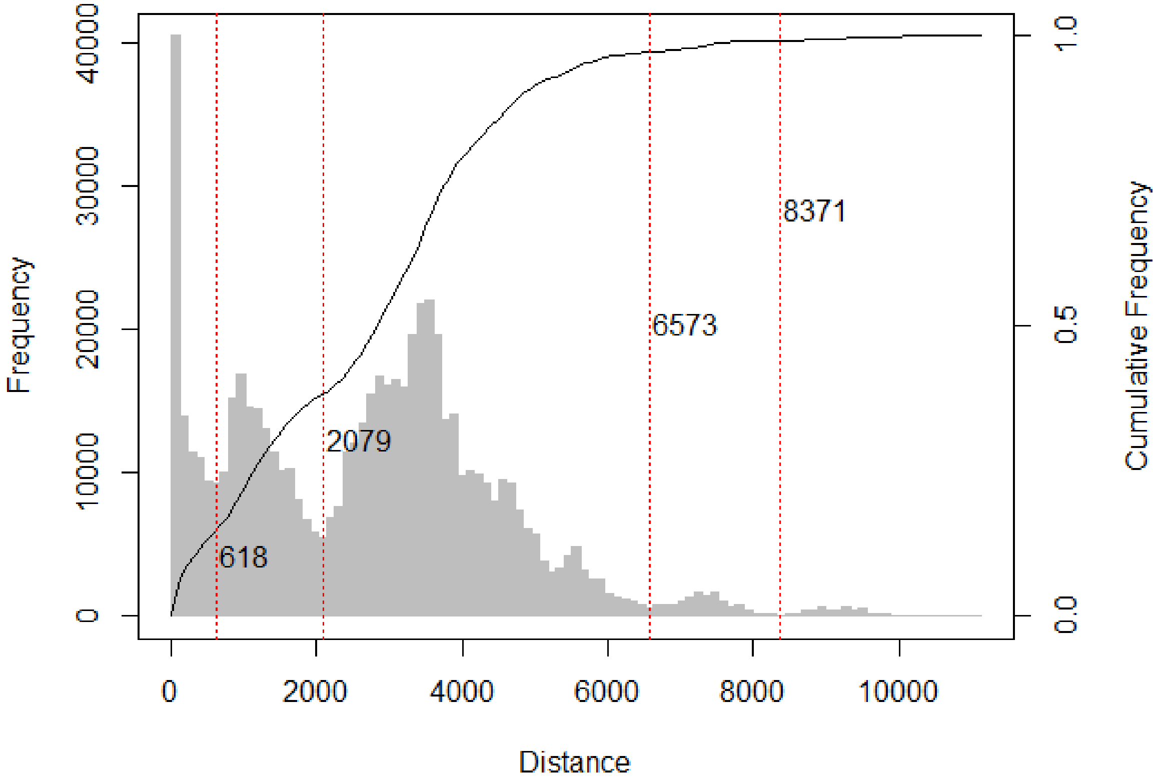


Figure 2-2: Distance in metres between all simultaneous GPS tracking fixes. A significant peak of fixes occurs approaching 0 metres, likely representing the upper limit of within group spatial proximity of sounder members. However, some detail is lost at low distances due to coarse bin sizes.

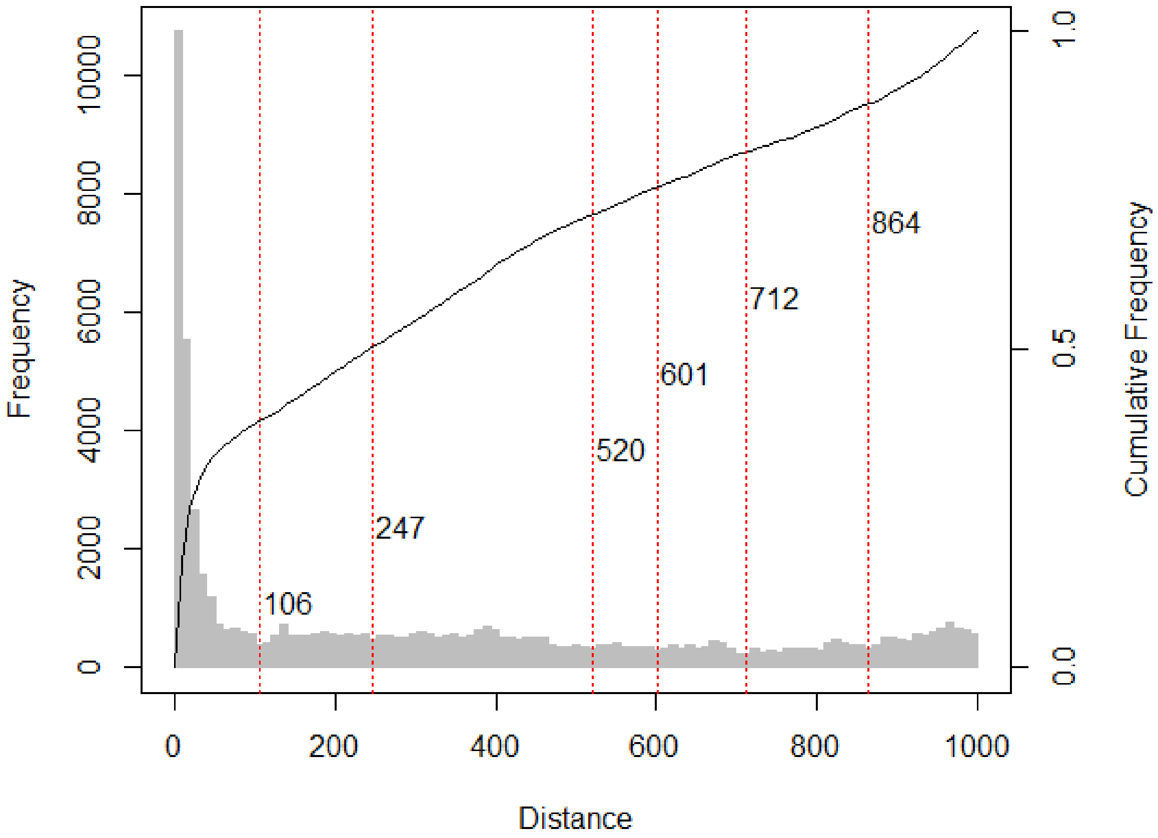


Figure 2-3: Distance in metres between all simultaneous GPS tracking fixes of individuals captured in the same trap. The break at 106 metres is taken to represent the upper limit of within group proximity of individuals (rounded to 100 metres).

2.2.5 Social network analysis

Contact rates (edges) between individuals (nodes) were used as a measure of spatial association to model wild pig social structure in a PBSN. The simple ratio index (SRI) was used as the measure of spatial association between individuals:

$$\mathrm{SRI} = \frac{x}{x+y_{AB}+y_A+y_B} \quad [2]$$

where x is the number of contacts between individuals A and B, y_{AB} is the number of simultaneous fixes without a contact, y_A is the number of individual A's fixes without a simultaneous fix of individual B, and y_B is the number of individual B's fixes without a simultaneous fix of individual *A*. SRI = 1 when two individuals are always recorded in contact with one another, and SRI = 0 when two individuals are never recorded in contact. SRI is appropriate for describing how often a pair of individuals is in contact when the recorded sample is continuous, and no inferences need be made about the times when animals were not observed (i.e. when fix success rate is very high across all individuals) (Cairns & Schwager, 1987; Farine & Whitehead, 2015). SRI has been used to quantify spatial associations in models of social structure in caribou *Rangifer tarandus* (Peignier et al., 2019), sleepy lizards *Tiliqua rugosa* (Spiegel et al., 2016), killer whales *Orcinus orca* (Parsons, Balcomb, Ford, & Durban, 2009) and others (Farine & Whitehead, 2015).

To determine if observed contact rates are due to social behaviour or other factors affecting regular space use such as resource distribution, the observed PBSN was compared to a reference distribution of 99 permutations of a PBSN created by data stream randomization. The GPS tracks of each individual in the study were divided into chunks one day in length and reordered by day independently of each other, keeping the daily structure of each GPS track intact. This permutation strategy preserves daily movement patterns within individual tracks to maintain the influence of environmental features, resource distribution and spatial-temporal constraints on movement. Accordingly, comparing the observed association rates to this null model distribution of networks provides a test where synchronous movement (i.e. being in the same place at the same time) is preserved in the observed network, but any synchronous movement is disrupted by the reordering of days in the randomized networks, where contact rates depend on being in the same place on different days (Fig. 2-4). Since movement tracks are preserved within individuals, individual home ranges in the observed and randomized data are essentially identical. The significance of the observed association rates is measured by a rank-permutation test, where the rank of observed SRI in the distribution of the 99 randomized permutations is used to determine the test statistic. The test statistic gives the probability of randomized iterations of the network giving greater SRI than observed: $P = 1 - (R/(n + 1))$ where R is the number of randomized iterations with equal or less SRI and n is the number of observed and randomized iterations. Therefore, when the observed SRI is greater than all randomized iterations, $P < 0.01$ (Benhamou, Valeix, Chamaillé-Jammes, Macdonald, & Loveridge, 2014; Berry, Johnston, & Mielke, 2011).

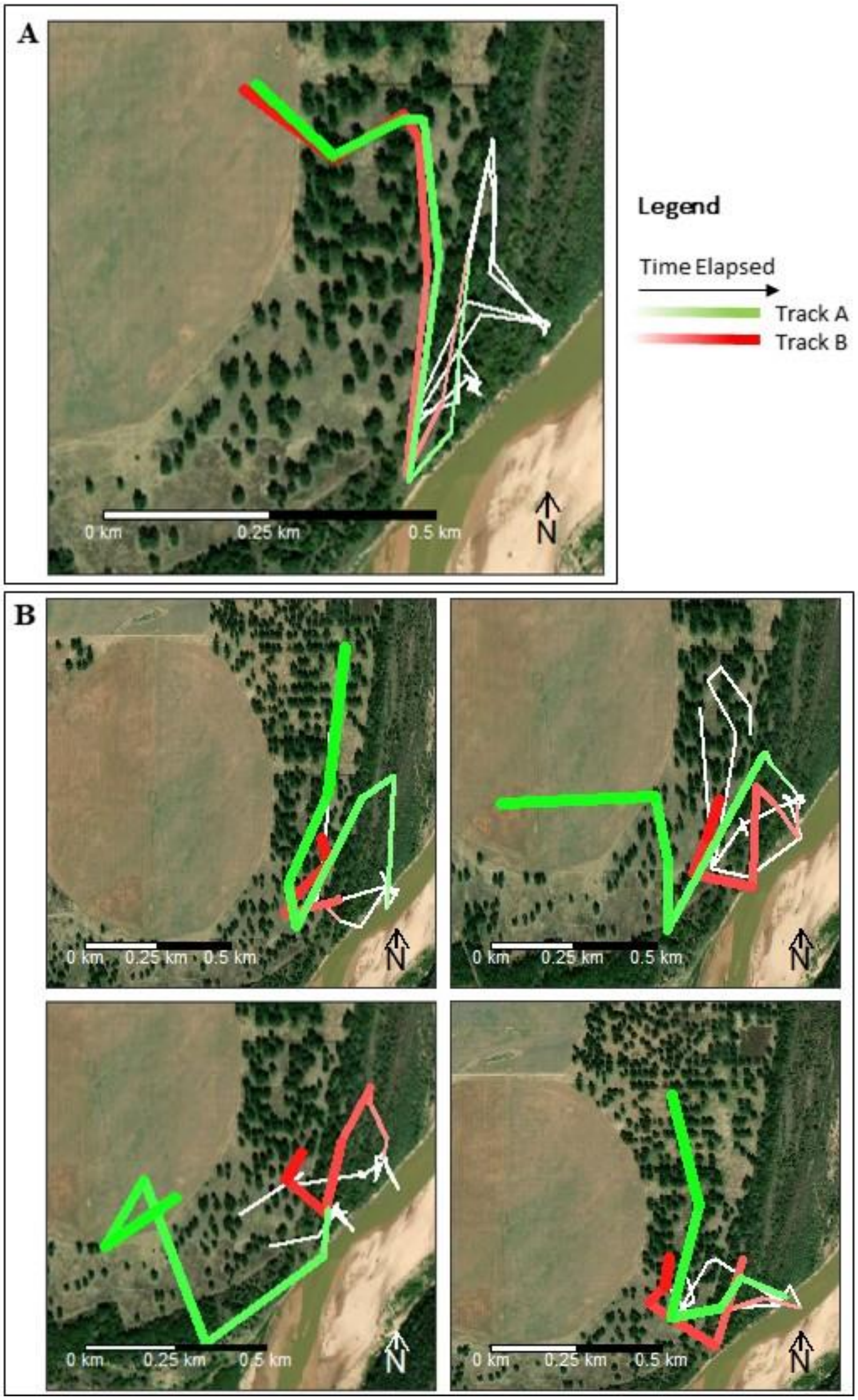


Figure 2-4: The effect of data stream randomization on wild pig movement paths for a social pair. Each frame shows ten consecutive fixes (five hours). The observed paths (A) display synchronous movement, where individuals are constantly in contact

along their paths. Each of the four bottom frames (B) show a permutation of the randomized data stream, where the same two individuals' paths are desynchronized and contacts are fewer but can occur due to spatial overlap.

BBUDs, Home ranges and VI were calculated using the R package *adehabitatHR* (Calenge, 2006). The R package *wildlifeDI* (Long et al., 2014) was used to generate frequency distributions of distances between fixes. The R packages *spatsoc* (Robitaille, Webber, & Vander Wal, 2019) and *asnipe* (Farine, 2013) were used to measure contacts, construct and randomize PBSNs.

2.3 Results

2.3.1 Home ranges

The mean home range size for each individual was 112.93 hectares ± 58.39 hectares, and the mean core area size was 9.82 hectares ± 5.84 hectares. The home range centroids of wild pigs expected to belong to the same sounder through trapping were mostly within 100 metres, while non-sounder home range centroids tended to be 1-2 km separated (Fig. 2-5). The home ranges and core areas of wild pigs expected to the same sounder from trapping tended to be moderately or very similar. Some outliers occurred in the case of individuals not expected to belong to the same sounder with moderately or very similar home ranges which were very close in geometric centroid proximity (Fig. 2-5).

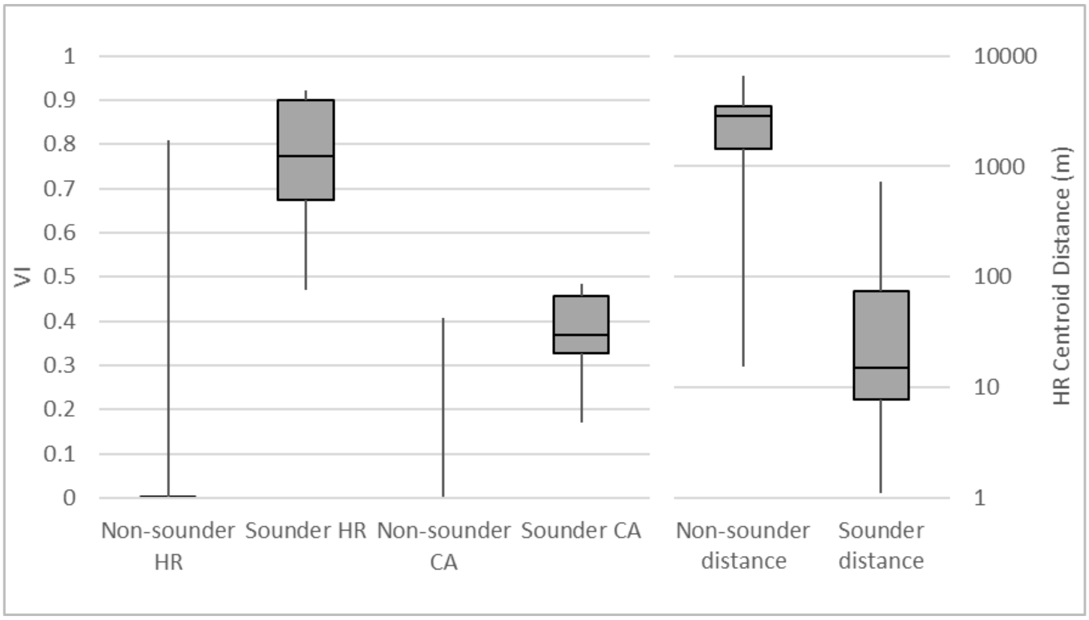


Figure 2-5: Non-sounder versus sounder by trapping home range and core area volume of intersection, and home range centroid distance. Most individuals not trapped together had very low measures of spatial overlap, although some outliers with high measures of spatial overlap also occurred.

