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When mum's away: a study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops* sp.)

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Early social development in long-lived social mammals has important implications for adult behaviour, 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.

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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

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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' in 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 and Macaca 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 (Wells 1991; Smolker et al. 1992; 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 km^2 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 to 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 opportunistic 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 to be 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

Table 1
Subjects and minutes of observation per age class

Mother–Calf pair			Age class*					Total minutes
Calf ID	Calf sex	Mother ID	1	2	3	4	5–8	
ASN	F	DEM	835	638	274	—	—	1747
CHS†	F	BLB	0	0	0	0	856	856
DOD	F	DEM	588	451	460	642	—	2141
DUR	F	DUN	0	409	105	—	—	514
EAT	F	EED	882	574	668	—	—	2124
EDE	F	PIC	823	618	181	—	—	1622
KIY	F	PUC	562	600	259	189	289	1899
MOU	F	MIN	972	890	1048	0	750	3660
PEG	F	SQU	1146	1026	991	861	953	4977
PIC	F	PUC	905	878	0	3147	1707	6637
SHC	F	SUR	0	409	971	689	0	2069
WHO	F	WED	651	88	505	1369	943	3556
YAD	F	NIC	489	648	652	366	—	2155
ZEP	F	ZIP	265	281	580	611	572	2309
BUD	M	SUR	643	682	630	223	—	2178
CAM	M	JFR	0	652	1267	—	—	1919
COO	M	CRO	1227	1373	1079	—	—	3679
GRT	M	JFR	704	706	727	—	—	2137
INI	M	PUC	591	333	603	597	—	2124
JSE	M	JFR	1378	946	898	934	—	4156
MIG	M	MOU	635	668	181	525	—	2009
NOM	M	NIC	639	450	311	—	—	1400
QUA	M	PSU	1002	1038	1011	877	907	4835
RAB	M	NIC	0	850	1002	—	—	1852
SMO	M	YOG	1089	974	1070	774	—	3907
SRY	M	SUR	740	582	295	436	—	2053
STA	M	PEG	675	667	694	362	280	2678
		Total	17441	17431	16462	12602	7257	71193

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.

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
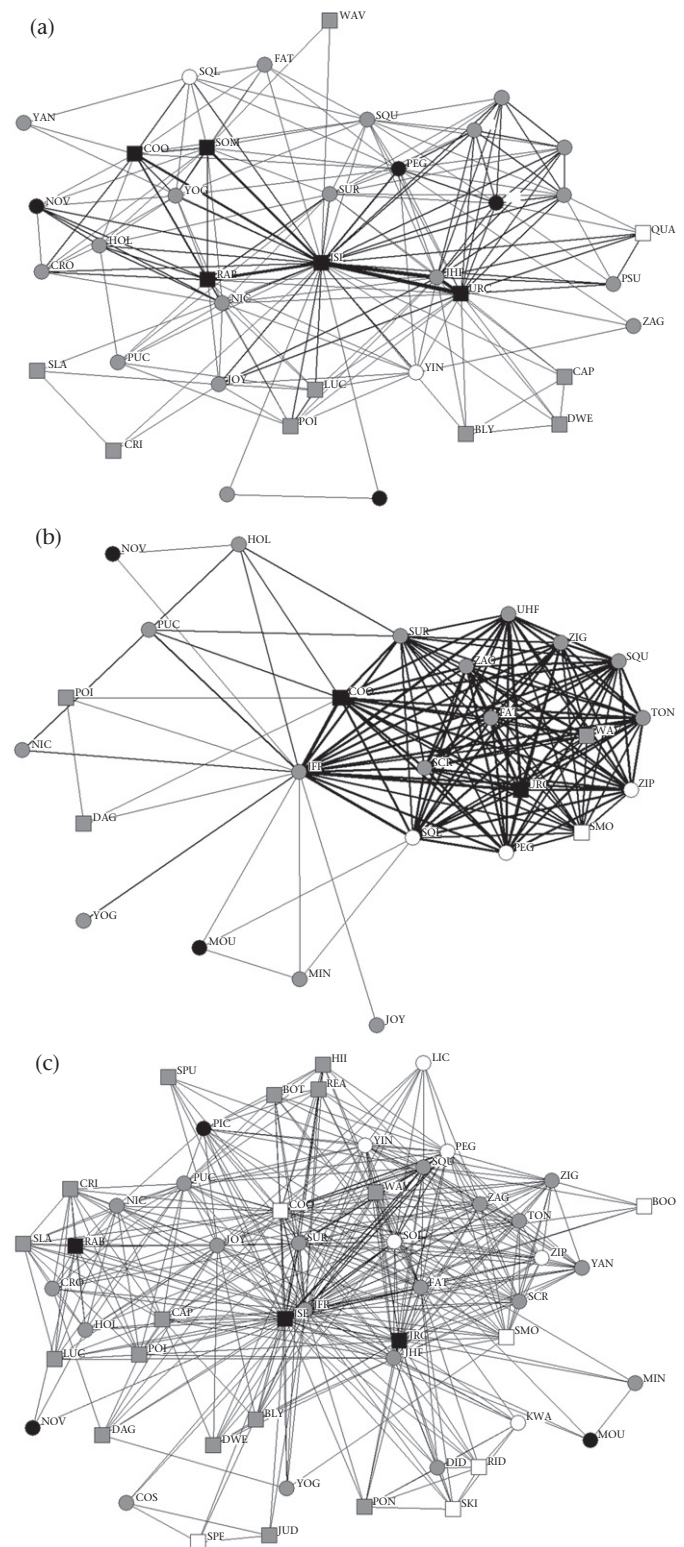

