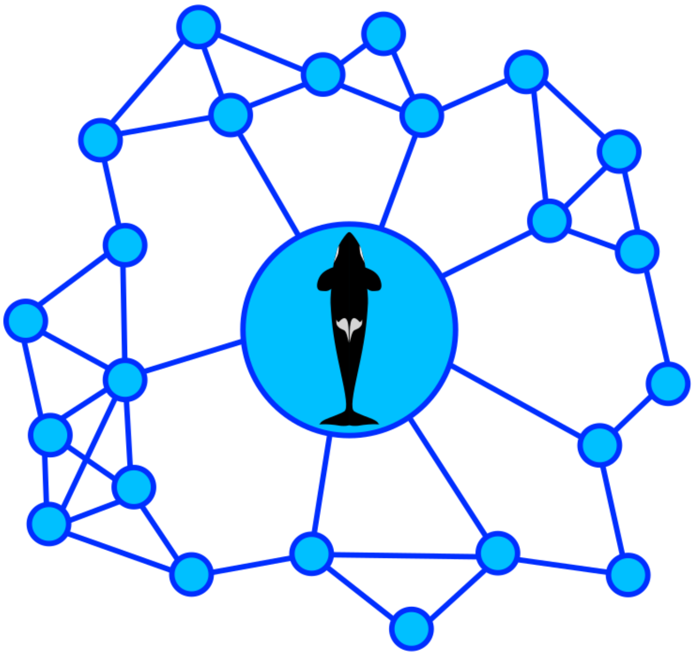
Developing methods and applications for the analysis of cetacean social networks



Submitted by Michael Nash Weiss, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology

July 8th, 2020

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other university.

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Abstract

Cetaceans, the whales, dolphins, and porpoises, represent a taxon of intense interest for researchers studying non-human social structure. Social network analysis has become a central tool for studying these species, however the collection, analysis, and application of cetacean social network data comes with numerous challenges. In this thesis, I address key research gaps in the study of cetacean social networks, using the well-studied southern resident killer whale populations as my study system.

In the first chapter, I present a systematic literature review on cetacean social networks, in order to identify open areas for future research and development.

In Chapter 2, I address the question of social complexity and its quantification. Using mixture models, I develop and test measure of social complexity based on relationship diversity that can be derived from association networks.

In Chapter 3, I demonstrate that a commonly used statistical procedure for regression in association networks does not specify a proper null hypothesis, and results in high type I error rates.

In Chapter 4, I use unmanned aerial systems methods to measure association and interaction networks within a group of southern resident killer whales, finding important differences in the structure of these different networks.

In Chapter 5, I use long-term photographic data to model the spread of a novel pathogen over the social network of the endangered southern resident killer whale community to assess overall risk and potential management strategies.

In Chapter 6, I use a multi-decade dataset of social associations, survival, and fecundity to test the link between aspects of the social environment and fitness in the southern resident killer whale population.

In the final chapter, I provide a general discussion and synthesis of my results, and suggest areas for future research, both generally and within the southern resident population specifically.

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During the course of my PhD work, I contributed to several published studies that are relevant to the topics covered in this thesis. These publications are included here as appendices.

* Joint first author

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Many of the ideas and thoughts in this thesis, particularly those related to developing novel methods for social network analysis, were developed largely during long, exciting, and sometimes frustrating whiteboard sessions with Dan Franks, who also was integral to the completion of most of the work presented here. This research would not exist if not for Dan’s knowledge, curiosity, and patience.

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Declaration

The work in this thesis involved collaboration with Hal Whitehead (HW), Sam Ellis (SE), Lauren Brent (LB), Matthew Silk (MS), Deborah Giles (DG), Charlie Grimes (CG), Mia Lybkaer Kronborg Nielsen (MLKN), Mike Cant (MC), Sadie Youngstrom (SY), Sam Wasser (SW), Mike Cant (MC), and Paolo Domenici (PD), whose specific contributions are listed below. My primary supervisor Darren Croft (DP) and Dan Franks (DF) were involved in all chapters. Ken Balcomb (KC) and Dave Ellifrit (DE) at the Center for Whale Research guided and oversaw all fieldwork, and collected and managed the long-term data on encounters and demography in the southern resident killer whale population, and were therefore crucial for all chapters involving empirical data from this population.

Chapter 2. HW conceived of the initial idea for a model of social complexity from mixture models, and coded the first version of the model in MatLab. HW additionally provided access to the empirical cetacean association datasets used to test the method. DF and DP provided guidance on simulations used to test the method, and on drafting the manuscript.

Chapter 3. MS and DF helped run simulation iterations, and MS, DF, DP, LB, and SE all contributed to the verbal arguments presented and in designing the simulation tests.

Chapter 4. I performed drone flights with help from DG, SW, PD, and SY, who served as captain on the research vessel, as well as observers during flights. KB, DE, DG, CG, MLKN, SW, MC, PD, SE, SY, DP, and DF all provided input on data analysis and writing.

Chapter 5. I analysed photographs collected and curated by DE and KC, with help from additional Center for Whale Research staff and volunteers. DF and MS provided guidance on coding the epidemic modelling and null models. DE, KC, DF, MS, DP, and MC all provided input on writing

Chapter 6. DE and KC managed the encounter and demographic database for the southern resident killer whales.

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Chapter 2:

Weiss, M. N., Franks, D. W., Croft, D. P., & Whitehead, H. (2019). Measuring the complexity of social associations using mixture models. *Behavioural Ecology and Sociobiology*, *73*(1). https://doi.org/10.1007/s00265-018-2603-6

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Chapter 1

Future directions in cetacean social network analysis: Methods, theory, and applications

1.1 Introduction

The whales, dolphins, and porpoises, collectively referred to as cetaceans, have long been the subject of popular and economic interest. For centuries, various cetacean species have been harvested for food, oil, and entertainment (Bigg & Wolman, 1975; Gambell, 1993), and many populations are currently the basis of a booming ecotourism industry (see Higham, et al., 2016). In the 1970s, several long-term projects began studying wild populations of cetaceans at the individual level. It quickly became clear that these animals have complex, individualised societies. It has become common to compare cetaceans to primates; both groups exhibit impressive cognitive abilities and intricate neurological anatomy, complex social structures, and diverse ecological roles, with some species (specifically killer whales *Orcinus orca* and humans *Homo sapiens*) inhabiting the apex predator position within their respective ecosystems. While apes and other primates have often been studied to provide insight into human evolution, cetaceans may serve as an out-group. Because the marine environment presents unique ecological challenges and opportunities, studies of cetacean societies allow researchers to piece apart the evolutionary and ecological forces shaping complex social structure, and how social evolution in the ocean may differ from in terrestrial systems (for review see Connor, 2000).

Besides the interesting comparison to apes and other terrestrial systems, the study of cetacean social structure has provided ways to investigate many other open questions in behavioural ecology. Understanding these social systems can give researchers insight into the interplay between sociality and culture (reviewed by Cantor & Whitehead, 2013), the ecological origins of social structures (reviewed by Pearson, 2011), and the relationship between social and cognitive complexity (e.g. Marino, et al., 2007). In addition, many cetacean populations are threatened or endangered (SSC

Cetacean Specialist Group, 2019), and understanding their social structure is often essential for developing effective management strategies for their conservation.

Although much progress has been made in our understanding of cetacean social systems, there are many aspects of their social lives that remain a mystery. There are significant challenges associated in addressing these knowledge gaps that relate to both the problems associated with data collection in the marine environment and available methods for the analysis of these often sparse and complexly structured datasets. Recent developments in methods for analysing animal social systems, particularly in the field of social network analysis, provide a number of exciting opportunities for quantifying the structure and function of cetacean societies. While previous work reviews both the general principles of social network analysis (Farine & Whitehead, 2015) as well as field studies and current knowledge about cetacean social systems (Rendell, et al., 2019), there is currently no up-to-date review of the application of social network theory to cetaceans. Such a review would be useful for summarizing variations in methodology, underlying themes, and highlighting research gaps in this subfield. In this chapter, I first provide an overview of cetacean social systems and how these can be represented as social networks. I then carry out a systematic literature review to identify key knowledge gaps that may provide fruitful directions for future research. I divide this later discussion into three main sections: theoretical questions, methodological directions, and potential applications.

1.2 Cetacean societies and social networks

Cetaceans as a group are extremely diverse in their life history, distribution, anatomy, and ecology. It is perhaps unsurprising, then, that cetaceans are also a behaviourally and socially diverse taxa. Despite this diversity, the social systems of cetaceans share some commonalities. All cetacean societies have some degree of fission-fusion dynamics, with group composition changing over time, however the timescale of these changes vary greatly (reviewed by Connor, 2000). All parental care is provided by the mother, and generally comes with a great deal of investment. This leads to females having a central position in most cetacean societies (Rendell, et al., 2019). Beyond these commonalities, however, cetacean social structures diverge greatly.

Perhaps the most complex social structures exist among the large, matrilineal toothed whales, with most well-known being the killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and pilot whales (*Globicephala* spp.). These social systems exhibit well defined, consistent social units embedded within larger social entities, such as the “pod” in killer whales, or “clans” in sperm whales (Gero, et al., 2015; Parsons, et al., 2009; Ottensmeyer & Whitehead, 2003). These species are therefore said to exhibit “multilevel” social structures (Grueter, et al., 2020), comparable to the tiered societies found in humans and other primates (Grueter, et al., 2012). Social units typically contain close maternal kin (Konrad, et al., 2018; Parsons, et al., 2009; Esteban, et al., 2016; Van Cise, et al., 2017; Alves, et al., 2013). Social associations within units are non-random, and may be driven by variation in kinship within the unit (Gero, et al., 2008). Associations between units are also non-random, however the role of kinship in defining these associations is variable. In short-finned pilot whales, between unit associations correlate positively with genetic similarity (Van Cise, et al., 2017), however in sperm whales and killer whales, kinship is not correlated with between-unit association (Deecke, et al., 2010; Konrad, et al., 2018). In sperm whales, males leave their maternal social units during puberty and form their own loose social network (Lettevall, et al., 2002). This system is strikingly similar to that of African elephants (*Loxodon africana,* Wittemyer, et al., 2005). In killer whales, in contrast, both males and females will often (and in some populations exclusively) remain in their mother's social unit for life (Parsons, et al., 2009; Esteban, et al., 2016), and do not appear to socially segregate from females (Esteban, et al., 2016; Williams & Lusseau, 2006). There is significant variation in sociality between populations within these species. In killer whales, strong differences are apparent in network structure between populations, with some populations exhibiting less structured, fission-fusion networks (Tavares, et al., 2017; Reisinger, et al., 2017), likely linked to differences in prey characteristics (Beck, et al., 2012). In sperm whales, there are differences in sociality between populations in the Atlantic and the Pacific (Whitehead, et al., 2012) and between vocal clans (Cantor & Whitehead, 2015), however the drivers of these differences are not clear.

The mid-sized coastal dolphins exhibit looser social networks. Group size is variable, and group membership changes frequently. Most of our knowledge about these systems comes from studies of bottlenose dolphins (*Tursiops* spp.), however, it is supplemented by recent studies of humpback dolphins (*Sousa* spp.), Atlantic spotted dolphins (*Stenella frontalis*), and Australian snubfin dolphin (*Orcaella heinsoni*). While populations of these species often exhibit multiple social communities, these do not represent consistent social units as in the matrilineal whales (Dungan, et al., 2012; Elliser & Herzing, 2012; Lusseau, et al., 2006). A possible exception may be in some isolated populations of humpback dolphins, where social modules appear to be highly disconnected from one another (Bouveroux, et al., 2019), and the strong, stable alliances formed by male bottlenose dolphins in some populations (Connor, et al., 2011). These species typically show some degree of social segregation by sex (Hawkins, et al., 2019; Lusseau & Newman, 2004; Mann, et al., 2012). In some populations of bottlenose dolphins, males form a separate, complex network of alliances, which appear to be key for ensuring access to mating opportunities. The role of kinship in these populations is varied. Kinship is sometimes a driver of association in both males and females (Moller, et al., 2006; Mann, et al., 2012), while in other populations little evidence of kin structure has been identified (Louis, et al., 2018). There is some evidence that the social structures of the deep-diving beaked whales, such as bottlenose whales (*Hyperoodon ampullatus*) and Baird's beaked whale (*Berardius bairdii*) show similar patterns, although more research is needed (Gowans, et al., 2001; Fedutin, et al., 2015). This similarity is particularly interesting given the striking ecological differences between the beaked whales, which primarily inhabit the open ocean and forage on deepwater squid and fish, and coastal dolphins.

The smaller dolphins exhibit similar social systems, but potentially with even weaker bonds and less social structure. For example, studies of Hector's (Brager, 1999), Commerson's (Coscarella, et al., 2011), dusky (Degrati, et al., 2019) and Guiana dolphins (Beirao-Campos, et al., 2016) have revealed similar patterns of loose social bonds and little structuring to social relationships, although associations are still typically non-random.

The social systems of baleen whales are not well understood, with few individual-level studies outside of humpback whales (*Megaptera noveaengliae*). Based on studies of this species, baleen whale societies appear to be loosely structured, however there is some evidence for kinship structure (Weinrich, et al., 2006), and multi-year associations (Ramp, et al., 2010).

The social structures of river dolphins, open ocean dolphins, porpoises, and monodonts (the belugas and narwhals) are poorly understood, with most of our information coming from measurements of group composition, isotopic, and genetic data, rather than measurements of individualised social relationships. In most cases, this is because individuals are difficult to identify individually and are difficult to locate. The open ocean dolphins are difficult to access, and in some species often occur in groups containing hundreds or thousands of individuals. While much of our knowledge of these species social structure comes from genetic analysis from stranding events (Viricel, et al., 2008), some studies have begun to piece together the social structure of deep water dolphins, particularly in areas where they tend to occur around archipelagos (Baird, et al., 2008; McSweeney, et al., 2009; Aschettino, et al., 2012). These studies have revealed a variety of potentially interesting social structures, such as that of spinner dolphins (*Stenella longirostris*), where individuals form extremely large, stable, mixed sex groups (Karczmarski, et al., 2005) and the apparent "stratified" social structure of Risso's dolphins (*Grampus griseus*), where males form stable pods, females remain relatively solitary, and juveniles form a flexible fission-fusion network (Hartman, et al., 2008). Monodonts live in remote areas in the arctic, and lack many of the features that are typically used for photographic identification, however evidence of matrilineality (O'Corry-Crowe, et al., 2018; Palsbøll, et al., 1997), ecological differentiation between social groups (Watt, et al., 2015) and sexual segregation (Stern, et al., 2006; Marcoux, et al., 2009), along with recent work highlighting their apparently prolonged post-reproductive lifespans (Ellis, et al., 2018) suggest that more in-depth analyses of these species' societies is warranted. River dolphins, such as the Boto (*Inia geoffrensis*), live in complex river systems with poor visibility, and typically lack dorsal fins or other identifying features, which has thus far precluded analyses of their social structure beyond analyses of group size and composition (Denkinger, et al., 2020). Porpoises, while often found in accessible, coastal areas, are typically cryptic and difficult to photograph, making analyses of associations at the individual-level challenging. Some evidence of population structure has been gained using genetic data (Escorza-Treviño & Dizon, 2000), and some progress has been made in understanding their social preferences using animal-borne sensors (Sakai, et al., 2011), however their social structure largely remains unknown.

Measuring and modelling the social structures of cetaceans is challenging. Fission fusion dynamics in these systems means that the characteristics of groups change frequently, even in the species with stable social units, so researchers cannot simply measure the size and composition of groups. In addition, relationships are typically highly individualised, and thus individuals are not interchangeable within the society. This combination of frequent changes in group composition and strong social preferences makes social network analysis an ideal framework with which to analyse cetacean societies.

Social network analysis has become a key tool for understanding social structure in animal populations. Originally developed in the social sciences to investigate the structure of human social relationships, social network analysis envisions society as a graph, with node representing social actors (typically individuals, although they may also represent groups) connected by edges representing social relationships. These edges may be binary, indicating the presence or absence of a relationship, or weighted to indicate the strength of a relationship. In humans, edges are often self-reported (Scott, 1988). In animal studies, however, edges are inferred based on the pattern of interactions or associations between identified individuals (Farine & Whitehead, 2015). As further research has been conducted on animal social networks, it has become clear that the structure of these networks has important implications for disease transmission (Craft, 2015), the spread of social information (Cantor & Whitehead, 2013), and a variety of other ecological and evolutionary processes (Kurvers, et al., 2014).

While social networks are an appealing technique for understanding cetacean societies, the construction and analysis of these networks presents a methodological challenge. In addition to the statistical issues present in all social network analysis, including the non-independence of network data (Dekker, et al., 2007), the influence of missing individuals and edges (Silk, et al., 2015), and dependency of network metrics on network size and density (Krivitsky, et al., 2011), it is particularly difficult to collect data on cetacean social relationships. Many species live in areas that are difficult to access, and it is harder still to repeatedly locate known individuals. In behavioural ecology, social relationships, and the resulting social structure, are generally considered to arise from repeated interactions between individuals (Hinde, 1976). The interactions important for forming and maintaining social relationships in animals will depend on the system, and the specific interaction relevant to a study will depend on research questions. Commonly used interactions include food sharing, grooming, and physical contact. In cetaceans, such interactions typically occur underwater, and thus out of view from traditional observation platforms.

Despite these challenges, robust methodologies have been designed to study these societies, primarily based on using photographic identification to monitor long-term association patterns, often based on co-occurrence of individuals within groups. These methods have been applied to a wide array of questions in behavioural ecology, and several different species of cetacean. In fact, a recent review suggests that cetacean social networks may be among the best studied of any animal group, surpassed only by the primates and passerine birds (Webber & Vander Wal, 2019).

Given the large body of research conducted on cetacean social networks over the last three decades, it is important that researchers reflect on this sub-field of study in order to identify key areas for future research. In particular, research into primate social networks has been guided by reviews of the literature that identify research gaps and promising areas for future research (Brent et al. 2011; Sueur et al. 2011). There are not, however, any such reviews of the application of social network methods to cetaceans. Here, I conduct a systematic review to identify trends and patterns in methodologies, themes in research topics, and research gaps that may be fruitful for future research.

1.3 Systematic literature review

To quantify trends, patterns, and gaps in the study of cetacean social networks, I undertook a systematic literature review using the Web of Science database. I performed initial searches combining one of three topic terms (“social network”, “social structure”, or “social organisation”) with one of four taxonomic terms (“cetacean”, “whale”, “dolphin”, or “porpoise”). This initial search yielded 732 unique documents. I restricted this analysis to studies that generated or analysed matrices representing pairwise social relationships between identified individuals or social groups. I did not include papers that generated other forms of networks (e.g. genetic) without measurement of social relationships. Several cetaceans exhibit multilevel social structure, in which individuals form stable core units. As such, many network studies on cetaceans use units, rather than individuals, as the nodes in the network; these studies were retained in our database. Many studies, particularly those published prior to the mid-2000s, do not use social network terminology, despite generating and analysing adjacency matrices describing individualised social relationships. These studies were also retained in the dataset. I excluded studies conducted on captive groups of animals.

I excluded publications from the grey literature, such as theses, book chapters, conference proceedings, and government reports, along with literature reviews that do not carry out quantitative analysis. I did not exclude methods papers using cetacean social network datasets to test or develop new analytical techniques for animal social networks. I did, however, exclude network science papers that used the Doubtful Sound bottlenose dolphin network as a benchmark dataset for algorithm development without reference to cetacean biology. After these exclusions, the dataset contained 181 unique entries.

1.4 Network methodology in cetacean studies

1.4.a Collecting social network data from wild cetaceans

As discussed above, the study of cetacean social systems comes with particular methodological challenges. In terrestrial systems, researchers can observe direct social interactions, such as grooming, sharing, and aggression, to derive detailed measures of social relationships. In cetaceans, however, the majority of these interaction occur underwater, and cannot be observed in all but the most permissive system. Therefore, studies of social relationships in these systems are typically based on surface observations of association patterns, rather than direct interactions. There are two primary assumption of such association analyses. The first is that association provides the opportunity for interaction, and thus individuals that associate more frequently are also likely to interact more often (Whitehead & Dufault, 1999). The second is that, if non-social factors are controlled for, frequent association reflects social affinity (Whitehead & James, 2015).

Association can be defined in a number of ways. The most common way in cetacean studies is to assign individuals to groups, typically defined as individuals within some distance of each other acting with some degree of coordination, and score all individuals within that group as associated (Whitehead & Dufault, 1999). This method was used in 164 out of the 181 studies in my dataset of cetacean social network studies. This method, while not particularly fine-grained, is a pragmatic choice in most cetacean social systems. As geographic barriers are limited, and cetacean populations typically have large home ranges, spatiotemporally distinct groups of individuals that are actively associating can often be identified with little ambiguity. When sampling is adequate, such group-based association networks can closely approximate the true patterns of social affinity within a population if the assumptions of association analyses hold (Franks, et al., 2010).

When discrete groups of active associates are difficult to distinguish from aggregations of individuals exploiting the same resources, or when more direct associations are desirable for a particular research question, other definitions of association are necessary (Figure 1.1). In these cases, studies typically use a time-based method for defining associations. Similar to methods for deriving social networks from time-series of detections at fixed sensors (Psorakis, et al., 2012), individuals are considered to be associated if they are photographed within a particular time window of one another. These windows can be defined *a priori* based on knowledge of the system, or determined using statistical analysis (Johnston, et al., 2017). An extreme version of this method is to define individuals as associated if they occur within the same photographic frame (Augusto, et al., 2017). These methods are particularly relevant to measuring cetacean relationships as simultaneous detection suggests not only spatial proximity, but some degree of synchrony. Synchrony is thought to be important for forming and maintaining social bonds in cetaceans (Connor, et al., 2006), and thus the measurement of synchronous behaviour is a potentially useful methods for measuring the strength of relationships. These time-based methods are much less common, having been used in 12 studies in our sample.

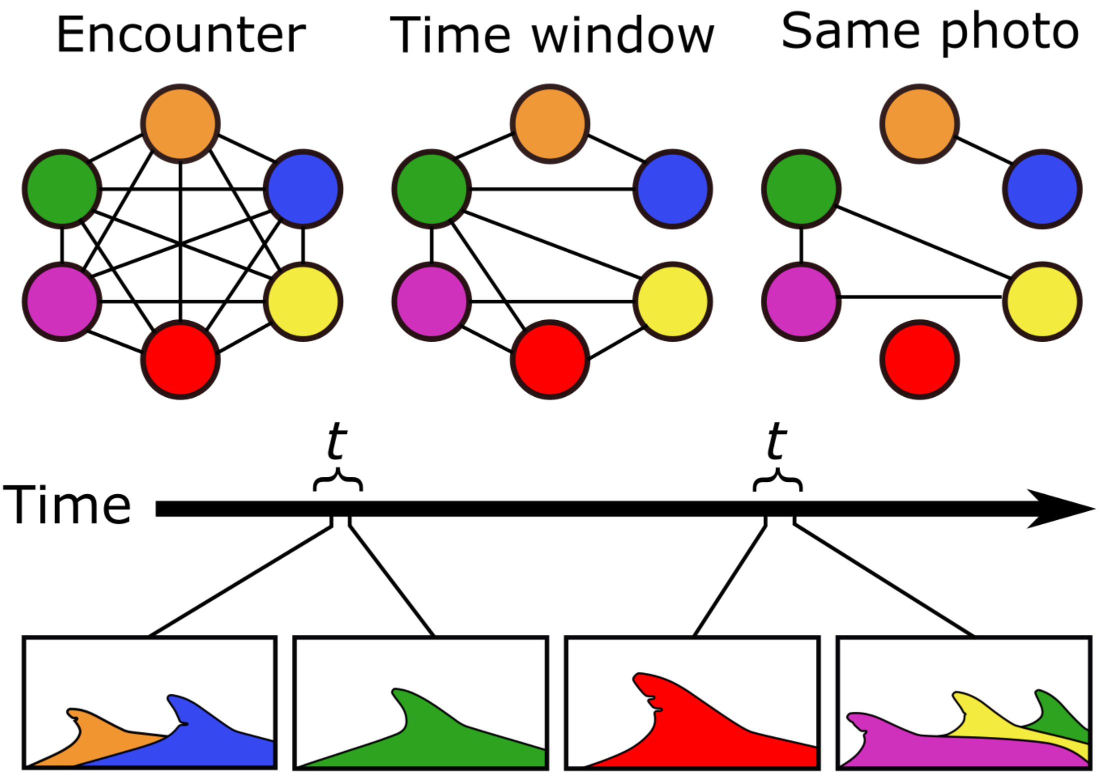

Figure 1.1 Methods for deriving association networks from photo ID surveys. Photographs from a single encounter (bottom) of identified individuals (colours) can be used to determine associations within a sampling period (top) either by assigning all individuals identified within the encounter to a single group, assigning associations based on time window t, or by restricting associations to individuals photographed simultaneously.

Animal-borne devices, such as telemetry tags, proximity sensors, and biologgers, have been used to derive social networks in several terrestrial systems (Krause, et al., 2013; Ryder, et al., 2013; Gelardi, et al., 2020). In cetaceans, their use has been more limited. I found 4 studies that utilised data from animal-borne devices to derive social networks. In three of these studies, social networks were based on spatial telemetry data, essentially collecting association data (Ortega-Ortiz, et al., 2012; Scharf, et al., 2016; Scharf, et al., 2018). An interesting methodological development was introduced by Sakai et al., (2011), who used biologgers to record synchrony and leader-follower behaviour in finless porpoises (*Neophocoaena phocoaenoides*). This data was derived from simultaneous deployment of devices on six individuals.

While commonly used for the collection of behavioural data on cetaceans (Mann, 1999) and for quantification of social networks in primates (Canteloup, et al., 2020), focal follow approaches have rarely been used to derive cetacean networks. We found only one paper that used data from focal follows to generate social networks in bottlenose dolphins (Stanton, et al., 2011).

It is notable that cetacean interaction networks have rarely been measured. While I found no studies in my systematic review that directly observed sub-surface social interactions, two studies have done so in bottlenose dolphins. Lusseau (2007) measured affiliative “mirroring” and aggressive “head-butting” behaviour between male bottlenose dolphins, finding that while aggression was negatively correlated with association, mirroring was not related to association rates. In contrast, Leu et al., (2020) found that synchronous surfacing, sexual contacts, physical touch, and association networks were all correlated. These results mirror the general conflicting results that are found when comparing associations and interactions; while these networks may be broadly correlated in many systems (Farine, 2015), there can be important differences in network structure depending on data collection technique (Castles, et al., 2014).

In most systems, it is difficult to observe direct interactions between cetaceans from traditional boat-based platforms. Technological developments, however, have made the possibility of measuring such interactions much more feasible. In particular, animal-borne devices and unmanned aerial systems have greatly increased researchers ability to observe and measure cetacean behaviour (Nowacek, et al., 2016), and the application of these methods to social network analysis could reveal aspects of social structure that are not currently well understood. While animal-borne devices have been applied, data other than spatial location and movement, such as footage from animal-borne cameras and bio-loggers (Aoki, et al., 2013; Pearson, et al., 2019) could be used to identify particular types of interaction. Unmanned aerial systems provide the potential for observing the social behaviour of several individuals simultaneously. The benefits of aerial observation in cetacean research have long been recognised (Nowacek, et al., 2001), but efforts to utilise these technologies in understanding cetacean social relationships have only recently been implemented (Hartman, et al., 2020).

1.4.b Quantifying cetacean social relationships

Once data have been collected, the next step is determining how relationships should be quantified from these data. In the case of association data, this is typically done through the use of association indices, which seek to estimate the probability that a pair of individuals associate in a given sampling period. The most intuitive of these is the simple ratio index (SRI). For a given pair of individuals i and j, SRI_{ij} is the number of sampling periods in which i and j were seen together divided by the number of periods in which at least one of i or j was seen. Other indices, such as the half-weight index (HWI) attempt to correct for potential biases in data collection, such as the case where individuals are more likely to be observed when they are apart.

In cetaceans, the HWI has consistently been the most popular method for quantifying social relationships in network studies (Figure 1.2). The SRI saw a steady decrease in popularity after the early 2000s, but there are possible signs of a recent resurgence, likely due to recent work highlighting its unbiased properties, and the arbitrary nature of the correction applied by the half-weight index (Hoppitt & Farine, 2018).

In human social networks, it is very common for networks to be binary, simply indicating the presence or absence of a social relationship. These methods have been applied to animal social networks as well, with “relationships” being defined based on randomisation techniques, thresholding, or simply by ignoring edge weights. This method has significant downsides; in animal social networks, much of the information about social structure is contained in edge weights, rather than topology (Rankin, et al., 2016), and thresholding can lead to severe and unexpected artefacts during analysis (Farine & Whitehead, 2015). Interestingly, these methods were briefly the second most common in cetacean studies, being used in nearly 40% of studies between 2004 and 2007 (Figure 1.2); this corresponds to a period when explicit network analytic methods were becoming popular in animal systems, but methods for weighted networks were not well developed. However, as further work has highlighted the issues with these methods, they have become less common, having been used in less than 5% of studies between 2016 and 2019 (Figure 1.2).

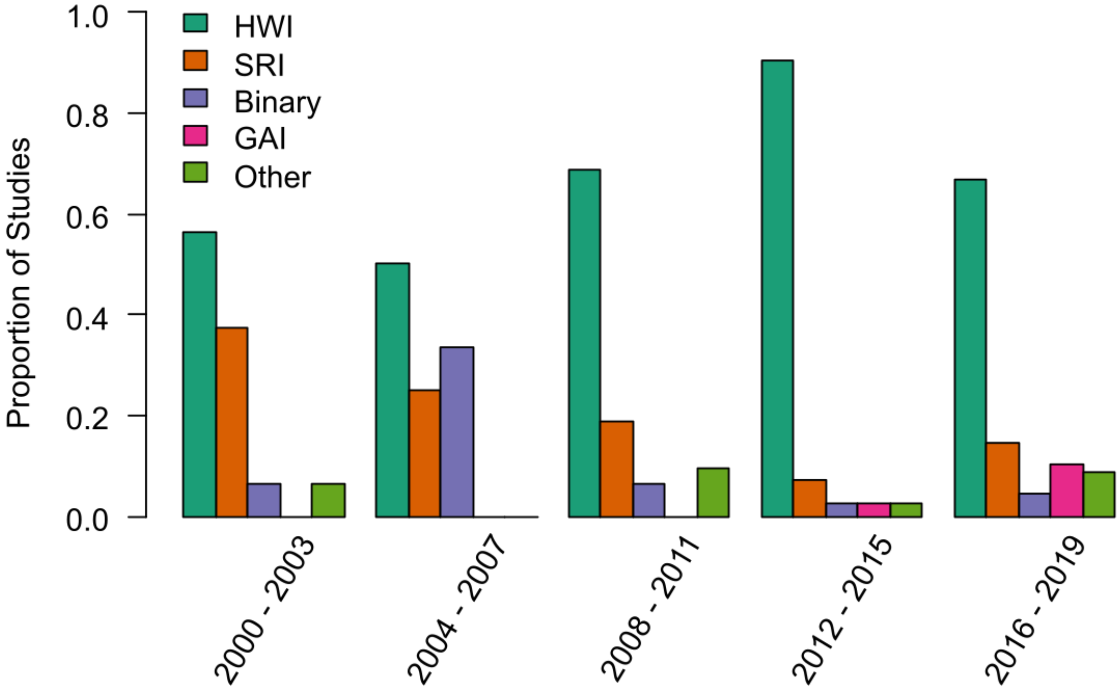

Figure 1.2 Trends in the definition of social relationships in cetacean social network studies. HWI = half-weight index, SRI = simple-ratio index, GAI = generalized affiliation index. Note that some studies used multiple edge definitions, and therefore bars may not sum to one in some periods. Further note that the GAI was not introduced until 2015.

There are potential problems with relying on association indices (or, worse, the simple presence of association) to summarise social relationships. First, presence in the same group or area can be driven by factors outside of social relationships, such as common resources or shared space use. Second, social representations using only a single relationship measure are likely to miss many of the nuances inherent to sociality. In primates, the use of multiple relationship measures has allowed researchers to gain a deeper understanding of species' social system through the classification of particular relationship types (Fischer, et al., 2017) and the calculation of composite indices of social relationships (Sapolsky, et al., 1997). Similar measures that account for many aspects of sociality would naturally be useful in cetacean systems.

To address this first problem, a useful tool that was developed relatively recently is the generalised affiliation index (GAI). GAIs use generalised linear to regress observed association rates on potential confounds, such as shared space use, temporal overlap in the study area, or gregariousness. The residuals of these models are then used as measures of how more or less dyads associate than expected given these confounds. It has therefore been suggested that GAIs better represent social affiliations than raw association indices (Whitehead & James, 2015). Introduced in 2015, this method has is gaining traction in cetacean research (Figure 1.1). The drawback is that, unlike association indices, GAIs do not have a simple interpretation with respect to the biology of the system. While association indices can be interpreted as an estimated probability of association, GAIs can only be interpreted as a relative measure of affiliation within the social system. GAIs are therefore not likely to be appropriate for network studies that are interested in the flow of disease, information, or resources through empirical social networks.

Addressing the second problem is less straightforward. Deriving multiple relationship measures for animals that are difficult to observe is challenging. Part of the solution may lie in the technological advancements discussed in the previous section, which may allow for relationship measures other than association to be used. In addition, the calculation of behaviourally-specific associations may warrant broader adoption. This method identifies a set of relevant behavioural states (such as foraging, travel, rest, and socialising) and calculates separate matrices of association for each state. This method has been applied in 7 studies in bottlenose (Machado, et al., 2019; Baker, et al., 2018; Kovacs, et al., 2017) and dusky dolphins (Pearson, et al., 2017), often finding that association networks have significantly different structures depending on behavioural state. While it may not always be necessary, the collection of behavioural state data alongside photo identification likely warrants universal adoption, so such analyses can be conducted where appropriate.

1.5 Open theoretical questions in cetacean social networks

Initial studies into cetacean social systems tended to be taxon based, rather than question based, focusing on understanding the social systems of specific species of cetacean more than testing particular hypotheses. However, as the field has matured, evidence from studies of cetacean social systems, and comparisons to existing theory and results from other systems, have prompted numerous hypotheses about the evolutionary mechanisms and functions of cetacean social network structure.

In this section, I turn towards some of the broader areas of behavioural ecology that are particularly relevant to researchers investigating cetacean social structure. I will review some of the key hypotheses in these areas, and evaluate how the cetacean social network literature has addressed these topics, and the ways in which future analysis may continue to uncover new information.

1.5.a The social cetacean brain

The comparison between apes and cetaceans has a long history. These groups are similar in their high degree of behavioural diversity, impressive social learning abilities, and complex social structures (Marino, 2002). Cetaceans, particularly the dolphins and sperm whales, also share the well-studied primate trait of large and complexly structured brains (Marino, et al., 2007). In primatology, one of the most intensely debated hypotheses is the "social brain hypothesis," which suggests that increased cognitive abilities and their associated neurological structures co-evolved with complex sociality (Dunbar, 1998). Support for this hypothesis has been mixed in primates, with some studies finding correlations between brain structure and aspects of social structure (Kudo & Dunbar, 2001; Pasquaretta, et al., 2014), while other analyses have indicated a greater role for ecological forces (DeCasien, et al., 2017; González-Forero & Gardner, 2018). Because they evolved complex sociality and large brains separately from the primates, cetaceans provide a second taxon in which the social brain hypothesis can be investigated.

Previous studies of the social brain hypothesis in cetaceans have used measures such as group size, descriptions of group composition, and bibliometric "social repertoires" as proxies for social complexity (e.g. Fox, et al., 2017). I found no studies that used social network statistics to investigate these questions in cetaceans. This review did, however, reveal a robust dataset of descriptive studies of cetacean social networks, including data on 20 genera of cetacean. As methods are generally comparable (group-based observation with half-weight index used to quantify relationships), this provides at the very least the beginnings of a comparative dataset for such analyses. Many of these studies report similar metrics, such as modularity (59 studies), social differentiation (47 studies), and the mean and standard deviation of association indices (113 studies). Careful thought will be needed to understand which of these measures indicate social complexity, and whether these measures are comparable between networks of different completeness and size, which are sampled at different rates. Furthermore, while there is an impressive degree of diversity in terms of number of genera, a great deal of research effort has been focused on bottlenose dolphins and killer whales. Robust comparative analyses will require information on a greater diversity of species. Members of Balaenopteridae, Ziphidae, and Phocoenidae were each represented by fewer than six studies each (Figure 1.3). Many families of cetaceans, including Monodonts, river dolphins, and remaining baleen whales, were not represented in our dataset.

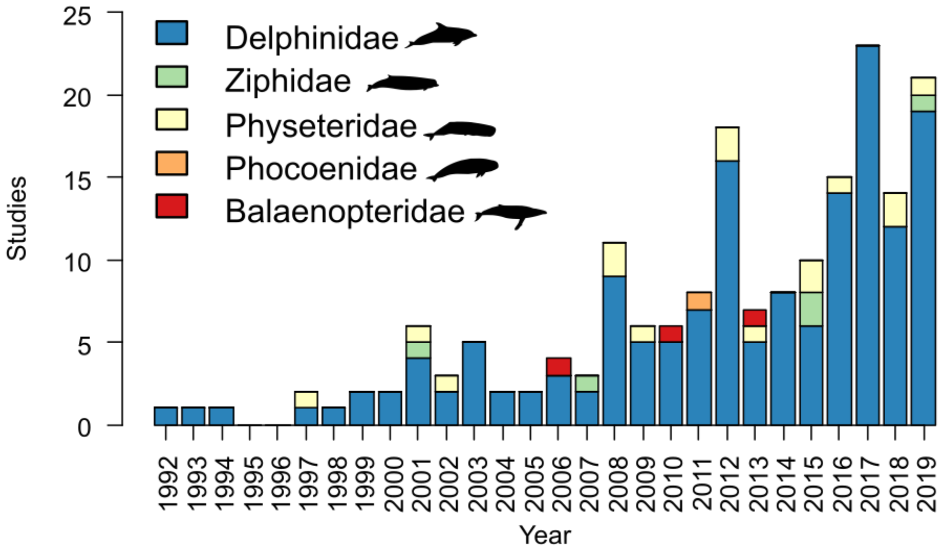

Figure 1.3 Trends in taxonomic diversity in cetacean social network studies. Bars indicate the number of studies within each family per year.

1.5.b Social networks and culture

Information about the behaviour of conspecifics can influence individuals' behaviour. This broad array of processes are referred to as "social learning" mechanisms. In some cases, these social learning processes result in large-scale spread of behavioural phenotypes and result in persistent, group-specific behaviours, or culture (Lanald & Janik, 2006). As a group, cetaceans are well known for their propensity for social learning. Experiments in captivity have demonstrated that cetaceans are capable of both vocal learning (Abramson, et al., 2018) and motor imitation (Abramson, et al., 2013). This learning ability, in concert with their complex social structures makes them an excellent system in which to investigate the interplay between social relationships and culture.

As is common in disease studies (see below), social networks can represent the opportunities for social transmission from one individual to another within the population, although the transmission dynamics may be more complex for information than in the case of pathogens (Firth, 2020). When combined with other variables such as genetic data or environmental covariates, social networks can reveal the relative importance of social learning in determining behavioural phenotypes (Hoppitt & Laland, 2011).

There are two primary methods for measuring social influence on behavior in wild populations. When only a "snapshot" of behavioural phenotypes is available, the most popular method is to perform matrix correlations between behavioural similarity and social connections, while controlling for other potential covariates such as genetic similarity and spatial distances. This method is philosophically aligned with the "method of exclusion" that has often been used to detect culture in animals, in which the presence of culture is confirmed if behavioural variations between social groups cannot be attributed to environmental or genetic differences (Schuppli, et al., 2019). These methods have been used to investigate foraging specialisation in killer whales (Esteban, et al., 2016) and bottlenose dolphins (Daura-Jorge, et al., 2012), particularly with reference to human-related foraging tactics. In some cases, isotopic data can be used to investigate the relationship between social affiliation and broader foraging niche (Louis, et al., 2018; de Stephanis, et al., 2008). In these analyses, these correlations have almost always found that associations were stronger between individuals of the same foraging class, suggesting social transmission. These methods have also been used to investigate the role of association in shaping the vocal dialects of the matrilineal whales, particularly sperm whales and killer whales. In sperm whales, association cannot explain vocal variation (Konrad, et al., 2018), while results in killer whales are mixed (Deecke, et al., 2010; Filatova, et al., 2017). Therefore, while experimental and observational studies have confirmed that adult killer whales are capable of vocal learning (Foote, et al., 2006; Abramson, et al., 2018), it is currently unclear if horizontal transmission is an important aspect of vocal culture in these species.

Matrix correlations, however, do not reveal the mechanisms of social learning. It is not possible, given a significant correlation between social association and behavioural similarity, to determine if the correlation is due to social learning. Many animal social networks exhibit behavioural trait assortment, with individuals preferentially socialising with individuals of similar behavioural phenotype, and such correlations could equally be due to these processes (see Croft, et al., 2009 for review).

A more powerful method for examining social learning is to explicitly model the spread of novel behaviours using network-based diffusion analysis (Hoppitt & Laland, 2011). If the timing or order in which individuals acquired the information is known, along with a relevant social network and asocial confounds, this method can be used to quantify the evidence for social transmission of the behaviour. Because the order of trait acquisition in cetacean studies is often not known, this method has rarely been applied. In humpback whales, diffusion analysis revealed that a novel foraging tactic followed the population’s social network, suggesting significant horizontal transmission (Allen, et al., 2013). In Shark Bay bottlenose dolphins, in contrast, the “sponging” foraging technique appears to be almost exclusively transmitted vertically from mother to offspring, rather than horizontally between associates (Mann, et al., 2012; Wild, et al., 2019).

A challenge for cetacean researchers going forward is to gain empirical evidence of the social learning mechanisms shaping observed patterns of cultural behaviour. This will be particularly difficult in the case of vocal dialects, which are multi-generational cultural traditions. Agent-based models have suggested likely social learning mechanisms for dialect evolution in killer whales (Filatova & Miller, 2015) and sperm whales (Cantor, et al., 2015), but direct empirical tests in wild systems are difficult. One potential way forward may be to monitor the simultaneous evolution of social and acoustic structure over several decades; in killer whales, dialect change has been recorded over several years (Deecke, et al., 2000), and if such changes could be mechanistically linked to association patterns, we may learn a great deal about the processes underlying dialect formation in toothed whales.

Also of interest is the broader, between-population relationship between social network structure and the diversity of culturally determined behaviour. Agent-based models suggest that there should be strong relationships between the structure of social networks, particularly the presence and strength of subgrouping, and the speed with which information transmits and the diversity of culturally determined behavioural phenotypes (reviewed by Cantor & Whitehead, 2013). Given the apparent role of social learning in shaping both vocal behaviour and foraging strategies in cetaceans, comparative studies linking diversity in these domains to network structure could serve as useful tests of these hypotheses. It would be expected that populations with greater degrees of subgroup structuring would occupy broader ecological niches, and have a greater diversity of vocalisations. Such comparisons could also, in theory, be carried out within populations at different time points.

1.5.c Fitness effects of social structure

All proposals about the evolutionary roots of particular forms of sociality hinge on underlying hypotheses about how sociality effects the fitness of individuals. In studies of animal and human social systems, there is ample evidence that sociality and fitness are indeed linked, with social species generally showing correlations between increased sociality and components of fitness such as survival and reproduction (Snyder-Mackler, et al., 2020; Ostner & Schülke, 2018).

In cetaceans, the relationship between sociality and fitness has primarily been investigated by linking position within the population social network to survival outcomes. In my systematic review, I found three studies that explicitly linked social structure to survival. In bottlenose dolphins in Shark Bay, immature males with higher eigenvector centrality (a measure of indirect connectedness in the network) have a higher probability of surviving to adulthood (Stanton & Mann, 2012). In killer whales, two studies have demonstrated a link between social network structure and survival. Ellis et al., (2017) found that males that were more directly and indirectly connected within their local networks had lower mortality, particularly in years of low resource abundance. Busson et al., (2019) further found a positive link between sociality and survival, reporting that individuals with higher average association indices had higher annual survival probabilities.

Interestingly, no study in our systematic review directly linked social network structure with observed reproductive success. Connor et al., (2001) found some evidence linking social structure and reproductive success in the Shark Bay bottlenose dolphin population. The authors of this study found that males that formed more stable alliances had higher rates of consortship with females. An additional study, not included in our sample, supports this link between alliance characteristics and male reproductive success, finding males in larger alliances had higher rates of paternities in another population (Wiszniewski, et al., 2012).

It has been hypothesised that many of the social structures found in cetaceans, particularly the highly social odontocetes, primarily function to increase reproductive success through cooperative care of young between females (reveiwed by Rendell, et al., 2019). It is an important gap, then, that no study appears to have explicitly investigated the link between social network structure and reproductive success in these systems. One study, not included in our systematic review, did find that associated female dolphins had correlated reproductive success (Frère, et al., 2010), however this a very different question from whether particular aspects of sociality, such as strong, stable bonds, increase reproductive success. A previous study analysing the relationship between median group size and female reproductive success did not find any relationship, however, this study did not quantify dyadic relationships between females (Mann, 2000). Future studies should attempt to address this question, particularly in systems where alloparental care is thought to be an important feature of society.

1.5.d Ecological drivers of social structure

The ecological conditions a population experiences, such as the abundance of food, the distribution of resources, and the degree of predation risk, can have significant implications for social dynamics. Because experimental manipulation of the ecological conditions experienced by wild cetacean groups is not possible, understanding these aspects of cetacean social structure are typically based on temporal dynamics within populations or comparative studies of multiple populations.

Long-term analysis of social dynamics paired with data on temporal variation in the availability of prey can reveal links between ecology and sociality. This is particularly tractable in populations that are specialists on particular prey items. In resident killer whales, variation in the abundance of Chinook salmon, their primary prey source, is linked to social network structure (Foster, et al., 2012). In other dolphin populations, social network structure appears to change between seasons, suggesting ecological variation may influence social structure. For example, in dusky dolphins, social bonds appear to weaken during the summer when prey are more abundant (Degrati, et al., 2019). Further evidence that characteristics of prey can influence social structure come from comparisons of killer whale populations feeding on different prey types in the north Atlantic (Beck, et al., 2012).

Along with variation in resources, research has analysed habitat variation to understand the link between ecology and sociality. In bottlenose dolphins, the characteristics of coastal habitats appear to influence social network structure. In the Indian River Lagoon, individuals with home ranges in narrower habitat have higher centrality measures (Titcomb, et al., 2015). Similarly, in Shark Bay, male bottlenose dolphins in shallower, more marginal habitat form smaller alliances, potentially resulting in decreased mating opportunities (Connor, et al., 2017).

There is also evidence that social structure may feedback on a population’s ecological niche. Evidence from stable isotopes suggests that social clusters exhibit distinct foraging niches in pilot whales (de Stephanis, et al., 2008) and bottlenose dolphins (Louis, et al., 2018). The mechanism by which this niche partitioning occurs is not well resolved, although social learning of prey choice and ranging patterns are both likely.

Less well studied than the influence of resources and habitat is the influence of predation risk on patterns of social behaviour. Protection from killer whales and sharks is thought to be one of the drivers of sociality in cetaceans, particularly in sperm whales (Whitehead, et al., 2012) and smaller dolphin species (Gowans, et al., 2007). However, robust tests of these hypotheses are lacking. There is evidence for differences in social structure between sperm whale populations with different levels of killer whale predation pressure (Whitehead, et al., 2012), and the general trends in network structure between species seem to support the idea that more vulnerable, smaller species may form larger, less stable groups. However, testing hypotheses about the role of predation pressure in shaping sociality will require tests that quantify both predation risk (either between or within populations) and relevant aspects of social structure (such as the diversity and stability of social bonds). Such studies have been carried out in other systems (Heathcote, et al., 2017; Muller, et al., 2019; Muller, et al., 2018), and replication within cetacean populations will help evaluate and refine socioecological hypotheses of whale and dolphin sociality.

1.6 Applying social network theory to conservation

There have been growing calls for behavioural ecologists to more fully apply their knowledge and research efforts to conservation efforts (Bro-Jørgensen, et al., 2019; Dill, 2017). Animal behaviour is highly relevant to conservation. Behaviour can itself influence population vital rates and growth, and is also often the first indications of population-level responses to environmental and anthropogenic disturbances. Quantification of behavioural patterns can thus serve to assess and manage endangered populations, and as a monitoring tool to detect disturbance (see Berger-Tal, et al., 2011 for a review). Social networks have been proposed as a particularly relevant conservation tool (Snijders, et al., 2017).

Many cetacean species are currently threatened or endangered, due to historical exploitation, bycatch from fisheries, or reduced prey supply due to environmental changes (Parsons, et al., 2015). As all cetaceans are social to some degree, the structure of cetacean societies has been proposed as an important aspect of conservation planning in these systems (Whitehead, et al., 2004; Brakes, 2017; Wade, et al., 2012). Here, I turn towards the past applications of social network theory to the management and conservation of cetacean populations, and discuss potential areas for further development.

1.6.a Defining management units

In cetaceans, the application of social networks to conservation has primarily been in the context of defining management units. In these studies, social networks are derived to identify either disconnected components or well-defined communities within the network (Foote, et al., 2010; Oudejans, et al., 2015; Chabanne, et al., 2017; Esteban, et al., 2016). These methods can be combined with spatial, genetic, or isotopic analyses to define units that require distinct management plans. Continued application of social network methods for these tasks is certainly necessary, particularly in populations that are poorly understood. Long-term analyses should focus on determining not only if these distinct management units are present, but whether they exhibit different overall vital rate (e.g. Ward, et al., 2011) or respond differently to temporal variations in ecological factors (e.g. Whitehead & Rendell, 2004) or management interventions.

1.6.b Anthropogenic drivers of social network structure

Human disturbances can have significant consequences for animal behaviour, which may be relevant for conservation efforts. The best studied sources of anthropogenic impacts on cetacean social structure are marine aquaculture and fisheries. Cetaceans, particularly bottlenose dolphins, often learn to opportunistically or cooperatively interact with fisheries and aquaculture as a primary foraging tactic. In these cases, it is common for individuals that interact with fisheries and aquaculture to form a distinct social cluster in the population (Methion & Diaz Lopez, 2020; Kovacs, et al., 2017; Diaz Lopez, 2019). While in many cases it is difficult to determine whether this result is due to homophily or social learning, temporal analysis in some populations has provided strong evidence that the anthropogenic activity itself leads to population splits. In Moreton Bay, bottlenose dolphins formed two distinct social clusters, one of which interacted with fisheries (Chilvers & Corkeron, 2001). When fishery activity reduced, the social modules rejoined, suggesting that the population split was in fact driven by foraging behaviour (Ansmann, et al., 2012). There is further evidence that individuals that interact with aquaculture are less central in their social networks (Pace, et al., 2012).

There are few studies linking direct human-induced mortality to changes in social structure in cetaceans, although historical whaling pressure has been suggested as a contributor to population-level differences in social structure in sperm whales

(Whitehead, et al., 2012). One such study was recently carried out in killer whales in the Crozet Islands, where mortality from illegal toothfish fisheries appears to have strongly disrupted the population's social structure (Busson, et al., 2019).

Even less well studied are the impacts of non-lethal anthropogenic disturbance and exploitation, such as noise pollution and ecotourism, on social network structure. There is ample evidence that these two sources disrupt social behaviour in some species (Senigaglia, et al., 2016; Visser, et al., 2016; Dunlop, et al., 2020), which is likely to have effects on social bonds. However, the empirical evidence for a link between these sub-lethal disturbances and social network structure is lacking. Future studies investigating the link between social network structure and exposure to disturbance such as whale watching may reveal broader implications of these disturbances on population structure (Bond, et al., 2020).

While the disruptions to social structure from aquaculture and fisheries are well studied, it is unclear whether these disruptions have implications for population viability. While it is theoretically likely that anthropogenic social disturbance has consequences for gene flow, social support, and information and disease spread (Kurvers, et al., 2014), the direct link between disruptions to social structure and changes in vital rates has not been established. Researchers should seek to address this gap in our knowledge by quantifying both social disruption and changes in vital rates in response to human disturbance.

1.6.c Social network robustness and its consequences

As animal social systems are non-random and often individualised, it is predicted that the removal of certain individuals will have an outsized effect on the structure of the social network, which may have knock-on effects for population cohesion. The degree to which social systems are robust to perturbations, and what specific perturbations are likely to result in greater changes, are key pieces of information for management efforts (Snijders, et al., 2017).

The robustness of social networks can be investigated in three primary ways. The most simple is to measure an empirical network and test its robustness using simulated removal experiments, which consist of analysing the network when some subset of nodes and their edges are removed. While potentially informative, this method does not account for any re-wiring of the social system that may occur after realized removals of individuals. Ideally, experimental removals can also be performed, in which the baseline network is measured, particular individuals are removed, and the post-removal network is also measured. While powerful, this method is not possible in wild cetacean populations. A potential stand-in for these experiments is to analyse long-term datasets to investigate how the network responds to natural (or human-induced) turnover.

In cetaceans, simulated removal experiments have been used to investigate the robustness of social networks in killer whales, bottlenose dolphins, and humpback dolphins. While the networks of bottlenose dolphins appear to be robust to removals, even of very central individuals (Lusseau & Newman, 2004; Lusseau, 2003), the networks of humpback dolphins and killer whales are prone to fracturing when central individuals are removed (Hawkins, et al., 2019; Williams & Lusseau, 2006).

Long-term analysis during periods of demographic upheaval have revealed different degrees of network robustness in cetaceans. Matching the results of simulated removal experiments, the social networks of killer whales appear to be vulnerable to removals. During a period of fisheries induced mortality, the killer whale population of the Crozet Islands experienced decreased social cohesion, and this effect remained after the excess deaths ended (Busson, et al., 2019). Similarly, heightened mortality from two major hurricanes caused a split in the social network of bottlenose dolphins in the Bahamas (Elliser & Herzing, 2011). Interestingly, the networks of Atlantic spotted dolphins responded quite differently to excess mortality. While the spotted dolphin network retained its structure after the death of over 30% of individuals (Elliser & Herzing, 2014), the subsequent immigration of individuals caused significant social restructuring (Herzing, et al., 2017).