2.3.2 Spatial-temporal contacts

A total of 41444 contacts were detected over both study years (max = 6108, min = 0). All individuals except for three had more than 1000 contacts, and only one individual had zero contacts detected (Fig. 2-6). Because each pairwise contact was counted as a unique contact, several individuals were observed with more contacts than recorded GPS tracking fixes, indicating these individuals had significant amounts of contacts with more than one other individual in the study area (Fig. 2-6, Appendix A).

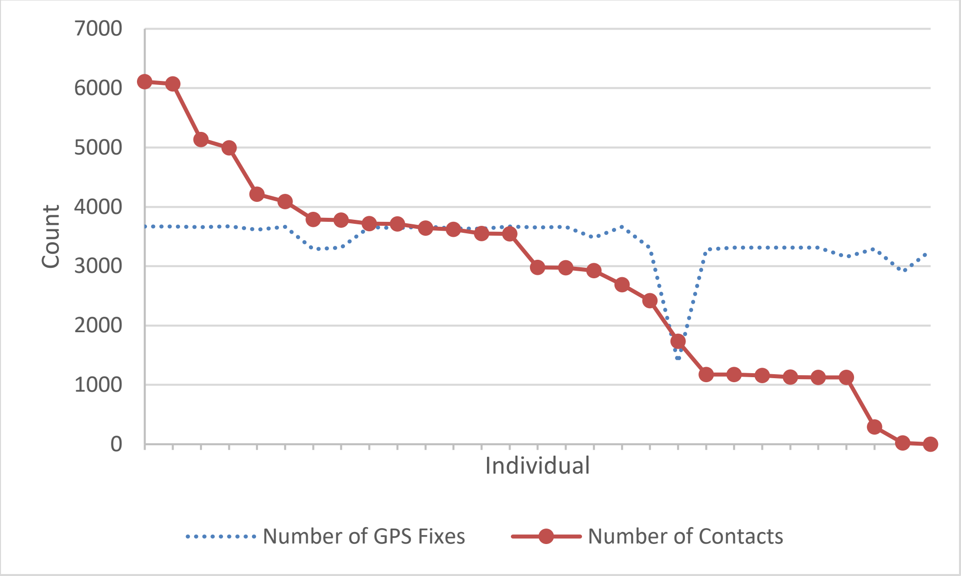
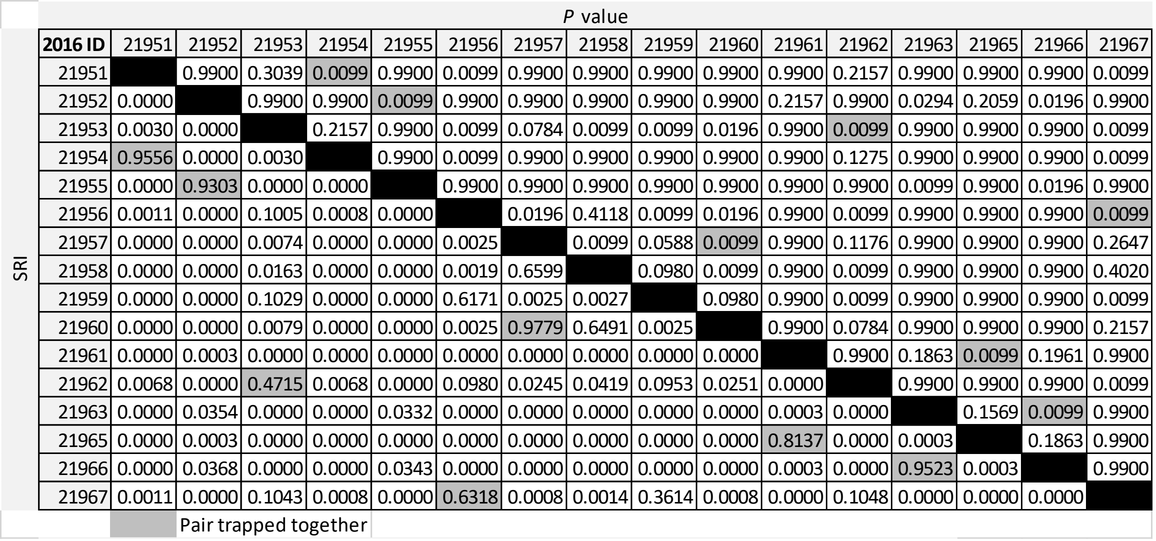


Figure 2-6: Number of contacts compared to number of GPS fixes recorded for each individual over both study years (*n* = 29). Since the maximum number of fixes recorded for any one individual was < 3700, individuals with more contacts than total fixes were frequently in contact with more than one other individual.

2.3.3 Social network analysis

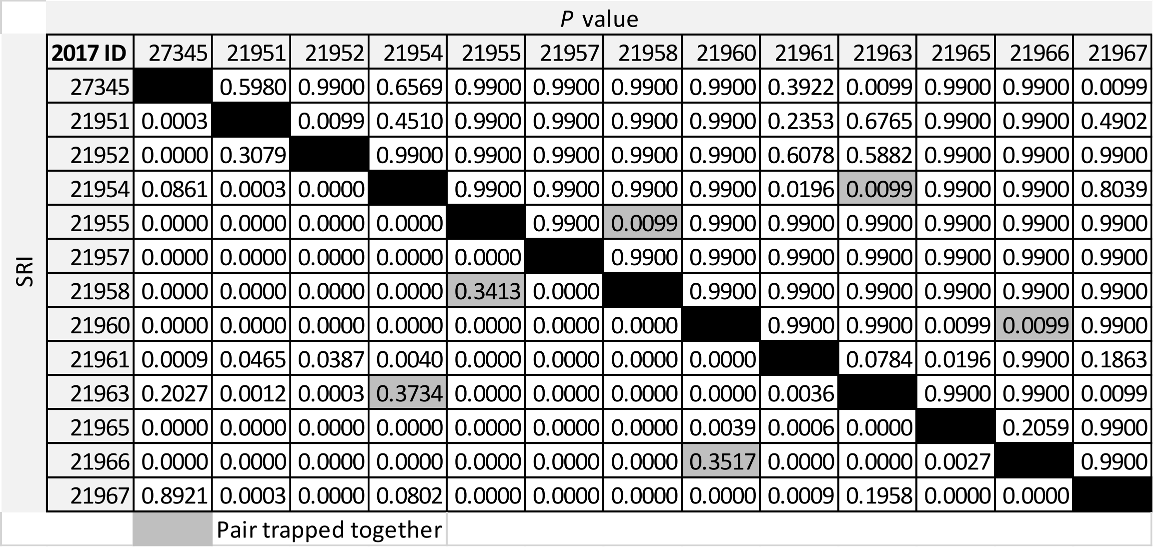
A PBSN was constructed using the contact rates derived from the GPS tracking data. Each pair of wild pigs expected to belong to the same sounder from trapping had relatively high contact rates, while some pairs not expected to belong to the same sounder also had high contact rates. Two triads with high association rates that were not expected to belong to the same sounder based on trapping were also detected. Many pairs had no contacts at all, while some pairs in both study years had very few contacts (e.g. SRI < 0.01, < 37 contacts) (Table 2-1). The data stream randomization test provided a distribution of contact rates that could be expected under regular space use activity to which observed contact rates were compared (Fig. 2-7). The observed SRI of all individuals expected to belong to the same sounder ranked higher than all randomized association rates, indicating their spatial association rates were dependent on synchronous movement. The observed SRI of some other pairs not trapped together also ranked greater than all randomized iterations, as did some very low SRI pairs (SRI < 0.01), representing very short social interactions or rare contacts never occurring in any randomized iteration of the data stream due to very low spatial overlap (Table 2-1).

Table 2-1: Social network of GPS tracked wild pigs split by study year. For each unique pair, contact rate (SRI) is shown in the lower triangle and the significance of the rank-permutation test (*P*) is shown in the upper triangle. Pairs that were captured in the same trap, and therefore were expected to belong to the same sounder are highlighted.



		P value															
	2016 ID	21951	21952	21953	21954	21955	21956	21957	21958	21959	21960	21961	21962	21963	21965	21966	21967
SRI	21951	■	0.9900	0.3039	0.0099	0.9900	0.0099	0.9900	0.9900	0.9900	0.9900	0.9900	0.2157	0.9900	0.9900	0.9900	0.0099
	21952	0.0000	■	0.9900	0.9900	0.0099	0.9900	0.9900	0.9900	0.9900	0.9900	0.2157	0.9900	0.0294	0.2059	0.0196	0.9900
	21953	0.0030	0.0000	■	0.2157	0.9900	0.0099	0.0784	0.0099	0.0099	0.0196	0.9900	0.0099	0.9900	0.9900	0.9900	0.0099
	21954	0.9556	0.0000	0.0030	■	0.9900	0.0099	0.9900	0.9900	0.9900	0.9900	0.9900	0.1275	0.9900	0.9900	0.9900	0.0099
	21955	0.0000	0.9303	0.0000	0.0000	■	0.9900	0.9900	0.9900	0.9900	0.9900	0.9900	0.9900	0.0099	0.9900	0.0196	0.9900
	21956	0.0011	0.0000	0.1005	0.0008	0.0000	■	0.0196	0.4118	0.0099	0.0196	0.9900	0.0099	0.9900	0.9900	0.9900	0.0099
	21957	0.0000	0.0000	0.0074	0.0000	0.0000	0.0025	■	0.0099	0.0588	0.0099	0.9900	0.1176	0.9900	0.9900	0.9900	0.2647
	21958	0.0000	0.0000	0.0163	0.0000	0.0000	0.0019	0.6599	■	0.0980	0.0099	0.9900	0.0099	0.9900	0.9900	0.9900	0.4020
	21959	0.0000	0.0000	0.1029	0.0000	0.0000	0.6171	0.0025	0.0027	■	0.0980	0.9900	0.0099	0.9900	0.9900	0.9900	0.0099
	21960	0.0000	0.0000	0.0079	0.0000	0.0000	0.0025	0.9779	0.6491	0.0025	■	0.9900	0.0784	0.9900	0.9900	0.9900	0.2157
	21961	0.0000	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	■	0.9900	0.1863	0.0099	0.1961	0.9900
	21962	0.0068	0.0000	0.4715	0.0068	0.0000	0.0980	0.0245	0.0419	0.0953	0.0251	0.0000	■	0.9900	0.9900	0.9900	0.0099
	21963	0.0000	0.0354	0.0000	0.0000	0.0332	0.0000	0.0000	0.0000	0.0000	0.0000	0.0003	0.0000	■	0.1569	0.0099	0.9900
	21965	0.0000	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.8137	0.0000	0.0003	■	0.1863	0.9900
	21966	0.0000	0.0368	0.0000	0.0000	0.0343	0.0000	0.0000	0.0000	0.0000	0.0000	0.0003	0.0000	0.9523	0.0003	■	0.9900
	21967	0.0011	0.0000	0.1043	0.0008	0.0000	0.6318	0.0008	0.0014	0.3614	0.0008	0.0000	0.1048	0.0000	0.0000	0.0000	■

▨ Pair trapped together



		P value												
	2017 ID	27345	21951	21952	21954	21955	21957	21958	21960	21961	21963	21965	21966	21967
SRI	27345	■	0.5980	0.9900	0.6569	0.9900	0.9900	0.9900	0.9900	0.3922	0.0099	0.9900	0.9900	0.0099
	21951	0.0003	■	0.0099	0.4510	0.9900	0.9900	0.9900	0.9900	0.2353	0.6765	0.9900	0.9900	0.4902
	21952	0.0000	0.3079	■	0.9900	0.9900	0.9900	0.9900	0.9900	0.6078	0.5882	0.9900	0.9900	0.9900
	21954	0.0861	0.0003	0.0000	■	0.9900	0.9900	0.9900	0.9900	0.0196	0.0099	0.9900	0.9900	0.8039
	21955	0.0000	0.0000	0.0000	0.0000	■	0.9900	0.0099	0.9900	0.9900	0.9900	0.9900	0.9900	0.9900
	21957	0.0000	0.0000	0.0000	0.0000	0.0000	■	0.9900	0.9900	0.9900	0.9900	0.9900	0.9900	0.9900
	21958	0.0000	0.0000	0.0000	0.0000	0.3413	0.0000	■	0.9900	0.9900	0.9900	0.9900	0.9900	0.9900
	21960	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	■	0.9900	0.9900	0.0099	0.0099	0.9900
	21961	0.0009	0.0465	0.0387	0.0040	0.0000	0.0000	0.0000	0.0000	■	0.0784	0.0196	0.9900	0.1863
	21963	0.2027	0.0012	0.0003	0.3734	0.0000	0.0000	0.0000	0.0000	0.0036	■	0.9900	0.9900	0.0099
	21965	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0039	0.0006	0.0000	■	0.2059	0.9900
	21966	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.3517	0.0000	0.0000	0.0027	■	0.9900
	21967	0.8921	0.0003	0.0000	0.0802	0.0000	0.0000	0.0000	0.0000	0.0009	0.1958	0.0000	0.0000	■

▨ Pair trapped together

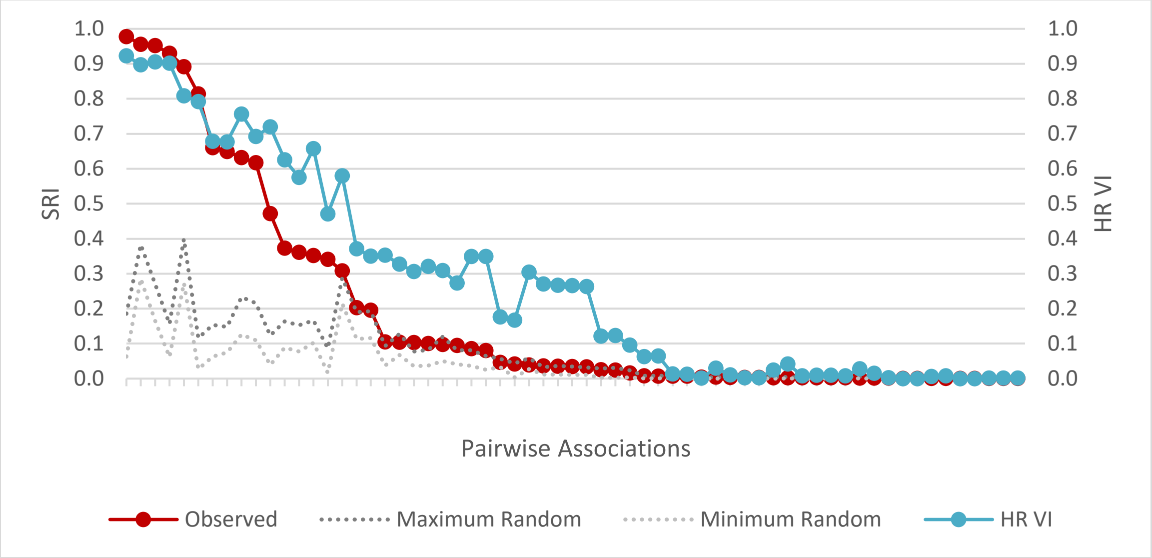


Figure 2-7: Observed and all randomized contact rates of all pairs, ordered by observed contact rate rank. The edge weights of pairs with very high observed contact rates were different from random contacts expected under regular space use, indicating observed contact rates in these pairs depended on synchronous movement. In the right tail, randomized edge weights were higher than some observed pairs' observed contact rates, indicating some pairs' interactions could be explained by random associations due to spatial overlap.

Individuals with very close home range centroids had very high to moderate contact rates, which decreased with distance between home range centroids and ceased to occur when home ranges were > 1 – 2 km separated (Fig. 2-8). Individuals with very similar home ranges and core areas had very high contact rates, though contact rates increased at an increasing rate as home range VI increased (for home range VI: $SRI = 1.36*VI^2 + 0.15*VI$, $R^2 = 0.98$) (Fig. 2-9, Fig. 2-10). The individuals not expected to belong to the same sounder from trapping with significant association rates (Table 2-1) are seen in figures 2-8 to 2-10 among the expected sounder pairs with moderate to high home range proximity, similarity and contact rates.

