SOCIAL NETWORKS AND FITNESS CONSEQUENCES OF EARLY SOCIALITY IN WILD BOTTLENOSE DOLPHINS (*Tursiops* sp.)

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By

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SOCIAL NETWORKS AND FITNESS CONSEQUENCES OF EARLY SOCIALITY IN WILD BOTTLENOSE DOLPHINS (TURSIOPS SP.)

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ABSTRACT

Despite recent investigations into the relationship between adult social bonds and fitness in socially complex species, remarkably little attention has focused on the consequences of early sociality. For this dissertation I used social network analysis (SNA) to examine social patterns in wild bottlenose dolphin (Tursiops sp.) calves of Shark Bay, Australia. Bottlenose dolphins exhibit a complex fission-fusion social organization with dynamic group membership and sex-segregation in adult behavior. The extensive Shark Bay dataset provided a unique opportunity to investigate calf social networks and potential fitness consequences of early sociality.

Chapters 1 – 2 discuss challenges in studying sociality and the application of SNA to studies of animal societies with a focus on primates and cetaceans. Chapter 3 presents a case study to illustrate the variety of social measures available to researchers to capture multiple dimensions of social behavior.

Chapter 4 investigates the reliability and precision of common social network metrics. SNA is increasing in popularity, but the error and bias introduced by sample size and method is underappreciated. Social network metrics responded differently to both sample size and method. Also, weighted metrics are arguably appropriate for ameliorating some error.

Chapter 5 uses SNA to investigate social patterns during temporary mother-calf separations. Calves had larger, less dense networks than their mothers, suggesting that calves use
these opportunities to expand their networks. Male calves had strong associations with other male calves, foreshadowing adult male alliance formation. Since Shark Bay dolphins exhibit bisexual philopatry, calf associations can last into adulthood and early sociality likely has implications for future success.

Finally, Chapter 6 directly investigates fitness by testing whether calf social networks predict juvenile survival to age 10. Significantly more males died as juveniles; however the probability of male survival increased with the metric eigenvector centrality. Interestingly, as calves, males who died had stronger ties to juvenile males than those males who survived. Thus, while some aspects of early sociality have a fitness benefit, certain associations appear costly. These results suggest that selection is acting on this early life-stage and have implications for the evolution of social behavior and the causes and consequences of sociality.
This thesis is dedicated to my friends and family for their constant love and support.

Many thanks,
MAGGIE
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DISSERTATION INTRODUCTION

Theoretically, group living evolves when the benefits of frequently associating with conspecifics (e.g. protection from predators, resource defense, or mate availability) outweigh the potential costs (e.g. increased competition, exposure to disease, and conspicuousness to predators) (Krause & Ruxton 2002). Presumably, certain conditions select or allow for more complex social structures featuring long-term, individually specific relationships, dynamic group membership, and long-term alliance formation. Several versions of the social brain hypothesis ("Machiavellian Intelligence" Byrne & A. Whiten 1988; "Social Brain" Dunbar 2003; "Cultural Intelligence" Whiten & van Schaik 2007) have been proffered to suggest that selective pressures of group living have shaped increasing social complexity along with brain size. Highly encephalized, socially complex species also tend to have extended life histories characterized by lengthy infancy and juvenile periods, which possibly allow for the development of the social competency necessary for adulthood (Pereira & Fairbanks 2002). Given what appear to be costly correlates of social complexity, these patterns of sociality are presumed to persist because they provide some fitness advantage. Empirical research into the fitness benefits of social bonds in species exhibiting the hallmarks of complex sociality is gaining momentum, but little attention has focused on social development or the fitness consequences of the early social environment.

The study of animal sociality is hindered by a lack of consensus concerning the definition of sociality itself, as well as a definition of social complexity. Chapter 1 introduces this problem as one of four challenges facing the studies of animal sociality, with an emphasis on primates and cetaceans. Despite a phylogenetic distance of 90-95 million years, primates and cetaceans,
particularly odontocetes (toothed whales), exhibit remarkable convergence concerning
behavioral, cognitive, and social traits (reviewed in Marino 2002). Several genera in both orders
are characterized as having relatively large brains for their body size, prolonged periods of
development, delayed sexual maturity, coordinated feeding strategies, cooperative alliances and
nested hierarchies, and behavioral traditions. Due in part to the interest generated by this
convergence, Chapter 1 focuses on the large body of primate and cetacean literature, but the
challenges discussed are applicable to other social species.

In order to better address questions concerning animal sociality, animal behaviorists and
behavioral ecologists are increasingly turning to the suite of analytical techniques known as
social network analysis (SNA). SNA allows for the quantification of multi-actor interactions,
thereby providing a more realistic representation of social patterns and relationships. Chapter 2
provides a brief introduction to social network analysis, including a review of primate and
cetacean social network literature, and techniques for network comparison and dynamic network
analysis developed in the social sciences that could benefit the animal behavior community.

Bottlenose dolphins are attractive candidates for the application of SNA due in part to
their complex fission-fusion social organization characterized by dynamic, temporally variable
groups (Connor et al. 2000). In Shark Bay, Western Australia, researchers have studied the
resident bottlenose dolphins since 1982. Using two calves from the Shark Bay dataset, Chapter 3
presents a case study intended to provide an example of the variety of social measures available
to researchers, including both traditional measures as well as network metrics. In particular, this
example case study advocates the use of multiple measures of sociality with careful
consideration of what dimensions were captured before making inferences.
Because SNA is becoming such a popular and powerful means for investigating animal societies, some attention must be paid to the reliability and scope of inference of network studies, specifically when metrics are calculated from networks consisting of samples from a larger population (Croft et al. 2011). As biologists move beyond using SNA for descriptive purposes to answer specific hypothesis driven questions, understanding the potential error and bias introduced by sample size and sampling method is imperative. Surveys, also known as sighting records, are more commonly used to construct animal social networks because they are relatively independent from each other and useful for gathering basic demographic information from a population. However, previous research on non-network measures indicates that more intensive focal follows on a specific individual(s) provide greater detail in terms of individual social variation, particularly for hard to identify individuals such as dolphin calves (Gibson & Mann 2009). Chapter 4 not only investigates the influence of sample size on four standard network metrics, but also how this influence differs for networks built from datasets collected via two commonly used sampling methods.

The extensive dataset, as well as the natural variation in behavior observed in the Shark Bay population, presents the unique opportunity to utilize SNA to examine calf social relationships and the possible future fitness consequences of early sociality. Chapter 5 focuses on the unusual ability of physically precocious bottlenose dolphin infants to engage in temporary separations from their mothers. These separations provide calves with the opportunity for self-socialization in the absence of direct maternal influence and allow calves to begin forming their own social network. Since Shark Bay bottlenose dolphins exhibit bisexual philopatry, relationships have the potential to begin early and persist into adulthood. This chapter
specifically investigates sex differences in bottlenose dolphin calf social patterns during temporary mother-calf separations.

Finally, to directly address the potential fitness consequences of early sociality in bottlenose dolphins, Chapter 6 investigates whether metrics calculated from calf social networks predict survival as a juvenile from weaning to age 10 years. Due to the dynamic nature of bottlenose dolphin society, newly weaned individuals must navigate a complex social landscape without the buffer of a stable kin group, presumably relying on social skills and bonds developed as calves. Adult male bottlenose dolphins form relatively stable, long-term hierarchical alliances in order to consort with females (Connor et al. 1992; Connor et al. 2001; Krützen et al. 2004), whereas females do not form alliances and instead exhibit highly variable social patterns (Smolker et al. 1992; Gibson & Mann 2008a). Given the sex-segregation in adult behavior, the post-weaning risks are greater for young males, who also associate less with their mothers than females (Tsai & Mann 2012). We hypothesized that differences in social partner preference between males and females begin as calves (Gibson & Mann 2008a; Gibson & Mann 2008b; Chapter 5) and certain attributes of these associates, including age-sex class, would have fitness consequences. In addition to overall social metrics, Chapter 6 examines calf association strength with different age-sex classes in relation to juvenile survival outcomes.

Network theory is becoming an increasingly valuable tool for research endeavors ranging from the identification of terrorist networks to the mapping of gene and protein interactions (e.g. Krebs 2002; Giot et al. 2003). For the field of animal behavior, network analysis offers an innovative approach to the study of animal societies. This investigation addresses critical methodological and sampling questions concerning both the collection and analysis of social
network data. However, most notably, this research effort applies this powerful tool to increase the currently limited understanding of the potential fitness consequences of early sociality in a free-living complex society.
REFERENCES


INTRODUCTION

Despite a phylogenetic distance of ~95 million years, primates and cetaceans both exhibit a wide variety of social systems and share many features of complex sociality, including long-term relationships and alliances. Primatologists have contributed a rich theoretical framework for understanding how such patterns evolved in mammals, and more recently cetologists have developed a variety of tools for measuring sociality over larger and more variable temporal and spatial scales. In this chapter, we bring these advances together and discuss the concept of sociality, particularly how it relates to primate and cetacean societies. We see four major challenges to the study of sociality in primates and cetaceans. First, how is social complexity defined and measured and on what scale? Second, what is the role of cognition in either fostering or constraining social phenomena? Third, what role does prolonged development, characteristic of primates and toothed whales, play in socially complex taxa? And, fourth, does social skill or complexity have individual fitness outcomes? This chapter is primarily focused on the first challenge, but will also review key literature regarding the other three.

DEFINING SOCIAILITY

* Authorship for paper: Margaret A. Stanton & Janet Mann
The term 'sociality' is often equated with the term 'group living' despite the presence of such contradictions as orangutans (*Pongo pygmaeus*) who spend the majority of their adult lives in relative solitude, but are still considered a social species (van Schaik & van Hoof 1996). Even bottlenose dolphin (*Tursiops* sp.) females spend approximately 50% of their time alone with their dependent offspring (Mann & Watson-Capps 2005; Gibson & Mann 2008a; Gibson & Mann 2008b) and some females spend >80% of their time alone (Mann *et al.* 2008). Whitehead (2008) addressed the elusive definition of sociality by describing “a baseline minimum condition for sociality [where] the members of a population interact behaviorally. If there are no interactions, so that no behavior of any animal has a direct effect on the behavior of any other, then there is no sociality” (p.245). This baseline excludes courtship interactions that result in offspring.

In order to facilitate the study of social structure and evolution, Hinde (1976) introduced a three level conceptual framework. The most fundamental level of this framework consists of interactions between two or more individuals. According to Hinde, descriptions of these interactions should include “what the individuals are doing together (its content) and how they do it (quality)” (p. 3). Example interactions include individual A grooming individual B or individual C chasing individual D. Successive interactions between individuals result in relationships, the second level of Hinde’s framework. Relationships should be described not only by the presence of interactions, but also by their temporal patterning. Repeated agonistic interactions between individuals A and B resulting in submissive behaviors by A would indicate that the relationship between these two individuals is B dominant to A. Most measures of social interaction and relationships are very basic, focusing on association, proximity, affiliation, and agonism. The third and final level is the surface structure of the group defined as “the nature,
quality, and patterning of relationships” (p. 3). Obviously, these three levels build upon each other, but are not unidirectional. In most systems, relationships likely influence interactions and social structure likely influences relationships. The basic appeal of Hinde’s framework is its applicability to a wide variety of social systems; however Kappeler & van Schaik (2002) introduced an additional system for defining social structure more specific to primates. This framework involves three non-mutually exclusive structural elements, social organization, mating system, and social structure, which are shaped by different selective forces. Social organization consists of demographic information such as group size and sex composition as well as the interaction of individuals in space and time. According to Kappeler & van Schaik (2002), the social organization of primates can be described as solitary, pair-bonded, or group-living. If the latter is the case, aspects such as group size, the ratio of males to females, and group cohesion should be described. The second element, social structure, is roughly equivalent to surface structure in Hinde's earlier framework as it is based on the patterning of relationships. Finally, mating system includes the traditional classifications of monogamy, polyandry, etc. and represents a particular subset of social interactions. It is important to note that although past studies have defined societies based on a single component, such as mating system, we maintain that an adequate description of a social system is not complete without consideration of all three elements.

SOCIAL COMPLEXITY
Non-human primates and delphinids attract so much interest in part because, like humans, they exhibit social complexity. Of course this statement begs the question: what is social complexity? Although frequently addressed in the primate literature and beyond, no consensus currently exists as to the definition of social complexity or the elements a society must exhibit to be considered complex. Blumstein & Armitage (1998) define the concept using information theory, which contends that a more complex system requires more information to describe (e.g. 10 behaviors are more complex than 1 behavior. This reasoning is not unique as group size is often used as a proxy for social complexity with the argument that the greater the group size, the greater the number of potential relationships (e.g. when \( N_{\text{group}} = 4 \) then \( N_{\text{relationships}} = 6 \), but when \( N_{\text{group}} = 6 \) then \( N_{\text{relationships}} = 15 \)). According to the authors, this definition also takes individual variation into account as greater variation takes additional information to describe. Despite a precedent for using group size to measure complexity, most researchers currently agree that the nature of relationships must also be accounted for when assessing complexity. As stated by Shultz and Dunbar (2007), “A ‘complex’ social environment may be more the result of an individual’s role within the group and its relationships with other group members rather than the total number of individuals with whom it associates” (p.2429). In order to attempt interspecific comparative analyses, some researchers have constructed social complexity metrics. Not surprisingly, Blumstein and Armitage (1998) used information theory to create a metric for quantifying social complexity across ground-dwelling sciurids where complexity increased with an increasing number of individuals in different social roles (e.g. yearling, juvenile, adult). Shultz and Dunbar (2007) created two indices of social intensity with which to compare social complexity across genera. The first index measures a genus’ degree of social bondedness by
calculating the proportion of species that exhibit either a pair-bonded (socially monogamous) or
female-female bonded social structure. The second index is simply the species mean of the total
daytime devoted to social activities. While attempts to quantify complexity are crucial for
comparison across taxa, the results thus far are study-specific, and no universally accepted
measure exists.

Despite disparities in defining complexity, the presence of alliances is traditionally
considered indicative of increased social complexity. Alliances are defined as “long-term
cooperative relationships” with cooperation defined as “an acting together of two or more
individuals such that at least one amongst them stands to gain benefits unavailable through
solitary action” (Harcourt & de Waal 1992, p.vi). Alliances are generally considered complex
due to their triadic nature and the implied ability to discern third-party relationships (Harcourt
1988; Harcourt 1992). For example, if individuals A and B are fighting, C may support animal A
because A is more dominant; thus C would support the likely winner. Alternately, C might
support B and consequently remove A from the top of the dominance hierarchy. Such decisions
become exponentially more complicated the greater the number of actors (Harcourt 1988). The
complexity increases to an even greater degree when considering hierarchical alliances such as
those observed in male bottlenose dolphins in Shark Bay, Australia where the decision to
compete or cooperate must be made both within and between individual alliances of 2-3 males
(Connor et al. 1992). The ability to recognize third-party relationships (triadic awareness) was
used in the past to differentiate between primates and non-primates (Harcourt 1992); however
evidence indicates this ability is present in spotted hyaenas (*Crocuta crocuta*) (Engh et al. 2005).
This feature is suggested, but not substantiated in bottlenose dolphins. Captive studies reveal the
ability to recognize relationships between objects and the observed alliance formation strongly suggests that the capacity is present (Herman et al. 1989; Connor 2007). By definition, alliances require repeated interactions between the same individuals, but alliance formation alone should not determine whether a society is complex. For the purposes of this chapter, we use the de Waal & Tyack (2003) definition of complex sociality that requires the presence of long-term, individually specific relationships, but we extend the definition to include flexible group membership and hallmarks such as alliance formation. Finally, some scientists define social complexity by the psychological mechanisms that underlie complex social cognition (e.g., theory of mind, episodic memory, imitation, joint attention, and teaching), with particular focus on attributes that are limited to humans and occasionally other large-brained species. Although beyond the scope of this chapter, we believe that consideration of both observational data and cognitive mechanisms are necessary to move the field forward.

FISSION-FUSION SOCIETIES

Even without a clear definition of complexity, many researchers agree that fission-fusion societies where long-term relationships are maintained are some of the most complicated in the animal kingdom. This social system is exhibited by a variety of primate species including humans, chimpanzees, bonobos, and spider monkeys (Ateles spp.), as well as other mammals such as elephants, spotted hyenas, lions, some bats, and bottlenose dolphins (Goodall 1986; Wells et al. 1987; Symington 1988; Rodseth et al. 1991; Smolker et al. 1992; Holekamp et al. 1997; Kerth & König 1999; Packer 1986). The details of fission-fusion societies vary across
species, but all are social systems in which members of the community are rarely, if ever, all together; group size and composition vary temporally; and preferential associations are present. The complexity of fission-fusion systems lies in the dynamic nature of these spatially and temporally variable groups and the resulting irregular availability of social information. Since relearning social standing with every encounter would presumably waste time and energy, the cognitive demands on these species include the need to remember individuals not encountered on a regular basis, as well as the interactions between these individuals (Aureli et al. 2008). Also, since not all interactions are witnessed by all members of the community, the ability to infer changes in third-party relationships based on patchy information would further assist individuals in such a social system (Engh et al. 2005). The benefit of a fission-fusion system appears to be the capability to quickly respond to fluctuating ecological pressures thus maximizing the benefits of grouping, while minimizing the cost of within-group competition. Evidence for this trade-off includes the observed linear relationship between feeding party size and patch size in populations of spider monkeys and chimpanzees (Symington 1990). Also, fission-fusion patterns responded to demographic changes in chimpanzees of the Tai forest, Ivory Coast, with increased party size, duration, and altered party composition as the overall community size decreased (Lehmann & Boesch 2004; Aureli et al. 2008). Due to the variation observed across fission-fusion species, researchers recently suggested that the term “fission-fusion society” be replaced with “fission-fusion dynamics” and employed to describe a continuum representing “the extent of variation in spatial cohesion and individual membership in a group over time” (Aureli et al. 2008 p628). Chimpanzees, spider monkeys, and humans are all considered to be "higher" fission-fusion taxa
due to the observed variability in subgroup number and composition (Symington 1988; Aureli et al. 2008).