Future work could focus on understanding these processes in greater detail. This will require a greater understanding of which individuals occupy central positions in these populations' social networks, and how their society responds to the removal of individuals with different social positions. While simulated removals inherently assume that individuals with central positions are key to maintaining network cohesion, individuals may serve to maintain social structure in ways other than occupying central positions. In macaques, for example, the removal of particular "policing" individuals causes a loss of cohesion beyond what is expected from simulated removals (Flack, et al., 2006). While sudden, catastrophic events serve as useful natural experiments for testing network robustness, they make it difficult to understand the role of particular individuals in maintaining structure. Analysis of long-term turnover, or events in which particular classes of individual are removed, in relation to social change may provide more detailed information (e.g. Goldenberg, et al., 2016). In addition, individual-level measures of sociality in relation to the loss of social partners may reveal individual re-wiring strategies which may help maintain network structure in the face of demographic turnover (e.g. Firth, et al., 2017).

1.6.d Disease prediction and management

Social network structure has long been recognised as a key factor in the spread of infectious disease (Klovdahl, 1985), however practical application of network science to managing disease in animal populations has only been implemented in the last two decades (Craft, 2015). In terrestrial and amphibious animal species, social network methods have been used to predict the severity of hypothetical outbreaks, understand individual disease risk, and design vaccination strategies (Silk, et al., 2017).

In cetaceans, the application of social network methods to disease ecology questions has been limited. In our dataset, only 3 studies directly linked social structure and disease dynamics. These three studies each looked at different stages of disease modelling. Guiamares et al., (2007) modelled the spread of a hypothetical pathogen over the social network of a sub-population of mammal-eating killer whales, finding that both the topology and distribution of edge weights in the network make it more vulnerable to disease outbreaks. Felix et al., (2019) analysed the occurrence of skin lesions on bottlenose dolphins, finding that the occurrence of this disease appeared to be concentrated in particular social clusters. Finally, Wierucka et al., (2014) found that excess mortality in pilot whales following a morbillivirus outbreak was limited to a subset of social clusters, suggesting sociality had a role in containing disease outbreaks.

These studies demonstrate the potential relevance of association networks to disease spread, likely because these association networks largely correlate with the true interactions of interest. This result has been confirmed by recent work using randomisation techniques to show that association networks are relevant for epidemiology of tattoo skin disease in bottlenose dolphins (Powell, et al., 2020). However, recent analysis has demonstrates how the specific transmission mode a pathogen utilises likely has impacts on relative exposure risk between classes of individuals (Leu, et al., 2020).

Future analysis could focus on two major domains: predicting the severity of future outbreaks and understanding the transmission dynamics of observed disease spread. In the first of these domains, we recommend that studies simulate pathogen spread over the social networks of vulnerable populations. In order to have maximum utility, these studies should be parametrised to a specific pathogen; the social network should represent relevant transmission pathways, and the parameters of the simulated pathogen should, to the degree to which these quantities are known, represent those of the real world pathogen (Craft, 2015). Another way to predict the relative risk of disease outbreaks in wild populations would be through comparative studies. If data on social network structure and pathogen prevalence can be obtained, comparative studies could reveal what aspects of social network structure are relevant to disease dynamics in these systems (e.g. Griffin & Nunn, 2012).

The second domain could take observed data on the prevalence of disease and social contacts to model the spread of disease through social networks, perhaps using analytical methods similar to network based diffusion analysis. Such analyses would be able to resolve important epidemiological parameters, such as the secondary attack rate (the probability that a given contact transmits the disease). If multiple types of social contacts are observed, the contacts most relevant to infection could be determined to understand transmission pathways. These results would be theoretically interesting, as they may help elucidate how transmission pathways differ between terrestrial and marine systems (McCallum, et al., 2004), as well as being useful for conservation efforts.

1.7 Southern resident killer whales

While my review here revealed a need for greater taxonomic diversity in cetacean social network studies, it is often useful to develop novel methods and applications in well-studied systems. The southern resident killer whale population is among the most well studied wild populations of cetaceans, or indeed of any mammal, in the world. These whales range across the coastal waters of the northeastern Pacific between southern California and southeastern Alaska, however, their core summer habitat is the inland waters of southern British Columbia and Washington state, an area known as the Salish Sea (Olson, et al., 2018) (Figure 3). This population has been continuously studied at an individual level since the 1970s by the Center for Whale Research, which produces an annual census with perfect detection. For individuals born since the start of the study, age, sex, and maternal relationships are known with certainty.

Besides being a tractable system, resident killer whales are of particular theoretical interest to behavioural ecologists. These whales exhibit a unique social structure, characterised by bisexual philopatry within a multilevel social network (Parsons, et al., 2009). The primary social unit is the matriline, a group of 2-9 individuals representing females and their descendants. The population is divided into three “pods,” collections of strongly associated and likely closely related matrilines (Bigg, et al., 1990). Pods exhibit distinct vocal dialects (Ford, 1991) and ranging patterns (Hauser et al., 2007), and are consistent social entities in this population (Parsons, et al., 2009). This unique social structure is paired with strange life history traits. Resident killer whale females are post-reproductive at approximately 40 years old, but may survive well into their 80s. This represents the longest known post-reproductive lifespan in any non-human mammal (Foote, 2008), a trait apparently driven by the indirect benefits females gain by helping their sons and grandoffspring survive (Foster, et al., 2012; Nattrass, et al., 2019; **Appendix B**) and the costs of continued reproduction due to reproductive conflict (Croft, et al., 2017).

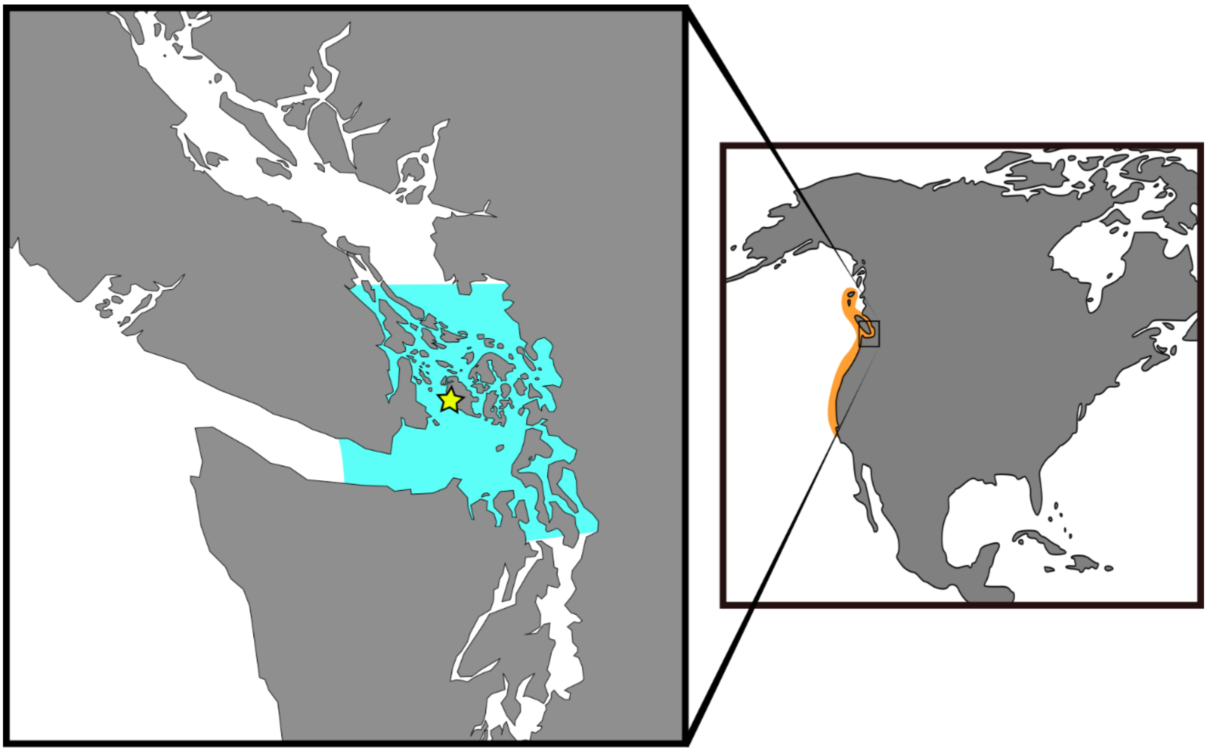

Figure 1.4 Southern resident killer whale range and study area. Right: Map of North America, with southern resident killer whale range marked in orange. Left: Salish Sea, with primary study area marked in blue, and the location of the Center for Whale Research marked in yellow.

The southern residents have been well-studied using social network methods. Past studies have analysed both broad and fine scale association networks to understand the temporal dynamics of social structure (Parsons, et al., 2009), the influence of prey abundance on social structure (Foster, et al., 2012), and the relationship between social network position and survival (Ellis, et al., 2017). The wealth of previous studies on this population's social structure allows us to develop and test novel methodologies, and draw on a long timeseries of social and demographic data to test hypotheses. In addition, the fragile state of this population means that additional information is vital to informing effective management. In the final chapters of this thesis, I attempt to develop methods for analysing this population's relationships in more depth, predict the risk of infectious disease within this population, and measure the relationship between social environment and vital rates.

1.8 Thesis outline

The study of cetacean societies has advanced a great deal since the initial studies of individual cetaceans began over five decades ago. In that time, the field has seen methodological improvements, theoretical advancements, and movement towards integrating our understanding of these societies into conservation and management. This progress, along with advancements in behavioural ecology as a whole, and new technological development, opens the door for exciting expansions in this field. Here, I have reviewed the literature to present the state of the science in terms of methods, theory, and applications, and identified likely areas for future work.

In the remaining chapters of this thesis, I will seek to address some of these research topics. Chapters 2 and 3 focus on analytical methods for the forms of association data commonly found in cetacean social studies. In Chapter 2, I develop a method for measuring an aspect of social complexity from association indices, with the goal of developing a method that could be used for comparative studies of cetacean social complexity. In Chapter 3, I evaluate a widely used method for uncovering the factors that influence social network structure, and show that this method is not an appropriate statistical technique. In Chapters 4, 5, and 6, I turn to analyses of empirical data derived from the southern resident killer whale community. In Chapter 4, I apply a novel data collection protocol to evaluate the degree to which associations and surface behaviour reflect sub-surface interaction rates in a killer whale social group. In Chapter 5, I apply social network methods to assessing the risk of infectious disease in this population, and the evaluation of potential management strategies. Finally, in Chapter 6, I analyse the relationship between the social environment and vital rates in this population using a long-term sightings and demographic dataset.

Chapter 2

Measuring the complexity of social associations using mixture models

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Abstract

We propose a method for examining and measuring the complexity of animal social networks that are characterized using association indices. The method focusses on the diversity of types of dyadic relationship within the social network. Binomial mixture models cluster dyadic relationships into relationship types, and variation in the preponderance and strength of these relationship types can be used to estimate association complexity using Shannon's information index. We use simulated data to test the method, and find that models chosen using integrated complete likelihood give estimates of complexity that closely reflect the true complexity of social systems, but these estimates can be downwardly biased by low intensity sampling and upwardly biased by extreme overdispersion within components. We also illustrate the use of the method on two real data sets. The method could be extended for use on interaction rate data using Poisson mixture models, or on multidimensional relationship data using multivariate mixture models.

2.1 Introduction

Social complexity is a much used concept in behavioural ecology (Kappeler, 2019). However, definitions vary widely, and often are not operationalized. Measures of social complexity have been sought and used for a variety of reasons, perhaps most notably to test the social intelligence hypothesis for the evolution of cognition (Kwak, et al., 2018; Kappeler, 2019), and the social complexity hypothesis for the evolution of communication (Freeberg, et al., 2012).

In studies of non-human societies, the term social complexity has primarily been used in two broad ways. First, social complexity is used to describe the number of different types (roles) of individuals that make up a social group (Blumstein & Armitage, 1997; Groenewoud, et al., 2016). Second, social complexity is used to describe the complexity of social relationships among individuals within a social group or population (Fischer, et al., 2017). Recent work has highlighted the importance of considering these two aspects of social complexity separately. These two types of complexity appear to evolve under different patterns of local relatedness. In social mammals complex social relationships are associated with groups that have low relatedness, while members of groups composed of close relatives are more likely to show a diversity of roles (Lukas & Clutton-Brock, 2018). While both aspects of social complexity have important implications, it is the measurement of the complexity of social relationships that we attempt to address here.

To have utility, measures of social complexity should be comparable across populations within species, as well as across species, perhaps within some higher taxon. This is challenging. Populations are typically of different sizes, demographics, and may use space and interact socially in different ways. Furthermore, they are studied with different protocols and with differing intensities. Ideally, we seek a measure that is: i) unaffected by network size, so the social complexity calculated from a full social network is similar to that calculated from any substantial random portion of it; ii) little influenced by the addition of distantly connected individuals into the study network; iii) not biased high (suggesting false complexity) by uneven sampling of individuals; and iv) not biased low (obscuring complexity) by low-intensity sampling. Measures of social complexity can potentially be multidimensional, with different dimensions capturing elements of the concept (Fischer, et al., 2017; Whitehead, 2008).

There have been two general perspectives to measuring social complexity using network data. The top-down approach looks at complexity as a network property, using measures such as size, diameter, modularity, dimensional coupling, disparity and computational complexity (Butts, 2001; Whitehead, 2008). These measures tend to be affected by network delineation, so causing problems with issues i) and ii) outlined above. Indeed, these problems are common to many attempts to develop measures to compare the structure of social networks (Faust, 2006).

An alternative, bottom-up approach, is to consider social complexity from the perspective of the individuals within a society. Hinde (1976) defined social structure as the “nature, quality, and patterning of relationships”. Then, social complexity can be thought of as the complexity of dyadic relationships. If we operationalize relationships using “relationship measures” such as interaction rates and association indices (Whitehead, 2008), these can be used to estimate social complexity. Bergman & Beehner (2015) suggest a simple definition of social complexity as “the number of differentiated relationships that individuals have”. A good example of this relationship-based approach to social complexity is Fischer et al.’s (2017) method. Using detailed observations of affiliative and agonistic interactions, each dyadic relationship is quantified, and then these are clustered into one of four relationship classes. Social complexity is quantified using the diversity of relationships experienced by an individual, and individual-level complexities are aggregated into measures of group complexity. While Fischer et al.'s (2017) is an appealing and rich approach, it depends on the availability of detailed data on direct social interactions (e.g., grooming and aggression) which are often difficult to observe in studies of the social structure of wild animals.

Many studies of social structure employ association indices, estimates of the proportion of time that a dyad is associated (Cairns & Schwager, 1987). These association indices are used to infer the structure of social relationships within the population. Association indices (the “simple ratio index”, the “half-weight index”, etc.) are typically calculated as ratios: the number of times that the dyad was observed associating divided by the number of times that they could have been observed associating—a binomial process. Using this attribute of association indices, we introduce a method, which in some respects parallels that of Fischer et al., (2017), for deriving a measure of social complexity, which we call association complexity, from association indices. We use binomial mixture models on association data to model the distribution of relationships within a population (see Figure 2.1). The mixture models represent the associations as belonging to several classes, each with a mean strength of association and rate of occurrence within the population (Mcnicholas, 2016). The mixture modelling finds how many classes are best supported by the data, and then estimates these parameters. These are then input to a Shannon index of entropy (Shannon & Weaver, 1949) to give a measure of diversity among the associations experienced by individuals, which we use to measure complexity.

Here we first explain the method, then test it against simulated data. We explore the effects of sampling rate as well as within-class variability on our estimates of association complexity. Finally, we illustrate the process with real data and discuss potential extensions.

2.2 Methods

2.2.a Binomial mixture model

We assume that each dyad, *ij*, has a real association index R_{ij} that is the actual proportion of time that they are in association, and that each R_{ij} belongs to an unknown discrete relationship class. So, for instance there might be some tight "bonded" relationships with $R_{ij} = \mu_1 = 0.75$, some pairs of "friends" with $R_{ij} = \mu_2 = 0.20$, and some "casual acquaintances" with $R_{ij} = \mu_3 = 0.03$.

The relationship between individual *i* and individual *j* belongs to relationship *class* $k_{ij} \in \{1, 2, 3, \ldots, K\}$, where K is the number of classes in the population. If there are d_{ij} observation occasions (representing the denominator of the association index), the number of observed associations, x_{ij}, is binomially distributed:

$$x_{ij} \sim \text{binomial}(d_{ij}, \mu_{k_{ij}}) \qquad (1)$$

We do not know the number of relationship classes K, the means for each class, $\{\mu_k\}$, or the proportion of relationships in each class, $\{\alpha_k\}$ $[\Sigma\ \alpha_k = 1]$. However, mixture models allow us to estimate these parameters. Mixture models assume that an observed distribution is a mixture of several unknown distributions, and estimate the nature and importance of these different components (McNicholas 2016). In our case, we are trying to dissect a distribution of relationship measures into its components, with each of the components representing a different class of relationship. The parameters [{μ_k}, {α_k}] of the binomial mixture model are estimated using maximum likelihood via an expectation-maximization (EM) algorithm (see below). The number of classes, *K*, is estimated by fitting a set of candidate models with different values of *K*, and choosing the best one based on criteria such as the Bayesian Information Criteria (BIC), Akaike Information Criterion (AIC), or the Integrated Completed Likelihood (ICL) (Mcnicholas, 2016). We calculate ICL as BIC + 2*E*, where *E* is the entropy of the classification matrix. Thus, ICL penalizes models in which the relationship class of dyads is uncertain.

2.2.b EM Algorithm

Our model is estimated using an expectation-maximization algorithm that treats components memberships of each dyad *ij* as missing data to be estimated. For a set of denominators d_{ij} and numerators x_{ij} of dyadic association indices, and a predefined number of components *K*, the algorithm is initialised by randomly choosing μ_k and setting $\alpha_k = 1/K$. The algorithm then iterates through an expectation (E) and maximization (M) step. The E step consists of:

1. Calculating the likelihood of each observation under each binomial component (L_{ijk})

$$L_{ijk} = \left(\binom{d_{ij}}{x_{ij}} \mu_k^{x_{ij}} (1 - \mu_k)^{d_{ij} - x_{ij}} \right) \cdot \alpha_k \qquad (2)$$

2. Calculating membership probabilities (z_{ijk}) of each component for each dyad

$$z_{ijk} = \frac{L_{ijk}}{\sum_{k=1}^{K} L_{ijk}} \qquad (3)$$

In the M step, we then calculate new parameters (association strengths) and weights (frequencies) for each component, with weights calculated as

$$\alpha_k = \frac{\sum_{ij=1}^{N} z_{ijk}}{N_{dyad}} \tag{4}$$

which is the overall probability than an observation belongs to each components given the current values of *z,* and new parameters calculated as

$$\mu_k = \frac{\sum_{ij=1}^{N} z_{ijk} x_{ij}}{\sum_{ij=1}^{N} z_{ijk} d_{ij}} \tag{5}$$

which is the maximum likelihood estimate of the binomial probabilities for each component based on the current *z*. This process is repeated until the improvement in the log-likelihood is less than a tolerance value (by default 1e-6) or the maximum number of iterations (by default 1,000) is reached.

While the EM algorithm is guaranteed to converge, these models are known to converge to local optima and be sensitive to starting values (Mcnicholas, 2016). To ensure consistent results, we perform multiple repetitions of the algorithm. We repeat the fitting process until the results of 5 runs are within the tolerance of the maximum log-likelihood obtained in the model runs, or until a maximum number of repetitions is reached (by default 20). We then use the repetition with the highest log-likelihood as our final model.

2.2.c Quantifying complexity

The mixture models suggest that relationships of class *k* occur with frequency α_k and these dyads associate at a rate of μ_k (the strength of the association index). Thus, the frequency of associations in the population between two individuals with relationship class k is:

$$q_k = \mu_k \cdot \alpha_k \,/\, \Sigma\, \mu_k \cdot \alpha_k \qquad (6)$$

Then, the diversity in association can be expressed by Shannon and Weaver's (1949) entropy index:

$$S = -\, \Sigma\, q_k \cdot \ln(q_k) \qquad (7)$$

And this is our proposed measure of association complexity.

This measure has the desirable quality that, in general, social structures with more relationship classes will have a higher value of S. In addition, this measure also quantifies differences in the diversity of associations between social structures with the same number of relationship classes. A society will have higher complexity when the frequency with which classes occur decreases as the strength of association increases. Maximal complexity for a given number of classes is achieved when

$$\alpha_k = {\mu_k^{-1}} \Big/ {\sum \mu_k^{-1}} \qquad (8)$$

as under these conditions, associations of all classes are equally frequent. Deviations from (8) lead to differences in the frequency of associations of each class, which results in less diversity in association types. Societies with the same value of K can have very different values of S, and difference in values of K will not always reflect differences in S. Stated another way, S indicates the degree of uncertainty in the relationship class of a given association. As an example, consider three hypothetical societies, one with $K = 5$ and $q = \{0.2, 0.2, 0.2, 0.2, 0.2\}$, another with $K = 5$ and $q = \{0.9, 0.025, 0.025, 0.025, 0.025\}$, and a third with $K = 2$ and $q = \{0.5, 0.5\}$. The first two societies have the same number of relationship classes, but in the first the frequency of associations of each class is the same, and thus the diversity of associations is extremely high (*S* = 1.61), while in the second, one class dominates, reducing the association complexity (*S* = 0.47). Furthermore, while the third society has only two relationship classes, associations of both class are equally likely, leading to an estimate of complexity higher than the second society (*S* = 0.69). We illustrate the variation in *S* within and between values of *K* in our simulations (see below).

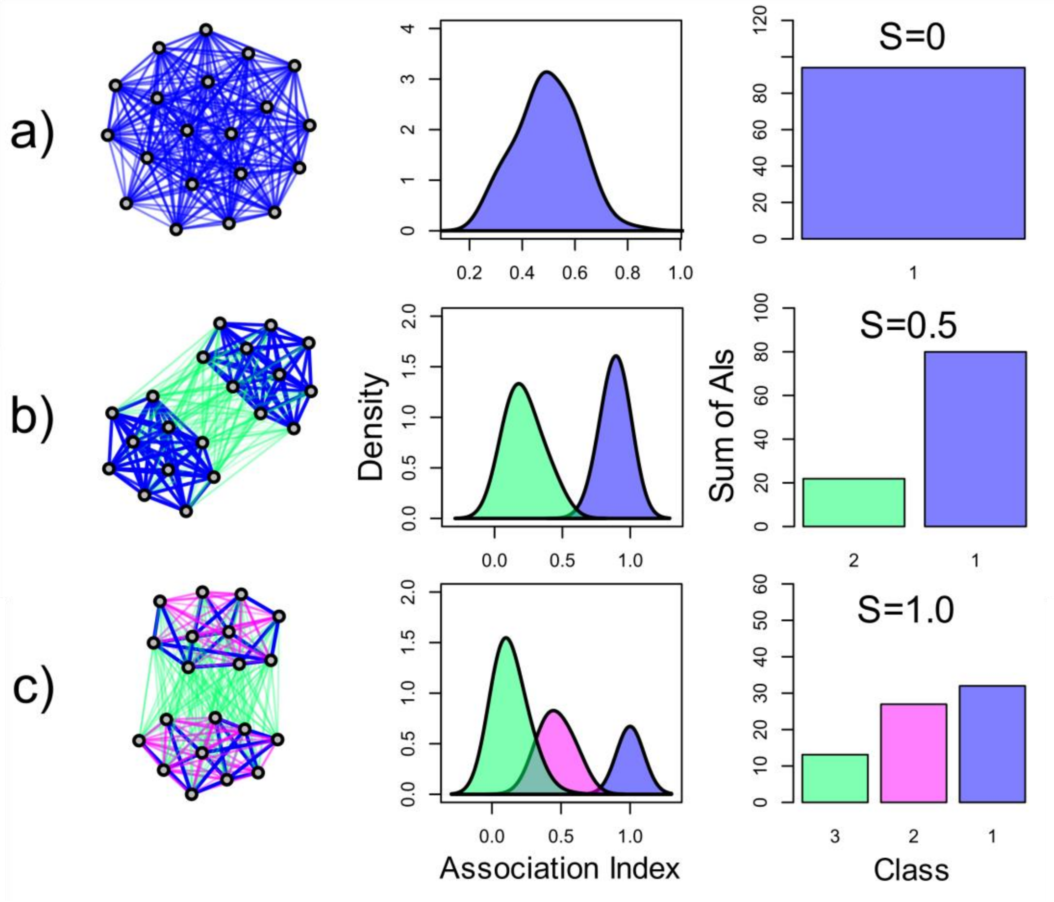

Figure 2.1 Illustration of our dyadic concept of association complexity, illustrated for societies of low (a), medium (b), and high (c) complexity. Social networks (left) contain different numbers of relationship types (represented by edge colours), each with a unique distribution of true association indices (center). We measure complexity as the uncertainty that an association is of a particular relationship type, visualised here as the sum of association indices of each type (right).

2.2.d Testing the method

We used simulated data to test our proposed method. We were particularly interested in which criterion to use for selecting the number of components (AIC, BIC, ICL), as well as how the sampling effort, indicated by the denominator of the association index (d_{ij}) might affect estimates of the number of classes of social relationship (K) and association complexity (S). In addition, we sought to more closely simulate real world data by including overdispersion within relationship classes. Overdispersion represents how much more variable observations are than a particular model assumes. In practice, overdispersion from a theoretical distribution could be caused by a variety of behavioural, psychological, environmental or measurement issues. Overdispersion in binomial data is often modelled via beta-binomial distributions. The beta-binomial distribution results from binomial trials in which the probability of success is not constant but follows a beta distribution with shape parameters β_1 and β_2. In this context, we have found it more useful to consider an alternate parameterization based on the mean, $\mu = \beta_1/(\beta_1+\beta_2)$, and the overdispersion parameter $\rho = 1/(\beta_1+\beta_2+1)$.

The simulations used Poisson and beta-binomial distributions to produce sets of d_{ij} and x_{ij}, respectively. These simulations were parameterized to reflect the characteristics of real world datasets. We examined six real association datasets (two of which are used as examples, below) from individually identified wild cetaceans, calculating mean(d_{ij}) and estimating overdispersion, ρ, for each. Overdispersion, ρ, was estimated using maximum likelihood assuming the number of components (K), as well as values of $\{\mu_k\}$ and $\{\alpha_k\}$ are as estimated by the binomial mixture models (using ICL; see below). These suggested reasonable ranges of mean(d_{ij}) from 15-100, and ρ from 0-0.01. We draw our ρ values from a broader distribution (0 – 0.015) to ensure that the upper end of the empirical range is well represented in our simulated examples.

We simulated a population of N associating individuals (N_{dyad} = (N(N-1))/2). We simulated social structure by setting the number of relationship classes, choosing frequencies and distributions of association probabilities for each type, assigning dyads to types, and then generating true dyadic association probabilities. We then simulated observational sampling of associations from this social structure. More specifically, in a given simulation run with K relationship classes, we

1. Drew relative α_k from a uniform distribution on [0,1], with the constraint that $\min(\alpha_k) > 0.1/K$
2. Drew μ_k from a uniform distribution on [0,1], with the constraint that they were at least 0.1 apart
3. Drew ρ_k from a uniform distribution on [0,0.015]
4. Assigned $k(ij)$ to dyads with probability α_k
5. Generated R_{ij} for each dyad from a beta distribution with mean $\mu_{k(ij)}$ and overdispersion parameter $\rho_{k(ij)}$
6. Generated d_{ij} from a Poisson distribution with mean D
7. Generated x_{ij} from a binomial distribution with probability R_{ij} and d_{ij} trials

Since the parameter D indicates the mean denominator of the association indices, it is an indicator of sampling intensity in our simulations. From these simulated social structures, we measured realized association complexity from the $k(ij)$ and R_{ij}, and then fit a series of binomial mixture models with K = 1, 2, 3, 4, 5, 6, 7, 8, and 9 to the x_{ij} and d_{ij}. We chose a best value of K based on BIC, ICL, and AIC, and recorded estimates of S based on the models chosen by each of these criteria.

We systematically varied the values of N, K, and D across simulations to test the method under different population sizes, social structures, and sampling effort. We ran 20 simulation runs for every combination of the following parameters: $N = 20, 50$; $K = 1, 2, 3, 4, 5$; $D = 20, 40, 60, 80, 100$.

To examine model performance at estimating S and K, we analysed the mean error in model estimates under different conditions. This gave us a measure of the degree to which our model accurately reflects actual complexity under different conditions, as well as allowing us to examine the model output for bias. We also estimated the correlation between true and estimated values of S for each criterion and under different conditions, to determine the degree to which we can expect the output of the model to reflect differences in complexity between societies.

We also tested our model for sensitivity to systematic increases in overdispersion. Using $N = 20$, $K = 1, 2, 3, 4, 5$, and $D = 20, 40, 60, 80, 100$, we ran simulations in which we defined a common overdispersion parameter ρ for all components. We used $\rho = 0.005, 0.01, 0.015, 0.02$, running 20 simulations for each combination of parameters. We examined our model for biases introduced by increased overdispersion by analysing the mean error in estimates of S and K in relationship to overdispersion, social structure, and sampling.

2.3 Results

2.3.a Testing the method

As expected, most variation in S in our simulations was driven by differences in the number of relationship classes, as demonstrated by a high correlation between true values of S and K ($r_S = 0.93$, Fig. 2). However, when only considering cases in which

$K > 1$ (as when $K = 1$, S is always 0), the correlation was much lower ($r_S = 0.67$), and a significant degree of overlap in values of S between different values of K was apparent (Figure 2.2). While the number of relationship classes greatly affects the complexity of associations, the frequency and strength of relationship classes is also an important factor.

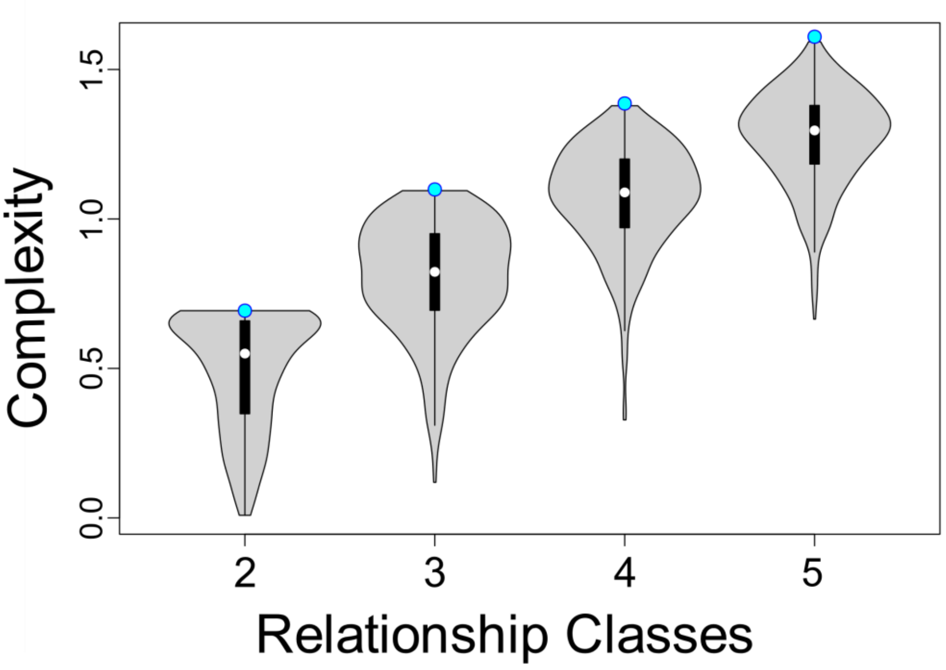

Figure 2.2 Distributions of realized complexity values (S) between societies with different numbers of relationship classes (K). Violin plots represent density estimates and quartiles of true S values for each value of K used. Simulation runs for K = 1 are not plotted as these runs, by definition, have S = 0. Blue points represent the maximum possible entropy for each value of K as defined by eq. 8. Each distribution represents the results of 500 simulation runs.

The results of our simulation study largely suggest that ICL is the best criterion to use for these models. The correlation (r_S) between the estimates of S via ICL and true complexities across all parameters was 0.9, while AIC and BIC had overall correlations of 0.79 and 0.78, respectively. This high correlation for ICL across sampling efforts, network sizes, and social structures, indicates that estimates of S based on models chosen via ICL are highly comparable between networks. At low sampling efforts ($D <$ 40), ICL does give estimates of S less correlated with true complexities than AIC or BIC, but rapidly tends towards a perfect correlation with increased sampling effort. In contrast, the correlations between true and estimated complexities obtained by AIC and BIC do not increase with sampling effort, and are consistently below 0.9 (Figure 2.3, left).

AIC and BIC were both likely to overestimate the complexity of a social structure, and this overestimation was exacerbated by increased sampling effort. In contrast, the estimates obtained by ICL are downward biased at low sampling rates, but the bias decreases as sampling effort increases. This indicates that ICL estimates are unlikely to be overestimates of true complexity, but large amounts of data ($D >$ 80) are likely needed to ensure accurate estimates. However, even at low sampling rates, the bias is less than 0.5 (Figure 2. 3, right).

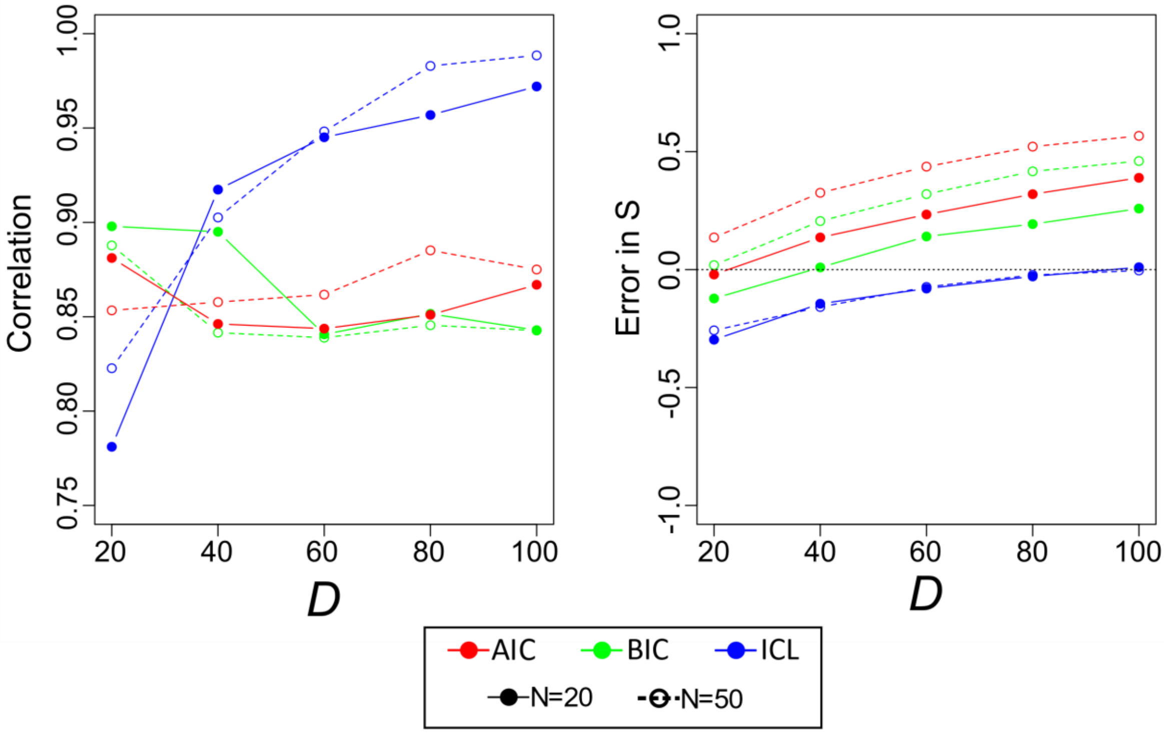

Figure 2.3 Correlation between real and estimated S (left) and mean error in estimates of S (right) for each criterion under different levels of sampling effort (expressed as mean denominator, D) and network sizes (in number of individuals, N). Each data point is based on 250 simulation runs (50 runs for each value of K). Dotted black line indicates a mean error of 0.

In addition, both AIC and BIC provide estimates that are sensitive to network size in our simulations, with larger networks having added positive bias. In contrast, ICL did not give estimates biased by network size (Figure 2.3), and thus provide an estimate of complexity that is comparable between social networks of different sizes and levels of completeness (a reasonable, roughly random subset of a larger network should provide a similar estimate as the full network).

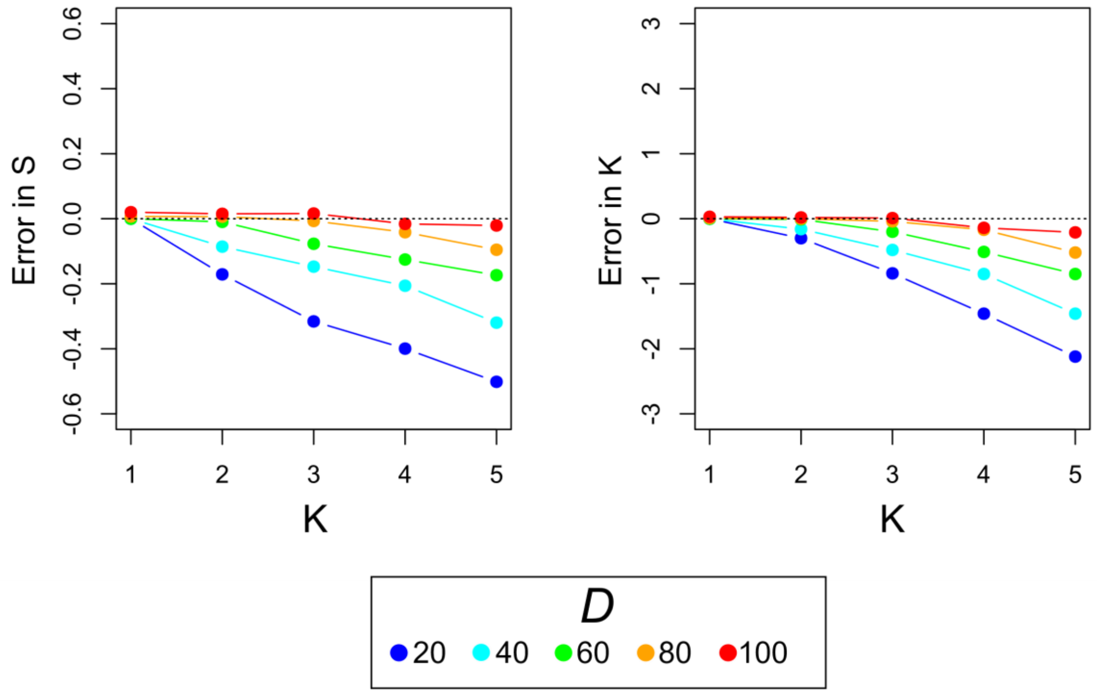

Figure 2.4 Relationship between input value of K and error in estimates of S and K obtained from models chosen via ICL. Colours indicate simulated sampling effort (as expressed by mean denominator of association indices, D). Results are presented based on runs with N = 20, and each data point represents the mean of 50 simulation runs. Dotted black line indicates a mean error of 0.

ICL was prone to underestimating both *S* and *K* at low sampling rates. This tendency was exacerbated by social structures with more relationship classes. This bias was relieved with increased sampling effort. In addition, ICL rarely found multiple relationship classes in social structures in which there was only one class of dyad (Figure 2.4). Therefore, while we suggest the use of ICL to choose the number of components in these models, as it gives good estimates that are comparable between networks, we caution that these estimates will likely be underestimated with low sampling intensity, particularly for complex social structures.

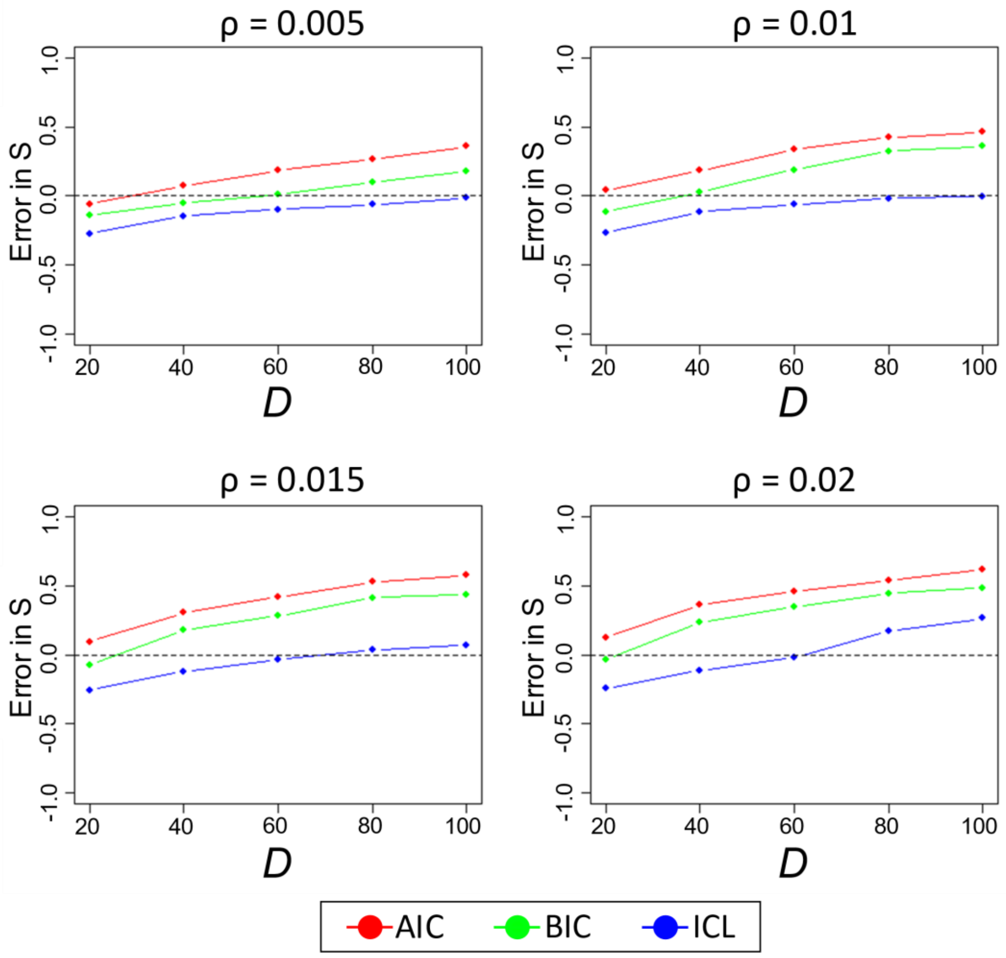

Figure 2.5 Results of overdispersion simulation. Values shown are mean error in estimates of S for all runs with a given overdispersion parameter. Colours indicate criteria used to estimate the number of components. Dotted black line indicates a mean error of 0.

All criteria were somewhat sensitive to systematic increases in overdispersion. High levels of overdispersion led to overestimates of complexity, particularly under high sampling intensity. However, ICL was far less sensitive to overdispersion than AIC or BIC. At values of $\rho < 0.015$, ICL converged towards zero bias as sampling effort increased towards *D* = 100, and even at $\rho = 0.015$, upward bias at high sampling intensity was small. At $\rho = 0.02$, upward bias at high sampling intensities became more pronounced (Figure 2.5).

2.3.b Illustration using real data

The distributions of simple ratio association indices for the northern bottlenose whale and sperm whale data sets are shown in Figure 2.6. Mixture models suggested 2 relationship classes for the northern bottlenose whales with an association complexity of S = 0.69, and 3 relationship classes for the sperm whales with an association complexity of S = 0.91. The mean denominators of the association indices and estimates of overdispersion were D = 34.6 and ρ = 0.010 for the northern bottlenose whales, and D = 59.9 and ρ = 0.007 for the sperm whales. Using the simulation data in Fig. 4, these suggest that our model estimates may have small (< 0.2) downward biases.

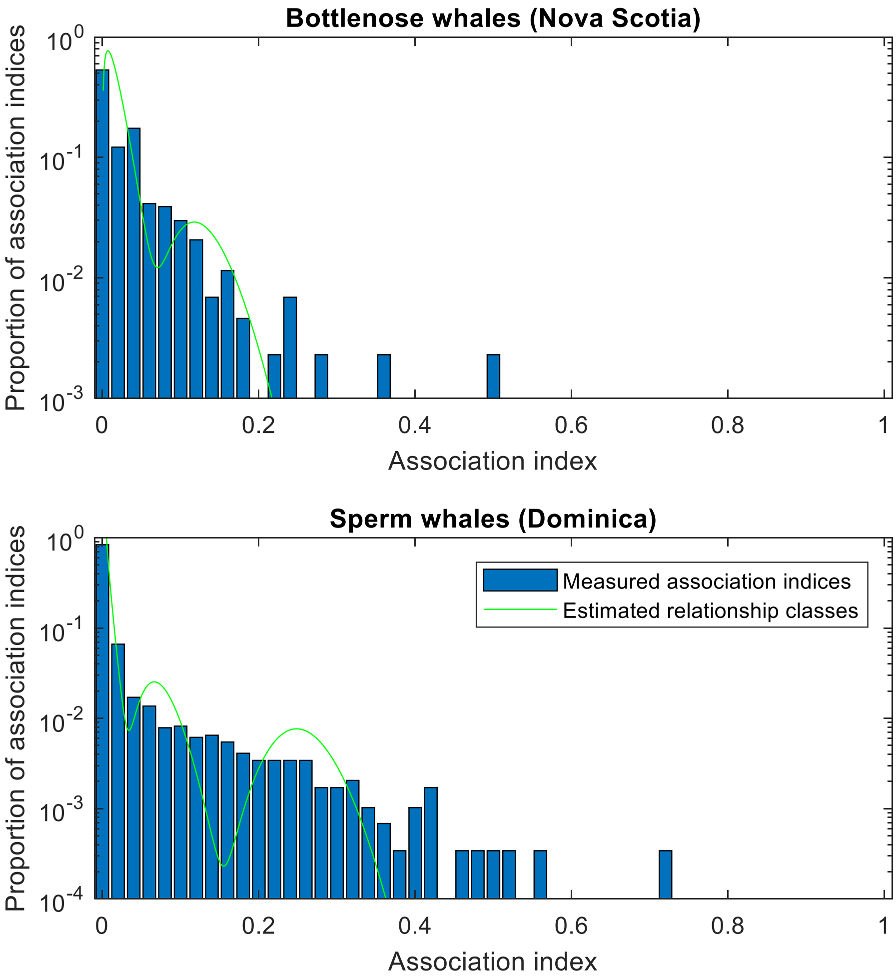

Figure 2.6 Distribution of measured association indices for northern bottlenose (above) and sperm (below) whales together with estimated relationship classes from binomial mixture models with ICL, with intra-class dispersion estimated using maximum likelihood.

Fig. 2.6 shows the estimated distribution of real association indices from the binomial mixture models and estimates of overdispersion. While they roughly match the distribution of measured association indices, the matching is not too good, but it is must be remembered that the measured association indices include sampling error while the estimated real association indices do not. In other words, while the histogram represents the distribution of estimated association indices *x*/*d* with equal weight given to each dyad, the fitting of relationship classes is based on maximizing the likelihood of the observed x given their sample sizes d.

Both species have a preponderance of extremely low association relationships (μ_1 = 0.017 and α_1 = 0.88 for the northern bottlenose whales; μ_1 = 0.002 and α_1 = 0.90 for the sperm whales), as well as some low association relationships (μ_2 = 0.125 and α_2 = 0.12 for the northern bottlenose whales; μ_2 = 0.072 and α_2 = 0.07 for the sperm whales). The sperm whales additionally have a much smaller class of fairly strong association relationships (μ_3 = 0.252 and α_3 = 0.03). These latter correspond to relationships within social units (Gero, et al., 2014).

2.4 Discussion

We have presented a method for quantifying the complexity of association networks based on dyadic sighting histories. We use binomial mixture models to estimate the number of different classes of relationship and the association frequencies of each class and take the diversity of these frequencies as our measure of association complexity. Our results show that this approach can generally be used to effectively model the dyadic associations and measure network complexity, and is comparable between networks.

Hinde (1976) defined social structure as the “nature, quality, and patterning of relationships”. Ideally, we would measure complexity from all three of these elements. However, it is well-known that measures of the global patterning of relationships – such as metrics from network analysis – are not comparable between networks, due to the dependency of these measures on network size and density (Faust, 2006; Rito, et al., 2010; van Wijk, et al., 2010). This is a significant problem for the field of animal social networks because it makes the comparative approach difficult. Our method instead examines social complexity through the nature and quality of dyadic relationships – providing a bottom-up measure of complexity that can be fairly compared between association networks. Our method can therefore be used with a comparative approach to examine drivers of social complexity across populations, species and potentially taxa.

A previous approach to measuring dyadic complexity (Fischer et al., 2017) is a promising way forward for many systems, but is not appropriate for association data, because it requires classes of interaction to be known and pre-defined in the complexity measure. The researcher needs data more detailed than just who was with whom (associations) and on whether an interaction is of the class aggressive or the class affiliative. Our approach instead seeks to automatically identify different classes of dyad based on the patterns of associations. The same limitations that apply to any analysis using association indices apply to our method. Since all that is being measured and modelled is the proportion of time individuals spend together, the nuances of social relationships are perhaps not captured by these measures. For example, our method would not be able to distinguish between two relationship classes that associate with the same probability but interact in different ways while associated. We suggest that our model will be a useful comparative tool when the collection of detailed interaction data is impractical, such as in studies of wild cetaceans.

Our complexity measure is unaffected by network size; since our measure is based on dyads, the association complexity of a reasonably well-sampled social network will be similar to that of the full network. Our measure is also fairly robust to the existence of individuals that are distantly connected to the network and thus observed infrequently. Although our method rarely estimates a higher level of complexity than that of the true network, low-intensity sampling biases it towards estimating artificially lower levels of complexity. It is a common feature of social network analysis that low-intensity sampling produces metrics that are unreliable (Franks, et al., 2010; Farine & Whitehead, 2015; Whitehead, 2008), and we therefore suggest that caution is taken when interpreting results from this model on sparsely sampled data.

Because the complexity measure is partly based on unevenness of dyadic weights, we might expect a network sampled with the gambit of the group to have a higher level of complexity than a network sampled by observing pairwise associations (e.g., by focal sampling). This is because there will be more casual acquaintances in the network as an artefact of the gambit sampling method. For example, both individuals A and B might only be observed together because they are both associating with individual C. Thus, when adopting a comparative approach, differences in sampling protocol will need to be considered.

Finally, the driver of association complexity needs to be considered for each social system, because complex social structures can arise through a number of mechanisms. Complex social structures, such as multilevel societies, can arise from cognitively demanding behavioural processes such as cultural transmission (Cantor, et al., 2015). However, complexity can also be driven by simple differences between individuals in their social behaviours (Firth, et al., 2017). Furthermore, there is increasing recognition of the role that features of the physical environment play in shaping social structure (He, et al., 2019). Therefore, it could be that the social decisions of individuals do not produce a complex network, but instead social complexity is driven by patterns of space use or the complexity of the environment

(Titcomb, et al., 2015; Leu, et al., 2016). Complex patterns of overlapping space use could lead to higher estimates of social complexity with our method. It is therefore important that our proposed metric not be interpreted as a measure of the complexity of individuals' social decision-making, but rather as a feature of the social structure of the population.

If our measure of association complexity is to be widely used, it needs some measure of confidence. We suggest the temporal jackknife, in which different temporal segments of data are omitted in turn. This method is appropriate with behavioural association data when the nonparametric bootstrap cannot be used (as randomizing identities produces self-associations) (Whitehead, 2008). Additionally, it would be helpful to give analytic estimates of the bias due to sampling rates and overdispersion that are indicated by our sensitivity analyses. There also could be more robust measures of association complexity from mixture model data that perform better than the Shannon index, but we have not yet found any.

The method that we have proposed could be varied or extended in several potentially productive ways. Using the same data set, two or more measures of association could be defined, based on different behavioural states or ways of associating (Gero, et al., 2005). These then constitute multivariate relationship measures, which could be clustered using multivariate mixture models (Mcnicholas, 2016). To obtain our univariate measure of association complexity, using equations 2 and 3, we need some way of compounding the now vector-valued centroids of the clusters (μ's), perhaps using principal components analysis. However, we could also calculate separate measures of complexity for each association measure, so that, for instance, complexity could be compared between behavioural states or modes of communication. Our association complexity measure(s) could also be used in parallel with other network or relationship measures, such as modularity (Newman 2006), to give a more nuanced comparison between social networks.

Many social network data are in the form of interaction rates (Farine & Whitehead, 2015). Poisson mixture models would be appropriate in these cases, perhaps with offset variables indicating effort. These interaction rate data could be combined with each other, or with association data, in a multivariate mixture analysis. Offset variables may be useful more generally. For instance, generalised affiliation indices are the residuals from a regression of the measures of association or interaction on structural predictor variables, such as gregariousness or spatiotemporal overlap (Whitehead & James, 2015). Inputting generalised affiliation indices into mixture models, either directly into Gaussian mixtures or as offsets in binomial or Poisson mixtures, could control for use of space and other confounds.

An interesting comparison can be made between our measure of social complexity, which rests on the idea of differentiated types of social relationship that may be functionally similar, to ideas of complexity derived from analysis of fission-fusion dynamics. One of the key components of fission fusion systems is the degree to which fission and fusion creates uncertainty in the composition of individuals' social groups (Aureli et al. 2008). Quantifying this uncertainty has recently been proposed as a way to measure aspects of social complexity (Ramos-Fernandez et al. 2019). In groups where every relationship is individualized, this measure would capture how unpredictable, and thus potentially cognitively demanding, and individuals social environment would be. It may be useful to consider how these two measures would differ in their estimates of complexity. From an individual perspective, the maximum uncertainty (for a given average group size) in group composition occurs when all individuals have equal probability of co-occurring in groups. In societies where individuals exhibit clear social preferences, the uncertainty of group membership will be reduced; Ramos-Fernandez et al. found that the multilevel society of geladas exhibited far lower uncertainty in group membership than the less structured social networks of chimpanzees. This leads to an interesting prediction that these two measures of social complexity should in fact be inversely related; a society with $K = 1$ and $S = 0$ will in fact have the greatest complexity at an individual level. Future work could calculate these two measures on multiple datasets and test this prediction. The difference here rests in our assumption that relationships of the same type are to some extent equivalent to individuals. The validity of this assumption will vary depending on species and social system. Furthermore, which form of “complexity” researchers wish to measure will depend on whether researchers are interesting in measuring the structure of social relationships (the mixture model method) or the unpredictability of fission-fusion dynamics.