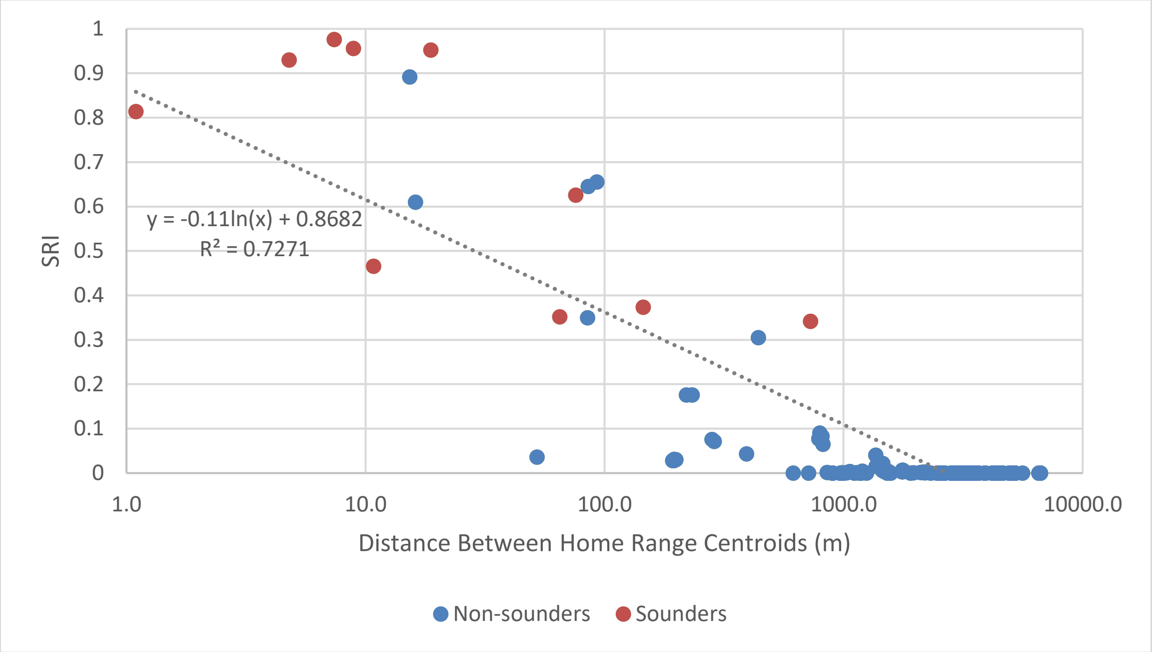


Figure 2-8: Pairwise distance between home range centroids and contact rates (SRI) of individuals compared by individuals trapped together (sounders) versus individuals not trapped together (non-sounders)

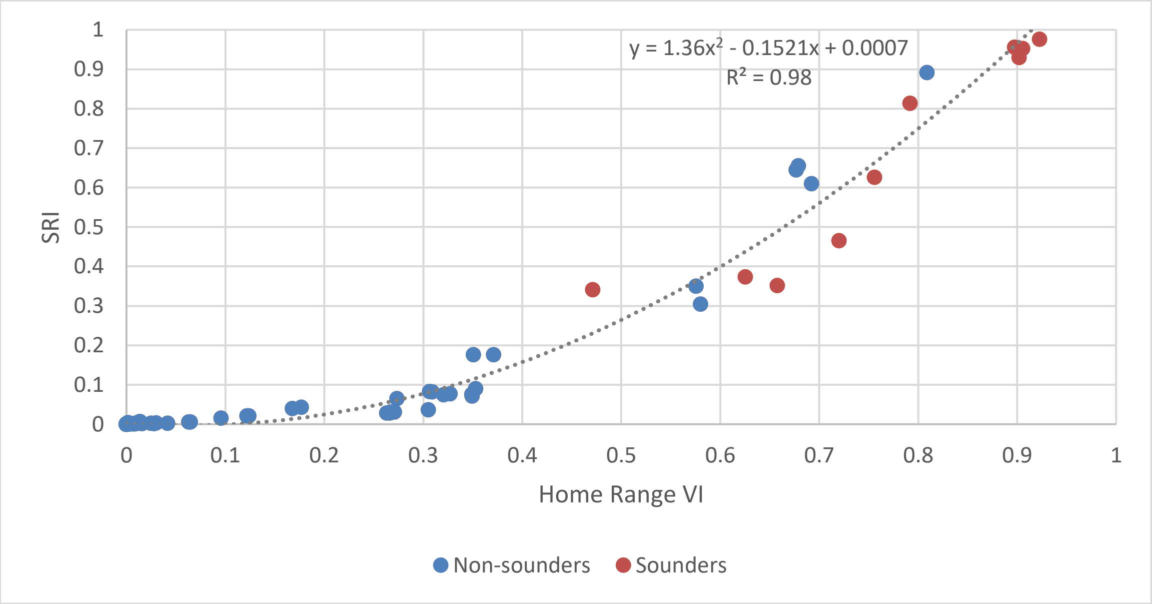


Figure 2-9: Pairwise home range similarity (home range VI) and contact rates (SRI) of individuals trapped together (sounders) versus not trapped together (non-sounders)

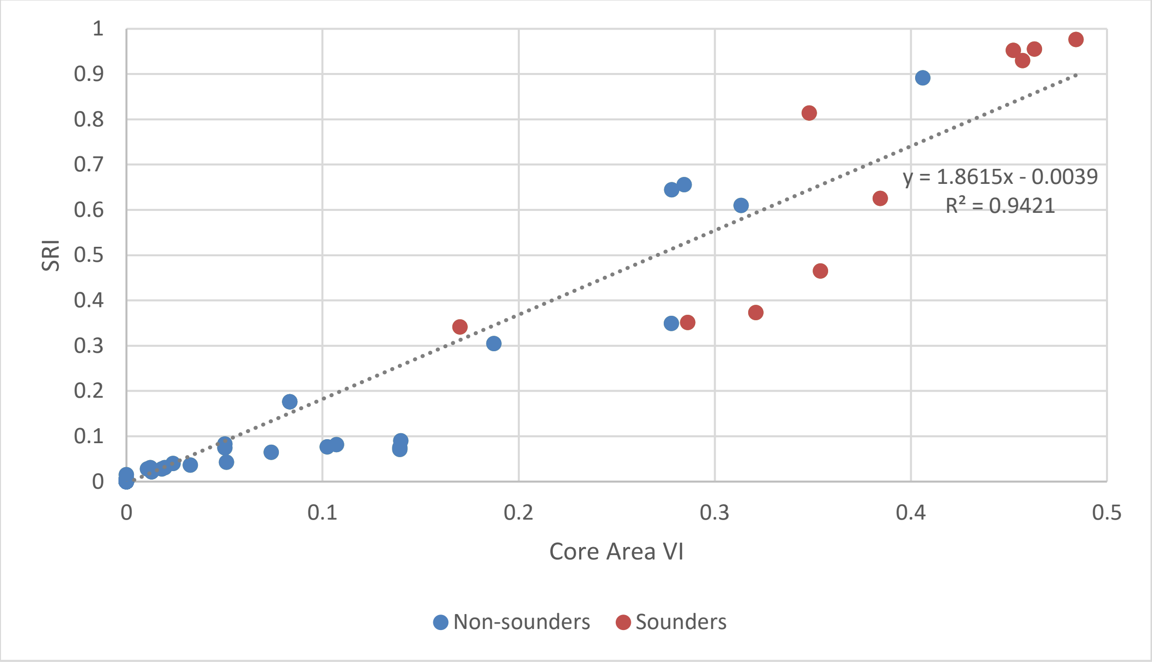


Figure 2-10: Pairwise core area similarity (core area VI) and contact rates (SRI) of individuals trapped together (sounders) versus not trapped together (non-sounders)

2.4 Discussion

2.4.1 Home ranges, contacts and social network

Wild pigs were trapped in groups and adult females were fitted with GPS tracking collars to collect fine spatial and temporal resolution movement data. From the GPS tracking data, home ranges were modelled and compared for each individual using BBUDs, contact heterogeneity in the population was detected and used to model a proximity based social network, and a hypothesis test was performed to separate the effects of environmental constraints and social behaviour on observed spatial associations (Spiegel et al., 2016). This provided an analysis workflow that demonstrates the non-random social structure of wild pigs based on interaction. Common social network randomization hypothesis test cannot provide insight into factors driving observed spatial associations, as randomizing network attributes only describes completely random associations that ignore the constraints of space and time on animal movement and lack ecological meaning. Therefore, incorporating the temporal structure of the GPS tracking data in all aspects of analysis provided more informative observations and hypothesis testing opportunities.

The use of BBUDs benefitted both the modelling and comparison of home ranges by preserving space use heterogeneity within the home range. The incorporation of the temporal sequence of fixes in the Brownian bridge method improves home range estimation by enforcing temporal constraints on movement, thereby reducing type 1 error compared to geometric and other kernel based home range estimators (Horne et al., 2007; Walter et al., 2015). Accordingly, comparing utilization distribution home ranges accounts for the independent space use heterogeneity of each individual not captured in simple home range geometric intersections. By comparing utilization distribution similarity between individuals using the VI index, spatial overlap is measured as a continuous value by the joint likelihood of space use (Fieberg & Kochanny, 2005). Home range and core area similarity (VI) were found to be good predictors of contact rates in the study area, where contact rates increased as home range and core area similarity increased. However, the relationship between contact rates and home range VI was found to be non-linear, due to lower contact rates occurring until home range VI increased above 0.6 to 0.7. This indicates individuals with low or moderate home range similarity do not interact relatively as much as individuals with very similar home ranges, and the relationship between home range similarity and contact rates changes depending on how similar two individual’s home ranges are.

Some research on wild pigs group effects includes identifying groups based on home range overlap threshold (Yang et al., 2021), although inferring social interaction from spatial overlap could lead to bias as shown here and in previous research, especially in pairs with low or moderate spatial overlap (Fig. 2-9) (Long et al., 2014; Podgórski et al., 2014). Though home range similarity and contact rates were strongly related, the occurrence of spatial overlap does not directly translate to direct interaction between individuals, which can only be determined from measuring dynamic interaction. Previous research has found population density and spatial overlap does not fully explain wild pigs social structure, as wild pigs with significant opportunity to interact often do not (Podgórski et al., 2014). However, the distance between home range centroids can influence between sounder contacts (Pepin et al., 2016; Podgórski et al., 2018). This finding was mirrored here, as lack of home range overlap and significant distances between home range centroids corresponded to a lack of contacts (Fig. 2-8, Fig. 2-9).

Measures of spatial association should reflect the spatial and temporal characteristics or requirements for the ecological phenomenon of interest to occur (Farine & Whitehead, 2015). Here, the high spatial-temporal resolution and duration of the GPS tracking data allowed for the measurement of distance between simultaneous fixes of all individuals, representing spatial structure of individuals in the data. Having captured multiple pairs of individuals during trapping, the GPS tracking data was used to estimate an appropriate distance between individuals belonging to the same social group (Fig. 2-2, Fig. 2-3). The within-group proximity of individuals was found to be frequently less than 100 metres, and within this distance, proximity trended towards 0 meters. Previous research has noted the trend towards 0 metres within group distances, but allowed for more spatial error characteristic of the radio telemetry technology used in their studies compared to GPS tracking data used here (Podgórski et al., 2018, 2014; Tomkiewicz et al., 2010).

The simple ratio index was used to quantify contact rates, which requires no compensation for missing fixes in the data set such as the popular half-weight index (Cairns & Schwager, 1987). Therefore, the GPS tracking data collected was sufficiently continuous (i.e. high fix success rate, spatial-temporal resolution) to use more conservative measures of spatial association than similar research on wild pigs social structure (Iacolina et al., 2009; Podgórski et al., 2014). Because contact distances were based on observed within-group distances and measured more conservatively by SRI, observed contact rates were likely an accurate reflection of the real spatial association rates between socially interacting female wild pigs (Cairns & Schwager, 1987; Farine & Whitehead, 2015; Hoppitt & Farine, 2018). Other research on the ecological effects of contact rates and social structure have used even finer spatial and temporal resolution contact thresholds that reflect specific requirements for the ecological phenomenon of interest, such as disease transmission (Pepin et al., 2016; Yang et al., 2021).

In the PBSN, multiple pairs were found to have non-random spatial associations where the strength of spatial association depended on synchronous movement behaviour. Randomized network edge weights were lower than observed for these individuals, signifying contact rates were affected by sociality as they were greater than contact rates that could be expected by chance during regular space use (Fig. 2-7). This result aligns with previous research on social structure in wild pigs which found that female wild pigs form spatial-temporally distinct social groups (Podgórski et al., 2014). All ten expected wild pigs sounder pairs identified from trapping and six additional pairs not previously identified as belonging to the same sounder were found to have significant test results, indicating social associations in these pairs (Table 2-1). Though trapping was an effective way to identify sounder members, as no false positives were detected, trapping failed to identify the six additional socially interacting pairs. This exemplifies the benefit of looking within wildlife telemetry data to generate evidence of social structure rather than risk missing social group membership or ignoring social group dynamics when treating group membership as an individual attribute based on spatial overlap or trapping.

Though some individuals were almost always in contact over the duration of the study, cohesiveness in social pairs varied within the 78 day period, shown by the occurrence of moderate contact rates dependent with significant data stream randomization test results. This indicates social processes in wild pigs could occur at daily, weekly or monthly time scales, as less cohesive socially interacting and rare/random contacts occurred. Also, the coarseness of testing contact rates over the duration of the entire study period makes the nature of the very rare contacts between individuals observed here unclear. It is possible that the indicated non-random association in these low observed contact rate pairs was caused by the rare contacts never occurring in any iteration of the randomized network due to very low spatial overlap, resulting in observed contact rates out-ranking all randomized iterations, or it is possible that contacts were indeed short bursts of social movement behaviour. For example, Podgórski et al. (2014) found some female-female interactions occurred and ended within a day, but the driver of these interactions is still not known. In a later study, Podgórski et al. (2018) found yearling female boars had more between group contacts (an effect of dispersal from the natal group), indicating strength of associations within and between groups could be affected by age. More research is needed to identify why rare or between group contacts occurred, and why some socially interacting pairs had much lower contact rates than others.

Social networks modelled without testing for temporal dependencies in spatial associations can identify non-random associations in observed social structure (Bejder, Fletcher, & Bräger, 1998; Chaverri et al., 2007; Gorman et al., 2006; Kemp & Manly, 1997; Smolker et al., 1992), which can be useful for describing various phenotypic patterns, however, randomizing network attributes usually cannot describe the influence of various drivers affecting spatial association rates (Croft et al., 2011; Farine & Whitehead, 2015; Spiegel et al., 2016). This method provides a social network analysis workflow in which social organization and evidence of group membership is an emergent property of spatial associations, rather than an individual attribute. Using this analysis method, non-random observed association rates dependent on social movement behaviour were identified.

2.4.2 Applications and limitations

The data stream randomization test used here provides evidence of specific movement relationships measured to generate spatial associations used in a social network. However, there are a few other methods of using the temporal component of GPS tracking data to gain similar proof of the importance of interdependent movement in observed spatial association rates. First, Podgórski et al. (2014) use a lagged association rate, which is the probability that individuals remain together after being observed together at a given time interval previously, to determine if observed contact rates were more temporally stable than random associations. The authors found that lagged association rates in observed data was greater than lagged association rates of randomized permutations, thus the temporal structure of the data was critical to observed contact rates in their study. However, the authors used a null model of completely random associations made by swapping network attributes. Because individuals cannot have had contacts in places where one or both could not physically have been based on distance and maximum travel speed, completely random network attribute randomization tests do not account for the spatial-temporal autocorrelation of individuals’ movement. In randomization procedures performed at the network level, it is possible that individuals could have very different home ranges entirely in given permutations of the network to their actual home range, and null models lack spatial ecological meaning. This is an undesirable property in a social network based on spatial associations which are inherently constrained in space and time (Farine, 2017). A similar test to the lagged association rates test was also discussed by the authors of the article describing the methods used here (Spiegel et al. 2016). The authors hypothesize that a data stream offset, where the entire track of individuals are temporally offset independently (e.g. by one hour, or any other time interval) should create a null model of movement where temporal dependencies of spatial associations are disrupted but other effects are preserved in the intact paths of the individuals. This should achieve similar results to the methods used here for separating the role of social movement behaviour and regular space use, while preserving spatial-temporal movement paths within individuals.

The data stream randomization test could suffer from bias based on temporally segmenting paths at a coarser or equal temporal scale as environmental influences or other non-social influences on animal movement and social behaviour. For instance, if spatial association rates are influenced by forage availability, but social organization is based on roosting associations (tent-making bats: Chaverri et al., 2007) or preferential associations are an emergent effect of foraging activity and habitat complexity in an otherwise randomly structured population (Giraffes: Muller, Cantor, Cuthill, & Harris, 2018). In cases such as this, spatial association rates would likely not be significantly different than contacts expected due to spatial overlap and environmentally driven associations (e.g. forage availability). Similarly, static social effects on movement such as territoriality and scent marking would likely be undetectable in this method due to their long temporal duration and indirect influence of sociality on individual movement (sleepy lizards *Tiliqua rugosa*: Leu, Jackson, Roddick, & Bull, 2016; leopards *Panthera pardus*: Rafiq et al., 2020; Spiegel et al., 2016). However, the duration of the path segments which are reordered could be adjusted to target ecological processes of interest, such as seasonal effects on spatial associations (Butt, 2010; Dorning & Harris, 2019; van Overveld et al., 2020).

