

Female bisexual kinship ties maintain social cohesion in a dolphin network

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Social assortativity, where individuals preferentially mix with certain conspecifics, is widespread among a diverse range of taxa. Animals may assort by a variety of characteristics and receive substantial benefits from these interactions, such as a reduction in predation risk, increased foraging efficiency or greater access to resources. We investigated the social network structure of an embayment population of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, using a long-term photoidentification data set, and examined the impact of sex and kinship in maintaining the cohesion of the social network. We applied recently developed social network techniques that incorporate uncertainty into statistical measures to delineate four smaller social groups within two previously defined communities. Temporal stability of associations within social groups was substantially greater than among individuals from different groups. We also found that the dolphin population was not strongly segregated by sex and both males and females had similar degrees of social connectivity in the network. Moreover, genetic analyses showed that relatedness had a greater influence on female than on male social relationships, as association strength was positively correlated with genetic relatedness between females and between female and male pairs, but not between males. These results suggest that females and males may target kin interactions with females and that kinship appears to be important for maintaining the cohesiveness of this dolphin social network.

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Social assortativity, where individuals preferentially mix with conspecifics sharing similar traits, is widespread among a diverse range of taxa. Animal populations assort by a variety of characteristics including sex (reviewed in Ruckstuhl 2007), age (Smith et al. 2002; Silk et al. 2006a; Wolf et al. 2007; Manno 2008), kinship (reviewed in Silk 2002), reproductive status (Sundaresan et al. 2007; Manno 2008; Möller & Harcourt 2008), morphological traits (Croft et al. 2005), sociability (Lusseau et al. 2006; Manno 2008), behaviour (Pike et al. 2008) and familiarity (Pinter-Wollman et al. 2009). The prevalence of assortative mixing may relate to benefits that individuals obtain by associating with others that have similar capabilities or share similar resource requirements. This includes a potential reduction in predation risk, increased foraging efficiency and greater access to resources (Krause & Ruxton 2002). Social assortativity combined with individual variation in connectivity can substantially affect a population's social network structure and have significant

consequences for population-level processes (Krause et al. 2007; Wey et al. 2008). For instance, shorter path lengths between individuals increase the rate of information exchange and disease transfer through the population, while tighter clustering and assortative mixing of individuals restricts diffusion to smaller subgroups in the network (e.g. Guimarães et al. 2007; Naug 2008).

Large variability in centrality measures is also a common feature of many animal social networks. Individuals with high centrality are either connected to many others or have associates from different social clusters. These individuals are often few, but can have a disproportionate effect on the social cohesion of the population (Lusseau & Newman 2004; Williams & Lusseau 2006), quality and duration of individual and social group interactions (Flack et al. 2006; Manno et al. 2007), group-level decisions (Lusseau 2007) and reproductive success of close associates (McComb et al. 2001). As a result, the consequences of losing individuals from a population, through either death or emigration, vary not only with population size but also with the individual's functional role and the structural properties of the network (Lusseau & Newman 2004; Williams & Lusseau 2006; Manno 2008; but see Flack et al. 2006).

Bottlenose dolphins (genus *Tursiops*) commonly live in fission–fusion societies, where individuals have been shown to assort preferentially by sex (Wells et al. 1987; Smolker et al.

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1992; Lusseau & Newman 2004); females by their reproductive state (Möller & Harcourt 2008) and kinship (Duffield & Wells 1991; Möller et al. 2006), and males by kinship in some populations (Krützen et al. 2003; Parsons et al. 2003), but not in others (Möller et al. 2001; Owen 2003). Associations between females and males in bottlenose dolphin societies appear to be primarily driven by the reproductive state of females and mating season (Connor et al. 2000; Owen et al. 2002). However, the influence of genetic relatedness on associations between females and males and the potential role of sex and kinship in maintaining the cohesiveness of dolphin social networks have not been examined.

Kin selection theory predicts that individuals can obtain indirect fitness benefits by cooperating with kin (Hamilton 1964). Females across several mammalian taxa have been found to direct their affiliative behaviour towards maternal relatives. These preferential associations may be displayed in various ways including spatial proximity (Gero et al. 2008; Wolf & Trillmich 2008), physical contact (e.g. grooming, Silk et al. 2006a; Perry et al. 2008), coalitionary support during agonistic interactions (Smith et al. 2010) and allomaternal care (O'Brien & Robinson 1991; Jesseau et al. 2009). Furthermore, it appears that females may receive substantial fitness benefits from these targeted kin interactions (reviewed in Silk 2007). Males, on the other hand, associate closely and cooperate with male relatives more rarely, but do so in some populations of highly social species such as lions, *Panthera leo* (Packer et al. 1991) and chimpanzees, *Pan troglodytes* (Mitani 2009). In only very few societies are female and male relatives known to form strong, long-term social bonds (e.g. pilot whales, *Globicephala melas*: Amos et al. 1993; bonobos: *Pan paniscus*, Hohmann et al. 1999; killer whales, *Orcinus orca*: Baird & Dill 2000; baboons, *Papio cynocephalus ursinus*: Palombit et al. 2001; humans, *Homo sapiens*: Neyer & Lang 2003). Embayment populations of bottlenose dolphins generally show a high degree of site fidelity; females are highly philopatric (Duffield & Wells 1991; Connor et al. 2000; Möller & Beheregaray 2004) and males also show some degree of philopatry (Krützen et al. 2004; Möller & Beheregaray 2004; Sellas et al. 2005). Bottlenose dolphins also appear capable of identifying maternal kin by their unique acoustic signature whistles (Sayigh et al. 1990; Janik et al. 2006). Together, these observations suggest that opportunities for kin selection to act on the social behaviour of both females and males are present within these populations.