Here, we have focused on developing methods to empirically compare multiple social networks. In the next chapter, I turn towards an arguably much more common case, in which researchers may be interested in understanding the drivers of structure within a single network. Rather than developing new methods, in the next chapter I evaluate a currently widespread method for understanding the drivers of social network structure, and discuss some potential alternative methods

Chapter 3

Evaluating datastream permutations for regression in animal social networks

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Abstract

Social network methods have become a key tool for describing, modelling, and testing hypotheses about the social structures of animals. However, due to the non-independence of network data and the presence of confounds, specialized statistical techniques are often needed to test hypotheses in these networks. Datastream permutations, originally developed to test the null hypothesis of random social structure, have become a popular tool for testing a wide array of null hypotheses. In particular, they have been used to test whether exogenous factors are related to network structure by interfacing these permutations with regression models.

Here, we show that these datastream permutations typically do not represent the null hypothesis of interest to researchers interfacing animal social network analysis with regression modelling, and use simulations to demonstrate the potential pitfalls of using this methodology. Our simulations show that utilizing common datastream permutations to test the coefficients of regression models can lead to extremely high type I (false-positive) error rates (> 30%) in the presence of non-random social structure. The magnitude of this problem is primarily dependent on the degree of non-randomness within the social structure and the intensity of sampling. We strongly recommend against utilizing datastream permutations to test regression models in animal social networks. We suggest that a potential solution may be found in regarding the problems of non-independence of network data and unreliability of observations as separate problems with distinct solutions.

3.1 Introduction

Social structure, defined as the patterning of repeated interactions between individuals (Hinde, 1976), represents a fundamental characteristic of many animal populations with far-reaching consequences for ecology and evolution, including for gene-flow, social evolution, pathogen transmission, and the emergence of culture (Kurvers, et al., 2014). The last two decades have seen widespread adoption of social network methods in animal behaviour research to quantify social structure (Webber & Vander Wal, 2019). The network framework is appealing because it explicitly represents the relationships between social entities from which social structure emerges (Hinde, 1976), and thus allows tests of hypotheses about social structure at a variety of scales (individual, dyadic, group, population). Social networks can be based on direct observations of interactions, or inferred from other data types, such as groupings of identified individuals (Franks, et al., 2010), GPS tracks (Spiegel, et al., 2016), proximity loggers (Ryder, et al., 2012), or time-series of detections (Psorakis, et al., 2012).

The analysis of animal social network data presents a statistical challenge. Specifically, two separate issues must be addressed. First, network data are inherently non-independent, thus violating the assumptions of independent observations inherent to many commonly used statistical tests. Second, factors outside of social structure, such as data structure and observation bias, may influence the structure of observed animal social networks, potentially leading to both type I and type II errors in statistical tests (Croft, et al., 2011).

To address the problem of non-independence, a wide array of statistical tools have been developed, primarily in the social sciences. These methods include permutation techniques that allow for hypothesis testing in the presence of non-independence.

These permutations normally test relationships between exogenous variables and network properties, such as the presence and strength of social ties, or the centrality of nodes in the network. These methods typically build empirical null distributions by randomly assigning the location of nodes in the network, while holding the network structure constant (“node-label permutations”). The resulting null distribution maintains the non-independence inherent to the network while breaking any relationship that exists between network structure and potential covariates (Dekker, et al., 2007).

While these methods are useful for dealing with the issue of non-independence, they do not address the second issue, from which studies of animal social systems in particular often suffer. Because the methods developed in the social sciences only permute the final constructed network, they do not inherently account for common biases in the collection of the raw observational data used to construct the final network. These biases may be introduced by the method of data collection (e.g. group-based observations), individual differences in identifiability, or demographic processes (James, et al., 2009). For example, consider a situation where researchers are interested in differences in social position between sexes, but females are more cryptic and thus observed with a lower probability. This would lead to incorrect inferences due to biases in the observed network structure that are unrelated to the true social processes of interest (Farine, 2017). To deal with these problems, a suite of alternative permutation procedures has been developed. Rather than permuting the final network, these methods permute the raw data used to construct the network. These methods are therefore sometimes referred to as “datastream permutations.” The goal is to construct permuted datasets that maintain structures of the original data that may influence the observed network structure (e.g. the number of times individuals were observed and the sizes of observed groups), while removing the social preferences that underpin the social network (Farine & Whitehead, 2015).

The original datastream permutation technique for animal social data was proposed by Bejder et al., (1998), based on the procedure outlined by Manly (1997) for ecological presence-absence data. Bejder et al.'s procedure was designed to test whether a set of observed groupings of identified animals showed signs of non-random social preferences. This procedure permutes a group-by-individual matrix, where rows are groups and columns are individuals, with 1 representing presence and 0 indicating absence. The algorithm finds 2 by 2 "checkerboard" submatrices, with 0s on one diagonal and 1s on the other, that can be "flipped" (i.e. 0s replaced with 1s and vice versa). These flips maintain row and column totals (the group size and observations per individual, respectively), but permute group membership. In biological terms, matrices generated with this procedure represent the null hypothesis that individuals associated completely at random, given the observed distribution of group sizes and the number of sightings per individual.

Refinements of this method were later developed that constrained swaps within time periods, classes of individual, or locations (Whitehead, et al., 2005). One alteration also controls for gregariousness, and allows for permutation of association data not constructed using group membership (Whitehead, 1999). Controlling for gregariousness and sighting history is possible when each sampling period is represented as a square matrix, where 1 indicates that individuals associated in that period and 0 indicates no association. In this format, the data can be permuted in a way that maintains the number of associates each individual had in each sampling period.

In recent years, datastream permutation methods have been developed that can handle more complex data structures, such as GPS tracks (Spiegel, et al., 2016), time-series of detections (Psorakis, et al., 2015), and focal follow data (Farine, 2017). All of these methods have in common that they essentially randomise raw observations of social association (or interactions) data and thus remove social structure while maintaining most other features of the data, including features potentially causing biased measurements of social structure. They thus provide a robust null distribution to test for non-random social structure in a dataset, which is a key step in understanding the behavioural ecology of wild populations.

Many empirical studies and methodological guides have suggested interfacing these null models with other statistical techniques, particularly regression models (including ordinary least squares, generalised linear models, and mixed-effects models), to test hypotheses about network structure. The logic of this recommendation is that permutation-based null models allow researchers to account for sampling issues when testing hypotheses using these common statistical models. However, it is important to recognize the limitations of this approach, and to think carefully about the null hypothesis that these methods specify. In common datastream permutation null models, the null hypothesis specified is that the population's social structure is random, once we control for the structure of the data and other confounds. For a particular quantity of interest, such as edge weights, node centralities, or differences between networks, this null hypothesis can be equivalently stated as proposing that all variance in a given value or network metric is due to data structure, confounds, and residual variance. In network terminology, this null hypothesis is a random network, within a set of constraints. This null hypothesis is by design, because this form of permutation procedure was specifically created to test for non-random social structure.

However, we feel there has been a lack of consideration about whether this null hypothesis is appropriate in other contexts, such as regression modelling. We show here that these procedures do not provide an appropriate null hypothesis for testing the null hypotheses of regression models.

Consider the basic linear model:

$$Y = \beta X + \varepsilon \tag{1}$$

where Y is a response variable, X is a matrix of predictor variables, ε is the error term, and β is a vector of estimated coefficients. We are typically interested in testing the null hypothesis $\beta = 0$, representing no relationship between the response Y and the predictor(s) X. In permutation based hypothesis testing procedures, researchers specify this null distribution by randomising either X or Y, often with constraints, thus maintaining the distribution of values but breaking any covariance between the variables (Anderson & Robinson, 2001). This is the logic behind traditional node-label permutation tests of regression in social networks (Croft, et al., 2011).

Datastream permutations, however, do something very different, which is inappropriate for testing this hypothesis. By permuting the data underlying network measures and then re-calculating the response variable, these procedures change the distribution of Y, instead of breaking relationships between the variables. If the network has non-random social structure, even structure entirely unrelated to X, then we will typically see a reduction in the variance of Y as we permute the raw data. When Y has a larger variance in the observed data than in the permutations, more extreme values of β are more likely to occur in the observed data, even if the null hypothesis is true. This procedure is therefore likely to result in much higher rates of false-positive type I error than is acceptable (Figure 3.1).

Changes in variance between the observed and permuted data is more than just a technical issue. There is a fundamental problem with this approach when it comes to testing hypotheses using regression models. When researchers fit regression models to predict network properties from exogenous variables, the null hypothesis they will be testing against can be stated as “the variation in network structure is not related to the exogenous variable.” This, however, is not the null hypothesis tested by the commonly used datastream permutation methods. Rather, the null hypothesis that is proposed by these datastream permutations could be stated as “the degree of variation in network structure and its relationship to the exogenous variable are both due to random interactions of individuals within constraints.” The researcher cannot disentangle the null hypothesis of no relationship between the network and the predictor from the null hypothesis of random social structure. In other words, a significant result from this procedure could be due to a relationship between the predictor and the network, or because individuals do not interact at random, whether or not the true social structure is related to the predictor. This fundamental mismatch between the null hypothesis of interest and that tested by the datastream permutation algorithm makes tests of regression models using this procedure nearly uninterpretable.

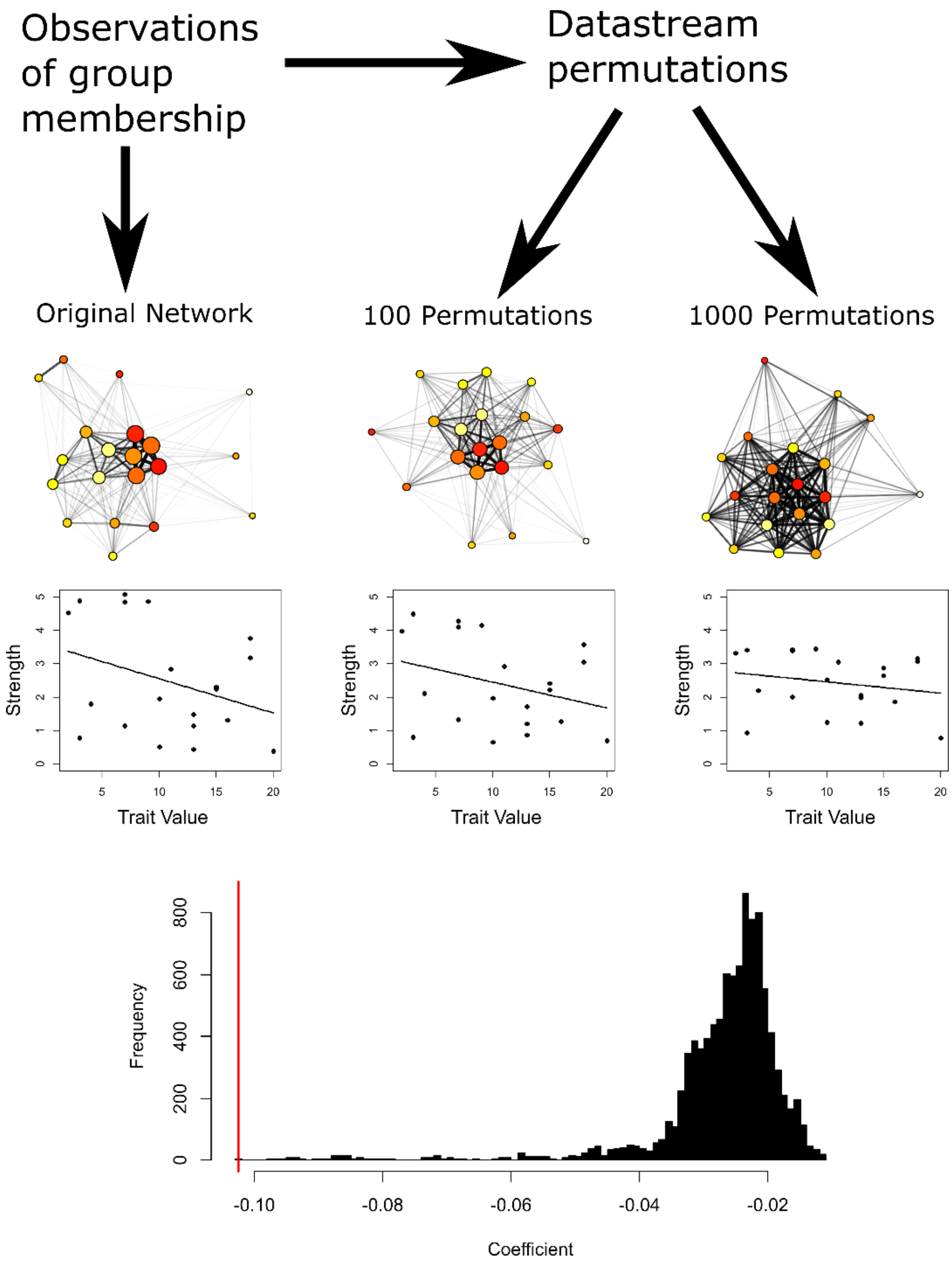

Figure 3.1 Example of the mechanism by which datastream permutations may lead to false positives in linear regression. In the original network, there is variation in strength among individuals driven by differences in gregariousness (represented by node size in the social networks). Individuals are assigned a trait value (represented by colour in the social network) unrelated to their network position. By chance, there is a slight negative relationship between network strength and trait value in the observed network. After several permutations, there is a reduction in the variance in the strength of individuals in the permuted network, and thus the magnitude of the relationship is reduced. The bottom histogram shows the distribution of null coefficients after 10,000 permutations (black), and the coefficient from the original linear model (red).

Here, we demonstrate the problems that occur when combining datastream permutations of animal social network data with regression using two simulated scenarios. In these scenarios, we generate datasets with simple non-random social structure. We then introduce a random exogenous variable that has no relationship to social structure, and test for a relationship between network structure and this variable with linear models, using datastream permutations to determine statistical significance. We show that even in the absence of any true relationship between exogenous variables and social structure, datastream permutations are highly prone to producing significant *p*-values when social structure is non-random. We caution against using these datastream permutations to test the coefficients of regression models, and we discuss possible solutions and alternative methods for regression analysis in social networks.

3.2 Methods

3.2.a General framework

To illustrate the problems with using datastream permutations to test the coefficients of regression models, we carried out simulations across two different scenarios, reflecting common research questions in animal social network analysis. The first scenario simulates a case in which researchers are interested in whether dyadic covariates (e.g. kinship or phenotypic similarity) influences the strength of social bonds, which we will refer to as a case of “dyadic regression”. The second scenario simulates a case when researchers are interested in how a quantitative individual trait (e.g. age or personality) influences individual network position, which we refer to as “nodal regression.”

While the methods of network generation differ slightly for each scenario, the general steps are the same:

1. Generate observations of a network in which the quantity of interest (edge weight or node centrality) has inherent variation.
2. Generate values for a trait that are unrelated to this variation.
3. Fit a linear model with the network property as the response variable and the trait as the predictor
4. Create permuted versions of the observed network via a common datastream permutation
5. Compare the original model’s coefficient to those fit to the permuted data to calculate a *p*-value

For each simulation, we perform 200 runs, with varying parameter values (Table 3.1). For each run of both simulations, we produce four outputs. The first two outputs are the coefficient of the fitted linear model and the *p*-value from the permutation test. The other two outputs give information about the characteristics of the dataset. The first is the standard deviation of the response variable (either the edge weights or weighted degrees), indicating the degree of non-randomness in the social structure, and the second is the average number of sightings per individual, a common measure of sampling effort in social network studies.

3.2.b Dyadic regression: Does trait similarity predict the strength of social relationships?

In our first simulation, we investigate the case in which the researcher is interested in the influence of a dyadic predictor (such as similarity in phenotype or kinship) on the rates at which dyads associate or interact. Our simulation framework is heavily inspired by those of Whitehead & James (2015) and Farine & Whitehead (2015). We simulate a population of N individuals, and assign each dyad an association probability p_{ij} from a beta distribution with mean μ and precision ϕ ($\alpha = \mu\phi$, $\beta = (1-\mu)\ \phi$). By assigning association probabilities in this way, we create non-random social preferences in the network, and thus larger variance in edge weights than would be expected given random association (Whitehead et al., 2005).

Table 3.1 Ranges for varied parameters used in simulations

Parameter	Meaning	Dyadic	Nodal	Range
N	Number of individuals in population	✓	✓	20 – 100
μ	Mean association probability	✓		0.01 – 0.5
t	Number of sampling periods	✓		20 – 200
ϕ	Precision of beta distribution for association probabilities	✓		1 – 10
o	Observation probability per sampling period	✓		0.1 – 1
G	Number of observed groupings		✓	20 – 500
M	Maximum grouping size		✓	5 – 10
σ	Standard deviation of group size preference		✓	0.1 – 2.0

We then simulate t sampling periods. For simplicity, individuals are sighted in each sampling period with a constant probability o, and associations between dyads where both individuals are sighted occur with probability p_{ij}. We then build the observed association network by calculating dyadic simple-ratio indices:

$$SRI_{ij} = \frac{X_{ij}}{D_{ij}} \qquad (2)$$

Where X_{ij} is the total number of sampling periods in which *i* and *j* were observed associating, and D_{ij} is the total number of periods in which either *i* or *j* was observed (including periods where they were observed, but did not associate with any individuals).

We then assign each individual a trait value from a uniform distribution (0,1). We do not need to specify what this trait represents for our simulation, but it could represent any quantitative trait used as a predictor in social network studies (age, personality, cognitive ability, dominance rank, parasite load, etc.). Note that the trait value is generated after the observations of association and has no influence on any network property.

We then fit the linear model:

$$SRI_{ij} = \beta_0 + \beta_1 \left| trait_i - trait_j \right| + \varepsilon \qquad (3)$$

and save the estimate of β_1. We compare this coefficient to a null model generated using the sampling period permutation method proposed by (Whitehead, 1999). There are several algorithms available to perform these swaps. We use the “trial swap” procedure described by Miklos & Podani (2004) and suggested for social network studies by Krause et al., (2009). For each trial, this procedure chooses an arbitrary 2 by 2 submatrix of the lower triangle within a random sampling period. If a swap is possible, it is performed (and symmetrized), otherwise the matrix stays at its current state. These steps when the matrix is not changed are referred to as “waiting steps.”

This algorithm is ideal because it ensures that the Markov chain samples the possible matrices uniformly, while other algorithms that do not include waiting steps exhibit biases in their sampling of the possible matrices (Miklós & Podani, 2004). We generate 10,000 permuted datasets for each simulation, with 1,000 trial swaps between each permutation, and re-fit our linear model to each permuted dataset, recording the coefficient. We then use this distribution of coefficients to calculate the *p*-value of the linear model's coefficient. Across the 200 runs, we vary the parameters of the simulation by drawing μ, ϕ, N, o, and t randomly using Latin hypercube sampling (Table 3.1).

3.2.c Nodal regression: Do individual traits influence network centrality?

We next investigate the same concept in the context of nodal regression. This form of analysis tests whether some individual attribute is related to variation in network position. This is perhaps the most common use of datastream permutation null models for testing the significance of linear regression coefficients in animal social networks (Cowl, et al., 2020; Poirier & Festa-Bianchet, 2018; Zeus, et al., 2018). For simplicity, we focus on weighted degree, which is simply the sum of an individual's edge weights.

In this simulation, we consider the case where networks are derived from patterns of shared group membership ("gambit of the group"). This form of data collection is extremely common in animal social network studies, and was the basis for the original datastream null model developed by Bejder et al., (1998).

The framework for this simulation is based on that used by (Firth, et al., 2017). We simulate G observations of groupings in a population of N individuals. Each group is assigned a group size S from a discrete uniform distribution on $[1,M]$. We assign each individual a preference for a particular group size P from a truncated normal distribution with mean (1+M)/2, standard deviation σ, lower bound 0, and upper bound M. Higher values of σ will therefore lead to higher variation in gregariousness in the population. For each group g, membership is determined by sampling S_g individuals without replacement, with individual sampling probability determined by the size of group g and each individual's group size preference:

$$P(i \text{ in } g) \propto \frac{1}{(S_g - P_i)^2} \tag{4}$$

This gives the simulation the property that individuals with higher assigned gregariousness scores tend to be seen in larger groups, and vice versa. This leads to non-random differences in gregariousness (and thus weighted degree) between individuals. We then calculate the association network, again using the SRI:

$$SRI_{ij} = \frac{X_{ij}}{X_{ij} + Y_i + Y_j} \tag{5}$$

Where X_{ij} is the number of groups in which the dyad was seen together, and Y_i and Y_j are the number of groups in which only i or only j were seen, respectively. After calculating the network, we determine each individual's weighted degree. We again generate a trait value for each individual at random from a uniform distribution on (0,1) and fit the linear model

$$\sum_j SRI_{ij} = \beta_0 + \beta_1 trait_i + \varepsilon \tag{6}$$

and again save the estimate of β_1. We compare this coefficient to random coefficients fit to networks generated using the group-based permutation procedure proposed Bejder et al., (1998).This procedure again sequentially permuted the observed dataset, while maintaining the size of each group and the number of groups per individual. We again use the trial swap method to perform these permutations, generating 10,000 permuted datasets with 1,000 trials per permutation, and derived *p*-values in the same way as above. We vary the parameters of this simulation by using Latin hypercube sampling to draw values of *N*, *M*, *G*, and *σ* (see Table 3.1 for ranges).

3.3 Results

3.3.a Dyadic regression

The overall type I error rate for the dyadic regression case was high, with 35% of runs giving false positive results (70 out of 200 runs). Sensitivity analysis suggested that the most important factors influencing type I error rate in our simulations were the average number of sightings per individuals and the variance of association probabilities. As the average number of sightings increased, so did the false positive rate (*β* = 0.012 ± 0.004, *z* = 3.149, *p* = 0.002, Figure 3.2c). Similarly, networks with higher variance in edge weights experienced higher type I error rates (*β* = 8.35 ± 8.93, *z* = 2.37, *p* = 0.02, Figure 3.2a). There was a less clear, but statistically significant relationship between network size and type I error rates, with networks of larger size typically having lower type I error rates (*β* = -0.014 ± 0.007, *z* = -2.02, *p* = 0.04, Figure 3.2b).

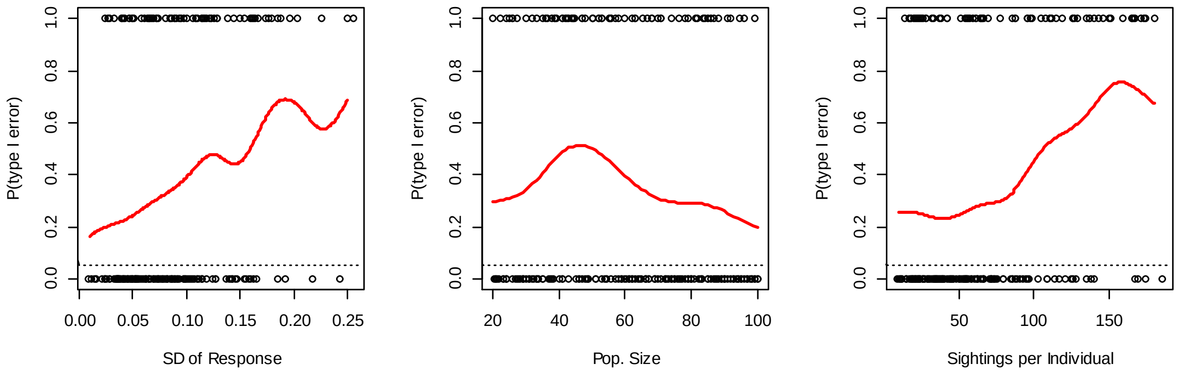

Figure 3.2 Conditional probability plots from dyadic regression simulation. Points indicate results of individual simulation runs (1 = significant p-value, 0 = non-significant

p-value). Red lines are smoothed condition probabilities of a significant p-value. Dotted line indicates target type I error rate of 0.05.

3.3.b Nodal regression

The nodal regression case resulted in even higher type I error rates than the dyadic case, with almost half of runs giving false positive results (95 out of 200 runs; 47.5%). The rate of type I errors was strongly influenced by the variance in weighted degree; as the standard deviation of the response increased, so too did the false positive rate (β = 1.18 ± 0.50, z = 2.34, p = 0.019, Figure 3.3a). In contrast, as the size of the network increased, the false positive rate decreased, although never approaching the target false positive rate of 0.05 in our simulations (β = -0.02 ± 0.01, z = 2.89, p = 0.004, Figure 3.3c). In this simulation, the number of sightings per individual did not appear to significantly influence the type I error rate (β = 0.018 ± 0.013, z = 1.43, p = 0.153, Figure 3.3b). This may be because, in networks with few groupings but high sightings per individual, there were fewer possible permutations of the observed network, and therefore the permuted networks were more similar to the original network.

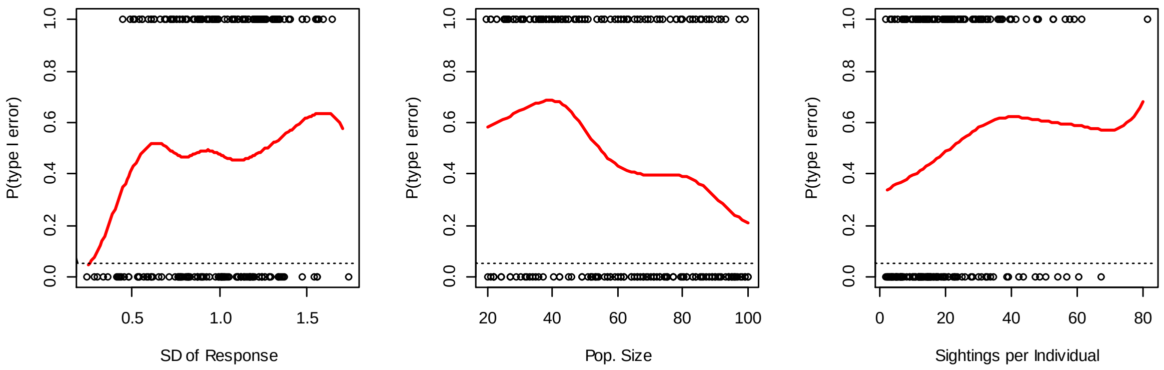

Figure 3.3 Conditional probability plots of type I error rates for the nodal regression simulation. Points indicate the outcome of individual runs (1 = significant p-value at 0.05, 0 = non-significant p-value). Red lines are smoothed conditional probabilities of a significant p-value. Dotted lines indicate the target error rate of 0.05.

3.4 Discussion

These two simple simulated scenarios show that the commonly used datastream permutation procedures for animal social network data produce extremely high and thus unacceptable false-positive rates when applied to regression models. This is because datastream permutations do not generate appropriate null distributions for testing the significance of model coefficients. We therefore strongly warn against using this procedure.

We now turn to some potential solutions to this problem that may still facilitate inference in these situations. This is not intended to be a comprehensive guide to hypothesis testing in social networks, and other solutions are certainly possible. We encourage other researchers to consider these and other possible solutions.

3.4.a Transforming the response variable

If variations in social behaviour are present in the network, datastream permutations undesirably eliminate social influence and reduce the variance in the response of a regression model. A potential fix for this problem is to simply standardize the variable of interest, perhaps to have a mean 0 and standard deviation 1 (Z-scores), and to repeat this process for all permutations. While this is likely to reduce type I error rates, we caution that this is a quick fix of the symptom and does not address the cause: that the null model generated does not test the desired hypothesis. We therefore do not consider this to be an adequate solution in itself.

3.4.b Alternative test statistics

Another potential solution could be found in using a test statistic other than the coefficients from the model. Here, we've used the estimated regression slopes, but other statistics, particularly pivotal statistics such as partial correlation coefficients and *t* values, may be more useful. In the context of node-label permutations such as MRQAP, *t* values and partial correlation coefficients perform better in hypothesis testing contexts than the raw coefficient value (Dekker, et al., 2007). While previous authors have recommended against using the *t* or *Z* statistic, because they represent deviations from a parametric distribution rather than direct features of the data (Farine, 2017), such statistics could experience a lower type I error rate than those reported here, as they explicitly account for uncertainty in model estimates. However, as in the case of transforming the response, this does not address the larger issue of an incorrectly specified null hypothesis. We therefore do not view the adoption of alternative test statistics from regression models compared to datastream permutations as an appropriate solution.

3.4.c Separating the issue of non-independence from biases in the data

We suggest that the way forward for hypothesis testing in animal social networks is to recognize that the problems of non-independence of network measures and the influence of data structure underlying networks are separate issues, requiring separate solutions. Not all animal network data will be subject to the issue of unreliability (e.g., in cases where sampling is balanced across subjects and relevant contexts) and in some instances the data may be complete and unbiased. In these cases, node permutations or other statistical network models are appropriate (Croft, et al., 2011). In instances where structure in the data needs to be controlled we propose two potential methods; other solutions are certainly possible, and we encourage further work on this matter.

The first method would utilize generalised affiliation indices (GAIs) (Whitehead & James, 2015) or similar corrections to account for confounding variables that may influence observed edge weights. GAIs fit the observed data associations or interactions as the response in a binomial or Poisson generalised linear model, with confounding factors such as space use, sightings frequency, or joint gregariousness as predictors. The residuals of this model are then used as measures of affiliation, as they reflect the difference between observed and expected association rates given the confounding factors. While a flexible and appealing approach, GAIs require that potential confounds be properly specified in terms of dyadic covariates, and that the relationship between confounds and edge weights be linear. This second issue, however, may be addressed by fitting generalised additive models (GAMs), where relationships are represented by smooth functions.

A related, but slightly different approach would be to incorporate confounds in the inferential model itself. Rather than deriving new edge weights via GAIs, if researchers identify likely confounds and summarize them quantitatively for each dyad or individual, these could be used directly in the final model. Where potential non-linearity between confounds and responses exist, data transformations, polynomials, and smooth functions may present a possible solution.

We feel that these methods have the potential to address the current issue that we have identified and we strongly encourage new work to explore and validate these approaches. It is important to note that the methods we propose are only useful if the question of interest is about the structure of social affinity, rather than the empirical pattern of encounters between individuals. If, instead, researchers are interested in the actual rates of contact (as is the case in disease research and studies of social learning), this approach may not be appropriate. Extensions of recent work using hidden state modelling may be more appropriate for disentangling true association patterns when detections are potentially biased or imperfect (Gimenez, et al., 2019).

3.4.d Building better null models

The problems we have identified here arise because the commonly used null models for animal societies do not generate datasets representing the null hypothesis of interest in a regression setting. These models were specifically designed to test the null hypothesis of random social structure, not the null hypothesis that aspects of social structure are unrelated to exogenous factors. An obvious way forward would be the development of permutation procedures that generate datasets that correctly represent the relevant null hypothesis. In the case of dyadic regression, these datasets would maintain the structure of the data (e.g. sightings per individual, associations per sampling period, spatial patterns of observations), randomise identities of associated individuals, and simultaneously preserve the variance in edge weights. In the case of nodal regression, permuted datasets would maintain the same (or at least a similar) distribution of individual centrality within the network, in addition to structural confounds such as the size of groups, sightings per individual, and timing of sightings. The design of such procedures is far from trivial, and is beyond the scope of this paper, but we suspect that the development of algorithms that simultaneously maintain aspects of data structure and features of the social system will be an important area of methodological research going forward.

3.5 Conclusion

The development of permutation techniques that control for sampling biases while maintaining temporal, spatial, and structural aspects of the raw data is an important development in the study of animal social systems, and we suspect that these procedures will remain a key tool for hypothesis testing in ecology and evolution. However, a lack of consideration regarding the matching up of the null hypothesis being tested with the null model being generated using datastream permutations has led to unwarranted application of these techniques, particularly in the context of hypothesis testing using regression models.

We recommend that researchers think critically and carefully about the null hypothesis they wish to test using social network data, and ensure that the null model they specify does in fact represent that hypothesis. We suspect that in most cases, the null hypothesis of random social structure will clearly not be appropriate, and therefore traditional datastream permutations will not be a viable approach. We hope that our discussion of this issue and the results of our simulations will result in reconsideration of how researchers employ null models when analysing animal social networks, promote further research and discussion in this area, and lead to the development of procedures that correctly specify null hypotheses and allow robust inference in animal social network studies.

These first two chapters have been concerned with the statistical analysis of social network data, either within or between networks. Left unaddressed are the challenges of collecting social network data in hard to observe systems, such as cetaceans. In the next chapter, I turn toward developing novel data collection methods for cetacean sociality, and work to understand the consequences of different forms of behavioural data on researcher’s inferences about social structure.

Chapter 4

Aerial observation of killer whale social interactions reveals differences between association, synchrony, and contact networks

Abstract

Measuring the patterns of social relationships in a population is a key priority in behavioural ecology, as social structure can have important consequences for ecological and evolutionary processes. For marine species, direct social interactions are difficult to observe, and therefore most social network studies in these systems use the rate of associations, representing how frequently individuals have the opportunity to interact. There is currently a lack of research, however, investigating whether social networks measured in this way are representative of interaction patterns, and if surface observations reflect sub-surface behaviour. Here, we test the relationships between association, surface interactions, and sub-surface behaviour in resident killer whales. We use the unmanned aerial systems (UAS) to observe association patterns alongside two affiliative social interactions: synchronous surfacing and physical contact. We find that while associations were correlated with both interaction patterns, and interaction rates were correlated with each other, there were important differences in structure between these three networks. Interactions occurred non-randomly between associated individuals, and sub-surface physical contact interactions were significantly more differentiated than synchronous surfacing interactions. In addition, while association patterns showed no correlation with sex or age similarity, both interaction networks showed significant assortment by both age and sex. This study highlights the potential pitfalls of using association as a proxy for interaction, and the immense potential of UAS for collecting data on the fine-scale social structure of wild cetaceans.

4.1 Introduction

In highly social species, the structure of relationships within groups or populations can have profound implications for biological processes, including disease spread (Craft, 2015), social learning (Cantor & Whitehead, 2013), and ecological processes (Kurvers, et al., 2014). In addition, an individual's position within their society can have impacts on their survival, growth, and reproduction (Ostner & Schülke, 2018). Quantifying the social structure of wild animal populations is thus central to addressing key behavioural, ecological and evolutionary research questions. Over the last decade, social network theory has been rapidly adopted to quantify the structure of animal societies at different levels of organisation (e.g. individual, social group, community and population). Social networks model social structure as a set of nodes, representing social actors such as individuals or groups, and the set of edges connecting them. The behavioural definition of edges in social network studies should be driven by research questions (Carter, et al., 2015). The "gold standard" for quantifying social relationships is the measurement of relevant, direct social interactions, however such data are not always available. In some cases, such as when social interactions are difficult to observe, it may be necessary to use proxies for the interactions of interest. One way to do this is to quantify the frequency with which pairs of individuals are close enough in time and space that they have the opportunity to interact. Such data are commonly referred to as "associations." Association is typically defined by co-membership within groups or spatiotemporal co-occurrence. As individuals that associate more regularly have more opportunities for interaction, it is typically assumed that association patterns will correlate strongly with interaction rates, and thus social networks constructed from association with generally be representative of interaction networks. There can be important differences, however, in network structure depending on whether edges are based on association or interaction, and what kinds of interactions are measured (Castles, et al., 2014). These differences can affect our estimates of overall network structure, the apparent position of individuals within the network, and our understanding of what factors, such as age, sex, and kinship, underly social processes. For example, if individuals do not exhibit assortment by sex in their associations, but associates of the same sex are more likely to interact, analysis of associations alone may lead researchers to incorrectly conclude that the species does not exhibit social homophily by sex. It is therefore important to test these assumptions where possible, and to attempt to determine their impact on our inferences about social structure.

Cetaceans, particularly the toothed whales, are often highly gregarious and exhibit a wide array of complex social structures (reviewed in Chapter 1 and Rendell, et al., 2019). It is perhaps unsurprising that, along with the passerine birds and primates, cetaceans are among the animal groups that have been studied most intensely using social network methods (Webber & Vander Wal, 2019). To date however, social interactions among cetaceans have been inferred almost exclusively from observed associations among individuals, because direct interactions are typically difficult to observe. Associations are generally defined either by shared group membership or by a spatial or temporal cut-off at a broad scale (Farine & Whitehead, 2015). Some studies have attempted to uncover much more fine-scale social relationships by examining patterns of surface interaction, particularly synchronized surfacing (Augusto, et al., 2017; Dungan, et al., 2016). Synchronous surfacing is thought to be a useful behaviour for cetacean social network analysis due to its apparent role in social bonding (Connor, et al., 2006), and because it is measurable from boat-based observations of surfacing individuals.

New technological advances, particularly animal-borne sensors and unmanned aerial systems (UAS), have made it feasible to analyse the sociality of free-ranging marine animals at a much finer scale than is possible with photo-identification techniques alone (Nowacek, et al., 2016). Animal borne sensors have been used to analyse synchrony (Aoki, et al., 2013) and gregariousness (Pearson, et al., 2019) in wild cetaceans, and to understand individualized social relationships in semi-free ranging porpoises (Sakai, et al., 2011). This approach, however, is limited by the number of deployments that can be carried out simultaneously in the case of proximity sensors and biologgers, and by the ability of researchers to identify individual social partners from animal-borne cameras. While UAS has the drawback of only being able to observe near-surface behaviour, it provides a platform from which to observe the social interactions of multiple individuals simultaneously, and thus may serve as a useful tool for understanding social networks in marine species. Recently, UAS have been successfully applied towards quantifying the drivers of social relationships in cetaceans, by simultaneously monitoring patterns of surface interactions and spatial configuration in Risso's dolphins (*Grampus griseus*) (Hartman, et al., 2020). In addition to the ability to monitor entire groups, an aerial perspective provides the ability to observe sub-surface interactions in systems where researchers typically only observe associations at the surface. This presents the opportunity to determine both whether association patterns reflect interaction rates, and to what degree surface and sub-surface interaction patterns are correlated.

While the benefits of an aerial platform for the study of cetacean behaviour have long been recognized (Nowacek, et al., 2001), it has not been widely practical until recently. The use of UAS greatly increases the observation time for marine mammals, particularly when submerged (Torres, et al., 2018), and is non-invasive when aircraft are flown at appropriate altitudes (Fettermann, et al., 2019; Ramos, et al., 2018). UAS have been to observe the behaviour of cetaceans (Nielsen, et al., 2019; Torres, et al., 2018) and other surface-oriented marine species (Rieucau, et al., 2018). We propose that UAS may serve as an important tool for quantifying social interactions in wild cetaceans.

In this study, we use UAS to observe multiple types of affiliative social interaction between identified individuals in a group of free-ranging killer whales (*Orcinus orca*). We use this data to understand the impact of using association as a proxy for interaction, and the choice of interactions observed, on inferences about the structure of killer whale social groups. Specifically, we test four questions:

1. Are networks derived from association and different forms of interaction broadly correlated?
2. Do interactions occur randomly between associated individuals? If not, how does the structure of interaction networks differ from what would be expected given random interactions?
3. Are networks derived from different forms of interaction (contact and synchronous surfacing) interchangeable with one another?
4. How does our choice of association or interaction measure influence inferences about the role of age, sex, and kinship in structuring social relationships?

4.2 Methods

4.2.a Study population

The southern resident killer whale population is a small (72 individuals at time of writing), closed population of killer whales inhabiting the coastal waters of the northeastern Pacific, with their core habitat being the inland waters of Washington, USA and British Columbia, Canada. This population has been subject to an annual census carried out by the Center for Whale Research since 1976. All individuals can be visually identified using unique markings, body shapes and sizes, and scarring, allowing most birth years and maternal relationships to be known with certainty.

The southern residents exhibit a multilevel social structure based on maternal kinship. Individuals in this population exhibit extreme bisexual social philopatry, with both males and females staying in their mother's group their entire lives. The basic social unit is the matriline, composed of close relatives with a recent common maternal ancestor. Closely related matrilines form pods, larger social groups with a shared vocal dialect (Bigg, et al., 1990). In this population, pod membership has been a significant predictor of association patterns in the southern resident population in all years in which they have been studied (Parsons, et al., 2009). The southern resident population contains three pods, designated J (22 individuals), K (18 individuals), and L pod (32 individuals).

4.2.b Field observations

During the summer of 2019, we collected video observations of southern resident killer whales using a small unmanned aircraft (DJI Phantom 4 Pro V2) launched from a small motorized vessel (21 ft. Grady White), or using a larger unmanned aircraft (DJI Matrice

600) launched from shore. Groups of whales were located by observers prior to launching the aircraft. Groups were primarily chosen for follows based on logistical factors, such as distance from the launch point and the presence of whale watch and research vessels around the whales. Preference was typically given to larger groups to maximize the possible number of interactions observed over a given period. In addition, the aircraft was simultaneously used to help locate fecal samples for a separate research project, and follows of larger groups increased the probability of observing defecation. During on-water operations, the vessel maintained a low speed (< 7 kts) when within 1 km of whales. The vessel was usually positioned behind groups of whales, at a distance of 200-400 m to minimize potential disturbance to the whales while allowing visual contact (see Ayers et al., (2012) for details).

When in the air, one crew member piloted the aircraft, while another served as a visual observer to aid in maintaining visual line-of-sight and situational awareness. A third team member was designated as a general observer, tasked with monitoring whale behaviour during research flights and assisting with operations. Recordings were started whenever whales were within the visual field of the aircraft's camera. The aircraft maintained an altitude between 30 and 120 meters while operating above whales, and was typically positioned to the side of the animals, with the camera at an angle. Camera angle and position of the aircraft were adjusted to minimize glare from the water's surface.

Operations were limited to conditions appropriate for the safe operation of the UAS and clear observation of animals below the water (no rain, wind below 10 kts, sea state less than Beaufort 3). During the course of the summer, we collected 12 hours of footage of southern residents over 13 days. For the majority of these days (10 days, 11 hours), only members of J pod were present. We therefore chose to restrict our analysis to observations of J pod only, and excluded data collected on days when other pods were present.

4.2.c Ethical considerations

The southern resident killer whales are protected in the United States under both the Marine Mammal Protection Act and the Endangered Species Act. Therefore, all research was conducted under permits issued by the National Marine Fisheries Service (NMFS permits 21238 and 22141), and the aircraft was always operated by a trained pilot licensed under Federal Aviation Administration Part 107. Previous studies suggest that operating UAS at an altitude of 30 m or more has minimal effect on cetacean behaviour (Fettermann, et al., 2019; Ramos, et al., 2018) and that killer whales in particular do not show any signs of disturbance from UAS research operations (Durban, et al., 2015). In our study, we monitored the whales to determine if clear behavioural responses (increased surface active behaviours or sudden direction changes) occurred as the UAS approached. If such disturbances were noted, our protocol was to cease observation of that individual or group for the remainder of the day. However, no behavioural responses were observed during the study. These research activities have been approved by the University of Exeter College of Life and Environmental Sciences ethics committee.

4.2.d Video analysis

From the video, we sought to quantify the dyadic rates of two types of direct interaction, synchronous surfacing and physical contact, as well as patterns of spatiotemporal co-occurrence (association) between individuals. All videos were analysed using BORIS software (Friard & Gamba, 2016). Previous studies have established that individuals in this population can be consistently identified from aerial photography (Durban, et al., 2015). All video analyses were performed by an observer experienced in identifying individual killer whales in this population, with individuals identified by their unique markings, body shapes and size, and scarring.

Analysis of each video clip proceeded by first identifying all whales that were visible at any point during the video. Then, in random order, the observer sequentially followed each whale for the entirety of the video, recording when it was visible, what interactions it had, and the identity of its interaction partners. We did not record interactions where either of the interacting individuals was not identified.

We coded visibility as a state variable, indicating when each individual was on screen and identifiable in each video. Association was then measured based on each pair of individuals' periods of visibility. We use the term “association” following Whitehead & Dufault (1999), meaning that associated individuals are those pairs of individuals with the opportunity to interact at a given time. We therefore consider individuals to be associated if they were simultaneously observed and identified in the video footage. We coded two forms of direct interaction: physical contact and synchronous surfacing (Figure 4.1). These two types of interactions were chosen because both synchrony and physical touch have been suggested to play important roles in cetacean social bonding (Connor, et al., 2006; Nakamura & Sakai, 2014). In addition, these interactions provided a potential contrast between interactions observable from traditional, boat-based platforms (surfacing) and those that would typically not be visible without the use of an aerial platform (contact).

We code physical contact as a point event, coded at the moment when individuals initially come into contact. As we were interested in patterns of affiliative social relationships, we excluded aggressive interactions such as fluke strikes and biting. We also excluded observations of nursing, as these represent feeding behaviour rather than strictly social interactions. Potential sexual contacts were not excluded, as previous studies suggest that affiliative socialization often includes sexual behaviour in this population (Noren & Hauser, 2016; Osborne, 1986). It was not possible to unambiguously assign individuals as initiator and receiver for the vast majority of contact behaviours, and contact was therefore coded as an undirected behaviour.

Synchronous surfacing was also coded as an undirected point event and was defined as individuals respiring together within one adult female body length (approximately 6 m). We use a strict temporal cut-off, such that individuals were only considered to have breathed in synchrony if at some point during their surfacing sequence both individuals' blowholes were simultaneously above the water's surface. Individuals could be recorded synchronously surfacing with multiple partners in a single surfacing sequence if more than one individual met this criteria. Note, however, that we did not use a chain-rule for coding these interactions, and therefore synchronous surfacing interactions were not transitive (i.e. individual *A* can synchronously surface with both *B* and *C* without *B* and *C* synchronously surfacing with one another).

Our sequential follow protocol, if all interactions are correctly recorded, generates two records of each interaction (one per individual), potentially coded by the observer at slightly different time points. We checked the data by first ensuring all recorded interactions were symmetric. Any asymmetric interactions were re-analysed in the original video to determine whether the asymmetry was the result of a false positive (interaction recorded when it should not have been) or a false negative (failure to record interaction for one individual), and was corrected accordingly. Once interactions were checked, we assign a "true" time for all interactions as the midpoint between the two records of the interaction. The differences in coding time were small, typically less than half a second for both interaction types (surfacing: median = 0.20 s, IQR = 0.29; contact: median = 0.44 s, IQR = 0.66). In addition, we checked the data to ensure that all individuals were coded as visible during all of their recorded interactions, with inconsistencies again corrected by re-analysis of the video.

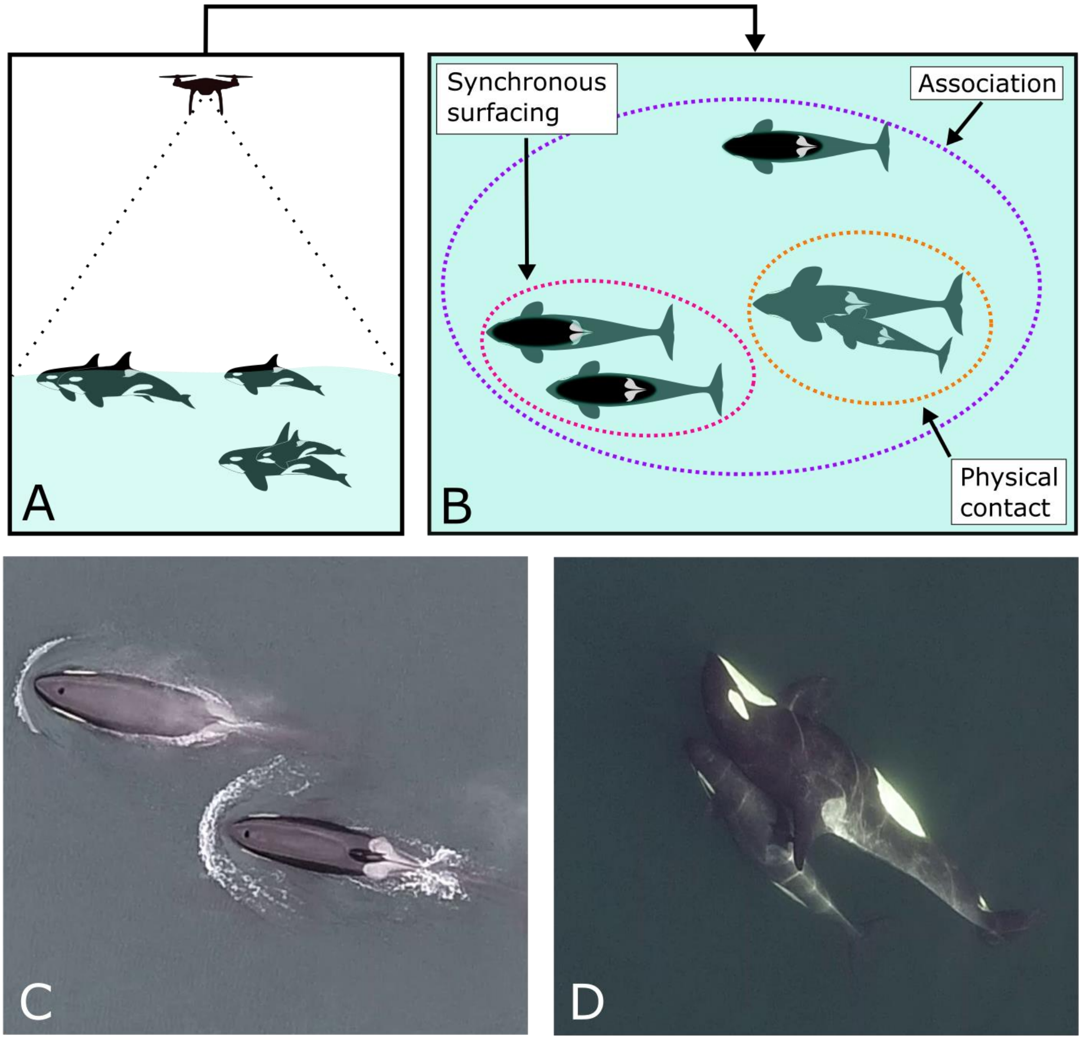

Figure 4.1 Observing killer whale interactions using UAS. A-B: The aircraft is flown over focal killer whale groups (A). All individuals detected simultaneously were considered to be associated, and both synchronous surfacing and physical contact interactions were recorded between identified individuals (B). C-D: Example video

stills of synchronous surfacing between individuals J36 and J47 (C) and physical contact between individuals J44 and J53 (D).

4.2.e Social network construction

We constructed interaction networks by counting the total number of interactions between each dyad, and then dividing this count by the observation time of each dyad to estimate interaction rates. As in the case of association indices, the denominator here represents the amount of time during which an interaction could have occurred because at least one of the individuals was observed. Each dyad's observation time was summarized as the total amount of time that one or both of the individuals was visible

$$rate_{ij} = \frac{interactions_{ij}}{time_i + time_j + time_{ij}} \tag{1}$$

Here, *interactions*$_{ij}$ is the number of interactions between individuals *i* and *j*, *time*$_i$ and *time*$_j$ are the total time only *i* or *j* were visible (excluding time in which they were on-screen simultaneously), and *time*$_{ij}$ is the amount of time both *i* and *j* were visible simultaneously. We calculate interaction rates and resulting networks separately for synchronous surfacing and contact networks.

We also construct a network representing the degree to which individuals tended to co-occur in our observations:

$$association_{ij} = \frac{time_{ij}}{time_i + time_j + time_{ij}} \tag{2}$$

Where the variables definitions are the same as in equation 1. This index is comparable to the "simple ratio index" commonly used in animal social network analysis (Cairns & Schwager, 1987), but using continuous measures of time rather than counts of sampling periods. Like other association indices, the edges in this network range from 0 (never co-occurred) to 1 (always observed together).

4.2.f Correlations between networks

As association provides the opportunity for interaction, we assessed the degree to which associations reflected pairwise interaction rates, and whether interactions of different type were correlated. To do this, we measure the correlation between each pair of networks using Spearman’s correlation coefficient (r_s). We determine the statistical significance of these correlations using a Mantel test implemented in the “vegan” R package (Oksanen, et al., 2019).

4.2.g Network metrics

We were interested in testing whether important aspects of interaction networks can be inferred from association patterns, and whether different forms of interaction were representative of one another. To do this, we measure aspects of the global structure of the interaction networks using four network metrics. These metrics were chosen as they indicate biologically meaningful aspects of social structure, such as the variation in relationship strength, the number of interaction partners, and the transitivity of social relationships. These metrics are described in Table 4.1. Briefly, we measured the number of interaction partners individuals had (average degree), the degree to which social relationships were transitive (clustering coefficient), the degree to which individuals were exclusive in their social relationships (disparity), and the overall variability in interaction rates (coefficient of variation). Note the subtle but important difference in interpretation between disparity and coefficient of variation. A high coefficient of variation reflects overall variation in interaction rates, and can therefore arise from differences in gregariousness between individuals, even if each individual has relatively homogenous relationships. In contrast, disparity measures the average variation in social relationship strength within each individual, correcting for gregariousness.

All analyses were conducted in R (R Core Team, 2020). Calculation of most statistics was performed using custom code, however weighted clustering coefficient was calculated using the "tnet" package (Opsahl, 2009).

Table 4.1 Summary of metrics calculated for each social network

Metric	Mathematical definition*	Biological interpretation
Average degree	$\frac{1}{N}\sum_{i=1}^{N}\sum_{j=1}^{N} I(\omega_{ij} > 0)$	The average number of social partners that individuals have.
Clustering coefficient	$\frac{total\ value\ of\ closed\ triplets}{total\ value\ of\ all\ triplets}$	The propensity for individuals with mutual social partners to have strong relationships with each other.
Average disparity	$\frac{1}{N}\sum_{i=1}^{N}\sum_{j=1}^{N}\left(\frac{\omega_{ij}}{\sum_{k=1}^{N}\omega_{ik}}\right)^2$	The variation in the strength of each individual's social bonds.
Coefficient of variation	$\frac{\mathrm{SD}(\omega)}{\overline{\omega}}$	The overall variation in relationship strength

*ω is the weighted adjacency matrix, N is the total number of individuals in the network, and I is an indicator function that takes the value 1 if its arguments are true, and 0 otherwise.