Data stream randomization could easily be extended to research on phenotypic effects on animal associations which are quite popular (e.g.: Gorman et al., 2006; Levin et al., 2018; Smolker et al., 1992; Zonana, Gee, Bridge, Breed, & Doak, 2019). This could improve spatially based social network tests where node attributes are of focal interest by retaining socio-environmental context in the null model and splitting by phenotypic traits during or after analysis (Farine, 2017). In fact, this analysis would be immediately relevant as follow up to this research, as differences in wild pigs space use and social associations can occur by sex (Kay et al., 2017; G. Massei et al., 1997; Podgórski et al., 2014; François Spitz & Janeau, 1990) and age differences (Keuling, Stier, & Roth, 2008; Podgórski et al., 2018), which could be of interest in explaining the variance in social group strength of spatial associations observed. Similarly, data stream randomization could benefit research into the effects of social structure on other ecological processes such as disease transmission. Network attribute randomization would describe if disease spread among individuals with particular network properties (e.g. high node degree, edge weight) whereas data stream randomization would identify particular spatial associations and behaviours explaining the risk of disease transmission between individuals.

2.4.3 Conclusion

GPS tracking data was used to measure spatial associations in a proximity based social network of female wild pigs. Using data stream randomization to generate evidence of social structure identified likely social pairs not detected during trapping, providing a more accurate model of social structure in the study area. Wild pigs in the study area exhibited contact heterogeneity, where they were frequently in contact with sounder members and less often or never contacted others in the study area. However, the strength of association within groups varied (SRI between 0.47 – 0.97), indicating some pairs with social movement behaviour spent significant amounts of time not in contact with each other. These non-contact times, as well as the occurrence of rare contacts in the study area could have harmful consequences such as disease transmission between groups. Consideration for the variance in social group strength of association and potential for non-group like behaviour should be incorporated into research on spatial and social effects on disease transmission and social behaviour in wild pigs, as this factor can improve understanding of within and between group spatial relationships and dynamic interaction.

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Chapter 3

3 How cohesive are wild pig social groups? Measuring association patterns in wild pig social groups over time

3.1 Introduction

Animals, especially mammals, often live in social groups to increase survival and general fitness (J. B. Silk, 2007; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015). Female wild pigs (*Sus scrofa*) live in matrilineal social groups (sounders) usually composed of one to several breeding age pigs (sows) and their young. Male wild pigs are usually solitary, but briefly join sounders to mate with sows (Graves, 1984; Podgórski et al., 2014). In North America, wild pigs are an invasive species that cause significant damages to agriculture, livestock, wildlife and the natural environment which warrant significant management efforts to mitigate their impact, remove populations and prevent their spread (Barrios-Garcia & Ballari, 2012; Bevins et al., 2014). Much of the regular activity and space use of sows is tied to social group behaviour, such as co-parenting young, scrounger-producer foraging, learning from conspecifics and site selection (Giraldeau & Caraco, 2000; Graves, 1984; Janeau et al., 1995; Morelle et al., 2015; François Spitz & Janeau, 1990). Because of the influence of sociality on their regular activity, sociality also has important impacts on the harmful effects of wild pigs such as disease transmission (Pepin et al., 2016, 2021; Yang et al., 2021) and response to management actions (Bastille-Rousseau et al., 2021; Hanson et al., 2009; Sparklin, Mitchell, Hanson, Jolley, & Ditchkoff, 2009). This makes wild pig sociality an important consideration in both their movement ecology and their management (Giovanna Massei et al., 2011; Morelle et al., 2015). Knowledge of wild pig spatial and social behaviour can inform their management by providing better understanding of the causes and effects of density in established ranges, the risk of expansion into new ranges, developing and evaluating the performance of control measures, and modelling disease transmission (Beasley et al., 2018; Keiter et al., 2017). But despite the importance of wild pig sociality and spatial behaviours in these research studies and control measures, the group dynamics and temporal cohesiveness of wild pig sounders remains an under-studied aspect of invasive wild pigs (Beasley et al., 2018).

Like other socially structured animals, wild pig populations are spatially structured and exhibit contact heterogeneity, where individuals in the same group are more frequently in contact than individuals in different groups (Pepin et al., 2016; Podgórski et al., 2014). This is seen in sows forming long-lasting preferential associations with their kin while interacting less with spatially adjacent sounders (Podgórski et al., 2014). However, between-sounder interactions can occur and are related to individual age, spatial proximity of sounders and the fission of large sounders (Gabor, Hellgren, Bussche, & Silvy, 1999; Pepin et al., 2016; Podgórski et al., 2018). Within sounders, individual behaviours also affect social group dynamics; sows temporarily leave the sounder to give birth (Janeau et al., 1995) and the age and sex of young wild pigs influence exploratory ventures away from the natal group before natal dispersal (Truvé & Lemel, 2003). Sounder dynamics can also be affected by mortality or interruption by predation or human interference, where wild pigs will rejoin groups of unrelated individuals in response to predation or deliberate relocation or removal by humans (Delgado-Acevedo et al., 2021; Gabor et al., 1999; Iacolina et al., 2009). In addition to long term social structure, these social group dynamics have important implications for transmitting or limiting disease spread between groups, as well as population expansion (Gabor et al., 1999; Pepin et al., 2016, 2021). However, wild pig research often only considers these effects over long study periods or ignores within-study period variability in sociality and space use (Johann et al., 2020).

In wildlife populations that exhibit contact heterogeneity such as wild pigs, measuring animal social relationships has become an increasingly popular research topic in ecology, especially through social network analysis (Farine & Whitehead, 2015; Wey et al., 2008). In social network analysis, researchers can use telemetry data to quantify spatial associations between individuals to gain insight into spatial and social animal behaviours (e.g. spatial associations used to identify social structure: Podgórski et al., 2014; or social grouping used in a predictive model of spatial associations: Yang et al., 2020). Spatial associations between individuals can be quantified in terms of spatial overlap, often measured by home range overlap (Fieberg & Kochanny, 2005), or by dynamic interaction, where spatial relationships are measured in space and time (Long et al., 2014). Studies of spatial associations that use dynamic interaction often measure contacts (co-occurrences between individuals within a given space and time threshold), which are used to model spatially-based social networks, a.k.a. contact networks or proximity based social networks (PBSN's). PBSN's provide opportunity for hypothesis testing ecological questions by simulating contact networks under conditions different from observed (termed data stream, or pre-network randomization), such as non-random spatial associations (Bejder et al., 1998; Croft et al., 2011; Farine & Whitehead, 2015). Data stream randomization tests have been used to identify social associations in contact networks in sleepy lizards *Tiliqua rogosa* (Spiegel et al., 2016), caribou *Rangifer tarandus* (Peignier et al., 2019) and gannets *Morus serrator* (Jones et al., 2020).

In such contact network analyses, the definition of a 'contact' between individuals that is used to quantify associations should reflect the ecological phenomenon of interest, such as the distance between individuals in a social group (Farine & Whitehead, 2015; Whitehead, 1997; Whitehead & Dufault, 1999) or the interaction requirements to transmit a disease (Craft, 2015b). One of the strengths of network analysis of animal populations is preservation of contact rate heterogeneity between individuals, which provide important information concerning the characteristics of the ecological phenomenon of interest (Lusseau, Whitehead, & Gero, 2009; Wey et al., 2008). However, as hypothesis testing social networks has become more popular (Farine, 2017), research questions or data are often tied to individuals and/or individual characteristics, such as does individual A socially interact with individual B (Lusseau et al., 2006; Spiegel et al., 2016). And while these tests are important for understanding factors affecting inter-individual relationships in animals, attention should be paid to the relationship between the ecological question and the observed spatial associations. For instance, what behavioural implications might the occurrence of small, indirect or statistically insignificant associations in a contact network have? Moreover, the ecological meaning of any variance between observed association rates in different individuals that might have the same test result, or even contrasting test results can go undiscussed. For instance, if individual A and B socially interact, how much interaction constitutes this social association? And if individual C and D also socially interact, what is the range of association rates that can constitute a social association? Finally, individual-level research questions potentially ignore variability in the temporal scale of factors affecting sociality and social group dynamics, which in the case of wild pig social networks relate to their harmful effects such as disease transmission (Kay et al., 2017; Pepin et al., 2016).

Therefore, to better understand wild pig social group dynamics, GPS tracking data of wild pigs from four study locations is used to measure a proximity based social network, which is tested for significant social associations using a data stream randomization test. This provides individual-level evidence of social interaction (a significant or non-significant test result) while preserving heterogeneity in strength of pairwise associations in the observed contact network. Variability in the strength of associations in high contact rate pairs is then explored between pairs and within pairs over time to examine potential differences in pair cohesion and interruptions in social associations. By considering between and within-pair contact rate variability in a wild pig contact network, we aim to improve understanding of association patterns, space use and movement behaviour within and between wild pig social groups.

3.2 Methods

3.2.1 Study area and data collection

Wild pig GPS tracking data was collected from four sites: Noble Research Institute’s Oklahoma Red River Ranch (RRR) and Oswalt Road Ranch (ORR), and the US Department of Energy’s South Carolina Savannah River Site (SRS) and the Florida Archbold Buck Island Ranch (ABIR). RRR is a 1316 hectare agricultural research and demonstration farm, with cattle and pecan operations on the northern bank of the Red River. ORR is a 2028 hectare cattle operation, consisting of a mixture of wooded and open areas (Gaskamp et al., 2021). The SRS consists of a 24500 hectare area, part of the Savannah River National Environmental Research Park, characterized by a mixture of pine and hardwood forest (Keiter et al., 2017). Finally, ABIR is a 4230 cattle ranch consisting of a mixture of "seminative" and modified cattle pastures, grassland and wetlands (Swain, Boughton, Bohlen, & Lollis, 2013). All study sites have established wild pig populations, consistent with the existing range and expansion of wild pigs in the Southern United States (Bevins et al., 2014; Mayer & Brisbin, 1991).

At RRR, 29 sows were captured and attached with GPS collars over two separate study seasons (*n* = 16 in autumn 2016 and *n* = 13 in autumn 2017) using suspended drop enclosures designed to capture entire sounders of wild pigs, minimizing interruptions to social group structure (Gaskamp et al., 2021). At ORR, 39 wild pigs were captured over the course of three years. At RRR and ORR all trapping and handling followed the Oklahoma Wild Pigs Control Act (O.S. § 6-601) and the America Society of Mammologists approved guidelines (Sikes, 2016). SRS and ABIR GPS tracking data was retrieved from Yang et al. (2020) via online repository, and consisted of 19 wild pigs at SRS, and 19 wild pigs at ABIR. Ethics and detailed capture information are available in their article. GPS tracking information by study site is presented in Table 3-1.

Table 3-1: GPS tracking data statistics by study site

Study Site		**RRR**	**ORR**	**SRS**	**ABIR**
Fixes/Individual	*mean*	3405	4320	3383	7460
	min	1383	153	288	1697
	max	3672	11458	6344	18053
Fix Rate		1 fix/30 min	1 fix/60 min	1 fix/60 min	1 fix/30 min
Fix Success Rate		99.1 ± 2.4%	98.5 ± 7.6%	82.9 ± 18.8%	89.5 ± 20.3%
Duration (days)	*mean*	72	184	179	210
	min	30	6	12	35
	max	78	447	378	315
Sex	*Female*	29	20	13	14
	male	0	19	6	5
Age (months)	*>=36 (adult)*	19	19	14	19
	<36 (subadult)	3	3	5	0
	Not Recorded	6	17	0	0

3.2.2 Spatial-temporal contacts and social network

To measure spatial associations between individuals in the GPS tracking data, contact rates were calculated for each unique pair of individuals. Contacts are defined by the co-occurrence of GPS tracking fixes within a given temporal and distance threshold that reflect the spatial proximity of individuals in a social group. To determine an appropriate contact distance threshold, the distance between all simultaneous (recorded within 15 minutes) fixes was measured for each study site data set. Anticipating some pairs of individuals would belong to the same sounder and exhibit contact heterogeneity, a peak in the frequency distribution of distance between simultaneous fixes was expected approaching zero metres, representing the usual distance between individuals belonging to the same sounder (Podgórski et al., 2014). Peaks in the frequency distributions of distances between simultaneous GPS fixes reveal high amounts of simultaneous fixes were recorded within 100 metres at all four study sites, which increase in frequency approaching distance = 0 metres (Fig. 3-1). Therefore, for the purposes of measuring social associations in wild pigs, a contact was defined as a co-occurrence between two individuals within a temporal threshold of <= 15 minutes and a distance threshold of <= 100 metres. 100 metres is more conservative contact distance threshold than those used in other studies measuring spatial structure of wild pig sociality (Iacolina et al., 2009; Podgórski et al., 2014).

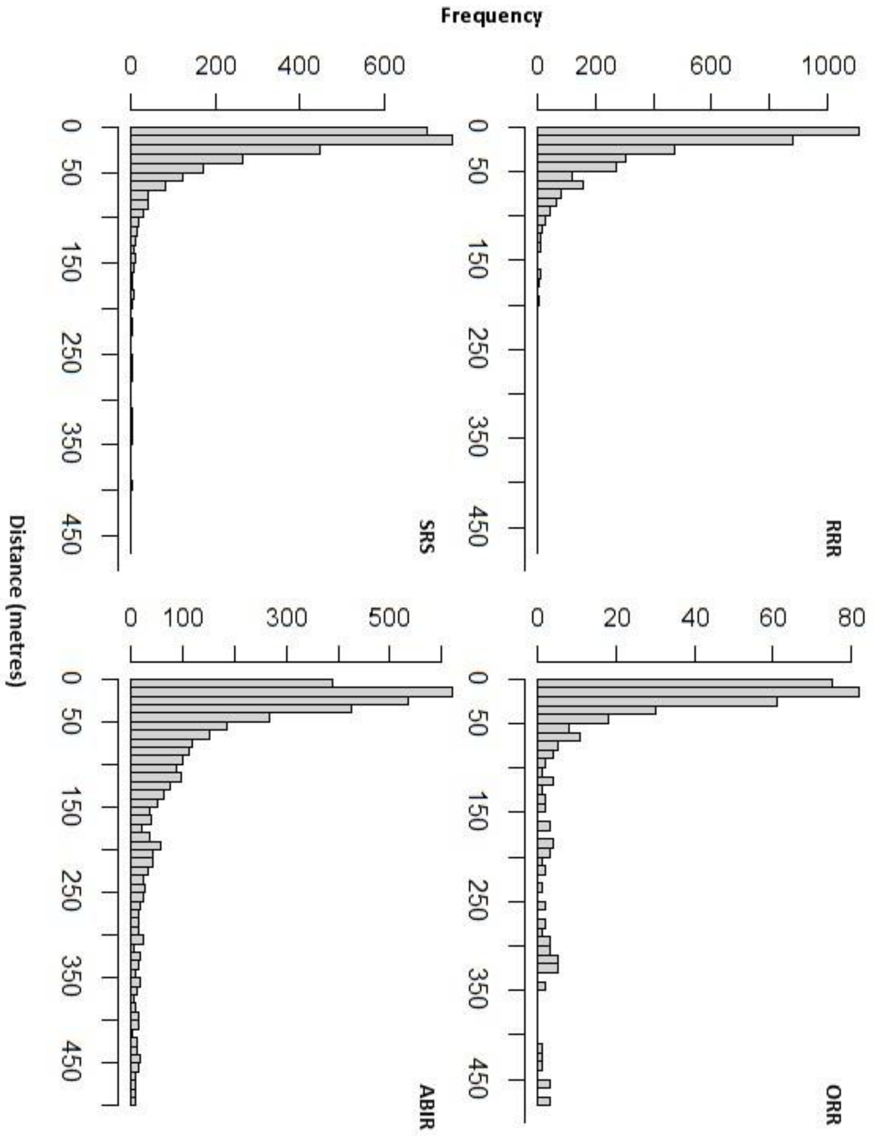

Figure 3-1: Frequency distribution of distance between simultaneous GPS tracking fixes of a selection of pairs from each study site. These individuals have a high amount of fixes within 100 metres of each other, likely representing the upper limit of distance between individuals within social groups.