Recently, a hierarchical organization in association patterns was found for an embayment population of Indo-Pacific bottlenose dolphins, *T. aduncus*, inhabiting Port Stephens, southeastern Australia. In this area, two mixed-sex communities inhabiting ecologically different regions of the embayment were subdivided into several smaller groups (Wiszniewski et al. 2009). In the present study, we critically assessed the delineation of individuals into smaller social groups using recently developed network techniques and examined the temporal stability of associations within these groups. Using this information, we then examined the role of sex and kinship in maintaining the cohesion of the dolphin social network and tested whether individuals born locally in Port Stephens are more integrated in the social network than immigrants. To the best of our knowledge, this is the first study to assess the influence of kinship on long-term associations between male and female bottlenose dolphins.

METHODS

The study was conducted in the Port Stephens embayment, located 200 km north of Sydney on the New South Wales coast of southeastern Australia (32°42'S, 152°06'E). Indo-Pacific bottlenose

dolphins inhabiting the embayment are genetically distinct from communities on the adjacent Hunter coast population, while the two socially segregated eastern and western communities within Port Stephens also show some genetic differences (Möller et al. 2007; Wiszniewski et al. 2010). The core areas of the two communities coincide directly with a change in habitat type: the larger eastern community consists of at least 90 dolphins and inhabits a typically marine environment with sandy bottom and sea grass beds, while about 30 western individuals range over a larger and more estuarine region of the port, characterized by a mud bottom and mangroves (Wiszniewski et al. 2009).

Data on school membership were obtained from 180 systematic transect surveys conducted during seven breeding seasons (December to April) and three nonbreeding seasons (June to August) between 1998 and 2007 using standard photo-identification techniques (for further details see Möller et al. 2006; Wiszniewski et al. 2009). No photoidentification surveys were conducted in 2003 and 2004. A school was defined as all individuals within a 100 m radius (Irvine et al. 1981), and if travelling, the animals were heading in the same direction (Shane 1990; Möller et al. 2006). Schools were excluded from analyses if a minimum of 75% of the estimated school size were not reliably photographed, a fusion event occurred during photoidentification, an identical school was resighted during the day, or individuals were re-encountered within 1 h of the first sighting with different associates (Wiszniewski et al. 2009).

Sample Collection and Genetic Analyses

Skin samples for this study were collected from adults and juveniles during sampling surveys in the Port Stephens embayment between 1999 and 2008. We used the PAXARMS biopsy system (PAXARMS N.Z. Ltd, Timaru, New Zealand), which was specifically designed for sampling small cetaceans and has been shown to cause minimal short-term impacts to the dolphins (Krützen et al. 2002). Samples obtained were usually 5 mm in diameter and 1 cm in length and included both skin and blubber tissue. Individuals were recognized at the time of sampling using photoidentification techniques. Our targeted sampling scheme for known individuals and the short time allocation for sampling individuals within a school ensured minimal stress to the dolphins. Biopsy sampling and photoidentification surveys were conducted under licences from the Department of Environment and Climate Change and Marine Parks Authority and under approval by the Macquarie University Animal Ethics Committee.

Samples were preserved in 20% dimethyl sulphoxide saturated with sodium chloride (Amos & Hoelzel 1991) or 100% ethanol. The sex of individuals was determined by extracting DNA from skin samples of identified individuals using the salting-out procedure (Sunnucks & Hales 1996) and amplifying fragments of the *ZFX* and *SRY* genes using the polymerase chain reaction (PCR; as described in Möller et al. 2001). Females were alternatively identified by the repeated presence of a dependent calf (Möller et al. 2006).

Two sets of genetic markers were used to test for an association between genetic relatedness and association patterns among individuals: a 460-bp fragment of the mitochondrial DNA control region, which was amplified by PCR according to Möller & Beheregaray (2001) and a set of 10 nuclear DNA microsatellite loci markers (EV1, EV14: Valsecchi & Amos 1996; MK5, MK6, MK8, MK9: Krützen et al. 2001; TG20: Caldwell et al. 2002; KW2, KW9, KW12: Hoelzel et al. 2002). PCR conditions were as reported in Möller & Beheregaray (2004), except for EV14, KW9 and TG20, where each 10 µl radiolabelled reaction contained 0.6 mM MgCl₂ and was amplified using a 32-cycle 'touchdown' (59–51 °C for EV14 and KW9; and 63–55 °C for TG20). Tests for significant deviation

from linkage equilibrium and Hardy–Weinberg equilibrium were performed in GENEPOP 3.4 with the Markov chain method with 1000 iterations (Raymond & Rousset 1995).

