

Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia

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Abstract Kinship has been shown to be an important correlate of group membership and associations among many female mammals. In this study, we investigate association patterns in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting an embayment in southeastern Australia. We combine the behavioral data with microsatellite DNA and mitochondrial DNA data to test the hypotheses that genetic relatedness and maternal kinship correlate with associations and social clusters. Mean association between females was not significantly different from a random mean, but the standard deviation was significantly higher than a random standard deviation, indicating the presence of nonrandom associates in the dataset. A neighbor-joining tree, based on the distance of associations between females, identified four main social clusters in the area. Mean genetic relatedness between pairs of frequent female associates was significantly higher than that between pairs of infrequent associates. There was also a significant correlation between mtDNA haplotype sharing and the degree of female association. However, the mean genetic relatedness of female pairs within and between social clusters and the proportion of female pairs with the same and different mtDNA haplotypes within and between clusters were not significantly different. This study demonstrates that kinship correlates with associations among female bottlenose dolphins, but that kinship relations are

not necessarily a prerequisite for membership in social clusters. We hypothesize that different forces acting on female bottlenose dolphin sociality appear to promote the formation of flexible groups which include both kin and nonkin.

Keywords Female associations · Kinship · Bottlenose dolphins · Microsatellites · Mitochondrial DNA · *Tursiops aduncus* · Mammals

Introduction

Many female mammals live in groups. By living in groups, females may benefit through reduced risk of predation, better protection from sexual coercion by males, increased access to food resources, and assistance for infant rearing (e.g., Wrangham 1980; Wrangham and Rubenstein 1986; Smuts and Smuts 1993). However, there are also costs associated with living in groups, such as increased competition for food resources and mating opportunities (e.g., Alexander 1974; Wrangham and Rubenstein 1986). Individuals therefore need to decide whether or not to join groups, and which groups to join, so as to maximize their fitness. Individuals may enhance their fitness directly by maximizing their own reproduction (Williams 1966) and, indirectly, by maximizing the reproduction of their relatives (Hamilton 1964).

Kin selection theory (Hamilton 1964) suggests that individuals should preferentially associate and cooperate with kin whenever the inclusive benefits outweigh the costs. In most mammalian species, females remain within their natal area or group throughout their lives (Greenwood 1980; Pusey and Packer 1987) and therefore have enhanced opportunities to associate with kin. Not surprisingly, kin-

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biased associations and kin-biased behaviors are commonly observed among many female mammals. Female kin spend more time in close proximity and are more likely to aid each other [e.g., several primates, reviewed in Silk (2002)], may share territories [e.g., great gerbils (Randall et al. 2005)] and foraging grounds [e.g., greater horseshoe bats (Rossiter et al. 2002)], may breed communally [e.g., house mice (Rusu and Krackow 2004)], may allosuckle [e.g., lions (Pusey and Packer 1994)], and may gain higher reproductive success by forming coalitions with kin (e.g., red howler monkeys (Pope 2000)).

Coastal bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*) live in fission–fusion societies, where individuals show flexible grouping patterns while maintaining long-term associations with specific individuals (Würsig and Würsig 1977; Wells et al. 1987; Smolker et al. 1992; Möller et al. 2001). Information on association patterns from two populations (one of *T. truncatus* and one of *Tursiops* sp.) suggests that adult females, apart from forming strong social bonds with their calves, usually show stable, moderate level associations with other females within social clusters named “bands” or “cliques” (Wells et al. 1987; Wells 1991; Smolker et al. 1992).

Potential advantages of group living for female bottlenose dolphins include protection from predators and defense against sexual coercion by males (Connor et al. 2000a). Several shark species are known to prey on bottlenose dolphins (Corkeron et al. 1987; Cockcroft et al. 1989), and they may focus on calves and their mothers (Corkeron et al. 1987; Mann and Barnett 1999). Another potential cause of calf mortality may be infanticide by males. Although acts of infanticide have not been observed directly in bottlenose dolphins, indirect evidence suggests that it is likely to occur (Ross and Wilson 1996; Patterson et al. 1998). Both predation by sharks and the possibility of infanticide suggest that assistance for infant rearing may also be important for female bottlenose dolphins. In several studies, it has been reported that bottlenose dolphin group size increases when calves are present (e.g., Wells et al. 1987; Möller et al. 2002). In addition, females seem to form coalitions to protect themselves from male harassment (Connor et al. 2000a).