Some evidence suggests that an additional cognitive enhancement in higher fission-fusion taxa is the ability to inhibit behavior based on context. Chimpanzees, for example, inhibit aggressive behavior when challenged if no support is available; by contrast, high-ranking juvenile Japanese macaques continue to challenge lower-ranking individuals in the absence of familiar support, resulting in the loss of dominance rank (Chapais 1992; Aureli & de Waal 1997; Aureli et al. 2008). Enhanced inhibition may also help to explain the tolerance of bottlenose dolphin females. Unlike males who must compete with each other for mates, female bottlenose dolphins are not in direct competition with each other for resources and do not steal fish or exhibit intrasexual aggression (Mann & Sargeant 2003; Scott et al. 2005). A recent study investigated the possibility of enhanced inhibition by comparing the results of three non-fission-fusion species (capuchin monkey, *Cebus paella*; long-tailed macaque, *Macaca fascicularis*; and gorilla, *Gorilla gorilla*) and four fission-fussion species (bonobo, *Pan paniscus*; spider monkey, *Ateles geoffroyi*; chimpanzee, *Pan troglodytes*; and orangutan, *Pongo pygmaeus*) presented with five tasks assessing motor and temporal inhibition. Members of fission-fusion taxa consistently performed better than those of non-fission-fusion taxa and a cluster analysis based on the tasks' results grouped the species based on social dynamics regardless of phylogeny (Amici et al. 2008). The results of this inhibition study indicate that further comparative research into the cognition of fission-fusion species across taxa is necessary to understand the cognitive demands of this dynamic social system.
SOCIAL BRAINS

Across mammalian taxa, numerous studies have found a relationship between social complexity and relative brain size (Dunbar 1992; Dunbar 1998; Kudo & Dunbar 2001; Shultz & Dunbar 2006). Consistent with two similar and prominent theories implicating social factors in the evolution of large brains, the “Machiavellian Intelligence” and the “Social Brain” hypotheses (Byrne & Whiten 1988; Dunbar 1992; Dunbar 1998), Marino (1996) found a positive correlation between encephalization quotient and group size across odontocete families. Primate studies have gone much further, showing that a variety of social and ecological factors independently correlate with overall (or non-visual) neocortex size including: grooming clique size (Kudo & Dunbar 2001), mating system (Sawaguchi & Kudo 1990; Pawlowskil et al. 1998), social learning (Reader & Laland 2002), rate of deception (Byrne & Corp 2004), degree of frugivory (Sawaguchi & Kudo 1990; Barton 1998), diurnality (Barton 1996), innovation rate (Reader & Laland 2002), and tool use (Reader & Laland 2002). Thus, social and ecological pressures are likely to be important in brain evolution (Barton 1996; Reader & Laland 2002). Similar correlations have been found in birds (Lefebvre et al. 1997; Lefebvre et al. 2002; Lefebvre et al. 2004; Sol et al. 2005; Emery et al. 2007) and ungulates (Shultz & Dunbar 2006). Whiten & van Schaik (2007) suggest that it is the combination of innovation (novel individual learning) and social learning that allow species to both solve ecological problems and capitalize on the discoveries of others. Both are necessary for the evolution of traditions and culture, presenting spiraling selection pressures on “cultural intelligence” in a species (Cultural Intelligence Hypothesis: Whiten & van Schaik 2007). However, behavioral complexity remains ill-defined
(Healy & Rowe 2007), a limitation likely to foster circularity where complexity is assumed for large-brained animals and dismissed for those less endowed. To avoid this, social complexity must be carefully operationalized at each turn.

DEVELOPMENT

Highly encephalized species such as delphinids and primates also tend to have slow life histories, especially a lengthy period of immaturity (Harvey et al. 1987). Many explanations for this correlation focus on the expense of brain growth and energetic trade offs between brain growth and body growth (Deaner et al. 2003, but see Barton & Capellini 2011). Other hypotheses for extended life-histories, not mutually exclusive from those emphasizing brain growth, focus on socioecological pressures or releases from constraint (Deaner et al. 2003). Prolonged immaturity in particular may allow for the development of the social competency necessary for adulthood (Fairbanks 2002). If reproductive success as an adult is dependent on social savvy, then the extension of the developmental period prior to adulthood would allow individuals to obtain necessary social knowledge and skills. In support of this argument, Joffe (1997) found a correlation between the non-visual neocortex ratio and the proportion of life spent in the juvenile period, but no correlation between non-visual neocortex ratio and proportion of life spent in gestation or infancy. Furthermore, the proportion of life spent in the juvenile period was correlated with mean group size, but no correlation was detected between mean group size and proportion of life spent in gestation or infancy. A more recent analysis, however, did not find support for a direct correlation between brain size and length of the juvenile period, but the
authors do not dismiss the possibility of large brains providing benefits such as allowing for increased behavioral flexibility in complex environments (Sol 2009; Barton & Capellini 2011).

Whether a prolonged infancy and/or juvenile period is essential to the development of social skills is difficult to test. How much social experience, and what kind, is necessary for social competence? How is it measured? Is the number or quality of relationships important? Is it beneficial to be connected or close to an important individual or key player? Experimental work cannot selectively deprive animals of one type of social experience without depriving them of many. Developmental research, however, can provide insights by showing how the variation in early social experience predicts social rank, social integration, survival, or reproductive outcomes.

FITNESS AND SOCIALITY

Although social complexity is presumed to persist because it increases survival and reproduction, historically few studies empirically tested how intraspecific individual variation in sociality directly relates to fitness, although this area of research is currently gaining momentum (Silk 2007; Silk et al. 2010; Schülke et al. 2010). For logistical reasons, such studies were most often conducted in species with short life-histories (reviewed in Silk 2007). The degree to which sociality might affect fitness appears to vary depending on ecological conditions and type of social system. For example, group size and reproductive success tend to be negatively or not correlated when infants are reared either individually or communally, as is the case with yellow-bellied marmots (Marmota flaviventris) (Armitage & Schwartz 2000). This negative relationship
is most likely attributable to increased within-group competition and, in species such as lions, increased infanticide (Packer et al. 1990). However, in cooperatively breeding species such as the meerkat (*Suricata suricatta*), group size has a positive relationship with offspring survival (Clutton-Brock et al. 2001). While providing important evidence for fitness consequences of sociality and a direction for future research endeavors, these studies only scratch the surface of an expansive topic.

The relationship between socially complex features and fitness in particular has received remarkably little attention. Many studies of fission-fusion societies, for example, are interested in the ecological or social conditions that favor the evolution of this system, but this research fails to directly address the fitness benefits provided to an individual living in a such a dynamic society. Examples of recent studies relating complex social bonds and fitness include a study of savannah baboons (*Papio cynocephalus*) that investigated the relationship between variation in female social integration and infant survival. A female's social integration was quantified by a composite sociality index consisting of measures of proximity and grooming and was found to be a significant predictor of infant survival to age one. This relationship remained when dominance rank and environmental conditions were statistically removed and when data were restricted to when females did not have young offspring to avoid inflated composite sociality indices due to other females’ attraction to infants (Silk et al. 2003; Silk et al. 2009). Strong and consistent social bonds were also associated with longevity in adult female baboons (Silk et al. 2010). An increasing amount of attention has also begun focusing on the fitness consequences of male social bonds. While cooperation in reproductive coalitions and alliances has long been considered beneficial due to its influence on dominance hierarchy and access to mating
opportunities, a recent study in macaques (*Macaca assamensis*) linked strong male-male bonds to coalition formation, social dominance, and paternity success (Schülke *et al.* 2010). Our own recent work also uncovered a fitness consequence of social bonds for male bottlenose dolphins (*Tursiops* sp.). In this study a social measure calculated during the infancy period predicted future male survival as a juvenile (Chapter VI). Aside from these recent investigations, the historical lack of empirical support for the adaptive value of complex social bonds is not surprising given the difficulty of collecting the necessary data, especially in apes and delphinids.

Once data are obtained and social complexity is defined, another obstacle to overcome is the selection of appropriate analyses that are capable of biologically relevant quantification of social relationships. Innovative social network analysis provides a powerful response to this challenge. Traditional studies of social relationships and structure focus on dyadic interactions, whereas network analysis applies graph theory to quantify multi-actor interactions, thereby providing more realistic representations of complex societies (Wasserman & Faust 1994). Lusseau and colleagues have already demonstrated the applicability of social network theory to cetaceans by describing bottlenose dolphin societies at two sites in New Zealand and Scotland (Lusseau 2003; Lusseau & Wilson 2006) and killer whale social structure in the northeastern Pacific (Williams & Lusseau 2006). Primatologists have also used social network analysis to describe and analyze social patterns, particularly grooming interactions, in a number of species including baboons (*Papio anubis*) (Lehmann & Ross 2011), chimpanzees (Lehmann & Boesch 2009), and macaques (*Macaca nemestrina*) (Flack *et al.* 2006; see Brent *et al.* 2011; Chapter 2 for reviews). Recent methodological developments have provided researchers with procedures for incorporating uncertainty introduced by sampling bias as well as exciting new variations of
metrics for analyzing networks where ties between individual actors represent not just the presence of a relationship, but also its strength (Lusseau et al. 2008; Whitehead 2008). In general, social network analysis allows researchers to address those questions that are difficult or impossible to answer using more traditional methods, specifically when considering complex sociality.

CONCLUSION

In this chapter, we discuss four major challenges in the study of sociality and social complexity, with a focus on primates and toothed whales. A universal definition for social complexity remains elusive; however, certain characteristics such as alliance formation and fission-fusion social patterns are generally considered complex. Continued input from both behavioral observation studies as well as cognitive research will aid in the understanding of this complicated phenomenon. Additionally, we consider developmental research essential for understanding the prolonged developmental period characteristic of species typically considered socially complex as the survival and/or reproductive outcomes of early social development are likely to be crucial to the understanding of the causes and consequences of sociality. Clearly, there are a number of diverse social measures available and discovering what features are important, either because they help define complexity or have fitness outcomes, is a significant undertaking. We advocate using as many approaches and tools as are available, particularly those that capitalize on recent computational advances, such as social network analysis. In the broad sense, primatologists have typically focused on the types of social interactions (e.g., grooming,
coalitionary aggression) and selective forces that shape social structure. Also, for practical, disciplinary, and historical reasons, primatologists are far ahead of cetologists in terms of experimental research on the underlying psychological mechanisms of social cognition, whereas cetacean biologists, although newer to this domain, have concentrated on how to characterize large, socially complex societies. By merging these efforts, a clearer picture of complex animal societies is sure to emerge.
REFERENCES


INTRODUCTION

A powerful quantitative tool with which to address the causes and consequences of sociality is social network analysis (SNA). Indeed, social network theory has potential in any discipline that requires the description of complex systems including physics, psychology, sociology, ethology, neuroscience, cell and molecular biology, ecology, mathematics, military intelligence, and computer science (Wasserman & Faust 1994; Freeman 2004). A social network is defined as actors (or nodes, points, vertices) linked by relationships (edges, links, ties) and the visual representation of these nodes and edges is referred to as a graph (Fig. 1). This type of analysis was popularized in the 1970s after Stanley Milgram (1967) examined the distance between individuals in the U.S., the results of which are commonly referred to as "Six Degrees of Separation." Later, Watts & Strogatz (1998) formalized Milgram's idea in their description of small-world phenomena, where tightly knit sub-groups of individuals are closely connected to each other, but with at least one member maintaining a connection to a separate sub-group.

With recent advances in computing power, SNA has gained momentum in the field of animal behavior (Krause et al. 2007; Wey et al. 2008). Traditional studies of social relationships and structure focus on dyadic interactions, whereas network analysis applies graph theory to quantify multi-actor interactions, thereby providing more realistic representations of the complex

* Authorship for this paper: Margaret A. Stanton & Janet Mann
societies typically observed in primates and cetaceans. Additionally, by providing more direct measurements of social relationships, rather than proxies such as group size, social network analysis allows for more in-depth investigations into complex sociality. By quantifying multi-actor interactions SNA accounts for the unavoidable data dependency, which is problematic for traditional statistical analyses. Take for example, an investigation into the relationship between dominance rank and relationship quality in a savanna baboon troop. With traditional methods, female rank and/or relationship quality are treated as independent, when in fact, they are not. A female who grooms (bonds with) one female cannot simultaneously be grooming (bonding with) another. Rank is determined by who is above and below, so is by definition, not independent. SNA treats the relational nature of data as part of the analysis. A network's edges can be directed or undirected, weighted or unweighted. Undirected edges indicate that the relationship is symmetric, as in the case of a mutual friendship. However, if one individual identifies another as a friend and the sentiment is not reciprocated, the relationship is directed. Additionally, an unweighted edge indicates the presence of a relationship, while a weighted edge can indicate the presence and the strength of a relationship. Edges can also be either positive or negative, as might be quantified when individuals preferentially approach or avoid each other (Wasserman & Faust 1994; Croft et al. 2008; Wey et al. 2008). Network theory is useful and unique in that it is capable of analysis on multiple levels by characterizing individuals, their subgroups of neighbors, and the network as a whole. Some basic social network metrics including measures of centrality (a node’s connection to the rest of the network) and clustering (the tightness of subgroups or cliques) are described in Table 1, but it is most important to note at this juncture that distinct social network metrics provide different information about the same individual,
CONSIDERATIONS AND CAVEATS

Despite the usefulness of social network analysis and the increasing frequency with which these techniques are applied, a number of considerations and caveats are warranted prior to the initiation of a network study (see James et al. 2009; Croft et al. 2011 for review of SNA potential pitfalls). One important consideration is how to define a relationship. According to Hinde's (1976) framework for the study of social structure, a relationship is defined as successive interactions between individuals. In the study of animal behavior, however, interactions are often difficult to observe and quantify; therefore relationships are more often assessed in terms of association defined by shared group membership. Whitehead & Dufault (1999) refer to this method as the “gambit of the group” and for the purposes of SNA, researchers should be aware that networks built from group-defined association data may appear highly clustered due to this sampling method. These associations are also typically measured in terms of an association index, such as the half-weight index, that accounts for sampling effort (Cairns & Schwager 1987). Additionally, there is no universally accepted method for determining whether a biologically meaningful relationship exists and should be included in a social network for analysis or whether the observed association is random, erroneous, or biased by sampling method or effort (see Chapter 4). The best response to this uncertainty to date has been to filter and dichotomize data, thereby only including edges or nodes above a certain value when
constructing the network. However, the thresholds at which networks are filtered and dichotomized are arbitrary and the resulting binary networks are likely oversimplified. Recent methodological developments are providing researchers with exciting new variations on centrality and clustering metrics for analyzing weighted networks, which are exceedingly useful for investigating animal social networks (Table 1) (Lusseau et al. 2008).

Weighting edges by association should be considered whenever possible, and algorithm development is ongoing to facilitate further substantive interpretation of weighted graphs. Following construction of the network and calculation of network metrics, weighted or unweighted, the subsequent statistical analysis of network data must proceed with caution. Due to its very nature, network data violates the assumption of independence of traditional statistical methods. Therefore, when analyzing network data the scope of inference is generally constrained and the statistical significance of network metrics is typically assessed by carefully chosen randomized techniques. This particular caveat has important implications for network comparison and dynamic network analysis.

NETWORK COMPARISON AND DYNAMIC NETWORK ANALYSIS

Two networks can be compared with permutation tests (Manly 2007), determining whether specific network metrics means differ more than random expectations. However, care must be taken to ensure that the networks under comparison are similar in size and density or that measures have been normalized based on the maximum value for a node in that network because most network metrics vary with the number of nodes and edges. An additional methodology for
comparing networks regardless of differences in size, or even species, was suggested by Faust & Skvoretz (2002) and characterizes the network in terms of their structural properties and measures the similarity of these networks based on the parameter estimates for models that predict the probability of network ties. Dynamic social data present additional methodological obstacles and techniques for analyzing such data using network theory are still in development or untested on real-life data. Intuitively, social networks are dynamic with relationships forming and fading over time; however the vast majority of research has focused on static networks that are unable to capture information about changes in the network or the mechanisms related to observed dynamics. In the social sciences, Snijders (1996) and his colleagues (Steglich et al. 2010) developed some dynamic models used in the analysis of dynamic friendship networks. These dynamic models can identify what is likely driving change in social networks over time and could be particularly useful for studying animal social development. Research into dynamic network models is on-going and the availability of applied longitudinal datasets will facilitate the creation of exciting additional methodologies.

ANALYSIS OF PRIMATE AND DOLPHIN SOCIAL NETWORKS

In the field of animal behavior, social network analysis is employed, generally on static graphs, to describe complex social structure and to provide insight into studies of cooperation, disease and information transfer, the different roles of individuals in groups, and the consequences of anthropogenic disturbance on animal societies (See Krause et al. 2007; Wey et al. 2008 for excellent reviews). The specific applications of social network analysis to animal
behavior are too numerous to enumerate in further detail here; however it is worth noting some of the earliest and most commonly cited animal social network analysis was conducted on wild populations of bottlenose dolphins (*Tursiops* sp.) (Lusseau 2003; Lusseau & Newman 2004; Lusseau & Wilson 2006; Lusseau 2007). Bottlenose dolphins are attractive candidates for social network analysis due to their dynamic and complex society. For example, Lusseau (2003) described the network of a relatively small population (N=64) of bottlenose dolphins in Doubtful Sound, New Zealand and investigated the theoretical removal of random individuals compared to specific individuals with a large number of associates. The dolphin network appeared robust to removal of random individuals while the removal of individuals with high degree increased the network diameter, defined as the average shortest path-length between any two nodes, by 20%-30%. In a separate study, Lusseau *et al.* (2006) described the network of bottlenose dolphins (N=124) in the inner Moray Firth in eastern Scotland. This study addressed the possible relationship between social structure and geographic preference by assigning dolphins to one of two categories; 1) always sighted in inner Moray Firth or 2) sighted in inner Moray Firth and elsewhere, and determining whether dolphins in these two categories constitute cliques in the network. The researchers conclude that composition of the two communities identified in the social network matched well with the categories of geographic preference.