Defining Associations and Social Group Structure

The strength of association among pairs of individuals was calculated using the half-weight index (HWI; Cairns & Schwager 1987) and was restricted to adults and juveniles (individuals at least 5 years of age, Mann & Smuts 1998) sighted more than 10 times over the entire study period (median = 11, mean \pm SE = 16.7 \pm 0.98; range 1–57). Calculation of HWI, network statistics and the permutation analyses described below were conducted in SOCPROG version 2.3 (Whitehead et al. 2005) in MatLab version 7.0.4 (The Mathworks Inc., Natick, MS, U.S.A.). All permutation analyses were repeated at least three times to ensure that *P* values were stable.

Social group structure was examined using the modularity matrix clustering technique described by Newman (2006) and Lusseau et al. (2008). Briefly, the modularity matrix is the association index (i.e. weight) between two individuals minus the expected weight if associations are randomly distributed in the population. The eigenvector of the dominant eigenvalue of the modularity matrix is then used to split the matrix successively into two clusters. This divisive procedure is then iterated on all resulting clusters. The most parsimonious division in the network is subsequently determined by the division that maximizes the modularity coefficient, *Q*. To assess the degree of confidence for the groups identified, we bootstrapped observed school membership samples 1000 times by resampling (with replacement) these samples. The replicates were obtained using daily sampling periods and had the same sample size as the real data. We then applied the modularity community division algorithm described above on each bootstrap replicate (Lusseau et al. 2008). A comembership matrix was then estimated, which corresponded to the proportion of times that two dolphins were clustered in the same social group over all bootstrap community division replicates. We subsequently carried out the modularity community division algorithm on this comembership matrix (Lusseau et al. 2008). The comembership matrix and resulting social group structure (determined by Q_{\max}) were visualized using the spring-embedding method (Kamada & Kawai 1989) in NETDRAW (Borgatti 2002). We then used lagged association rate (LAR) techniques in SOCPROG (Whitehead 1995) to compare the temporal stability of associations within and between these social groups. This combined approach has the advantage of distinguishing temporally stable social groups from the short-term clustering of individuals (Whitehead 2008). Each LAR was compared to the null association rate, which is the expected LAR in the absence of any preferred associations. The precision of the LARs were estimated using the jackknifing procedure, in which 30-day sampling periods over which the association data were collected, were sequentially omitted (Whitehead 1995).

Variability in Sociability

To determine whether dolphins differ significantly in sociability, schools were permuted 40 000 times, keeping the number of individuals in each school and the number of schools in which each individual was observed constant (Whitehead et al. 2005). The standard deviation of the typical group size (TGS), which is the size of a group as experienced by an individual (Jarman 1974), was used to identify individuals consistently found in larger or smaller schools.

Five egocentric network measures (strength, eigenvector centrality, reach, clustering coefficient and affinity) were then calculated to investigate differences in the centrality of individuals and groups. These measures were calculated in SOCPROG using the

weighted association matrix network and definitions described in Whitehead (2009). Briefly, strength is a measure of gregariousness and is the sum of the association indices for each individual (i.e. weighted degree); eigenvector centrality factors in the level of centrality of an individual's neighbours as well as its own; reach is a measure of indirect connectedness; the clustering coefficient is the proportion of an individual's neighbours that are themselves neighbours; and affinity determines whether individuals connect strongly to individuals that also have strong connections. Network metrics were compared to those of an expected network based on 1000 permutations (100 flips performed per permutation iteration) to test whether network structure is influenced by individual association preferences (Lusseau et al. 2008). Using individuals of known sex ($N = 84$), we tested whether sex could explain the variation observed among individuals in centrality levels. Differences in centrality were assessed using the Mann–Whitney *U* test with 10 000 Monte Carlo resamplings. To test whether individuals born locally in Port Stephens were more socially integrated in the network than immigrants, an assignment test was conducted in the program GENECLASS version 2 (Piry et al. 2004) using the Bayesian method described in Rannala & Mountain (1997). Here, the probability for each individual being born locally was estimated using their multilocus genotypes and the population allele frequencies of two potential source populations: Port Stephens and the adjacent Hunter coast (Möller et al. 2007). The assignment probability was then correlated with each of the five centrality measures using the Pearson correlation coefficient. Differences in group centrality were assessed by calculating the difference between observed and expected centrality values for each individual and averaged for each social group. The difference was used rather than the observed to account for sampling structure and differences in group size. Strength values were normally distributed ($P > 0.05$), so we used a one-way ANOVA to test differences in group means. As the distributions for the other four centrality measures deviated from normality ($P < 0.05$), intergroup differences were assessed using the Kruskal–Wallis tests and pairwise post hoc comparisons (Siegal & Castellan 1988). All statistical tests conducted on centrality measures were performed in SPSS version 15.0 (SPSS Inc., Chicago, IL, U.S.A.).

Finally, since association rates between dyads change over different timescales (Wiszniewski et al. 2009), we assessed whether the centrality of individuals remains consistent over time. For each individual that was present in two time periods of the study (P1: 1998–2002; P2: 2005–2007; $N = 132$), the difference in the centrality measures was calculated. We bootstrapped samples 1000 times within each of these two periods and recalculated centrality measures for each of those bootstrap replicates. We used these 1000 measures to derive the 95% confidence intervals for each centrality measure. We used these distributions to assess the likelihood that centrality measures estimated in P1 and P2 were taken from the same statistical population. A significant change in centrality measures between time periods was identified if less than 5% of the measures overlapped.