Figure 1. Three example networks of different ego types that differ in size, density and strength of ties: (a) male calf; (b) mother of male calf; (c) male calf together with mother. Nodes are individual dolphins and lines represent association based on shared group membership. The thickness of the lines 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

Metric	Definition
Ego size	Number of other individuals in an ego's network. Analogous to the ego's number of associates
Ego density	Number of observed ties/number of possible ties in the ego network
Homophily	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. $\leq$ 4 years), juvenile (ca. $\leq$ 10 years) and adult (ca. > 10 years) periods
Ego strength	Sum of the weights of the ties between an ego and his/her associates

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 $\pm$ SE frequency of 1.68 ± 0.11 separations/h. The mean $\pm$ SE duration of each separation was 9.09 ± 0.29 min. Calves were alone for $74.9 \pm 2.8\%$ of the time they spent separated, whereas mothers were alone for $88.3 \pm 2.1\%$ 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 ($F_{2,55.1} = 8.37$, $P = 0.0007$; 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.
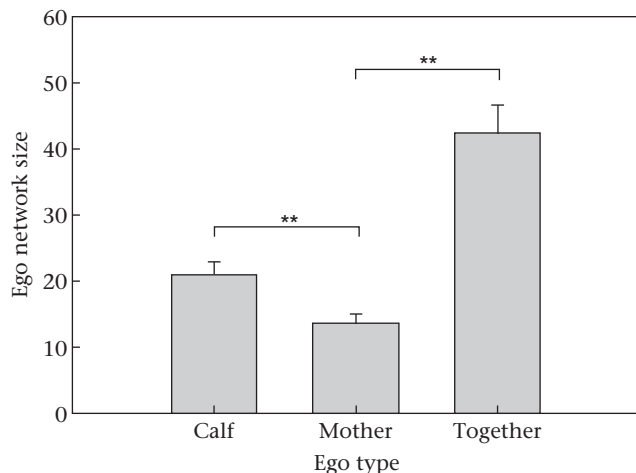
Ego density

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: $t_{12} = -4.24$,
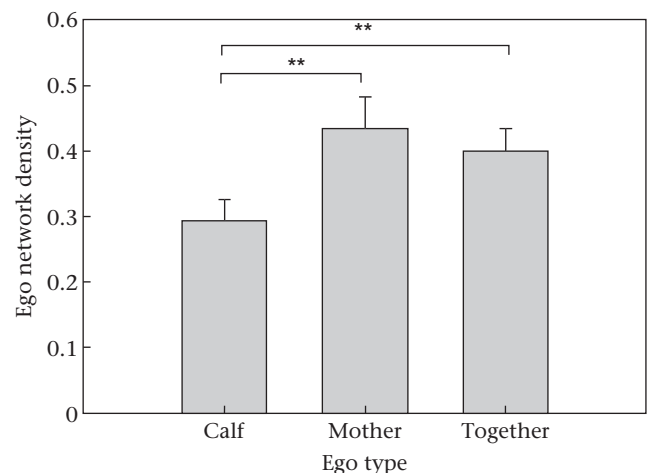

Figure 2. Mean $\pm$ SE ego network size of different ego types (**$P < 0.005$, Tukey multiple comparisons).