In primates, network theory has been applied to the analysis of grooming interaction networks as well as association networks (Flack *et al.* 2006; Lehmann & Boesch 2009). An interesting SNA study investigated the roles and structural positions of captive pigtailed macaques (*Macaca nemestrina*) in their social networks. In this case, dominant males perform a policing function by impartially intervening in conflicts between other members of the group.
Both the simulated and empirical removal of just a few of these policing individuals altered the macaque social network, in some cases significantly decreasing in the mean degree and increasing clustering coefficients, which the authors conclude destabilizes the group (Flack et al. 2006). Such investigations can be utilized as a means of predicting anthropogenic effects on free-ranging animal social networks. While many wildlife conservation management plans assume all animals are equal, research such as the macaque study described above, as well as an analysis of a killer whale (*Orcinus orca*) social network, indicates that certain individuals have a disproportionally large impact on their networks and should be differentially accounted for in conservation plans (Williams & Lusseau 2006). Many more primate studies use the term social network when referring to associating individuals and grooming interactions, but do not actually apply network theory when analyzing data. However, as the utility of SNA becomes increasingly apparent network theory is being applied to datasets from primate field sites to identify differences in association patterns between both individuals and age/sex classes and describe association trends over time (Lehmann & Ross 2011; Henzi et al. 2009; Ramos-Fernández et al. 2009).

ADDITIONAL SOCIAL NETWORK APPLICATIONS

The use of social network analysis in animal behavior is by no means confined to research in cetaceans and primates. Indeed the use of these methods now ranges from studies of insects (e.g. Fewell 2003), rodents (e.g. Wey & Blumstein 2010), ungulates (e.g. Sundaresan et al. 2007), and social carnivores (e.g. Smith et al. 2010). An exceedingly useful social network
The technique is quadratic assignment procedure (QAP) regression, which allows for the regression of explanatory matrices on a response sociomatrix representing associations or interactions (Krackhardt 1988; Dekker et al. 2007). QAP regression first calculates coefficients by performing an ordinary least squares (OLS) regression, then randomly permutes the response matrix and reruns the OLS regression X number of times to obtain a matrix-specific distribution of coefficients against which the observed matrix coefficients can be compared and statistical significance evaluated. This permutation-based approach avoids the inflation of type-I errors due to the correlational nature of network data (Krackhardt 1988). As with traditional multiple regression, multiple regression quadratic assignment procedure (MRQAP) allows for the inclusion of multiple factors that may account for variation in a sociomatrix, including factors that are not necessarily of interest that need to be controlled for. Animal behavior researchers are just beginning to recognize the usefulness of this analysis (Croft et al. 2011) and have thus far employed QAP regression to investigate factors influencing network structure in yellow-bellied marmots (Marmota flaviventris) (Wey & Blumstein 2010) and ring-tailed coatis (Nasua nasua) (Hirsch et al. submitted). We have also recently applied this method to our own investigation of the social function of tool-use in Shark Bay bottlenose dolphins (Tursiops sp.) (Mann et al. in review). In that study, the MRQAP was used to control for sex as well as geographic distance and maternal relatedness between individuals while investigating whether similarity based on the use of marine sponges as tools is a significant predictor of association and indicative of culture. This was the first study to examine whether tool-use or foraging similarity influences social preference. Such an examination is not possible with traditional non-network approaches.
CONCLUSION

As indicated above, we have begun applying SNA in our own work on bottlenose dolphin mothers and calves. Chapter 3 gives an example of ego networks (which consist of a focal dolphin or "ego" and all directly connected individuals) for two calves based on different measures of sociality including association and petting/grooming interactions. As evidenced by the pioneering animal network studies described above, social network analysis of cetacean and primate populations is exceedingly applicable to free-ranging primate and cetacean populations and the potential inquiries are plentiful.
REFERENCES


**Figure 1:** Social Network of Shark Bay adult and juvenile dolphins constructed from survey data from 1999-2007. Edges are weighted by half-weight coefficient and only those greater than the average (0.13) are included.

- Female
- Male
- Unknown Sex
<table>
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<tr>
<th><strong>Individual measures</strong></th>
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<tr>
<td><strong>Node degree:</strong> the number of edges to a focal animal; the number of other animals with whom the focal individual interacts or associates</td>
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<td><strong>Centrality:</strong> a measure of an individual’s structural importance based on its network position</td>
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<td><strong>Degree centrality:</strong> centrality based on the number of direct edges an individual has</td>
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<td><strong>Betweenness centrality:</strong> centrality based on the number of shortest paths between every pair of other nodes in the network that pass through the focal individual</td>
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<td><strong>Reach:</strong> A measure of indirect connectedness that is defined as the number of nodes two or fewer steps away</td>
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<td><strong>Affinity:</strong> Average degree of a node’s neighbors. A node with high affinity is connected to other nodes of high degree</td>
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<th><strong>Intermediate measures</strong></th>
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<tr>
<td><strong>Clustering coefficient:</strong> the density of the subnetwork of a focal individual’s neighbors; the number of observed edges between neighbors is divided by the number of possible edges between them</td>
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<tr>
<td><strong>Cliquishness:</strong> how much the network is divided into subgroups; a clique is a set of nodes where each node is directly tied to each other</td>
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<th><strong>Group measures</strong></th>
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<tr>
<td><strong>Average path length:</strong> the average of all path lengths between all pairs of nodes in the network</td>
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<td><strong>Density:</strong> the number of observed edges divided by the number of possible edges in the network</td>
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<td><strong>Diameter:</strong> the longest path length in the network</td>
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<th><strong>Weighted measures</strong></th>
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<tr>
<td><strong>Strength:</strong> A measure of weighted degree that is the sum of the weights on the edges connected to a node</td>
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<tr>
<td><strong>Betweenness:</strong> Sum of the inverses of the weights on each edge that equals the shortest path lengths that pass through the node</td>
</tr>
<tr>
<td><strong>Eigenvector:</strong> The appropriate element of the first eigenvector of the association matrix.</td>
</tr>
<tr>
<td><strong>Reach:</strong> Overall strength of a node’s neighbors</td>
</tr>
<tr>
<td><strong>Affinity:</strong> Average weighted strength of a node’s neighbors</td>
</tr>
<tr>
<td><strong>Clustering coefficient:</strong> A measure of cliquishness or how well connected neighbors are to each other considering the weight on all three edges of each triangle linking the nodes</td>
</tr>
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Table 1: Social network analysis terms. Definitions from Wey et al. 2008 p.334 and Whitehead 2008 p.172-175.
CHAPTER III

Shark Bay Bottlenose Dolphins: A Case Study for Defining and Measuring Sociality*

INTRODUCTION

Like primates such as humans (Homo sapiens), chimpanzees (Pan troglodytes), bonobos (Pan paniscus), and spider monkeys (Ateles spp.), bottlenose dolphins (Tursiops sp.) exhibit an intrinsically complex fission-fusion social organization characterized by the dynamic nature of compositionally and temporally variable groups (Goodall 1986; Symington 1988; Connor et al. 2000). Not surprisingly, measuring sociality in these complex societies is no easy task and often requires a multi-faceted approach with careful consideration of what inferences may be drawn from each available social metric. In this chapter, we use our long-term study of bottlenose dolphin mothers and calves to demonstrate the range of measures that can be used to capture some aspect of dolphin social life, particularly those achieved by employing social network analysis. This innovative technique is increasing in popularity due to its ability to quantify multi-actor interactions thereby providing more complete descriptions of complex societies. We provide examples of both association-based social networks, as well as interaction-based social networks that are more analogous to the grooming networks of chimpanzees.

Bottlenose dolphins of Shark Bay

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An important distinction between the above primate fission-fusion systems and that of bottlenose dolphins is the openness of bottlenose dolphin communities (Smolker et al. 1992). While chimpanzee, spider monkey, and the subgroups of most other fission-fusion species are composed of members from a larger closed social unit, bottlenose dolphin communities exist on an open-closed continuum. At some sites, bottlenose dolphin communities are closed or semi-closed (e.g., Wells et al. 1987; Lusseau et al. 2003), but in Shark Bay, Australia, the community is unbounded with an overlapping mosaic of hundreds to thousands of individuals (Connor et al. 2000). A consequence of openness is that the potential relationships are not constrained by social unit size. Additionally, while the fissions and fusions of terrestrial social groups are limited by the cost of locomotion, this constraint is considerably less restrictive in the aquatic environment of the bottlenose dolphin (Williams et al. 1992), facilitating more frequent interaction with larger groups of individuals on an irregular basis. As a consequence, variation in patterns of association within a population of bottlenose dolphins is exceptionally large (Smolker et al. 1992; Gibson & Mann 2008a). Average group size among bottlenose dolphins in Shark Bay is 4.8 individuals; however the size and composition of these groups is likely dependent on social context (Smolker et al. 1992). Male bottlenose dolphins in Shark Bay form hierarchical alliances cooperating to obtain and sequester females for mating. "First-order alliances" consist of pairs or trios of individual males, whereas teams of these first-order alliances, referred to as "second-order alliances," cooperate to steal female consorts from other alliances or prevent thefts (Connor et al. 1992). Males in first and second order alliances are more highly related than expected by chance, suggesting inclusive fitness benefits to alliance formation (Krützen et al. 2003). An alternative strategy, termed a "super-alliance," is a second-order alliance consisting of labile first-order
alliances whose members frequently switch partners (Connor et al. 2001). Interestingly, members of super-alliances appear no more related to each other than expected by chance (Krützen et al. 2003). Recent research suggests a third level of alliance formation and the nested nature of male bottlenose dolphin alliances is arguably more complex than cooperation behavior in any non-human mammal (Connor et al. 2011).

Unlike males, female bottlenose dolphins of Shark Bay do not form alliances and vary widely in degree of sociality, forming loose social networks with the number of known lifetime associates ranging from 1 - >160 (Smolker et al. 1992; Gibson & Mann 2008, Chapter 4). Females do appear to have preferred associates, but typically spend less than 30% of their time with these top associates (Smolker et al. 1992). Interestingly, female dolphins depend on non-defensible ephemeral food patches (e.g. schools of fish) and are thus tolerant, yet selfish about access to food (Mann et al. 2007); therefore defense of resources does not explain patterns of female sociality. Predation on calves is also unlikely to be the main cause of these groups as shark predation does not appear to be a primary predictor of calf mortality (Mann & Watson-Capps 2005), although group sizes are larger in the newborn period (Mann et al. 2000). In Shark Bay females give birth to a single calf after a 12-month gestation period. Calves are weaned at an average age of 4 years, but females do not have their first calf until age 11-12 years (Mann et al. 2000). Unlike primates who spend their extended developmental period buffered by their natal social group (Leigh & Blomquist 2007), bottlenose dolphins do not spend the juvenile period in stable groups and must negotiate a complex social environment in the absence of direct maternal care (Mann et al. 2000; Tsai & Mann 2012). A recent examination of the possible function of female bottlenose dolphin social groups in Shark Bay found some support for the protection of
young calves (first year of life) from predators since mothers with young calves tended to form larger groups. However, the formation of mother-calf groups was better explained overall by the hypothesis that grouping enables calves, particularly males, to develop social skills before the lack of social savvy incurs a reproductive cost (Gibson & Mann 2008b). Interestingly, bottlenose dolphin calves also vary in degree of sociality ($N_{associates} = 1-77$) and have the ability to separate from their mothers and form unique associates. Since bottlenose dolphins show bisexual philopatry, calf social relationships often persist into adulthood (Tsai & Mann 2012), but despite the attention given to the adult bottlenose dolphin’s fission-fusion society, the first in-depth investigation into bottlenose dolphin calf social development was only recently published (Gibson & Mann 2008a). Using the number of associates and the proportion of time spent in groups when together and separated from each other as measures of sociality, Gibson & Mann (2008a) assessed predictors of individual variation in the social patterns of mothers and calves in Shark Bay. Not surprisingly, the results of this study indicate that the number of associates, time spent in groups, and time spent separated from their mothers changes as calves approach weaning. The researchers also found differences based on calf sex and maternal sociality. With age, males increased their time in groups during separations while this measure decreased in females. In addition, the number of calf associates was strongly related to their mother’s number of associates, especially for females (Gibson & Mann 2008a). We recently employed social network analysis to investigate calf social networks during temporary mother-calf separations and found that calves had larger, less dense ego networks than their mothers. Additionally, male calves appeared to preferentially associate with other male calves during separations (Stanton et al. 2011). These results suggest that during separations calves are independently developing the
social skills and/or bonds necessary for future success, particularly males who rely on alliance formation for mating opportunities as adults. The function and consequences of individual variation in calf sociality are just beginning to be explored, and are critical for understanding both prolonged development and social complexity in bottlenose dolphins. The next step is to examine these patterns in greater depth. In order to highlight individual social variation as well as some of the numerous methods with which social patterns can be quantified, we present a series of social measures calculated for two Shark Bay bottlenose dolphin calves.

METHOD

Researchers have studied the bottlenose dolphin females, calves, and their associates (N>1500) of Shark Bay, Australia since 1988. This research is facilitated by a large number of identifiable individuals and an extensive 27-year dataset. Existing Shark Bay data include both “snapshot” survey data and more intensive focal follow data. Boat-based focal follows of specific mother-calf pairs provide detailed behavioral information including group composition, activity, location, and specific social interactions using standard quantitative sampling techniques including point, scan, and continuous sampling (Altmann 1974). Party composition is scanned for every minute during a focal follow and association is conservatively determined using a 10m chain rule where one dolphin is considered to be in a group with another dolphin if they are separated by 10m or less. Individuals are identified by dorsal fin using photo-identification techniques (Smolker et al. 1992). Focal follows of individuals involve intensive sampling, but provide greater detail and precision in terms of individual social variation, particularly when
examining mother-calf pairs, by allowing for more reliable identification of young calves and better assessment of calf behavior during temporary long-distance separations from their mothers (Gibson & Mann 2009). Two calves, one male (MIG) and one female (LEN) were observed for ~33 hours and ~40 hours respectively during their first four years of life. These calves were chosen because both were observed for four years and both possess similarly sized networks, which facilitates comparison. Using MIG and LEN’s focal follow party composition data, we first calculated a variety of traditional, non-network measures of individual sociality as described in Table 1.

In order to employ social network analysis on this dataset, we used SocProg 2.3 (Whitehead 2009) and UCINET6 (Borgatti et al. 2002) software to construct the ego-networks of LEN and MIG from focal follow party composition data (Fig. 1). An ego network is a type of social network consisting of a focal individual or “ego” and only those individuals directly connected to the focal. All networks were drawn in NetDraw using the spring-embedding algorithm (Borgatti 2002). Two individuals were connected to each other by an edge if they were observed in the same group and the strength of their relationship was calculated by taking the average proportion of observations (APO) two individuals were observed together. The average is necessary to account for biases based on sampling effort. For example, if two dolphins SMO and COO were observed together for a total of 120 minutes and SMO was observed for 180 minutes total, while COO was observed for 480 minutes total, then SMO spent 0.75 of his time with COO, whereas COO spent 0.25 of his time with SMO. In order to create a symmetric sociomatrix so as not to imply a false sense of directionality in the relationship, these two proportions would be averaged for an APO = 0.5. It is important to note that this measure does
not directly translate into the percent of time two individuals were seen together. An APO of 0.5 does not indicate that two animals were observed together 50% of the time. However, higher APOs are considered indicative of stronger relationships.

Association, however, is not the only social measure from which social networks may be constructed; indeed, measuring association is generally considered a proxy for interaction data since interactions are often difficult to observe in the field. Grooming in primates and petting (an affiliative behavior where one dolphin actively moves their pectoral fin on a body part of another dolphin, Fig. 2) in dolphins provide excellent interaction data from which to build social networks. We constructed social networks based on petting interaction events observed during all focal follows of Shark Bay mother-calf pairs during the first four years of LEN and MIG's lives (Fig. 3). Due to the difficulty of obtaining this data, we did not wish to assign too much meaning to the number of observed interactions; therefore these petting networks are binary, meaning a line between two individuals indicates the presence of a relationship, but contains no information about strength. These interaction networks provide an additional dimension to the investigation of social patterns provided by association networks that assume that associated individuals interact with each other. It is important to note at this juncture that the networks presented here are static and were constructed by combining four years of data to create a single network. While multiple years provide more data with which to determine associations, it is likely that each calf's social network differs from year to year with relationships forming and fading over time. Dynamic social network analysis, however, presents novel methodological obstacles that are beyond the scope of this case study. More detailed descriptions of the metrics
calculated from both the association and petting networks are available in Chapter 2 of this dissertation.

RESULTS AND DISCUSSION

The results of various traditional non-network measures of individual sociality are presented in Table 2, while the social network analysis results are presented in Table 3.

While we cannot draw inferences from the analysis of two calves, our intention here is to emphasize varying aspects of sociality and the measures with which to address them. For example, MIG spends a larger portion of his time alone than LEN, which may lead to the conclusion that MIG is less social than LEN. However, while in a group MIG spends more than twice as much time socializing with other dolphins. Additionally, as expected by her greater amount of time in groups, LEN spends more time with every age sex class than MIG with the exception of male calves. It is interesting that MIG, a male calf, spends considerably more time with other male calves than LEN, a female calf. Finally, while fission-fusion social systems receive a great deal of attention in the literature, the rate of change in group composition is rarely reported. In this case, LEN’s fission-fusion rate is greater than that of MIG, which is also not surprising given the difference in time spent alone versus time spent in groups.