Genetic Relatedness and Network Structure

Pairwise genetic relatedness among the 65 individuals genotyped at 10 microsatellite loci was estimated using Queller & Goodnight's (1989) relatedness coefficient, *r*. The coefficient, ranging from –1.0 to 1.0, was calculated by comparing the alleles shared by two individuals with the frequency of that allele in the population in the program RELATEDNESS version 5.04 (K. F. Goodnight, Rice University, Houston, TX, U.S.A.). Average genetic relatedness was then calculated for each of the social groups identified, with standard errors obtained by jackknifing over all loci (Queller & Goodnight 1989).

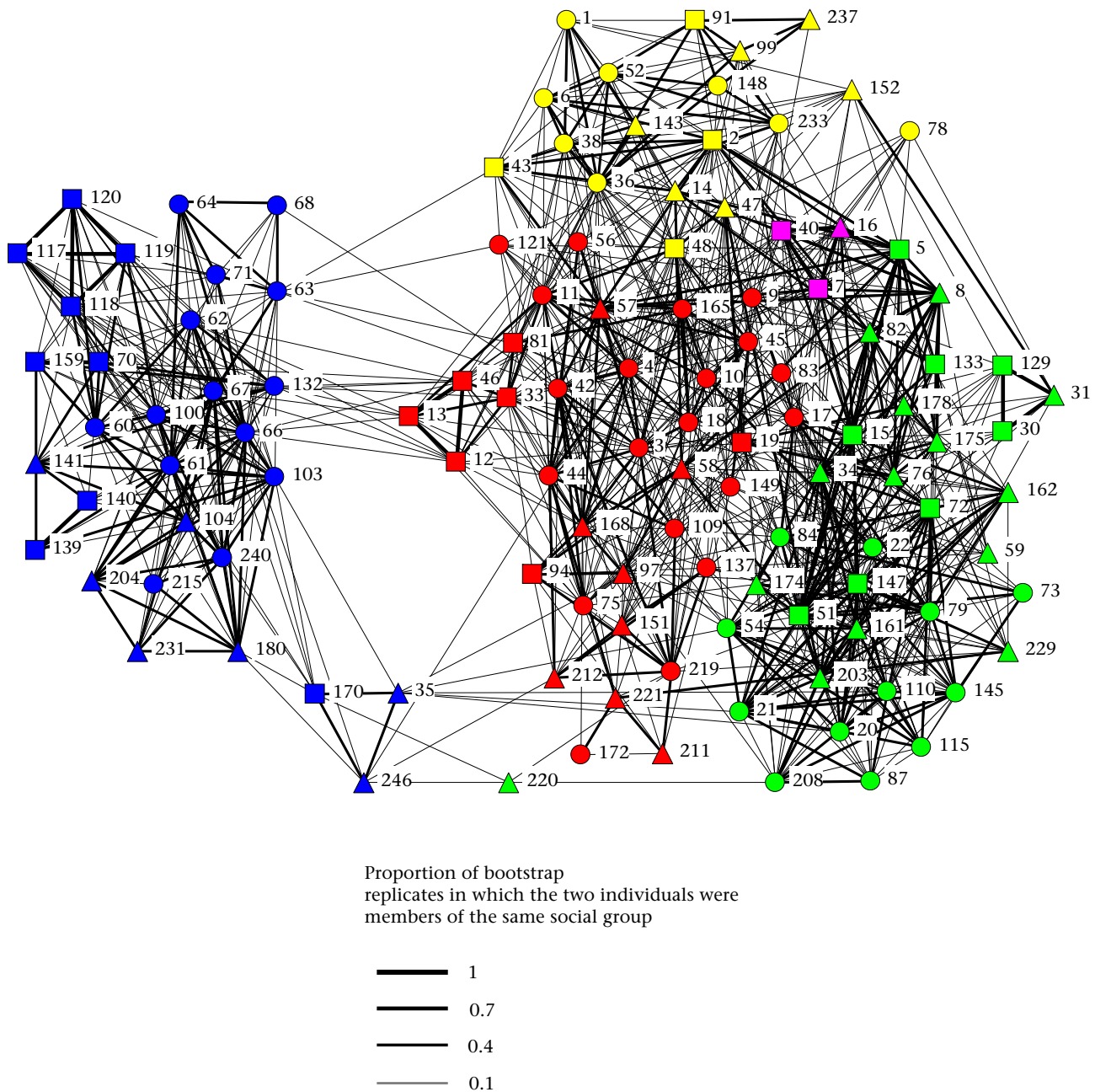


Figure 1. The Port Stephens dolphin social network based on bootstrap replicates of the association matrix. Each individual in the network is represented by a node and unique photoidentification number. Social group structure was identified using the modularity matrix technique and membership in the five clusters is displayed by colour and broadly defined by their ranging patterns (blue = Western; red and purple = Central, with purple representing a set of three individuals that clustered separately; yellow = River; green = Heads). Social groups were composed of both males (squares) and females (circles) and individuals of unknown sex (triangles). The thickness of the edge running between the two individuals represents the probability of individuals belonging to the same social group.