Contact rates were then measured between individuals to model wild pig social structure in a PBSN. The simple ratio index (SRI) was used as the measure of contact rates between individuals: SRI = $x/(x + y_{AB} + y_A + y_B)$ where x is the number of contacts between individuals A and B, y_{AB} is the number of simultaneous fixes that are not contacts, y_A is the number of individual A's fixes without a simultaneous fix of individual

B, and y_B is the number of individual B's fixes without a simultaneous fix of individual A (Cairns & Schwager, 1987; Farine & Whitehead, 2015). Therefore, SRI ranges from 0 to 1, where SRI = 0 for two individuals that have no contacts, and SRI = 1 for two individuals that are always in contact have. SRI provides a more conservative measure of spatial associations between individuals than more simple contact rates such as proximity analysis ($= x/(x + y_{AB})$) and the popular half-weight index ($= x/(x + y_{AB} + 0.5(y_A + y_B))$) because all recorded fixes for each individual are incorporated rather than only all simultaneous fixes, and no adjustments are made based on the likelihood of recording one individual without the other (however SRI simplifies to $x/(x + y_{AB})$ when fix success rate = 100%) (Cairns & Schwager, 1987; Farine & Whitehead, 2015; Hoppitt & Farine, 2018; Long et al., 2014). Because of uneven starting dates and durations of GPS fix collection between individuals at ORR, SRS and ABIR, SRI was calculated only within subsets of overlapping GPS tracking fixes for each pair.

To test for non-random spatial-temporal associations in the PBSN, a data stream randomization test was performed, where the GPS tracking data were reordered by day for each individual randomly, while within-day order of fixes was preserved and contact networks reconstructed from the randomized data. This randomization technique provides a null model contact network where synchronous movement between contact rates should be interrupted by the reordering of days between individuals, while the preservation of movement within each day maintains the influence of other factors affecting wild pig contacts such as spatial overlap and resource distribution (Cooper, Morgan Scott, De La Garza, Deck, & Cathey, 2010; Pepin et al., 2016; Spiegel et al., 2016). Full details on the data stream randomization test methodology are described in chapter two of this thesis. The randomization process was performed 99 times, and the observed network compared to the distribution of randomized network contact rates by rank permutation test. The probability of a randomized iteration being greater than the observed value is given by $P = 1 - (R/(n + 1))$ where R is the number of randomized iterations equally or less extreme than the observed and n is the number of observed and randomized iterations (Benhamou et al., 2014; Berry et al., 2011). Therefore, for individuals with $P < 0.01$, the observed contact rates were dependent on the observed order of days and are greater than contact rates that could be expected by chance due to spatial overlap, indicating these individuals' spatial associations are likely driven by social movement behaviour (Spiegel et al., 2016).

3.2.3 Measuring contact patterns within and between wild pig sounders

As the goal of this chapter is to explore variation in the strength of associations in wild pig social structure, a subset of the GPS tracking data was performed where the GPS tracking data of wild pigs with moderate to high contact rates, and/or social movement behaviour were selected. The selections were performed based on the PBSN and data stream randomization test, where individuals with SRI >= 0.10 were selected. This selection of pairs of individuals provides the opportunity to analyze contact patterns likely sounder members/socially interacting pairs when $P < 0.01$ and gain insight into the social and spatial dynamics of wild pig social pairs.

The GPS tracking data of each selected individual was then partitioned into two categories of periods based on the occurrence or non-occurrence of contacts over 24 hour periods, the first being non-contact periods, and the second being contact periods. Non-contact periods are defined as continuous periods with no contacts between the two individuals over at least 24 hours, while contact periods are all other fixes (at least one contact within 24 hours). Therefore, the minimum duration of a non-contact period is 24 hours, while a contact period can consist of a single contact between pairs (Fig. 3-2). Contacts were defined in the same way as in the construction of the social network, as the co-occurrence of individuals within a temporal threshold of 15 minutes and a distance threshold of 100 metres. 24 hours was chosen as a temporal partitioning threshold between periods because the absence of contacts over a 24 hour or greater period should more accurately reflect a departure from regular daily activity relating to social associations in wild pigs. This allows for occasional and/or short ventures apart within a 24 hour period that ultimately are a regular part of wild pig daily activities such as foraging for food that do not reflect a departure from regular social associations (Graves, 1984; Janeau et al., 1995). Finding 24 hour contact versus non-contact periods will show variation in the strength of association within social pairs over time.

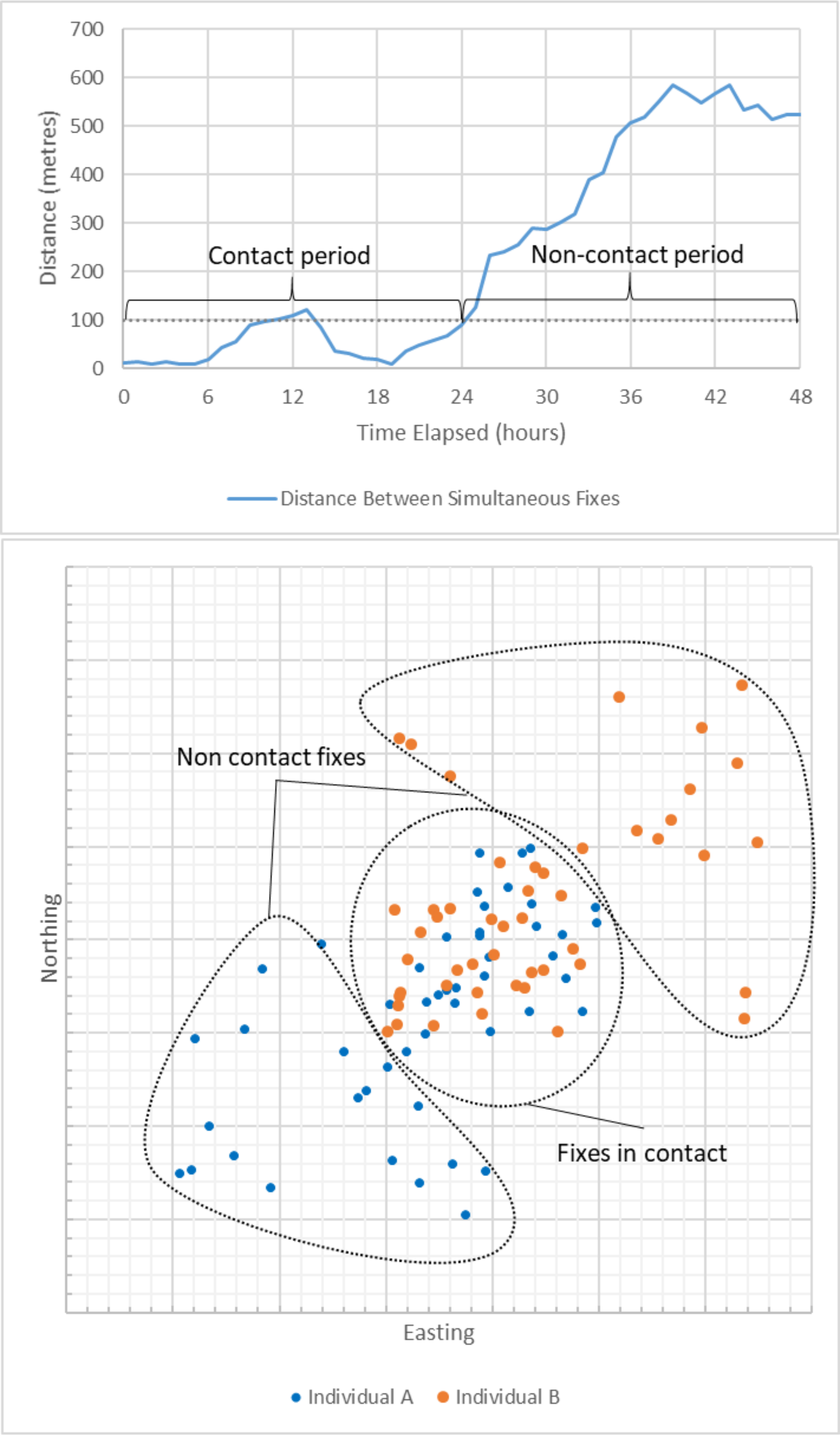

Figure 3-2: Simulated example of contact versus non-contact periods in the GPS tracking data. From the GPS tracking data of individuals A and B (bottom), the

data is segmented based on whether or not at least one contact has occurred in the past 24 hours (top). Shorter non-contact events can occur within a 24 hour period that still constitutes a contact period.

The occurrence of non-contact periods was compared between pairs in terms of the sex of paired individuals, age of the paired individuals, the number of non-contact periods, and contact rate. The sex and age of pigs was measured during trapping and provided in the raw GPS tracking data, with age being measured at the start of GPS tracking. Wild pig age was defined as adult (> three years old) and subadult (< three years old). Different combinations of pairs such as female-female or male-male, and adult-adult or adult-subadult might have more or less cohesive associations related to wild pig ecology such as sounder forming and natal dispersal, which could explain variability and interruptions in spatial associations measured here (Podgórski et al., 2018, 2014; Truvé & Lemel, 2003).

To measure the interrelatedness of space use and movement within pairs during contact and non-contact periods, the duration, median distance between individuals, difference in median distance from each individual’s home range centroid and movement correlation metric DI was calculated for each unique contact and non-contact period within pairs. Home range centroids were the median easting and northing coordinates of each individual (Pepin et al., 2016). The DI metric is composed of two movement components which are compared between the two movement paths of each individual, the first being path bearing, and the second being path distance. DI provides a measure of the correlation of two paths’ bearing and distance on a scale of -1 to 1, where -1 indicates negative correlation, 0 indicates no correlation and 1 indicates positive correlation (Long & Nelson, 2013a). Comparing movement and spatial relationships within pairs of individuals during contacts versus non-contact periods will provide more detailed knowledge of the spatial relationships between wild pigs with high contact rates, including social pairs, over time.

3.3 Results

3.3.1 Social network and pair selection

The PBSN and data stream randomization test are shown in figure 3-3. A number of strongly associated pairs with observed contact rates greater than all randomized iterations were observed at all four study sites. In the ORR data, two pairs of individuals had very high randomized contact rates compared to observed, and all other randomized iterations. It is hypothesized that these peaks in SRI in the randomized iterations could be due to the short durations of overlapping data in these two pairs resulting in smaller home ranges and therefore more contacts in randomized iterations, or due to contacts during resting behaviour occurring in the randomized iterations, though these hypotheses were not thoroughly analyzed. Based on the contact networks constructed, 23 pairs consisting of 30 unique individuals were selected from RRR, 17 pairs of 29 unique individuals were selected from ORR, seven pairs consisting of 12 unique individuals were selected from SRS, and ten pairs consisting of 14 unique individuals were selected from ABIR for a total of 57 pairs consisting of 85 unique wild pigs (Fig. 3-4, Table 3-2).

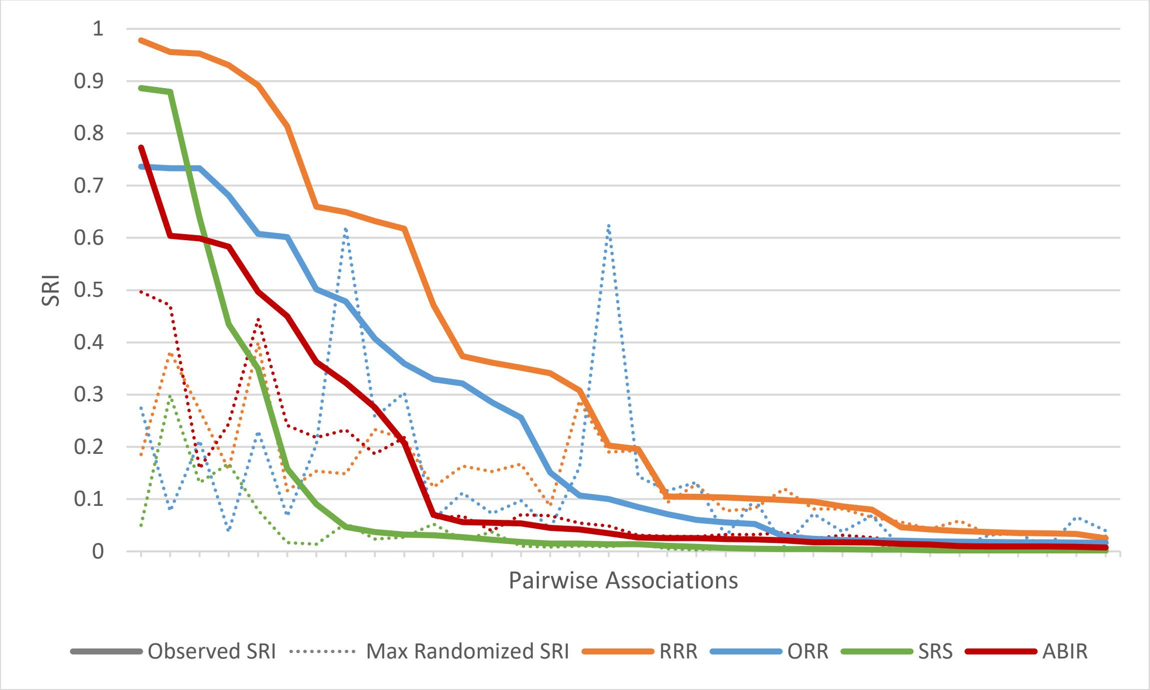

Figure 3-3: Observed SRI and maximum SRI generated from the data stream randomization test for each study site. For pairs with observed SRI > maximum randomized SRI, observed contact rates depended on synchronous movement, providing evidence these individuals' spatial associations are social in nature (Spiegel et al., 2016).

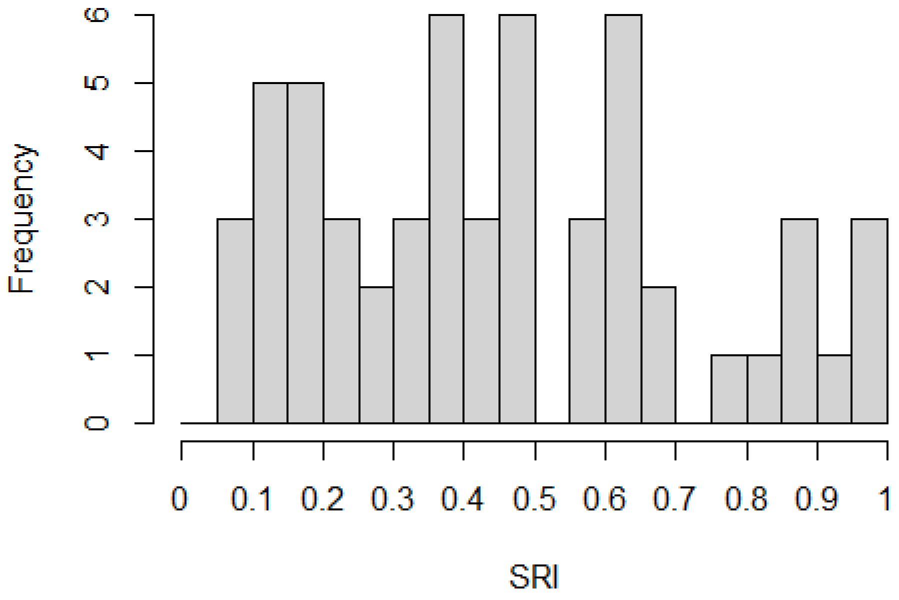

Figure 3-4: Frequency distribution of SRI of pairs selected from all four sites (*n* = 57 pairs). Pairs were selected to gain an understanding of cohesiveness of wild pig social groups based on their contact rate being SRI >= 0.1, representing moderate to strongly associated pairs with social interactions.

Table 3-2: Number of pairs selected by age and sex from all four sites. Pairs can be female-female (F-F), female-male (F-M) or male-male (M-M). Age was measured at the time of capture and divided in to two categories for analysis purposes: adult (> 3 years old) or subadults (< 3 years) old. Pairs could be adult-adult (A-A), adult-subadult (A-S) or subadult-subadult (S-S). In some individuals age was not measured, therefore in pairs where one or both individuals have no age data, age is defined as not recorded.