As for the association-based ego-networks, LEN and MIG had a similar number of associates at 57 and 62 respectively. Visual inspection of these graphs suggest that LEN and her mother are in the center of a large subgroup, while MIG and his mother are more peripherally connected to a couple of subgroups (Fig. 1). Thus, MIG’s ego network also appears to contain
more clusters, some of which are adult males likely consorting MIG’s mother near the end of his infancy. However, while visual inspection of networks is a useful investigation technique, observed patterns should be verified using appropriate network metrics. For example, most network metrics both at the individual and whole ego-network level are similar between the two calves with the exception of the network-wide clustering coefficient, which is higher in MIG’s ego network.

The most obvious differences between the association-based ego-networks (Fig. 1) and the petting networks (Fig. 3) are size and density, defined as the number of actual edges divided by the number of possible edges in the network. While LEN and MIG’s ego-networks have unweighted densities of 0.55 and 0.36 respectively, the entire petting networks containing LEN as a calf and MIG as a calf have much lower densities of 0.03 and 0.04. Although LEN and MIG were associated with 57 and 62 other dolphins respectively, petting was only observed between LEN and six others, and MIG and three others, which may suggest stronger social relationships between these individuals; however considerably more data are necessary to draw any conclusions.

The aim of this case study is to illustrate some of the diverse social measures available to researchers and the desirability of using multiple measures to discover those features most important to a given society or research query. We particularly advocate capitalizing on recent advances in social network analysis that allow for the quantification of multi-actor interactions. A thorough investigation including multiple dimensions of sociality coupled with careful consideration of the inferences drawn from each measure is necessary to provide the detail required for a more complete understanding of animal societies.
REFERENCES


Tsai, Y., & Mann, J. 2012. Dispersal, philopatry and the role of fission-fusion dynamics in bottlenose dolphins. \textit{Marine Mammal Science}. 

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**FIGURES AND TABLES**

<table>
<thead>
<tr>
<th>Measure of Sociality</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average group size</td>
<td>Average size of groups in which the calf was observed defined by 10-m chain rule. Includes mother and calf.</td>
</tr>
<tr>
<td>% time alone</td>
<td>Percent of observation time in which the calf was not in a group with any other individual.</td>
</tr>
<tr>
<td>% time in groups</td>
<td>Percent of observation time during which the calf was observed in a group containing an individual other than the calf’s mother.</td>
</tr>
<tr>
<td>% time socializing</td>
<td>Percent of observation time in which the calf was actively socializing.</td>
</tr>
<tr>
<td>% time in group with:</td>
<td>Percent of observation time in which the calf was observed in a group consisting of:</td>
</tr>
<tr>
<td>Mother only</td>
<td>Mother only</td>
</tr>
<tr>
<td>All females</td>
<td>One or more females excluding the mother</td>
</tr>
<tr>
<td>All males</td>
<td>One of more males</td>
</tr>
<tr>
<td>Mixed sex</td>
<td>Both males and females excluding the mother</td>
</tr>
<tr>
<td>% time associated with:</td>
<td>Percent of observation time in which the calf was observed in a group consisting of at least one of the following age sex classes:</td>
</tr>
<tr>
<td>Adult Female</td>
<td>Adult female excluding mother</td>
</tr>
<tr>
<td>Adult Male</td>
<td>Adult male</td>
</tr>
<tr>
<td>Juvenile Female</td>
<td>Juvenile female</td>
</tr>
<tr>
<td>Juvenile Male</td>
<td>Juvenile male</td>
</tr>
<tr>
<td>Calf Female</td>
<td>Calf female</td>
</tr>
<tr>
<td>Calf Male</td>
<td>Calf male</td>
</tr>
<tr>
<td>Average fission-fusion rate</td>
<td>The average # of times per hour the calf’s group composition changes including the mother</td>
</tr>
</tbody>
</table>

**Table 1**: Non-network social measure definitions
Figure 1: Weighted ego-networks of a) LEN and b) MIG. Thicker edges indicate stronger relationships. Only those edges with an APO > 0.50 are shown for clarity; however all associations were included in the analysis. The mother is the closest node to the focal calf found near the center of the graphs. Mother’s are LIC and MOU respectively.

● Female □ Male △ Unknown
Figure 2: Two juvenile dolphins petting
Figure 3: Main component of social networks built from petting interaction data for a) Years LEN was a calf (2002-2005) and b) Years MIG was a calf (2004-2007). LEN and MIG’s petting ego-networks appear in the insets.

● Female □ Male △ Unknown
<table>
<thead>
<tr>
<th></th>
<th>LEN♀</th>
<th>MIG♂</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average group size</td>
<td>6.9</td>
<td>5.3</td>
</tr>
<tr>
<td>% time alone</td>
<td>4.6</td>
<td>16.1</td>
</tr>
<tr>
<td>% time in groups</td>
<td>70.4</td>
<td>54.1</td>
</tr>
<tr>
<td>% time socializing</td>
<td>2.5</td>
<td>5.8*</td>
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<tr>
<td>% time in group with:</td>
<td></td>
<td></td>
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<tr>
<td>Mother only</td>
<td>25.0</td>
<td>30.0</td>
</tr>
<tr>
<td>All females</td>
<td>21.2</td>
<td>4.7</td>
</tr>
<tr>
<td>All males</td>
<td>0.0</td>
<td>3.5*</td>
</tr>
<tr>
<td>Mixed sex</td>
<td>47.8</td>
<td>42.9</td>
</tr>
<tr>
<td>% time associated with:</td>
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<td></td>
</tr>
<tr>
<td>Adult Female</td>
<td>63.8</td>
<td>49.0</td>
</tr>
<tr>
<td>Adult Male</td>
<td>31.4</td>
<td>18.5</td>
</tr>
<tr>
<td>Juvenile Female</td>
<td>52.5</td>
<td>23.8</td>
</tr>
<tr>
<td>Juvenile Male</td>
<td>23.4</td>
<td>9.8</td>
</tr>
<tr>
<td>Calf Female</td>
<td>40.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Calf Male</td>
<td>27.1</td>
<td>42.3*</td>
</tr>
<tr>
<td>Average fission-fusion rate</td>
<td>7.5</td>
<td>5.9</td>
</tr>
</tbody>
</table>

**Table 2:** Non-network social measures results based on LEN and MIG focal follow data. *LEN had higher levels of association overall, but MIG associated more often with young males and spent a greater percentage of observation time socializing.*
<table>
<thead>
<tr>
<th></th>
<th>LEN</th>
<th></th>
<th>LEN</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Individual</td>
<td>Ego-network average</td>
<td>Individual</td>
<td>Ego-network average</td>
</tr>
<tr>
<td>Strength</td>
<td>31.45 [0.06]</td>
<td>12.70 [0.14]</td>
<td>33.15 [0.06]</td>
<td>12.48 [0.17]</td>
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<tr>
<td>Eigenvector Centrality</td>
<td>0.26 [0.00]</td>
<td>0.12 [0.00]</td>
<td>0.24 [0.00]</td>
<td>0.11 [0.00]</td>
</tr>
<tr>
<td>Weighted Clustering Coefficient</td>
<td>0.23 [0.00]</td>
<td>0.44 [0.00]</td>
<td>0.2 [0.00]</td>
<td>0.57 [0.01]</td>
</tr>
</tbody>
</table>

Table 3: Social network metrics calculated from LEN and MIG’s association ego-networks at both the individual and ego-network levels. Individual metrics refer to those of LEN and MIG, while ego-network metrics are the average of all individuals in the ego-network. Metrics were calculated in SOCPROG 2.3 using all available associations. Square brackets contain bootstrap standard errors using 1000 replicates. Strength indicates how connected an individual is to others by summing the weights of his/her associations. Eigenvector centrality is an additional measure of connectedness, but also considers the associations of an individual’s neighbors (e.g. an individual may have high eigenvector centrality by being strongly linked to many individuals or by being linked to fewer well-connected individuals). Weighted clustering coefficients show how ‘cliquish’ or tight the subnetworks are (all individuals within a clique are also tightly associated). More detailed descriptions of these metrics are available in Chapter 2 of this dissertation or in Whitehead (2008)
CHAPTER IV

Snapshot or Movie? How Sample Size and Sampling Method Influence Social Network Metrics

Social network analysis (SNA) is becoming increasingly popular in the field of animal behavior for describing complex social structure, investigating cooperation, tracking disease and information transfer, examining the roles of individuals in groups, and determining the consequences of anthropogenic disturbance on animal societies (Croft et al. 2008; Wey et al. 2008). In a social network, social entities, such as individuals, are referred to as nodes connected by edges, which represent some type of relationship. Although SNA has been used in several disciplines for decades (e.g. Erdős & Rényi 1959; Freeman 2004), the potential biases generated by the quantity and type of data used in analyses are not always appreciated. SNA data are collected using a variety of methods from questionnaires, to opportunistic observations, to twitter feeds (e.g. Lusseau 2003; Carrasco et al. 2008; Scanfeld et al. 2010); however the particular collection method may bias results and the amount of data collected may introduce significant error. For example, an individual may respond to a questionnaire with the names of three individuals they spend the majority of their time speaking to via cell phone, whereas an analysis of cell phone data may indicate one or more of these identifications are not accurate. To fully apply the power of social network analysis in hypothesis driven research, the sources of bias and error must be addressed. Specifically, the error referred to here is sampling error defined the difference between the sample and the population. Sampling error is generated by random

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variation in sampling because not all members of the population are accounted for. Sampling bias is also how different a sample is from the population, but bias is caused by a systemic discrepancy in sampling. For example, observers may inadvertently focus on more obvious behaviors or individuals, or one age group may be more likely to respond to a survey than another, or males might be easier to capture and tag than females (Fowler 2009). Here we use the 27-year multifaceted Shark Bay Bottlenose Dolphin dataset to investigate sampling error and bias by determining the effects of sample size, data collection method, and minimum data threshold on several social network metrics.

Past studies have addressed how sample size introduces error into social network metrics using networks constructed from interorganizational linkages or name generator surveys (Galaskiewicz 1991; Costenbader 2003). Researchers randomly removed increasing proportions of these binary network datasets and resampled with replacement. These studies found that the response to changes in sample size varied based on both the type of social network metric and network characteristics, such as size and density. Sampling error has also been investigated using simulated network data. For example, Borgatti et al. (2006) investigated the robustness of centrality metrics introduced by error by randomly deleting and/or adding edges and nodes to both simulated dense and sparse random networks and found that (1) centrality metrics (measures of node ‘importance’) decline consistently with the amount of error and that (2) edge deletion had a greater impact on dense than sparse networks. However, overall, dense networks were impacted less by error than sparse networks. The networks simulated by Borgatti et al. (2006) are known as ‘random networks’ because they are generated with an edge having an equal probability of existing between any two nodes (Erdős & Rényi 1959). Analyses of
simulated random networks are valuable because the entire network is known, but real world networks, including animal networks, are often nonrandom (e.g. an edge may have a higher probability of existing between certain nodes, such as nodes of the same sex), and may respond differently to sampling error.

The recent surge in SNA popularity in animal behavior and related fields has prompted considerable interest in similar methodological questions. Similar to Borgatti et al. (2006), Perreault (2010) randomly removed an increasing proportion of edges from simulated networks. Unlike Borgatti et al. (2006), Perreault generated ‘small-world’ networks and a ‘scale-free’ network, as well as random networks. Small-world networks are defined as having short mean path length between any two nodes in the network as well as high mean clustering coefficient (Watts & Strogatz 1998) and there are many examples of real-world networks displaying small-world properties (e.g. Watts 1999; Lusseau 2003; Croft et al. 2005). Scale-free networks follow a power-law degree distribution such that there are a relatively large number of nodes with a high number of connections (Ravasz & Barabási 2003); therefore these networks are considered to be more robust to random node removal than are random networks. Some real-world networks are reported to be scale-free; however some researchers make the persuasive argument that animal networks do not generally display a large enough degree distribution to determine whether or not they are scale-free (Croft et al. 2008). Perreault (2010) found that edge number affected various network measures in different ways with both mean degree and mean clustering coefficient increasing linearly with edge sample size. Also, metrics, particularly density and betweenness, from the random, small-world, and scale-free networks differed the most from one another at low sample sizes. Most importantly, the results showed that while one metric might be well
represented by a given subsample of edges, another could be completely different than its original value. The author also highlighted the danger of misrepresenting or misinterpreting results from networks constructed from data that underrepresent the number of edges.

Using real-world data, Voelkl et al. (2011) investigated the stability and reliability of measures of primate networks created from grooming interactions. The results of this study also found that some social network metrics fared well with respect to random edge removal, while others were extremely sensitive. Similar to Borgatti et al (2006), network structure (size and density) proved relevant even though the primate networks analyzed represented closed, relatively small (4 - 35 individuals) stable groups. Since larger sample sizes are considered to be more similar to the population, it is not surprising that those networks created from a large number of observations of grooming interactions (>2,000) were more robust to edge removal than network created from a small number of observations (<100). The Voelkl et al. (2011) study addressed critical sampling issues facing behavioral ecologists, including the potential for misidentifying individuals or behaviors, but has limited application to other animal networks due to the focus on small, stable, closed groups. Additionally, because interactions are often difficult to observe and quantify in field settings, many investigators rely on association defined by shared group membership as a proxy for relationships (Cairns & Schwager 1987; Whitehead 2008a). Thus, all individuals in a group are presumed to interact with each other; an assumption known as the gambit of the group (GoG) (Whitehead & Dufault 1999). In such cases, researchers are collecting observations of group membership and each group may contain a variable number of individual members (nodes). Since GoG assumes that all members of a group are connected to each other, each observation with a different group size will have a different number of edges.
Therefore, researchers collecting association data are likely to be concerned with the influence of the number of observed groups on network metrics rather than the number of interactions as investigated by Voelkel et al. (2011).

Regardless of whether interactions or associations are used as edges, an underlying consideration is how to quantify biologically significant relationships. Unfortunately, there are no universally accepted criteria for identifying biologically meaningful relationships (i.e., a minimum number of interactions or association strength) and no prescription for determining whether an observed relationship is based on biases introduced by sampling effort or method. For example, one observed interaction between A and B in a month might be spurious, but 20 interactions are unlikely to be. Observer effort, sampling method, and sampling rate all play a critical role. The common response to this uncertainty has been to filter and dichotomize data to create a binary network where edges or nodes above a certain value are included and those below are excluded. However, these thresholds at which networks are filtered and dichotomized are arbitrary and the resulting binary networks are likely to be oversimplified. An alternative to filtering and dichotomizing networks is the analysis of weighted networks. Weighted networks retain information about the value of edges, such as the number of times two individuals were seen together. The inclusion of edge weights is particularly relevant to animal networks or any network where ties between nodes are inferred from observations of shared group membership (Lusseau et al. 2008, but see Whitehead 2008b for discussion concerning the precision of associations). However, most traditional SNA studies of sample size include only binary networks and metrics, although Voelkl et al. (2011) did include weighted degree in their analyses.
Recently, Franks et al. (2010) proposed a novel method for sampling simulated networks constructed using the gambit of the group. To test this technique, the researchers inserted a known biological signal, trait assortativity, into simulated data and investigated how well this signal was represented, as well as how a variety of network metrics were influenced by increasing sample size (number of simulated observations) and proportion of the population sampled. The inclusion of assortativity is noteworthy because researchers addressing hypothesis driven questions are often not only interested in structurally based properties, such as centrality, but also semantic or attribute data, such as age, sex, or presence/absence of a behavior. Assortivity (hereafter referred to as homophily) is preferential interaction or association between individuals based on similarity and is of particular interest as a force driving the formation of network connections (McPherson et al. 2001). Franks et al. (2010) also compared simulated weighted network analysis to binary network analysis with edges filtered at three different thresholds (association index = 0.2, 0.5, & 0.8). Their results emphasize the robustness and usefulness of weighted networks over filtered binary networks when calculating mean degree, clustering coefficient, betweenness, and trait assortativity, as well as the importance of the number of samples over the proportion of the population sampled. Here, we also investigated error when sampling the gambit of the group, but we used a real world bottlenose dolphin dataset to examine sampling error by determining how network size, density, strength, and age-sex class homophily changed as a function of sample size. We also took our analyses a step further, and investigated bias by examining how metrics calculated from networks created using two common sampling methods in animal behavior (survey and focal follows; see below for definitions) fared as a function of sample size.
Bottlenose dolphins are attractive candidates for social network analysis given their dynamic and complex society. Similar to humans, bottlenose dolphins inhabit a fission-fusion social system where group composition changes over time and all members of the community are rarely, if ever, together (Smolker et al. 1992; Connor et al. 2000). Indeed, some of the most commonly cited animal social network studies are descriptions of bottlenose dolphin populations in Doubtful Sound, New Zealand, the Moray Firth, Scotland, and Port Stephens, Australia (Lusseau 2003; Lusseau & Wilson 2006; Wiszniewski et al. 2010). In Shark Bay, Australia the average group size is 3-4 individuals (Smolker et al. 1992; Gibson & Mann 2008) and sex segregation in behavior is apparent. Adult males form alliances of 2-3 individuals to herd and consort females (Connor et al. 2011), while the females themselves vary greatly in terms of sociality, with the greatest lifetime number of known associates exceeding 160 (Gibson & Mann 2008).