To test for a correlation between associations and genetic relatedness, we used Mantel tests (Mantel 1967; Schnell et al. 1985) and partial Mantel tests which control for social group structure (Smouse et al. 1986), between the association matrix (HWI) and the corresponding matrix of pairwise relatedness estimates. The analysis was repeated for each sex class separately (female–female; female–male; male–male). The HWI matrix was also correlated with a pairwise mtDNA haplotype similarity matrix generated using a binary scale (1 = identical sequence; 0 = different sequence). The significance of all correlations was assessed using 10 000 random permutations (Schnell et al. 1985) in SOCPROG. We then assessed whether genetic relatedness was higher within than

between social groups using permutation tests in the program PERM (Duchesne et al. 2006). This program firstly sums r values for all pairs of individuals belonging to the same group. The r values are then randomly permuted 1000 times across groups while maintaining the original group structure. Significance is assessed by comparing the distribution of permuted intragroup sums to the observed sums. The stability of P values estimated over 10 iterations was used to determine the number of permutations required. For mtDNA data, the proportion of individuals that are expected to match haplotypes was calculated using the formula $\sum (p_i)^2$, where p is the frequency of the i th haplotype in the data set (Ott & Longnecker 2001). This probability was then compared to the

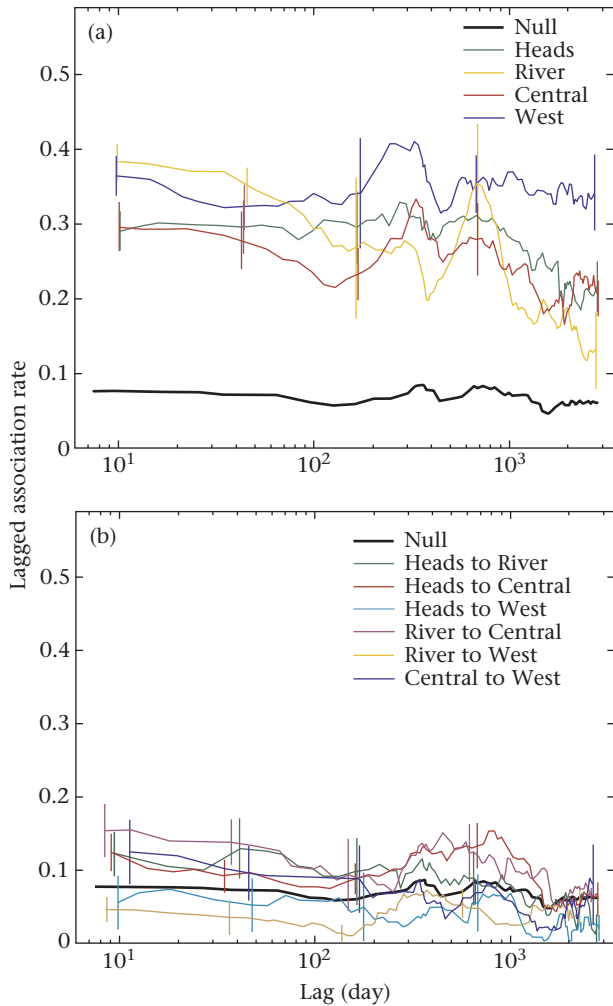


Figure 2. Lagged association rate for (a) within and (b) between the four social groups identified in the Port Stephens dolphin network. The null association rate was estimated from all individuals using 40 000 permutations. Standard errors of the lagged association rates were computed by jackknifing over 30-day periods and are displayed as a ± 1 SE interval around the mean.

observed proportion of haplotypes matches within each of the identified social groups.

RESULTS

Social Network Structure and Temporal Stability

Analysis of social network structure was based on 120 individuals from 737 schools that met the restriction and sighting criteria. This included 54 females, 30 males and 36 individuals of unknown

sex. The sex of some dolphins was undetermined owing to the lack of genetic data and behavioural observations of a dependent calf with the individual. Applying the modularity matrix technique on bootstrap replicates of the association matrix initially divided the population into three social groups ($Q_{\max} = 0.28$). The partition corresponded to the western community and two groups in the eastern community. Since the western community is clearly segregated from the eastern community and shows temporally stable association patterns (Wiszniewski et al. 2009), the analysis was repeated for eastern individuals to investigate fine-scale group structure within this larger community. This resulted in a division of one of the previously defined eastern groups into two mixed-sex groups and a set of three individuals ($Q_{\max} = 0.19$; Fig. 1). Lagged association rate analysis confirmed the segregation of the western community and three social groups in the eastern community, as associations within each of the four groups were temporally stable and remained above the null association rate over the entire study period (Fig. 2a). This was in contrast to LARs calculated between individuals of different social groups, which were substantially lower and stayed close to the null association rate (Fig. 2b). The three eastern groups are hereafter referred to ‘Heads’, ‘Central’ and ‘River’ based on their tendencies to occupy different areas of the embayment (Wiszniewski et al. 2009).

Temporal analysis of centrality measures between the first (1999–2002) and second (2005–2007) time periods demonstrated that individual dolphins maintain their social position over time and the network is generally stable ($P > 0.05$ for all measures). Overall, strength was significantly correlated with affinity ($r = 0.56 \pm 0.08$, $P < 0.05$), indicating that individuals preferentially associated with others with similar numbers of associates (equivalent to degree homophily in binary networks). Newman’s assortativity coefficient between association strength and sex was nonsignificant ($N = 84$; $r \pm SE = 0.251 \pm 0.009$, $P > 0.05$), suggesting that the population is not strongly segregated by sex. Averages of the centrality measure, strength, were also similar within and between sexes (female–female: $N = 1431$; mean $\pm SE = 3.88 \pm 0.30$; female–male: $N = 1431$; 1.93 ± 0.40 ; male–female: $N = 1431$; 3.48 ± 0.25 ; male–male: $N = 435$; 2.49 ± 0.18).