4.2.h Comparing interactions to associations

We first tested whether the structure of interaction networks could be explained solely by dyadic co-occurrence and non-dyadic factors. In addition to co-occurrence, the observed networks could be influenced by temporal variation in the rate at which interactions were observed. We therefore construct a null model for our interaction networks that maintains both individual detection history and temporal variation in the observed rate of interactions. For each observed interaction, we permute the identities of interacting individuals by randomly sampling two individuals coded as visible at the time of the interaction. This generates a dataset in which the timing of observed interactions and individual occurrence history are maintained, but the identities of interacting whales are randomized. We then re-calculate dyadic interaction rates and the resulting network statistics. We repeat this procedure 10,000 times to build a distribution of our network statistics under the null hypothesis that the structure of interactions could be explained by random interactions, association tendencies, and temporal variation in overall interaction rate.

4.2.i Comparing surfacing and contact networks

Next, we investigated differences in structure between the two interaction networks. We again use a randomization based null model, this time representing the null hypothesis that the two types of interaction are interchangeable, but potentially with different overall rates. We use the randomization procedure proposed by (Franz & Alberts, 2015) to do this. Each observed interaction is given a label indicating what form of interaction, surfacing or contact, it represented. These labels are then randomized, and the two resulting networks are calculated. We again repeat this procedure 10,000 times, re-calculating our 4 network statistics for each randomization. Here, our test statistics are the differences in each network metric in Table 4.1 between the two networks. If the observed difference lies outside the 95% confidence interval of the randomizations, we reject the null hypothesis of no structural difference between the networks.

4.2.j Influence of age, sex, and kinship on social network structure

Finally, we test how the choice of behaviour defining network edges can influence inferences about the role of age, sex, and kinship in structuring social networks. We construct three predictor matrices for our analysis. The first is maternal kinship, estimated from maternal pedigrees derived from long-term observations. We calculated these values from the pedigree data using the “kinship2” R package (Sinnwell & Therneau, 2020). While some paternities are known in this population from genetic sampling (Ford, et al., 2018), we estimated maternal relatedness by assigning each individual a unique father in the pedigree. This method assigns individuals with no shared maternal ancestor in the known pedigree a maternal relatedness of 0, despite the fact that resident killer whale pods tend to be closely related (Pilot, et al., 2010). This variable is therefore a relative measure of shared maternal ancestry, rather than an estimate of genetic similarity. This variable is both more analytically tractable than an estimate of genetic relatedness for this analysis, and is more behaviourally relevant for this matrilineal social system. The second predictor is a binary similarity matrix, indicating whether individuals belong to the same sex or not. All whales in J pod are of known sex based on obvious sexual dimorphism in adults, and photography of the genital region in immature individuals. The final predictor was a continuous measure of age similarity. In J pod, all surviving individuals have birth years known with certainty. We quantify age similarity as the negative absolute difference between individuals’ ages, in years.

To quantify the relationship between both synchronous surfacing and contact rates and our predictors, we use generalised linear models (GLM), which can be expressed as:

$$interactions_{ij} \sim \text{Quasipoisson}(\lambda_{ij}, \theta) \tag{3}$$

$$\log(\lambda_{ij}) \;=\; \beta_0 + \beta_1 kin_{ij} + \beta_2 age_{ij} + \beta_3 sex_{ij} + \log(time_{ij} + time_i + time_j)$$

where $\lambda_{i,j}$ and θ are the mean and dispersion parameter for the quasipoisson distribution, respectively, kin_{ij} is the estimated kinship between *i* and *j*, sex_{ij} indicates whether *i* and *j* are of the same sex, age_{ij} is the negative absolute difference between *i* and *j*'s age, and the β are estimated regression parameters. The term $\log(time_{ij}+time_i+time_j)$ is an exposure term, allowing the modelling of rates of interaction rather than interaction counts. This is possible because the above equation can be re-arrange to reflect that the expected rate of interactions over time is related to the predictors through an exponential function:

$$\frac{\lambda_{i,j}}{time_{ij}+time_i+time_j} = \exp\left(\beta_0 + \beta_1 kin_{ij} + \beta_2 age_{ij} + \beta_3 sex_{ij}\right) \tag{4}$$

Similarly, we quantify the relationship between our predictors and dyadic co-occurrence with the model:

$$association_{ij} \sim \text{Beta}(\mu_{ij}, \phi) \tag{5}$$

$$\text{logit}(\mu_{ij}) \;=\; \beta_0 + \beta_1 kin_{ij} + \beta_2 age_{ij} + \beta_3 sex_{ij}$$

where μ_{ij} and ϕ are the mean and precision parameter of the beta distribution. In this model, dyadic sampling effort was included as a proportional weight in the fitting process, meaning that dyads with more sampling (and thus greater measurement certainty) were given more influence over model fit. In addition, as there were zeros in the co-occurrence data, we transformed these values using the procedure suggested by Smithson & Verkuilen (2006). We fit these models in R, using the betareg package for beta regression (Cribari-Neto & Zeileis, 2010).

Because the responses in these models are network edge weights, they do not constitute independent observations. Therefore, we use a permutation procedure to determine the statistical significance of regression coefficients. We use the double-semi-partialling method developed by Dekker et al., (2007) with 10,000 randomizations, using the pivotal statistics (*t* for quasipoisson, *z* for beta) as our test statistics. Our method is equivalent to the well-established multiple regression quadratic assignment procedure (MRQAP), but fitting GLMs instead of least squares regression. We therefore refer to this procedure as a generalised linear model quadratic assignment procedure (GLMQAP). We have made this procedure available in the "aninet" R package, accessible through GitHub (https://github.com/MNWeiss/aninet).

While double-semi-partialling is generally robust to multi-collinearity, we checked for collinearity between our predictors to ensure that our analysis could efficiently separate out the effects of kinship, age, and sex. Mantel tests showed no strong correlations between these three predictor matrices (*kin* vs. *age*: r = -0.07, p =0.927; *kin* vs. *sex*: r = -0.07, p = 0.881; *age* vs. *sex*: r = -0.044, p = 0.749).

4.3 Results

4.3.a Sampling effort

Over 10 days of sampling, we collected 651 minutes of video. We collected video of all members of J pod (22 individuals). All individuals were observed on at least 3 different days. Each individual whale was videoed for a mean of 125.96 minutes (SD = 57.65), and each pair of animals was observed for an average of 213.68 minutes

(SD = 58.17). During our observations, we recorded 831 instances of physical contact between identified individuals, and 1617 synchronous surfacing interactions (Table 4.1). Pairs of whales were visible simultaneously for an average of 38.24 mintues (SD = 30.61). Observations of both forms of interaction were consistently observed over the 10 days of sampling; 9 days contained at least 50 surfacing interactions, while 7 days contained at least 50 contacts (Figure 4.2). Both surfacing and contact interactions occurred regularly between associated individuals. While individuals were associated, they came into contact at an average rate of 0.06 per minute (SD = 0.13), and performed synchronous surfacing at a rate of 0.12 per minute (SD = 0.17).

Table 4.2 Summary of individual attributes and observation effort for each individual in J pod in the summer of 2019.

Matriline	ID	Birth Year	Sex	Observation time (min)	Sync. surfacings	Contacts
J11	J27	1991	M	85	63	4
	J31	1995	F	206	315	91
	J39	2003	M	121	77	45
	J56	2019	F	203	302	141
J14	J37	2001	F	137	232	119
	J40	2004	F	173	218	114
	J45	2009	M	134	134	58
	J49	2012	M	163	195	95
J16	J16	1972	F	28	18	9
	J26	1991	M	46	14	17
	J36	1999	F	37	29	28
	J42	2007	F	34	20	20
J17	J35	1998	F	166	227	105
	J44	2009	M	159	139	75
	J46	2009	F	219	259	190
	J47	2010	M	145	163	99

	J53	2015	F	181	223	190
J19	J19	1979	F	86	50	15
	J41	2005	F	131	219	120
	J51	2015	M	140	176	78
J22	J22	1985	F	77	93	30
	J38	2003	M	99	68	32

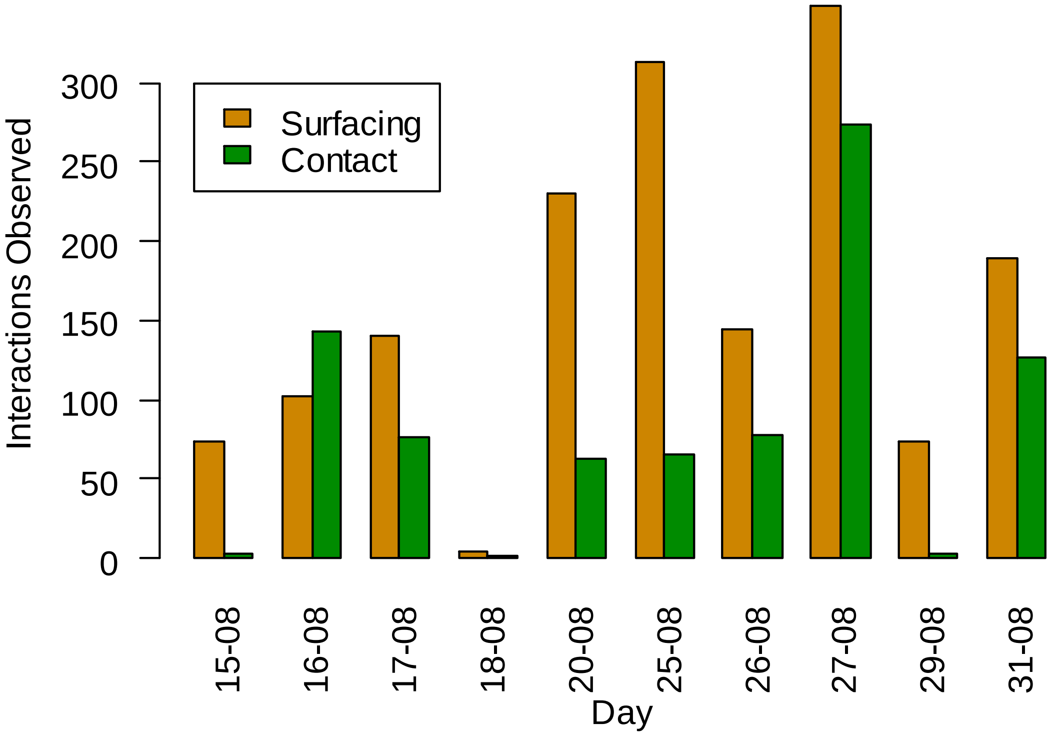

Figure 4.2 Temporal patterns of observed interactions across the sampling period.

4.3.b Interaction and association networks

Within J pod, the association, synchronous surfacing, and contact networks all formed a single connected component (Figure 4.3). The association network was extremely strongly connected; all but 6 dyads had association values greater than 0, indicating some degree of co-occurrence and the opportunity for interaction. The two interaction networks were distinctly sparser than the association network; not all individuals that associated engaged in direct interactions.

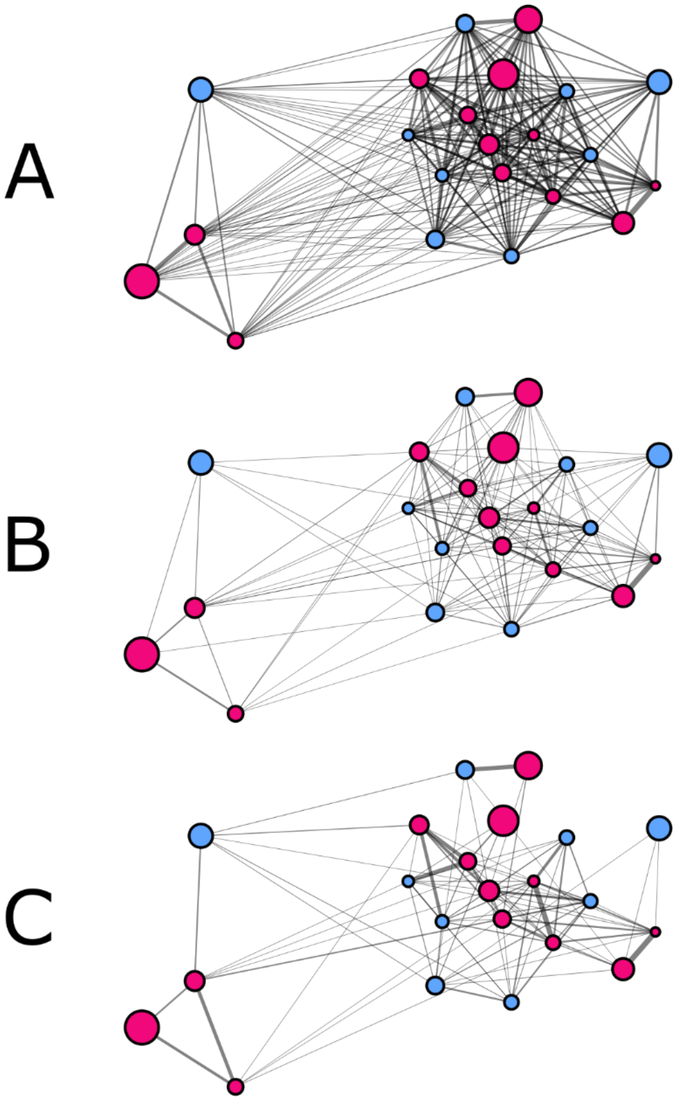

Figure 4.3 Social networks within J Pod. Networks are plotted for **A:** association, **B:** synchronous surfacing, and **C:** physical contact. Node colour indicates sex (blue = male, red = female), and node size is scaled by age. Edge thickness is proportional to association/interaction rate. Figure produced using Gephi (Bastian, et al., 2009). Nodes are positioned based on the ForceAtlas2 layout algorithm applied to the association network.

4.3.c Correlation between networks

Matching the assumptions of association analyses, both the interaction rates were significantly positively correlated to association rates based on pairwise Mantel tests, with the surfacing network being more strongly correlated with association rates (surfacing: $r_s = 0.79$, $p < 0.001$; contact: $r_s = 0.59$, $p < 0.001$). In addition, the two interaction rates were significantly positively correlated with each other ($r_s = 0.72$, $p < 0.001$).

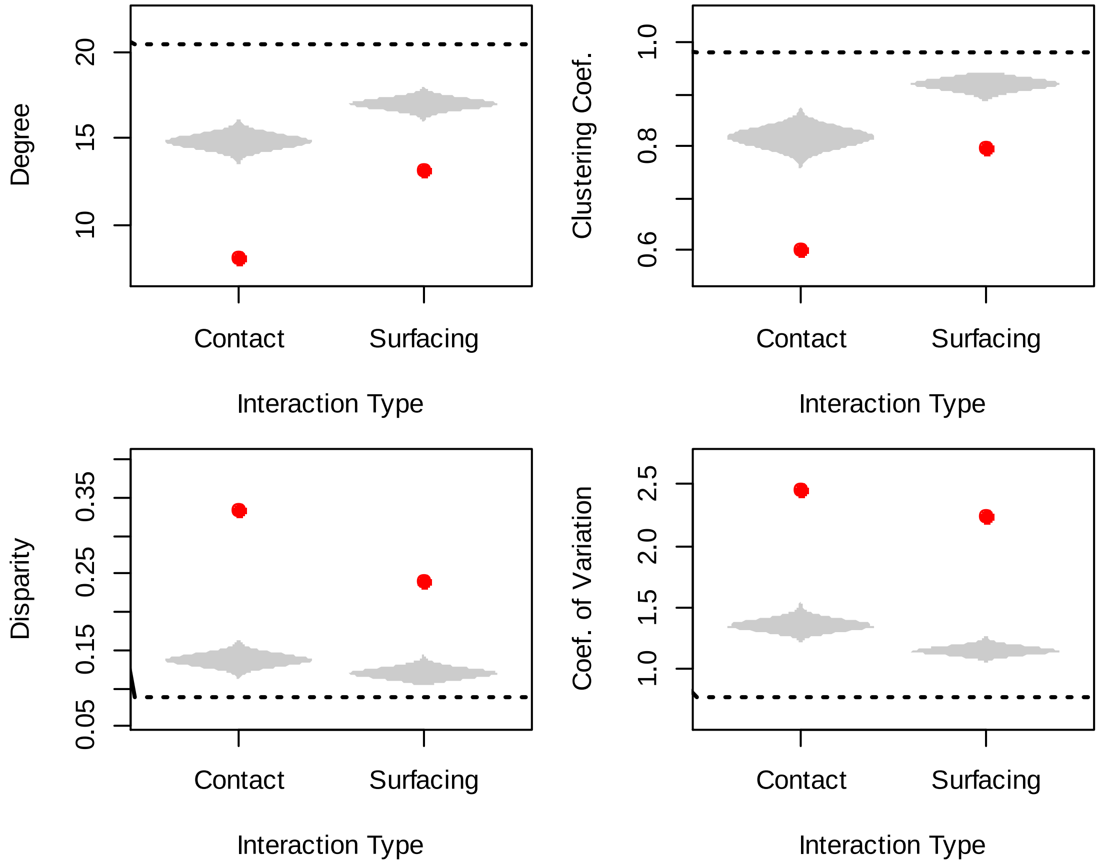

Figure 4.4 Difference between interaction and association networks. Red points indicate observed values of each metric in the interaction networks, and grey violins represent the null distribution from randomizations. The dotted lines indicate the values of the statistics in the association network.

4.3.d Comparing interactions to association patterns

The values of all network statistics for the synchronous surfacing and contact networks differed significantly from the null model of random interactions between associated individuals (all $p < 0.001$; Figure 4.4). In both interaction networks, the observed average degree was lower than the association network, while the disparity and coefficient of variation were significantly higher. This indicates that individuals interacted with fewer individuals and had greater variation in interaction rates than expected from the association patterns. Interestingly, both interaction networks exhibited significantly lower clustering coefficients than in the randomized datasets, indicating that interaction rates were less transitive than expected.

4.3.e Comparison of interaction types

The contact network had a significantly lower mean degree ($p < 0.001$) and higher disparity ($p < 0.001$) than the surfacing network, indicating that individuals had more differentiated relationships with fewer individuals in the contact network. In addition, the clustering coefficient of the surfacing network was significantly higher ($p < 0.001$), indicating a greater degree of transitivity in social relationships. The contact network had a higher CV than the surfacing network, however this difference was not outside of that expected based on our randomization procedure ($p = 0.068$; Table 4.3).

Table 4.3 Comparison of network metrics between interaction types.

Metric	Surfacing	Contact	*P*-value[a]
Degree	13.09	8.09	< 0.001

Clustering coefficient	0.80	0.60	< 0.001
Disparity	0.24	0.33	< 0.001
Coefficient of variation	2.23	2.46	0.068

[a]*P*-values derived from 10,000 randomizations of the interaction data

4.3.f Influence of age, sex, and kinship

Our GLMQAP analysis showed that both interaction networks, as well as the co-occurrence network, were significantly positively correlated with kinship. However, the co-occurrence network did not show structuring by age or sex. In contrast, both interaction networks showed statistically significant positive assortment by both age and sex, with larger effect sizes in the contact network (Table 4.4).

Table 4.4 Results of GLMQAP analyses of co-occurrence and interaction networks.

Predictor	Response	Estimate	SE	*P*-value[a]
Maternal kinship	Co-occurrence	3.54	0.48	**<0.001**
	Surfacing	6.40	0.45	**<0.001**
	Contact	7.49	0.61	**<0.001**
Age similarity	Co-occurrence	0.02	0.01	0.068
	Surfacing	0.04	0.01	**0.010**
	Contact	0.09	0.02	**<0.001**
Sex similarity	Co-occurrence	0.14	0.11	0.183
	Surfacing	0.67	0.18	**0.008**
	Contact	1.21	0.22	**<0.001**

a. Reported *p*-values derived from 10,000 randomizations.

4.4 Discussion

The analysis of animal social structure is always influenced by the choice of which behaviours constitute a social connection between individuals. In cetaceans, social analyses are almost exclusively based on observations of surface behaviour, using either associations or synchronous surfacing, with the relationship between surface and underwater behaviour rarely investigated. In this study, we analysed networks derived from surface and underwater interactions, as observed from an aerial platform.

Both surfacing and physical contact interaction networks were significantly different from null expectations given the patterns of association for all metrics used. This suggests that analyses of social structure using associations may be somewhat misleading with respect to interaction patterns. Specifically, association patterns may overestimate the degree of clustering and density of the true interaction networks, and underestimate both the overall degree of relationship differentiation, and the role of age and sex in structuring relationships. These and other potential issues with associations as a proxy for interactions have been extensively discussed in the methodological literature (Farine, 2015; Whitehead & Dufault, 1999; Carter, et al., 2015), and have been demonstrated empirically in terrestrial systems (Castles, et al., 2014), however these issues have rarely been empirically addressed in marine mammals. We note that, while there are important discrepancies in network structure between the interaction networks and co-occurrence patterns, all networks were significantly positively correlated. While interactions occur non-randomly between associates, association still provides the initial opportunity for interactions, and thus association rates still generally correlate with interaction rates. Together, these results indicate that although some association network properties may be misleading, associations are still useful in describing general patterns of affiliation in marine mammals, especially if data on interactions are not available.

Similarly, there are both similarities and differences between the structure of synchronous surfacing interactions, which can be measured using traditional surveying methods, and physical contacts. These networks were strongly positively correlated, but differed significantly in global network properties. These results suggest that surface-based observations are likely to provide useful information about other forms of affiliative interaction in this population, but may still underestimate the degree to which social relationships are individualized. Interestingly, while both interaction types were significantly positively correlated with age and sex similarity, the size of these effects were approximately twice as large in the contact network (Table 2).

Few previous studies have explicitly investigated how different behavioural definitions of social network edges effect inferences about the structure of affiliative relationships in cetaceans. Lusseau (2007) found no correlation between affiliative interactions and association rates in male Doubtful Sound bottlenose dolphins. In contrast, Leu et al., (2020) found that physical contact, sexual contact, synchronous surfacing, and association were all positively correlated in Shark Bay bottlenose dolphins, but there were differences in the patterns of centrality across age-sex classes. In both of these studies, boat-based photography and ad libitum behavioural observation were used to record associations and interactions between individuals. Our results show similar patterns to those reported by Leu et al., (2020), with all social networks being positively correlated, but with important differences in social network structure depending on edge definition.

Some cetacean social network studies have used extremely restricted definitions of association to quantify fine-scale social relationships, such as synchronous surfacing (Leu, et al., 2020; Dungan, et al., 2016; Hartman, et al., 2020). Our analysis suggests that, while other forms of affiliative behaviour are correlate with surface synchrony in resident killer whales, there are potentially important differences in the patterns of these interactions. Within J pod, physical contact interactions suggested individuals had fewer social partners (lower mean degree), more differentiated social relationships (higher disparity), and less transitive relationships (lower clustering coefficient) than in the synchronous surfacing network.

Previous studies have shown that maternal kinship plays a dominant role in determining association patterns in this and other killer whale populations (Bigg, et al., 1990; Esteban, et al., 2016), and our results confirm that maternal kinship shapes both association and interaction patterns in the southern resident population. Previous analyses of killer whale association networks tend to suggest no role of age or sex assortment in determining association patterns (Esteban, et al., 2016; Tavares, et al., 2017; Williams & Lusseau, 2006), despite apparent sexual segregation during foraging (Beerman, et al., 2016) and the occurrence of all-male groups during socialising (Rose, 1992). Our results agree with these findings, showing no assortment by age or sex in killer whale association patterns. Importantly, however, our analysis did demonstrate clear age and sex assortment in physical contact and synchronous surfacing patterns. This pattern suggests that maternal kinship drives association patterns, with age and sex having little influence, while interactions between associated individuals are determined in part by age and sex similarity. Interestingly, this mirrors findings in other coastal dolphin species, where assortment by age and sex appears to be a common feature of social network structure (Galezo, et al., 2018; Hawkins, et al., 2019; Lusseau & Newman, 2004).

There are several important extensions possible to the work reported here. In particular, networks derived from entire populations, rather than a single social group, may reveal more about these social systems. Of special interest in the killer whale system would be analyses focused on understanding which individuals may act as “social brokers” by maintaining relationships with individuals of other pods (Lusseau & Newman, 2004). Additional information could also be gained from refining the behavioural definitions used here, perhaps by separating out different forms of physical contact, or by including additional behaviours. Of particular interest for future studies would be the analysis of interactions with potential fitness consequences, such as food sharing (Wright, et al., 2016), and interactions with clear directionality, such as leader-follower interactions (Brent, et al., 2015). Our understanding of this social system may further be aided by analysing non-affiliative interactions, such as aggression and competition. Combining multiple forms of interaction to measure relationships, perhaps using a composite sociality index (Sapolsky, et al., 1997) or multi-layer networks (Silk, et al., 2018), may also be an important next step. Finally, as a potentially important benefit of analysing interactions rather than associations is the ability to measure differentiated relationships over a relatively short timescale, the observation methods we employ here have the potential to strengthen analyses of social network dynamics (Pinter-Wollman, et al., 2014). Importantly, these networks were derived from behaviours that, while often occurring below the surface, were still necessarily observed near the surface. Further work, perhaps in smaller species, could use animal borne devices to determine if patterns of proximity and synchrony are consistent when individuals are further below the surface.

These first three chapters have been concerned with various aspects of social network methodology in cetaceans, particularly the statistical comparison of social structure within and between networks, and the impact of data collection on inferences about social network structure. In the next two chapters, I will turn towards more applied questions. In Chapter 5, I use social network methodology to investigate the potential impacts of disease outbreaks in the southern resident killer whales, while in Chapter 6 I will use social network data to better understand the links between sociality, mortality, and reproduction in this population

Chapter 5

Modelling cetacean morbillivirus outbreaks in an endangered killer whale population

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Abstract

The emergence of novel diseases represents a major hurdle for the recovery of endangered populations, and in some cases may even present the threat of extinction. In recent years, epizootics of infectious diseases have emerged as a major threat to marine mammal populations, particularly group-living odontocetes. However, little research has explored the potential consequences of novel pathogens in endangered cetacean populations. Here, we present the first study predicting the spread of infectious disease over the social network of an entire free-ranging cetacean population, the southern resident killer whale community (SRKW). Utilizing 5 years of detailed data on close contacts between individuals, we build a fine-scale social network describing potential transmission pathways in this population. We then simulate the spread of cetacean morbillivirus (CeMV) over this network. Our analysis suggests that the SRKW population is highly vulnerable to CeMV. The majority of simulations resulted in unusual mortality events (UMEs), with mortality rates predicted to be at least twice the recorded maximum annual mortality. We find only limited evidence that this population's social structure inhibits disease spread. Vaccination is not likely to be an efficient strategy for reducing the likelihood of UMEs, with over 40 vaccinated individuals (>50% of the population) required to reduce the likelihood of UMEs below 5%. This analysis highlights the importance of modelling efforts in designing strategies to mitigate disease, and suggests that populations with strong social preferences and distinct social units may still be highly vulnerable to disease outbreaks.

5.1 Introduction

Infectious diseases, particularly novel pathogens emerging in naïve populations, can have severe consequences for animal populations (Daszak, et al., 2000). The consequences of these pathogens are exacerbated in small, endangered populations, where disease can contribute to elevated extinction risk (Pedersen, et al., 2007). The prediction of infectious disease outbreaks through epidemic modelling, and the subsequent design of mitigation strategies, is therefore a key task in endangered species management. Traditional epidemic models assume that contact rates are homogenous within a population (Allen, 2008). However, this is rarely the case. In populations that are strongly spatially or socially structured, these assumptions may hamper efforts to predict the severity and patterning of disease outbreaks.

Network-based models have been increasingly used for analyzing disease dynamics in animal populations, because they can incorporate spatial and social structure (Craft & Caillaud, 2011; Godfrey, 2013; Silk, et al., 2017). In social network models, social entities (i.e. individuals or groups) are represented as nodes in a graph, with the edges between nodes representing social connections and thus the opportunity for disease transmission. A great deal of research has modelled disease outbreaks over the social networks of terrestrial mammal populations, with the goals of predicting outbreak sizes, estimating temporal trends in susceptibility, and designing vaccination strategies (e.g. chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*): Carne et al., 2014; raccoons (*Procyon lotor*): Reynolds et al., 2015; Japanese macaque (*Macaca fuscata*): Romano et al., 2016; chimpanzees: Rushmore et al., 2014; African buffalo (*Syncerus caffer*): Cross et al., 2004; Verreaux's sifakas (*Propithecus verreaxi*): Springer et al., 2017; European badgers (*Meles meles*): Rozins & Silk et al., 2018). This work has highlighted the importance of considering non-random social structures in wildlife epidemic modelling, and has suggested a role for social structure in containing epidemics in natural populations.

Emergent infectious disease is of increasing concern for populations of cetaceans, many of which are already threatened or endangered (Gulland & Hall 2007; Van Bressem et al., 2009). Relatively little work, however, has been done modelling the disease consequences of cetacean social structure. Guiamares et al., (2007) modelled the spread of a hypothetical pathogen in a subnetwork of mammal eating killer whales (*Orcinus orca*), finding that the network was particularly vulnerable to disease outbreak. In this analysis, the dynamics of the simulation were not tuned to any particular pathogen. More recently, unweighted versions of networks derived from bottlenose dolphin populations (*Tursiops truncatus*) have been analyzed as part of comparative and theoretical studies (Sah et al., 2017; Sah et al., 2018). Importantly, no previous study has modelled the spread of specific pathogens over cetacean social networks with the goal of predicting the severity of outbreaks, and none have modelled the spread through a complete population.

Due to the logistical challenges of observing social interactions in wild cetaceans, the vast majority of cetacean social network studies are based on association indices, which estimate the probability that dyads associate in a given sampling period. Criteria for “association” are varied, but researchers typically set a temporal or spatial threshold at which two individuals are considered to be together. A mismatch between association criteria and disease transmission scales may have hampered previous epidemiological studies; most cetacean social network studies that use a spatial threshold define associations on broad scales, from 100 m (Lusseau, et al., 2006) up to 10 km (Foster, et al., 2012). While these association criteria are often justified when trying to understand the patterns of social relationships within a population, many pathogens of interest are typically transmitted over smaller spatial scales, e.g. when animals exchange viruses through the respiratory tract. This mismatch between contacts relevant to infection and network definitions may lead to incorrect inferences about the dynamics of disease outbreaks (Craft, 2015).

A pathogen of particular concern in gregarious cetacean species is cetacean morbillivirus (CeMV). CeMV is an RNA virus belonging to the family *Paramyxoviridae*, which also contains measles virus, phocine distemper virus, canine distemper virus, feline morbillivirus, and peste des petits ruminants virus (Afonso et al., 2016). CeMV is implicated as the cause of several unusual mortality events in wild cetaceans (Van Bressem et al., 1999; Di Guardo et al., 2005). This virus is highly infectious, with high potential for interspecies transmission (Jo et al., 2018) and is likely transmitted via the respiratory tract through the inhalation of aerosolized virus (Van Bressem et al., 2014). Several factors may increase a population's susceptibility to CeMV, including high polychlorinated biphenyl (PCB) load (Aguilar & Borrell 1994), poor nutrition (Aguilar & Raga 1993) and inbreeding (Valsecchi et al., 2003).

In this study, we use detailed social network data to model disease dynamics in an endangered killer whale population, the southern resident killer whales (SRKW). The SRKW population is an extremely small (less than 80 individuals), closed population of killer whales in the northeastern Pacific, frequenting the inland waters of Washington and British Columbia. This population faces long-term threats from a variety of environmental and anthropogenic factors. The three factors identified as primary hazards to this population are the decline in abundance and quality of their primary prey, Chinook salmon (*Oncorhynchus tshawytscha*), anthropogenic noise, and persistent organic pollutants (Lacy *et al.,* 2017). In addition, recent analysis of the respiratory microbiome of this population has highlighted pathogens as a potential fourth threat (Raverty et al., 2017). Previous analysis has emphasized CeMV as a pathogen in need of further study and monitoring in this population (Gaydos et al., 2004).

Killer whales are susceptible to CeMV infection; a killer whale that stranded in 2002 was found to be seropositive for CeMV antibodies, indicating recent exposure (Rowles et al., 2011). Morbillivirus epizootics have not yet been recorded in any killer whale population and the virus has not been detected in Pacific killer whales, but CeMV has high spillover potential from reservoirs into novel populations (Van Bressem et al., 2014). SRKWs have been observed interacting with other cetacean species which are known carriers of CeMV, including harbor porpoise (*Phocoena phocoena*), humpback whales (*Megaptera novaengliae*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), providing a potential pathway for the introduction of this pathogen into the population. In addition, many of the factors that are thought to increase a population's susceptibility to CeMV are present in the SRKW community, including high PCB load, inbreeding, and nutritional stress (Krahn et al., 2007; Ford et al., 2018; Ford et al., 2010).

The SRKW live in stable, multilevel social groups, and individuals form distinct social clusters (Bigg, et al., 1990; Ellis, et al., 2017; Parsons, et al., 2009). The smallest, most stable social unit is the matriline, composed of females and their descendants, which usually contain 2-9 whales. Closely related matrilines form pods that may contain over 40 individuals and exhibit distinct vocal dialects. The southern resident community contains 3 pods, referred to as J, K, and L (Bigg, et al., 1990). This social organization creates a modular social network structure, although the implications of this multilevel social structure for disease transmission in this population has yet to be established.

Modular networks have been hypothesized to provide fitness benefits to social species by trapping disease within modules and preventing large-scale epidemics. Simulation studies predict that modular contact networks result in smaller disease outbreaks than non-modular networks (Nunn et al., 2015; Sah et al., 2017; Rozins & Silk et al., 2018). Recent comparative work has suggested that network subgrouping may decrease outbreak size and epidemic probability, dependent on the characteristics of the disease and strength of the subdivisions (Sah et al., 2018). An analysis of parasite load in primate social groups supports the hypothesis that modular organization inhibits disease spread, with individuals in more modular groups generally having lower parasite load (Griffin & Nunn, 2012). In addition, the presence of pronounced social preferences may itself aid in preventing disease spread. Strong social preferences result in increased variance in edge weights (Whitehead, 2008), and social networks with greater variance in edge weight are predicted to generally experience smaller outbreaks of infectious disease (Yang & Zhou 2012; Wang et al., 2014). It is currently unclear if the modular structure and strong social preferences of the SRKW community are capable of significantly reducing disease spread. Previous work in a closely related species with a similar social structure, the long-finned pilot whale (*Globicephala melas*), demonstrated that increased mortality after a CeMV epizootic was limited to a subset of social groups (Wierucka, et al., 2014), potentially indicating that modular social structures can effectively trap this disease.

Recently, there has been growing interest in applying individualized medical treatment to the SRKW population (e.g. Gaydos et al., 2019), following the model of wildlife veterinary care that has been applied in terrestrial systems such as mountain gorillas (Robbins et al., 2011). Such individualized care may include prophylactic vaccination strategies. Although no morbillivirus vaccine is proven to be effective in any cetacean species, a DNA vaccine for CeMV has been tested in bottlenose dolphins (Vaughan et al., 2007) and recent genomic studies could further inform the development of new vaccines (Batley et al., 2018). Logistical challenges and ethical considerations, however, may preclude vaccinations on a large scale in wild populations. Nonetheless, network-based vaccination strategies to mitigate morbillivirus spread have been successfully implemented in another endangered marine mammal, the Hawaiian monk seal (*Monachus schauinslandi*; Robinson et al., 2018). Furthermore, herd immunity is thought to be more easily induced in modular social networks, as individuals that bridge communities can be targeted for vaccination, preventing global disease spread (Salathe & Jones 2010). It is currently unclear whether vaccinating a realistic portion of the SRKW population would be effective at preventing epizootics.

Here, we use five years of detailed, fine-scale association data to inform a stochastic, network-based model of pathogen spread through the SRKW population. We focus on simulating the epidemic characteristics of cetacean morbillivirus based on previously published research, given its role in mass mortality in other populations and the risk it poses to the SRKW. We further use null models of the social network to determine the role that social structure has in shaping disease outbreaks. Finally, we simulate both random and network-based vaccination strategies to determine if prophylactic treatment could efficiently mitigate epizootics in this population.

5.2 Methods

5.2.a Field observations

Social associations were recorded over five years (2011-2015) of opportunistic photographic identification surveys in the inland waters of Washington and British

Columbia conducted by the Center for Whale Research (CWR). The purpose of these surveys was both to capture clear images of every whale present during each encounter and to acquire photographs that could be used for assessment of body condition and social affiliations. As the SRKW are protected by federal law in both the United States and Canada, all field work was carried out under federal permits issued by both countries (NMFS 15569; DFO SARA 272). Surfacing whales were photographed using Canon or Nikon DSLR cameras. Encounters only occurred on days when clear photographic identification was possible (i.e. no rain and sea state less than Beaufort 4). As the CWR has been conducting annual surveys of the SRKW population since 1976, all individuals in this population are well known. Individuals are easily identifiable throughout their lives by unique pigmentation patterns behind their dorsal fins ("saddle patches"), as well as by dorsal fin shape, knicks, and scars they acquire throughout their lives (Bigg, et al., 1990). Surveys were typically conducted from small motorized vessels (5.5 m Boston Whaler), although shore-based photographs of sufficient quality to identify individuals and associations were also analyzed. Only in-focus, clear photograph sequences in which all individuals were identifiable were analysed. Photographs were managed and analysed using ACDSee Photo Studio.

5.2.b Social network construction

As CeMV is thought to be contracted primarily through the inhalation of aerosolized virus, our contact network was constructed to reflect close surface associations, with the goal of estimating the frequency of "respiratory contact" between dyads. While much is still unknown about the transmission dynamics of CeMV, including how long the virus remains infectious in the air after exhalation, we chose a restricted association criteria to ensure that our estimates of disease spread were conservative. Therefore, we considered individuals surfacing synchronously or successively within one body length to be in respiratory contact. Synchronous and successive surfacings were recorded from photographic series capturing surfacing sequences. A surfacing was considered successive or synchronous when an individual began surfacing before the previous individual became completely submerged (Figure 5.2a).

Individuals and social groups within the SRKW population differ in their use of the study area, and were not continuously followed. Therefore, we are unable to directly estimate the total number of contact events between individuals. Instead, we estimate the probability that each dyad came into contact on a given day. We estimated daily respiratory contact probabilities by calculating dyadic simple ratio indices (SRI) (Cairns & Schwager, 1987):

$$\mathrm{SRI}_{ij} = \frac{X_{ij}}{D_{ij}} \tag{1}$$

where X_{ij} is the number of days in which individual i was photographed in respiratory contact with individual j, and D_{ij} is the total number of days on which either i or j were photographed. SRI values represent an estimated daily association probability, and thus range from 0 to 1, with zero indicating individuals were never observed in respiratory contact, while 1 indicates individuals were observed in respiratory contact on every day that either was observed. Many cetacean network studies use a half-weight index (HWI) to correct for biases in data collection, namely that individuals are often more likely to be seen apart than together. However, in line with our goal of being conservative in our estimates of disease spread, we chose to use SRI, as a dyad’s SRI value will always be less than or equal to the same dyad’s HWI value.

During surveys, the primary objective was to photograph all whales present, with secondary goals of recording social groupings and assessing the health of individuals. Groups of whales could not be continually followed for all hours of the day, and it was therefore not possible to quantify the amount of time associated dyads spend together on a given day. Moreover, not all individuals could be simultaneously monitored and surveys were likely to miss surface associations. Therefore, our SRI values are prone to underestimating daily contact probabilities, which may lead to overly-conservative estimates of disease outcomes.

We limit our dataset to sampling days occurring in the summer months (May to September) of each year. This is the period in which the southern residents are most frequently in the study area as they follow returning Chinook salmon runs, and therefore provides the most detailed data on association patterns. Movement patterns of the SRKW change significantly during the winter, and it is therefore unclear to what degree contact rates during the summer reflect winter contacts. While some aspects of SRKW social structure change over longer time-scales, relationships are consistently structured by pod and matriline, and changes are not predictable (Parsons, et al., 2009). Therefore, we aggregate association data across the entire study period, as this aggregation allows for more precise estimates of dyadic contact probabilities (Whitehead, 2008). In order to avoid biases in estimated contact probabilities due to the births and deaths of individuals, only individuals that were alive for the entire study period were included in our analysis.

To confirm the suitability of this approach, we compared all pairs of networks derived from each year of data collection by calculating the Spearman correlation coefficient between dyadic SRI values across the two years, with Mantel tests with 1,000 permutations to assess statistical significance of the correlations (Hobson et al., 2013).

We also tested for seasonal changes within the summer months by constructing aggregated networks for each study month (May-September) across all years and carrying out the same comparison procedure described above.

While the aggregation of several years of data allows for more precise estimates of contact probabilities, it also presents the potential for increasing the density (i.e. number of edges) in our simulated networks relative to the empirical annual contact patterns. Overestimating the density of contact networks can lead to overestimation of disease spread in epidemiological simulations (Risau-Gusman 2011). We carry out a simulation study to confirm that simulations based on the aggregated network do not result in higher density networks than would be expected for a single year of associations. For each year, we simulate associations for each dyad from a binomial distribution, using the observed annual dyadic sampling effort (D_{ij} in eq. 1) as the sample size and the aggregated SRI value as the probability of success. The expected mean annual density is then calculated from these simulated networks. We carry out this procedure 10,000 times to build a distribution of mean densities for our simulations, which is then compared to the mean density of the observed annual networks. If aggregation results in increased density, the observed mean density would be significantly lower than the simulated mean densities.

SRI networks were constructed in R (R Core Team, 2020) using the asnipe package (Farine 2018) and custom code, and the vegan package was used to conduct Mantel tests (Oksanen, et al., 2019).

5.2.c Network metrics

To evaluate the precision of our social network, we estimated the correlation between our measured association indices and the underlying association probabilities. We first calculate the coefficient of variation (CV) of our observed SRI values, and then estimate the CV of the underlying association probabilities (*S*) via maximum likelihood, assuming the underlying associations follow a beta distribution. The ratio of *S* to the observed CV is an estimate of the portion of variance in SRI values that is accounted for by the variance in association probabilities, rather than sampling variance, and therefore approximates the correlation between true and observed association indices. Correlations greater than 0.4 are generally considered to indicate useful representations of the underlying social structure (Whitehead, 2008). Parameter fitting was performed in R, using the VGAM package for beta-binomial likelihood calculation (Yee 2018).

We measure the extent to which individuals formed subgroups by performing community detection on the contact network. We use a walktrap community detection algorithm implemented in the igraph R package to detect communities (Csardi & Nepusz 2006). The modularity of the community division found by this algorithm is a network-level measure of how strongly individuals associate within rather than across social clusters.

5.2.d Temporal independence of respiratory contacts

A key assumption of our disease transmission model (see below) is that the probability of a dyad coming into respiratory contact on a given day is constant, and therefore independent of contacts in previous days. Biologically, this would indicate that contacts dissolve and reform within a single day according to constant contact probabilities, leading to temporal independence of associations.

We test this assumption by calculating the lagged association rate (LAR) across several time-lags in our dataset. The LAR at time-lag τ estimates the probability that a dyad associated in a given day will also be associating τ days later. Most analyses of LAR analyze extremely large values of τ (i.e. over 1,000 days) in order to investigate the long-term temporal structure of associations. However, as we are interested in transmission dynamics over considerably shorter timescales (see below), we only investigate LARs for values of τ from 1 to 20 days.

Whitehead (1995) suggests comparing LARs to null association rates that represent the expected patterns if individuals associated randomly. As our model does not assume random mixing, but rather temporal independence, we use an alternative null association rate that approximates the expected LAR if associations dissolve and reform between each sampling period with a constant probability of association for each dyad. Let a_{ij} be the probability of an association between individuals i and j in each sampling period (approximated by SRI_{ij}). The probability that i and j associate twice in any two sampling periods, given independence, is then a_{ij}^2. The expected LAR across all time-lags under temporal independence (LAR_{null}) is then:

$$\mathrm{LAR}_{null} = \frac{\sum_i \sum_j a_{ij}^2}{\sum_i \sum_j a_{ij}} \qquad (2)$$

We calculated 95% confidence intervals for LARs at each τ using jackknife resampling (Whitehead 1995). LAR_{null} represents our null hypothesis of temporal independence, and we rejected this null hypothesis at a given τ if the 95% confidence interval of the LAR at τ did not include LAR_{null}. All temporal analyses were performed using custom R code.

5.2.e Disease outbreak model

We simulate the spread of CeMV using a stochastic individual-based susceptible-infected-removed (SIR) model over the killer whale respiratory contact network. Note that in SIR models, there is no difference between dead and recovered, immune individuals; they are removed from the population and cannot become infected again or spread the pathogen to others. While this framework is potentially overly simplistic for some pathogens, recovery from CeMV confers life-long immunity and the virus has no carrier state, meeting the basic assumptions of an SIR model (Van Bressem et al., 2014).

The model simulates a situation in which an interaction with a CeMV infected individual of another species (e.g. Pacific white-sided dolphin, humpback whale, harbor porpoise) leads to the introduction of the disease to the SRKW population via a single seed individual. Interspecific interactions are rarely observed, and therefore we assume no further interspecific transmission after the initial introduction. As CeMV has not been detected in this population in over 40 years of observations, all non-infected individuals start as susceptible. Each time-step in the model represents a single day. We therefore model the probability that an infected individual j transmits the disease to a susceptible individual i at time t (λ_{tij}) as the joint probability that i and j come into contact on that day and that a given contact effectively transmits the disease. As the fine-scale transmission dynamics of CeMV have not been resolved, we make the simplifying assumption that for each day a susceptible individual is exposed to an infected individual, there is a constant probability of transmission. We further simplify the model by assuming that daily contacts are independent of one another. We use our estimated SRI values to approximate daily contact probabilities, and so

$$\lambda_{tij} = \beta \cdot \mathrm{SRI}_{ij} \cdot I_{tj} \tag{3}$$

where β is the transmission coefficient, representing the per-contact probability of transmission, and I_{tj} is an indicator variable that takes the value of 1 if *j* is infected at time *t*, and 0 otherwise. The probability that susceptible individual *i* will become infected during timestep *t* (T_{ti}) is then

$$T_{ti} = 1 - \prod_j \left(1 - \lambda_{tij} \right) \tag{4}$$

The probability that individuals already infected at the beginning of timestep *t* will be removed by timestep *t*+1 is denoted by α (mean infectious period = 1/α). Individuals that become infected during *t* cannot infect others or be removed until timestep *t*+1. The model run is terminated when there are no infected individuals left, or until the time limit is reached. We limit the number of daily time-steps to 150, as our dataset represents association patterns during a five-month period of the year. We do not include non-pathogen induced baseline mortality in the model, as mortality rates over a single 5-month period would be too low to have a significant impact on model predictions. The disease simulation model was coded in R.

5.2.f Model parameters and output

The outcome of our model is influenced by the removal probability α, and the transmission coefficient β. We therefore sought to estimate values of these parameters that most closely resemble those of previous CeMV outbreaks in wild odontocetes. In the absence of data on CeMV outbreaks in killer whale populations, we estimate the likely range of epidemic parameters of CeMV from previously published epidemic modelling and social network studies of western Atlantic bottlenose dolphins. We note that CeMV strains vary in their epidemiology, and that there are likely differences in recovery rates and infectiousness between host species (Jo et al., 2018). The derived parameter values should therefore be viewed as rough estimates based on the best available knowledge.

Morris *et al.,* (2015) estimated a reproductive ratio for CeMV (the average number of secondary cases expected from a single infected individual, R) of 2.58 during the peak of an epidemic (95% CI = 2.08-3.17) and a removal rate of 0.12 (95% CI = 0.1-0.14). While the overall rate at which infected individuals infect others was estimated in this analysis, this study did not estimate a per-contact transmission probability.

To estimate the per-contact transmission probability of CeMV during this previously observed epidemic, we use a social network study carried out by Titcomb et al., (2015) on a subpopulation of western Atlantic bottlenose dolphins in the Indian River Lagoon to estimate the mean strength $\langle s \rangle$ of association networks in this population. This study is the only large-scale social network study we are aware of in this species that uses the same daily sampling period as our analysis, and spatially overlaps the CeMV outbreak from which the other epidemic parameters were derived. This study reports a mean weighted degree in the dolphin social network of 1.88 (95% CI = 1.63-2.13). We note that this study defined associations over broader spatial scales than our analysis (100 m) and HWI was used, rather than SRI. These factors are likely to produce estimates of $\langle s \rangle$ larger than our methodology, potentially leading to an underestimation of the transmission coefficient for CeMV and making our estimates of CeMV spread conservative.

For each set of simulations, we generate a set of α, $\langle s \rangle$, R_0, and seed individuals via Latin hypercube sampling using the “lhs” R package (Carnell 2019). This sampling technique allows for a more efficient exploration of the entire parameter space than sampling each variable independently (Seaholm et al., 1988). Parameter values for α, $\langle s \rangle$, and R_0 were drawn from continuous uniform distributions with ranges equal to their reported 95% confidence intervals, while the seed individual is draw from a discrete uniform distribution on [1, *N*], where *N* is the total number of individuals in the network (Table 5.1). We then calculate β for each parameter set using a simple estimate of the reproductive ratio for epidemics on weighted graphs (Kamp *et al.,* 2013):

$$R_0 = \frac{\beta \langle s \rangle}{\alpha} \tag{5}$$

which can be re-arranged to

$$\beta = \frac{R_0 \alpha}{\langle s \rangle} \tag{6}$$

Our baseline simulation to assess overall vulnerability of the network consisted of 100,000 model runs. We evaluate the outcome of the model first by calculating the probability that an outbreak results in an “unusual mortality event” (UME; Gulland & Hall 2007). We use a simple heuristic to define UMEs, and say a UME has occurred when a simulation results in predicted mortality at least 2x higher than the highest recorded annual mortality rate in this population, which was 8.24% in 2016. Therefore, our definition of a simulated UME was a simulation in which at least 16.47% of the population is predicted to die. While the mortality rate of CeMV infected cetaceans is not known, individuals infected with viruses of this family tend to exhibit mortality rates of 70% - 80% (Diallo et al., 2007). We therefore assume that mortality rates due to CeMV were 70% of the final outbreak size, and thus our threshold outbreak size for UMEs was 23.53% of the population infected. While we use this threshold in the rest of the text, our general results were robust to alterations to this heuristic. We also calculated the mean and standard deviation of the outbreak size (the proportion of the population infected) during runs in which UMEs occurred as a measure of predicted UME severity.

We also conducted a sensitivity analysis to determine which of our two parameters, α and β, was most influential on the outcome of our simulation. We did this by calculating partial Spearman rank correlation coefficients for the final outbreak sizes of our 100,000 model runs and their respective values of these two parameters (Wu et al., 2013). Higher absolute values of these coefficients indicate a greater amount of variance in the outcome of the simulation being due to variance in the parameter of interest, controlling for other parameters.

Table 5.1 Parameters and values used for disease simulations. All parameter ranges were derived from studies of social interactions and CeMV epizootics in western Atlantic *T. truncatus.*

Parameter	Interpretation	Value	Source
α	Probability of removal per day	0.10 – 0.14	Morris *et al.* 2015
1/ α	Mean infectious period	7.14-10.00	Morris *et al.* 2015
R_0	Mean number of secondary cases per infected individual during an outbreak	2.08 – 3.17	Morris *et al.* 2015
$\langle s \rangle$	Mean number of contacts per individual per day	1.63 – 2.13	Titcomb *et al.* 2015
β	Per-contact transmission probability	$\frac{R_0\alpha}{\langle s \rangle}$	Kamp *et al.* 2013

5.2.g *Influence of social structure on disease outbreaks*

We next sought to determine the extent to which the structure of SRKW social relationships shapes disease spread. We do this by performing simulations of disease outbreaks on two null models. The first is a mean-field null model, in which all contact probabilities between individuals are set to the mean contact probability in the observed network. This model simulates a population that associates entirely at random, and is therefore equivalent to traditional epidemic models that assume random mixing. The second null model is an edge randomization, in which observed edge weights are randomly shuffled between dyads. This retains the heterogeneity of social preferences, but removes the higher-order structure of the network. In both null models, the mean strength (i.e. an individual's average contacts per time step) from the observed network is retained.

We carry out the same simulation procedure outlined above on the null-model networks, and examine the influence of network structure on disease dynamics by comparing the UME probability and mean UME size between the observed network and the two null models.

5.2.h Effectiveness of vaccination

We next investigated whether a prophylactic vaccination strategy would be effective in this population. We simulate the implementation of three potential vaccination strategies. The first is a random vaccination, in which *V* randomly chosen individuals are set as removed prior to the start of the simulated outbreak. The other two strategies are both based on individuals' centrality in the network. In many networks, targeting vaccinations towards individuals with high weighted degree is the most effective strategy to induce herd immunity (Rushmore et al., 2014), however in networks with community structure, targeting high betweenness individuals that bridge communities is sometimes more effective (Salathe & Jones 2010). We simulate scenarios in which individuals are targeted either based on their weighted degree or weighted betweenness. In both scenarios, the *V* individuals with the highest centrality are set as removed prior to the start of the simulation.

We evaluate vaccination effectiveness relative to a “conservative coverage threshold” (Rushmore *et al.,* 2014). We therefore define an effective vaccination coverage when UMEs do not occur in 95% of simulations. We simulate values of *V* from 1 to 50 (coverage of 1%-70%), with 50,000 simulations for each value of *V* and each vaccination strategy. We stress that safely vaccinating 50 free-ranging killer whales is most likely an unrealistic management goal, even if a safe and effective CeMV vaccine is developed for this species. Nonetheless, we simulate these high values to better illustrate the degree to which vaccination may be effective in this population.

5.3 Results

5.3.a Respiratory contact structure

The final respiratory contact network contained a total of 72 individuals sighted over the course of 314 days of observation. All individuals were photographed on at least 30 different days throughout the study period, with a median of 82 days per individual. Estimation of social differentiation and subsequent comparison to the observed CV suggested a highly differentiated social structure and a good correlation between our observed network and the true underlying association probabilities (S = 1.50, r = 0.70).