While predation pressure and sexual coercion by males may favor grouping among female bottlenose dolphins, in coastal areas groups usually split up during foraging (Connor et al. 2000b; Möller et al. 2002). Furthermore, female bottlenose dolphins have not been observed cooperating to defend resources against conspecifics (Connor et al. 2000a), which may affect the pattern of social relationships. In other female mammals, competition for food is considered a major determinant of relationships (Wrangham

1980; van Schaik 1989). Female primates often emigrate and form loose or variable social bonds when food competition is relaxed, while they tend to be philopatric and form strong bonds with kin when competition for food is strong (Wrangham 1980; van Schaick 1983).

It remains largely unknown whether female bottlenose dolphin associations correlate with kinship. In Shark Bay, Western Australia, field data suggest that female *Tursiops* sp. have remained in their natal area and continued to associate with their mothers after conceiving calves (Smolker et al. 1992). In Sarasota Bay, Florida, field observations of female *T. truncatus* that have returned to their natal band when their first calf was born, along with preliminary genetic analyses, suggest that bands may be largely composed of maternal relatives (Wells 1991; Duffield and Wells 1991).

In this study, we investigate association patterns in female *T. aduncus* (Indo-Pacific bottlenose dolphin) inhabiting Port Stephens, southeastern Australia. We then combine the behavioral data with information from microsatellite DNA markers and mitochondrial DNA (mtDNA) sequences to test the hypotheses that genetic relatedness and maternal kinship correlate with associations and social cluster membership. Previous genetic analyses have shown that females in this population are highly philopatric to their natal site (Möller and Beheregaray 2004) and there is, therefore, the opportunity for association between female kin.

Materials and methods

Study area and population

Port Stephens (32°42' S, 152°06' E) is a shallow, predominantly sandy bay of approximately 140 km² located in New South Wales, southeastern Australia. Bottlenose dolphins are observed in Port Stephens year-round, with about 90 individuals regularly sighted within the Port (Möller et al. 2002). A molecular phylogenetic analysis revealed that this population belongs to the Indo-Pacific species of bottlenose dolphin *T. aduncus* (Möller and Beheregaray 2001).

Behavioral data and biopsy sampling

The composition of 218 dolphin groups was determined by photographic identification of individuals (Würsig and Würsig 1977) during 38 boat surveys conducted between December 1998 and April 2000. Dolphins were defined as part of the same group if within a 100-m radius (Irvine et al.

1981) and, if the animals were traveling, they were heading in the same direction (Shane 1990). Individuals in a group were usually found within a 10 to 20-m radius but were frequently more widespread when foraging. Group size ranged from one to 30 individuals, with a mean of 6.75 (SD=0.37) dolphins (Möller et al. 2002).

Small skin samples were collected from 87 free-ranging dolphins using a remote biopsy system (Krützen et al. 2002) during 26 additional boat surveys between March 1999 and April 2000. Biopsies were preserved in a salt-saturated solution of 20% dimethyl sulphoxide (Amos and Hoelzel 1991). We identified individuals during biopsy sampling by either photo-identification or visual recognition by one of the authors (LMM). While in the boat, resampling of individuals was minimized by checking a photo-identification catalogue which identified previously sampled individuals.

Genetic analysis

DNA was extracted from biopsy samples following a salting-out protocol described in Sunnucks and Hales (1996). The sex of sampled dolphins was determined by amplification through the polymerase chain reaction (PCR) of the genes ZFX and SRY using a protocol developed by Gilson et al. (1998). Nine cetacean microsatellite loci were amplified by PCR: Ev1 and Ev37 (Valsecchi and Amos 1996), Mk5, Mk6, Mk8, and Mk9 (Krützen et al. 2001), D8 (Shinohara et al. 1997), and Kw2 and Kw12 (Hoelzel et al. 1998), as described in Möller and Beheregaray (2004). Tests for linkage disequilibrium revealed that there were no significant locus-pair comparisons at the 5% level, none of the loci showed departures from Hardy–Weinberg equilibrium, and probability tests did not detect excess or deficiency of heterozygotes at any locus (Möller and Beheregaray 2004). A fragment of approximately 460-bp of the mtDNA control region was amplified by PCR according to Möller and Beheregaray (2001). Samples were sequenced with an ABI 377 DNA sequencer. Alignment of the resultant sequences and identification of distinct mtDNA haplotypes within a 403-bp mtDNA segment were performed by eye.