Variability in Sociality

Dolphins in Port Stephens differed significantly in their levels of gregariousness (observed SD of TGS = 2.08; random SD of TGS = 1.79; $P < 0.001$), but sex-specific comparisons of all five centrality measures suggested there were no significant differences between males and females in their levels of social connectivity (Mann–Whitney U test: $P > 0.05$ for all comparisons; Table 1). We also found no correlation between the probability of being born locally and centrality scores (strength: $r = -0.106$, $P = 0.400$; eigenvector centrality: $r = -0.167$, $P = 0.183$; reach: $r = -0.143$, $P = 0.257$; clustering coefficient: $r = -0.075$, $P = 0.555$; affinity: $r = -0.162$, $P = 0.197$). Individual variability in centrality measures,

Table 1

Average network measures calculated using association strength (HWI) for all individuals and for each social group and sex

Group	N	Strength	Eigenvector centrality	Reach	Clustering coefficient	Affinity
All	117	0.038 (0.016)	-0.002 (0.001)	0.610 (0.500)	-0.024 (0.002)	0.003 (0.023)
Heads	34	0.221 (0.018)	-0.007 (0.001)	3.77 (0.327)	-0.025 (0.002)	0.214 (0.022)
Central	35	-0.047 (0.025)	-0.001 (0.001)	0.434 (0.159)	-0.035 (0.002)	0.074 (0.024)
River	18	-0.032 (0.025)	-0.002 (0.001)	-0.259 (0.230)	-0.042 (0.003)	-0.002 (0.029)
West	30	-0.029 (0.023)	-0.012 (0.001)	-2.243 (0.304)	0.002 (0.006)	-0.318 (0.030)
Female	54	0.036 (0.020)	-0.003 (0.001)	0.198 (0.289)	-0.026 (0.003)	-0.024 (0.003)
Male	30	-0.008 (0.041)	-0.003 (0.002)	0.479 (0.646)	-0.017 (0.006)	-0.001 (0.058)

Standard errors are reported in parentheses.

Table 2

Correlation coefficients between association strength (HWI) and relatedness estimates (microsatellite DNA; r) and between association strength and matriline membership (mtDNA)

	Relatedness (r)	Matriline membership
All ($N = 2080$)	0.067**	0.051*
Females ($N = 575$)	0.184**	0.239**
Male–female ($N = 1054$)	0.105**	0.051*
Males ($N = 465$)	−0.007	−0.042

* $P < 0.05$; ** $P < 0.01$; Mantel tests based on 10 000 random permutations.

however, may be to some extent attributed to group membership. Dolphins in the Heads social group had significantly higher measures of strength, reach and affinity compared to the other groups (Kruskal–Wallis test: $P < 0.001$ for all comparisons; Table 1). Western individuals, on the other hand, showed the highest level of clustering and lowest levels of three other centrality scores (eigenvector centrality, reach and affinity: $P < 0.001$), but formed the most enduring bonds (as shown by LAR analysis; Fig. 2a).

Genetic Relatedness and Network Structure

Genetic data were available for 65 of the 120 individuals used for social analysis. Following Bonferroni corrections, there were no significant departures from Hardy–Weinberg equilibrium expectations and linkage disequilibrium among the 10 microsatellite loci used. For both microsatellite and mtDNA markers, pairwise matrices of association strength and genetic relatedness were positively correlated when considering all individuals (Table 2). Correlations were, however, stronger when considering only females (Table 2). All correlations involving females (female–female, female–male) were significant, regardless of whether group membership was controlled for using the partial Mantel tests. In contrast, there was no correlation between association strength and relatedness when considering only males (Table 2).

At the social group level, within-group relatedness was significantly higher for the West and River groups compared to the expected within-group values if individuals were grouped randomly (Table 3). In both cases, high within-group relatedness appears to be mainly driven by higher mean relatedness among female pairs (Table 3). In contrast, mean relatedness within the Heads and Central groups was not significantly different from random expectations. We also found that dolphins in the Heads social group had a significantly lower likelihood of being born locally compared to the other three social groups (Kruskal–Wallis test: $P < 0.05$ for all comparisons; Table 3). Similar patterns were observed when mtDNA haplotype membership was used as the measure of genetic relatedness. Positive correlations were observed when considering only females and male–female pairs, but not when only males were considered. The River and West social groups were composed predominately of one haplotype (SEAust 2; Fig. 3) and as a result, 64% and 72% of dyads matched haplotypes

Table 3

Average pairwise relatedness (r) values within groups (as shown in Fig. 1) and among females (F) and males (M)

Group	N (F/M)	r (All)	r (F–F)	r (M–M)	AI (All)
Heads	18 (10/8)	−0.119 (0.07)	−0.149 (0.06)	−0.079 (0.09)	0.37 (0.06)
Central	16 (9/7)	−0.014 (0.07)	0.001 (0.08)	−0.03 (0.08)	0.72 (0.06)
River	10 (6/4)	0.065 (0.04)*	0.098 (0.03)	0.016 (0.09)	0.64 (0.08)
West	19 (9/10)	0.088 (0.12)**	0.114 (0.11)	0.062 (0.13)	0.64 (0.06)

The average probability of being born locally (assignment index, AI) is also displayed for each social group. Standard errors are given in parentheses.