All pairs of yearly networks were significantly positively correlated (range of r values= 0.41-0.58, all $p < 0.001$), as were monthly networks (range of r values = 0.38-0.56, all $p < 0.001$). We therefore conclude that there is no evidence for significant changes in the patterns of social relationships within the summer months during our study period, nor was there evidence that social structure shifted significantly across the 5 years of the study. The mean density of annual networks was not different from the expected density given aggregated SRI values and sampling effort (Figure 5.1).

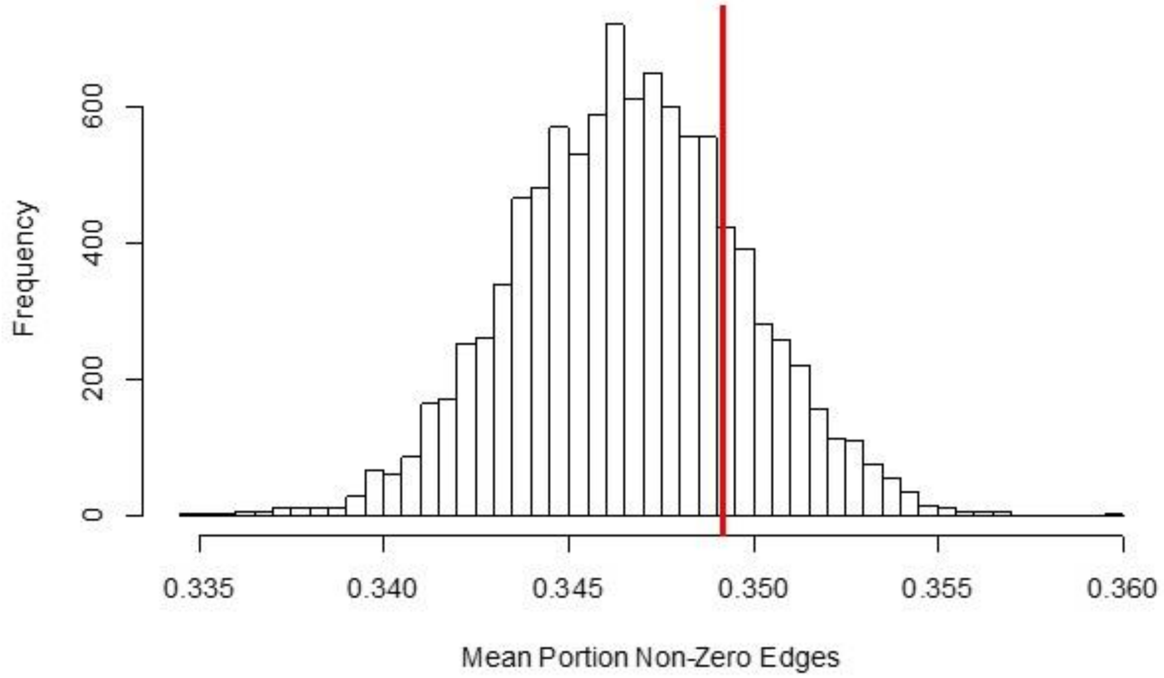

Figure 5.1 Results of simulation comparing density of annual networks to aggregated network. Histogram represents the mean density of annual networks simulated from the aggregated contact probabilities and yearly dyadic sampling effort. Red line indicates the observed mean density of annual networks.

The aggregated SRKW respiratory contact network formed a single, highly connected component (Figure 5.2b). Over 70% of dyads had a non-zero contact probability during the study period. Non-zero edge weights ranged from 0.005 to 0.62, with the mean contact probability over all dyads being 0.03 (median = 0.01, IQR = 0.03).

In agreement with previous studies (Ellis, et al., 2017; Parsons, et al., 2009), the network was distinctly modular (*Q* = 0.52) and was divided into six social clusters. All but one cluster contained members of a single pod, the exception being J pod’s cluster, which contained individual L87, an adult male that has frequently changed social affiliation since his mother's death in 2005 and has travelled with J pod since 2010 (Center for Whale Research 2018). L pod showed the most significant sub-pod structure, with three identified social clusters. In contrast, J pod formed a single, large cluster (Figure 5.2).

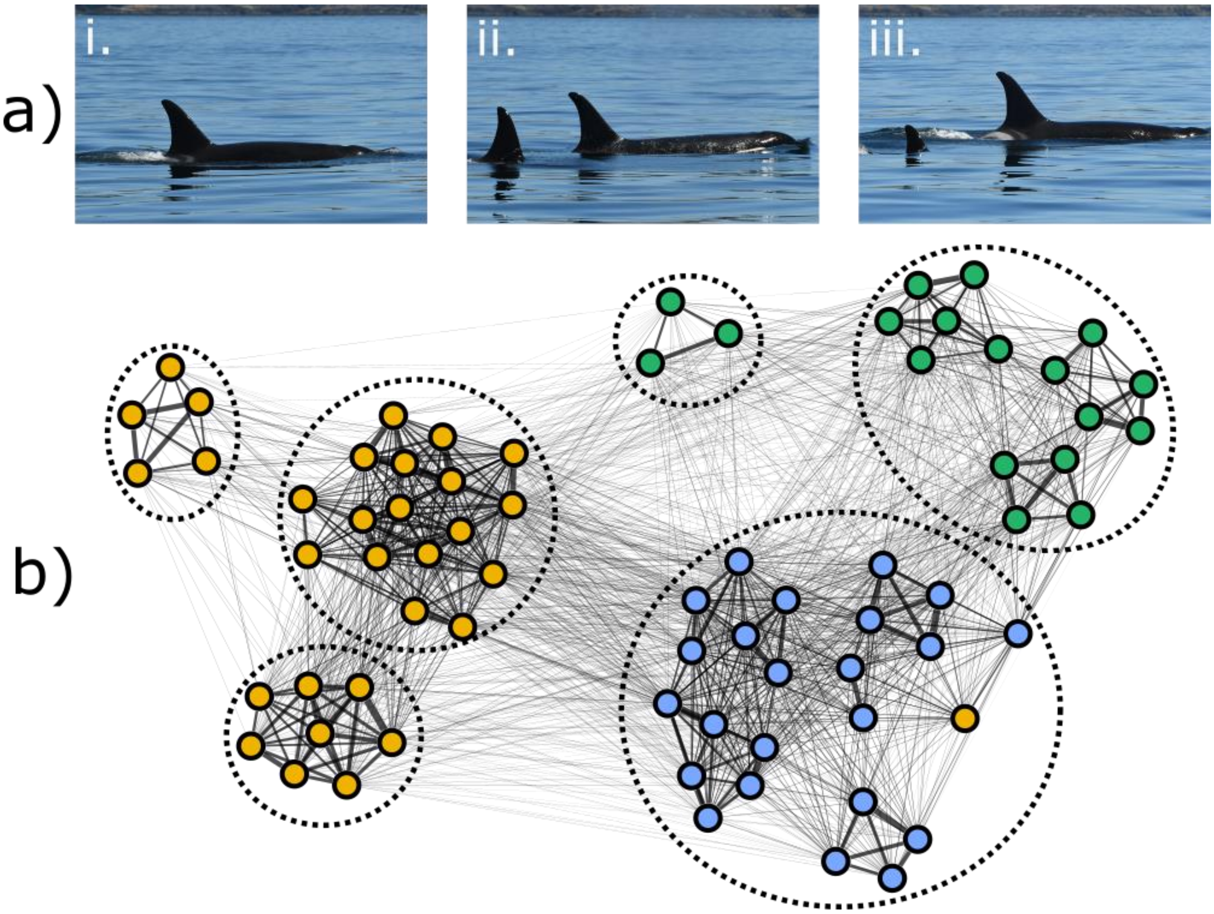

Figure 5.2 Respiratory contacts in the southern resident killer whale population. a) Example photographic sequence of a successive surfacing between two individuals (J42 and J16). Individual J42 is identifiable from her saddle patch in (i), and as J42 begins to submerge in (ii), individual J16 begins surfacing within one body length. In (iii), J16 is fully identifiable. b) Final respiratory contact network for the population from 2011 to 2015. Edge thickness corresponds to estimated daily probabilities of respiratory contact. Node colours indicate pod membership (blue = J, green = K, orange = L) and dotted lines indicate clusters found by walktrap community detection algorithm.

Analysis of lagged association rates showed that the temporal patterns of association in the observed data are largely similar to the expected patterns under temporal independence, given the observed association preferences. While the LAR is typically slightly above the expected LAR, jackknifed 95% confidence intervals overlap LAR_{null} (Figure 5.3). We conclude that our model's assumption of temporal independence is unlikely to significantly bias the results of our simulations.

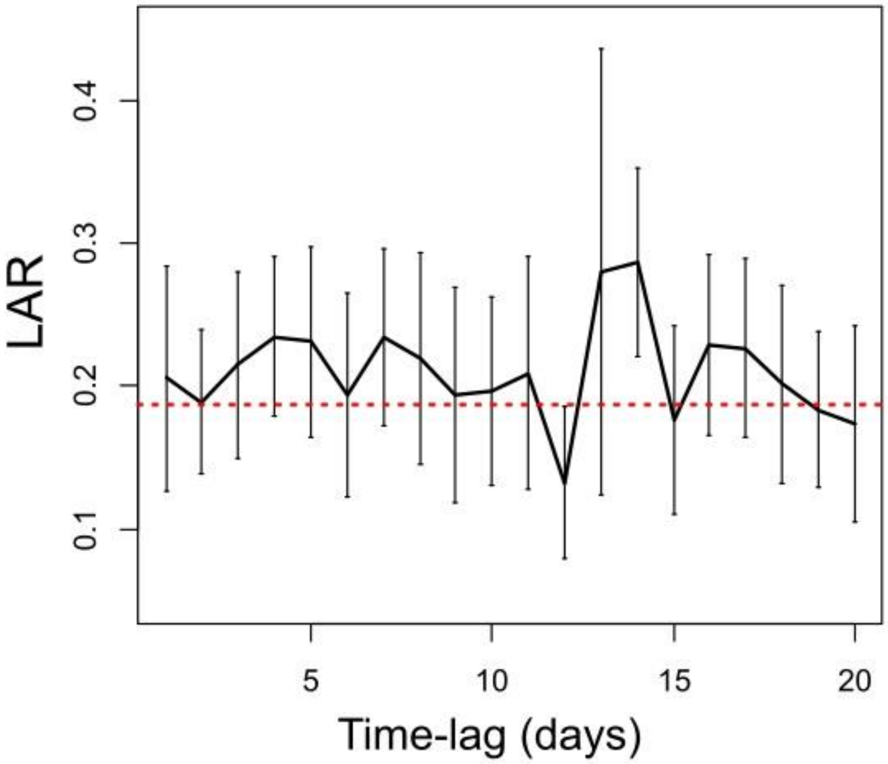

Figure 5.3 Lagged association rates of respiratory contacts. Black line is the calculated LAR at each daily time-lag, with error bars indicating jackknifed 95% confidence intervals. Dotted red line indicates the expected LAR under temporal independence, given the observed association preferences (as in equation 2).

5.3.b Simulated disease outbreaks

As expected, the outcome of the baseline simulation showed distinct bimodality; the disease either failed to spread far beyond the initially infected individual, or most of the population became infected. The network was extremely susceptible to simulated CeMV outbreaks (Figure 5.4). The majority of simulations resulted in unusual mortality events (UME probability = 0.69). When UMEs occurred, the disease typically infected around 90% of the population (mean UME size = 0.89, SD = 0.09).

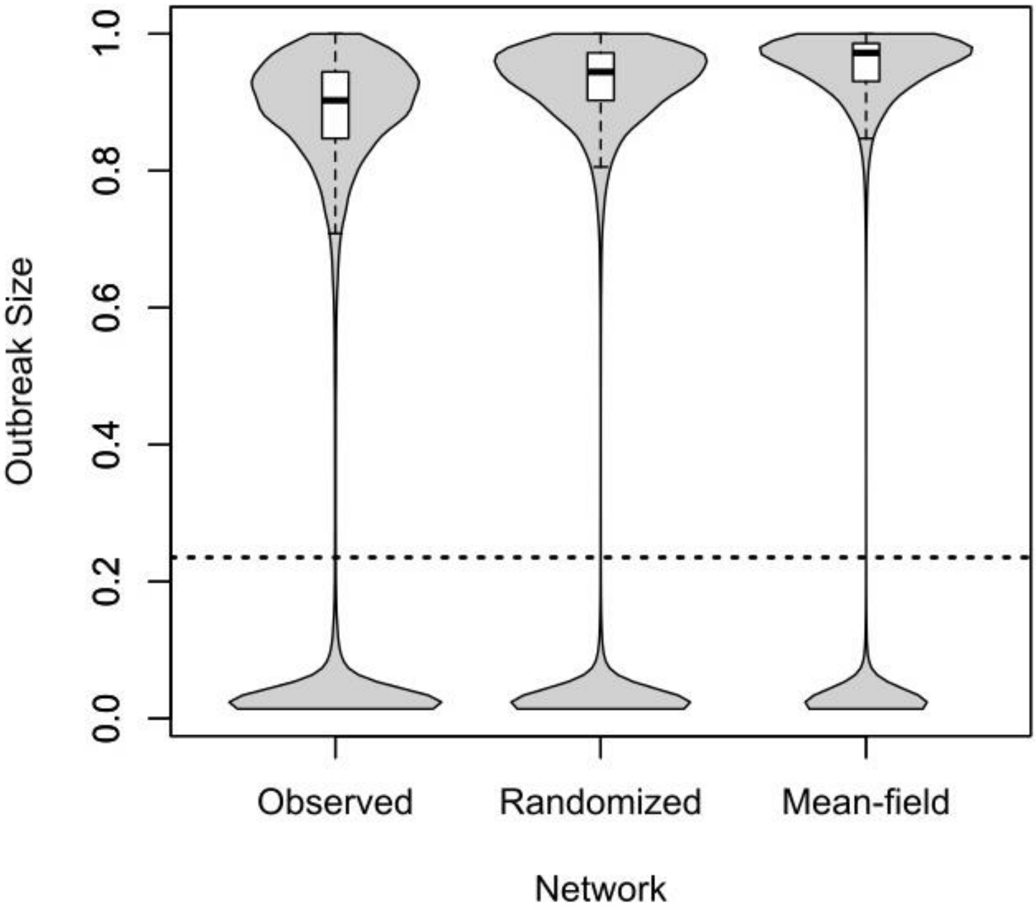

Figure 5.4 Distribution of disease outcomes in the observed network and two null models. Violin plots indicate the density of disease outcomes (in proportion of the population infected). Dotted line indicates our threshold for an unusual mortality event. Boxplots indicate quantiles for the runs in which the epidemic resulted in a UME.

Sensitivity analysis using partial correlation coefficients suggested that the outcome of our model was more sensitive to variation in the per-contact transmission rate than the recovery rate. The partial rank correlation between outbreak size and transmission rate was 0.33, while the correlation with removal rate was -0.18. This is not surprising, as our values of the removal rate were based on the results of explicit epidemic modelling, while our estimates of the transmission rate were derived from a combination of previously reported epidemic parameters and social network metrics. The uncertainty in our estimates of the transmission rate therefore incorporate the uncertainty in recovery rate, basic reproductive number, and contact rates. While our range of recovery rates was 0.1 to 0.14, our final values of the transmission rate ranged from 0.1 to 0.27. This result highlights the need for further studies into the transmission dynamics of CeMV to inform modelling and management efforts. We note, however, that our estimates for the per-contact transmission rate of CeMV are highly conservative compared to the known transmission rates of other morbilliviruses (e.g. the 90% transmission rate found in measles; Hamborsky et al., 2015).

5.3.c Influence of social structure on disease outbreaks

Comparison of results of simulations on the observed network to the two null models revealed that the structuring of contacts in the observed network provided limited protection from disease outbreaks (Figure 5.4). While UME probability was larger in the null models, the changes in UME probability were small (mean-field UME probability = 0.74; edge-randomized UME probability = 0.72). Similarly, the size of UMEs was slightly larger in both null models (mean-field: mean = 0.95, SD = 0.05; edge-randomized: mean = 0.93, SD = 0.06). In terms of number of individuals infected during UMEs, these differences amount to an average increase of 3 individuals in the edge-randomized model, and 5 individuals in the mean-field model. While these results suggest that both the strength and patterning of social preferences may lead to measurable reductions in epidemic probability and size, they also clearly demonstrate that these effects are likely not significant from the perspective of conservation planning in this population.

5.3.d Effectiveness of vaccinations

Our network measures used to design vaccination strategies, weighted degree and betweenness, were not strongly correlated (Spearman's $r = 0.24$), indicating that there would be significant differences between vaccination strategies based on these measures. Both targeted vaccination strategies performed better than the random vaccination strategy at reducing the probability of outbreaks, and both targeted strategies performed similarly to one another (Figure 5.5). However, the differences in conservative coverage thresholds were modest. Given random vaccination, 45 individuals (62.5% coverage) were required to reduce UME probability below 0.05, compared to 40 individuals (55.6% coverage) in the betweenness strategy and 42 individuals (58.3% coverage) in the weighted degree strategy.

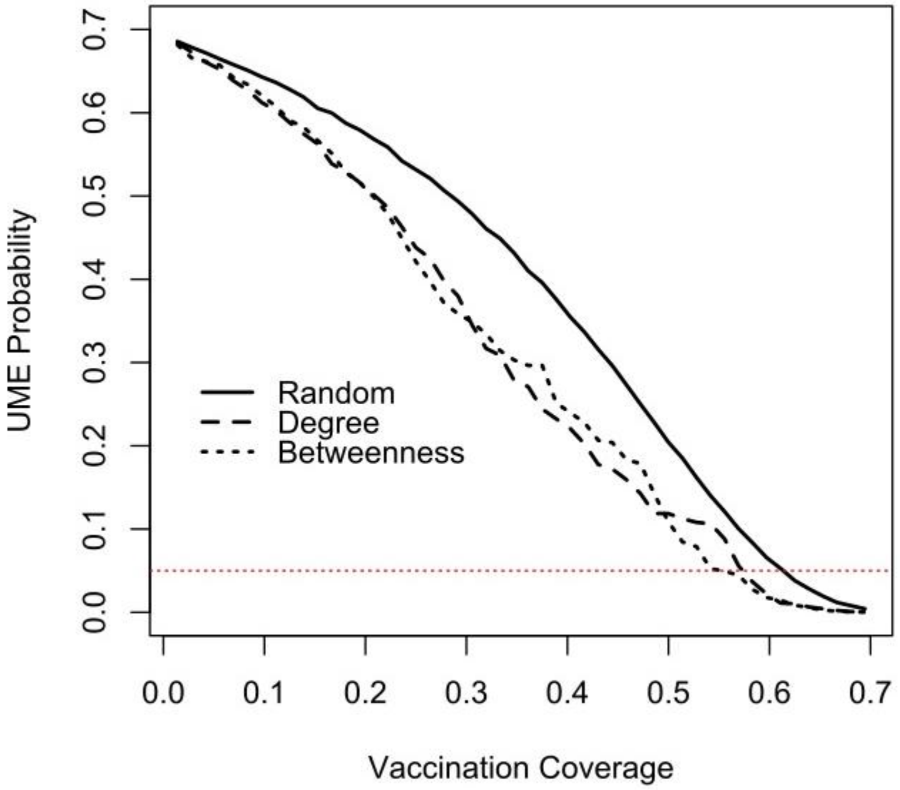

Figure 5.5 Results of simulated vaccination strategies. Lines indicate UME probability for each vaccination strategy (solid = random, dashed = weighted degree, dotted = betweenness) under different levels of coverage. Red dotted line indicates our conservative vaccination target, at which UMEs are predicted to occur in less than 5% of cases.

5.4 Discussion

In this study, we assessed the vulnerability of a critically endangered killer whale population to outbreaks of an infectious disease that has previously been identified as a potential hazard. In our analysis, designed to replicate the observed properties of cetacean morbillivirus, most simulations resulted in outbreaks that would likely result in unusual mortality events, and in these cases nearly the entirety of the population became infected. Our results further suggest that the social structure of this population offers only limited protection from disease outbreaks, and that vaccination programmes, even with relatively high coverage and ideal targeting of individuals, are unlikely to efficiently reduce the risk of outbreaks. Given its fragile state, it is unlikely that this population would recover from the sudden increase in mortality that would result from a majority of the population becoming infected with CeMV. While this model was specifically parameterized to simulate the spread of CeMV, the general vulnerability suggested by this analysis is likely to be applicable to other highly infectious pathogens that can be spread via aerosols.

Theoretical models and comparative studies suggest that subgrouping in social networks reduces the risk of disease spread (Griffin & Nunn 2012; Sah et al., 2018). Our findings generally support this result, with the important caveat that the protection provided seems unlikely to be significant in a conservation context for this population. This agrees with recent simulation experiments suggesting that disease spread is only significantly inhibited at extreme modularity values, and that network fragmentation may be more important than modularity (Sah et al., 2017). We suggest that this lack of significant protection is due to the sheer density of connections in the killer whale network; while there were clear preferences for associating within clusters, associations across clusters were still common. In addition, modular structures are predicted to be most effective at trapping disease with low transmissibility (Sah et al., 2018). Social structure may therefore be less effective at trapping pathogens such as morbilliviruses, which are highly transmissible.

Both the distribution of contact probabilities and the degree of subgrouping had small but measurable effects on the outcomes of simulated epidemics. The effect of edge weight variance may partially be driven by the density of non-zero edges, as all individuals had the opportunity to interact in the mean-field model, while the edge-randomization maintained the portion of edges from the original network, although overall interaction rates were the same between the two models. In most cases, both the portion of non-zero edges and variance in edge weights are the result of social preferences in association networks (Whitehead, 2008). Therefore, our findings suggest that both the intensity of social preference and the patterning of relationships may be determinants of disease spread on animal social networks. However, our study also demonstrates that small populations with strong social preferences and clear divisions between social units may still be highly vulnerable to the emergence of novel pathogens.

It is important to note that factors not included in the model, such as potential changes in social behaviour after infection (e.g. Lopes et al., 2016; Stroeymeyt et al., 2018), the duration of daily social contacts, transitivity effects in the daily contacts, the potential for continued interspecies transmission, and variation in epidemic parameters, are likely to influence the actual outcome of CeMV outbreaks in this population. Our analysis draws particular attention to current uncertainty about the per-contact transmission rate of CeMV. We suggest that future empirical work address these knowledge gaps to better inform management efforts. Regardless, the results of our model are concerning, and suggest that the possibility of widespread disease outbreaks and their potential impact on SRKW vital rates should be accounted for in future population assessments.

Our results demonstrate that it is difficult to induce effective herd immunity in the SRKW population by partial vaccination of the population, even when vaccinations are ideally targeted based on network centrality. At least 40 vaccinations (> 50% of the network) were required to reduce UME probability below 0.05, even with network-informed vaccination strategies. Modularity in contact structures is thought to generally make targeted vaccination more effective (Salathe & Jones 2010), however the multilevel nature of resident killer whale society complicates this; since family groups typically move together, there are no single individuals responsible for the majority of the spread between modules that can be targeted for vaccination. The logistical challenges of vaccinating and monitoring individuals at sea and the potential stress these activities may cause the animals likely make the prospect of wide-scale vaccinations impractical, as well as potentially unethical.

As individualized treatment is unlikely to be efficient, we suggest that management of potential disease outbreaks is likely best addressed by increasing the overall health of the population. Since the 1990s, the SRKW population has declined from nearly one hundred individuals to 73 at the time of writing. The most severe pressure contributing to this ongoing decline is reduced availability of prey (Lacy et al., 2017). As a result of consistently low food availability, visibly poor body condition is widespread in this population (Fearnbach et al., 2018), as is hormonal evidence of nutritional stress (Ayres, et al., 2012). Poor nutrition may increase this population's vulnerability to CeMV and other pathogens (Aguilar & Raga 1993). While inbreeding and PCB concentration are also of concern due to their link to CeMV outbreaks (Aguilar & Borrell 1994; Valsecchi et al., 2003), these hazards are less readily addressed by conservation efforts. Therefore, in line with previous recommendations, we suggest that management actions designed to increase the abundance of Chinook salmon available to the SRKW are critical to mitigating the potential impact of epizootics in this population.

Our analysis highlights the importance of applying modelling techniques in conservation planning, while also highlighting the limitations of targeted vaccination as a disease management strategy. As conservation interventions are always limited by both resources (Bottrill et al., 2008) and potential negative impacts on individual animals (e.g. Woodroffe 2001), maximizing the payoff of management actions is crucial. Individualized medical interventions in general, and vaccinations in particular, are increasingly central to a number of conservation efforts. Previous work has demonstrated that modelling techniques can often inform low-impact, effective, and efficient vaccination programs in endangered wildlife populations, particularly in primarily solitary species (Robinson et al., 2018) and in group-living species with well-defined territories (Haydon et al., 2006). Our analysis suggests that such actions may be less effective in highly social, group-living populations with frequent social contact between subgroups, even when these groups are well defined. These social structures may also be generally vulnerable to disease outbreaks, despite their apparent modularity. Such social structures are prevalent in several taxa of conservation concern, including cetaceans, elephants, and primates (Grueter et al., 2012; Grueter et al., 2020). We recommend that similar simulation studies be implemented when evaluating infectious disease risk and management strategies in these systems.

In this chapter, I have examined the influence of social structure on population fitness by focusing on the potential for outbreaks of novel disease. While understanding these potential risks are important, social structure can also influence vital rates in more consistent ways, outside of single catastrophic events. In the next chapter, I turn towards investigating the link between social structure and observed deaths and births in the southern resident population.

Chapter 6

The influence of social environment on survival and fecundity in resident killer whales

Abstract

The social environment can serve as an important factor shaping individual fitness, particularly in highly social species. Numerous studies have demonstrated links between components of fitness and individuals' number of social partners, strength of social relationships, and centrality within their social networks in a variety of social mammals. These studies, however, often ignore potentially important differences in behaviour between potential social partners which may impact the effect that social relationships have on health, survival, and reproduction. Here, we investigate the link between social environment and both survival and fecundity in resident killer whales using a detailed long-term database of social associations and demographic turnover. As resident killer whales exhibit strong sex differences in behaviour, we explicitly test for a link between the age-sex composition of the social environment and these outcomes.

The results of this analysis provided strong evidence that the age-sex class of social partners is a significant factor influencing components of individual fitness. Models that included information about the age-sex class of associations fit the data better than models including no information on the social environment and models that viewed all associates as equivalent. In the case of survival, we found that adult male associates significantly increase mortality hazard in a given year. In the case of fecundity, adult female associates significantly increased the probability that females reproduced in a given year, while immature associates decreased reproduction probability. This second result is the first evidence that female social bonds increase reproductive output in cetaceans. These results demonstrate the importance of accounting for the characteristics of social partners when linking social relationships to fitness outcomes.

6.1 Introduction

In social species, the number and quality of social partners that individuals have, and the nature of their relationships to those partners, regulates how individuals obtain social information (Duboscq, et al., 2016), individual predation risk (Janson, 1998), the outcome of intergroup competition (Cheney, 1992), and individuals' access to food and other resources (Stevens & Gilby, 2004). Because of this, aspects of the social environment such as the strength and stability of social bonds, social network centrality, and dominance rank have been linked to aspects of health and fitness in numerous social mammals, including humans, non-human primates, ungulates, and cetaceans (Snyder-Mackler, et al., 2020). In this study, I focus on three potential ways that the social environment may be linked to fitness. First, the total strength of social relationships (e.g. group size, network strength) that individuals have may be linked to fitness. Second, specific types of individuals (e.g. sex, age, phenotype) may have different direct effects on the fitness of their associates. Finally the overall composition of the social environment may impact group performance, and thus impact the fitness of individuals.

In the context of social networks and dyadic social relationships, most studies have investigated the link between sociality and fitness by quantifying social network centrality or the total strength of social bonds, and then correlating these measurements with health and fitness variables (Ostner & Schülke, 2018). An inherent assumption of this form of analysis is that the social partners included in the analysis represent relationships with similar fitness implications, as each unit of social connection is modelled as contributing equally to the outcome of interest. This assumption may often be a reasonable one, particularly when analyses are constrained to a single class of individual, or relevant direct interactions are used as the measure of social relationships. In many cases, however, researchers may only have access to data on association tendencies, rather than direct interactions, and may wish to understand the impact of the full social environment, rather than a particular class of relationship, on individual outcomes. In these cases, it is likely necessary to account for differences in the behaviour of potential social partners in analysing of the relationship between fitness and sociality.

Individuals within a population are not behaviourally homogeneous, with variation in behaviour driven by numerous factors such as genetics, sex, and ontogeny. These behavioural differences often manifest in social contexts that effect not only the fitness of the individual performing the behaviour, but the fitness of that individual's social partners. In some cases, these effects are due to dyadic interactions between individuals. For example, particular individual may be more likely to directly benefit their social partners by sharing resources (e.g. Wright et al. 2016), or performing anti-predator behaviour (e.g. Dimitriadou, et al., 2019), while other individuals may be more likely to represent fitness costs by competing for resources (e.g. Michelena, et al., 2008; Nakano 1995), or directly causing injury and mortality through aggression (e.g. Boydston et al. 2001; Kulik et al. 2015). In these cases, we would expect components of fitness to correlate not with overall social connectivity, but the connectivity to individuals of specific phenotypes.

In contrast to these direct dyadic effects, the composition of behavioural phenotypes within groups, and thus the composition of individuals' social environment, can also have implications for the efficiency with which groups perform collective tasks (Farine et al. 2015; Jolles et al. 2020), such as cooperative foraging (e.g. Carere et al. 2018) and intergroup conflict (Cassidy, et al., 2015). In these cases, we would expect that fitness may not correlate with the strength or number of social bonds that individual have at all, but rather with the relative composition of phenotypes within their social environment, either at the ego network or group level.

In more fluid, fission-fusion societies, individuals can adjust their social environment when the costs of their current social partners outweigh benefits (Aktipis, 2011), but in populations with stable, impermeable group structure, the ability of individuals to perform such adjustments may be limited by the physical and social costs of dispersal (Bonte, et al., 2012). In these latter cases, demographic processes can significantly impact individual social environment, leading to differential outcomes in terms of individual survival and fecundity.

One well-studied group of animals with well documented sex and age related variation in social behaviour are the coastal dolphins (Gibson & Mann, 2008; Marley, et al., 2013; Smolker, et al., 1992). Because of these differences, it is common for dolphin populations to exhibit distinct sexual segregation, with males and females forming separate social networks (Hawkins, et al., 2019; Lusseau & Newman, 2004). As with these other dolphin species, killer whales (*Orcinus orca*) exhibit sex differences in many behavioural domains as adults. In fish-eating resident killer whales, males are more likely to forage alone in deeper water (Beerman, et al., 2016), and are less likely to share prey that they capture (Wright, et al., 2016), despite taking more dives to foraging depth (Tennessen, et al., 2019). In addition, adult females, particularly older individuals, are more likely to lead group movement (Brent et al., 2015). Males are considerably larger than females, and are therefore likely a greater energetic cost to their social group (Noren, 2011), and receive considerably more social support from their mothers (Foster, et al., 2012; Wright, et al., 2016), while apparently also relying more on close social bonds in general, particularly when prey abundance is low (Ellis, et al., 2017**, Appendix A**).

Despite these sex differences in multiple domains of social behaviour, killer whale populations differ from other dolphins in that they do not exhibit sexual segregation in their association networks (Esteban, et al., 2016; Williams & Lusseau, 2006). In the case of fish-eating “resident” killer whales, both males and females stay with their mother’s social group their entire lives, and matrilines tend to associate with a set of other, likely closely related matrilines to form semi-stable social groups referred to as pods (Bigg, et al., 1990). Mating typically occurs between members of different social groups, although some inbreeding has been observed (Ford et al. 2018). This social structure, in which individuals of both sexes belong to stable kin groups, does not provide the opportunity for the sexes to significantly segregate in space and time. While the sexes do partially segregate while foraging in resident killer whales (Beerman, et al., 2016), these separations are temporary (over the course of a few hours) and over small spatial scales (less than a kilometre), and individuals remain within the same waterway.

The combination of strong sex differences in social behaviours and a lack of sexual segregation provides an interesting opportunity to understand how social partner behaviour influences relationships between sociality and fitness. Aspects of sociality have previously been demonstrated to be important determinants of survival in killer whale populations (Busson, et al., 2019; Ellis, et al., 2017), however the dependence of these effects on age and sex related variation in behaviour have not been investigated. As male killer whales are less likely to provide directed help via food sharing (Wright, et al., 2016), exhibit less information sharing through leadership (Brent, et al., 2015), may participate less in cooperative prey foraging (Hoelzel 1993) and appear to be a source of greater food competition than females due to their higher metabolic needs and foraging rates (Noren, 2011; Tennessen, et al., 2019), it is likely that associations with different age-sex classes have very different impacts on survival and fecundity.

Here, I investigate the degree to which social effects on fitness are dependent on age and sex related differences in the behaviour of individuals' associates. Using over 30 years of data on demography and social structure, I estimate the impact of different age-sex classes of associate on individuals' survival and reproduction. I test the three mechanisms outlined above:

1) Total strength of social relationships and size of social environment predicts fitness
2) The strength of bonds to different classes of individuals have different fitness implications
3) The relative composition of the social environment influences fitness by impacting group performance

I hypothesize that having more adult male associates means that individuals have more competition for food, while adult female associates may provide a source of resources and information. In addition, it is possible that groups with relatively fewer males may be less efficient in cooperative foraging. Together, I predict that associations with adult females provide fitness benefits, while associations with adult males will present fitness costs.

6.2 Methods

6.2.a Field observations

Opportunistic photographic identification encounters were carried out year round in the Salish Sea, with the primary study area being the San Juan Islands. Photographs were collected either from a small motorized vessel (5.5 m Boston Whaler) or from shore. From 1976 to 2003, film cameras were used, while after 2003 digital cameras have been utilized. The primary goal of every encounter was to acquire photographs of the left and right side of every individual present, with the ultimate goal of obtaining an accurate annual census. As this population is small and closed, and has been monitored since the 1970s, every individual can be easily individually identified. For each encounter, at least one photograph of every identified individual was saved to a folder for that individual in that year, along with information about the date, time, location, and sequence number of that photograph. This provided a record of the encounters in which each individual was identified in each year.

The dataset contained 31 years of data from 1987 to 2017 and a total of 1,701 sampling days, with the number of sampling days per year ranging from 13 to 100. After excluding individuals that died in their first year and thus had missing social variables (see below), the final datasets contained 96 births and 85 deaths. The survival dataset contained 2,514 annual observations of 160 unique whales. The fecundity dataset contained 745 whale years for 60 unique females.

6.2.b Assigning age, sex, life history stage, mortality, and fecundity

Several decades of study have revealed no evidence of immigration or emigration in the southern resident killer whale population, and individuals belong to consistent, discrete social units (Parsons, et al., 2009). The CWR therefore assigns mortality when individuals are repeatedly missing from otherwise full censuses of their social group. Individuals that have had mortality assigned this way have not reappeared at any point during the study.

Fecundity was recorded based on observations of new calves and their association patterns. Calves can be unambiguously assigned to mothers based on their close spatial proximity and synchrony with particular adult females (Bigg, et al., 1990). Subsequent genetic evidence has universally agreed with maternities assigned in this way (Ford, et al., 2018). As the detection of a new calf relies on both a successful pregnancy and the calf surviving long enough to be detected, the measurement of fecundity here expresses the probability that a female produces a calf that survives long enough to be photographed while alive (Ward, et al., 2009).

Sex was determined either by photography of the genital region in immature individuals, or based on obvious sexual dimorphism in adults. For individuals that were observed in their first year of life, ages can be determined with certainty, while individuals born prior to the start of the study were assigned estimated years of birth based on life history characteristics (Olesiuk, et al., 1990). Based on previous analysis of growth rates (Fearnbach, et al., 2011), individuals were assigned to one of 3 broad age-sex classes in each year: immature (< 15 years), adult females (15+), and adult males (15+). While more fine-grained separations are possible (e.g. separating reproductive and post-reproductive females), these broad classes are used as to not over-parameterize our models of survival and reproduction.

6.2.c Measuring social associations

As with the life history data, measures of individual social environment were based on photo-ID encounters. Following Parsons et al. (2009) and Foster et al. (2012), individuals identified within the same encounter are considered to be associated, as these individuals are potentially foraging in the same waterway and are within vocal range. Associations were measured using a daily sampling period, using the simple ratio index (SRI) to estimate daily association probabilities. The SRI between individual *i* and *j* in year *t* is calculated as

$$\mathrm{SRI}_{t,i,j} = \frac{x_{t,i,j}}{d_{t,i,j}} \tag{1}$$

Where $x_{t,i,j}$ is the number of days in year *t* in which *i* and *j* were photographed during the same encounter, and $d_{t,i,j}$ is the number of days on which either *i* or *j* was photographed. While the SRI is used to summarize social structure, subsequent analysis accounts for uncertainty in these measures (see below).

6.2.d Social network structure and precision

I first used the association data to determine whether the annual social networks provided reasonable representations of social structure. Social differentiation (*S*) was measured in each year. The value of *S* is the estimated coefficient of variation of the true underlying association probabilities, which is estimated assuming that the underlying probabilities follow a beta distribution. This quantity is therefore estimated by fitting the parameters of a beta-binomial model to the numerators and denominators of the simple ratio index. This estimate can further be compared to the observed coefficient of variation (CV) to derive an estimate of the correlation between true and observed association indices (Whitehead 2008):

$$r = \frac{s}{\mathrm{CV}} \tag{2}$$

I further investigated how well the estimated networks represented “ground truth” social structure by measuring the degree to which associations correlated with social unit membership in each year. This was done by fitting binomial generalised linear models to the SRI values in each year, using the denominators as the sample size. As predictors, I used two binary similarity matrices, representing shared pod and matriline membership. Matriline membership was determined based on individuals having a known shared maternal ancestor, following Parsons et al., (2009). I then applied the double-semi-partialling quadratic assignment procedure with 1,000 permutations to derive *p*-values for these effects (Dekker et al., 2007).

6.2.e Modelling survival

Survival was modelled using extended Cox mixed effects models. This modelling framework seeks to predict the mortality hazard λ based on a set of time-varying covariates. These models took the form:

$$\lambda_{t,i} = \lambda_{0,s_{t,i}}\left(a_{t,i}\right) \cdot \exp\left(\sum_p \beta_p X_{p,t-1,i} + \varepsilon_t\right) \tag{3}$$

$$\varepsilon_t \sim N(0, \sigma)$$

Here, $\lambda_{0,s_{t,i}}$ is the baseline hazard function specific to each life history stage *s* (the broad age-sex classes defined above), $a_{t,I}$ is individual *i*’s age in year *t*, β is a vector of estimated coefficients, *X* is a matrix of *p* social environment terms, and ε is an annual random effect, assumed to be identically and independently normally distributed with estimated standard deviation σ.

Social variables are taken from the year prior to the recording of survival because mortality assignment is based on individuals being consistently missing from encounters in which their social unit is observed. Therefore, individuals inherently have lower levels of social affiliation at a broad scale in years in which they die. Taking the measurement from the previous year breaks this inherent correlation caused by the structure of the data. This one-year time lag is theoretically justified; previous analysis have found that variation in environmental quality is most closely correlated with next-year mortality (Ford, et al., 2010) and the survival impacts of social disruptions, such as the death of mothers and grandmother, can last for multiple years (Foster, et al., 2012; Nattrass, et al., 2019; **Appendix B**). Note that because of this methodology, the final dataset does not include the first year of each individual’s life. This model was fit using the coxme R package (Therneau, 2020). Results are presented with the coefficients β with their bootstrapped standard errors (see below), as well as the hazard ratio $Hz = \exp(\beta)$, indicating the relative change in mortality risk with a single unit change in predictor value.

6.2.f Modelling fecundity

Fecundity was modelled using binomial generalised linear mixed models. Following Ward et al., (2009), the years immediately before and after a female gives birth are excluded to account for the 18 month gestation period of killer whales. Ward et al. (2009) found that a 4th order polynomial best explained the relationship between fecundity and age in resident killer whales, and this relationship has been confirmed and utilized for conservation planning in subsequent analyses (e.g. Ward et al. 2013). This formulation allows the rate of reproductive maturity in early life and the rate of senescence in later life to be asymmetric. While newer methods, such as generalised additive models (GAMs), would allow for more flexible modelling of this relationships, we maintain the 4th order polynomial structure, both to ensure comparability with these previous studies, and because of potential analytical issues in combining GAMs with non-parametric bootstrapping (see below). I further exclude females younger than 9 and older than 43 from this analysis. These were the youngest and oldest ages of reproduction in this population, respectively. Killer whales typically do not reach sexual maturity until their early teens, and are post-reproductive after their mid-40s. Older and younger individuals were removed to prevent possible social differences between these ages from influencing the results of this analysis. Using the remaining binary outcomes for each female in each year (1 = was observed with a calf, 0 = was not observed with a calf), the probability of individual *i* being observed with a new calf in year *t* ($\theta_{t,i}$) is modelled as:

$$\text{logit}\left(\theta_{t,i}\right) = \sum_{k=0}^{4} \rho_k a_{t,i}^{k} + \gamma L_{t,i} + \sum_p \beta_p X_{p,t-1,i} + \delta_i + \varepsilon_t \qquad (4)$$

$$\delta_i \sim N(0, \sigma_{ind})$$

$$\varepsilon_t \sim N(0, \sigma_{year})$$

X is again a matrix of *p* social environment terms, and $a_{t,I}$ is again individual *i*'s age in *t*. *L* is an indicator variable, taking the value of 1 if individual *i* is lactating in *t* and 0 otherwise. Individuals were assumed to be lactating if they had a surviving offspring under the age of 4 in year *t*, as isotopic evidence suggests that individuals gradually wean up until the age of 4 in this population (Newsome, et al., 2009). The terms ρ_k, β_p, and γ are estimated fixed effects, while δ and ε are individual and year level random effects. This model was fit using the lme4 R package (Bates, et al., 2015).

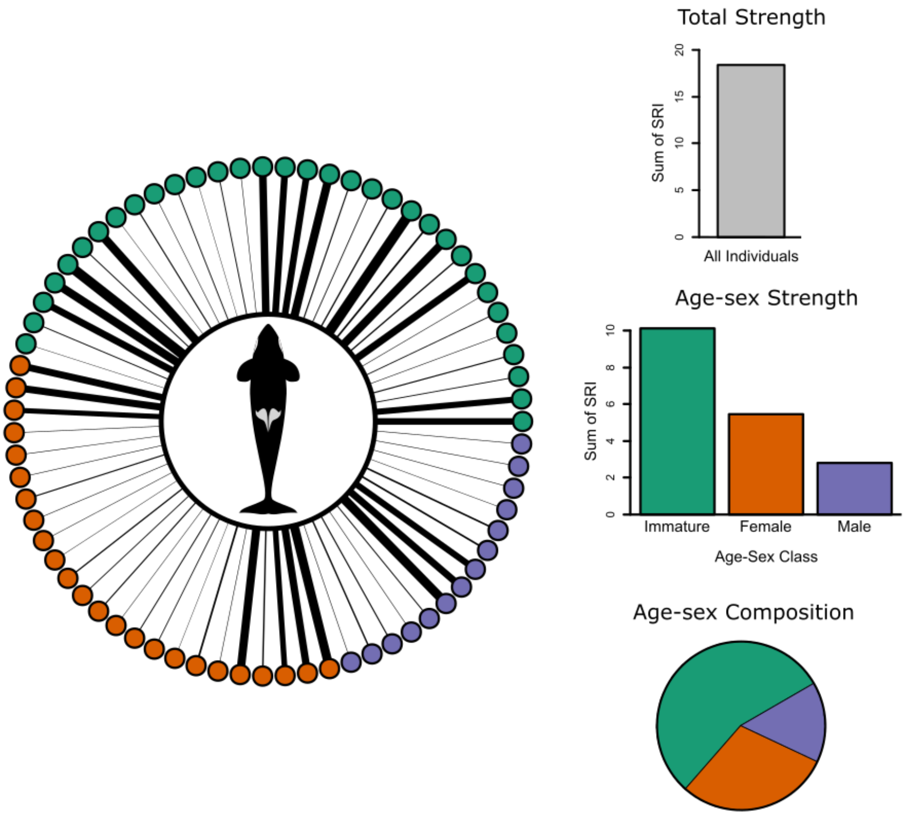

Figure 6.1 Diagram of social environment measures. Left: Ego network for individual J16 in 2017, showing their connections to males (blue), females (orange), and immature individuals (green). Edge thickness is proportional to simple ratio index. Ego networks are then used to derive three kinds of social environment measures: total strength (sum of SRI values), strength to each age-sex class (sum of SRIs to each class), and age-sex composition (portion of SRI to each class).

6.2.g Measuring individual social environment

The association data was used to derive several measures of the social environment, and multiple models were fit to determine which terms, if any, predicted vital rates (Figure 6.1). First, I derived a measure indicative of the total size of each individuals' social environment. This was measured by individual strength centrality, which is the sum of an individual's SRI values in a given year. This measure is an approximation of individual typical group size (Whitehead 2008). Models with this measure propose that individual reproduction and survival are dependent on the number of associates they typically have, regardless of the characteristics of those associates. I refer to these models as "total strength models". Note that these measures incorporate the size of individuals' matrilines and pods, as well as the frequency with which they associate with members of other social groups.

Next, I tested whether the strength of connections to different types of associate influenced fitness. I refer to models incorporating these terms as "age-sex class strength models." These models propose that survival and reproduction are linearly related to the number of social partners in each class, and different classes have different impacts on survival. This was measured as the sum of SRI values to each of the three main age-sex classes in each year. As above, the sum of SRI values to each age-sex class is an estimate of each individual's typical number of associates of that class. These three measurements were significantly positively correlated (male associates vs. female associates: $r_S = 0.68$; male associates vs. immature associates: $r_S = 0.49$; female associates vs. immature associates: $r_S = 0.73$), suggesting that they are driven by underlying factors, specifically pod, matriline, and populations size. While this collinearity may not be ideal for linear modelling, we note that this will only have the effect of decreasing the precision of our estimates, but does not effect model selection or result in increased false positives (Morrisey & Ruxton 2018). Our estimates from these models should be viewed as conservative based on these correlations.

The final measurements expressed the composition, rather than absolute size, of the social environment. We refer to models using these predictors as "age-sex composition models”. These measures propose that the composition of behavioural types in an individual’s social environment, rather than the number in each class, influences fitness. This would be expected to be the case if the age and sex of individuals in a group influenced the efficiency with which the group completed collective tasks, such as the cooperative prey searching that this population apparently exhibits (Hoelzel 1993). Using the sum of SRI values to each age-sex class, we derive the portion of each individual’s associations that connect them to individuals of each age-sex class, creating compositional covariates. These compositional data were transformed using the isometric log-ratio to derive a two-dimensional measure of ego network composition (Kogovsek et al., 2013). Models including these terms propose that the size of individuals’ ego networks and the absolute number of associates in each class do not determine survival or reproduction, but rather the relative representation of each age-sex class is the relevant information. This method cannot handle components with values of 0. Therefore, to calculate these measurements, I add a small number (0.0001) to all values to remove zeroes. All social variables were *Z*-scored prior to model fitting.

6.2.h Bootstrap-based inference

Social network measures derived from observational data are only a sample of the true social system, and thus have inherent uncertainty (Lusseau et al., 2008). In the context of regression modelling, predictor variables are typically assumed to be measured without error, and therefore the raw social network measures used here break the assumptions of regression modelling when used as predictors. To derive estimates and confidence intervals for the survival and fecundity models, I therefore develop an adaptation of a two-step bootstrap procedure previously proposed to estimate measurement error models (Haukka 1995). This procedure combines a traditional case-resampling bootstrap for regression (Thai et al., 2013) with the bootstrap procedure recommended by Lusseau et al., (2008) for group-based association data. This involved performing two bootstraps; the first resamples the association data to account for uncertainty in network measures. The second resamples the final model-frame to account for uncertainty in model fit. The steps of this algorithm are:

1. For each year, generate a bootstrapped dataset by resampling observation days with replacement and calculate annual association networks from these datasets.
2. From these bootstrapped networks, derived bootstrapped social measures for each model.
3. Create a bootstrapped dataset of responses and predictors by sampling rows of the data frame (each representing a whale-year) with replacement.
4. Fit the survival and fecundity models to this final bootstrapped dataset.

I first carry out bootstrap-based model selection to determine which of the social environment measures (or the null model) are best supported as relevant to vital rates. For each bootstrap, AIC was calculated for each of four models for both fecundity and survival:

- Null model: No social environment terms
- Strength model: Sum of all SRI values
- Age-sex strength model: Sum of SRI values to each age-sex class
- Age-sex composition model: Isometric log-ratio measurements of the age-sex composition of the social environment

For each bootstrap replicate, the algorithm then select the best model via AIC. We perform model selection by determining which model was selected in the most bootstrap replicates. I refer to the portion of bootstraps in which a particular model was chosen as that model's "model selection frequency" (Lubke et al., 2017). For the models that were selected the most frequently, I also examine the bootstrapped distribution of coefficients to infer the direction and size of social effects on both survival and fecundity. In particular, I focus on the mean and standard errors for all estimated coefficients to infer the size and direction of social effects on survival and fecundity, as well as two-tailed *p*-values for each parameter.

6.3 Results

6.3.a Social network structure

The annual social networks were extremely dense, with most individuals being associated on at least one occasion (density mean ± SD = 0.92 ± 13) and the mean association strength was similarly high (average SRI mean ± SD = 0.25 ± 0.05). Social differentiation was generally intermediate to high (*S* mean ± SD = 0.65 ± 0.21), and estimated correlations between true and observed association indices were high (*r* mean ± SD = 0.81 ± 0.07). In all years, both shared pod membership ($\bar{\beta} = 1.49 \pm 0.91$, all $p < 0.01$) and shared matriline membership ($\bar{\beta} = 1.07 \pm 0.27$, all $p < 0.01$) predicted higher dyadic association probabilities, suggesting that our annual networks are sampled adequately to reflect the underlying "ground truth" social structure of the population.

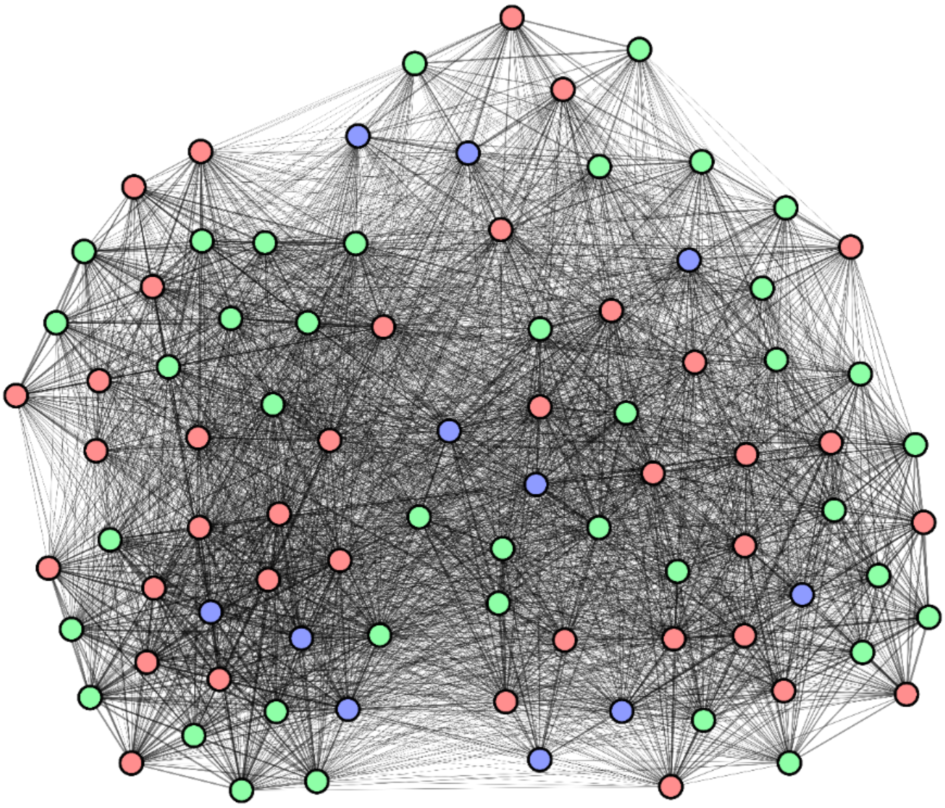

Figure 6.2 Example social network for the southern resident killer whale population. Node colour indicates individual age-sex class (green = immature, red = adult female, blue = adult male). Edges width is proportional to the simple ratio index between individuals.

6.3.b Social environment and fecundity

The best model for fecundity was the age-sex class strength, containing terms for the sum of SRI values to each of the three broad age-sex classes (bootstrap selection frequency = 0.456), although this model was only marginally better than the compositional model (bootstrap selection frequency = 0.372). Together, these two models were selected in 82.8% of bootstrap replicates (Table 6.1). This indicates that while the age-sex class of associates is relevant for fecundity, it is less clear whether the absolute strength of social associations or the composition of the social environment are the relevant factor. In contrast, the total strength model was selected much less frequently than the null model (bootstrap selection frequency = 0.048), suggesting that individuals' typical group size is not an effective predictor of fecundity. For simplicity, and because inferences from coefficients in the age-sex class strength and composition models were similar, I focus further analysis on the age-sex class strength model.

As expected, lactation had a negative impact on fecundity (β = -1.45 ± 0.44, $p < 0.001$), and the relationships between age and fecundity followed the pattern previously reported by Ward et al., (2009), with a fast increase to a peak around 20 years old, followed by a decline and plateau at 30 years, followed by a decline towards post-reproductive age (Figure 6.3). Adult female associates had strong positive impacts on fecundity (β = 1.13 ± 0.46, $p = 0.016$). In contrast, immature associates had a smaller, but significant negative impact on fecundity (β = -0.73 ± 0.35, $p = 0.032$). Male associates did not have a statistically significant impact on fecundity (β = -0.32 ± 0.32, $p = 0.294$).

Table 6.1 Bootstrap model selection frequencies for fecundity and survival models. Best models are in bold.

