Chapter 6
Shark Bay Bottlenose Dolphins: A Case Study for Defining and Measuring Sociality

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Abstract Bottlenose dolphins are attractive candidates for the application of social network analysis (SNA), in part because of their complex fission–fusion social organization characterized by dynamic, temporally variable groups. In Shark Bay, Western Australia, researchers have studied the resident bottlenose dolphins since 1982. Using data on two calves from the Shark Bay dataset, here we present a case study 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.

Keywords Association • Bottlenose dolphins • Fission–fusion • Interaction • Primates • Social metrics • Social network analysis

6.1   Introduction

Similar to primates such as humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and spider monkeys (*Ateles* spp.), bottlenose dolphins (*Tursiops* sp.) and other delphinids 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; Brager 1999; Coscarella et al. 2011). Not surprisingly, measuring sociality in these complex societies is no easy task and often requires a multifaceted 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 has rapidly increased in popularity because of its ability to quantify multi-actor interactions, thereby providing more complete descriptions of complex societies. We provide examples of both association-based social networks and interaction-based social networks that are more analogous to the grooming networks of chimpanzees.

6.1.1   Bottlenose Dolphins of Shark Bay

An important distinction between the foregoing primate fission–fusion systems and that of bottlenose dolphins is the openness of bottlenose dolphin communities (Smolker et al. 1992). Although the subgroups of chimpanzee, spider monkey, and 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 semiclosed (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 (Mann et al. 2012). A consequence of openness is that the potential relationships are not constrained by social unit size. Additionally, although 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 and 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 nonhuman mammal (Connor et al. 2011).

In contrast to 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 to 160 (Smolker et al. 1992; Gibson and Mann 2008a, b). In a recent comparison of male and female social network metrics, we found that males and females do not differ in the their total number of associates (degree), but as expected given male alliance formation, males have stronger associations and are more cliquish (Mann et al. 2012). That said, 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 nondefensible 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 and 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). In contrast to primates who spend their extended developmental period buffered by their natal social group

(Leigh and 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 and Mann 2013). 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 because 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 and Mann 2008b). This hypothesis was borne out by a subsequent study showing that early (pre-weaning) social networks predict juvenile (post-weaning to age 10 years) male mortality (Stanton and Mann 2012).

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. Because bottlenose dolphins show bisexual philopatry, calf social relationships often persist into adulthood (Tsai and Mann 2013), but despite the attention given to the adult bottlenose dolphin fission–fusion society, there are few in-depth investigations into bottlenose dolphin calf social development. 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 and Mann (2008a) assessed predictors of individual variation in the social patterns of Shark Bay mothers and calves. 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 whereas 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 and Mann 2008a). We recently employed social network analysis to further 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 formed stronger bonds with other male calves during separations (Stanton et al. 2011). These results suggest that during separations calves are independently developing the social skills and bonds necessary for future success, particularly males who rely on alliance formation for mating opportunities as adults. Juvenile males, however, appear to harass male calves and may be detrimental to male calf future fitness (Stanton and Mann 2012). The function and consequences of individual variation in calf sociality, which are just beginning to be explored, are critical for understanding both prolonged development and social complexity in bottlenose dolphins. The next step is to examine these patterns in greater depth. 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.

6.2   Method

Researchers have studied the bottlenose dolphin females, calves, and their associates ($N > 1,500$) of Shark Bay, Australia, since 1988. This research is facilitated by a large number of identifiable individuals and an extensive 30-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 10-m chain rule where one dolphin is considered to be in a group with another dolphin if they are separated by 10 m 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 and Mann 2009). Two calves, one male (MIG) and one female (LEN), were observed for ~33 h and ~40 h, respectively, during their first 4 years of life. These calves were chosen because both were observed for 4 years and both possess similarly sized networks, which facilitates comparison. Using MIG's 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 6.1.

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. 6.1). 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) when 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 min and SMO was observed for 180 min total, although COO was observed for 480 min total, then SMO spent 0.75 of his time with COO, whereas COO spent 0.25 of his time with SMO. To create a symmetrical 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.

Table 6.1 Non-network social measure definitions

Measure of sociality	Description
Average group size	Average size of groups in which the calf was observed defined by 10-m chain rule; includes mother and calf
Time alone (%)	Percent of observation time in which the calf was not in a group with any other individual
Time in groups (%)	Percent of observation time during which the calf was observed in a group containing an individual other than the calf's mother
Time socializing (%)	Percent of observation time in which the calf was actively socializing
Time in group (%) with	Percent of observation time in which the calf was observed in a group consisting of
Mother only	Mother only
All females	One or more females excluding the mother
All males	One or more males
Mixed sex	Both males and females excluding the mother
Time (%) associated with	Percent of observation time in which the calf was observed in a group consisting of at least one of the following age-sex classes:
Adult female	Adult female excluding mother
Adult male	Adult male
Juvenile female	Juvenile female
Juvenile male	Juvenile male
Calf, female	Calf, female
Calf, male	Calf, male
Average fission–fusion rate	The average number of times per hour the calf's group composition changes, including the mother