* $P < 0.05$; ** $P < 0.01$; based on 10 000 random permutations.

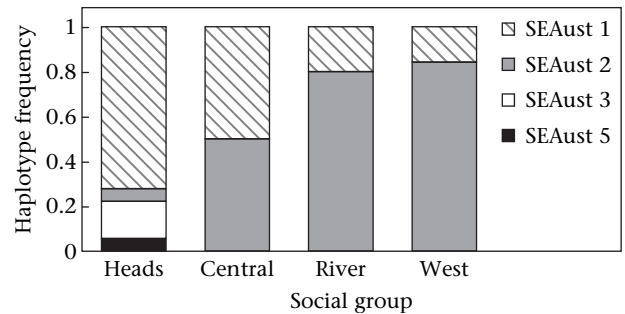


Figure 3. Frequency distribution of mtDNA control region haplotypes within each of the four social groups in Port Stephens.

within each group, respectively. The percentage of haplotype matches expected at random was comparatively lower at 45%, which was closer to the observed number in the Heads and Central groups (53% and 47%, respectively). The Heads group also had the highest haplotypic diversity (Fig. 3) as a result of two additional haplotypes (SEAust 3 and SEAust 5) observed in the group.

DISCUSSION

Social Network Structure and Temporal Stability

This study shows that the Port Stephens dolphin population is partitioned into four social groups within two larger communities. While there was some uncertainty surrounding membership for individuals positioned between social group cores, results from LAR analysis indicated that within-group associations were temporally stable. The segregation of the three eastern social groups is also consistent with findings of three distinct female clusters in this community (Möller et al. 2006). Furthermore, we demonstrated that the Port Stephens population is not strongly segregated by sex and that constant companionships occur between males and females. Segregation by sex has been reported in some bottlenose dolphin populations (Connor 2000; Rogers et al. 2004), but stable intersexual associations are known to be present in at least one other population (Doubtful Sound, New Zealand, Lusseau et al. 2003). In contrast to this study, however, the presence of stable bisexual bonds in the Doubtful Sound population and in other species living in ‘fission–fusion’ societies (e.g. spinner dolphins, *Stenella longirostris*, and chimpanzees) appear to be the result of geographical isolation (Boesch 1996; Lusseau et al. 2003; Karczmarski et al. 2005).

Variability in Sociality

Despite significant differences in association patterns between the sexes in Port Stephens (i.e. small, stable alliances, Möller et al. 2001; large female clusters, Möller et al. 2006), variation in centrality measures among dolphins could not be attributed to sex. We also found that dolphins with a lower likelihood of being born locally appear to be just as socially integrated as those with higher probabilities. The behavioural plasticity of bottlenose dolphins appears to be similar to that of African elephants, *Loxodonta africana*; elephants translocated into a new population were able to assimilate into the existing social system after just a short period of time (Pinter-Wollman et al. 2009). Dolphins in the Heads social group, which are closest in proximity to the Hunter coastal dolphin population, were the most diversely connected in the Port Stephens network (high strength and reach combined with low clustering) and, on average, had the lowest probabilities of being born locally

and the lowest levels of pairwise relatedness. In general, the centrality measures strength, reach and affinity decreased in social groups located at increasing distances from the Port's entrance into more estuarine conditions, while mean relatedness among individuals and probabilities of being born locally in these groups increased. Thus, there appears to be a close relationship in Port Stephens between association patterns and genetic composition of social groups and the ecological and social environment that the social group inhabits (Wiszniewski et al. 2009).

Individual differences in sociability may also relate to individual characteristics or to the strategies used by particular individuals to maximize their access to resources. For instance, differences in sociability between female bottlenose dolphins in Shark Bay, Western Australia, have been attributed to differences in foraging strategies and the time devoted to these activities (Mann & Sargeant 2003; Sargeant et al. 2007; Gibson & Mann 2008). Conversely, variability in alliance sizes observed in some populations such as Port Stephens (Möller et al. 2001) and Shark Bay may be related to differential mating strategies or dominance ranking (Connor et al. 2000), as well as the number of males competing for each female within a given population (Whitehead & Connor 2005). In several long-lived social species, age has also been identified as a predictor of sociality, hierarchical rank and/or structure of associations (Hauser & Tyrrell 1984; McComb et al. 2001; Widdig et al. 2001; Corr 2003; Silk et al. 2006b; Evans & Harris 2008; Fraser et al. 2008). Thus, age may concurrently affect levels of gregariousness in Port Stephens dolphins, but data to test this hypothesis are currently unavailable for this population. Finally, variation in sociality could be influenced by distinguishing behavioural features among individuals that persist over time and across contexts (i.e. personality, as defined by Pervin & John 1997). In humans, stable personality descriptors such as degree of extroversion and neuroticism appear to affect the size and quality of an individual's social network (Asendorpf & Wilpers 1998; Kalish & Robins 2006; Roberts et al. 2008). Individual variability in temperament has also been shown to influence social relationships in some primate (e.g. Weinstein & Capitano 2008) and fish species (e.g. Pike et al. 2008). For example, in guppies, *Poecilia reticulata*, Croft et al. (2009) found that individuals that were shy and engaged in less risky behaviour in the presence of predators generally associated within a larger social network and formed stronger associations than bold individuals. Although the effects of personality traits on social network structure is not well understood for most species, these studies and the recent detection of distinct personalities in bottlenose dolphins (Highfill & Kuczaj 2007) suggest that individual behavioural traits may influence structural properties of dolphin networks.