Model	Fecundity	Survival
Null	0.124	0.229
Strength	0.048	0.054
Age-sex class strength	**0.456**	**0.507**
Age-sex class composition	0.372	0.210

While males are the primary beneficiaries of maternal care later in life, it is possible that the apparent link between female association and fecundity was driven by benefits provided to females by their mothers. If mothers increase their daughters' fecundity, and individuals with surviving mothers have more female associates (as their mother would be a near constant adult female associate), this could lead to the relationship between fecundity and sociality that we found. To check this, I fit a linear mixed effects model with strength to adult females as the response, an indicator variable for mother state (1 = alive, 0 = dead), a fourth order polynomial term for individual age, and individual and year level random effects. This model only included reproductive aged females with known mothers. This model found no significant effect of maternal state on the sum of SRI values to adult females (likelihood ratio test: $\chi^2 = 0.10$, $p = 0.747$), and in fact the sign of the effect of the maternal effect was slightly negative ($\beta = -0.02 \pm 0.09$). I therefore conclude that there is not significant positive covariance between having a surviving mother and having greater network strength to adult females, and the effects found in the fecundity model cannot be explained solely by any positive effect that mothers may have on their daughters' reproductive output.

6.3.c Social environment and survival

In the context of survival, bootstrap model selection frequencies suggests that, as in the case of fecundity, the best fitting model included terms for the sum of SRI values to each age sex class. Note, however, that the null model had considerably more weight in the survival analysis than in the fecundity model, being selected in 22.9% of bootstrap replicates compared to 50.7% for the age-sex class strength model. As in the case of fecundity, the total strength model performed considerably worse than the null model (bootstrap selection frequency = 0.054), suggesting that individuals' typical group size is not an effective predictor of mortality. Again, the two models that use information about the age-sex composition of the social environment combined were largely supported, being selected in a combined 71.7% of replicates. As above, I focus on interpretation and inference from the age-class strength model, as it was selected more frequently than the age-sex composition model, and inferences from their coefficients were similar.

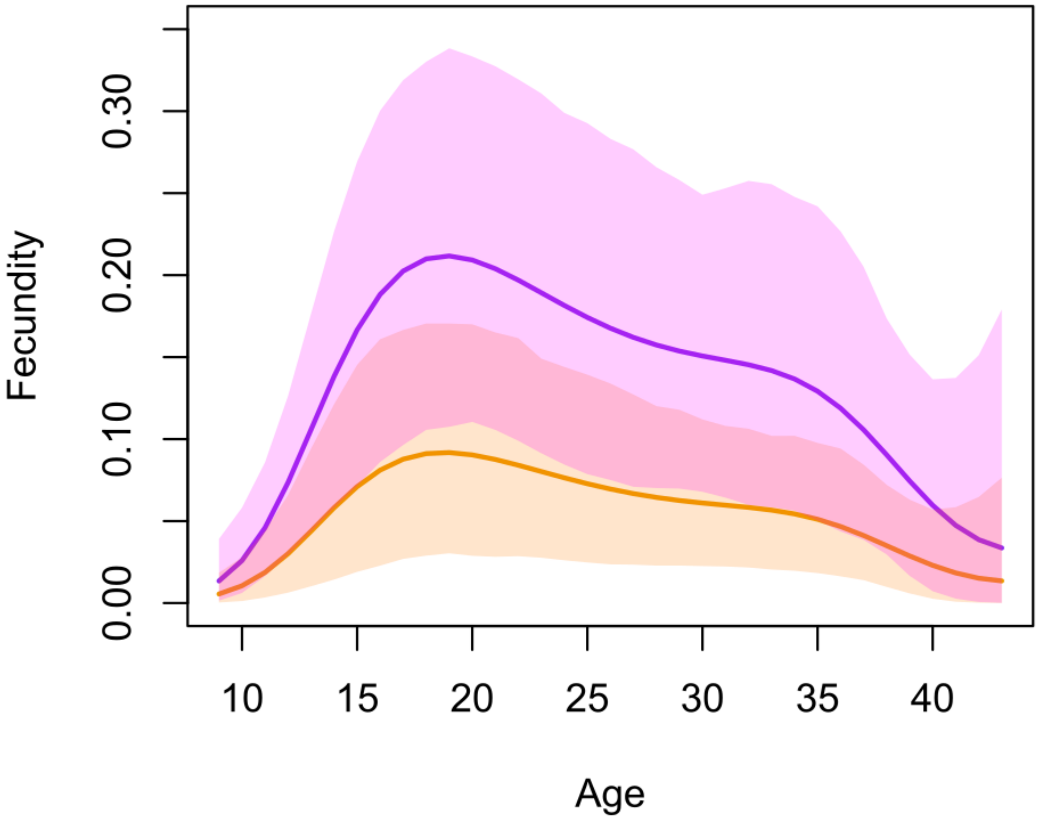

Figure 6.3 Effect of age and sociality on fecundity. Curves are bootstrapped mean and 95% confidence intervals for predicted fecundity for females with different typical adult female associates (purple = 10, orange = 7). Associations to other age-sex classes are held constant to their means, and random effects are marginalized.

The only significant social effect in this model was that of adult male associates. The sum of individuals' SRI values to adult males significantly increased their mortality hazard in the next year ($\beta = 0.55 \pm 0.26$, $Hz = 1.80$, $p = 0.034$). Social connections to adult females had a non-significant effect on mortality hazard ($\beta = -0.74 \pm 0.38$, $Hz = 0.51$, $p = 0.052$), as did social connections to immature individuals ($\beta = 0.31 \pm 0.30$, $Hz = 1.43$, $p = 0.292$).

6.4 Discussion

The results presented here indicate that the social environment is an important determinant of both survival and fecundity in the southern resident killer whale population. Models that included information about the age-sex class of associates were better supported by the data than models that viewed all individuals equivalently, and models that included no information about the social environment. In particular, male associates increase mortality hazard, while female associates increase fecundity and juvenile associates decrease fecundity. These effects cannot be attributed to the size of the social environment (or underlying factors such as matriline size and pod size). For both vital rates, the model including network strength, a measure of typical group size, fit the data significantly worse than the models including age-sex classes. In these total strength models, the effect of network strength was small and non-significant for both mortality ($\beta = -0.01 \pm 0.16$, $p = 0.952$) and fecundity ($\beta = 0.17 \pm 0.20$, $p = 0.394$). Although the mechanisms by which associates of different age-sex classes influence vital rates cannot be determined from this analysis some potential mechanisms can be proposed based on our current understanding of killer whale life history and social behaviour.

The first striking effect in this analysis is the strong positive influence of adult female associates on female reproductive success. Similar effects have been observed in female feral horses (Cameron, et al., 2009) and baboons (McFarland, et al., 2017), but to the best of our knowledge this is the first demonstration that female social relationships can increase reproductive success in cetaceans. In previous work, Frere et al., (2010) found that associated female bottlenose dolphins (*Tursiops aduncus*) exhibited correlated reproductive output, but this study did not demonstrate an increase in reproductive success with increased sociality. The mechanisms underlying correlations between sociality and reproductive output are not entirely clear, in this or other systems. A likely explanation is that adult female associates increase foraging success and prey intake by sharing knowledge about prey distribution, cooperatively finding and exploiting discrete prey patches, and sharing prey that they catch, however these explanations all require further testing. The lack of clarity in these results between the age-sex strength models and the age-sex composition model makes it more difficult to determine the precise mechanisms by which the social environment is influence fecundity.

The second notable effect revealed in this analysis is the negative impact of males on survival, with social connections to adult males increasing an individual's risk of mortality within a year. It is likely that these cost are due in part to differential prey intake as a result of the patterns of helping and harming behaviour within social groups. These changes in prey intake could be driven by decreases in received prey sharing due to other social partners preferentially provisioning males (Wright, et al., 2016) or direct competition between individuals for limited food resources (Hoelzel, 1993). It is also possible that this decrease in survival is the result of direct aggression and harassment, although potentially lethal aggression appears to be very rare in wild killer whale populations, particularly within single social groups (Robeck, et al., 2019). An additional possibility is that individuals may invest heavily in their adult male associates, sacrificing their own survival to increase the survival and reproduction of these males. This may be an evolutionary advantageous strategy given that killer whales tend to be highly related to their social partners, and males have the potential to be extremely reproductively dominant if they survive to an old age (Ford et al. 2018).

The analysis also shows that associating with immature individuals has a small but significant negative impact on fecundity. It seems likely that limitations in females' ability to care for immature individuals may lead them to limiting further reproduction. While the model used for this analysis accounted for decreased reproduction during lactation, it does not account for possibly depressed reproduction when individuals have surviving weaned offspring. Previous analysis suggests that, particularly for males, some degree of maternal dependence is present well into adulthood (Foster, et al., 2012), and females may thus continue to suppress reproduction even when their surviving offspring are weaned, but are still dependent on their mother sharing prey with them. It is further possible that individuals may forgo reproduction when their social group has several dependent young, to avoid competition between calves of similar age (Croft et al. 2016). On the other hand, it's possible that immature associates are less capable of contributing to cooperative foraging due to a lack of experience (Guinet & Bouvier, 1995), resulting in decreased prey intake and nutritional condition for their social partners.

If adult male killer whales decrease the survival of their associates, why does this population exhibit bisexual philopatry, rather than male dispersal? While the answers to this question are beyond the scope of this study, they likely lie in the potential indirect fitness benefits provided by provisioning close male kin. While female reproduction is constrained by high maternal investment and long gestation periods, male reproduction has no such constraints. Genetic evidence suggests that reproduction in this population is dominated by a few males, particularly the oldest individuals (Ford et al., 2018). In addition, because of the social structure of this population, the offspring of males are typically born into a different social unit, and therefore do not contribute to any within-group competition for resources (Croft, et al., 2017). Therefore, it may be that the ideal reproductive strategy for these killer whales is to heavily invest in keeping male kin alive until they are old enough to be highly reproductively successful, potentially at the expense of the survival of the rest of their associates. It may further be the case that these negative effects are particularly prevalent in this population due to general limitations on food availability (Ayres, et al., 2012; Ford, et al., 2010), and that such effects would not be apparent in more stable populations. Replication of this analysis in other populations of resident killer whale could reveal whether or not this is the case.

The findings presented here differ from previous results from studies of killer whale sociality. Most recently, Busson et al., (2019) found that individual mean association strength was positively correlated with survival in Crozet Islands killer whales, however this study lacked information on individual life history stage. In addition, this study aggregated associations across an entire multi-decade study period, rather than deriving networks in each year as in the current analysis. As killer whale social systems tend to be dynamic, this may have missed important aspects of sociality in each year. In addition, this aggregation naturally biases the associations of individuals that die during the study downwards, while our study accounts for this inherent correlation between association and demographic datasets.

Another previous study in the southern resident population found that social network centrality predicted survival in males, but not females (Ellis et al., 2017; **Appendix A**). This study analysed associations at a different scale than our analysis, defining associations as individuals surfacing within close physical proximity in contrast to our definition based on co-occurrence within encounters. While this more restricted definition is more likely to reflect individualized social relationships, the association definition used here reflects the broader social environment. Future work could repeat this analysis using different definitions of association to examine at which scale these effects occur. In addition, this previous study analysed males and female survival separately. The larger number of parameters in the models used here, specifically the fact that we include up to three social parameters in addition to annual random effects, precludes such analysis in the current study without overfitting our model.

Analysis of killer whale reproduction has previously suggested that demography, both at the population, pod, and matriline level, did not have an impact on fecundity (Ward et al., 2009). Importantly, this study used as covariates either the total number of adult males in each level, or the total number of individuals, with the assumption that reproduction would either be constrained by access to mates or by overall density dependence. The findings of the current study are in fact entirely compatible with these results: the total size of an individuals' social environment, and the sum of their connections to adult males, do not influence reproduction. This updated analysis therefore confirms that restricted access to mates and density dependence are likely not driving variations in female reproductive output in this population. Instead, the effects of associates on reproduction is determined by the typical number of female and juvenile associates.

While initially it may seem that the results of the survival analysis and fecundity analysis are not compatible with one another, particularly if the underlying mechanisms are likely derived from the effects of social partners on food intake, this is in some ways a result of statistical significance thresholds, rather than the size or direction of effects. While the effect of males was only statistically significant in the survival model, the direction of the effect for the fecundity model was also negative. Similarly, while juveniles and females significantly decreased and increased fecundity probability respectively, they both had non-significant effects on mortality in the opposite directions (Figure 6.5). It is also significant that the same social effects model was chosen for both demographic rates. These results suggest that it is plausible that the same underlying mechanisms are at play for the social effects on both survival and fecundity, but more data is needed to confirm this.

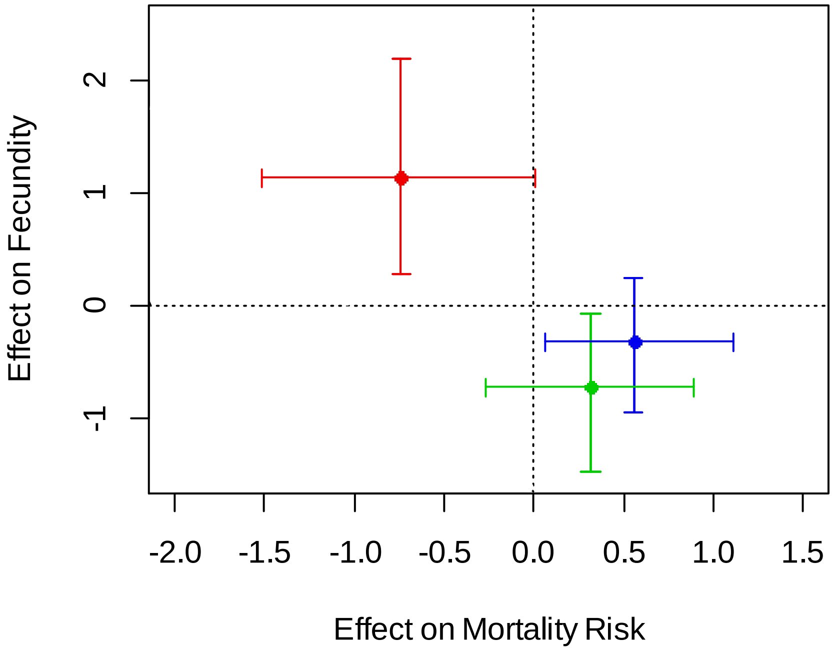

Figure 6.4 Effects of associate age sex class on mortality and fecundity from the best fit models. Colour indicates age-sex class (red = adult females, blue = adult male, green = immature). Points are bootstrapped means, and error bars indicate 95% confidence intervals. Dotted lines indicates no effect.

In total, the results of this analysis provide strong evidence for social effects on vital rates that could not be captured through previous modelling efforts. Future work should focus both on understanding the mechanisms for these effects, as well as their consequences for the evolution of killer whale social structure, and the conservation of this population.

Chapter 7

General discussion and future directions

The last decades of behavioural ecology research have demonstrated the importance of social structure for populations' ecology, evolution, and conservation. Social network analysis has proven to be a particularly powerful methodological framework to examine these processes in a variety of systems. Because of the centrality of social relationships to many aspects of their lives, understanding the patterning and consequences of social relationships is particularly key for cetacean species.

In this thesis, I have addressed a wide range of topics in social network analysis, with particular focus on the unique challenges and opportunities presented in studies of cetacean populations. I addressed gaps in the analysis of the association networks commonly measured in cetacean populations, specifically the questions of how to measure social complexity in these systems and how to use regression modelling to understand the factors underpinning social network structure. I further applied modern technology to collect data on direct interactions between wild cetaceans, including sub-surface interaction. In the final two chapters, I applied social network analysis to long-term datasets to understand the risk of disease and the social impacts on vital rates in the endangered southern resident killer whales.

In this chapter, I will discuss some of the implications of these findings, and highlight potential directions for future research.

7.1 Social complexity and comparative analysis

The first data chapter of this thesis is concerned with deriving a potentially useful measure of social complexity that is applicable to association networks. Clearly, the ultimate application of such a measure would be as a tool for comparative analysis, particularly within taxa where associations are the most common form of information about social structure, such as cetaceans.

In Chapter 2, we discuss the idea that a similar mixture model framework could be applied to interaction data, or multidimensional measures of social relationships. In Chapter 4, we demonstrate that unmanned aerial systems are a powerful tool for observing direct social interactions in cetaceans. A potentially interesting area for future research would be comparing measures of social complexity derived from association indices to those derived from detailed data on direct interactions. Our results in Chapter 4 show that associations generally correlate with interactions, however the increased differentiation within interaction rates may lead to higher measures of social complexity. Studies collecting both association and interaction data on multiple populations or groups, calculating multiple measures of social complexity, and quantifying the correlation between these measures, would help elucidate the degree to which association complexity can be expected to represent interaction complexity.

Besides the question of whether association complexity represents the complexity of social interactions, there is a broader question of how to conduct comparative studies using this, or any, network measure. The first problem is that any network measure derived from observational data has uncertainty associated with it, which should be accounted for in phylogenetic analyses (Lusseau et al., 2008). We did not derive a method for measuring the uncertainty of association complexity measures here, however the current version of SOCPROG includes a jackknife resampling procedure for this task. While this seems to perform adequately, a deeper investigation of how to identify bias and precision in the calculation of association complexity is likely an important piece of future analysis.

Another question is how to account for non-social influences on social network measures in comparative analyses. Recent work has suggested using datastream permutations for this task (Farine & Aplin 2019). In Chapter 3, however, we demonstrated that datastream permutations have significant drawbacks. While in that chapter we focused on within-network regressions, the problems present there are also present when comparing networks. Specifically, if datastream permutations are used to compare networks, they test the null hypothesis that all social networks are random, which is clearly not useful in most cases.

While this remains an open question, it is likely that the way forward is to include data about potential confounds in the statistical model. Information such as network size and average sampling days per individual as covariates may help to reveal the effect of the covariate of interest on social network structure. This is the solution my co-authors and I suggest in our work on calculating effect size when performing within-network regressions (Franks & Weiss et al., 2020; **Appendix C**). In many cases, the effects of sampling may be non-linear, requiring the use of smooth terms via generalised additive models. The fitting of non-linear sampling intensity effects may further help identify points at which additional sampling no longer influences network measures, if these curves are found to be asymptotic.

7.2 Using social networks as predictors in statistical models

In Chapter 3, I highlighted issues with a common statistical procedure for regression in animal social networks, and suggested potential solutions (see Franks & Weiss et al., 2020 and **Appendix C** for further discussion of the statistical analysis of network data using regression models). Left untested in that chapter was the situation in which social network data is not the response in a statistical model, but rather is one of the predictor variables.

It is common for researchers to utilize node-label permutations for this situation, often with the same justification as is presented in the case of a network-based response variable that the observations are not independent. This, however, misunderstands the assumption of regression models. Consider the simple linear model that was examined in Chapter 3:

$$Y = \beta X + \varepsilon \tag{1}$$

$$\varepsilon \sim N(0, \sigma)$$

Where Y is the vector of responses, X is a matrix of predictor variables, β is a vector of estimated coefficients, and ε is the error term. Note that the only distributional assumption is that the errors are identically and independently normally distributed around 0; the distributions of Y and X themselves are not subject to any assumptions. When Y is derived from network data, it is likely (and for some measures assured) that the error term ε is not i.i.d. normal, and thus permutation procedures are necessary. However, the process giving rise to X is not considered in this model. In fact, the distribution and correlation structure of X has no effect on linear model fits when the other assumptions are met (Figure 7.1). Therefore, such permutation procedures are not necessary when Y is derived from non-network data while X is a network measure.

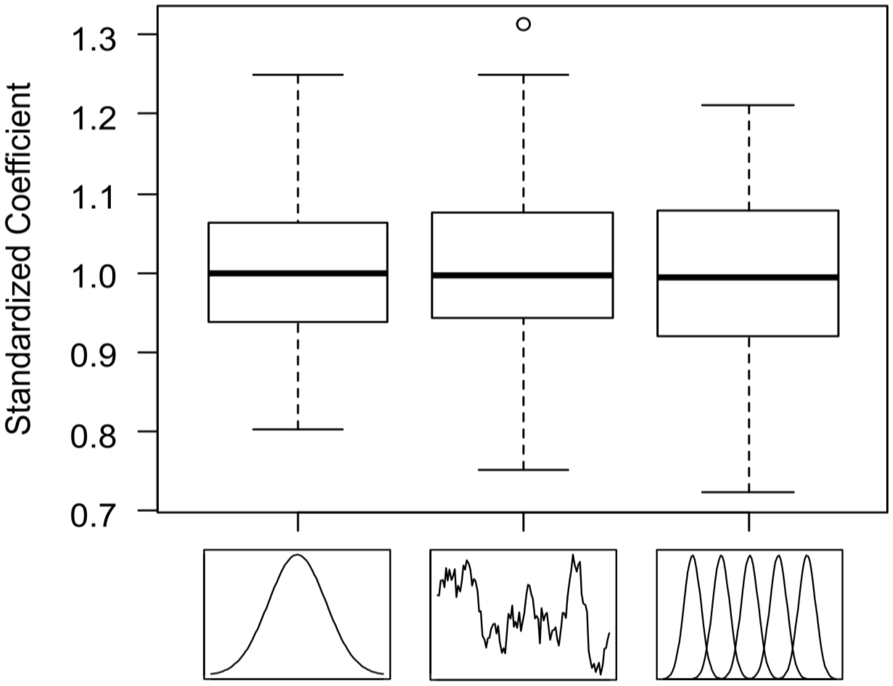

Figure 7.1 Example of the invariance of linear regression to predictor dependence structure. We simulate responses Y_i with a mean of X_i and a standard deviation of 1, and save the standardized coefficient. *X* values were generated either as a single normal distribution (left), a random walk (middle), or from multiple groups with different means (right). We run 100 simulations and plot the distributions of estimated standardized coefficients, showing that estimation is not effected by the dependence structure of the *X* variable.

Network autocorrelation, in which the traits of nodes are related to the traits of their direct and indirect alters, is prevalent in social networks, often due to the transmission of information or trait homophily. There are statistical methods available to model these processes, specifically network autocorrelation models, however the underlying statistical mechanisms are not different from typical regression models. The key to network autocorrelation models comes not from particular formulations of error structure or any randomization procedure, but by specifying the correct network-based covariate for regression modelling (Leenders 2002).

This is not to say that using social network measures as predictors in animal research comes without challenges. If biases are present in data collection that influence observed network structure, this will effect model fits and subsequent inference. This is particularly problematic if the factors giving rise to bias also correlate with the outcome variables, independent of social factors. Another, less well recognized issues, is that because social network data are only a subsample of the true social network, they violate a separate assumption of regression modelling, namely that predictor variables are measured without error. The first problem likely needs to be addressed similarly to how we recommend researchers deal with data collection bias in Chapter 3 and in Franks & Weiss et al., (2020; **Appendix C**). Namely, likely confounding variables should be identified and included in the statistical model, or edge weights can be derived from generalised affiliation indices before calculating network statistics. The second issue is potentially more distinct and challenging, but we can draw on the literature regarding measurement error models to address this.

In Chapter 6, I used a two-step bootstrap approach to account for measurement error. This method uses bootstrapping to first generate values for the predictor accounting for uncertainty, and then resamples the full regression model frame to account for model uncertainty. This method may be worth more broad application, however I note that it does not account for biases in data collection, and the way to do this is not clear. Therefore, while useful for these applications, I believe further work is necessary to derive and test measurement error methods in animal social networks.

Perhaps a more theoretically justified method for this task would be a latent variable approach using Bayesian inference. If we treat the true network edges as a latent variables that produce the observations through a process that we can formulate as a probability distribution (i.e. binomial trials for associations or Poisson events for interactions), this latent variable can be used in further regression. These models can be easily implemented in Bayesian software such as JAGS (Plummer 2003), however the computational cost of fitting them to large datasets, particularly datasets with multiple social networks, is likely to be high. This is because, under this framework, each edge is a stochastic, unobserved variable in the model. Future work could seek to more formally apply these methods, and test how well they perform compared to the typically implemented (but again, not strictly necessary) network-based randomization approaches. Regardless, the task of accurately measuring the relationships between social network structure and outcome variables, along with correctly quantifying uncertainty in these estimates, is a key task not just for behavioural ecology research, but for the application of social network data to conservation questions.

7.3 Disease spread in cetacean social networks

In Chapter 5, I investigated the role of social structure in shaping simulated disease outbreaks in the southern resident killer whale population. The results of this analysis suggest that the population is highly vulnerable to outbreaks of cetacean morbillivirus-like pathogens, and that vaccination is not effective for controlling these outbreaks. While potentially important for conservation planning, there are numerous areas for further exploration from this analysis.

As noted in Chapter 5, our model assumes that individual social relationships stay the same after infection, as we have no data on how killer whales or any cetaceans alter their social relationships when ill. However, changes in social relationships could have significant impacts on disease spread. If individuals become socially isolated when noticeably ill, then disease spread may be curtailed (Lopes, et al., 2016; Stroeymeyt, et al., 2018). In contrast, if sick individuals receive increased social support, this may increase the spread of disease. It is therefore crucial to understand how social relationships change when individuals become sick to inform more detailed modelling efforts.

One way to investigate this question would be to use the long-term photographic record of the southern resident killer whales. While the cause of death for most individuals in this population can never be known, as their bodies are not recovered, many individuals exhibit distinct changes in body condition prior to death, indicative of serious health problems. In recent years, these changes in body condition have been quantified using drone imagery (Fearnbach et al., 2019), however severe cases can be identified from traditional photo-ID methods. This visible decrease in body condition is commonly referred to as “peanut head,” because of the shape that whales’ profile take on when their fat supply is depleted (Figure 7.2). This poor body condition does not appear to occur in all members of a social unit simultaneously, suggesting that the condition is not caused entirely by reduced access to prey, but likely has a disease component. A potential way to quantify how social position changes during illness would be to quantify social relationships of individuals before and during their periods of peanut head. These parameters could then be incorporated in further modelling efforts.

Figure 7.2 Example of "peanut head," indicative of poor body condition and potential illness. Photograph shows individual J50 exhibiting severe peanut head, characterized by the deep indentation behind the blowhole (indicated by white arrow). J50 was declared deceased less than a month after this photograph was taken.

Also of importance is work investigating the empirical patterns of disease spread within the population. While our analysis focused on a potential emerging disease, previous work suggests that there are numerous pathogens currently circulating within the southern resident community that may be impacting population growth (Raverty et al., 2017). If data on disease occurrence within a reasonable subsample of the population, methods similar to those implemented by Powell et al., (2020) could determine whether social network structure is relevant to the spread of these diseases. In addition, if genetic data on particular pathogens could be derived from fecal or breath sample, more specific understandings of transmission pathways could be derived via phylogenomic analyses (Ray et al., 2016). These disease prevalence and genomic data could be combined not just with association networks, but with interaction networks derived from aerial observation to understand which, if any, social interactions are relevant to the spread of pathogens. If specific disease transmission pathways could be determined, the differences in structure between association, physical contact, and synchronous surfacing networks could contribute to determining which pathogens are most prevalent within the population.

7.4 Mechanisms of social effects on fitness

Numerous studies have found links between the social environment and aspects of fitness in social mammals (Snyder-Mackler et al., 2020). Less well understood are the mechanisms by which sociality influences survival and reproductive success in these species (Ostner & Schulke 2018). In Chapter 6, I found impacts of the broader social environment on southern resident killer whale fitness. In particular, social bonds to females increased female fecundity, which social bonds to males decreased annual survival probability. While differences in competitive effort and cooperation during foraging are likely to contribute to these effects, it is unclear what precise mechanisms underlie these relationships.

In recent years, methods have been developed to monitor fine-scale aspects of health in wild cetaceans. Breath samples allow researchers to monitor pathogens (Raverty et al., 2017), fecal samples provide information about prey consumption (Ford et al., 2016) and various forms of stress (Ayers et al., 2012), and aerial photography can give further information about body condition (Fearnbach et al., 2019). Combining these methods with social network measures could provide further evidence about what aspects of health and physiology are effected by the social environment.

In the case of survival, the negative effect of adult males are likely due to competition for food resources. This could be confirmed by repeating the analysis presented in

Chapter 6, but using body condition indices and hormonal measures of nutritional stress rather than survival as the response variable. The next question would be at what level this competition occurs. Competition could be happening during foraging, when individuals are attempting to catch the same fish that their adult male associates are also chasing. However, as prey sharing is a key aspect of resident killer whale social structure (Wright et al., 2016), competition could be also be occurring after fish are already caught, as individuals compete to be the recipient of food sharing. Further behavioural observations using UAS, and re-analysis of historical data on prey sharing, will help to reveal whether this second form of competition occurs regularly.

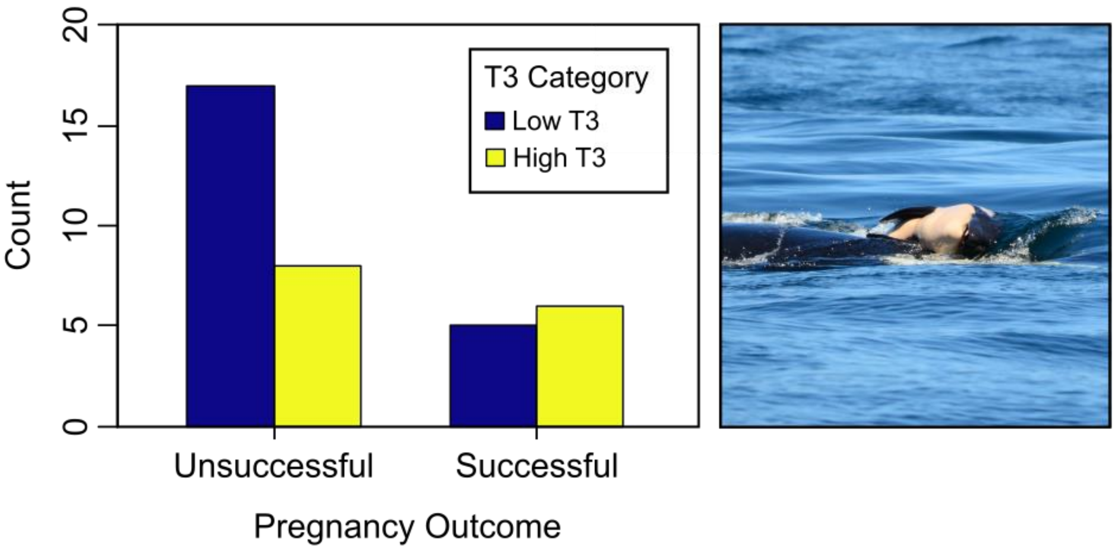

Figure 7.3 Pregnancy success in the southern resident killer whales. Left: Pregnancy outcomes and thyroid hormone (T3) concentration in southern residents. Low T3 indicates prolonged nutritional stress. Data from Wasser et al., (2017). Right: Photograph of dead neonate carried by J35, an example of late pregnancy failure. This neonate is believed to have died approximately half an hour after birth.

In the case of fecundity, the mechanisms are less clear. As this analysis only looks at the final outcome of reproduction (i.e. the observation of a live calf), it’s unclear at which stage the social environment is regulating reproduction in females. It’s possible that the regulation is occurring prior to pregnancy by female reproductive decisions. Females with fewer female associates to serve as potential alloparents, and with more dependent juvenile associates, may decide to forgo reproduction in a given year. It is also possible that the effect is due to differences in pregnancy success caused by social effects on nutrition. Recent evidence suggests that over half of all southern resident pregnancies end either in abortion or the calf dying prior to detection, and these abortions are linked to hormonal evidence of nutritional stress (Wasser et al., 2017; Figure 7.3). These two mechanisms could be disentangled by using hormonal data to assign pregnancy and pregnancy success, and using these variables as responses to the social environment, rather than fecundity itself.

7.5 Population trajectories and social structure

This thesis has highlighted two ways in which social structure can have impacts on population vital rates. First, disease transmission can cause both acute and long-term decreases in survival and reproduction, and is shaped by the structure of social contacts. Second, the behaviour of individuals' social partners can serve to either increase and decrease individuals survival and reproduction. Both of these processes have the potential to impact the overall population growth rate in ways that may not be predictable without information on social structure.

A particularly useful tool in animal conservation is population viability analysis (PVA). This method uses information on vital rates and population composition to project population size into the future under various scenarios, to derive probabilities of extinction within some set time frame. These methods can be individual-based or matrix projections, and can incorporate numerous possible influences on vital rates

(Lacy 2019). Recent work has recognized the influence that aspects of social structure can have on population growth, particularly in how social structure can influence patterns of reproduction (Vucetich et al., 1996; Walters et al., 2002). Less well explored is the role of social relationships themselves in shaping population growth. In the southern residents, there is evidence for the death of mothers and grandmothers increasing mortality hazards of individuals (Foster et al., 2012; Nattrass et al., 2019; **Appendix B**), interactions between sociality and environmental conditions (Ellis et al., 2017; **Appendix A**), and, in this thesis, relationships between the age-sex class of individual associates and vital rates. Such effects have not been included in population viability analyses, but may have significant impacts on projections of population size over time, particularly in extremely small populations. In addition, while the potential for disease spillover have been included in population viability analyses (Haydon et al., 2002), these efforts have not explicitly included social network structure in their predictions of disease spread. Including information about social networks and demography into viability analyses that include the possibility of large scale disease outbreaks could help inform risks associated with disease outbreaks in endangered population (Silk et al., 2019).

In the case of the effects found in Chapter 6, the dependence of social effects on demographic characteristics of associates makes it particularly important to incorporate these factors into population projections. As the population is small, the demographic composition of the southern residents is prone to dramatic changes over time. In particular, births in the southern resident community appear to be biased towards males, and the adult sex ratio of the population, while still biased towards females, shows trends towards greater male representation (Figure 7.4). This change in age-sex composition likely will have implications for individual social environment, and subsequently for survival and fecundity.

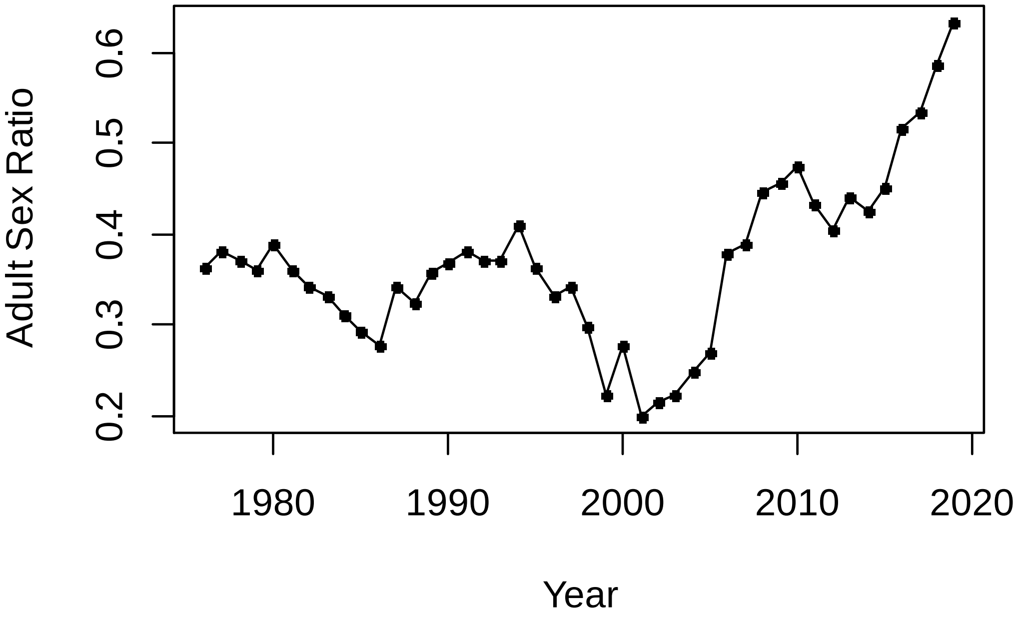

Figure 7.4 Adult sex ratio in the southern resident population. Sex ratio is expressed as the number of adult males divided by the number of adult females.

There are several unknowns that will need to be resolved in order to fully incorporate sociality in population viability analyses. Most importantly, the relationship between population dynamics and social network structure needs to be disentangled (Shizuka & Johnson 2019). Recent empirical (Firth et al., 2017; Goldenberg et al., 2016) and theoretical work (Farine 2019; Ilany & Akcay 2019) has suggested multiple mechanisms that could shape social network dynamics in animals, however these processes are likely to be different between systems. If these dynamics could be incorporated with individual-based models of population dynamics, changes in social effects on survival and fecundity, and changes in population vulnerability to disease outbreaks, could be incorporated in to predictions of population size over time, providing important information for management efforts.

7.6 Concluding remarks

Cetaceans, as a group, present difficulties to behavioural ecology research. These species present the opportunity to study deeply interesting questions about the evolution and consequences of sociality and cognition in the ocean. Simultaneously, the very traits that make them interesting, their large home ranges, aquatic lifestyle, slow life histories, and dynamic social systems, make them extremely challenging to study in their natural environment, both from the perspective of data collection and data analysis. These challenges are compounded by the urgent need for deeper knowledge about the factors influencing population trajectories in cetacean populations, the majority of which are threatened or endangered.

Here, I have attempted to contribute towards solving these problems more deeply by focusing on one particularly powerful tool, the application of social network analysis to wild cetacean populations. In this thesis, I have highlighted the strengths of social network analysis for quantifying social complexity, measuring social structure, evaluating disease risk, and determining which aspects of the social environment are relevant for survival and reproduction, while also drawing attention to the methodological challenges and drawbacks of these methods. It is my hope that this work will promote further investigations into these questions. In particular, I hope that the empirical results presented here will provide some small bit of extra information to inform the future management of the endangered southern resident killer whale population.

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Appendix A

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Author for correspondence:
S. Ellis
e-mail: s.ellis@exeter.ac.uk

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Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance

S. Ellis[1], D. W. Franks[2], S. Nattrass[2], M. A. Cant[3], M. N. Weiss[1], D. Giles[4], K. C. Balcomb[4] and D. P. Croft[1]

[1]Centre for Research in Animal Behaviour, University of Exeter, Exeter EX4 4QG, UK
[2]Department of Biology, University of York, York YO10 5GE, UK
[3]Centre for Ecology and Conservation, University of Exeter in Cornwall, Penryn, Cornwall TR10 9FE, UK
[4]Center for Whale Research, 355 Smugglers Cove Road, Friday Harbor, WA 98250, USA

SE, 0000-0001-9019-6040; MAC, 0000-0002-1530-3077

An individual's ecological environment affects their mortality risk, which in turn has fundamental consequences for life-history evolution. In many species, social relationships are likely to be an important component of an individual's environment, and therefore their mortality risk. Here, we examine the relationship between social position and mortality risk in resident killer whales (*Orcinus orca*) using over three decades of social and demographic data. We find that the social position of male, but not female, killer whales in their social unit predicts their mortality risk. More socially integrated males have a significantly lower risk of mortality than socially peripheral males, particularly in years of low prey abundance, suggesting that social position mediates access to resources. Male killer whales are larger and require more resources than females, increasing their vulnerability to starvation in years of low salmon abundance. More socially integrated males are likely to have better access to social information and food-sharing opportunities which may enhance their survival in years of low salmon abundance. Our results show that observable variation in the social environment is linked to variation in mortality risk, and highlight how sex differences in social effects on survival may be linked to sex differences in life-history evolution.

1. Introduction

An individual's mortality risk, their chance of dying at a given time, has fundamental evolutionary consequences [1]. Many aspects of life history have been shown to be linked to mortality risk such as age at first reproduction, parental care strategy and senescence [2]. Interestingly, males and females of the same species often have differing mortality risks due to their differing reproductive strategies [3]. For example, costly displays and intrasexual aggression increase the risk of male mortality in many mammal and bird species [4–6]. This has in turn been linked to life history; for example, higher rates of senescence have been reported in males of some polygynous species [7]. Understanding factors that govern the mortality risk of individuals has the potential to explain many important aspects of life history and behaviour, and why they vary between the sexes.

Social behaviour is important for many species and may affect individual mortality risk. In humans, for example, mortality risk has been linked to a variety of aspects of sociality (e.g. [8–10]). Social behaviours are usually direct, occurring between pairs or groups of individuals. However, an important feature of social behaviour is that these direct interactions form part of a complex network of interactions. An individual's position within this network, their social position, depends partly on their own interactions and partly on the interactions of others. An individual's social position will determine in part its access to resources and social information (information that can be learnt by observation of, or interaction with, other individuals [11–16]) and may therefore have implications for their mortality risk. Indeed, in several species social position has been linked to early life mortality risk [17–20]. However, the difficulty in collecting long-term dynamic social data means that the proximate mechanism by which sociality can affect mortality risk over the lifetime of individuals are largely unknown. To understand the ultimate processes driving the evolution of life-history strategies, and why these strategies may differ between the sexes, it is important to understand the link between social position and mortality risk.

Killer whales (*Orcinus orca*) are a particularly interesting species in which to study the relationship between sociality, sex, ecology and mortality risk. They are highly social: resident killer whales off the Pacific Northwest coast of the USA and Canada live in hierarchical societies [21], the social structure of which changes in different ecological conditions [22]. Social information is important to allow whales to find food, especially when resources are scarce [23], and family relationships also have important effects on the survival of individuals [24,25]. Male killer whales differ from females in their body mass [26], feeding habits [27] and likelihood of responding to social information [23]. In addition, resident killer whales have sexually divergent lifespans, with females who reach maturity predicted to live to 53, whereas males who reach maturity are unlikely to survive past 29 [25]. Killer whales are also one of only three mammals where females are known to have an evolutionary significant post-reproductive lifespan [28]. The importance of social relationships, their sexually divergent lifespans and their unusual life histories make killer whales a good species in which to study the relationship between sociality and mortality risk.

Here, we test the hypothesis that social position is linked to mortality risk in resident killer whales using 34 years of social and demographic data. Specifically, we (i) quantify the relationship between social position and survival in male and female resident killer whales and (ii) link this to resource abundance, to give an insight into the proximate mechanisms driving the relationship between sociality and mortality.

2. Methods

(a) Study site

This study was conducted on the southern resident killer whales inhabiting the waters off the coast of Washington State, USA and British Colombia, Canada. The population has been studied by annual photographic census undertaken by Orca Survey since 1976. In the summer, the southern residents inhabit the area around the San Juan islands, feeding almost exclusively on Chinook salmon (*Oncorhynchus tshawytscha*) [29,30]. The abundance of salmon in a given year has a significant impact on the mortality risk of resident killer whales [29,30]. The southern residents are a closed population of 71–98 individuals (between 1976 and 2010), with no social or genetic exchange with other sympatric killer whale populations [31,32]. Resident killer whales inhabit a hierarchical society. The smallest unit is the matriline consisting of the offspring and grand offspring of a female [21] and neither sex disperse, staying in close association with their matriline their whole life [21]. Higher levels include pod, community and clans, sharing broadly similar dialects and movement patterns [21].

(b) Data

Social associations were taken from the annual photographic census of whales between 1976 and 2010. Whales photographed within three body lengths (or within three body lengths of another group member) were considered to be part of the same group (electronic supplementary material, S1). Association groups were defined within an encounter (an observation of a group/groups of whales; see electronic supplementary material, S1). Group sizes ranged from single individuals to aggregations of 24 whales, with a mean of 2.5 whales per group. Each whale was observed a mean ($\pm$standard error) of 31.3 ± 0.67 times per year. Pairs of whales were observed together from 1 to 149 times per year with a mean ($\pm$standard deviation) of five ($\pm$7.9) observations per dyad. We use these association groups to construct a social network based on the 'gambit of the group' paradigm with the strength of association between two individuals calculated based on simple ratio indices [33,34] (see electronic supplementary material, S1). Whales in close association have the opportunity to hunt together and share food [27]. Our association measure therefore indicates the frequency with which individuals hunt, travel and socialize together. For the years 1990–2010, all data from a given year were used to calculate a single social network for each year. Between 1976 and 1989, there was a comparatively lower sampling effort and photographic data were sparser than in later years. To ensure that we had sufficient data to reliably infer social structure [33], in these early years we combined data into 2-year sampling periods to construct the social networks. The southern resident killer whales are monitored when they are inshore during the salmon runs in the summer. Over winter, they are usually further offshore and not observed. Most deaths occur over the winter. A whale is considered to have died in a given sampling period if they are not observed in the next summer (electronic supplementary material, S1).

Salmon abundance in the Pacific Northwest varies greatly between years based on the El Niño–Southern Oscillation and, more recently, fishing activity [35,36]. We use the salmon index calculated from test fisheries (begun in 1979) taken in the summer range of the southern resident killer whales as an estimate of salmon abundance ([37]; also used in [22,23]). The absence of data means that data from 1976 to 1978 are not included in the analysis including salmon abundance. Approximately half of all whale deaths occur in years with the lowest quartile of salmon abundance (34 of 65 deaths). For analysis, we classify the years with this lowest quartile of abundance as low salmon years, and the other years as high salmon years.

(c) Social communities

Resident killer whales preferentially associate with a small number of individuals [21]. This is reflected in the distribution of social association strength in the community [38], which is characterized by some strong bonds and many weaker bonds (mean $\pm$ s.d. social differentiation, $S = 1.09 \pm 0.18$; electronic supplementary material, S1). The biologically relevant social position for a whale with regard to survival and ecology is most likely to be within these smaller groups of important associates, rather than over the whole population. In this study, we therefore concentrate on an individual's social position within these networks of preferential associates.

We use community analysis to allow the groups of preferential associations to emerge from the patterns of social interaction. Communities were detected in each weighted annual social structure using a random walk algorithm [39]. Communities were defined independently in each network (example: figure 1). These communities are a good representation of the social structure of the population as a high proportion of social associations

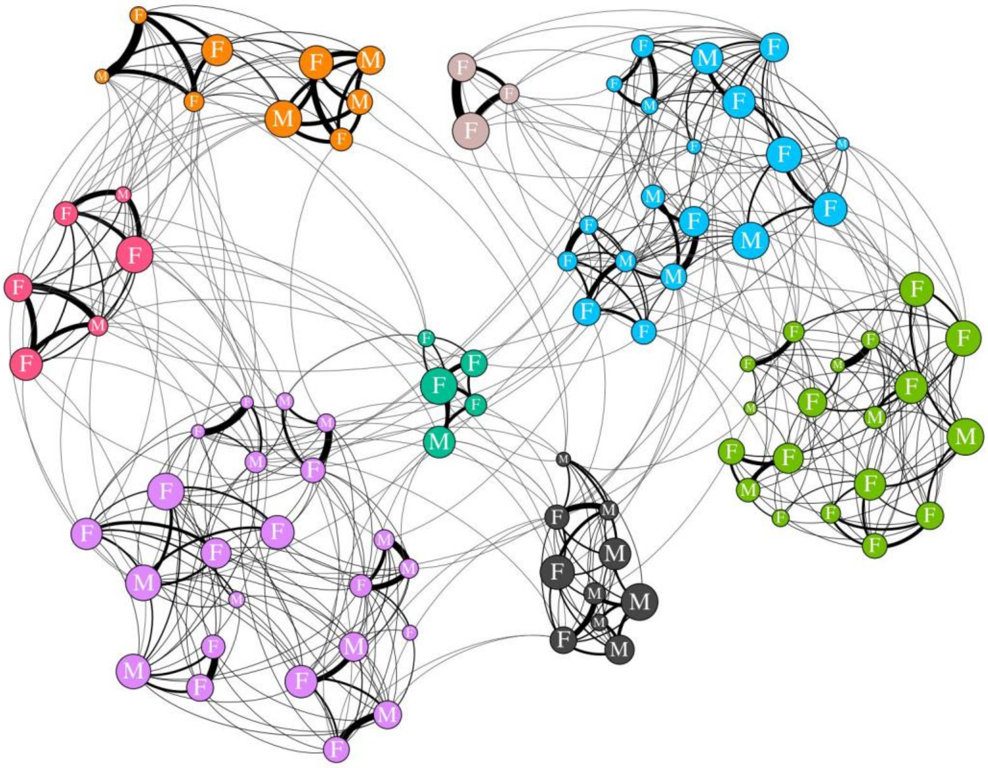

Figure 1. An example annual social network for the southern resident killer whale population (1996). Node colour shows community membership. Node size is scaled by a whale's normalized rank indirect centrality (within-community closeness). Node labels represent sex: M = male, F = female. Edge width is based on the simple rate index between two whales. Network visualized in Gephi.

are within, rather than between, communities: modularity was in the range 0.63–0.84. The killer whale population is significantly more modular than random (1000 data-stream permutations [see below], $p < 0.001$ in all years; median modularity of permuted datasets was 0.13 [interquartile range = 0.07–0.23]). The assignment of individuals to communities is robust. Individuals assigned to the same community in the original dataset are consistently grouped together in 1000 bootstrapped replicates: $r_{\mathrm{com}} = 0.81 \pm 0.01$ (mean ± standard deviation; electronic supplementary material, S1; [40,41]). As a measure of confidence in our calculated within-community network structure, we estimated the correlation between our observed association indices and the 'true' association indices [38]. Our within-community association indices are a good (greater than 0.4, [38]) reflection of the 'true' association pattern: mean (±standard deviation) annual $r = 0.75 \pm 0.09$ (electronic supplementary material, S1; [38]).

Annually, the population contained a median of six large (greater than five whales; see below) communities (range 5–9). Each large community contained an average of 11 ± 5.9 (mean ± standard deviation) whales. Communities tend to consist of a matriline, extended matriline or group of regularly associating matrilines. Throughout this study we use 'community' to refer to the small units derived from the social associations, rather than the larger separation between the northern and southern resident populations, which have also sometimes been referred to as communities [21].

(d) Quantifying social position

Social centrality is perhaps the most commonly used measure of social position. In essence, social centrality describes how well connected an individual is to others in their social system [33]. Social centrality therefore describes how well positioned an individual is to receive, for example, information, resources or disease from other members of their society [11–15]. In practice, an individual's likelihood of accessing resources or information held by other individuals will depend on two factors: (i) their direct connections to others, governed partly by their own social decisions, and (ii) their indirect connections to others in their community, which partly depend on the social choices of others [42]. We use two measures to capture the indirect and direct aspects of social centrality: closeness and degree. Closeness is the inverse of the average path length: the (weighted) number of steps from one individual to all others in the community. A high closeness indicates small number of weighted steps to all other individuals in the community and therefore a high social centrality. Degree is a simple unweighted count of a whale's associates. This can be seen as a measure of the number of social partners an individual has and hence their potential access to information and resources held by other members of the community [33]. Closeness depends on an individual's social position in the network and the indirect interactions, and the strength of the interactions, it has with other individuals. In contrast, degree depends only on an individual's direct associations. In this study, we are interested in an individual's social position within their network of close associates, their community. We therefore calculated centrality measures (community closeness and community degree) within an individual's local social community. To account for differing sizes of communities and annual populations, both measures were normalized for analysis. Measures were not calculated on communities with fewer than five whales, as patterns of social connection are limited in such small groups. Additionally, as closeness is highly skewed, it was also ranked within the network before normalization. These two measures quantify different but related aspects of social centrality. As would be expected, the measures are correlated, but the correlation is weak and highly variable (see electronic supplementary material, S2).

(e) Statistical analysis

We use survival analysis to investigate the social factors affecting the mortality of whales over their observed lifetime. Survival analysis describes an individual's probability of surviving beyond a specified time [43]. We analyse mortality risk using Cox proportion hazard (Cox PH) models which describe how the instantaneous risk (hereafter risk) of death occurring at a given time is affected by covariates. We use extended Cox PH

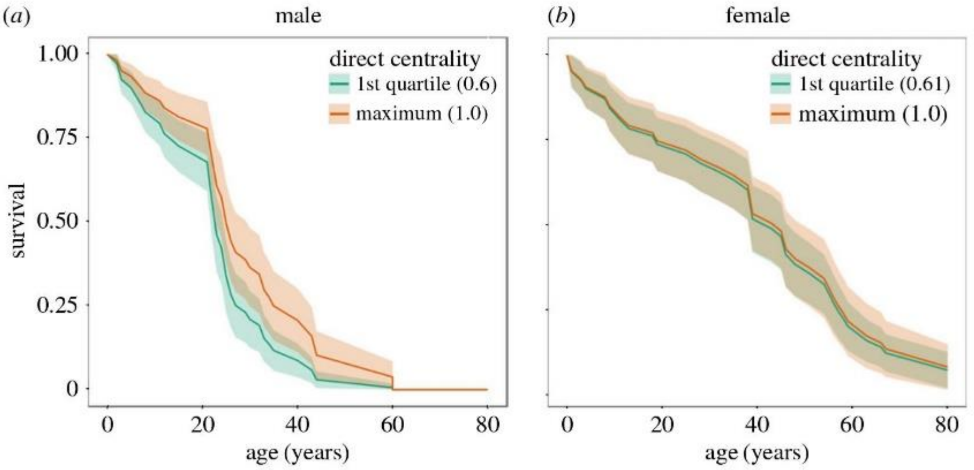

Figure 2. The survival of male (*a*) and female (*b*) killer whales based on their network centrality predicted by Cox PH survival models. The two curves represent the predicted survival of whales with the first quartile and maximum direct centrality (degree) of whales observed in the study. The survival of male whales is significantly related to their centrality within their social community (Haz. = 0.21 ± 0.14; Cox PH, $z = -1.95$, $e = 41$, $p = 0.0009$), whereas female survival is not (Haz. = 0.85 ± 0.66; Cox PH, $z = -0.005$, $e = 40$, $p = 0.112$).

models to investigate how a whale's probability of survival is affected by their position within the social network, which can change with time. For each Cox PH model we report the estimated hazard ratio (Haz.: calculated as the exponential of the model coefficient). A hazard ratio of exactly 1 indicates no differences in risk of mortality as the variable changes; a hazard ratio of less than 1, therefore, indicates a decreasing risk of mortality with a higher value of the variable. The hazard ratio is directly equivalent to increases (or decreases) in mortality risk per unit of variable i.e. a hazard ratio of 0.25 indicates a 75% decrease in the risk of mortality per unit of variable. Generalized linear mixed-effect models (GLMMs) were used for analyses not investigating survival. All GLMMs have a binomial error structure with whale identity as a random effect.