In order to capture the complexity of behavior in animal species such as bottlenose dolphins, researchers have developed and employed a variety of sampling techniques. Two methods often applied are surveys (sighting records) and focal follows. Surveys are most commonly used to construct animal social networks as they are relatively independent from each other and useful for gathering basic demographic information. These observations represent relatively brief snapshots of animal association and behavior. Focal follows are systematic sampling of a focal individual or individuals over a longer period of time and are more similar to taking a video recording (Altmann 1974; Mann 1999). Previous research showed that focal follows provide greater detail in terms of individual social variation, particularly for hard to identify individuals such as dolphin calves (Gibson & Mann 2009). This study also showed that,
depending on the social measure of interest, different amounts of data were required before the measurement became uncoupled from sampling effort. This problem is compounded with social network analysis because the metrics are by their nature dependent on one another. Thus, if some individuals are well-sampled and others are not, even those metrics calculated for the well-sampled individuals will be biased in addition to the network level metrics.

In this paper we address two main questions concerning the effects of sampling error and bias on social network metrics. (Q1) How does setting a minimum sample size per individual threshold (i.e. only including individuals with x minutes of follow time or x number of surveys) affect social network metrics and does this influence differ between focal and survey-based networks? (Q2) How does sample size affect four different ego network metrics and does this influence differ between those metrics calculated from focal and survey data? To answer this second question, we used ego networks (a focal, or ego, and all directly connected individuals) since the focal follow data for a given individual or pair essentially represent their ego network. Notably, these analyses compare how social network metrics of 20 different individuals sampled over the same period of time using a longitudinal real-world animal dataset.

METHOD

Study site and data collection

Data for these analyses were collected as part of a longitudinal study of the resident population of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia (25°47’S, 113°43’E) where research is facilitated by shallow water, relatively low human disturbance, and a large
number of identifiable individuals (N>1500 since 1984). The main study area includes 300 km$^2$ off the east coast of Peron Peninsula where researchers have studied dolphin life history, ecology, genetics, and behavior since 1984. The data collection methods of interest in the present analyses are surveys and focal follows. Surveys, or sighting records, are opportunistic, boat-based observations that typically last ~5 minutes. Information including group composition, speed, predominant behavior (from scan sampling), and instantaneous environmental variables such as water depth, sea state, and seafloor substrate are recorded. Focal follows involve more intensive sampling during which a specific individual or pair of individuals (such as a mother and calf) are followed for 1 – 9 hours and detailed information including group composition, activity, location, and social interactions are recorded using standard quantitative sampling techniques, including point, scan, and continuous sampling (Altmann 1974). Group composition is assessed every minute during focal follows by scan sampling. During both surveys and focal follows, group composition is determined using a 10 meter chain rule in which one dolphin is considered to be in a group with another dolphin if they are separated by 10 meters or less. Focal follows used in these analyses are of either mother-calf pairs or adult females and were collected as part of a continuous longitudinal mother-infant study initiated in 1988.

**Subjects**

*Q1 Threshold analysis*
Subjects for Q1 were 31 adult females (>10 years old) with a minimum of 10 surveys and 60 minutes of focal follow data collected between the years 1999-2007 (N=31). In this analysis all animals under 5 years of age, including most dependent calves, were excluded.

Q2 Sample size

Individuals included in these analyses were adult females who had each been followed and surveyed during the same time period for a minimum of 8 and a maximum of 10 years from 1988 – 2008 (N=20). Focal follows focused on the mother-calf pair as the focal unit. The date each survey occurred on was available for survey subsamples, but not focal follow subsamples; therefore animals under 5 years of age were identified by subtracting their birthdate from the survey date and removed from the survey dataset, but not from the focal follow dataset.

Analyses

Q1 Threshold analysis

Two sets of social networks were created: one using group composition from the first five minutes of surveys and another using group composition from focal follows of mother-infant pairs (Fig. 1). To facilitate comparison with follow data, each group composition included in the survey networks contained at least one of the 31 focal females. All networks were undirected and binary with edges present between all pairs of individuals with any shared group membership. For both survey and follow datasets the minimum number of observations necessary for an individual’s inclusion in the network was increased at regular intervals (Table 1). Two-way
permutation-based ANOVAs (Anderson 2001) were conducted to assess the influence of observation method and observation threshold on the network average normalized degree and clustering coefficient. Degree is simply the number of edges connected to a given node, whereas clustering coefficient measures how well connected a node’s neighbors are to one another and represents a measure of network cohesion. Metrics were normalized based on the maximum value of a node in a network in order to compare between networks of different sizes.

Subsequent two-sample permutation tests with a Bonferonni correction to the critical $P$-value addressed difference between simple-effect means (Rice 1989).

**Q2 Sample size**

To investigate the influence of number of surveys on ego network metrics, ego networks were constructed from a sample size of 1 - 100 surveys for each female. For example: A female’s ego network was constructed from one randomly sampled survey containing that female, then an ego network was constructed from two randomly sampled surveys etc. up to an ego network including 100 surveys. This process was repeated 500 times for each sample size and the mean and standard deviation calculated. To compare the influence of the opportunistic nature of survey samples versus the more directed focal follow samples, five minute “slices” of focal follow data were randomly sampled from each female’s dataset. The number of focal follow slices was increased at intervals of 10 and resampled similar to the survey data up to 100 focal slices. All sampling was done with replacement.

We calculated four metrics from each ego network: ego size (number of associates); ego strength (also known as weighted degree which is the sum of the weights of the ties between an
ego and his/her associates); ego density (the number of observed ties over the number of possible ties in the network and is a measure of network cohesion); and ego age-sex class homophily (in this analysis, the proportion of adult-female individuals in each female’s ego network). Because ego networks consisted of multiple years of data, age-sex class homophily was calculated for each year and averaged. Since individuals < 5 years were excluded from the survey dataset, age classes were broadly defined (in years) as juvenile: 5 - 9.99; and adult: >10. Again, since dates were available for survey subsamples, but not focal follow subsamples, the age of each individual in an ego network could only be established for survey networks, and not focal follow networks. Therefore, age-sex class homophily could be calculated for survey networks, but not focal follow networks. For the calculation of strength, survey network edges were weighted based on a given dyad’s half weight coefficient. The half weight index is a commonly used measure of association that controls for the sighting frequency of different individuals according to the formula: \( X/(X+0.5(Y_a +Y_b)+Y_{ab}) \) where \( X \) is the number of sampling periods (days) that A and B were observed together in the same group; \( Y_a \) is the number of sampling periods A was observed without B; \( Y_b \) is the number of sampling periods B was observed without A, and \( Y_{ab} \) is the number of sampling periods A and B were both observed, but in separate groups (Cairns & Schwager 1987). Follow network edges were weighted by the proportion of each female’s focal follow slices in which a given dyad was observed together. For example: if JFR and JOY were observed together in 50 out of 100 slices, the weight of the edge between them would be 0.5.

To further clarify differences between sampling method, we conducted Spearman’s rank correlation tests comparing the relative ranks of the 20 females based on each metric calculated from survey versus focal follow networks and averaged across sample sizes.
RESULTS

Q1 Threshold analysis

Both survey and follow networks decreased in overall size (number of included individuals) as the observation threshold increased; however the change in survey network size was greater than that of focal follow networks (Table 1). We also found a significant interaction between sampling method and observation threshold for both average normalized degree ($P < 0.0005$, 5000 iterations) and average clustering coefficient ($P < 0.001$) (Fig. 2).

Q2 Sample size

Ego size

Mean ego size calculated from both the survey and focal datasets increased with increasing sample size; however focal ego size increased more gradually and was consistently smaller than survey ego size (Fig. 3ab). The standard deviation in ego size changed little with changes in sample size, although for some females, standard deviations decreased as sample size increased. Overall, focal networks had smaller standard deviations in ego size than survey networks (Fig. 3cd). The relative ranks of females based on ego network size were similar between survey and follow networks (Spearman rank correlation: $r_s = 0.857$, $N = 20$ ranks, $P < 0.0001$).

Ego strength
Since survey and focal ego strength were calculated slightly differently, the direct comparison of maximum strength values is inappropriate; however a comparison of the trends shows that mean ego strength was the most reliable metric we investigated. Mean survey ego strength plateaued after ~10 surveys, while mean focal ego strength remained constant regardless of sample size (Fig. 4ab). Both survey and focal mean ego strength also had relatively low standard deviations, particularly at sample sizes >10 (Fig. 4cd). The relative ranks of females based on ego network strength were also similar between survey and follow networks ($r_s = 0.887, N = 20$ ranks, $P < 0.0001$).

**Ego density**

Mean ego density was the only metric we investigated to have an inverse relationship with sample size (Fig. 5ab). Both survey and focal mean ego density decreased with increasing sample size, however survey density gradually decreased to range from ~0.4 – 0.5, whereas mean focal ego density quickly dropped to ~0.3 – 0.5 and then gradually decreased from there to ~0.2 – 0.4. Standard deviations varied greatly for both survey and focal based calculations; however while focal ego density standard deviations fluctuated initially, they decreased to a generally lower level than those of survey ego density (Fig. 5cd). Interestingly, the relative ranks of females based on ego network density were different between survey and follow networks ($r_s = -0.290, N = 20$ ranks, $P = 0.214$).

**Ego Homophily**

Age-sex class based homophily from survey ego networks was also fairly robust to increases in sample size with rapidly decreasing standard deviations (Fig. 6ab).
DISCUSSION

Similar to the studies discussed earlier (Borgatti et al. 2006, Perreault et al. 2010, Franks et al. 2010, Voelkel et al. 2011), the various social network metrics calculated from Shark Bay bottlenose dolphin data responded differently to varying sample size. Additionally, we found that sampling method influenced both the reliability and precision of social network metrics.

In terms of sampling error, the weighted metric ego strength was the most robust to changes in sample size, while ego size was the most susceptible. As for bias introduced by sampling method, it has been previously suggested that surveys suffer from observer bias since larger groups tend to be easier to locate in the field (Gibson & Mann 2009). This tendency may account for some of the relative differences in metric values between survey and focal follow networks. Because GoG assumes that all members of a group are connected, networks built from large survey groups grow faster than networks built from smaller focal follow groups, especially in these dolphin data where group membership is dynamic and therefore likely to vary from one observation to another. The tendency of surveys to include larger group sizes and focal follows to include smaller group sizes helps explain some of the variation between sampling methods discussed below.

Q1 Threshold analysis

Both sampling method and threshold influenced bottlenose dolphin social network metrics. However, networks constructed from follow data were less affected by changes in
sampling threshold than the survey networks. Ego size was particularly large in survey networks at low thresholds, but quickly fell to below that of focal follow networks as the threshold was raised. This more extreme response may be related to the group size bias discussed above and it may result in more solitary individuals appearing gregarious due to a few spurious observations. In general, restriction to individuals with more observations may increase accuracy and identify biologically relevant relationships, but potentially biases against less sociable individuals (Granovetter 1973). Thus, if it is important to capture social network metrics for less gregarious individuals in a binary network, focal sampling may be a better measure to use.

Q2 Sample size

One of the most interesting results of the sample size analysis was the observed variance between individuals both within and between sampling methods. Metrics from the survey and focal ego networks of most females had similar distributions over the range of sample sizes (either increasing or decreasing similarly with increasing sample size), but, as mentioned above, the value of focal metrics tended to be lower than survey metrics. For example, the maximum survey ego network size ranged from 28 – 120 nodes, while the maximum focal follow ego network size ranged from just 5 – 78 nodes. This focal metric tended to be lower despite the fact that this dataset included individuals less than 5 years of age while the survey dataset did not. Again, this result is likely due in part to GoG and larger survey group sizes. Additionally, while there was a great deal of variation between females for each network metric, the relative ranks of ego network size and strength were similar between survey and follow networks. One notable instance in which a female’s metric responded differently to sample size than those of other
females was that of BOM’s focal ego density, which increased with sample size as opposed to
decreasing. Ego density was also the only metric with dissimilar individual relative ranks
between survey and focal networks as more solitary animals such as BOM were ranked higher in
the focal dataset than the survey dataset. Since BOM is a highly solitary female, it may be more
difficult to capture an accurate representation of her associates and characterize the ties among
those individuals. The initial high individual variation in the standard deviations of mean follow
density indicates that larger sample sizes are particularly advisable for more precise measures of
network density from focal follow data. Focal follow networks are constructed from smaller
groups on average, which means there is a lower and more variable potential for any two
individuals in the focal network to be connected to each other via GoG than in survey networks.
As the number of samples increases, the potential for individuals to be observed together in at
least one sampled group increases, and the calculated density becomes less variable between
trials, resulting in the observed decrease in the standard deviations of focal density.

While GoG does appear to drive some of the patterns we observed, this is not to say that
researchers should not use GoG. In many cases interactions are impossible or difficult to observe
in the field and attempting to characterize relationships with such imperfect data would be
misleading. Also, shared group membership, particularly in the bottlenose dolphin fission-fusion
society, is important in itself since it may represent individual decisions about with whom to
spend time. The effects of GoG are important to understand and consider, but they do not
preclude the use of GoG when conducting social analyses.

Conclusion
Low sample sizes and the potential for sampling error and bias are always a concern in empirical research, but this issue is of particular importance when considering the observations or events used to construct social networks due to the dependent nature of network data. Here, ego strength was considerably more reliable than ego size for both survey and focal follow networks. Thus, our results echo those of previous studies that encourage the use of weighted network metrics. Focal follow metrics in general had lower standard deviations than survey metrics and focal metrics were also less susceptible to changes in threshold. Based on these results as well as previous findings (Gibson & Mann 2009), the intensive nature of focal follows appears to better capture the more elusive social patterns of less social animals and provides more precise measurements than surveys. That is, surveys may not capture the solitary tendencies of less gregarious individuals. Future work will determine the impact of calculating survey versus focal follow network metrics on answers to hypothesis driven questions. However, here we cannot make overarching recommendations for one sampling method or sample size over another since such decisions will depend on the nature of the research question of interest; however we do recommend that sample size, sampling method, and the resulting scope of inference be carefully considered when drawing conclusions from social networks.
REFERENCES


### FIGURES AND TABLES

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<tr>
<th>Survey</th>
<th>Threshold (Min. # Obs.)</th>
<th>Mean # Obs. per individual ± SE</th>
<th>Network Size</th>
<th>Mean Normalized Degree ± SE</th>
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<th>Mean Normalized Degree ± SE</th>
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<td>22.41±1.16</td>
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Table 1: Descriptive statistics. Normalized degree = \( \frac{k}{(n-1) \times 100} \) and clustering coefficient = \( \frac{2t_i}{k_i(k_i-1)} \)

where for any node i, n=network size (# of individuals in the network), k = degree (or an individual’s # associates), and t = # of ties or edges.
Figure 1. Shark Bay bottlenose dolphin social networks constructed using a) ≥ 10 surveys and b) ≥ 50 minutes of follow data. Circles represent individual dolphins and lines are ties between individuals. Blue: male; red: female; yellow: unknown sex.
Figure 2. a) Mean normalized degree ± SE by sampling method and observation threshold. All differences in means were significant at $P < 0.0033$ except those indicated by N.S. b) Mean clustering coefficient ± SE by sampling method and observation threshold. ***, $P < 0.0033$. 

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**Figure 3ab.** a) Mean survey ego size with increasing sample size. b) Mean focal ego size with increasing sample size.
Figure 3cd. c) Standard deviation in survey ego size with increasing sample size. d) Standard deviation in focal ego size with increasing sample size.
Figure 4ab. a) Mean survey ego strength with increasing sample size. b) Mean focal ego strength with increasing sample size.
Figure 4cd. c) Standard deviation in survey ego strength with increasing sample size. d) Standard deviation in focal ego strength with increasing sample size.
Figure 5ab. a) Mean survey ego density with increasing sample size. b) Mean focal ego density with increasing sample size.
**Figure 5cd.** c) Standard deviation in survey ego density with increasing sample size. d) Standard deviation in focal ego density with increasing sample size.
Figure 6ab. a) Mean survey ego age-sex class homophily with increasing sample size. b) Standard deviation survey ego age-sex class homophily with increasing sample size.
CHAPTER V

When Mum’s Away: A Study of Mother and Calf Ego Networks During Separations in Wild Bottlenose Dolphins (Tursiops sp.)*

ABSTRACT

Early social development in long-lived social mammals has important implications for adult behavior, particularly in taxa that exhibit stable long-term bonds. In one such species, bottlenose dolphins, calves have precocious locomotion, enabling them to separate from their mothers soon after birth and associate with other dolphins in the absence of direct maternal influence. To investigate mother and calf social patterns while together and separated, we analysed the ego networks of 27 mother–calf pairs constructed using group composition data from focal follows and evaluated differences based on calf sex. When separated, all calves had larger, less dense ego networks than their mothers, whereas ego networks of mother and calf when together were similar in size to those of calves, but significantly less dense. Most intriguingly, during separations, male calves’ relationships with other male calves were stronger than expected, foreshadowing the long-term bonds between adult male alliance partners. Female–female calf relationships were not stronger than expected, but when together, mothers and female calves had strong relationships with juvenile females. These results support the social bonds hypothesis and suggest that temporary separations allow calves to build and strengthen their social networks. Since bottlenose dolphins show bisexual philopatry and infant

relationships can persist into adulthood, calf independence and early social development probably have implications for future success.