		SEX			
		F-F	F-M	M-M	Total
AGE	A-A	27	4	0	31
	A-S	7	2	0	9
	S-S	1	0	1	2
	Not Recorded	14	1	0	15
	Total	49	7	1	57

3.3.2 Measuring cohesiveness within pairs over time

43 pairs had one or more non-contact periods, while 14 pairs had no non-contact periods, for a total of 383 unique non-contact periods (mean = 8.91, max = 27), and 418 contact periods (mean = 7.33, max = 27) per pair observed across all four study sites (Fig. 3-5). The single long contact period of those 14 pairs with no non-contact periods are included in the analysis, causing the higher average but lower total of non-contact periods per individual compared to contact periods. Non-contact periods tended to be shorter in duration compared to contact periods (t = -6.19, df = 398.23, $P < 0.01$), and contact periods ranged in duration more widely (Fig. 3-6). During non-contact periods, median distance between pairs was greater than during contact periods (t = 12.94, df = 636.97, $P < 0.01$), and DI index values were lower (t = -12.136, df = 416.36, $P < 0.01$) indicating movement between individuals was less correlated compared to contact periods. The difference in distance of each Individual from their home range centroid was higher in non-contact periods compared to contact periods, meaning one individual was usually further displaced from their home range centroid than the other during non-contact periods (t = 6.86, df = 549.21, $P < 0.01$) (Fig. 3-6). This, in combination with the greater median distance between pairs, could indicate non-contact periods often occur when one individual travels away from the centre of the home range.

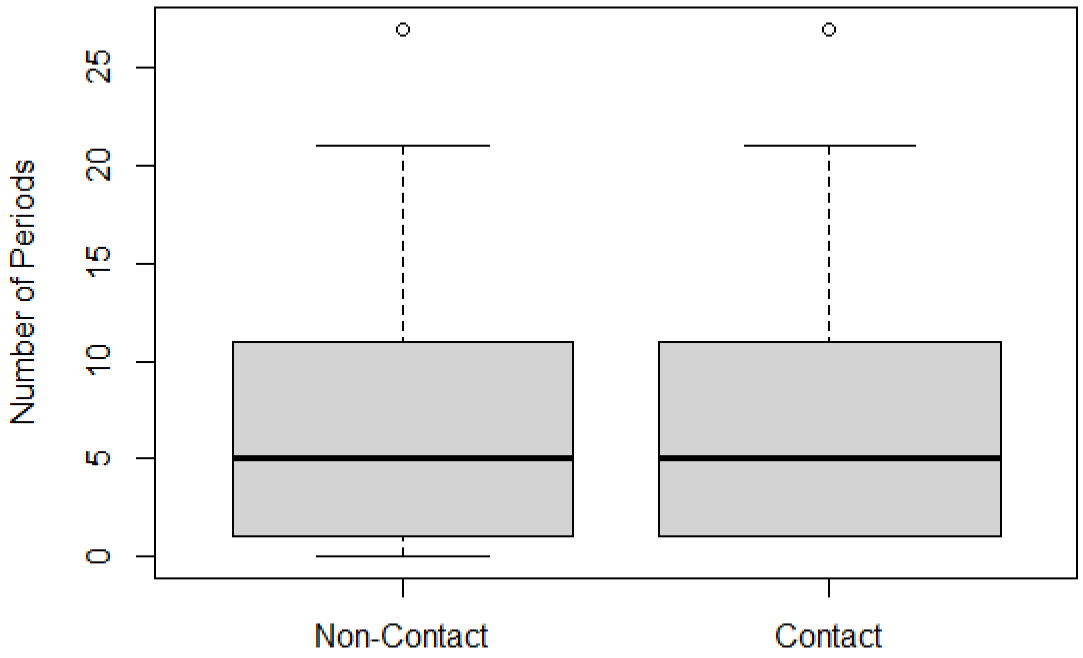

Figure 3-5: The number of observed non-contact and contact periods by unique pair. Because only individuals with contact rates >= 0.1 were selected, all pairs must have at least one contact period, but can have no non-contact periods. By definition, the number of contact periods per pair is equal to the number of non-contact periods ± 1.

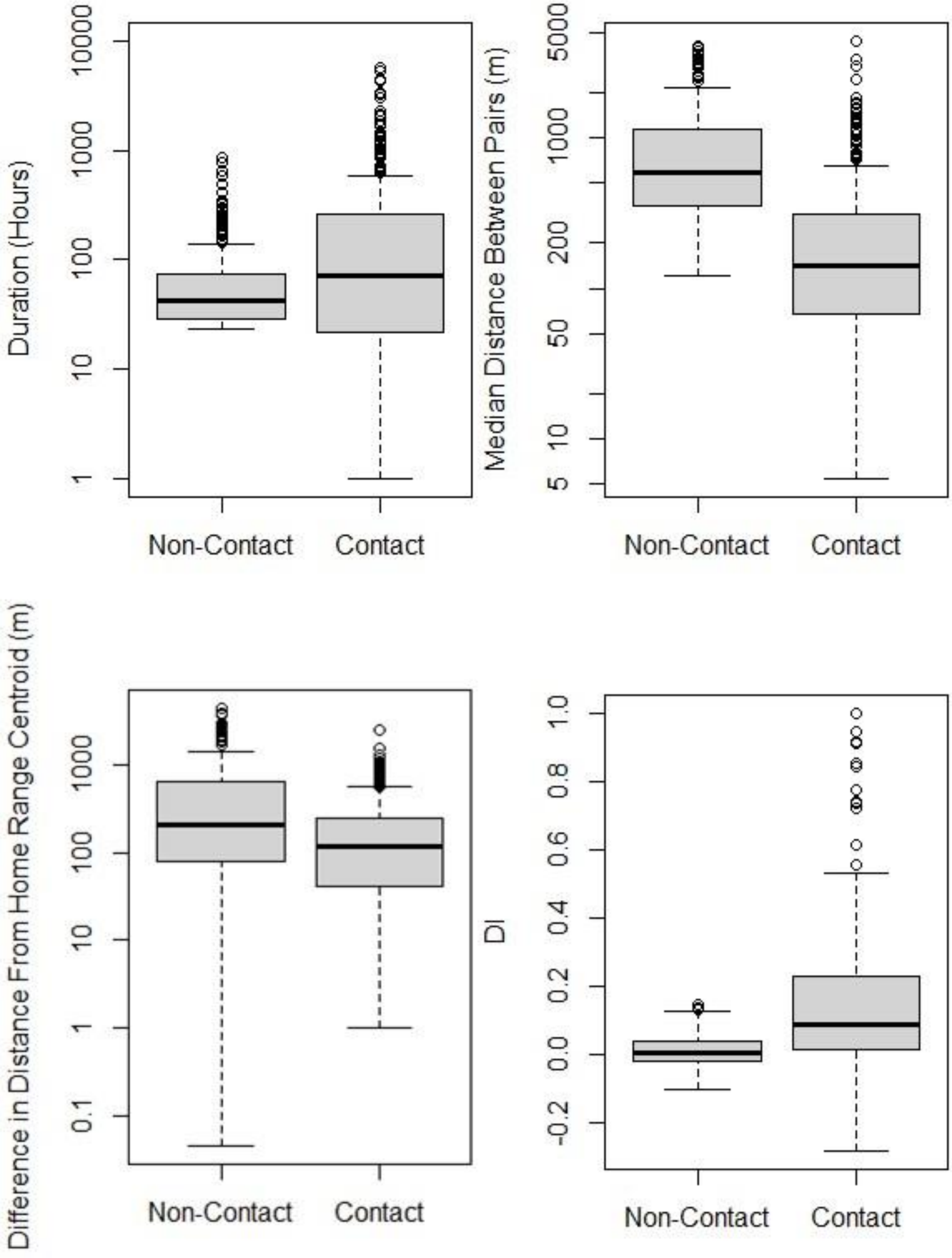

Figure 3-6: Duration, median distance between individuals by pair, the difference in median distance from home range centroid between individuals by pair, and DI

index in all observed non-contact periods versus contact periods. Non-contact periods are segments of data with no contacts between a dyad of wild pigs in >= 24 hours, while contact periods are the inverse (at least one contact within 24 hours). Therefore, contact periods can consist of only one contact fix (<= 30 minutes or 1 hour depending on fix rate).

3.3.3 Comparing cohesiveness between pairs

95% of non-contact periods observed were in female-female pairs (*n* = 364), which made up 90% of the unique pairs with SRI >= 0.10 selected (*n* = 49). Similarly, the majority of non-contact periods occurred in adult-adult pairs (56%, *n* = 225), which represented 54% (*n* = 31) of the pairs with SRI >= 0.1. Behind adult-adult pairs, 32% (*n* = 15) of non-contact periods were in pairs with no recorded age in one or both individuals (Table 3-2, Table 3-3). All combinations of sex and age pairs had at least one pair with no non-contact periods, although the lone male-male pair was one of only two subadult-subadult pairs, and the only to have no non-contact periods (Table 3-3). Though the majority of non-contact periods occurred in female-female pairs, the difference in number of non-contact periods between female-female and female-male pairs was not statistically significant at the 0.01 level (t = 2.70, df = 13.63, P = 0.02). No significant difference was observed in the number of non-contact events between different age combination pairs (t = 1.26, df = 14.65, P = 0.23). Due to the very high proportion of female-female pairs and the many pairs with missing age data, caution is warranted when interpreting differences in cohesiveness between pairs based on sex or age of paired individuals.

Table 3-3: Number of non-contact periods by pair sex (F-F: female-female, F-M: female-male, M-M: male-male) and age (A-A: adult-adult, A-S: adult-subadult, S-S: subadult-subadult, not recorded: no age data for one or both individuals in the pair) across all study sites. Non-contact periods are defined as the passing of >= 24 hours without a contact, defined in the same way as a contact used to calculate contact rates, in the pairs' GPS tracking data.

		SEX			
		F-F	F-M	M-M	Total
AGE	A-A	210	15	0	225
	A-S	37	2	0	39
	S-S	1	0	1	2
	Not Recorded	126	5	0	131
	Total	374	22	1	397

Pairs with high contact rates tended to have fewer non-contact periods, although pairs with a wide range in contact rates could have no non-contact periods (SRI ranged from 0.10 to 0.97 in pairs with no non-contact periods). Pairs with lower contact rates had the highest number of non-contact periods within pairs, but could also have few non-contact events, causing heteroscedasticity in the relationship between pair contact rate and number of non-contact periods (Fig. 3-7). The wide range in contact rate of pairs with no non-contact events pairs could have been caused by differences in tracking data duration, as pairs with no non-contact periods tended to have shorter overlapping GPS tracking data (t = -5.37, df = 54.55, $P < 0.01$). Female-female pairs ranged in contact rate and number of non-contact periods per pair more widely than female-male pairs, but contact rate and number of non-contact periods ranged across all age combinations. Only female-female pairs had very high contact rates (SRI > 0.75), but high contact rates occurred in all age combinations (adult-adult, adult-subadult, subadult-subadult and not recorded) (Fig. 3-8).

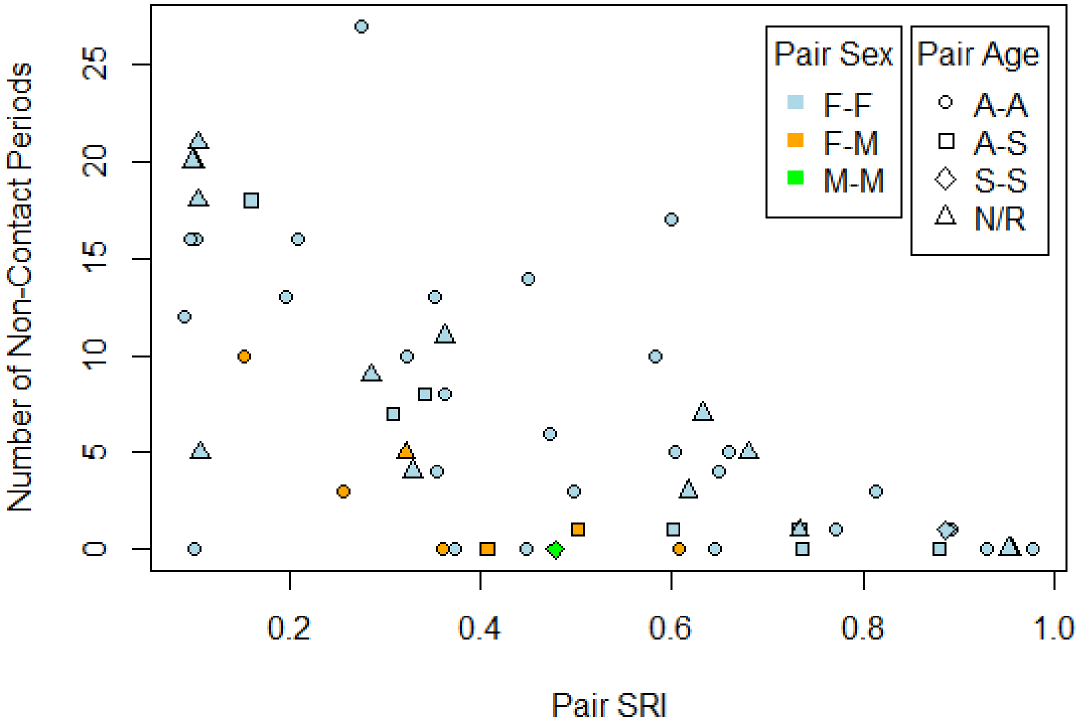

Figure 3-7: SRI and number of non-contact periods for by pair symbolized by sex (colour) and age (shape). Cohesiveness is compared between pairs by sex (F-F: female-female, F-M: female-male, M-M: male-male) and age (A-A: adult-adult, A-S: adult-subadult, S-S: subadult-subadult, N/R: age not recorded) to determine if some types of pairs tend to be more or less cohesive. For example, we might expect female-male pairs to not be as cohesive as female-female pairs, resulting in lower contact rates, or adult-subadult pairs to have a higher number of non-contact periods characteristic of exploration and natal dispersal (Janeau et al., 1995; Truvé & Lemel, 2003).

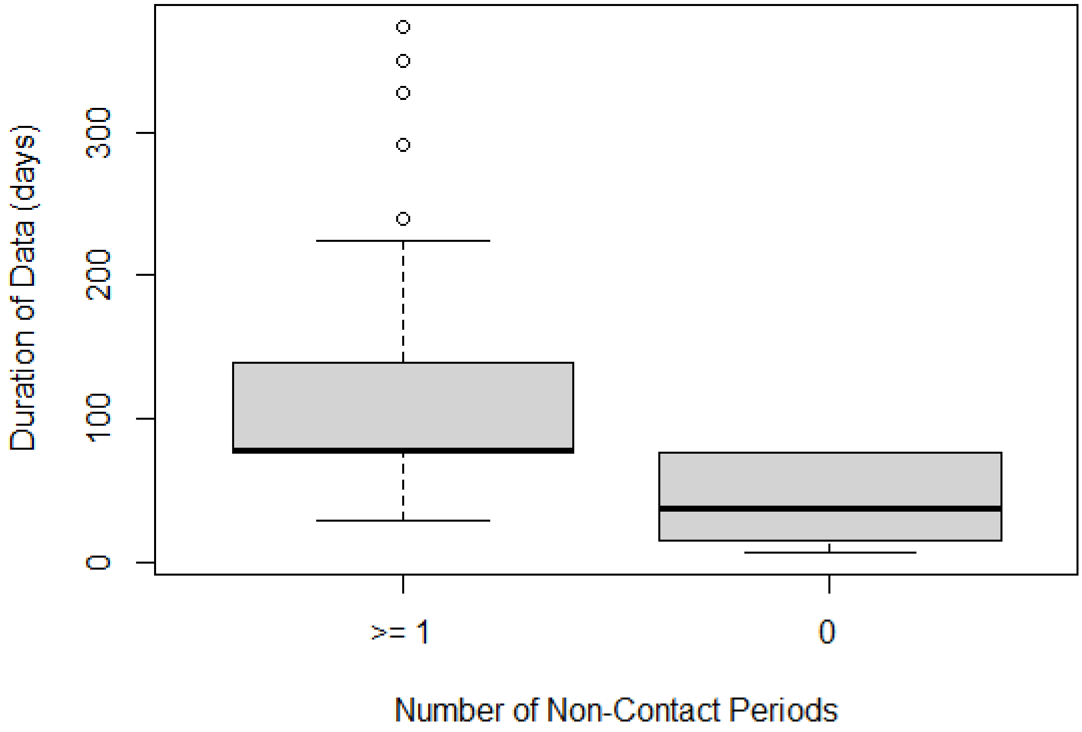

Figure 3-8: Duration of overlapping GPS tracking data in pairs with no-non contact periods versus pairs with one or more non-contact periods. Variance in the duration of overlapping tracking data was caused by uneven start and lengths of GPS tracking data in individuals

Non-contact and contact periods were compared within and between pairs by contact rate to determine if movement data segments are similar or different across pairs with varying strengths of association. Non-contact periods were similar in duration across all pairs regardless of contact rate, while contact periods were longer in duration in higher contact rate pairs (SRI > 0.75) compared to lower contact rate pairs (t = 3.70, df = 11.46, $P <$ 0.01). In the lowest contact rate pairs (SRI < 0.25), the durations of non-contact periods and contact periods were not significantly different (SRI < 0.25: t = 1.74, df = 298.91, P = 0.08), though there was a significant difference in the duration of non-contact and contact periods across all pairs, as mentioned previously. Therefore, low contact rate pairs could have short and frequent non-contact periods, and only sometimes had longer non-contact periods (Fig. 3-8, Fig. 3-9). Individuals in pairs with SRI > 0.75 were closer to each other during contact periods compared to lower contact rate pairs (t = 5.70, df =

24.93, $P < 0.01$), though distance between individuals during non-contact periods was consistent across high and low contact rate pairs ($t = 0.01$, df = 5.17, $P = 0.98$). This suggests low contact rate pairs are even less cohesive within the contact periods as defined in this study compared to high contact rate pairs, and could frequently be more than 100 metres separated during their contact periods (Fig. 3-9). Individuals in high contact rate pairs were more even distances from their home range centroids during contact periods compared to low contact rate pairs, meaning one individual was further from their home range centroid than the other in lower contact rate pairs during contact periods ($t = -7.55$, df = 31.26, $P < 0.01$). Contrarily, within high contact rate pairs, distances from home range centroids was more uneven during non-contact periods than contact periods, but the difference was not statistically significant (Fig. 3-9). Put plainly, it appears individuals travel away from their home range centroid during non-contact periods in high contact rate pairs, but this pattern occurs during contact periods in low contact rate pairs. This provides evidence that low contact rate pairs could belong to different social groups due to the uneven distances from each individuals' home range centroid during contact periods. Finally, there was no significant difference in DI in non-contact periods or contact periods between pairs by contact rate (Fig. 3-9).