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 because interactions are often difficult to observe in the field. Grooming in primates and petting (an affiliative behavior where one dolphin actively moves the pectoral fin on a body part of another dolphin; Fig. 6.2) 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 4 years of the lives of LEN and MIG (Fig. 6.3). Because of the difficulty of obtaining these 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 4 years of data to create a single network. Although 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
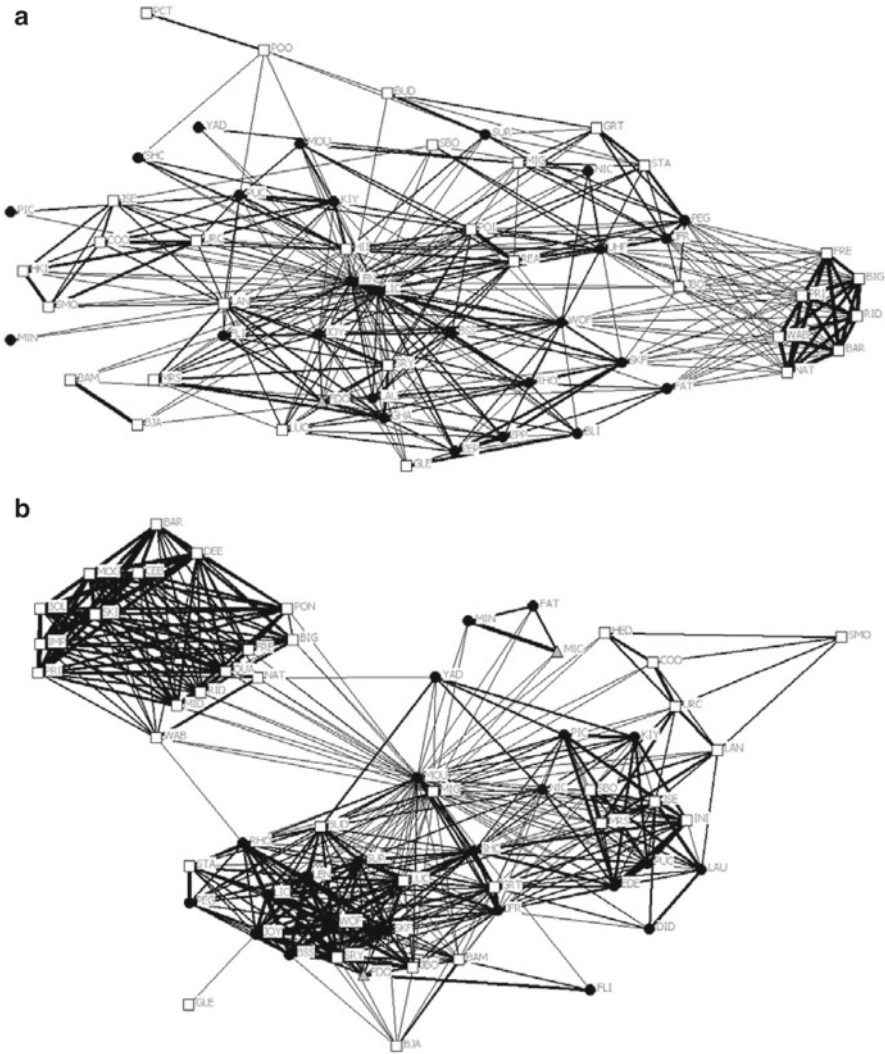
Fig. 6.1 Weighted ego networks of the calves LEN (**a**) and MIG (**b**). *Thicker edges* indicate stronger relationships. Only those edges with an average proportion of observations (APO)>0.50 are shown for clarity; however, all associations were included in the analysis. The mother is the closest node to the focal calf found near the center of the graphs. Mothers are LIC and MOU, respectively. *Circles*, females; *squares*, males; *triangles*, unknown

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 Chap. 10 of this volume.

Photo by Jana Watson–Capps

Fig. 6.2 Two juvenile dolphins petting

6.3 Results and Discussion

The results of various traditional non-network measures of individual sociality are presented in Table 6.2, and the social network analysis results are presented in Table 6.3.