INTRODUCTION

In species characterized by long-term bonds and high fission–fusion dynamics, social development is presumably highly variable and challenging, and therefore likely to have fitness outcomes. While offspring in social groups are typically buffered from challenges during infancy and the juvenile period (e.g. primates: Pereira & Fairbanks 1993; spotted hyaenas, *Crocuta crocuta*: Holekamp & Smale 1991, 1993; African elephants, *Loxodonta africana*: Lee 1986), bottlenose dolphin juveniles must negotiate a complex social environment with little protection from their maternal social group after weaning. Such conditions are likely to foment pressures on calves to develop their ‘own’ social network while still dependent on their mothers. Otherwise calves would be highly vulnerable after weaning, especially in Shark Bay bottlenose dolphin society where multilevel alliances of males (Connor et al. 2010) act aggressively towards both sexes (Scott et al. 2005) and adult female sociability is highly variable (Smolker et al. 1992; Gibson & Mann 2008a, b; Mann et al. 2008). Because of this variability, juveniles cannot rely upon stable maternal groups to reliably protect, buffer or assist them in somatic effort. Without at least some close associates, juvenile males and females might be more vulnerable to attacks or harassment by males and would be less exposed to critical social or ecological (e.g. prey, predator) information.
During early development, calves engage in temporary separations from their mothers during which they occasionally join groups and form their own social bonds (Mann & Smuts 1998; Mann & Watson-Capps 2005; Gibson & Mann 2008a, b). Because of these separations, we can examine the nature of calf social networks and social preferences independent from their mothers. The current study focuses on maternal and calf social networks and how these reflect the divergent interests of mothers and their offspring. Our study is the first to characterize social networks for dependent offspring and provides a unique perspective on the social demands of early development.

Infant care strategies in mammals can constrain or determine patterns of early social development. Such strategies are related to predator avoidance and habitat and typically fall into three categories; cache, carry, or follow (Lent 1974; Ross 2001). Caching species (e.g. rodents and carnivores) hide their young in vegetation or dens and are thus observed in habitats that provide adequate cover or have few predators. ‘Following’ species (e.g. some ungulates and macropods) are more common in open habitats and their offspring begin following their mothers almost immediately after birth (Estes 1992; Fisher et al. 2002; McGuire & Bemis 2007). Only 6 of 19 eutherian mammalian orders carry infants for appreciable distances and this strategy is particularly common among primates (Ross 2001). Ross (2001) suggested that carrying occurs when following is difficult or dangerous, such as in arboreal or volant species. Beyond predator avoidance, carrying and following are more common in ungulates, macropods and primates when litter size is small, maternal body size is large and life histories are slow (Ross 2001; Fisher et al. 2002).
Bottlenose dolphin offspring are relatively precocious in that neonates must immediately swim, surface to breathe and follow their mothers, similar to ‘following’ ungulates (Ralls et al. 1987; Mann & Smuts 1998). While Noren (2008) suggested that echelon (close, parallel) swimming is a form of infant carrying in terms of the hydrodynamic benefits to the calf (Norris & Prescott 1961; Noren et al. 2008) and the costs to the mother, the calf must still actively swim and surface to breathe, and cannot be restrained by the mother. Paradoxically, bottlenose dolphins follow their mothers from an early age yet show relatively long periods of dependence, nursing for an average of 4 years (Mann et al. 2000). Furthermore, unlike offspring left hidden alone, in crèches, or reared in stable groups, bottlenose dolphins’ precocial locomotion allows calves as young as 0–3 months to actively join or leave their mothers and other individuals (Mann & Smuts 1998; Mann & Watson-Capps 2005). These temporary separations continue throughout the infancy period, thus some calf associations occur in the absence of direct maternal influence and calf social bonds are not restricted to maternal associates. The independence and opportunities for self-socialization available to these precocial offspring probably have implications for social behaviour and relationships during subsequent juvenile and adult life stages. In other mammals, early social experience has a profound impact on social development, and a number of studies highlight the influence of social environment on subsequent social behaviour (e.g. nonhuman primates: Harlow et al. 1971; Berman et al. 1994; Maestripieri 2001; Suomi 2005; rodents: Van den Berg et al. 1999; Branchi 2009; humans: Fries et al. 2005). For example, in captive macaques, Macaca arctoides & M. mulatta, cross-fostered individuals developed the social tendencies of their foster species or population (de Waal &
Johanowicz 1993), while in rodents, male Wistar rats reared without the opportunity to play showed abnormal adult social behaviour (Meaney & Stewart 1979; Van den Berg et al. 1999).

Mother–calf separation patterns emulate the fission–fusion dynamics exhibited by bottlenose dolphin adults. The details of fission–fusion dynamics vary among species, but in all cases, members of the community are rarely, if ever, all together, group size and composition vary temporally, and preferential associations are evident. The complexity of these fission–fusion systems lies in the dynamic nature of these spatially and temporally variable groups and the resulting irregular availability of social information. Because relearning social standing with every encounter would presumably waste time and energy, the cognitive demand on these species includes the need to remember individuals not encountered on a regular basis, as well as the interactions among these individuals (Aureli et al. 2008). A benefit of a fission–fusion system appears to be the capability to quickly respond to fluctuating ecological pressures, thus maximizing the benefits of grouping while minimizing the costs of within-group competition. In addition to providing dolphin calves with social options in the absence of their mothers, separations may allow calves to develop the fission–fusion ‘fluency’ necessary in adult society.

Despite an average weaning age of 3–4 years, Shark Bay bottlenose dolphin calves begin catching fish at 4 months of age (Mann & Sargeant 2003). As previously mentioned, bottlenose dolphins cannot rely on maternal support during a juvenile period that begins at weaning and extends until individuals become sexually mature at age 10–15 years (Mann et al. 2000). Past investigations into calf activity budgets indicated that calves spend an increasing amount of time socializing during the first year of life, at which point socializing appears to peak (Mann & Watson-Capps 2005; Gibson & Mann 2008a). During the newborn period (0–3 months) calf
socializing includes rubbing, petting and chasing other individuals, including their mothers, and young calves frequently initiate rubbing behaviour with their mothers (Mann & Smuts 1999). Calves of all ages also engage in a variety of sociosexual play behaviours (e.g. mounting, beak-to-genital contact), and calf social partners tend to be other calves and predominantly male (Mann 2006). Indeed, the rate of sociosexual behaviour between male calves is higher than that between wild bonobo, *Pan paniscus*, females. Regarding separations, previous studies revealed that calves initiate and terminate over 90% of mother–calf separations and that during this time apart, bottlenose dolphin mothers mainly forage, while calves both socialize and forage more than when together with their mothers (Mann & Watson-Capps 2005). As they approach weaning, calves of both sexes spend more time separated from their mothers, but only female calves decrease their time in groups during separations while increasing their overall foraging time. Mother–calf sociality (number of associates) was also positively correlated with calf sociality during separations, but this relationship did not hold for the percentage of time in groups (Gibson & Mann 2008a). Grouping is clearly important for calves, particularly males, in developing social skills before a lack of social savvy incurs a reproductive cost (Gibson & Mann 2008b). This research, however, did not account for relationship strength or the cohesiveness of social networks. Therefore, despite the attention paid to mother–calf separations by Gibson & Mann (2008a, b), particularly concerning the calves’ experiences, the differences between maternal and calf social environments (networks) are not well understood. Since individual differences in sociality may have fitness implications, network development is worthy of investigation.
A social network is defined as actors, in this case individual dolphins, linked by relationships. Social network analysis quantifies multi-actor interactions and provides a more realistic representation of complex societies than traditional dyadic approaches. The dynamic and complex society of bottlenose dolphins is an attractive candidate for social network analysis and such techniques were applied to survey data to characterize populations in New Zealand, Scotland and southeastern Australia (Lusseau 2003; Lusseau & Newman 2004; Lusseau et al. 2006; Wiszniewski et al. 2010). The current study analysed ego networks, which are a type of social network consisting of a focal individual (the ego) and all directly connected individuals. Ego networks provide a means for describing and quantifying an individual’s immediate social neighbourhood, while allowing for the incorporation of more traditional statistical techniques.

Since maternal and calf interests differ (Trivers 1974), we anticipated that network composition during separations would reflect those interests. In the current study we examined three nonmutually exclusive hypotheses concerning mother–infant separations in bottlenose dolphins: (1) the social bonds hypothesis (Fairbanks 1993; Mann & Watson-Capps 2005; Gibson & Mann 2008a, b); (2) the learning to parent hypothesis (Lancaster 1971; Fairbanks 1990; Mann & Smuts 1998); and (3) the babysitting (or allomaternal care) hypothesis (Brown & Norris 1956; Riedman 1982; Wells 1991; Whitehead 1996; Mann & Smuts 1998). According to the social bonds hypothesis, calves gain associates and/or the social experience and skills necessary for future success. If voluntary separations allow calves to expand their social horizons beyond those provided by their mothers, then ego networks of calves during separations will be larger than those of their mothers and larger than those of mother–calf pairs when together. Additionally, there is a general pattern of sex-segregated bonds in adult bottlenose dolphin society in which
males form alliances with other males of the same age cohort (and often relatedness; see Krützen et al. 2003), while females have a variable number of strong ties to their matrilineal kin and female associates (Smolker et al. 1992; Wells 1991; Rogers et al. 2004; Möller et al. 2006). Therefore, male calves preparing for a less certain social future of alliance formation outside the protection of maternal kin will have larger networks than their female counterparts and more male calf and juvenile associates. The learning to parent hypothesis suggests that nulliparous females gain parenting experience by associating with calves and it predicts that the presence of juvenile females in calf networks will be greater than expected regardless of calf sex. Similar to the learning to parent hypothesis, the babysitting hypothesis suggests that juvenile and/or adult females accompany calves during separations to protect calves rather than to learn parenting skills, although the two are by no means mutually exclusive. The babysitting hypothesis predicts a large proportion of juvenile and/or adult females in calf separation networks of both sexes regardless of parity status. That is, females that have successfully reared offspring would still associate and potentially care for unrelated offspring under the babysitting hypothesis, but such females would not under the learning to parent hypothesis. Under any of the hypotheses, mothers and calves are likely to avoid aggressive males. Finally, while we do not directly address predation risk here, Mann & Watson-Capps (2005) found that predation was not the primary cause of infant mortality. Also, calves often have solitary separations, undermining predation and protection-based hypotheses (Mann & Smuts 1998; Mann & Watson-Capps 2005; Gibson & Mann 2008a, b). That calves often engage in solitary separations from their mothers further suggests that calves have the option of whether or not to associate and with whom. In examining the social networks of dependent offspring, which are often excluded from such analyses, this
study provides a novel approach to the investigation of early social development in a wild mammal.

METHOD

Study Site and Data Collection

Data for this study were collected as part of a longitudinal study of bottlenose dolphins (Tursiops sp.) in Shark Bay, Australia (25°47’S, 113°43’E). The main study area extends 300 km² off the east coast of Peron Peninsula, where researchers have studied the life history, ecology, genetics and behaviour of the resident bottlenose dolphin population since 1984. Research in Shark Bay is facilitated by clear, shallow water, relatively low human-related disturbance, and a large number of identifiable individuals (N>1500 since 1984) well habituated to small boats (4–6 m). Boat-based focal follows of specific mother–calf pairs provide detailed information on group composition, activity, location and specific social interactions using standard quantitative sampling techniques, including point, scan and continuous sampling (Altmann 1974). Focal subjects are part of a long-term study initiated in 1988 and, on a given day, are ranked according to priority based on the number of observation hours that year. One of the top three mother–calf pairs is typically followed during daylight hours and the focal follow length (from ~1–9 h) is determined a priori based on sample size and field conditions. Follows are terminated primarily because of low-light (end of day), maximum/criteria observation time reached, deteriorating weather conditions and/or losing sight of the animals. One of the authors/observers (J. M.) trained all other observers to over 90% agreement. Group composition
is scanned for every minute during a focal follow and association is conservatively determined using a 10 m chain rule, where one dolphin is in a group with another dolphin if they are separated by 10 m or less (Smolker et al. 1992). Individuals are identified by dorsal fin using photographic-identification techniques and sex is determined by presence of dependent offspring, by opportunist views of the genital region (Smolker et al. 1992), or by DNA (Krützen et al. 2004). If not precisely known, calf age is estimated by physical and behavioural characteristics of the calf and long-term sighting records of the mother (Mann et al. 2000; Gibson & Mann 2009). All calves in the current study were of known age.

**Subjects and Ego Network Construction**

Ego networks were constructed from the focal data set described above for 27 mother–calf pairs ($N_{Mothers}=18$, $N_{FemaleCalves}=14$, $N_{MaleCalves}=13$) followed for a minimum of 5 h each (mean ± SD = 8.2 ± 4.2 h) while separated from each other (Table 1). Separations were defined as when the mother and calf were more than 10 m apart with no other dolphins linking the pair. Ten metres is likely out of visual range and far enough that calves could easily be harmed by sharks or aggression from other dolphins. Additionally, in only 16.5% of all distances recorded during separations ($N_{distances}=14551$) were mothers 10–20 m away. Mothers and calves were at a distance of 50 m or greater for 68% of these records and greater than 100 m for 35% of distance records. These 27 mother–calf pairs were well known to researchers and the mean ± SD total follow time per pair was 44.0 ± 22.7 h. We constructed separation-based ego networks (associates when mothers and calves were in separate groups) for each mother and calf from mother–calf focal follows. Together-based ego networks (associates when mothers and calves
were in the same group) were similarly constructed. A tie between individuals in an ego network existed if the two dolphins were observed in the same group. To obtain robust networks, we pooled the data from each individual calf’s entire infancy period (birth to weaning) to create that individual’s static ego network (Fig. 1). Most data (90%) were collected before age 4 (Table 1). Weaning age ranged from 2.6 to 8.1 years (mean ± SE = 4.29 ± 0.26). Each maternal network was similarly built based only on data collected during the dependent calf’s infancy period. We used focal data rather than sighting records to construct mother and calf ego networks as sighting data grossly overestimates the time that mothers and calves are together relative to focal data (see Gibson & Mann 2009).

Ego Network Analysis

Ego network metrics, including size, density and age–sex class homophily (see Table 2 for definitions), were calculated for each ego network and served as response variables in mixed model ANOVAs with ego type (mother, calf, or together) and calf sex as fixed effects and mother–calf pair and observation time (in minutes) included as random variables (SAS v. 9.2, Proc Mixed, SAS Institute, Cary, NC, U.S.A.). Shared group memberships were determined using SocProg 2.4 (Whitehead 2009), and ego network metrics were calculated in UCINET6 (Borgatti et al. 2002). Ego networks for these analyses were static and binary.

Ego Network Composition

To examine the age–sex class composition of the networks of different ego types, we calculated the proportion of each ego network belonging to each age–sex class and compared
them to the proportion expected based on population means. Because each ego network represents more than 1 year, an individual included in the network could have been observed with the focal in two age classes. In such cases, the age class with the majority of the observations was assigned to the individual. To determine whether the proportion of individuals in each age–sex class in each ego network differed from that expected based on the population, we subtracted the mean proportion of each age–sex class in the population from the observed ego network values. We compared the means of these corrected values to zero using independent one-sample $t$ tests. The expected population means were calculated from demographic records on 759 individuals of known sex and age class for each of the previous 3 years and averaged. A previous analysis indicated that population means in our study area do not differ by more than 2% over a 10-year interval (Gibson & Mann 2008b).

Although age–sex class proportion provides insight into ego network composition, their relative importance may be better accessed by determining the strength of the ego’s relationships to the members of those categories. We determined the weight of a tie between the ego and each associate in his/her network by dividing the number of minutes the associate was observed in a group with the ego by the number of total minutes the ego was observed. The ego’s total strength is the sum of these weights and is thus a function of both the number and weight of his or her ties. The weights of ties to members of each age–sex class in each ego network were summed to determine age–sex class strength. We calculated the expected age–sex class strengths for each ego network by multiplying the total strength of known age–sex individuals by the proportion of each age–sex class in that network. Expected values were subtracted from observed values and the means were compared to zero using independent one-sample $t$ tests. All tests were two tailed.
RESULTS

Separation Rate and Duration

The 27 mother–calf pairs separated from each other with a mean ± SE frequency of 1.68 ± 0.11 separations/h. The mean ± SE duration of each separation was 9.09 ± 0.29 min. Calves were alone for 74.9 ± 2.8% of the time they spent separated, whereas mothers were alone for 88.3 ± 2.1% of time they spent separated from their calves. This difference was significant (paired t test: \( t_{26} = 5.21, P<0.0001 \)).

Ego Network Metrics

Ego size

Results of the mixed model ANOVA for ego size revealed no significant difference based on calf sex \( (F_{2,24.9} = 0.12, P = 0.7364) \) and no interaction between calf sex and ego type \( (F_{2,49.5} = 1.10, P = 0.3412) \); however, ego types (mother versus calf) significantly differed in size \( (F_{2,55.1} = 8.37, P = 0.0007; \text{Fig. 2}) \). Post hoc comparisons revealed that calves had larger ego networks than their mothers during separations. Additionally, mothers had smaller ego networks during separations than when together with their calves. Ego size of calf networks during separations and when together with their mothers were not significantly different.

Ego density
Ego density did not differ based on calf sex (mixed model ANOVA: $F_{2,24.9} = 0.06, P = 0.8030$), and there was no interaction between calf sex and ego type ($F_{2,49.5} = 0.33, P = 0.7188$), but ego densities of mothers and calves differed significantly ($F_{2, 55.1} = 8.72, P = 0.0005$; Fig. 3). Separation networks of calves were less dense than those of their mothers and less dense than ego networks of mothers and calves when together. The ego density of maternal separation networks and mother–calf together-based networks were not significantly different.

Ego homophily

Age–sex homophily between mothers and calves differed during separations (Fig. 4). Calf ego networks showed significantly less homophily than those of their mothers (mixed model ANOVA: $F_{1,25} = 93.53, P = 0.0001$); however, there was no significant difference based on the interaction of calf sex and ego type ($F_{1,25} = 0.02, P = 0.8991$) or calf sex alone ($F_{1,24} = 0.09, P = 0.7712$).