Genetic Relatedness and Social Network Structure

The significant correlation between association strength and genetic relatedness indicates that dolphins in Port Stephens spend more time with others to which they are more related. The low correlation values found may be expected given that female reproductive condition considerably influences the short-term association preferences of females (Möller & Harcourt 2008). Other factors such as familiarity may also be influencing male and female association patterns (e.g. Ferkin 1988; Pinter-Wollman et al. 2009). Nevertheless, decisions made by individuals to associate with kin may convey benefits to the population by increasing levels of social cohesion between social groups (e.g. Flack et al. 2006). Such a mechanism can be explained solely from individual selection processes, population-level benefits essentially emerging from the sum of benefits for individuals (Lusseau & Conradt 2009). African elephant societies show these cohesive mechanisms where group

fusion events occur more often between groups containing related matriarchs or between groups from the same maternal lineage (Archie et al. 2006). Similarly, Wey & Blumstein (2010) found that social cohesion in a population of yellow-bellied marmots, *Marmota flaviventris*, was maintained through the affiliative interactions of relatives that are of similar age. In Port Stephens, mean relatedness within two of the four dolphin groups (the River and Western groups) was significantly greater than expected. Based on shorter-term associations, Möller et al. (2006) also found that female clusters in the River and Western groups (clusters 'W' and 'K', respectively, in that study) had a higher mean relatedness than the Central group ('N' cluster) and Heads group ('S' cluster). For the Western group in particular, higher genetic relatedness may partly explain the stronger and temporarily more stable associations among individuals (Wiszniewski et al. 2009). The finding that females preferentially associate with their relatives suggests that female dolphins may gain inclusive fitness benefits from targeted kin interactions, as demonstrated in several other group-living mammals (e.g. Lambin & Yoccoz 1998; Hohmann et al. 1999; Armitage & Schwartz 2000; Pope 2000; Rusu & Krackow 2004; Archie et al. 2006; Silk 2007). In contrast, we found that males more often form stable partnerships with randomly related males. Since male alliances compete against each other for access to receptive females, males in this population may receive greater reproductive benefits from associating with a male of similar competitive ability than with a relative (Möller et al. 2001).

Moreover, we found evidence that genetic relatedness appears to play a role in the maintenance of social relationships between females and males. The prevalence of mixed-sex schools in Port Stephens (Wiszniewski et al. 2009) and the high and moderate degree of philopatry for females and males, respectively (Möller & Beheregaray 2004) perhaps provide opportunities for kin relations to develop (Connor et al. 2000). Stable intersexual associations among kin have only been documented in a few other vertebrate species to date, including some cetacean and primate species (e.g. pilot whales: Amos et al. 1993; bonobos: Hohmann et al. 1999; killer whales: Baird & Dill 2000; baboons: Palombit et al. 2001; humans: Neyer & Lang 2003). Hypothesized benefits that may be pertinent to bottlenose dolphins include reduced risk of infanticide (Dunn et al. 2002), lower levels of harassment of females by other males (Scott et al. 2005), group defence against predators (Connor 2000) and cooperative foraging leading to greater access to resources (Gazda et al. 2005; Lusseau 2007). Males may obtain inclusive fitness benefits if increased cooperation with kin results in increased survival of their siblings (Wells 1991; Connor et al. 2000). Since social clusters of females in Port Stephens consist of both related and unrelated individuals (Möller et al. 2006), a male may also benefit by associating with female relatives if this increases his familiarity with potential mating partners. Indeed, Owen et al. (2002) found that males in the Sarasota Bay (Florida) population preferentially associated with breeding females before the mating season and suggested that these interactions may increase a male's mating opportunities later on. Similarly, females may gain familiarity with prospective mating partners by associating with male relatives, which are allied to unrelated males (Möller et al. 2001). While intersexual bonds may significantly increase the risk of inbreeding in small populations, there is no evidence of inbreeding occurring in Port Stephens (Möller et al. 2007). Therefore, dolphins may recognize and avoid mating with relatives using kin recognition mechanisms such as phenotype matching using their signature whistles (Sayigh et al. 1990; Janik et al. 2006) or by familiarity with natal family members (reviewed in Pusey & Wolf 1996).

While the mechanisms generating differences in bottlenose dolphin societies are still not well understood, we have demonstrated that female bisexual kinship ties may be important for

preserving the cohesiveness of the Port Stephens' dolphin social network. Recent evidence suggests that role specializations resulting from an individual's heightened social or ecological knowledge (e.g. Lusseau 2007; Sueur & Petit 2008) can provide substantial fitness benefits to the social group as a whole (e.g. McComb et al. 2001). Despite difficulties in determining the influence of sociality on reproductive success in long-lived marine species such as dolphins, a stable network structure is likely to have important long-term implications for these fission–fusion societies.

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