To account for the inherent autocorrelation in network data, we used permutations to produce a null distribution to compare to the observed data. Unless indicated otherwise, analyses presented here are based within social communities. For this within-community analysis, we used 10 000 within-community node permutations to produce the null models (see electronic supplementary material, S1). When analysing at the population level (rather than the within-community level), we used 10 000 data-stream permutations to produce the null models (indicated by superscript $^{\text{d.s.}}$ by the test name; see electronic supplementary material, S1). Additionally within each permutation, for whales of unknown sex we assigned a sex at random with 1000 imputations per null model. The mean network statistic of these 1000 sex imputations was used as the network statistic for that iteration of the broader network permutation. Permuted null models were created for all Cox PH models [15], and GLMMs analysing networked data. For each permutation of the data the model (Cox PH or GLMM) is applied to the randomized data. These permuted data are used to create a null distribution of the test statistic which is then compared to the observed value [33]. For permuted analyses, reported *p* values indicate the number of times the simulated test statistic was greater than or equal to the observed test statistic (sample included in the numerator and denominator [44]). For analysis not including network statistics, permutations were not used (indicated by the superscript $^{\text{n.p}}$ by the test name). All analyses were performed in R using the igraph, ggplot2, lme4 and survival packages.

3. Results

(a) Sex, centrality and survival

Within social communities, both direct and indirect social centrality significantly relates to the survival probability of male, but not female killer whales. Males with a higher community closeness (a measure of indirect centrality) have a significantly lower mortality risk than whales with a lower community closeness (Haz. = 0.33 ± 0.2; Cox PH, $z = -1.67$, events (e) = 41, $p = 0.0366$; figure 2*a*). In contrast, the survival of female killer whales is unrelated to their closeness centrality (Haz. = 1.06 ± 0.72; Cox PH, $z = 0.03$, $e = 40$, $p = 0.6924$; figure 2*b*). Similarly, males associating with a larger number of individuals in their community (within-community degree) have a significantly lower mortality risk than individuals with fewer associates (Haz. = 0.21 ± 0.14; Cox PH, $z = -1.95$, $e = 41$, $p = 0.0009$). In contrast, female within-community degree does not significantly influence survival (Haz. = 0.85 ± 0.66; Cox PH, $z = -0.005$, $e = 40$, $p = 0.112$). The effect of social centrality on survival is not simply an artefact of social group size: network community size does not influence the survival of either sex (male, Haz. = 0.99 ± 0.02, Cox PH$^{\text{d.s.}}$, $z = -0.42$, $n = 860$, $e = 41$, $p = 0.8529$; female, Haz. = 0.406 ± 0.26, $z = -1.76$, $n = 1410$, $e = 39$, $p = 0.7999$).

(b) Centrality, survival and salmon

We find that both male (Haz. = 0.10 ± 0.09; Cox PH$^{\text{n.p.}}$, $z = -2.7$, $n = 825$, $p = 0.001$) and female (Haz. = 0.03 ± 0.03; Cox PH$^{\text{n.p.}}$, $z = -4.16$, $n = 1335$, $p < 0.001$) survival is significantly related to salmon abundance. Salmon abundance has an important influence on the relationship between social position and male survival; in years of low salmon abundance, males with high social centrality have a lower mortality risk (community degree: Haz. = 0.002 ± 0.006; Cox PH, $z = -3.24$, $e = 41$, $p = 0.0001$; community closeness: Haz. = 0.02 ± 0.038; Cox PH, $z = -2.28$, $e = 41$, $p = 0.014$; figure 3). In contrast, in years of higher salmon abundance, social centrality does not significantly relate to male mortality risk (community degree: Haz. = 0.641 ± 0.72; Cox PH, $z = -0.24$, $e = 41$, $p = 0.06$; community closeness: Haz. = 1.03 ± 0.92, Cox PH, $z = -0.10$, $e = 41$, $p = 0.4706$; figure 3). The survival of females is not significantly related to their social centrality in years of either low salmon abundance (community degree: Haz. = 0.36 ± 0.42; Cox PH, $z = -0.72$, $e = 39$, $p = 0.215$; community closeness: Haz. = 0.51 ± 0.52; Cox PH, $z = -0.53$, $e = 39$, $p = 0.3046$) or high salmon abundance (community degree: Haz. = 0.95 ± 1.2,

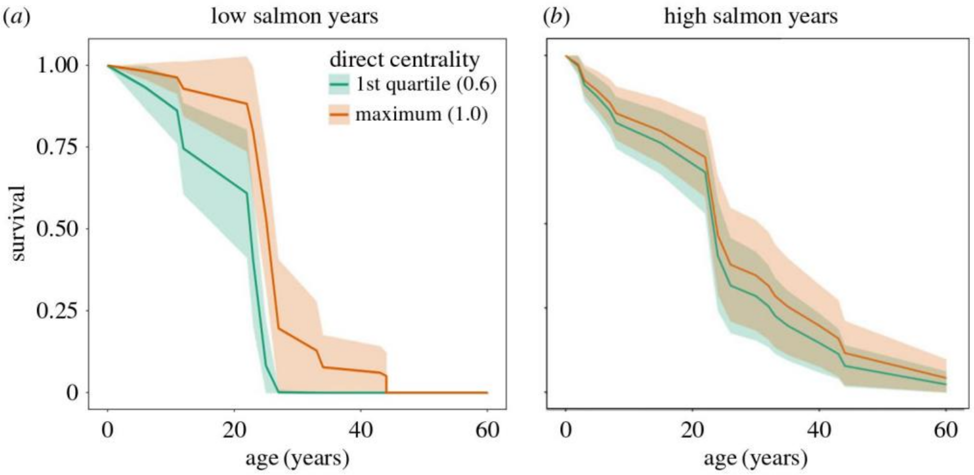

Figure 3. The survival of male killer whales in years of low (*a*) and high (*b*) salmon abundance. Lines show the survival of males with different direct social centrality as predicted by Cox PH models. Social centrality significantly relates to survival in years of low salmon abundance (Haz. = 0.002 ± 0.006; Cox PH, $z = -3.24$, $e = 41$, $p = 0.0001$) but not in years of high salmon abundance (Haz. = 0.641 ± 0.72; Cox PH, $z = -0.24$, $e = 41$, $p = 0.06$).

Cox PH, $z = 0.09$, $e = 39$, $p = 0.1168$; community closeness: Haz. = 1.54 ± 1.77, Cox PH, $z = 0.17$, $e = 39$, $p = 0.4706$).

Interestingly, males do not have a higher degree in years of low salmon abundance (GLMM: $\beta = 0.14$, $z = 0.46$, $n = 742$, $p = 0.2449$). This suggests that even though degree is important for survival in years when salmon are scarce, males do not appear to increase their direct centrality by associating with more individuals.

4. Discussion

Our results show that the survival of male, but not female, southern resident killer whales is significantly related to their social position in their local community. Males in the most central social positions (indirect centrality) have one-third of the mortality risk of those in the least central social positions. This is linked to salmon abundance: social position is only related to male survival in years of low salmon abundance.

Social position could affect the survival of males by mediating their access to resources via a number of mechanisms. For example, social information about the location of salmon has been shown to be important for resident killer whales who often follow post-reproductive females during collective movement, particularly during years of low salmon abundance [23]. A central social position may also increase a male's likelihood of receiving food from other whales. Resident killer whales, particularly females, often share fish that they catch with close associates [27]. An individual with more associates may be more likely to be the recipient of these food-sharing events, increasing their food intake, and in turn increasing their probability of survival. Other social factors may affect both social position and access to resources directly. Dominance, for example, could mediate both an individual's social position (e.g. [45–47]) and access to resources (e.g. [48,49]).

Social mechanisms will be most important when resources are scarce in years of low salmon abundance. Male killer whales may be more reliant than females on socially mediated resources because male resident killer whales are substantially larger than females: adult female southern resident killer whales are estimated to weigh up to 3338 kg, whereas adult males are estimated to weigh up to 4434 kg [26]. Males are estimated to require a 25% higher energetic intake to maintain this body size [26,50]. This higher energetic requirement of males will make them more vulnerable to starvation (e.g. [51–53]). A higher reliance on social information and food sharing may explain why the survival of males, but not females, depends on their position within the social structure.

Given the importance of the number of associates to the survival of male killer whales, it is interesting that they do not appear to increase their number of associates in response to low salmon abundance. There are possible behavioural and social explanations for this lack of social flexibility. Behaviourally, animals are time-limited, and face a trade-off between behaviours, including social and foraging behaviours [54]. In times of low resource availability, foraging pressures may reduce time available for social interactions, preventing males from increasing their social centrality, even when it would increase their probability of survival. The presence of such a trade-off is supported by observations of the behaviour of resident killer whales which have a lower rate of association in years of low salmon abundance [55] and a less interconnected social network [22], suggesting that they are engaging in less social behaviour. Competition for resources could also prevent males increasing their social centrality in years of low salmon abundance. Smaller group sizes in low resource conditions have been observed in a range of species (e.g. [56,57]). In a similar process, individuals may choose not to associate with a given male in times of low salmon abundance to reduce resource competition for themselves or their closer relatives. These non-exclusive mechanisms may explain why males appear unable to increase their social centrality in times of low salmon abundance.

Sociality can decrease an animal's mortality risk in a variety of ways. By living in groups animals can, for example, decrease their risk of predation or increase their foraging efficiency [58]. Recently the importance of heterogeneity in sociality has been highlighted, and a body of work shows that animals within a population can have a wide variety of social positions and social roles [59]. The heterogeneity of social bonds can have important fitness consequences. In several species, an individual's social bonds and affiliation (rather than social position) have been shown to affect their survival [60–62], reproductive success [18,63,64] and the survival of their offspring [17,18]. In addition, infant survival has been linked to social position in savannah baboons (*Papio cynocephalus*) [20]. However, to our knowledge, this is the first demonstration that social position is related to the survival of individuals in a complex society over their whole lifetime. In addition, we show that both the direct and indirect components of social position have survival implications and link these social effects to ecological conditions. Linking social structure and survival has many important evolutionary and ecological consequences [65]. For example, if fitness varies for different individuals within a group, we expect selection for individuals to move to these favourable social positions by changing their social strategy. However, an individual's position in the broader social structure is dependent on the behaviours and decisions of others in the population. Selection cannot, therefore, act directly on social position: it is difficult to imagine behavioural choices an individual could make to increase their indirect centrality. This highlights how behavioural phenotypes within a group interact to produce the fitness outcomes for the group members [66]. For male killer whales this means that their mortality risk partly depends on social factors outside their control which may contribute to their higher mortality rate in comparison to females. This may have fundamental life-history consequences, for example, by selecting for investment in reproduction in early life, and leading to an earlier onset of senescence [1,4].

In this study, we have shown that the survival of male resident killer whales is related to their position within a complex social system, especially in years of low resource abundance. Most models of social and life-history evolution assume a relatively constant and homogeneous social environment. In this study, we show that this may be an underestimation of the complexity of the evolutionary consequences of sociality, and that the heterogeneity and dynamics of social systems can have fundamental fitness consequences.

Ethics. Data were collected by the Center for Whale Research under federal permits (Marine Mammal Protection Act permit 532-1822 and/or Department of Fisheries and Oceans license 2006-08/SARA-34) in both the United States and Canada.

Data accessibility. Data to replicate the statistical tests are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.654sm [67]. Requests for access to raw data can be directed to the authors or the Center for Whale Research (www.whaleresearch.com).

Authors' contributions. S.E. and D.P.C. conceived the project in discussion with M.A.C., S.N. and D.W.F. S.E. conducted the analysis in discussion with D.W.F. and D.P.C. and with assistance from M.N.W., using data collected and managed by D.G. and K.C.B. S.E. made the figures and drafted the manuscript with input from all authors.

Competing interests. We have no competing interests.

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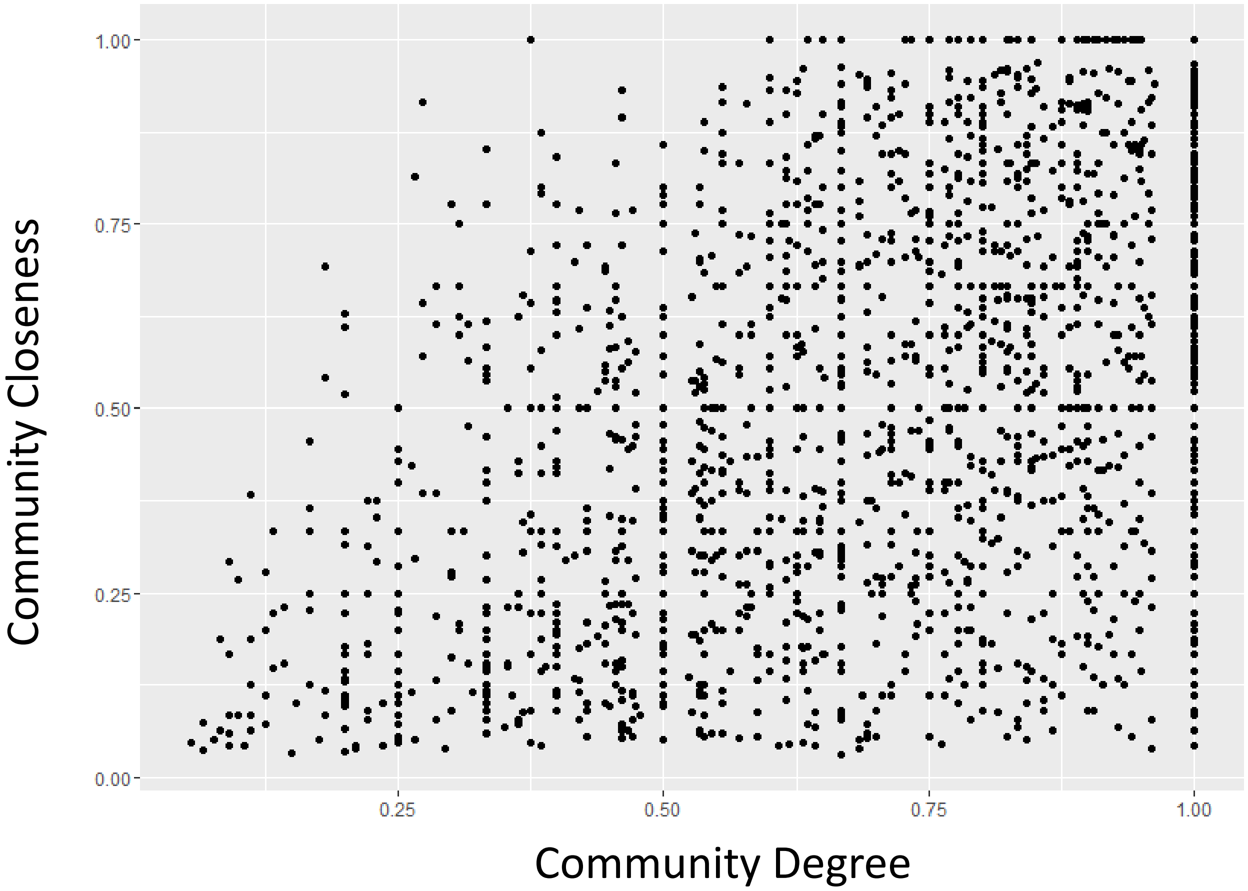
Supplemental material 1

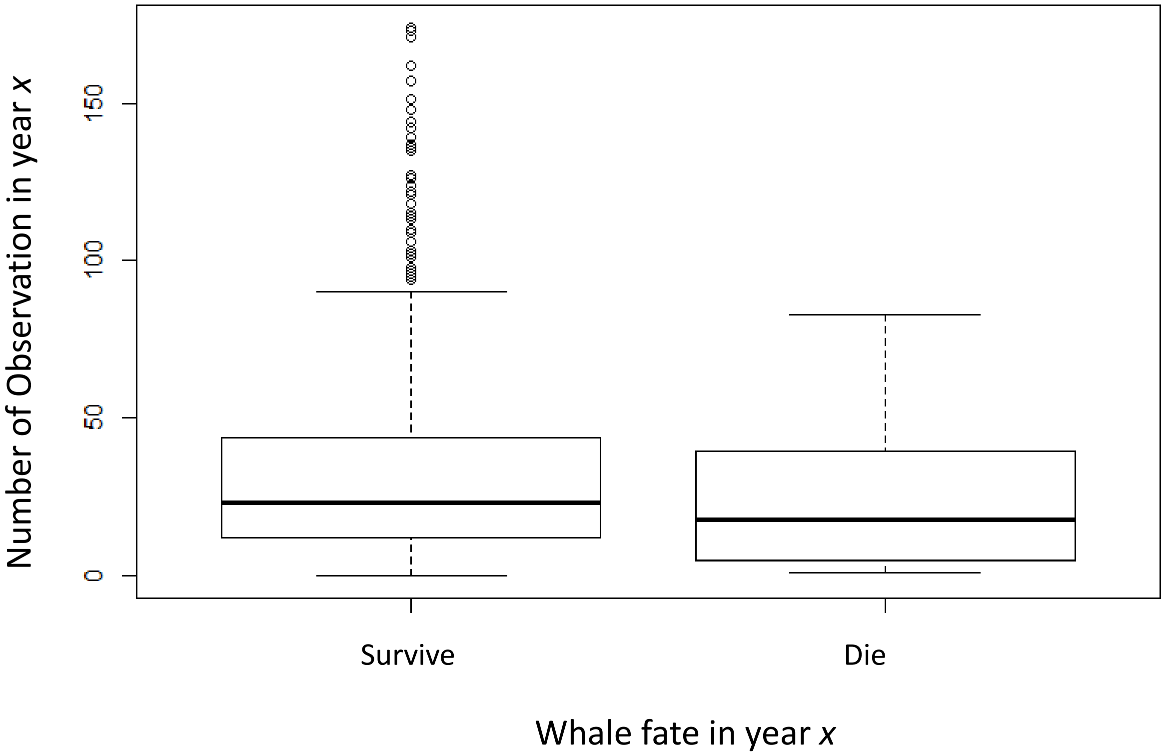
A) The Relationship between community degree and community closeness

There is a signficant relationship between community closeness and community degree (GLMM Est=4.26, z=16.079, n=2067, p<0.01). However, as can be seen from this figure this correlation is neither close nor consistent.



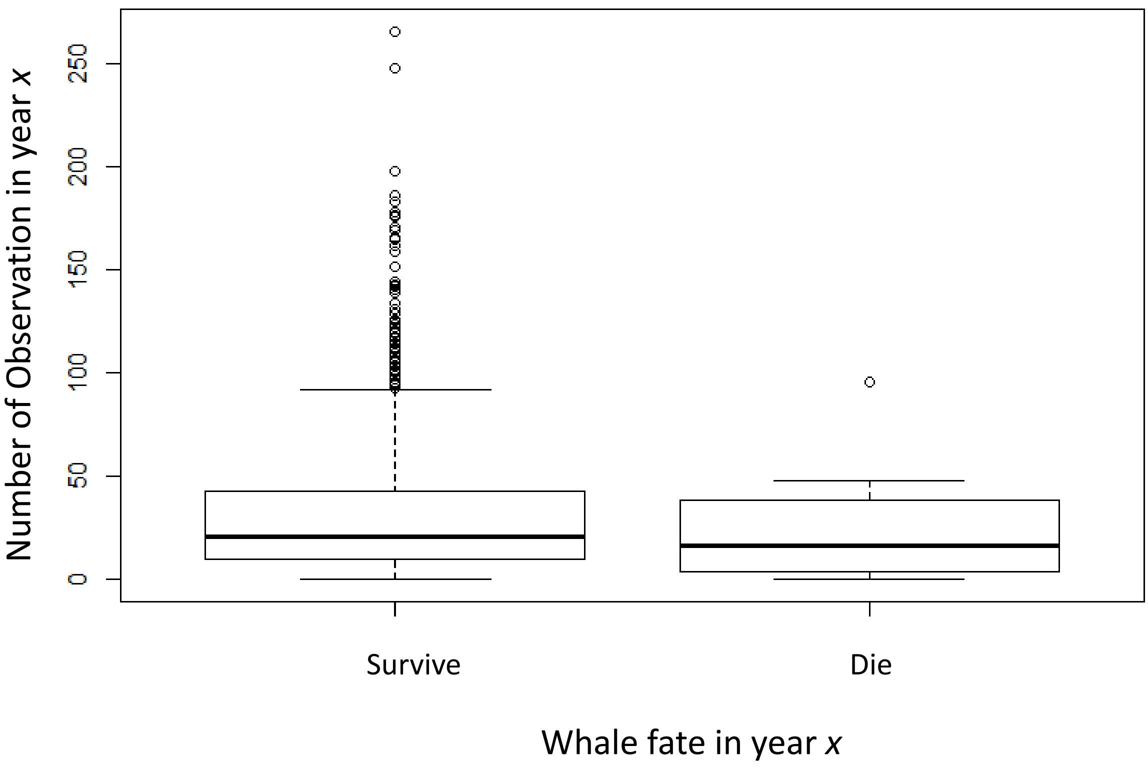
B) Relationship between observations and survival

Males



There is no significant difference between number of observations of males in years that they die and years in which they survive (Est= -0.009, z=-1.3, n= 860, p= 0.21).

Females



There is no significant difference between number of observations of females in years that they die and years in which they survive (Est= -0.0.13, z=-1.8, n= 1410, p= 0.08).

Supplemental material 2

Data collection

Annually between June and August Orca Survey performed regular *ad hoc* boat surveys in the feeding grounds of the resident killer whales of Washington State, USA and British Colombia, Canada. Whales were encountered on an average 43±4.45 (mean ± SE) survey days per year. During a survey whales encountered together were photographed with high quality cameras. Whales were individually identified based on unique marking patterns by experienced observers [1]. Marks are unique and distinctive and identification errors by experienced observers are very rare.

We use the gambit of the group paradigm: assuming individuals in close spatial association are interacting [2,3], which is a common approach in the study of animal sociality [4]. We define whales as within the same group if they are within three body lengths of one another. When encountered in groups whales were most commonly travelling, resting or socialising and occasionally foraging, though most commonly hunting was undertaken outside of the three body length distance [5]. Whales travelling and socialising have shallow (less than 3m) and short dives (less than 30 seconds) [6] and surface together or in very quick succession. Patterns of association above water are therefore likely to be representative of below water association. In addition we employ a chain rule [7] so individuals within three body lengths of an associate are still considered to be part of the same group. An average of 1043.29±142.24 encounters were observed per year.

Social network construction

We used our observed association groups to construct annual networks of social association. The strength of the association between two individuals was estimated based on simple ratio indices [4,8]. The simple ratio index for assessing the strength of social affiliation between two individuals and is given as the probability of each individual being observed [4,8]. Networks were calculated annually between 1990 and 2010, and for two years of association between 1976 and 1989 to control for the comparatively lower sampling effort in the earlier years of the study (mean annual observations: 1976-1990=228, 1990-2010=1053).

We calculated how the distribution of our calculated association indices reflect the distribution of the 'true' observed associations as a measure of confidence in our calculated network structure [9]. Social differentiation in the observed data (approximated using the methods described in [9]) was high: within-community S = 1.25 ±0.09; table S1. Within-communities the calculated association indices accurately reflect the estimated 'true' association pattern (r= 0.75 ± 0.09; table S1).

Statistical analysis

Individuals within social networks are, by definition, not independent, violating the assumption of most standard statistical tests [10]. To control for this it is necessary to create null model expectations based on permutations of the data [4,8,10].

Our analysis is based on measuring effects within communities. Using data stream permutations [4,11] in this case is inappropriate because all randomly constructed networks will have a different community structure. Data stream randomisations permute the groups individuals are associated in (in our case the observed association groups) [11]. Within a data-stream permutation, a given individual will occur in communities with very different structural properties, and will therefore have a very high variability in their within-community network position. Using data-stream randomisations will therefore overestimate the variability an individual experiences in their community network structure and will therefore overestimate the significance of any variable during analysis. Conversely using data-stream permutations, while preserving community structure will have insufficient variability to produce a useful null model. We therefore use node-based randomisations to construct the null models for within-community analysis**.** Node-based randomisations are based on permuting the properties of the nodes in a network to provide a randomised network with the same structural properties as the original observed network [8,7]. In our analysis individuals are assigned a permuted position within their community, the network properties are then calculated, which is used as the null model. Although node-based randomisations will not compensate for group size biases [11,12], it does allow us to preserve community structure which means it provides a more representative null model for this analysis. When testing the effect of community size on survival we used data stream permutations (10 000) as these analysis did not rely on consistent community structure (superscript $^{d.s.}$)

In both cases, from each permuted network the test statistic (*z*) is calculated, and compared to that from the real data. The reported p value is the proportion of times the test statistic from 10 000 permutations is larger than that from the real data. All p values testing network effects are based on this process.

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Table S1: Social differentiation (*S)* and how will this represents the calculated association indices (*r*), calculated using the methods described in [9]. A value of *S* near of greater than 1indicate a population where individuals have highly differentiated social relationships. *r* is limited to between 0 and 1. *r*=1 suggests a near perfect representation of the ‘true’ association patterns in the calculated association indices. Values *r* greater than 0.4 are considered to show the calculated indices are a ‘fair’ representation of the true structure [8,9]. Values of *r* greater than 0.8 are considered to be a ‘good’ representation of the data [8,9]. Community assortivity robustness, r_{com}, represents the how robust the assignment of a pair of individuals into the same community is given social structure and sampling [13]. All values are well above the 0.5 threshold suggested for a robust assessment of community structure [13]

Year	Within Community *S*	Within-Community *r*	*Community robustness (r_{com})*
1976/77	1.11	0.71	
1978/79	1.26	0.61	
1980/81	1.10	0.63	
1982/83	1.15	0.60	
1984/85	1.24	0.86	
1986/87	1.29	0.76	
1988/89	1.19	0.92	
1990	1.38	0.70	
1991	1.26	0.79	
1992	1.27	0.77	
1993	1.34	0.64	
1994	1.37	0.63	
1995	1.37	0.66	

1996	1.28	0.75
1997	1.18	0.82
1998	1.06	0.77
1999	1.27	0.73
2000	1.15	0.87
2001	1.23	0.85
2002	1.21	0.85
2003	1.30	0.78
2004	1.36	0.75
2005	1.38	0.72
2006	1.19	0.81
2007	126	0.79
2008	1.38	0.60
2009	1.1	0.85
2010	1.19	0.74
Mean (± std. dev.)	**1.25 (±0.09)**	**0.75 (±0.09)**

Appendix B

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Postreproductive killer whale grandmothers improve the survival of their grandoffspring

Stuart Nattrass[a,b], Darren P. Croft[c], Samuel Ellis[c], Michael A. Cant[d], Michael N. Weiss[c,e], Brianna M. Wright[f], Eva Stredulinsky[f], Thomas Doniol-Valcroze[f], John K. B. Ford[f], Kenneth C. Balcomb[e], and Daniel W. Franks[a,b,1]

[a]Department of Biology, The University of York, York YO10 5DD, United Kingdom; [b]Department of Computer Science, The University of York, York YO10 5DD, United Kingdom; [c]Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PY, United Kingdom; [d]Centre for Ecology and Conservation, University of Exeter in Cornwall, Penryn TR10 9FE, United Kingdom; [e]Center for Whale Research, Friday Harbor, WA 98250; and [f]Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC V9T 6N7, Canada

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Understanding why females of some mammalian species cease ovulation prior to the end of life is a long-standing interdisciplinary and evolutionary challenge. In humans and some species of toothed whales, females can live for decades after stopping reproduction. This unusual life history trait is thought to have evolved, in part, due to the inclusive fitness benefits that postreproductive females gain by helping kin. In humans, grandmothers gain inclusive fitness benefits by increasing their number of surviving grandoffspring, referred to as the grandmother effect. Among toothed whales, the grandmother effect has not been rigorously tested. Here, we test for the grandmother effect in killer whales, by quantifying grandoffspring survival with living or recently deceased reproductive and postreproductive grandmothers, and show that postreproductive grandmothers provide significant survival benefits to their grandoffspring above that provided by reproductive grandmothers. This provides evidence of the grandmother effect in a nonhuman menopausal species. By stopping reproduction, grandmothers avoid reproductive conflict with their daughters, and offer increased benefits to their grandoffspring. The benefits postreproductive grandmothers provide to their grandoffspring are shown to be most important in difficult times where the salmon abundance is low to moderate. The postreproductive grandmother effect we report, together with the known costs of late-life reproduction in killer whales, can help explain the long postreproductive life spans of resident killer whales.

menopause | grandmother effect | grandmothering | postreproductive life span | killer whales

Many mammals exhibit reproductive senescence, where fecundity declines with age (1). This reproductive senescence is typically aligned with somatic senescence—with both reproduction and survival gradually decreasing together with age (2, 3). In contrast, reproductive senescence is unusually accelerated relative to somatic senescence in humans (*Homo sapiens*), short-finned pilot whales (*Globicephala macrorhynchus*), belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and resident-ecotype killer whales (*Orcinus orca*; hereafter killer whales) (4). This manifests as a prolonged postreproductive life span: a long period of a female's life after reproduction where she can no longer reproduce (5). For example, approximately 3-quarters of women that survive into adulthood in hunter-gatherer societies do not give birth after 45 y, and they can expect to live into their mid-60s, on average (6, 7). Similarly, female killer whales also have extremely long postreproductive life spans; they stop reproducing in their late 30s and early 40s (4, 8) but can continue to live for decades thereafter (4, 5, 9); 64% of female killer whales that survive to the age of 10 y (approximately the point of sexual maturity) will live to be postreproductive (survive to at least age 45 y), at which point they will then have an expected postreproductive life span of 15.78 y.

Understanding why the female postreproductive life span has evolved in humans and some species of toothed whales has been a challenge for evolutionary biology. Research on humans suggests that the postreproductive life span has evolved, in part, due to the inclusive fitness benefits postreproductive females can gain by helping their kin (the grandmother hypothesis; refs. 10–12). In particular, the grandmother effect predicts that postreproductive grandmothers increase their inclusive fitness by supporting grandoffspring that are dependent on provisioned food for some time following weaning (13–15). There is substantial support for the grandmother effect across a range of human societies, including modern hunter-gatherer societies and preindustrial populations, which show that postreproductive grandmothers increase the survival of their grandoffspring, thus increasing their own inclusive fitness (10, 11, 14, 16–19). Although there is evidence for grandmother benefits in animals such as elephants (20, 21), there is no evidence for a postreproductive grandmother effect in nonhuman animals that have a prolonged female postreproductive life span.

For postreproductive females to be able to gain inclusive fitness benefits, they need both the opportunity to interact with grandoffspring and also a direct mechanism by which they can increase the survival of their kin. In killer whales—which are the best-studied species of toothed whales that exhibit a prolonged postreproductive life span—offspring do not disperse away from

Significance

Why humans and some species of whales go through menopause remains an evolutionary puzzle. In humans, postreproductive females gain genetic benefits by helping family members—particularly increasing their number of surviving grandoffspring. The extent to which these grandmother benefits are important in the evolution of menopause in whales remains unclear. Here, we test the grandmother effect in resident killer whales, where females can live for decades after their last reproductive event. We show that grandmothers increase the survival of their grandoffspring, and these effects are greatest when grandmothers are no longer reproducing. These findings can help explain why killer whales have evolved the longest postreproductive life span of all nonhuman animals.

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[1]To whom correspondence may be addressed. Email: daniel.franks@york.ac.uk.

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their mother (22, 23). This results in a close-knit family-based society, where grandmothers regularly group with both their offspring and their maternal grandoffspring. Previous research on killer whales has demonstrated a mother effect, with mothers increasing the survival of their weaned offspring (24). This effect is particularly strong for male offspring, but is irrespective of whether the mother is reproductive or postreproductive (24). In addition to supporting offspring to independence, postreproductive females might support grandoffspring directly by cooperative foraging and food sharing (25) or sharing ecological knowledge (26). This presents the clear potential for selection for helping grandoffspring in killer whales. Here we test the grandmother effect in killer whales by examining the survival of grandoffspring with living or recently deceased grandmothers. We also test whether postreproductive grandmothers support grandoffspring better than reproductive grandmothers. We control for the mother effect and for resource abundance in testing these hypotheses. Finally, postreproductive grandmothers can gain inclusive fitness benefits by reducing the interbirth interval of their daughters (18), and thus increasing their daughter's lifetime reproductive success; thus we also examine the effect of mothers on the interbirth interval of their daughters.

Methods

Study Populations. Demographic records were collected annually using photographic censuses for 2 resident killer whale populations: the southern (1976–2016) and northern (1973–2016) populations in the inshore coastal waters of Washington State and British Columbia, Canada (see refs. 9 and 27 for details). Resident killer whales are typically observed between May and November, when the animals frequent inshore waters. Individuals were identified by their unique fin shapes, saddle patches, and the presence of any nicks or scratches, and were sexed using distinctive pigmentation patterns around the genital slits and, in adults, differences in fin size. Genealogical relationships were inferred from long-term observations of social organization, and mothers were identified by their repeated association with young calves.

The data for each individual consisted of a year of birth, a year of death, and the identification (ID) of their mother when known. From this, we calculated age at death for all individuals, and maternal grandmother ID for those individuals whose mother had a known mother as well. Anonymized data can be accessed on OSF through the following link: https://bit.ly/2n5cBHU (28). Maternal grandmothers, and not paternal grandmothers, were assessed because there is no dispersal and thus paternal grandoffspring are raised outside of the group. For grandmothers born prior to the start of the annual censuses, we assigned estimated birth years based on birth histories and the ages of their offspring. We filtered the data ($n = 726$ individuals) to include only individuals with known maternal grandmothers, giving a sample size of 378 individuals (92 males, 76, females and 210 individuals of unknown sex who died before reproductive maturity). As there is no dispersal from either population, mortality was recorded if an individual's matriline was observed in the population within a given year but the individual did not appear.

Annual indices of Chinook salmon (*Oncorhynchus tshawytscha*) catch from test fisheries were used as a measure for region-wide salmon abundance within each year in the Pacific Northwest (e.g., ref. 26). The abundance in each year was calculated as the mean salmon abundance from 3 different sites, covering the entire key habitat range of the resident killer whale populations: southeast Alaska, northern British Columbia, and the west coast of Vancouver Island. This salmon index comes from the Chinook Technical Committee abundance indices, which are based on the output of the Pacific Salmon Commission Chinook model, and aggregated from 3 aggregate abundance-based management fisheries areas (29) and is scaled such that an index of 1 is the mean abundance for the period 1979–1982 (see appendix G in ref. 30). These data were available from 1979 to 2015. Individuals observed before 1979 were therefore left-censored, leaving a dataset of 4,578 whale-years lived across the 378 individuals. Individuals who died within the same year as their birth were assigned an age at death of 0.01 (see below for details).

Survival Model with Time-Dependent Effects. We used an extended Cox proportional hazards model to examine the consequences of a grandmother's death on grandoffspring survival, which accounts for right-censoring of data for some individuals (in this case, right-censoring occurred when an individual was still alive at the end of the study). The model was fit with maximum likelihood, and variations of the model were examined using Akaike information criterion (AIC) model selection; these are detailed below and are presented in further detail in *SI Appendix*. All analysis was implemented in R 3.5.0 (31) using the "survival" package (32).

Individual sex was coded as 0 for females and 1 for males, and individuals of unknown sex were coded as 0.5 (which gives equivalent results to randomizing sex). When a focal individual (of any age) died in the same year as their mother/grandmother (and thus we do not know for certain who died first), death order was randomized with equal chance of either dying first. The models ran with annual time steps, and, if the focal individual was determined to have died after their mother/grandmother, the age at death was set to the age in the year of death +0.01. This arbitrary small number is an implementation requirement, due to the model working in units of years, which allows us to capture the fact that the individual dies after its mother/grandmother, and could take any value between 0 and 1 with the same result. Because we are correlating mother/grandmother death with (grand)offspring death, not adding this number would implicitly add the assumption that (grand)offspring always die first. The death order matters because we examine mortality within a period following the mother's or grandmother's death. For each model, the population was run through 10,000 randomizations of the death order—for individuals with unknown death order—and the median coefficient, P values, and likelihoods were calculated.

There is a known effect of mother death in killer whales; adult sons are more likely to die in the 2 y following the death of their mother than similar-aged males with living mothers (24). Thus, we therefore controlled for grandoffspring who recently lost their mother by accounting for the contribution of the mother to the survival of her offspring. Previous work has shown that offspring show an increased mortality following the death of their mother, especially when the offspring are at least 30 y old when their mother dies. However, on the filtered dataset used here—of those individuals with a known grandmother—there were no individuals with a mother who died when the offspring was over 30 y old. We therefore did not include offspring age at mother death as a covariate. The best-fitting model of mother effect on survival on our current, reduced dataset captures the key significant short-term effect of mother death on the death of sons (24), and thus this term was retained in all statistical models to control for the mother effect (Eq. **1** and *SI Appendix*).

Our grandmother analysis took a variety of forms. We assign individuals to 3 categories depending on the status of their grandmother: 1) those with living grandmothers, which we consider as the baseline scenario; 2) those with grandmothers who died within the previous 2 y; and 3) those with grandmothers who died prior to the last 2 y. We chose a period of 2 y because we may expect some delayed effects of grandmother death on grandoffspring mortality. Within the 2 y, the calf might get by without its grandmother for a limited time, but, after surviving this period, the calf might be able to adjust, in a number of ways, to not having its grandmother around (e.g., by changing its social connections and gaining support from other females). Note that changing the threshold to 3, 4, or 5 y following the death of the grandmother does not significantly impact results, with the best-fitting model's AIC varying by less than 1 for these changes. As such, we report the results with a threshold of 2 y. We also allow the model (prior to model selection) to capture the possibility that any survival benefits from grandmothers may be sex-specific. Thus, we include a separate series of terms that only affect males. Potential differences between postreproductive and reproductive grandmothers were captured with a term reflecting whether a grandmother is postreproductive, which we conservatively defined as those over 45 y old, consistent with previous work (26).

To control for the effect of Chinook salmon abundance on mortality (33), salmon abundance was included as a time-dependent variable. An interaction between salmon abundance and grandmothering was also considered, and we fitted models including interaction effects of salmon with each of the grandmother terms in the final grandmothering survival model.

Cox proportional hazards models return 2 types of results. First, there are coefficients representing the contribution of a term (e.g., grandmother death) in a similar manner to those in linear models. Second, they return hazard ratios (HRs; the exponential of the coefficients), which are a factor by which the risk of death is multiplied. An HR of 1 indicates that there is no change in mortality between cases, whereas a value above 1 indicates an increased risk of death. Reported confidence intervals represent the range of parameters returned from the randomizations within the model.

Interbirth Interval Model. We used a generalized additive model to examine the consequences of a grandmother's status on her daughters' interbirth intervals. To test whether grandmothers decrease their daughters' interbirth intervals, we regressed a number of covariates on each interbirth interval.

Here we refer to "daughter"' as the female giving birth to the 2 calves in the interval, and "grandmother" as the mother of that daughter (and thus grandmother to the calves in the interval). We control for the daughter's age in the model by fitting it as a smooth term. This is defined as the daughter's age in the year when she gives birth to the second calf in the interval. We also included the following as covariates in the model: whether the first calf in the interval survived past the age of weaning [defined as 2 y (34)], whether the grandmother was alive 2 y into the birth interval (i.e., the time after which a surviving calf would be weaned), whether the grandmother was alive and postreproductive 2 y into the interval, and the mean salmon abundance during the interval. We note that—as with most long-term observational studies—the analysis is based on observed births, and there will be births that are unobserved due to calves dying very soon after birth (8). All full-model specifications can be found in *SI Appendix*, Table S12.

Results

Survival Model. We considered a number of models with a variety of terms (*SI Appendix*) including a general grandmother effect, and an additional effect of the grandmother being postreproductive. AIC differences between models were small. Each of the models with a close match to the best model (AIC differences of <2) show a general grandmother effect, and we therefore focus on the model with the lowest AIC value (*SI Appendix*). Schoenfeld residuals of the best-fitting model indicate that the grandmother effect is consistent across all ages, meeting the proportional hazards requirements ($\chi^2 = 1.71$, $P = 0.19$), as does the grandmother age at death ($\chi^2 = 1.28$, $P = 0.26$) and salmon index ($\chi^2 = 1.72$, $P = 0.19$). The best-fitting survival model (AIC = 1,254.1) for the effect of grandmother status on grandoffspring survival gives the mortality hazard of an individual at age t ($h(t)$) by

$$h(t) = h_0(t) exp\{2.9\, sMR + 4.3 GMR + 0.4 GMo45 - 2.8(slm \times GMR)\}, \quad [1]$$

where $h_0(t)$ is the baseline hazard at age t; sMR = sex when the focal individual's mother has died in the last 2 y; $GMR = 1$ when the focal individual's grandmother has died in the last 2 y; $GMo45 = 1$ when the grandmother has died, and was older than 45 at the time of her death; slm is the value of the annual salmon index; and model coefficients are rounded to a single decimal place (see *SI Appendix* for more precise values).

We find evidence for the grandmother effect in killer whales: The death of a grandmother reduces the survival of her male and female grandoffspring in the 2 y following her death. Grandoffspring whose maternal grandmother died within the last 2 y have a mortality HR 4.5 times higher than an individual with a living grandmother, when salmon is indexed at 1 (the mean abundance between years 1979 and 1982). Further, the model shows that those individuals who lose a postreproductive grandmother see their mortality increase above that of a reproductive grandmother by a factor of 1.5 (independent of salmon). Thus, an individual losing a postreproductive grandmother will see their mortality risk increase in total by a factor of 6.7 when the salmon index is 1. The AIC analysis shows that the GMR and $GMo45$ terms both have variable importance greater than 0.75. This means that the probability that these terms are in the Kullback–Leibler best model out of the candidate set is over 75%, demonstrating the importance of grandmothers and their postreproductive status in the model (*SI Appendix*, Table S2). Fig. 1 shows example survival trajectories for a 5-, 15-, and 20-y-old whale whose grandmother is alive (red line/circles), whose reproductive grandmother has recently died (blue line/squares), and whose postreproductive grandmother has recently died (green line/triangles). Adding the weaning status of grandoffspring (defining weaned as those over 2 y old) to the best-fitting model (AIC = 1,254.8; model 16) does not improve model fit, or show any indication that grandmother effects are specific to weaned or unweaned grandoffspring (*SI Appendix*, Tables S10 and S11).

When we consider interactions between the grandmother's death and salmon abundance, the coefficient for the effect of the grandmother's death decreases with a slope of −2.8 (95% CI: −6.5 to 1.5) per unit of salmon index. This means that an increase of salmon by the mean abundance (i.e., a doubling) reduces the coefficient of the grandmother effect by 2.8, while a decrease by the mean abundance increases the coefficient of the grandmother effect by 2.8. Thus, the grandmother effect operates when salmon index is lower than 1.536, which is above the mean salmon index. Seventy-eight of the 123 grandoffspring deaths occurred below this salmon threshold, despite survival being mitigated by grandmothers. When a grandmother is postreproductive, the threshold at which she provides benefits is raised further to a Chinook salmon index of 1.67.

Of the candidate models with ΔAIC < 2, all of the models included a mother effect (sMR) and grandmother effect (GMR). Six of these 7 models include the additional effect of a grandmother

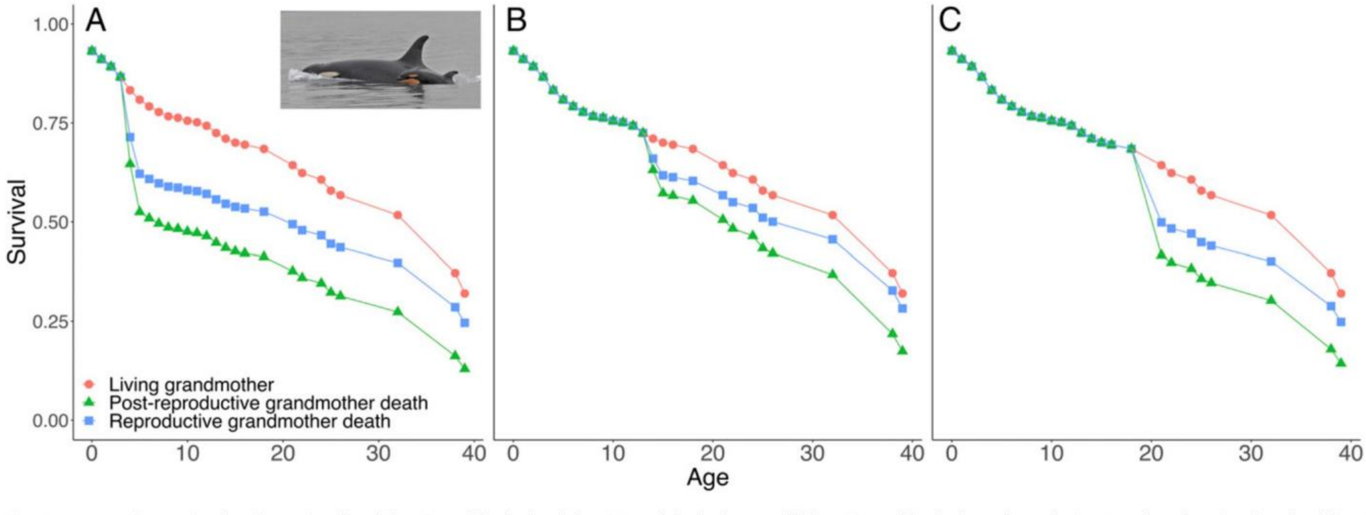

Fig. 1. Example survival trajectories for (*A*) a 5-y-old whale, (*B*) a 15-y-old whale, and (*C*) a 20-y-old whale, when their grandmother is alive (red line/circles), when their reproductive grandmother has recently died (blue line/squares), and when their postreproductive grandmother has recently died (green line/triangles), where the salmon index is fixed at 1 across all years. Survival is derived from the best-fitting extended Cox proportional hazards model for grandoffspring experiencing their grandmother's death at different ages (ages are in years). *Insert* shows grandmother J19 with her grandoffspring J51.

being postreproductive ($GMo45$), and only 1 includes the mother's age (but also includes the $GMo45$ term). The impact of salmon as an additive term (impacting all whales equally) appears in 2 of the 7 models, but also appears 3 times in an interaction with GMR. Our findings differ from a previous study examining the survival benefits of grandmothers in the study populations (35). One difference between the studies is sample size: We were fortunate to have 7 y of additional data, adding 88 births, 38 deaths, and an additional 26 grandmothers becoming postreproductive. Importantly, our approach separates short- and long-term effects of a grandmother dying, so that the impact of a grandmother dying in the last few years is different from the impact of a grandmother dying decades ago. Additionally, the mother effect we include controls for differences in survival impacts between sons and daughters. This follows theory and previous evidence that mothers invest more in their sons than their daughters (24). We also control for salmon and account for censoring with a survival model.

We did not detect any sex-specific effects of grandmother loss on the survival of grandoffspring (there is no term for this in the final model, above). While this may be influenced by the large number of unsexed individuals in the dataset—when filtered for only individuals with a known grandmother—our analysis of the mother effect in this paper clearly demonstrates sex differences in survival. The presence of the term sMR in our model only affects male offspring, suggesting that we have enough power to detect sex effects.

Interbirth Interval Model. We considered a number of models with a variety of terms (*SI Appendix*). The best-fitting model (AIC = 961.8445; model 2; see *SI Appendix* for full details) did not include an effect of grandmothers on their daughters' birth intervals,

$$IBI = 4.21 + s(DA) + 1.4208\ CA, \qquad [2]$$

where IBI is the length of the birth interval measured in years, DA is a smooth term for the daughter's age at the end of the birth interval (i.e., at the time of the birth of the second calf in the interval), and CA is 1 if the first calf in the interval survives more than 2 y into the interval (i.e., does the calf survive to weaning); otherwise it is set to 0.

The smooth term $s(DA)$ in this model was fitted with an estimated degree of freedom of 4.793. Two other models were, however, within $\Delta\text{AIC} < 2$ of this best-fitting model. Those models included both terms from the best-fitting model (model 2; *SI Appendix* and Eq. **2**) as well as the effect of grandmothers on their daughters' IBI (model 5; *SI Appendix*) and whether the grandmother was postreproductive (model 6; *SI Appendix*). In contrast to the hypothesized effects of grandmothers on their daughters' IBI, these models actually suggest that grandmothers (and particularly postreproductive grandmothers) have a small effect of increasing the birth interval if they are alive at the time of weaning for the first calf (*SI Appendix*, Table S12).

Discussion

We have shown that grandmothers bestow a survival advantage on their grandoffspring (a grandmother effect), and the effect remains after controlling for the mother effect. This is particularly the case when grandmothers are postreproductive, and thus provides evidence supporting the grandmother hypothesis in a nonhuman menopausal species. A key challenge in explaining the evolution of menopause across species is not just quantifying the benefits provided by postreproductive grandmothers—which explains why they live so long (36)—but also explaining why they do not continue reproducing. Here we have shown evidence that grandmother killer whales provide support to their grandoffspring, and that this is especially the case when the grandmothers are postreproductive. By stopping reproduction, postreproductive grandmothers not only avoid reproductive conflict with their daughters (23) but also offer increased benefits to their grandoffspring above that provided by reproductive grandmothers. Our data suggest that breeding grandmothers are not able to provide the same level of support as postreproductive grandmothers, and thus the evolution of reproductive termination increases a grandmother's capacity to help. There are a number of potential mechanisms that may explain this finding. For example, it is possible that, when grandmothers are supporting their own calves, their movement and activity patterns are constrained and they are not able to act as leaders in the same way as postreproductive females (23). Moreover, grandmothers with their own calves will require more food for lactation and thus are perhaps less likely to share food with other group members. Further observational studies are needed to study the behavioral interactions between grandmothers and grandoffspring in resident killer whales.

We do not find support for the hypothesis that grandmothers (either reproductive or postreproductive) reduce the interbirth interval of their daughters, with the best-fitting model not including this effect and other models demonstrating a postreproductive grandmother's presence being correlated with a small increase in the interbirth intervals of her daughters. We conjecture that this is because the grandmother would increase the survival of the first calf through the birth interval and thus impact her daughter in slightly delaying the birth of her second calf.

Our results further highlight the key role that postreproductive grandmothers play in killer whale societies in mitigating the impact of Chinook salmon abundance on the mortality risk of their grandoffspring. The impact of losing a postreproductive grandmother is highest in years with low and moderate salmon abundance. Killer whales forage selectively for Chinook salmon (30), and abundance of this prey species is known to have a strong negative correlation with killer whale mortality (33) and reproduction (8). Previous research has shown that postreproductive female killer whales act as repositories for ecological knowledge and that they provide an important leadership role for the group when foraging in salmon grounds (26). The importance of this leadership role in years of low Chinook salmon abundance may explain why the cost of losing a grandmother is slightly higher in years of low salmon abundance. As salmon populations continue decline, grandmothers are likely to increase further in importance for these killer whale populations (37, 38).

Consistent with previous findings—that postreproductive grandmothers confer benefits to their grandoffspring through a mechanism of leadership of the entire matriline (26)—we found no sex-specific effects of postreproductive grandmother loss on the survival of grandoffspring. This may be because the benefits of leadership around salmon foraging grounds cannot be directed toward specific kin, and both sexes of grandoffspring would be expected to benefit equally from leadership by their grandmother. This is in contrast to food sharing by mothers, which can be directed at specific individuals (such as males) within the group (25). There is no evidence that certain matrilines are more vulnerable than others (39), and so grandmothers are likely to be important across matrilines.

Outside of humans, menopause has only evolved in a small number of toothed whales (4, 5), and the long-term individual-based demographic data on resident killer whales provide a rare opportunity to test theoretical models on the evolution of menopause. In support of the grandmother hypothesis, we have shown that grandmothers increase the survival of their grandoffspring, and that postreproductive grandmothers are more effective helpers than grandmothers that continue to reproduce. These benefits to grandoffspring are necessary to explain why females have evolved to live long lives after they have terminated reproduction. Benefits alone, however, cannot explain why females terminate reproduction midway through life. Indeed, in other long-lived species that live in close-knit family groups, such as elephants, grandmothers provide benefits to grandoffspring while continuing to reproduce until the end of their long lives (20, 21). Examples such as this demonstrate that costs of continued reproduction are needed to explain why reproduction is terminated before the end of life (22). In killer whales and humans, intergenerational reproductive conflict has been found to provide such a cost, and thus select for early reproductive cessation. In killer whales, when mothers and daughters cobreed, the calves of mothers from older generation have significantly higher mortality (19, 23). Thus, for a complete understanding of the evolution of menopause, we need to move away from testing discrete hypotheses (e.g., mother, grandmother, reproductive conflict hypotheses) and instead take an integrated approach which considers both the fitness benefits of late-life helping to recipients (such as the grandmother effect reported here) and also the costs of late-life reproduction to breeders and other local group members (23). Only with this integrated approach can we fully explain why killer whales have evolved one of the longest postreproductive life spans recorded for all nonhuman animals.

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Supplementary Information for

Post-reproductive Killer Whale Grandmothers Improve the Survival of their Grandoffspring

Stuart Nattrass, Darren Croft P., Samuel Ellis, Michael A. Cant, Michael N. Weiss, Brianna Wright, Eva Stredulinsky, Thomas Doniol-Valcroze, John K.B. Ford, Kenneth C. Balcomb, Daniel W. Franks

Corresponding author: Daniel Franks

Email: daniel.franks@york.ac.uk

This PDF file includes:

Supplementary text

Tables S1 to S12

Data Description

Supplementary information

Parameter list for coefficients used in the model comparisons:

sex = 1 if individual is male, 0 if female, and 0.5 if unknown

MR = 1 if mother died in last 2 years

ML = 1 if mother died prior to last 2 years

sMA = *sex* if mother is living

sMR = *sex* if MR=1

sML = *sex* if ML=1

gmA = 1 if grandmother is living

gmR = 1 if grandmother died in last 2 years

gmL = 1 if grandmother died prior to last 2 years

sgmA = *sex* if *gmA* = 1

sgmR = *sex* if *gmR* = 1

sgmL = *sex* if *gmL*= 1

gmo45 =1 if the grandmother has died and was aged over 45 (post-reproductive) at death

slm = observed salmon abundance in given year

mageAlive = current age of the focal individuals mother if she is alive, 0 otherwise

Each binary parameter is set to zero if their respective conditions are not met.