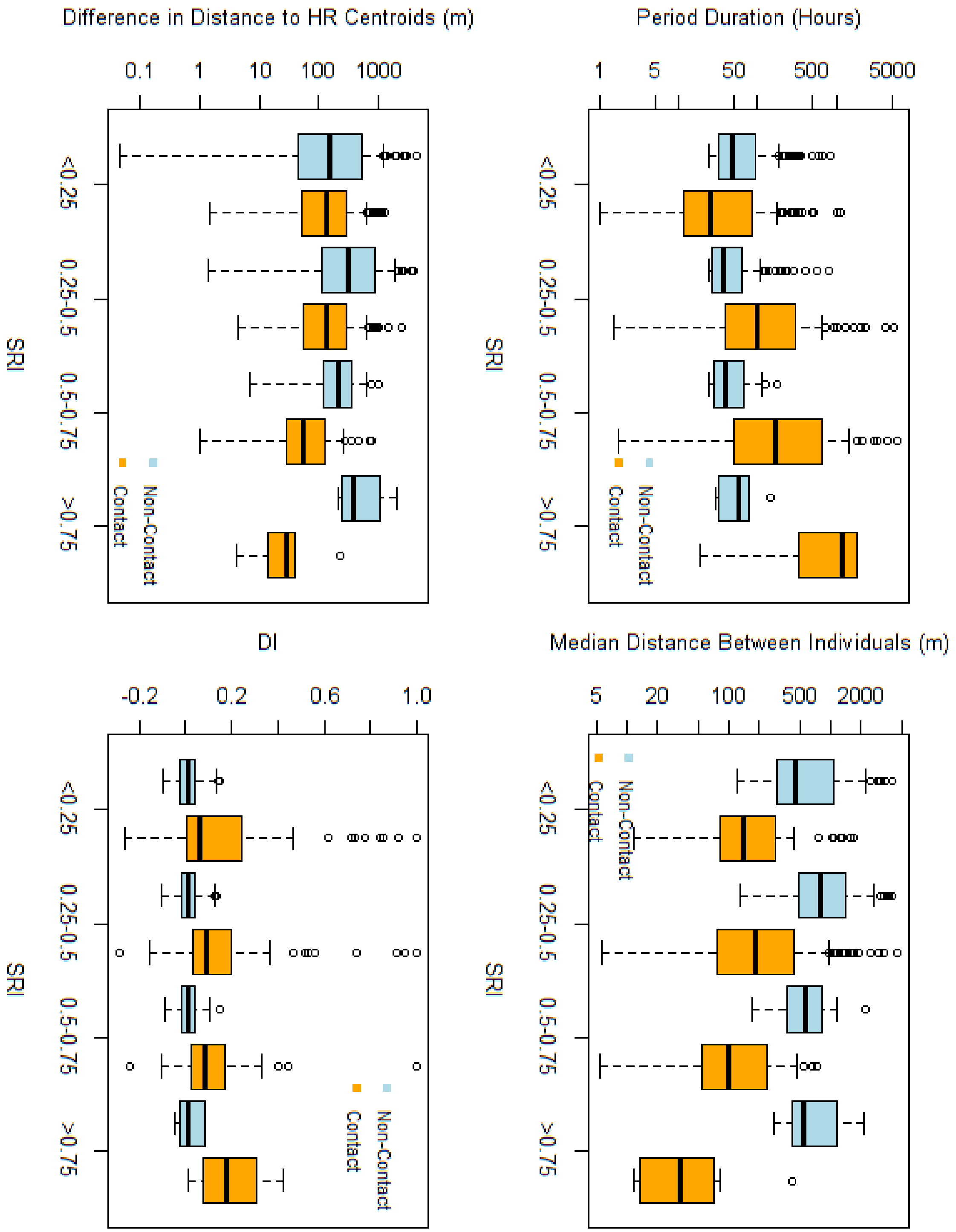

Figure 3-9: Duration, median distance between individuals in pairs, difference in the distance from home range centroids between individuals in pairs and DI in non-contact versus contact periods compared by contact rate.

3.4 Discussion

3.4.1 Non-contact periods in strongly associated pairs

Using GPS tracking data of wild pigs from four separate study sites, a PBSN was measured and tested for social associations through a data stream randomization test. A wide range in strength of association in wild pig social pairs was observed in pairs with significant data stream randomization test results. Due to the occurrence of unusually high peaks in the randomized contact rates of two pairs from ORR with short durations of overlapping tracking data, the effects of the duration of GPS tracking data on contact rates in the randomized data should be further analyzed to determine how duration of tracking data affects the results of the data stream randomization test. To measure and characterize the cohesiveness of wild pig social pairs, long lasting non-contact periods, defined as the passing of at least 24 hours without a contact between individuals were measured in the GPS tracking data of wild pig pairs with moderate to high contact rates. It was found that 43 wild pig pairs had one or more long lasting non-contact periods, while only 14 pairs had no 24 hour non-contact periods.

The occurrence of non-contact periods indicates associations within wild pig social pairs were not constant over time, and could be interrupted multiple times for long periods. Wild pig pairs that had no non-contact periods ranged widely in contact rates, which could be due to shorter overlapping GPS tracking data, especially in pairs with lower contact rates. Differences in the number of non-contact periods between pairs based on sex and age of paired individuals was inconclusive due to the high proportion and variability of female-female pairs, and high amount of pairs with missing age data, although female-female pairs did tend to have more non-contact periods than female-male pairs. Overall, non-contact periods were characterized by shorter durations, greater distances between individuals, less correlated movement and uneven distances from home range centroids within pairs, although some differences in these measures were found between pairs with high versus low contact rates.

Though overall wild pig social structure and contact heterogeneity has been researched (Pepin et al., 2016; Podgórski et al., 2014), the cohesiveness and contact patterns within social groups is not well known (Beasley et al., 2018). Wild pig pairs with high (and significant based on the data stream randomization test) contact rates likely belong to the same social group or at least have social interactions (Spiegel et al., 2016), but these pairs still had long non-contact periods characterized by different spatial association patterns within the timeframes of the study periods. By finding long non-contact periods in social pairs, we have shown that social and spatial associations in strongly associated pairs are not homogenous over the duration of the study periods. The occurrence of long non-contact periods has important implications for understanding contact heterogeneity in social animals as well as specific implications for the ecology, impacts and management of wild pigs as follows.

Firstly, identifying long non-contact periods is important for understanding contact rates and dynamics in socially structured animals, as the distribution of non-contact fixes might not be homogenous over time and can be concentrated into continuous periods without associations, contrasted by periods of very cohesive association. Though contact heterogeneity generally refers to the spatial structure of sociality where individuals contact socially associated individuals more than others, it should not be misconstrued that socially associated pairs are always in contact (subsequent analysis could explore from the opposite perspective; that non-associated pairs can have contacts). For instance, in social animals with moderate to high contact rates (e.g. >=50%), based on the results observed here one could possibly expect changes in the strength of association within the timeframe of measurement. So while the principle of contact heterogeneity is useful for analyzing attributes of strongly associated, more clearly structured groups, the reality may be that groups defined by strong associations are not as meaningful if interrupted or rare associations have important ecological consequences (this is known as the "strength of weak ties" theory: Granovetter, 1973; McFarland et al., 2017). The possibility of interruptions to spatial and social associations should be considered at various time scales as they relate to the ecological question of interest that defines the social network, as interruptions in social associations could provide the opportunity for non-group like behaviours or represent changes in factors influencing movement within the timeframe of the study periods (Kay et al., 2017).

Relating to wild pigs, when considering sociality over a weekly or monthly time scale, one should account for possible interruptions in usual contact heterogeneity and social structure. Varying social group cohesiveness has important implications relating to the harmful effects and management of wild pigs such as disease transmission, which can only require a short encounter between individuals to occur (Pepin et al., 2016; Podgórski et al., 2018). Therefore, when considering social structure as a factor affecting the likelihood of disease transmission (e.g. Yang et al., 2021) or in considering wild pig spatial ecology more generally, spatial and social interruptions in association should be accounted for in pairs belonging to the same social group. It is expected that sounder cohesiveness could be related to individual behaviours such as parturition (Graves, 1984), sounder fission and population expansion (Gabor et al., 1999), but more analysis is required to determine if non-contact periods observed here relate to any of these specific behaviours or social group dynamics. However, this analysis provides some understanding of the cohesiveness of wild pig social groups, an aspect of wild pig spatial ecology and sociality in need of research (Beasley et al., 2018).

Non-contact periods did not consider if contact with other individuals in the study area occurred during the interruption between the two individuals in the pair. Non-contact periods in some pairs could have involved contacts with a different individual in some cases, as some individuals had high contact rates with more than one other individual, and were included in more than one unique pair selected in this analysis. Individuals that had contacts and non-contact periods could have exhibited fission (group splitting) and fusion (group joining) behavior, or were part of a sounder with more than two GPS tracked sounder members. Evidence of wild pig sounder fission and fusion was found by Gabor et al. (1999) and related to preferred sub-groups within stable larger sounders, although behavioural associations between wild pigs were not measured in fine spatial-temporal resolution as in this research, thus the dynamics and timing of sounder fission-fusion events is unclear.

Detecting contacts with other individuals during non-contact periods would provide direct insight into some of the spatial/social effects implicated in this analysis such as disease transmission, and sounder fission-fusion events (Gabor et al., 1999; Pepin et al., 2016). Measuring the occurrence or non-occurrence of contacts with other individuals during a pair’s non-contact periods could provide not just descriptive measurements of sounder cohesiveness, but begin to explain why sounder interruptions occur, providing a better understanding of factors affecting sounder dynamics. However, whether or not non-contact periods were occupied by contacts with another individual in this analysis, it remains that the original pair had contact before/after separating for 24 hours or more, and thus contributed to measuring the cohesiveness of social pairs over time.

3.4.2 Comparing non-contact and contact periods between and within pairs

Different individual factors and behaviours recognized to affect wild pig sounder dynamics are related to the age and sex of individuals, and include mating, parturition, natal dispersal, site selection and others. For example, adult females usually show fidelity to daily sites and resting places, except during parturition when they isolate themselves, while subadults and males range more widely and may not exhibit daily site fidelity. (Graves, 1984; Janeau et al., 1995; François Spitz & Janeau, 1990; Truvé & Lemel, 2003). Accordingly, the age and sex compositions of wild pig pairs were compared in expectation that variability in cohesiveness of pairs would be related to different individual behaviours and social relationships of wild pigs of different ages and sexes. However, patterns of difference were not clear due to the overrepresentation and wide variability in female-female and adult-adult pairs in the selection of pairs with high contact rates. The finding that most pairs with moderate to high contact rates in the study areas were female-female pairs is unsurprising given the central role of females in wild pig social organization (Podgórski et al., 2014). So although the sex and age of paired individuals was not able to explain differences in pair cohesiveness here, the wide variation in contact patterns and cohesiveness between female-female pairs reinforces the finding that wild pig social groups can vary in strength of association between individuals as well as within pairs over time, and that contact heterogeneity in wild pigs is imperfect.

Some differences in spatial associations and dynamic interactions in contact and non-contact periods between pairs with different strengths of associations were observed, though duration of non-contact periods, median distance between individuals during non-contact periods, difference in distance from home range centroids during non-contact periods, DI index in non-contact periods and DI index in contact periods were not significantly different between pairs. The consistency in length of non-contact periods across pairs suggests pairs tend to re-associate regularly after a certain amount of time and that lower contact rate pairs do not necessarily have longer non-contact periods, but more (Fig. 3-6, Fig. 3-9). This means that more moderately associated individuals' contact patterns are less heterogeneous over time and involve more frequent associations and interruptions than more strongly associated pairs, which tended to have more cohesive contact periods and fewer non-contact periods. Large median distances between individuals, large differences in distance from home range centroids and no movement correlation (DI = 0) during non-contact periods in high contact rate pairs indicates one individual usually travels away from the other. This could be indicative of sounder fission events in high contact rate pairs during non-contact periods. Conversely, the higher difference in distance from home range centroids in lower contact rate pairs during contact periods indicates one individual travels further away from their home range centroid during contact periods, providing evidence of between-group contacts, or sounder fusion.

Due to the more frequent non-contact periods in lower contact rate pairs, it would be of interest to compare the node degree (number of unique connections with others) of individuals in these pairs to determine if these individuals might have more contact between groups, which can drive disease transmission (Dougherty, Seidel, Carlson, Spiegel, & Getz, 2018; Pepin et al., 2016). Recent research has found spatial spread of disease transmission in wild pigs is female biased, even though females are known to form spatially distinct social groups (Pepin et al., 2021; Podgórski et al., 2014). Therefore, the occurrence of female-female pairs with less cohesive spatial associations found here could support the findings of Pepin et al. (2021) that some females play important roles in between group contacts.

Although non-contact periods were frequently close to 24 hours in length, many longer non-contact periods were observed, including in strongly associated pairs. Because of evidence that lower contact rate pairs were less cohesive than higher contact rate pairs during contact periods, measuring shorter non-contact periods could provide insight into pair cohesiveness at shorter time scales. Examining this difference between pairs would a suitable question for future analysis, although measuring shorter non-contact periods would be a less clear departure from regular social associations, and could be a part of regular sounder dynamics such as forager-scrounger relationships (Graves, 1984). Some research on daily activities and habitat use of wild pigs already exists (Janeau et al., 1995; Johann et al., 2020; F. Spitz & Janeau, 1995; François Spitz & Janeau, 1990) that identifies and compares different daily movement behaviours and habitat use between different age and sex wild pigs, though comparisons of activity patterns between individuals within social groups are not made. Therefore, research on different daily association patterns within social groups would complement these studies and provide a more comprehensive understanding of the relationship between daily activity and sociality of wild pigs.

3.4.3 Methodological considerations

Calculating non-contact periods is based on time-groups of GPS tracking fixes (defined by the temporal threshold of a contact used here), so a fix of individual A without a fix of individual B would be considered a non-contact fix (because the distance between fixes is unknown, it is not considered a contact in this analysis). Missing fixes should have little impact on calculating non-contact periods, as it is unlikely that 24-48 or more consecutive fixes would be dropped causing a false-positive non-contact period due to the high fix success rate of the GPS tracking data used here (Table 3-1). A missed single contact fix during a non-contact causing a false elongation of the non-contact period would be unlikely, although a few contact periods were defined by single contact fixes. Therefore, considering only simultaneous fixes of both individuals should not change the measurement of non-contact periods significantly due to the high temporal resolution and fix success rate of the GPS tracking data used.

Because it was found that pairs with no non-contact periods tended to have shorter overlapping extents of GPS tracking data, further research should examine the frequency of long non-contact periods and determine if non-contact periods are increasingly likely to occur over time. Otherwise, GPS tracking data should be of sufficient and consistent duration to capture one to several days long non-contact and contact periods, such as 10 weeks or more (e.g. mean data durations in Table 3-1). Also, because of the high proportion and variability of female wild pigs and female-female pairs and the high amount of individuals with missing age data, further research that deliberately measures spatial/social associations in a range of sex and age wild pigs should be performed to clarify whether or not there is a significant difference in cohesiveness between pairs. Cohesiveness could also be compared across more age categories (or directly to the age of individuals) to better capture differences in cohesiveness of wild pigs at different life stages, such as piglets, yearlings, subadults and adults.