Figure 3. Mean $\pm$ SE ego network density of different ego types (**$P < 0.005$, Tukey multiple comparisons).
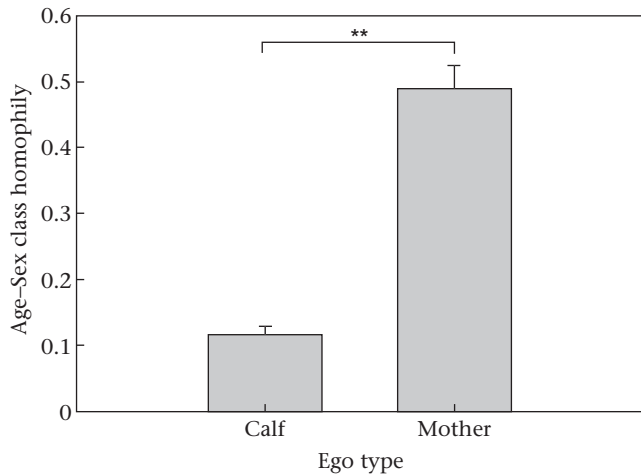
Figure 4. Mean ± SE ego network age–sex class homophily of different ego types (**$P < 0.005$, Tukey multiple comparisons).

$P = 0.001$). 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
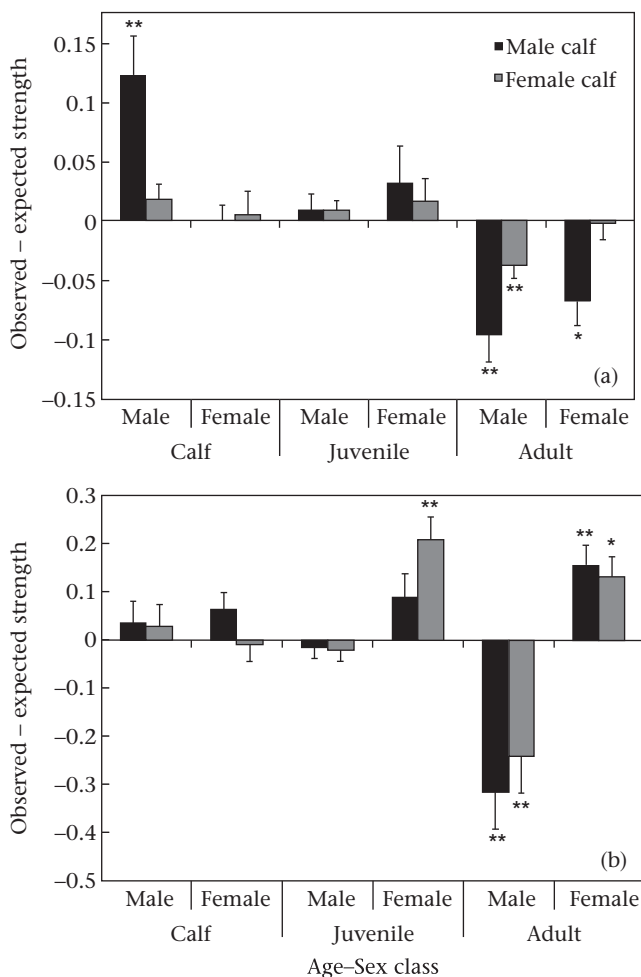

Figure 5. Average observed minus expected age–sex class strengths for (a) calf and (b) together networks (*$P < 0.01$ **$P < 0.005$, one-sample t tests).

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/km^2 (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 1993). 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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