Model Selection

Each table 3-6 presents the median hazard coefficients of the variables over 10,000 randomisations of the death order. The final column represents our model selection criteria, where the lowest AIC is considered the most parsimonious model. The best model is highlighted in bold. Mother effect models were used to determine which mothering terms were included in the models, with the terms from the best mother model being carried over.

All statistical models were compared via AIC. We calculate ΔAIC for each of *R* models by subtracting the minimum AIC value from all AICs, and then calculate model weights (*w*) for each model *i* as

$$w_i = \frac{\exp\left(-0.5 \cdot \Delta\mathrm{AIC}_i\right)}{\sum_{r=1}^{R} \exp\left(-0.5 \cdot \Delta\mathrm{AIC}_r\right)}$$

This quantity is often interpreted as the probability that a given model is the K-L best model out of the candidate set (table 1).

Table S1. Summary of models and selection criteria. All models with ΔAIC < 2 are in bold

Model	Terms	AIC	ΔAIC	w
1	MR + ML + sMA + sMR + sML	1263.629	9.569495	0.001598
2	sMA + sMR + sML	1260.415	6.355493	0.007972
3	sMR	1258.323	4.263298	0.022692
4	gmA	1272.207	18.1471	2.19E-05
5	MR + ML + sMA + sMR + sML + mageA	1265.129	11.06929	0.000755
6	sMA + sMR + sML + mageA	1262.144	8.084595	0.003358
7	sMR + mageA	1260.102	6.04215	0.009324
8	sMR + gmR + gmL + sgmA + sgmR + sgmL + slm	1259.384	5.324206	0.013351
9	sMR + gmR + gmL + sgmA + sgmR + sgmL + gmo45 + slm	1260.588	6.528728	0.00731
10	**sMR + gmR + gmo45**	**1254.824**	**0.764295**	**0.13052**
11	**sMR + gmR + gmo45 + slm**	**1255.435**	**1.375307**	**0.096161**
12	sMR + gmR + slm	1256.759	2.699272	0.049602
13	**sMR + gmR**	**1255.882**	**1.821992**	**0.076913**
14	sMR + gmR + gmo45 + slm + gmR:slm + gmo45:slm	1257.172	3.112457	0.040344
15	**sMR + gmR + gmo45 + slm + gmR:slm**	**1255.353**	**1.293509**	**0.100175**
16	**sMR + gmR + gmo45 + gmR:slm**	**1254.06**	**0**	**0.191267**
17	sMR + gmR + gmo45 + slm + gmo45:slm	1257.148	3.088062	0.040839
18	**sMR + gmR + gmo45 + gmo45:slm**	**1255.42**	**1.360516**	**0.096874**
19	**sMR + gmR + gmo45 + gmR:slm + mageA**	**1256.055**	**1.995649**	**0.070517**

20	sMR + gmR + gmR:slm + mageA	1257.169	3.109427	0.040405

A term’s model-averaged coefficient $\bar{\beta}$ is then

$$\bar{\beta} = \sum_{i=1}^{R} w_i \hat{\beta}_i$$

Where $\hat{\beta}$ is the estimated coefficient of the term in model *i*, which is 0 when the term is not included in the model.

Similarly, a term’s variable importance is simply the sum of the weights of the models in which that term is included (table 2).

Table S2. Model averaged coefficients and variable importance for all terms. Terms with variable importance > 0.9 are in bold.

Term	Model Averaged Coefficient	Variable Importance
motherrecent	0.001574	0.002353
motherlong	0.000934	0.002353
sexmotheralive	0.004516	0.013683
sexmotherrecent	**2.884683**	**0.999978**
sexmotherlong	0.003597	0.013683
motheragealive	8.53E-05	0.124359
gmalive	-8.66E-06	2.19E-05
gmrecent	**2.128937**	**0.954278**
gmlong	0.000734	0.020661
sexgmalive	0.001895	0.020661
sexgmrecent	0.008289	0.020661
sexgmlong	0.010244	0.020661
gmover45	0.37338	0.774007
salmon	-0.06953	0.347782
gmRslm	-1.11666	0.442708
gmo45slm	-0.05812	0.178058

Mother effect model selection

Model	MR	ML	sMA	sMR	sML	AIC
1	0.587 (-1.659: 2.903) P=0.594	0.276 (-0.789: 1.341) P=0.612	0.363 (-0.135: 0.861) P=0.153	2.503 (-0.327: 5.174) P=0.081	0.056 (-1.294: 1.409) P=0.935	1263.629
2			0.327 (-0.149: 0.805) P=0.179	3.079 (2.017: 4.155) P=1.0e-8	0.285 (-0.735: 1.305) P=0.584	1260.415
3				2.893 (1.831: 3.927) P=8.4e-8		1258.323

Table S3: Statistics for fitted models with only the mother survival terms, and sex terms.

Grandmother alive/dead only model

Model	gmA	AIC
4	-0.395 (-0.775: -0.015) P=0.042	1272.207

Table S4: Statistics for the fitted model with only the grandmother alive/dead survival term.

Mother effect model selection including mageAlive

Model	MR	ML	sMA	sMR	sML	mageAlive	AIC
5	0.841 (-1.507: 3.214) P=0.493	0.653 (-0.737: 2.046) P=0.358	0.347 (-0.149: 0.846) P=0.170	2.587 (-0.296: 5.313) P=0.077	0.045 (-1.316: 1.407) P=0.948	0.009 (-0.013: 0.032) P=0.413	1265.129
6			0.316 (-0.171: 0.804) P=0.204	3.150 (1.955: 4.357) P=2.6e-7	0.358 (-0.830: 1.546) P=0.555	0.002 (-0.154: 0.020) P=0.801	1262.144

7				2.968 (1.839: 4.100) P=1.8e-7		0.002 (-0.012: 0.017) P=0.763	1260.102

Table S5: Statistics for fitted models with only the mother survival terms, and sex terms, but with current mother age added to each model from table S3.

Grandmother model selection

Model	*sMR*	*gmR*	*gmL*	*sgmA*	*sgmR*	*sgmL*	*gmo45*	*slm*	*AIC*
8	2.622 (1.561: 3.683) P=9.7e-7	0.813 (-0.625: 2.254) P=0.268	0.082 (-0.589: 0.752) P=0.811	0.091 (-0.646: 0.826) P=0.809	0.408 (-1.413: 2.262) P=0.654	0.503 (-0.118: 1.126) P=0.113		-0.233 (-0.665: 0.200) P=0.292	1259.384
9	2.668 (1.597: 3.748) P=9.7e-7	0.652 (-0.852: 2.149) P=0.395	-0.049 (-0.790: 0.690) P=0.892	0.094 (-0.644: 0.830) P=0.804	0.389 (-1.448: 2.261) P=0.673	0.482 (-0.139: 1.104) P=0.128	0.253 (-0.288: 0.795) P=0.359	-0.232 (-0.665: 0.201) P=0.294	1260.588
10	2.926 (1.876: 3.974) P=4.5e-8	0.718 (-0.135: 1.570) P=0.099					0.386 (-0.019: 0.792) P=0.062		1254.824
11	2.863 (1.810: 3.915) P=1.0e-7	0.688 (-0.169: 1.544) P=0.116					0.384 (-0.022: 0.790) P=0.063	-0.237 (-0.672: 0.199) P=0.287	1255.435
12	2.823	0.887						-0.238	1256.759

	(1.777: 3.878) P=1.5e-7	(0.058: 1.716) P=0.036						(-0.673: 0.197) P=0.283	
13	2.899 (1.853: 3.940) P=5.3e-8	0.924 (0.097: 1.750) P=0.029							1255.882

Table S6: Statistics for fitted models with mother, grandmother, sex interactions, and additive salmon terms.

Interaction between grandmothering and salmon abundance

Model	*sMR*	*gmR*	*Gmo45*	*slm*	*gmR*slm*	*Gmo45*slm*	*AIC*
14	2.859 (1.802: 3.922) P=1.3e-7	1.477 (-1.683: 4.858) P=0.369	0.648 (-0.703: 2.001) P=0.347	-0.129 (-0.671: 0.414) P=0.643	-0.578 (-3.327: 1.997) P=0.671	-0.202 (-10108: 0.704) P=0.662	1257.172
15	2.853 (1.795: 3.912) P=1.3e-7	3.853 (-1.129: 8.169) P=0.107	0.369 (-0.041: 0.778) P=0.078	-0.193 (-0.632: 0.246_ P=0.388	-2.496 (-6.258: 0.246) P=0.194		1255.353
16	**2.898** **(1.842: 3.955)** **P=7.6e-8**	**4.318** **(-0.731: 8.544)** **P=0.086**	**0.368** **(-0.041: 0.778)** **P=0.078**		**-2.811** **(-6.542: 1.533)** **P=0.152**		**1254.06**
17	2.868 (1.816: 3.925) P=1.0e-7	0.657 (-0.202: 1.518) P=0.134	0.767 (-0.570: 2.103) P=0.261	-0.137 (-0.681: 0.406) P=0.621		-0.267 (-1.166: 0.632) P=0.561	1257.148
18	2.891 (1.843: 3.945) P=7.3e-8	0.657 (-0.202: 1.517) P=0.134	0.961 (-0.123: 2.046) P=0.082			-0.403 (-1.124: 0.318) 0.274	1255.42

Table S7: Statistics for fitted models that include an interaction between grandmother death and salmon index

Comparison of mother age and post-reproductive grandmother effects in best fitting model

Model	sMR	gmR	Gmo45	gmR:slm	mageAlive	AIC
19	2.894 (1.750: 4.037) P=7.8e-7	4.167 (-0.786: 8.432) P=0.086	0.372 (-0.046: 0.789) P=0.081	-2.704 (-6.441: 1.526) P=0.156	-0.0004 (-0.015: 0.014) P=0.917	1256.055
20	2.940 (1.793: 4.086) P=5.4e-7	4.519 (-0.375: 8.808) P=0.065		-2.847 (-6.618: 1.391) P=0.139	0.002 (-0.013: 0.017) P=0.789	1257.169

Table S8: Statistics for models comparing the best fitting model from Table S7 to that same model including current mother age, and replacing grandmother age at death with current mother age

Baseline hazard results for model 16

Age	survival
0	1
0.01	0.9317914
1	0.9109458
2	0.8922604
3	0.8662591
4	0.8325562
5	0.8086164
6	0.7917492
7	0.7774825
8	0.7666257
9	0.7630136
10	0.7554141
11	0.7515013
12	0.7428485
13	0.7245344
14	0.7102096
15	0.7001025
16	0.6948398
17	0.6948398
18	0.6842934
19	0.6842934
20	0.6842934
21	0.6432206
22	0.6233646
23	0.6233646
24	0.6067848

25	0.5789901
26	0.5674077
27	0.5674077
28	0.5674077
29	0.5674077
30	0.5674077
31	0.5674077
32	0.5171197
33	0.5171197
34	0.5171197
35	0.5171197
36	0.5171197
37	0.5171197
38	0.3716110
39	0.3202017
40	0.3202017
41	0.3202017

Table S9: The baseline hazard for the best fitting model 16. This baseline is the case where both mother and grandmother remain alive for the duration

Data Information

Each row of data accounts for a period of an individual whale's life. This time period is generally a single year, except in cases where multiple family members die within the same year. In this case, the period of time covered by a row is assigned a duration of 0.01 years.

The data as presented contains the assumption that the focal individual dies last whenever there are multiple family members who die within the same year. The column p.rowexists is then used to facilitate randomisation of death order (see below)

Variable Details

- Id
    - Anonymised identifier for the individual whale
- X.mother
    - Anonymised identifier for the mother of the focal individual. Hereafter referred to as "the mother"
- Grandmother
    - Anonymised identifier for the focal individual's grandmother. Hereafter referred to as "the grandmother"
- Sex
    - 1 if male, 0 if female. Individuals of unknown sex are assigned a value of 0.5, equivalent to randomised sex

- Salmon
    - Salmon index value for the time period considered
- Motheralive
    - 1 if the mother is still alive during this time period, 0 otherwise
- Motherrecent
    - 1 if the mother has died within the previous 2 years, 0 otherwise
- Motherlong
    - 1 if the mother has died prior to the previous two years, 0 otherwise
- Gmalive
    - 1 if the grandmother is alive during this time period, 0 otherwise
- Gmrecent
    - 1 if the grandmother has died within the previous 2 years, 0 otherwise
- Gmlong
    - 1 if the grandmother has died prior to the previous two years, 0 otherwise
- Sexmotheralive
    - The values of columns “sex” and “motheralive” multipled
- Sexmotherrecent
    - The values of columns “sex” and “motherrecent” multipled
- Sexmotherlong
    - The values of columns “sex” and “motherlong” multipled
- Sexgmalive
    - The values of columns “sex” and “gmalive” multipled
- Sexgmrecent
    - The values of columns “sex” and “gmrecent” multipled
- Sexgmlong
    - The values of columns “sex” and “gmlong” multipled
- Gmover45
    - 1 if the grandmother has died and was aged 45 or over at the time of death, 0 otherwise
- gmRslm
    - The values of columns “gmrecent” and “salmon” multipled
- gmo45slm
    - The values of columns “gmover45” and “salmon” multipled
- Startage
    - Age of the focal individual at the beginning of the time period
- Stopage
    - Age of the focal individual at the end of the time period
- Event
    - 1 if the individual dies during the time period, 0 otherwise
- p.rowexists
    - This column is used to determine the randomisation of death orders. 0 if the row is included in the analysis regardless of randomisation. 0.5 if the row is dependent on death order. If this is the case and p.rowexists=0.5, then the row will be excluded from analysis with probability 0.5, and the event signified with be moved to the previous row. This switches the assumed death order from 1) ancestors, 2) focal individual to 1) focal individual, 2) ancestors

Survival Model for weaned individuals

We extend our main models by taking the best fitting model (AIC = 1254.06; model 16) and adding parameters that consider the grandmother effects only for weaning individuals (define as those aged 2 or over). Neither of these models improve model fit, or show any indication that grandmother effects are specific to weaned or unweaned grandoffspring.

Weaning model 1: death ~ Sexmotherrecent + GMrecent + GMover45 + GMrecent*salmon + GMrecent*weaned

AIC = 1256.0

Parameter	coeff	CI	P value
Sexmotherrecent	2.90	1.84 – 3.95	8.1e-8 *
Gmrecent	1.98	-1.06 – 5.25	0.20
Gmover45	0.37	-0.040 – 0.78	0.077
gmRslm	-1.17	-3.87 – 1.58	0.39
Gmrecent*weaned	0.15	-1.56 – 1.88	0.78

Table S10: Statistics for weaning model 1, which takes the best fitting previous model (model 16) and includes the weaning status of grand offspring.

Weaning model 2: death ~ Sexmotherrecent + GMrecent + GMover45 + GMrecent*salmon + Gmrecent*weaned + GMver45*weaned

AIC = 1256.1

Parameter	coeff	CI	P value
Sexmotherrecent	2.91	1.85 – 3.97	7.4e-8 *
Gmrecent	4.67	-0.44 – 9.07	0.067
Gmover45	-0.11	-0.97 – 0.76	0.80
gmRslm	-2.73	-6.58 – 1.53	0.17
Gmrecent*weaned	-0.25	-2.04 – 1.59	0.77
Gmover45*weaned	0.65	-0.33 – 1.64	0.19

Table S11: Statistics for weaning model 2, which takes the best fitting previous model (model 16) and includes the weaning status of grand offspring.

Interbirth Interval Model

We used a generalized additive model with a Gamma error structure and identity link function, to examine the consequences of a grandmother's alive/dead status on her daughters' interbirth interval by regressing a number of covariates on each birth interval length. We used AIC to select between a number of models capturing a range of covariates:

- birth.interval
    - The length, in years, of the birth interval.
- daughter.age
    - The age of the daughter at the end of the birth interval (i.e. her age in the year when the second calf in the interval is born).
- first.calf.alive.post.weaning
    - 1 if the first calf in the interval survives more than 2 years into the interval (i.e. has been weaned), otherwise it is set to 0.
- gmother.alive.end.first.calf.weaning
    - 1 if the grandmother (mother of the daughter whose interval is being examined) is alive more than two years into the interval (the time after which the first calf in the interval will, if alive, have been weaned), otherwise is it set to 0.
- gmother.alive.and.postreproductive.end.first.calf.weaning
    - 1 if gmother.alive.end.first.calf.weaning = 1 and the grandmother is over 45 two years into the interval (i.e. she is alive and postreproductive by the time the first calf has had time to be weaned), otherwise it is set to 0.
- salmon
    - The mean salmon abundance during the entire interval.

Proposed Models

Model 1 (AIC: 975.453): birth.interval ~ s(daughter.age)

Model 2 (AIC: 961.8445): birth.interval ~ s(daughter.age) + first.calf.alive.post.weaning

Model 3 (AIC: 976.4604): birth.interval ~ s(daughter.age) + gmother.alive.end.first.calf.weaning

Model 4 (AIC: 962.9218): birth.interval ~ s(daughter.age) + first.calf.alive.post.weaning + gmother.alive.end.first.calf.weaning

Model 5 (AIC: 962.27): birth.interval ~ s(daughter.age) + first.calf.alive.post.weaning + gmother.alive.end.first.calf.weaning + gmother.alive.and.postreproductive.end.first.calf.weaning

Model 6 (AIC: 963.9162): birth.interval ~ s(daughter.age) + first.calf.alive.post.weaning + gmother.alive.end.first.calf.weaning + gmother.alive.and.postreproductive.end.first.calf.weaning + salmon

Model	*(intercept)*	*s(daughter.age)*	*first.calf.alive.post.weaning*	*gmother.alive.end. first.calf.weaning*	*gmother.alive.and.postreproductive. end.first.calf .weaning*	*salmon*	*AIC*
1	5.4820	Edf=4.645 (P=1.14e-12)					975.453
2	**4.2152**	**Edf=4.793** **(P=2.17e-09)**	**1.4208** **(P=1.55e-05)**				**961.8445**
3	5.2444	Edf=4.596 (P=6.25e-12)		0.3466 (P=0.301)			976.4604

4	4.0161	Edf=4.766 (P=5.68e-09)	1.4085 (P=1.85e-05)	0.3077 (P=0.341)			962.9218
5	3.93881	Edf=4.791 (P=4.13e-06)	1.48613 (P=4.13e-06)	-0.03823 (P=0.9166)	0.57121 (P=0.0824)		962.27
6	3.67903	Edf=4.823 (P=6.44e-10)	1.49564 (P=3.83e-06)	-0.04632 (P=0.8991)	0.57577 (P=0.0806)	0.21004 (P=0.6325)	963.9162

Table S12: Statistics for the proposed inter birth interval models. Model 2 is the best fitting, although models 4 and 5 are within ΔAIC < 2 of model 2.

Appendix C

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* Joint first author

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SPECIAL ISSUE ARTICLE

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Calculating effect sizes in animal social network analysis

Daniel W. Franks[1] | Michael N. Weiss[2] | Matthew J. Silk[3] | Robert J. Y. Perryman[4,5] | Darren P. Croft[2]

[1]Departments of Biology and Computer Science, The University of York, York, UK
[2]Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
[3]Environment and Sustainability Institute, University of Exeter, Penryn, UK
[4]Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia
[5]Marine Megafauna Foundation, Truckee, CA, USA

Correspondence
Daniel W. Franks
Email: daniel.franks@york.ac.uk

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Abstract

1. Because of the nature of social interaction or association data, when testing hypotheses using social network data it is common for network studies to rely on permutations to control for confounding variables, and to not also control for them in the fitted statistical model. This can be a problem because it does not adjust for any bias in effect sizes generated by these confounding effects, and thus the effect sizes are not informative in the presence of confounding variables.
2. We implemented two network simulation examples and analysed an empirical dataset to demonstrate how relying solely on permutations to control for confounding variables can result in highly biased effect size estimates of animal social preferences that are uninformative when quantifying differences in behaviour.
3. Using these simulations, we show that this can sometimes even lead to effect sizes that have the wrong sign and are thus the effect size is not biologically interpretable. We demonstrate how this problem can be addressed by controlling for confounding variables in the statistical dyadic or nodal model.
4. We recommend this approach should be adopted as standard practice in the statistical analysis of animal social network data.

KEYWORDS
animal social networks, social behaviour, social network analysis

1 | INTRODUCTION

Criticism of the use of *p* values (Amrhein, Greenland, & McShane, 2019; Halsey, Curran-Everett, Vowler, & Drummond, 2015) has arisen mainly due to researchers' past tendency to over focus on statistical significance, rather than a balanced consideration of it along with biological importance of model effects. Consequently, there is growing movement towards the use of approaches that place greater emphasis on biological importance through effect sizes, such as model comparisons and Bayesian inference (Burnham, Anderson, & Huyvaert, 2011; Cumming, 2014; Halsey, 2019), although careful use of *p* values alongside effect sizes remains largely supported. Nakagawa and Cuthill highlight that 'All biologists should be ultimately interested in biological importance, which may be assessed using the magnitude of an effect, but not its statistical significance' (Nakagawa & Cuthill, 2009, p. 1). Correctly using effect sizes enables interpretation of the extent of an effect, allows for comparisons of the relative importance of different effects, facilitates the use of results in meta-analyses and makes it possible to use results to predict future outcomes.

Daniel W. Franks and Michael N. Weiss are joint first authors.

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While the rest of ecology has been moving towards a balanced consideration of biological significance through careful assessment of effect sizes alongside statistical significance, studies of animal social networks have tended to focus mainly on statistical significance, and neglect effect sizes. A key reason for this is that many animal social network studies focus on permutation approaches for statistical inference; permuting data and comparing model results on the observed and permuted datasets (Croft, Madden, Franks, & James, 2011; Farine & Whitehead, 2015). Network and datastream (pre-network) permutations deal with the inherent non-independence of observations related to social network data that can violate the assumptions of some conventional statistical tests. While network permutations were originally introduced to tackle non-independence (Krackhardt, 1987, 1988), they have since been adapted in behavioural ecology to also control for a host of confounding factors inherent to observations of free-ranging individuals that influence observed associations between individuals. These include sampling effort, location, the number of times individuals are observed and observed group sizes (Bejder, Fletcher, & Brager, 1998; Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015; Whitehead, 2008). Indeed, most processes that influence associations between individuals have typically been controlled for by imposing constraints on data permutations in these null models, for example, by constraining swaps of pairs of observations to occur only within the same time period (e.g. a day or season) or location in which they were observed.

A common procedure in network studies has been to fit a statistical model to observed network data, derive a test statistic and then compare this test statistic to statistics derived from constrained permutations. In this procedure, confounds accounted for in the permutation are not controlled for in the fitted model. Thus, while permutations are intended to prevent these confounding effects from generating false positives or false negatives in the p value, they do nothing to adjust for any bias in estimated effect sizes generated by these effects. As such, it is even possible for a study to suggest a significantly positive effect, yet the effect size reported for the model is negative. For example, imagine a scenario where there are multiple locations at which associations between individuals are automatically recorded over multiple sampling periods. The observed associations between individuals could be purely the result of social preferences to associate with particular other individuals. There are, however, a host of additional ecological factors that could increase the probability of observing the individuals co-occurring at a given location, such as similarities in space use between individuals, uneven sex ratios, etc. (Farine, Firth, et al., 2015). If, in our example, individuals had a preference for associating with members of the other sex (disassortative mixing; i.e. males prefer to associate with females, and females with males) but males preferred one location and females preferred another, then it would appear in the observed network that individuals prefer to associate with others of the same sex, despite their actual social preferences being for individuals of the other sex. Permutations that control for location would show us that the observed effect sex on association rates is significantly greater than expected from permuted associations (i.e. compared to the null model) with the population been significantly disassorted. However, despite there being more disassortativity in the observed network than expected by chance, the effect size estimated by the original model would be negative and thus the opposite to the true direction of the effect. The effect size is then not biologically interpretable, and we are left to draw conclusions from the p value and direction of the effect alone, without any information on the biological importance of the effect.

Ultimately, whether this problem depends on the research question (Carter, Lee, & Marshall, 2015). If edges are intended to simply represent contacts between individuals, then the importance of using approaches that control for gregariousness or location preferences may be diminished because researchers are often more interested in quantifying emergent network structures than uncovering social preferences that drive social network structure. This would be the case for example, when studying disease or information spread (Farine, Aplin, Sheldon, & Hoppitt, 2015; Hamede, Bashford, McCallum, & Jones, 2009; Silk et al., 2017), or the impact of social contacts on survival (Ellis et al., 2017; Silk et al., 2009) or stress (Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011). However, if the question is related to social preferences or behaviour, such as whether individuals have non-random social preferences, whether particular types of individuals prefer to associate with each other (Aplin et al., 2013; Croft et al., 2009), what type of social system is in place or how complex a social system is (Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017; Ramos-Fernandez et al., 2018; Weiss, Franks, Croft, & Whitehead, 2019), then these factors need to be controlled for. This could be relevant, for example, when addressing questions about the evolution of social preferences, such as shy individuals preferring to associate with bold individuals rather than other shy individuals. However, even where the question relates to contact networks, it might be appropriate to control for certain confounding effects (e.g. bias resulting from individuals being monitored for different periods of time or bias resulting from being more likely to observe bold individuals over shy).

Many questions in animal behaviour focus on the level of either dyads or nodes. The basic idea behind dyadic models is that the outcome, such as the probability of associating, is affected by the characteristics of both individuals in the dyad. Dyadic regressions—where the analysis is at the level of connections between pairs of individuals—are used less in animal social network analysis than in other fields. In particular, other fields have developed methods for dyadic analysis, termed Actor–Partner Interdependence Models, which tackle the problem of interdependence without the use of or need for permutations (Chow, Claxton, & van Dulmen, 2015; Garcia, Kenny, & Ledermann, 2015; Kenny, 1996, 2018). In these models, controls can be included in the statistical model that examines predictors of the strength of connection between the two individuals or predictors of node-level network measures. An example of this is shown in a paper using dyadic regression that controls for new confounding factors and debunks a previous network analysis suggesting that obesity is socially transmitted (Cohen-Cole & Fletcher, 2008). Other methods such as exponential random graph models (ERGMs) (Silk & Fisher, 2017), latent space models (Hoff, Raftery, & Handcock, 2002) and Stochastic Actor-based Models (Fisher, Ilany, Silk, & Tregenza, 2017; Ilany, Booms, & Holekamp, 2015) can also be used for dyadic analysis.

For questions relating to any network-level statistics that rely on indirect connections (Brent, 2015), however, such as path length or clustering, then we may need to control for these factors in the association index itself. This is commonly done for overall gregariousness (Godde, Humbert, Cote, Reale, & Whitehead, 2013), but not for other key confounding factors. An underused method is to produce generalized affiliation indices (GAIs), which are produced from the residuals of a regression of observed contacts on confounding variables (Whitehead & James, 2015). GAIs are promising, although the biological meaning of these association indices can be difficult to interpret, and with values typically being both positive and negative it may be difficult to apply many traditional network analysis approaches that ecologists are familiar with. In particular, most weighted network statistics such as clustering coefficient and path length assume that edge weights are strictly positive (Newman, 2004).

Here, we focus on dyadic and nodal analysis and use two network simulation examples to demonstrate that relying solely on permutations to control for confounding variables can result in incorrect and biased effect size estimates of animal social preferences that are not biologically meaningful. Our second simulation, in particular, represents a common scenario where individuals are sampled in different locations. We show with our examples that this problem can best be addressed by controlling for confounding variables in the statistical model, before demonstrating that this approach remains effective when analysing an example using real-world data.

2 | MATERIALS AND METHODS

The code written in R 3.6.3 (R Core Team, 2018) for both simulated examples is available in Supporting Information. We have chosen two example simulations with each illustrating the effect of a different confounding factor. The first simulation captures observation bias and the second captures social preference along with location preference. Our simulation framework is inspired by those of Farine (2017), Farine and Whitehead (2015) and Whitehead and James (2015). We also demonstrate the method using a real-world example, with social data on reef manta rays *Mobula alfredi* from Perryman et al. (2019).

2.1 | Simulation 1: Sex differences in gregariousness and conspicuousness

We designed our first model to simulate a scenario in which a study is testing for a sex difference in gregariousness—a nodal analysis. We simulated a population of 100 individuals, with an equal sex ratio, in which females were more gregarious than males, but males were easier to observe. All individuals were assigned a level of gregariousness g from a truncated normal distribution (bounds 0 and 1) with a mean of G_F for females and G_M for males, and standard deviation of 0.1. Individuals were also assigned a sighting frequency s from the same distribution but with mean S_F for females and S_M for males. Females are assumed to be more gregarious and thus were assigned a higher gregariousness than males. Females were also assumed to be more difficult to observe than males (perhaps due to conspicuousness, size or behaviour) and thus are assigned a lower sighting probability than males. We systematically varied the values of G_F, S_F and S_M.

Using the *rgraph* function in the R package SNA (Butts, 2016), we then simulated $t = 100$ sampling periods. In each sampling period, every individual was always observed so that we had a reference case of perfect sampling for each run. The probability that any two observed individuals were observed associating was equal to the product of their gregariousness scores. Once sampling was complete, we generated the association network using the simple ratio index (SRI) (Cairns & Schwager, 1987) and measured the sum of the strength of connections (weighted degree) for each individual as a measure of their observed gregariousness. For each run, we then simulated sampling on the network, where each individual was observed with probability S_M for males and S_F for females. We do this by removing all associations involving individuals that were not sighted in a given sampling period.

We tested for a difference in strength between females and males using two different approaches. We expected females to have higher strength than males as a result of their higher gregariousness. First, we fitted a linear model to test the hypothesis that females have a higher strength than males:

$$S_i \sim \beta_0 + \beta_1 \, \mathrm{sex}_i + \varepsilon_i.$$

Second, we also fitted the same model but included the mean-centred number of observations as a covariate to control for sampling bias. As such, we also included an interaction of observations with sex as a covariate to control for sampling bias in the effect size:

$$\begin{aligned}\mathrm{Strength}_i \sim \beta_0 + \beta_1 \, \mathrm{sex}_i + \beta_2 \, \mathrm{observations}_i \\ + \beta_3 \, (\mathrm{observations} \times \mathrm{sex})_i + \varepsilon_i.\end{aligned}$$

In both models, we allowed unequal variance by sex. Sex was also included as an interaction with the mean-centred number of observations. This improved the model fit due to an interaction between gregariousness and sightings: because we know the sexes differ in their gregariousness, we would also expect that they would have different relationships between sightings frequency and strength. For a fair comparison across parameterizations of the model, the model then compares the effect of sex at the average level of sightings frequency, and we take the ratio there as our effect size. We found that a linear relationship with the number of observations was a good fit for this model.

We used a permutation procedure to determine the statistical significance of regression coefficients for the corrected nodal model. Although our study is about effect sizes, our intention is to demonstrate their use along with permutations. Recent work has highlighted problems with using datastream permutations with standard regression to test hypotheses such as the one we are interested here (Weiss et al., 2020). Thus, we instead use the double semi-partialling method outlined by (Dekker, Krackhardt, & Snijders, 2007) with 10,000 permutations of the residuals, using the pivotal statistics (*t* for quasi-poisson, *z* for beta) as our test statistics. This permutation procedure does not account for sampling or other confounding effects, but it does not need to, because we have already controlled for them in our statistical model.

2.2 | Simulation 2: Sex assortment and location preferences

We designed the second simulation to test the hypothesis that individuals of the opposite sex have stronger social preferences for each other than they do for individuals of the same sex. However, we also included a sex difference in location preference, that confounded the true social preferences of individuals—a dyadic analysis. We simulated 100 individuals, half of which were female and half of which were male. For all dyads of the same sex, we assigned an association preference from a truncated normal distribution with a mean $S_{\text{Same}} = 0.25$ and standard deviation of 0.1 (boundaries 0 and 1). We did the same for all pairs of individuals of a different sex, but used a mean of $S_{\text{Different}} = 0.5$. This association matrix was assumed to be symmetric. We assumed two sampling locations A and B and assigned a preference for location B to each individual, using a truncated normal distribution with a standard deviation of 0.1 and means of $L_M = 0.8$ for males (strong preference for Location B) and $L_F = 0.2$ for females. To examine the effect size without bias in location preferences, we also ran the simulation with a mean preference of $L_M = L_F = 0.5$ for location B (i.e. no preference) for both sexes for each set of parameter values for S_{same} and $S_{\text{different}}$.

We then simulated $t = 100$ sampling periods as before. In each sampling period, we assigned each individual to a location (A or B) according to their location preference. Individuals could then only associate if they were in the same location in that time point, and the probability that any two observed individuals were observed associating was proportional to the product of their association preferences. In each sampling census, we recorded whether each pair of individuals was observed associating.

We again used three different ways to test for negative assortativity by sex, calculating statistical significance by comparison to the results from the permutations. First, we fitted a binomial multiple membership GLMM with logit link as a dyadic regression to test the hypothesis that individuals of the opposite sex have a higher social preference for each other than they do for individuals of the same sex. We used default priors and the model:

$$
\begin{aligned}
(\text{assoc}, \text{not}-\text{assoc})_{ij} \sim \beta_0 + \beta_1\, \text{sameSex}_{ij} + \text{dyadID}_{ij} \\
+ \text{nodeID}_i + \text{nodeID}_j + \varepsilon_{ij},
\end{aligned}
$$

where nodeID is a random factor in the multiple membership model. This represents a random gregariousness or sociality effect or, in the case of uneven detection, a visibility effect for each individual. Note that including nodeIDs as standard random factors without the multiple membership model would represent a directed network scenario, but we are dealing with undirected associations here. MCMCglmm includes an observation-level random intercept as default and DyadID is therefore implicitly included as a random intercept. This glmm structure follows some aspects of implementations of the Actor-Partner Interdependence Model (Kenny, 1996, 2018) and the multiple membership approach is inspired by Rushmore et al. (2013).

Second, we fitted the same model, but included the proportion of censuses that the two individuals in the dyad were observed in the same location (which we centred on 0.5), as a covariate to control this non-social influence:

$$
\begin{aligned}
(\text{assoc}, \text{not}-\text{assoc})_{ij} \sim \beta_0 + \beta_1 \text{sameSex}_{ij} + \beta_1\, \text{locationOverlap}_{ij} \\
+ \text{dyadID}_{ij} + \text{nodeID}_i + \text{nodeID}_j + \varepsilon_{ij}.
\end{aligned}
$$

We used the multiple regression quadratic assignment procedure (MRQAP) to calculate significance for this corrected model. There are caveats with this approach. First, the GLMQAP deals specifically with the non-independence between edges that arises because they are connected to the same node, but this is already dealt with completely by the multi-membership random effect. As such, there is no need to use permutations with this approach. Additionally, MCMCglmm is a Bayesian approach, and thus *p* values are not a standard aspect of the analysis. However, we have included the permutation procedure here to demonstrate an appropriate permutation approach, should it be desired. MRQAP uses the double semi-partialling permutation method (Dekker et al., 2007) with 10,000 permutations. This method is equivalent to the multiple regression quadratic assignment procedure (MRQAP), but fitting GLMs instead of least squares regression. This GLMQAP procedure is available in the ANINET R package, accessible through GitHub (https://github.com/MNWeiss/aninet).

2.3 | Reef Manta Ray Data: Sex differences in gregariousness

Simulation is the best approach for testing our method because it allows us to know what the effect size should actually be. However, we also demonstrate the method on complex data. As such, we used group-based association data on reef manta rays (for full details, see Perryman et al., 2019). Individual reef manta rays were identified by standard photo-ID methods, and data on group compositions were collected from November 2013 to May 2018 in the Dampier Strait region of Raja Ampat, West Papua, by trained researchers diving using SCUBA equipment, or freediving, depending on the position of rays in the water column. In line with Perryman et al. (2019), we removed individuals observed fewer than 10 times to improve data reliability (Whitehead, 2008) and derived the SRI using a 15-day sampling period. In the resulting dataset, there are 70 unique females, 42 unique males, 1,257 female sightings, 643 male sightings, 17.96 mean sightings per female and 15.31 mean sightings per male. As such, there is a clear case of more females or oversampling of females.

We fitted a regression model to the network to test the hypothesis that one sex has higher strength than the other:

$$\text{Strength}_i \sim \beta_0 + \beta_1 \, \text{sex}_i + \varepsilon_i.$$

However, we know that these data are confounded by a bias towards observing females, which can bias the effect size in this respect. We also fitted the same model but included the mean-centred number of observations of each individual as a covariate to control for sampling bias in the effect size following the approach of our first simulation:

$$\text{Strength}_i \sim \beta_0 + \beta_1 \, \text{sex}_i + \beta_2 \, \text{observations}_i + \varepsilon_i.$$

We checked the fit of observations, and a linear relationship was appropriate in this case. Unlike our nodal simulation, we did not interact sex with observations because there was no difference between the sexes in how the observations impacted strength, and it did not improve the model fit.

3 | RESULTS

3.1 | Simulation 1: Sex differences in gregariousness and conspicuousness

The simulation created the desired effect that females are more gregarious than males, while males appear to be more gregarious when females are difficult to observe (Figure 1). Over 20 independent simulation runs, we found that the mean effect size of sex on strength was 29.16 (95% CI = 28.66, 29.65) when sampling was perfect and males and females were equally observable (equivalent to $S_F = 1, S_M = 1$).

For each simulation run, our expected effect size is from the perfectly sampled network under the given parameter values and the other two effect sizes are from the sampled network with the statistical model not accounting for observations and with the statistical model accounting for observations. Figure 2 shows the results of our analysis over systematically varied parameters S_F and S_M, where $S_M > S_F$ and $S_M + S_F = 1$ to keep sampling observations constant (Figure 2a), and also varying G_F ($G_F > G_M$) (Figure 2b). The results show that not accounting for confounding effects in the statistical model (and instead relying on permutations to account for them) produces effect sizes that are very different from the actual effect sizes and for a wide range of conditions. Indeed, this approach actually shows the opposite result to the reference model, in that females are shown to be less gregarious than males (points below the dotted line on Figure 2a). However, when we account for sampling in the statistical model, the results are extremely similar to the actual effect sizes.

Unlike the uncorrected model which would rely on permutations to correct confounds only in the *p* value, the effect of the corrected model can be biologically interpreted. For example, when $S_M = 0.7$ and $S_F = 0.3$ and $G_M = 0.5$ and $G_F = 1.0$ the corrected mean strength ratio can be interpreted as females being 87% more gregarious than males (reference 82%). This cannot be done for the uncorrected effect size which would be interpreted as males being 4% more gregarious than females. To demonstrate the use of the permutation method with the statistical model, for this example the *p* values for all 20 runs were significant with $p < 0.05$ in all cases.

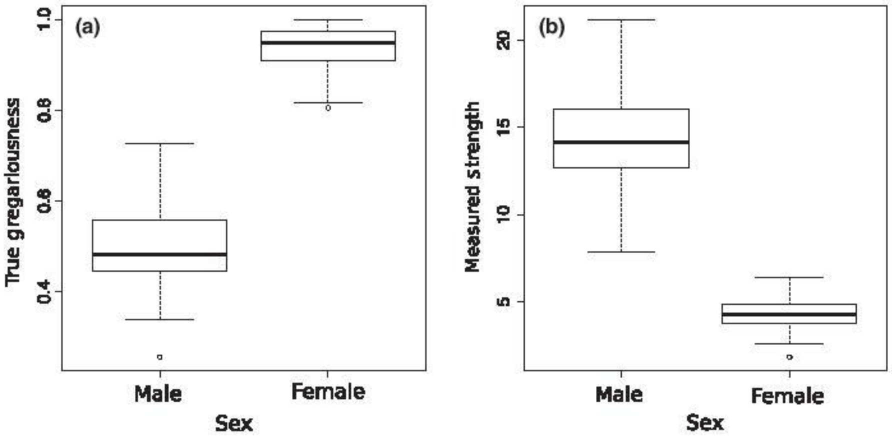

FIGURE 1 (a) The true gregariousness of individuals of each sex. (b) The measured strength of individuals of each sex from simulated observations, where $S_M = 1$ and $S_F = 0.1$. In both cases, $G_F = 1$ and $G_M = 0.5$. Plots are for a single representative run of the simulation. The contrast between the two panels (a) and (b) demonstrates that although females are more gregariousness, males incorrectly appear to be more gregarious when females are difficult to observe. For all box-and-whisker plots, the bottom and top of the box are the 25th and 75th percentiles, the middle band is the median, the upper whisker is Q3 + 1.5 IQR, the bottom whisker is Q1 + 1.5 IQR and open circles show outliers

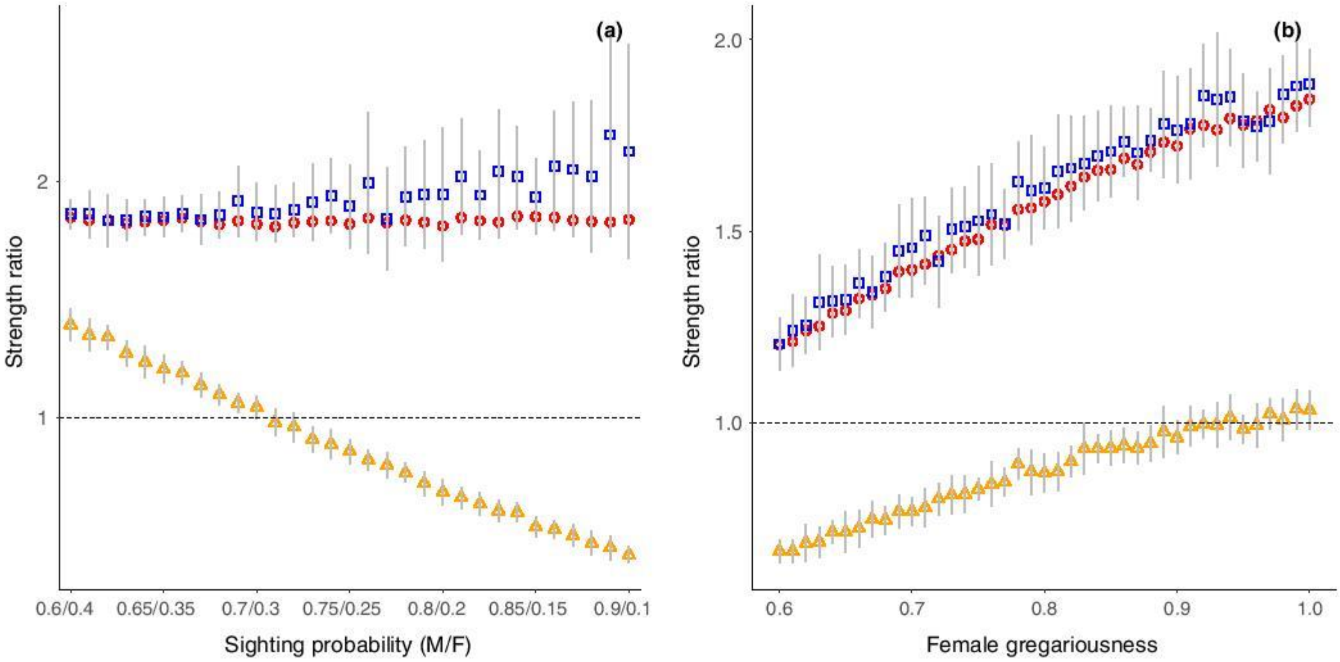

FIGURE 2 The sex effect size (ratio of strength between males and females) from the statistical models. Odds over 1 (dotted line) mean that females are more gregarious and have a higher strength than males. Red circles show the true effect size, orange triangles show the effect size of the uncorrected statistical model after biased sampling and blue squares show the effect size of the model statistically controlling for observation bias after biased sampling. Error bars show standard deviation. Panel (a) shows results when $G_F = 1.0$ and $G_M = 0.5$ while covarying S_F and S_M, and panel (b) shows results when $S_F = 0.3$, $S_M = 0.7$ and $G_M = 0.5$ while varying G_F. These figures show that failing to account for the bias in the statistical model gives incorrect effect sizes, and that this problem can be addressed by controlling for bias in the statistical model

3.2 | Simulation 2: Sex assortment and location preferences

The simulation created the desired effect that individuals of a different sex are more likely to associate while individuals of the same sex are more likely to be in the same location. Over 20 independent simulation runs when males and females had location preferences from the same distribution, we found that two members of a dyad being of the same sex was associated with a decrease in the logit-transformed dyadic association strength of 0.43 (95% CI = 0.42, 0.44). This is the mean (over 20 runs) of the mean posterior expected odds ratio for each simulation, meaning that individuals of the same sex were only 67% less likely to associate than individuals of a different sex at a given sampling event.

For each simulation parameterization, our reference/true effect size is from 20 runs of the network under the given parameter values but with location preferences equal for males and females ($L_M = L_F = 0.5$). Figure 3 shows the results of our analysis over systematically varied parameter S_{Same}, while $S_{Different} = 0.5$, $L_F = 0.8$ and $L_M = 0.2$ (Figure 3a), and over systematically covaried parameters L_F and L_M while $S_{Different} = 0.5$ and $S_{Same} = 0.25$ (Figure 3b). The results show that not accounting for confounding effects in the statistical model produces effect sizes that are very different from the actual effect sizes. Indeed, for a wide range of conditions, it actually shows the opposite result to the reference model, in that individuals of the same sex are more likely to associate than individuals of the different sex (points above the dotted line for both panels). However, when we account for sampling in the statistical model, the results are extremely similar to the actual effect sizes.

Unlike the uncorrected model, which would rely on permutations to correct confounds only in the *p* value, the effect of the corrected model can be interpreted biologically. For example, when $S_{Same} = 0.25$. $S_{Different} = 0.5$, $L_F = 0.8$ and $L_M = 0.2$ odds ratio of associating with the same sex is 0.44, which is extremely close to the true value of 0.43. This cannot be done for the uncorrected effect size which gives a mean odds ratio of 1.02. Under the conditions for this example, the *p* values for all 20 runs were significant with $p < 0.05$ in all cases.

3.3 | Reef Manta Ray Data: Sex differences in gregariousness

In the basic model (strength ~ sex), the effect size for sex (in this case being male) was −0.45 (SE 0.33), suggesting that males are less gregarious than females. However, in the second model that controlled for observations (strength ~ sex + number-of-observations), the effect size was −0.07 (*SE* 0.26) and not statistically significant (GLMQAP permutation test; $p = 0.78$). Thus, the second model shows that the original effect size was biased by the over sampling of females. The full table of results for both models is provided in the Supporting Information. This offers further support for our

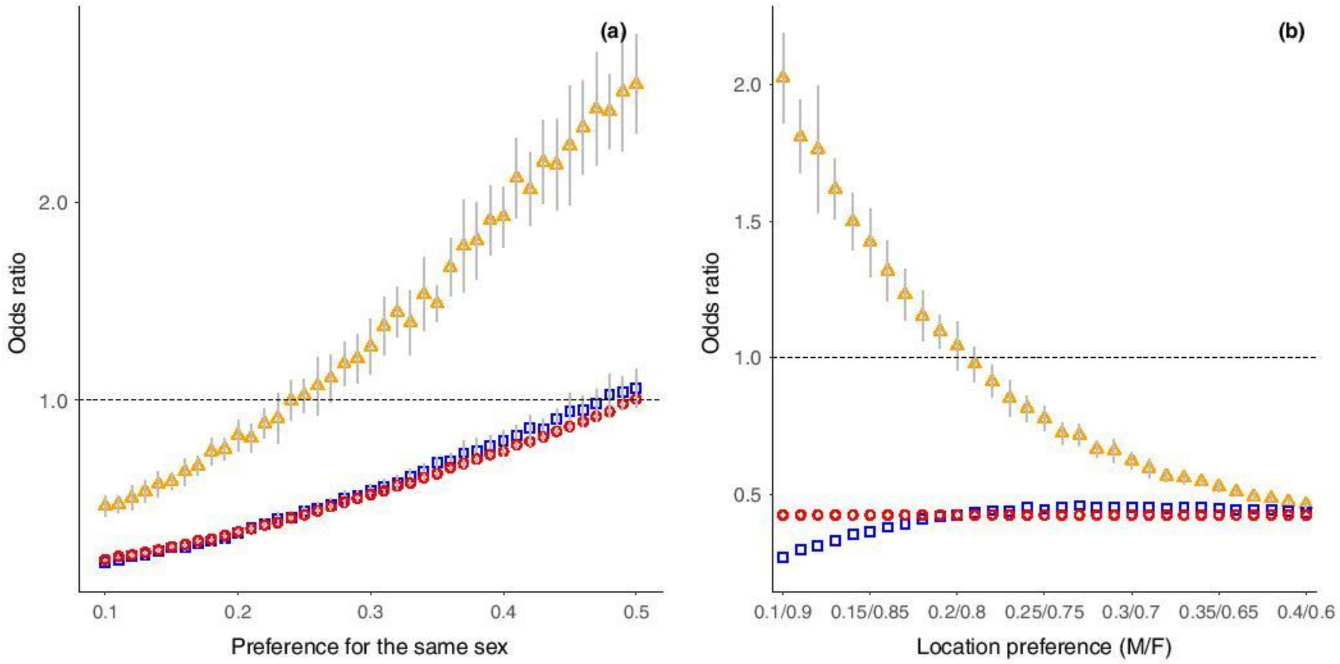

FIGURE 3 The effect size (odds ratio of associating with the same sex) from the statistical models. Red circles show the effect size for the reference case when males and females share equal location preferences ($L_M = L_F = 0.5$). Orange triangles show the effect size of the uncorrected statistical model, and blue squares show the effect size of the model statistically controlling for location overlap. Error bars show standard deviation. Panel (a) shows results when S_{Same} is varied while $S_{\text{Different}} = 0.5$, $L_F = 0.8$ and $L_M = 0.2$. Panel (b) shows results when L_F and L_M are covaried while $S_{\text{Different}} = 0.5$ and $S_{\text{Same}} = 0.25$. These figures show that failing to account for the bias in the statistical model gives incorrect effect sizes, and that this problem can be addressed by controlling for bias in the statistical model

finding from the first simulation using data with a more complex structure.

4 | DISCUSSION

Our study demonstrates that when answering questions related to social preferences, controlling for confounding factors in the fitted statistical model produces biologically meaningful effect size estimates that greatly help the interpretability of the results. Where confounding factors are only controlled for in the null model, as has been typical in animal social network analysis, the only information about the effect comes from the *p* value and the tail in which significance is found. The latter approach focuses on statistical significance and does not facilitate a careful and balanced assessment of biological importance. As such, it is not desirable to control for confounding factors in permutations alone, and we advocate a return to careful consideration of the statistical model specification.

Our study demonstrates examples of how animal social network analysis can be performed, in the light of recent work highlighting that that datastream permutations do not test the hypothesis that is typically desired with standard regression modelling (Weiss et al., 2020). The approach that we have demonstrated (a) accounts for confounding factors in the statistical model, (b) accounts for the relevant non-independence in the statistical model and (c) uses post-network permutations to further account for non-independence. Thus, we advocate careful thinking about constructing the statistical model to correctly fit the data, including confounding effects. Where possible non-independence structure should also be dealt with in the statistical model, although this can also be dealt with using post-network permutations. Our approach can help facilitate the use of Bayesian analysis, which has possibly been neglected due to the past focus on permutation tests and *p* values.

If confounding factors are controlled for in the statistical model, then it is unnecessarily to control for them again in the permutations. In some cases, no permutations are needed, such as when using dyadic regression with adequate variance/covariance structure (see e.g. our example simulation 2). When the structure to be controlled for is more complex, such as when performing a nodal analysis on a centrality measure, then appropriate permutations can be used, as demonstrated here, such as GLMQAP in the ANINET R package for a dyadic analysis (Weiss, 2020).

We found that controlling for confounding factors in the statistical dyadic model can help to either mitigate or eliminate the problem, depending on how well these confounding effects can be captured in the model. It often compensates for the extent of the bias, except where there are extreme differences in observations in the first simulation, where it still performs much better than not controlling for confounding factors. Our approach works the same with nonlinear approaches such as polynomial regression and GAMs, and we recommend careful examination of predicted model fits and relationships between variables to assess whether a nonlinear relationship might be best for the confounding factors.

When analysing with social preferences, there are many situations where confounding factors should be controlled for in the statistical models. Examples of confounding factors include group sizes, location, season and any known observation bias. When dealing with social preferences, anything that would be controlled for in the null model should ideally be controlled for in the statistical model. Even where the question relates to contacts, there will still be occasions where it is appropriate to control for bias in the effect size. For example, here we demonstrated an example of where there is bias for observing certain types of individuals over others, which distorts our observations of the actual interactions (see simulation 1). In situations such as this where differences in observation (or analogously bio-logger performance) may mask the structure of the true social network then controlling for its effect will be important in analysing all animal social networks. However, once confounding factors are controlled for in the statistical model, in most cases it will not be necessary to control for them again in the null model.

Gregariousness is often a key confound for which researchers control (Godde et al., 2013). However, in some study systems, gregariousness may be a mechanism underlying both the number of observations and the connectedness of individuals in the social network. Where this is the case controlling for the number of observations of each individual in a statistical model can be problematic and including it as a covariate in a model may mask differences in gregariousness between individuals. Another scenario where it is difficult to tease apart competing drivers of association is where social preferences drive use of locations (in addition to spatial preferences impacting association patterns). This is a general problem for networks constructed using data on spatial and temporal co-occurrence that still needs to be resolved, but the key to addressing it is understanding any observation bias and the study system. Simple simulations such as those we have presented here are useful tools in examining the impact of known confounding factors on social preferences prior to any analysis of animal social data, and studying whether they can be adequately controlled for.

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AUTHORS' CONTRIBUTIONS

D.W.F. conceived of the idea and D.W.F. and M.N.W. designed the simulations with input from M.J.S. and D.P.C.; M.N.W. and D.W.F. programmed the simulations; M.N.W. developed and coded the permutations; D.W.F. analysed the results with input from M.N.W., M.J.S. and D.P.C.; D.W.F. led the writing of the manuscript with input from M.N.W., M.J.S. and D.P.C. R.J.Y.P. collected and provided the reef manta ray data. All authors contributed critically to the final draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The manta data are available at https://osf.io/y5ts2/

ORCID

Daniel W. Franks https://orcid.org/0000-0002-4832-7470
Michael N. Weiss https://orcid.org/0000-0002-7422-0538

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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