Network Composition

Whether separated or together, mothers and calves preferentially associated with calves (of both sexes) and juvenile females. That is, ego networks of calves, mothers and mother–calf pairs all had more male calves (one-sample $t$ tests: calves: $t_{26} = 9.52, P <0.001$; mothers: $t_{26} = 4.53, P <0.001$; mother–calf pairs: $t_{26} = 10.94, P <0.001$), female calves (calves: $t_{26} = 7.63, P <0.001$; mothers: $t_{26} = 5.34, P <0.001$; mother–calf pairs: $t_{26} = 7.92, P <0.001$) and juvenile females (calves: $t_{26} = 5.51, P <0.001$; mothers: $t_{26} = 3.00, P =0.006$; mother–calf pairs: $t_{26} = 5.53, P <0.001$) than expected based on the population means. All three ego types also had fewer adult
males in their networks than expected (calves: $t_{26} = -14.59, P < 0.001$; mothers: $t_{26} = -17.63, P < 0.001$; mother–calf pairs: $t_{26} = -10.46, P < 0.001$); however, the proportion of juvenile males in these networks (calves: $t_{26} = 1.91, P = 0.068$; mothers: $t_{26} = 1.14, P = 0.267$; mother–calf pairs: $t_{26} = 1.99, P = 0.057$) and adult females (calves: $t_{26} = -0.46, P = 0.648$; mothers: $t_{26} = 1.47, P = 0.153$; mother–calf pairs: $t_{26} = -0.983, P = 0.335$) did not differ from that expected.

Age–sex class strengths revealed more differences (Fig. 5). The strength of the ego’s relationship to adult males was lower than expected in all calf and mother–calf together networks (female calf: $t_{13} = -3.37, P = 0.005$; male calf: $t_{12} = -4.25, P = 0.001$; female calf–mother: $t_{13} = -4.17, P = 0.001$; male calf–mother: $t_{12} = -4.24, P = 0.001$). However, the strength of ties to adult females was higher than expected for mother–calf together networks (female calf–mother: $t_{13} = 2.90, P = 0.013$; male calf–mother: $t_{12} = 4.31, P = 0.001$) and lower than expected only for ego networks of male calves when separated ($t_{12} = -329, P = 0.006$). The strength of ties to other male calves was significantly higher than expected for male ($t_{12} = 3.73, P = 0.003$) but not for female ($t_{13} = 1.46, P = 0.169$) calf ego networks. Finally, the strength of ties to juvenile females was significantly greater than expected for female calf–mother networks ($t_{13} = 3.42, P = 0.005$), but not for male calf–mother networks ($t_{12} = 1.81, P = 0.095$).

DISCUSSION

A common difficulty with investigating infant social behaviour is discerning whether associates are attracted to the mother or the offspring. Our approach differentiated between associations that occurred with and without the mother and helped distinguish between associates
or partners that were attracted or attractive to the calf from those that were attracted or attractive to the mother. Thus, we found that calf social networks during separations are indeed distinct from those of their mothers and from those when mother and calf are together. As expected, some of this disparity also varied by calf sex in ways similar to sex differences in adult association patterns. In terms of network size and structure, mothers had smaller, denser separation-based networks than their calves. It is important to note, however, that while our present results show that networks of mothers and calves differ during separations, mothers also have considerable impact on the social lives of their calves. When the mother and calf were together, the size of the ego network was similar to that of the calf’s separation network, yet the density was similar to the mother’s separation network.

Beyond size and density, maternal separation networks contained a greater degree of homophily, indicating that mothers primarily associated with other adult females during separations, whereas calves associated with members of age–sex classes that differed from that of their own. This result, however, may be driven by the higher availability of adult females than of calves in the population. At closer inspection, including a correction for the availability of associates, calf, mother and mother–calf together networks contained the expected proportion of adult females but few adult males. This apparent avoidance of males is not surprising since adult males form alliances to herd and consort females and are often aggressive (Scott et al. 2005; Connor et al. 2010).

While the similarity of age–sex class proportions between ego network types is notable, the differences in ego tie strength are particularly intriguing. Ties to other male calves were stronger than expected for male calves during separations, an outcome not observed between
female calves or among mothers and adult females. Associations with juvenile or adult females during separations did not differ from those expected for calves of either sex. Indeed, adult females’ relationships with male calves were weaker than expected. Additionally, mother–female calf networks had strong ties to juvenile females that were absent in mother–male calf networks. The age–sex class proportions that differed from expected further indicate that the observed social patterns were not based on random spatial distribution. Also, the estimated density of dolphins in Shark Bay is 2.4 Dolphins/km² (Watson 2005); therefore, random groups of individuals within 10 m of each other are highly unlikely. Although we did not analyse the strength of relationships with age–sex classes in maternal networks, the few associates in the mothers’ ego networks tended to be other adult females. Previous studies have shown that mothers primarily forage during separations and seem to take advantage of this time to hunt for prey without interference from calves (Mann & Smuts 1998; Mann & Watson-Capps 2005). Maternal foraging tends to be a solitary activity and is inversely related to a mother–calf pair’s number of associates and time spent in groups (Gibson & Mann 2008a); thus, the significantly greater proportion of maternal separation time spent alone and the small size of mothers’ networks while separated are not surprising.

**Social Bonds Hypothesis**

As predicted by the social bonds hypothesis, calves had larger ego networks than their mothers. We suggest that the larger, less dense calf networks and the smaller, more dense maternal networks indicate that mothers are maintaining established relationships with interconnected individuals, whereas calves are developing potential relationships by ‘casting a
wider net’. Although there was no sex difference in calf ego network metrics, the stronger ties observed between male calves may be an important antecedent to juvenile and adult male social structure, a pattern reflected in other male calf social interactions (Mann 2006). Relationships formed as calves could be critical during the juvenile period, particularly for young males that no longer benefit from maternal protection and are likely to be harassed and attacked by other males (see Scott et al. 2005). For reasons that are not understood, adult female sociality is more variable than that of males. While evidence suggests that the development of foraging skills is a greater priority for female calves than social skills per se (Mann & Sargeant 2003; Gibson & Mann 2008a), adult females still must inhabit a large fission–fusion-based society and they do have preferred associates (Smolker et al. 1992; Frère et al. 2010). There is also recent evidence that both genetic and social factors contribute to fitness variation in adult female bottlenose dolphins; therefore, female sociality may be more important than previously thought (Frère et al. 2010). The calf networks we analysed were consistent with the general pattern of sex-segregated bonds in adult bottlenose dolphin society discussed above.

Early sex differences in behaviour and partner preferences are well documented in mammals and have implications for adult behaviour and social structure. In ungulates, where adult males physically compete for females, young males play more frequently and with more contact (reviewed in Beckoff & Byers 1998). In cercopithecine primates, specifically vervet monkeys (*Chlorocebus aethiops*), where females live in matrifocal groups their entire lives while males emigrate at puberty, social partner choice reflects future social needs. Female vervet monkeys build bonds with maternal kin and older dominant females, while males focus efforts on older brothers or males they are likely to encounter after leaving their natal group (Fairbanks
A study of captive gorillas, *Gorilla gorilla gorilla*, also found sex differences in infant play behaviour based on adult social structure (Maestripieri & Ross 2004). Since bottlenose dolphins show bisexual philopatry, both sexes have the potential to form social relationships early in life that persist into adulthood. For example, some of the pairs and triplets of males that engaged in frequent sociosexual contact as calves were still together in adult male alliances (Mann 2006). Thus, calves may not just develop social skills per se, but may also develop relationships that will be important, if not critical, postweaning.

**Babysitting and Learning to Parent Hypotheses**

The babysitting hypothesis received no support. Calves did not preferentially associate with juvenile or adult females during separations and male calves’ relationships with adult females were weaker than expected. These results indicate that bottlenose dolphin females (juvenile and adult) do not help protect or guard calves during separations. As previously reported (Gibson & Mann 2008a), and supported by this data set, a large proportion of calf separations are solitary, further undermining the babysitting hypothesis. As for learning to parent, the idea that nulliparous females gain parenting experience with others’ calves cannot be completely disregarded given their presence in mother–female calf networks; however, their relative absence in mother–male calf networks does not support this hypothesis. It is possible that the aggregate nature of this data set swamped any early (first year of life) evidence of learning to parent. Previous research found that female attraction to calves occurs in the first months of life (Mann & Smuts 1998), but also suggests that relationships thereafter do not appear to be based on calf protection and support. Interestingly, juvenile females in mother–
female calf networks were often kin, such as the older sister or maternal aunt, suggesting that these juveniles might be more interested in their relationship with female kin than with calves in general.

Conclusion

Overall, we found the most support for the social bonds hypothesis. Social bonds and experience gained during infancy are likely to influence later life stages. The high fission–fusion nature of bottlenose dolphin society dictates that newly weaned juveniles must navigate a dynamic social and ecological landscape without the buffer of a stable maternal social group. Therefore, calf independence and social development are likely to impact survival and other fitness outcomes. This complex fission–fusion social organization also presents challenges to researchers attempting to capture the implications of dynamic multi-actor social associations and interactions. Social network analysis provides insight into complex sociality that is not available with traditional dyadic methods. The differences between the ego networks observed here, particularly those between male and female calves, suggest that calves are tending to their social interests and preparing for social challenges concerning the selection of associates. By harnessing more sophisticated network analysis techniques, future work will investigate the dynamics of calf social networks as they approach weaning and determine which, if any, aspects of early social experience influence future fitness.
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REFERENCES


FIGURES AND TABLES

Table 1. Subjects and minutes of observation per age class

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A ‘—’ indicates that the individual was weaned before it was observed in that age class.

*Age class (months): 0 (0–2.99); 1 (3–11.99); 2 (12–23.99); 3 (24–35.99); 4 (36–47.99); 5–8 (48–95.99).

†CHS was only observed as a calf during later age classes; however, her ego size, density and homophily values were well within 1 SD of the mean for female calves.
Figure 1. Three example networks of different ego types that differ in size, density and strength of ties: (a) male calf; (b) mother of male calf; (c) male calf together with mother. Nodes are individual dolphins and lines represent association based on shared group membership. The thickness of the lines is proportionate to the number of minutes that two dolphins were observed together during follows of the ego. Circles: females; squares: males; black: calf; white: juvenile; grey: adult.
### Table 2. Ego network metric definitions

<table>
<thead>
<tr>
<th>Metric</th>
<th>Definition</th>
</tr>
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<tr>
<td>Ego size</td>
<td>Number of other individuals in an ego’s network. Analogous to the ego’s number of associates</td>
</tr>
<tr>
<td>Ego density</td>
<td>Number of observed ties/number of possible ties in the ego network</td>
</tr>
<tr>
<td>Homophily</td>
<td>Proportion of individuals in an ego network that share a given attribute with the ego. Age–sex homophily refers to the proportion of individuals in an ego’s network that are the same sex and in the same age class as the ego. Age classes relate roughly to calf (ca. ≤ 4 years), juvenile (ca. ≤ 10 years) and adult (ca. &gt; 10 years) periods</td>
</tr>
<tr>
<td>Ego strength</td>
<td>Sum of the weights of the ties between an ego and his/her associates</td>
</tr>
</tbody>
</table>
Figure 2. Mean ± SE ego network size of different ego types (**P < 0.005, Tukey multiple comparisons).
Figure 3. Mean ± SE ego network density of different ego types (**P < 0.005, Tukey multiple comparisons).
Figure 4. Mean ± SE ego network age–sex class homophily of different ego types (\(*\*p < 0.005\), Tukey multiple comparisons).
Figure 5. Average observed minus expected age–sex class strengths for (a) calf and (b) together networks (*$P<0.01$ **$P<0.005$, one-sample $t$ tests).
ABSTRACT

Although empirical evidence linking adult social bonds to fitness is growing, little attention has focused on the fitness consequences of early social experience in any species. Given the connection between early ecological conditions and fitness, it follows that social conditions will also influence survival and reproduction in gregarious species. Here, we use social network analysis to determine if metrics calculated from calf networks predict juvenile survival in bottlenose dolphins (*Tursiops* sp.). The labile nature of bottlenose dolphin society demands that newly weaned individuals negotiate a complex social and ecological landscape without a stable kin group to buffer them. Bottlenose dolphins exhibit a complex fission-fusion social structure where the social bonds and skills developed during infancy may be critical for future success, particularly for males who form long-term alliances for mating access. We found that significantly fewer males survived the juvenile period than females. However, the probability of a male surviving increased with eigenvector centrality, a measure of social importance accounting for direct and indirect network connections. Additionally, those male calves who died post-weaning had significantly stronger ties to juvenile males, suggesting that juvenile males are a source of stress or harassment. In contrast, the link between female calf networks and survival is not obvious because of low female juvenile mortality. Our results

* Authorship for paper: Margaret A. Stanton & Janet Mann
support the connection between sociality and fitness in a naturally variable complex social system, and emphasize the need to examine potential selection at all life-history stages in order to more fully understand the causes and consequences of sociality.

INTRODUCTION

Although many organisms live in groups, few species have developed complex social relationships defined by features such as alliance formation, long-term, individually specific relationships, and flexible group membership (Harcourt & de Waal 1992; de Waal & Tyack 2003). Socially complex species, such as dolphins, elephants, and many primate species, also tend to possess large, metabolically expensive brains and exhibit extended life-histories characterized by long, slow periods of growth and delayed sexual maturation and reproduction (Harvey et al. 1987; Charnov & Berrigan 1993; Connor et al. 1998; Dunbar & Shultz 2007; Lehmann & Dunbar 2009). If these features reflect costly correlates of complex sociality, the benefits of maintaining social complexity presumably exceed those typically associated with aggregation alone (e.g. predator protection or resource defense) (Krause & Ruxton 2002; Silk 2007a). Empirical evidence establishing a link between complex social structures and fitness has been historically scarce given the difficulty of acquiring enough long-term data; however, such investigations are gaining momentum and producing intriguing results. For example, male coalitions and alliances have been linked to dominance and direct reproductive benefits for cooperating males (Bygott et al. 1979; Krützen et al. 2004; Duffy et al. 2007; Schülke et al. 2010). Social integration is positively associated with infant survival among adult female
savannah baboons (*Papio cynocephalus*) (Silk *et al.* 2003; Silk 2007b), and with increased foaling success among unrelated adult female feral horses (*Equus caballus*) (Cameron *et al.* 2009). Strong and consistent social bonds are also associated with longevity in adult female baboons, a finding that echoes those in the human social support literature (Uchino 2006; Holt-Lunstad *et al.* 2010; Silk *et al.* 2010), while low variance in strength and number of social bonds is related to adult longevity in groups of rock hyraxes (*Procavia capensis*) (Barocas *et al.* 2011). More recently, researchers have begun to adopt a quantitative genetics approach to addressing the evolution of sociality by calculating the additive genetic variance and heritability of social behavior and its relationship to fitness outcomes (Frère *et al.* 2010; Lea *et al.* 2010). Although these investigations show that adult social bonds relate to fitness, the fitness implications of early social development and social network structure have yet to be examined.

Investigating the link between sociality and fitness requires the selection of analyses that are capable of biologically relevant quantification of social relationships. Social network analysis allows for the quantification of multi-actor interactions, thereby providing more realistic representations of social bonds embedded in complex societies. While gaining in popularity, this powerful tool is currently underutilized as a method for testing biological hypotheses (Croft *et al.* 2011). In humans, aspects of social networks, such as number of connections and cohesiveness, are linked to lower rates of morbidity and mortality involving cardiovascular disease, cancer, and even infectious disease (Berkman & Syme 1979; Kawachi & Colditz 1996; Uchino 2006; Holt-Lunstad *et al.* 2010). Evidence suggests that social relationships may encourage healthy behavior, decrease blood pressure and levels of immunosuppressive hormones, and/or serve as a stress “buffer”. Human social support studies, however, are generally interested in clinical
outcomes and not fitness per se. Outside of humans, a study in long-tail manakins (*Chiroxiphia linearis*) found that the information centrality of adolescent male manakins predicted social rise as an adult, a feature correlated with mating success (McDonald 2007).

Aside from the manakin investigation (McDonald 2007), remarkably little attention has focused on the direct fitness consequences of early social bonds. Many studies have demonstrated the flexibility and influence of early social experience (e.g. nonhuman primates: Harlow *et al*. 1971; de Waal & Johanowicz 1993; Berman *et al*. 1994; Suomi 2005; rodents: Vanden Berg *et al*. 1999; Branchi 2009; humans: Fries *et al*. 2005), and it is well established that ecological factors such as food availability and weather conditions during early development can influence maternal condition and offspring survival and reproduction (Lindstrom 1999). Thus, given the long-term effects of social development on subsequent behavior, early social conditions are also likely to influence fitness, particularly in a long-lived, socially complex species such as the bottlenose dolphin (*Tursiops* sp.).