Although 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 does LEN, a female calf. Finally, although 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. 6.1).
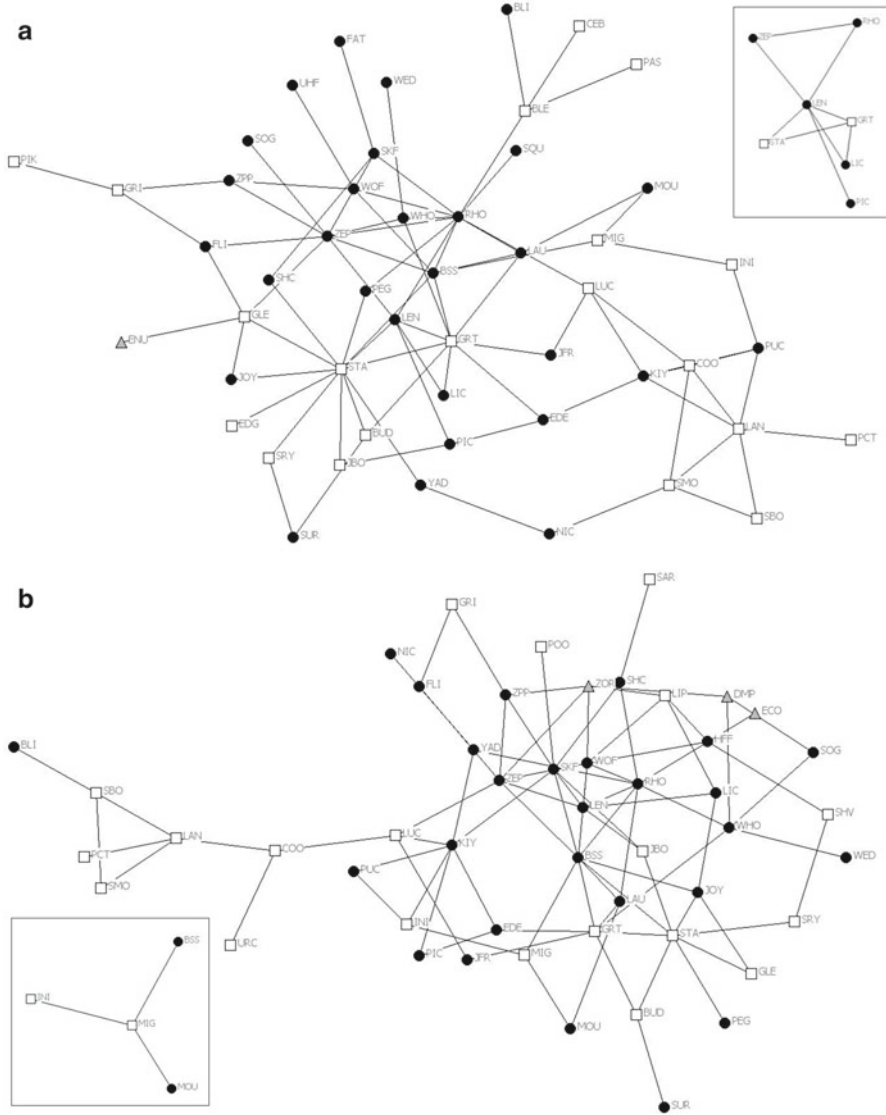
Fig. 6.3 Main component of social networks built from petting interaction data for (**a**) years LEN was a calf (2002–2005) and (**b**) years MIG was a calf (2004–2007). LEN's and MIG's petting ego networks appear in the *insets*. *Circles*, females; *squares*, males; *triangles*, unknown

Thus, MIG's ego network also appears to contain more clusters, some of which are adult males likely consorting with MIG's mother near the end of his infancy. However, although visual inspection of networks is a useful investigation tech-nique, observed patterns should be verified using appropriate network metrics. For example, most network metrics at both the individual and the whole ego network

Table 6.2 Non-network social measures results based on focal follow data for LEN and MIG

	LEN ♀	MIG ♂
Mean group size	6.9	5.3
Time alone (%)	4.6	16.1
Time in groups (%)	70.4	54.1
Time socializing (%)	2.5	5.8[a]
Time (%) in group with		
Mother only	25.0	30.0
All females	21.2	4.7
All males	0.0	3.5[a]
Mixed sex	47.8	42.9
Time (%) associated with		
Adult female	63.8	49.0
Adult male	31.4	18.5
Juvenile female	52.5	23.8
Juvenile male	23.4	9.8
Calf female	40.0	16.7
Calf male	27.1	42.3[a]
Mean fission–fusion rate (number/h)	7.5	5.9

[a]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 6.3 Social network metrics calculated from the association ego networks of LEN and MIG at both individual and ego network levels

	LEN		MIG	
	Individual	Ego network average	Individual	Ego network average
Strength	31.45 (0.06)	12.70 (0.14)	33.15 (0.06)	12.48 (0.17)
Eigenvector centrality	0.26 (0.01)	0.12 (0.01)	0.24 (0.01)	0.11 (0.01)
Weighted clustering coefficient	0.23 (0.01)	0.44 (0.01)	0.20 (0.01)	0.57 (0.01)

Individual metrics refer to those of LEN and MIG whereas 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 1,000 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 sub-networks are (all individuals within a clique are also tightly associated). More detailed descriptions of these metrics are available in Chap. 10 of this volume or in Whitehead (2008)

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. 6.1) and the petting networks (Fig. 6.3) are size and density, defined as the number of actual edges divided by the number of possible edges in the network.

LEN's and MIG's ego networks have unweighted densities of 0.55 and 0.36, respectively, but the entire petting networks containing LEN as a calf and MIG as a calf have much lower densities, of 0.03 and 0.04, respectively. Although LEN and MIG were associated with 57 and 62 other dolphins, respectively, petting was only observed between LEN and 6 others, and between MIG and 3 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.

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