3.4.4 Conclusion

Social associations in wild pigs were measured and tested using GPS tracking data in a proximity based social network and data stream randomization test. As a wide range in the strength of association in social pairs was observed, spatial associations in social pairs were measured over time. Most social pairs had long periods of 24 hours or more without any spatial associations, characterized by shorter durations, higher distances between paired individuals, more uneven distances from home range centroids, and less correlated movement compared to periods where spatial associations did occur. Having found long non-contact periods occur within pairs, spatial associations in wild pigs are not evenly distributed over time, but can occur in bursts of strong association contrasted by periods with no associations, even in wild pig social pairs with high contact rates. Therefore, when considering wild pig social structure, interruptions in social associations in wild pigs should be accounted for even in strongly associated pairs. Though differences in cohesiveness between pairs was inconclusive, some difference in the cohesiveness of pairs based on contact rate was found, where pairs with higher contact rates had stronger spatial associations during contact periods compared to lower contact rate pairs. Accordingly, even shorter periods without associations, such as within day periods should be examined to improve understanding of the cohesiveness of wild pig social groups over time.

3.5 References

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Chapter 4

4 Conclusion

Wild pig social structure is directly related to their harmful effects, especially disease transmission (Pepin et al., 2021; Yang et al., 2021), making it an important research priority (Beasley et al., 2018). Accordingly, it was the aim of this thesis to examine wild pig social structure in two ways: 1) heterogeneity in strength of associations between individuals, and 2) heterogeneity in strength of associations over time within specific dyads. In chapters two and three, GPS tracking data of wild pigs from four study sites across the southeastern United States are analyzed to address the research questions and objectives set forth in chapter one. The findings of chapters two and three are discussed here, as well as avenues for future work. Chapter two addressed the first and second research questions as well as the first research objective, aiming to quantify the strength of association between wild pigs to gain insight into wild pig social structure heterogeneity and identify social pairs using GPS tracking data. Chapter three addressed the first and third research question, as well as the second research objective.

In chapter two, spatial overlap and dynamic interaction was measured between wild pigs using GPS tracking data. The strength of association between individuals was quantified by measuring contact rates in a proximity based social network. A data stream randomization test was performed to test the hypothesis that observed spatial association rates were due to social movement behaviour (H_0: observed spatial associations were not different than association rates that could occur due to spatial overlap). It was found that wild pigs captured in the same trap all had moderate to very strong associations and significant data stream randomization test results, indicating these pairs likely belonged to the same social group. It was also found that there were a number of pairs that were not captured in the same track exhibiting strong evidence of social group belonging. Individuals with significant data stream randomization test statistics ranged widely in strength of association, indicating interaction within social pairs could vary from group to group.

In chapter three, the social network and data stream randomization methods of identifying social associations in wild pigs using GPS tracking data were applied to the Red River Ranch site, along with data from three additional study sites. As in chapter two, a number of pairs with high strengths of association and significant data stream randomization test results were observed, providing strong evidence of social group belonging in these pairs. To gain insight into the wide range in strength of association observed in social pairs in chapter two and three data, the GPS tracking data of strongly associated pairs were subset based on the occurrence of long periods of time elapsing (>24 hours) without a single contact between individuals (termed non-contact periods). The patterns of non-contact periods were compared based on the sex, age and strength of association of paired individuals to test for differences that could explain the wide range of strengths of association observed in social pairs. It was found that female-female pairs tended to have more non-contact periods, although female wild pigs and female-female pairs were overrepresented in the GPS tracking data. No significant difference in cohesion was found based on the ages of paired individuals, although many individuals in the GPS tracking data had no recorded age. Non-contact periods were characterized by long, continuous periods of less cohesive spatial and dynamic interaction patterns compared to the corresponding periods with associations within pairs, providing evidence of interruptions to social associations within pairs over time.

4.1 Thesis questions and objectives

4.1.1 Research objective 1: Quantify the strength of associations and identify social associations between wild pigs using GPS tracking data

Measuring a proximity based social network quantifies the relative strength of association between wild pigs in the study areas. By performing a data stream randomization test to generate a null model network that preserves the regular space use of individuals but desynchronizes movement, the effect of synchronous movement on contact rates can be determined. For pairs with significant test results, spatial association rates were driven by social movement behaviour and are greater than associations that could have occurred due to overlapping space use. The results of the test were supported by the high observed strength of associations in pairs with significant test results, as well as preliminary indications of group membership through trapping individuals in the same trap in chapter two, providing strong evidence of individuals belonging to the same social group.

4.1.2 Research objective 2: Measure and compare spatial associations within pairs over time, and between pairs by sex and age of paired individuals

The cohesiveness of pairs over time was measured by looking at associations within pairs at the GPS fix level, and identifying the occurrence of long continuous periods in which no contacts between individuals occurred. Due to the occurrence of long non-contact periods in many pairs, it was found that the strength of association within pairs was not evenly distributed over time, but concentrated into periods of association and periods without association. The number of non-contact periods within pairs was compared between pairs by the sex, age and strength of association of paired individuals, to examine differences in cohesiveness between pairs. The duration, median distance between individuals, difference in distance from home range centroids, and movement correlation (DI index) during non-contact and contact periods were compared between strongly and weakly associated pairs to determine how spatial associations varied over time.

4.1.3 Research Question 1: How heterogeneous are wild pig spatial and social associations between individuals and within associated pairs?

Based on the contact rates measured in the PBSN and the results of the data stream randomization test, a wide range in strength of spatial associations between GPS tracked wild pigs was found. Heterogeneity in the strength of association between individuals was related to social grouping and the distance between home ranges of wild pigs, as individuals with very strong associations were found to likely belong to the same social group through the data stream randomization test, and individuals with no associations tended to have home ranges separated by around two kilometres or more. However, heterogeneity was not perfect as many pairs with significant data stream randomization test results had moderate or weak strengths of association. Some rare interactions likely between groups were observed, and a range of contact rates in socially grouped pairs was also observed, indicating some interaction between groups and varying strength of association within groups occurred.

Within pairs, association patterns varied over time, as it was found that long periods of time without any spatial association occurred in the majority of pairs analyzed. As would be expected, spatial association and dynamic interaction patterns were significantly weaker during non-contact periods, as pair members were found to be further distances apart and have significantly less correlated movement. This, in combination with the length of non-contact periods demonstrates that spatial and social associations within pairs are heterogeneous and can temporarily be interrupted, often for substantive temporal periods of longer than 24 hours.

4.1.4 Research Question 2: How can individuals be assigned to groups based on spatial associations measured from GPS tracking data?

The data stream randomization test generated evidence of pairwise social group belonging by comparing observed association rates to association rates that could be expected by chance due to spatial overlap. The data stream randomization test results were supplemented by observed contact rates (providing a measure of strength of association between individuals) and records of which GPS tracked individuals were captured in the same trap, which agreed well with the observed association rates and results of the test. Therefore individuals with strong observed associations dependent on social movement behaviour determined by the proximity based social network and data stream randomization test likely belonged to the same social group.

4.1.5 Research Question 3: Does the cohesiveness of associated pairs vary based on the attributes of paired individuals?

Some evidence of difference in cohesiveness between pairs was found based on the sexes of the paired individuals, where female-female pairs had more non-contact periods on average than female-male pairs. However, this result requires further interrogation owing to the overrepresentation of females in the GPS tracking data. The number of non-contact periods within pairs did not vary by age, but age categories were coarse and many individuals did not have a recorded age. Individuals with stronger association rates had more cohesive contact periods characterized by longer durations, and smaller median distances between individuals compared to more weakly associated pairs. More weakly associated pairs tended to have more non-contact periods, but there was high variability in the relationship between the number of non-contact periods and contact rates. Due to the uneven amount of female and male wild pigs collared, missing age data and range in the number of non-contact periods occurring in weakly associated pairs, little evidence of difference in cohesiveness between pairs based on their attributes was found. Based on these results, adult female-female wild pig social pairs can vary in strength of association between pairs, and within pairs over time.

4.2 Discussion and future work

In chapter two, a wide range in strength of association in socially interacting pairs was observed providing more evidence that wild pigs exhibit contact heterogeneity in their social movement behaviour. Several pairs also had very low contact rates, indicating that in some dyads contacts only occur rarely. It was often the case that the very rare associations observed still exhibited significant data stream randomization test results. It is possible that these pairs do in fact have short bursts of social interaction, or that these significant results occur due to very rare associations between individuals with very low amounts of spatial overlap. So while the range in strength of association and differences between social or strongly associated pairs was analyzed in chapter three, further work is needed to further investigate the spatial and temporal patterns dyads exhibiting very rare associations. Measuring short and/or rare associations between individuals would further improve understanding of contact heterogeneity in wild pigs and disease transmission rates, as rare and short contacts between groups can still result in disease transmission and be a limiting factor in disease spread (Pepin et al., 2016).

Studying any differences in the cohesiveness of social pairs would benefit from data that includes a more even balance of males, females, juvenile, subadult and adult wild pigs, as the uneven balance of female wild pigs and missing ages in the data analyzed could have affected the results on differences in cohesiveness between pairs by sex and age. It should be expected that even if ages and sexes of wild pigs were more evenly balanced in the data, female-female pairs would still comprise the majority of social pairs (as was the case in chapter three) due to the focal role of adult females in wild pig social structure (Podgórski et al., 2014). However, with more balanced data one could be more certain about any differences between individuals that affect group cohesion. Some pairs in chapter three were also less than ideal due to uneven start times and varying durations of overlapping GPS tracking data, causing these pairs to have significantly shorter periods of data that could be analyzed. Insufficient length of overlapping data possibly affected the results of chapter three, as pairs with no non-contact periods had shorter overlapping data durations than pairs with one or more non-contact periods. As interruptions to social structure were found to be one to several days long, overlapping tracking data should be at least several weeks to several months in duration to allow sufficient time for social patterns and interruptions to emerge. Finally, the potential effects of un-collared wild pigs in the study areas is unknown. Trapping wild pigs should attempt to capture entire social groups, as was the case in at least two of the four study areas to try and ensure all wild pigs in the area are known (Gaskamp et al., 2021), but little can be known about transient wild pigs or interactions with wild pigs along the edges of study areas. Knowing the true population density of wild pigs in the study area is important for their harmful effects, as well as understanding their social structure, as found in chapter two in the relationship between distance between home range centroids and association rates (Keiter et al., 2017; Pepin et al., 2016).

A parameter of 24 hours was chosen in the definition of a non-contact period because it provided confidence that a lack of associations represented a meaningful interruption to social associations within pairs. This is in contrast with shorter wanderings or interruptions that could occur but might be a part of regular daily activities such as foraging (Janeau et al., 1995). It was found that less strongly associated pairs had less cohesive spatial and dynamic interaction compared to more strongly associated pairs while they were in contact, indicating cohesiveness might also vary at shorter time scales than the 24 hour periods considered here. For instance, more weakly associated pairs could have shorter non-contact periods or less spatial associations within periods of association compared to strongly associated pairs. Accordingly, social group cohesion should be studied at various time scales to further examine differences in cohesiveness between pairs over time. Social group cohesiveness could also be studied over longer time periods, such as over the entire life cycle of wild pigs, to examine differences in temporary or permanent social group splitting and gain insight into longer term sounder dynamics (Gabor et al., 1999; Truvé & Lemel, 2003).

Lastly, though chapter three described the heterogeneity of associations within pairs over time, it remains unknown why pairs' associations were interrupted. Explanations for non-contact periods are briefly explored based on social structure through measuring the difference in distance of each individual from their home range centroid to try and identify between-group associations, but further work is required to identify specific behaviours or even potential environmental factors that could affect wild pig social group cohesion. Future work should analyze movement behaviour (e.g. fast bursts, stationary) before and after separation to try and understand why social pairs split up, or habitat preferences or features that could cause interruptions. These factors should be studied as they relate to known wild pig movement ecology and behaviour, such as scrounger producer foraging relationships or parturition (Graves, 1984; Janeau et al., 1995; Truvé & Lemel, 2003) or the habitat requirements of different sex and age pairs (F. Spitz & Janeau, 1995).

Overall, the wide range of contact rates and variability in spatial association patterns over time in wild pig social pairs show that wild pig social structure is not static nor perfectly heterogeneous. Therefore, when considering wild pig sociality, one should account for the possibility of between-group interactions and non-social behaviour in social groups as they relate to ecological phenomenon of interest. More research is needed to understand what behaviours or environmental factors cause non-contact periods within wild pig social groups, as well as why rare contacts between individuals occur. In the case of the harmful effects of wild pigs, knowledge of the cohesiveness of social groups can inform management strategies by providing a better understanding of risk and optimizing management actions, as contacts and movement directly relate to space use, range expansion, disease transmission, and wild pig responses to management actions.

Effective management strategies are needed to mitigate the damages caused by wild pigs in their established range and their expansion across North America.

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Appendices

Appendix A: Red River Ranch GPS tracking information

Table A-1: Red River Ranch GPS tracking statistics by individual ID and year (burst column). Individuals trapped together are expected to belong to the same sounder, identified in the sounder column.

Sounder (by trapping)	Burst	Fix success rate (%)	Total fixes	Duration (days)
1	2016_21951	98.88405	3633	78
1	2016_21954	99.72782	3671	78
2	2016_21952	99.02014	3664	78
2	2016_21955	99.91835	3670	78
3	2016_21953	99.91832	3638	78
3	2016_21962	99.91835	3658	78
4	2016_21956	99.75504	3671	78
4	2016_21967	99.78225	3672	78
5	2016_21957	99.94256	3665	78
5	2016_21960	99.80947	3667	78
6	2016_21958	99.86286	3666	78
7	2016_21959	99.56451	3480	74
8	2016_21961	99.61884	3641	77
8	2016_21965	99.86324	3651	77
9	2016_21963	98.44856	3659	78
9	2016_21966	99.94556	3617	78
10	2017_21951	100	3312	70
11	2017_21952	100	3312	70
12	2017_21954	99.49713	1385	30
12	2017_21963	99.96981	3311	70
13	2017_21955	98.52053	3263	70
13	2017_21958	95.40924	3159	70
14	2017_21957	99.06401	3281	70
15	2017_21960	99.42616	3292	70
15	2017_21966	99.87923	3308	70
16	2017_21961	87.71135	2905	70
17	2017_21965	99.96981	3311	70
18	2017_21967	99.21498	3286	70
19	2017_27345	99.96981	3311	70

Appendix B: Fieldwork photographs

Figure B-1: An adult wild pig (*Sus scrofa*) photographed by Noble Research Institute (*n.d.*). Wild pigs are an invasive species in North America, responsible for significant damages to agriculture, livestock and the natural environment.

Figure B-2: A sounder of wild pigs consisting of two adult females and their associated young in a baited suspended drop enclosure designed to capture the entire sounder. Capturing the entire sounder increases the effectiveness of trapping for management and minimizes disruptions to social groups, avoiding unintended consequences such as disease transmission between groups. Photographed by Noble Research Institute (*n.d.*).

Figure B-3: An adult wild pig and several piglets captured in a suspended drop enclosure. Photographed by Noble Research Institute (*n.d.*).

Figure B-4: Research collaborator Dr. Stephen Webb measuring the shoulder height of a wild pig. A GPS tracking collar has been attached around the neck of the wild pig, which will be released, recovered and harvested at a later date. Photographed by Noble Research Institute (*n.d.*).

Curriculum Vitae

Name:	Jack McIlraith
Post-secondary Education and Degrees:	Trent University Peterborough, Ontario, Canada 2015-2019 B.Sc.
	Fleming College – Frost Campus Lindsay, Ontario, Canada 2017-2018 Ontario College Graduate Certificate
Honours and Awards:	Trent National Renewable Scholarship 2015-2016
	Western University Esri Canada Centres of Excellence Student Associate of the Year 2021
Related Work Experience	Teaching Assistant Western University 2019-2021
	Academic Assistant Trent University 2018
Other Related Experience	Organizing team: Special Session in Geospatial Data Science. 2021 Annual Meeting of the Canadian Association of Geographers
	Esri Canada Centres of Excellence Student Associate 2019-2021

Conference Presentations:

McIlraith, Jack., Long, Jed., Webb, Stephen. (2021 July 7-11). Data stream randomization for identifying social associations in GPS tracked wild pigs. *2021 Annual Meeting of the Canadian Association of Geographers*. Prince George, British Columbia, Canada [virtual]

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