Bottlenose dolphins exhibit an intrinsically complex fission-fusion social system in which members of the community are rarely, if ever, all together; group size and composition varies temporally; and preferential associations are present (Connor *et al*. 2000). Within this fission-fusion system female social relationships are highly variable and often include strong ties to matrilineal kin (Wells 1991; Smolker *et al*. 1992; Rogers *et al*. 2004; Möller *et al*. 2006; Frère *et al*. 2010), while male dolphins at some research sites, including Shark Bay, Australia, form alliances of 2-3 individuals, often of a similar age cohort (Connor *et al*. 1992; Connor *et al*. 2001; Krützen *et al*. 2003). Shark Bay bottlenose dolphins show bisexual philopatry (Tsai & Mann 2012); therefore social relationships have the potential to form early in life and persist into
adulthood. Shark Bay calves are weaned at ~3-4 years, but do not reach sexual maturity until age 10-15 years (Mann et al. 2000). Unlike primates, during the juvenile period between weaning and sexual maturity, bottlenose dolphins are not buffered by stable kin groups; therefore the post-weaning social and ecological challenges facing young bottlenose dolphins are even greater than those facing young primates (Mann et al. 2000; Leigh & Blomquist 2007). Our previous work suggests that both mother-calf grouping and temporary mother-calf separations enable calves, particularly males, to develop social skills and bonds before the lack of social savvy incurs a fitness cost (Gibson & Mann 2008a; Stanton et al. 2011). Relative to females, males associate infrequently with their mothers post-weaning (Tsai & Mann 2012), exhibit more aggression (Scott et al. 2005), and rely on alliances for mating access (Connor et al. 2001; Krützen et al. 2004); therefore the social skills and/or bonds acquired as calves are likely more important to males than females. This is not to say that female social bonds are unimportant since an interaction between social and genetic factors was recently shown to explain variation in adult female calving success (Frère et al. 2010). However, females do not form strong alliance-type bonds and maintain stronger associations with their mothers post-weaning than do males, suggesting that females do not face the same social challenges during the juvenile period as males. Previous work indicates that females benefit by emulating maternal hunting and social behavior, which tends to be extremely variable (Mann et al. 2008; Gibson & Mann 2008b; Sargeant & Mann 2009). Considering these previous findings, we hypothesize that individual differences in bottlenose dolphin calf sociality are likely to have fitness consequences, particularly for males.
In this study, we used social network analysis to test whether any of five individual-level metrics (binary degree, strength, weighted betweenness, eigenvector centrality, and clustering coefficient) calculated from the networks of 67 calves can predict juvenile survival from weaning to age 10 using generalized linear mixed-effects logistic regression. We did not examine social bonds during the juvenile period, only preceding it, in part because over half (57%) of the juvenile mortality occurred within a year or two after weaning; this resulted in an inadequate time period for reliable assessment of juvenile social bonds. This pattern of mortality also augments the argument that calf social patterns are critical to survival after weaning. To determine the nature of potential links between calf social bonds and future juvenile survival, we also investigated the strength of calf associations with members of each age-sex class in relation to survivorship. Given that male calves exhibit stronger than expected bonds with other male calves when separated from their mothers (Stanton et al. 2011), we predicted that those male calves who survived post-weaning had stronger ties to other male calves than those who did not survive.

RESULTS

Males were less likely to survive from weaning to age 10 than females (Pearson’s Chi-squared test: \(df=1, \chi^2 = 9.6635, P = 0.0019\)). The final GLMM logistic regression model selected by Akaike’s information criterion (AIC) included the fixed effects eigenvector centrality, strength, sex, and the interaction between eigenvector centrality and sex (Table 1). The effect of eigenvector centrality on the probability of survival differed significantly between males and
females as the probability of survival increased significantly with eigenvector centrality for males, but not for females (Table 1; Fig. 1). There was also a trend towards the probability of survival increasing with strength (Table 1).

As calves, males who died between weaning and age 10 had stronger ties to juvenile males than males who survived to age 10 (P=0.016, 10,000 permutations) (Fig. 2). However, calf tie strength with all other age-sex classes did not differ based on male juvenile survival status. Age-sex class strength also did not differ significantly between female calves based on survival status. Finally, the number of associates belonging to each age-sex class did not significantly differ among either male or female calves based on survival status.

DISCUSSION

Here we show that features of early social networks predict juvenile survival in bottlenose dolphins. Differential survival between males and females is common among mammals (Clutton-Brock et al. 1985), and our results are consistent with the observation that males are typically less likely to survive the juvenile period. However, here we identify a unique social component to the likelihood of survival, as males exhibiting higher eigenvector centrality were more likely to survive from weaning to age 10 than males with lower eigenvector centrality.

Eigenvector centrality is particularly interesting because this measure accounts for both direct and indirect ties and is therefore not detectable using non-network techniques. Binary degree, or number of associates, was not a significant predictor of survival, suggesting that when
considering social partners, quality is more important than quantity. Individuals with high eigenvector centrality are either themselves central to the network, or are connected to central individuals (Bonacich 2007). In this case, calves’ strong connections to their mothers are likely driving eigenvector centrality since mothers were present in the majority of the surveys and mothers had social network metric values similar to those of their offspring. Maternal social choices clearly influence the social environment experienced by calves, however in this analysis we controlled for maternal identity and still found that infancy networks were predictive of juvenile survival, which occurs after offspring have markedly decreased maternal association (Tsai & Mann 2012).

Another intriguing result was that male calves who did not survive as juveniles had significantly stronger ties to juvenile males than those male calves who did survive. We suggest that the presence of juvenile males in social groups is stressful for male calves. Additionally, juvenile males may directly harass male calves. In a previous investigation of socio-sexual interactions among Shark Bay bottlenose dolphins, male calves were the recipients of 49.4% of all events with juvenile male actors. Conversely, juvenile males were recipients of only 4.8% of socio-sexual events with male calf actors (Mann 2006). Larger juveniles do not appear to be playfully self-handicapping (Watson & Croft 1996) in these interactions by allowing small calves to mount them or exchange mounting, typical of interactions between male calves, suggesting that juvenile male mounting behavior towards calves might be more about dominance or intimidation than affiliation. While some social bonds do appear to have fitness benefits, chronic social stress has well documented detrimental effects. In rodent and non-human primate models social stress affects outcomes from abnormal aggressive behavior to organ weight,
plasma glucocorticoid levels, body weight, fat distribution, insulin production, testosterone levels, the dopamine and serotonin systems, and even hippocampal neuronal morphology (Tamashiro et al. 2005; Veenema 2009). Thus, our results indicate that while some aspects of social structure, specifically higher eigenvector centrality, increase the probability of survival, some types of associations are stressful and detrimental to future survival.

Contrary to our prediction, surviving males did not have stronger relationships with other male calves than non-surviving males. This prediction was based on our previous study that found stronger than expected bonds between male calves during temporary mother-calf separations (Stanton et al. 2011). However, this earlier study used focal follow data (continuous 1-9 h follows on specific mother-calf pairs) to target calf associations during separations when the calf is determining with whom to spend time. In contrast, survey data, while plentiful and effective for building social networks, are not as efficient as focal follow data at capturing calf behavior when separated from the mother (Gibson & Mann 2009). Male-male calf bonds are still likely to be important, and may even provide some protection from juvenile harassment. However, future work is needed using more discriminating techniques including directional interaction data to tease out the significance of these relationships.

Alliances are generally considered complex due to their triadic nature and the implied ability to discern third-party relationships (Harcourt 1988; Harcourt & de Waal 1992). Decisions about with whom to cooperate become exponentially more complicated the greater the number of actors. Recent evidence suggests three levels of alliances in adult male bottlenose dolphins, a level of complexity yet to be demonstrated in any species besides humans (Connor et al. 2011). Given the intense competitive nature of male relationships in this context, it follows that
establishing bonds or at least some form of social competency prior to reaching adulthood would benefit males in negotiating this complex social landscape. The logistic regression results presented here suggest that early social bonds or skills established as calves provide males with either a competitive advantage or a social buffer post-weaning. Since adult female bottlenose dolphins do not form alliances, the consequences of early sociality appear, not surprisingly, to differ from those of their male counterparts. As in baboons and horses, female social bonds in bottlenose dolphins are likely to have an impact on reproductive success rather than survival per se. Indeed, the interaction effect of associations and genetics on calving success in this population indicates social bonds do have some reproductive consequences (Frère et al. 2010).

Our results emphasize the importance of the early social environment in a naturally variable wild population of complex social mammals. The ability to predict juvenile survival from calf social network metrics suggests that selection is acting on social traits at this early life-stage, which has important implications for the evolution of social behavior and the causes and consequences of complex sociality. Future work will examine how social networks change over the course of the infancy periods and the influence of these dynamics on subsequent survival and reproduction.

METHOD

Study site and data collection

Data were collected as part of a long-term study of bottlenose dolphins in Shark Bay, Australia (25°47’S 113°43’E) where researchers have been investigating the life history,
behavioral ecology, and genetics of the resident population since 1984 (www.monkeymiadolphins.org). The present analyses included 14,948 surveys from 1988 – 2010. Surveys are brief (~5 min), opportunistic boat-based observations that represent “snapshots” of dolphin association and behavior. Group composition recorded during a survey is determined by a 10-meter chain rule in which one dolphin is considered in a group with another dolphin if they are within 10 meters of one another (Smolk er et al. 1992). Individuals are identified using photographic identification based on unique dorsal fins and body markings.

Subjects

All individuals included in this study (N_females=39, N_males=28) had known birth and weaning dates, were sighted on a minimum of 15 days pre-weaning (mean±sd: 67.2±53.0), and either died between weaning (~3-4 years) and 10 years, or survived past age 10. All individuals included in this study were sighted regularly by researchers. Since both sexes are philopatric (Tsai & Mann 2012), those individuals frequently sighted pre-weaning but not sighted for >4 years post-weaning were considered deceased. Birthdates were determined by the last sighting date of the mother without a calf as well as by physical characteristics of the calf upon first sighting. Weaning dates were determined by taking a midpoint between the last date a calf was observed in infant position, from which all nursing occurs, and when association between the mother and offspring decreased to less than 50% (Mann et al. 2000).

Social networks
For each subject, all surveys collected during their infancy period (birthdate – weaning date) were selected and the group composition data from this subset used to create the social network that that dolphin experienced during their infancy. Unknown or uncertain identifications were excluded (~8% of identifications). Two dolphins were considered connected in the network if they were observed in the same group. Connections, or ties, were weighted based on a given dyad’s half weight coefficient. The half weight index is a commonly used measure of association that controls for the sighting frequency of different individuals according to the formula: $X/(X+.5(Ya +Yb)+Yab)$ where $X$ is the number of sampling periods (days) that A and B were observed together in the same group; $Ya$ is the number of sampling periods A was observed without B; $Yb$ is the number of sampling periods B was observed without A, and $Yab$ is the number of sampling periods A and B were both observed, but in separate groups (Cairns & Schwager 1987; Whitehead 2008). In order to obtain robust measures, only individuals observed a minimum of 15 times were included in these infancy networks.

**Analyses**

Five social network metrics were calculated for each subject from their infancy network: binary degree, strength (weighted degree), weighted betweenness, eigenvector centrality, and clustering coefficient. Binary degree refers to the number of individuals directly connected to a node (# of associates); strength is the sum of the weights of all ties connected to a node; weighted betweenness quantifies how many shortest paths between two other individuals in the network pass through a node taking tie weights into account; eigenvector centrality refers to a node’s eigenvalue in the first eigenvector from a matrix of associations; clustering coefficient
measures how connected a node’s neighbors are to one another and represents local network 
cohesiveness (Wasserman & Faust 1994; Whitehead 2008). Metrics were normalized based on 
the maximum value for a node in that network in order to compare between networks of different 
sizes. These five metrics, as well as sex and all metric by sex interactions, served as fixed 
explanatory variables in a generalized linear mixed-effects logistic regression with individual 
subject, mother identity and weaning age controlled for as random variables, and survival to age 
10 (yes or no) as the binary response variable. The explanatory variables were standardized to 
the same scale (SD units) in order to provide a more interpretable model where one unit increase 
is the same for all variables, while not affecting statistical significance. The best model was 
selected by Akaike information criterion (AIC) and confirmed with likelihood ratio tests. 
Multicollinearity among explanatory variables was assessed using variance inflation factors. 

To further investigate infancy network composition, we counted the number of each 
subject’s associates in each age-sex class (adult female, adult male, juvenile female, juvenile 
males, calf female, and calf male). Because each infancy network spanned multiple years, an 
individual included in the network could have been observed in two age classes. In such cases, 
the age class with the majority of the observations was assigned to the individual. Age classes 
were broadly defined as: calf from 0 - 3.99 years, juvenile from 4 - 9.99 years, and adult from 
≥10 years. We then summed the weights of each subject’s ties to all members of each age-sex 
class to get age-sex class strength. We determined whether the number of associates in each age-
sex class or the strength of the relationship with each age-sex classes differed between 
individuals who survived and those who did not using two-sample permutation tests. Separate 
tests were conducted for males and females. All analyses were conducted in R (version 2.13.1;R
Development Core Team 2011) using the igraph package for network analysis (Csardi & Nepusz 2006), the lme4 package for GLMM logistic regression (Bates et al. 2011), and the perm package for permutation tests (Fay & Shaw 2010).
ACKNOWLEDGEMENTS

We thank members of the Shark Bay Bottlenose Dolphin Research Project and all research assistants who helped with data collection. We also thank the Western Australia Department of Environment and Conservation, the Monkey Mia Dolphin Resort and the Shark Bay Ecosystem Research Project for their support. Dr Kay Holekamp, Dr Peter Armbruster and Dr Lisa Singh provided helpful comments on previous versions of this manuscript. Research was approved by the Georgetown University Animal Care and Use Committee (protocol 07-041) and the West Australian Department of Environment and Conservation (license SF006897). Funding for this research was provided by The Explorer’s Club Washington Group, Georgetown University Center For the Environment, Georgetown University Graduate School of Arts and Sciences, and grants to Janet Mann: National Science Foundation (#s 0316800, 0820722, 0941437, 0918308, 9753044), Office of Naval Research- BAA (# 10230702), Georgetown University, Brach Foundation, Eppley Foundation for Research, and the National Geographic Society Committee for Research and Exploration.
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FIGURES AND TABLES

Table 1. Parameter estimates for fixed effects in the final GLMM logistic regression model

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<th>Estimate ± SE</th>
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<td>Intercept</td>
<td>3.01 ± 0.78</td>
<td>3.87</td>
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<td>Eigenvector</td>
<td>-0.89 ± 0.54</td>
<td>-1.66</td>
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<tr>
<td>Sex</td>
<td>-2.65 ± 0.87</td>
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<tr>
<td>Strength</td>
<td>0.86 ± 0.44</td>
<td>1.95</td>
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</tr>
<tr>
<td>Eigenvector* Sex</td>
<td>1.60 ± 0.74</td>
<td>2.17</td>
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</tbody>
</table>
Figure 1. Partial effect of standardized eigenvector centrality on the probability of survival for each sex. Each point represents an individual dolphin’s (N=67) probability of survival = Y based on their standardized eigenvector centrality as predicted by the final GLMM logistic regression model.
Figure 2. Average (±SEM) sum of associations (age-sex class strength) between male calf subjects (N=28) and members of each age-sex class. Significant differences between survival outcomes are denoted by an asterisk. Average sum of association with adult males appears to differ by survival status, however this measure was highly variable and not statistically significant (P = 0.268, 10,000 permutations).
DISSERTATION CONCLUSION

Although sociality was long presumed to be an adaptive response, the relationship between social complexity and fitness has only recently become the focus of empirical research. While evidence for the fitness benefits of social bonds in adults has grown precipitously in recent years, relatively little attention has been paid to the fitness consequences of early sociality. Given the prolonged development exhibited by many socially complex species, as well as the importance of early social environment on subsequent social behavior, and the fitness consequences of early ecological conditions, early sociality is also likely to relate to fitness outcomes. In this dissertation, I used social network analysis (SNA) to quantify the social patterns embedded in the complex Shark Bay bottlenose dolphin society in a unique investigation of infant social networks and the fitness consequences of early sociality.

While SNA has recently experienced an increase in popularity among behavioral ecologists and other scientists, the potential for error and bias introduced by sample size and sampling method is often ignored. The influence of increasing sample size on various social network metrics indicates susceptibility to sampling error; however some metrics were more sensitive to changes in sample size than others. Additionally, the comparison of ego network metrics calculated from networks created using different sampling methods indicates sampling bias, particularly concerning the value of ego size and the relative ranks of individuals’ ego density. Many of the observed patterns and differences appear to be driven by differences in the average group size between survey and focal follow samples in conjunction with the ‘gambit of the group’ (GoG) assumption of complete connectivity within groups of associated individuals.
The results of these comparisons do not preclude the use of GoG when conducting social analyses; however, the influence of GoG must be accounted for when constructing social networks from associations. In general, no all-encompassing ‘right’ answer exists concerning the appropriate sample size and sampling method when constructing social networks since these decisions will depend on the specific research question and social network metrics of interest; however these issues and the resulting sampling error and bias must be considered to avoid Type I or Type II errors.

Dependent offspring are often excluded or ignored in network analyses; therefore my study of mother and calf social networks during temporary separations represents a unique investigation into infant social network structure. The presence of these separations also allowed for the differentiation of maternal and calf associates, a distinction often difficult to make when mothers and offspring remain in close proximity to one another. The larger, less dense networks of calves, as well as the strong bonds between male calves lend support to the social bonds hypothesis and suggest that separations allow calves, particularly males, to develop the social bonds and skills while still reliant on their mothers and before there is a fitness cost. Indeed, results in this dissertation suggest that some of this fitness cost is incurred during the juvenile period when those males with lower eigenvector centrality, a direct and indirect measure of sociality, were less likely to survive the juvenile period to age 10. This result provides empirical support to the predicted relationship between early social environment and future fitness.

Overall, the results of this dissertation demonstrate the value of using social network analysis beyond the description of social structure to answer hypothesis driven questions. Interestingly, throughout these investigations of bottlenose dolphin calf social networks,
weighted metrics were often more important than binary metrics, such as age-sex class strength over proportion or eigenvector centrality over degree. This trend supports the argument that group size does not capture social complexity, and that the nature and strength of social relationships must indeed be taken into account. Most importantly, the revelation of a fitness consequence of early sociality for male calves indicates that selection is acting on social traits at this early life stage. The potential fitness consequences of social traits at all life stages must be investigated and accounted for in order to fully understand the evolution of sociality and the causes and consequences of social complexity.
APPENDIX A

Chapter 5 was published in the journal *Animal Behaviour*. This journal does not require that authors receive permission prior to publishing the authors’ articles in their own theses (http://www.elsevier.com/wps/find/authorsview.authors/rights?tab=2).