Data analysis

Of 218 groups observed in Port Stephens, 158 were selected for association analysis. Groups were selected if at least four times the visually estimated group size were taken in identification photographs and there was no apparent fusion with animals from other groups while the photographs were being taken.

From these groups, females identified on at least six occasions [the median number of sightings or higher

(Möller 2001)] were selected to calculate pairwise associations using the half-weight index (HWI) (Cairns and Schwager 1987) in SOCPROG 1.2 (Whitehead 1999b). Thirty-five known females were sighted six or more times (28 of these females had a closely associated calf) (Appendix). Associations were calculated as follows: association between two individuals A and B = $2N_{ab}/(N_a+N_b)$, in which N_{ab} is the number of times A and B were found together in the same group, and N_a and N_b are the total number of groups for A and B (Cairns and Schwager 1987). With the HWI, associations can range from zero for two dolphins never seen together in the same group to one for two individuals that were always sighted together. We defined frequent associates (FA) as pairs of females in the top 10% of the association coefficients and infrequent associates (IA) as pairs of females in the lowest 10% of the association coefficients and/or those which were not observed to associate. If a female was sighted more than once in a day, only the first sighting of that female was included for analysis. Individuals were classed as females if they were sampled and genetically sexed as such or by field observations of repeated association with a dependent calf. Female calves were excluded from the analyses.

Overall and pairwise associations were tested for departures from randomness within SOCPROG 1.2 (Whitehead 1999b), using the permutation procedure developed by (Manly 1995), adapted by (Bejder et al. 1998) for association data and refined by (Whitehead 1999a) to account for demographic effects (referred to as permutation test hereafter). In this case, the null hypothesis is that there are no preferred or avoided long-term (between sampling periods) nor short-term (within sampling period) companions, given the number of groups each individual was seen in during each sampling period (in our case, survey month). In this test, for each sampling period, the elements of the incidence matrix of groups by individuals are permuted, keeping row and column totals constant. Tests were two-tailed ($\alpha=0.05$) and based on 10,000 permutations. We kept increasing the number of permutations, starting at 1,000, until the *P*-value stabilized (Bejder et al. 1998), which occurred before we reached 10,000 permutations. Departures from randomness were tested for both the mean and standard deviation. Significant pairs (i.e., nonrandom associates) were defined as those emerging in every one of ten tests (Bejder, personal communication).

Association coefficients were converted to distance measures by subtracting them from one, and then displayed in a neighbor-joining tree (Saitou and Nei 1987) to visually explore the existence of main social clusters in the dataset.

Genetic relatedness based on microsatellites was estimated using the index of Queller and Goodnight (1989)

within RELATEDNESS 5.04 (Goodnight and Queller 1998). This genetic data was previously used to test for sex differences in the dolphins' dispersal patterns (Möller and Beheregaray 2004). Matrices of pairwise genetic relatedness and mtDNA haplotype sharing were constructed for genotyped females used for association analysis. These matrices were tested against an association matrix containing the same individuals using a Mantel matrix randomization procedure, where the significance is determined by making a direct comparison of the test statistic with the randomization distribution (Manly 1997b) (referred to as matrix randomization test hereafter). A randomization test (two-sample test) was also used to compare mean differences in pairwise genetic relatedness of (a) frequent against infrequent associates and (b) within and between main social clusters (referred to as two-sample randomization test hereafter). A randomized chi-square test (Manly 1997b) was used to compare frequency of female pairs with the same and different mtDNA haplotypes within and between bands (referred to as randomized chi-square test hereafter). Tests were carried out with RT 2.1 (Manly 1997a), with 10,000 randomizations. Bonferroni correction was applied

for multiple comparisons of pairwise genetic relatedness (three comparisons, adjusted $\alpha=0.016$) and mtDNA haplotype sharing (two comparisons, adjusted $\alpha=0.025$).

Results

Female associations and social clusters

Overall, the mean association between females was not significantly different from a random mean (permutation test, real mean=0.12, random mean=0.12, $P=0.303$). However, the overall standard deviation was significantly higher than a random standard deviation (permutation test, real SD=0.160, random SD=0.117, $p<0.01$). Of the 595 possible female pairings, 12 pairs associated significantly more often than expected by chance, and one pair associated significantly less often than expected (Table 1). Individual females had up to three nonrandom associates (Table 1).

A neighbor-joining tree, based on the distance of associations between females, identified four main social clusters in the area: *K*, *S*, *W*, and *N* (Fig. 1). This result is

Table 1 Associations of female bottlenose dolphins (HWI, Cairns and Schwager 1987) with six or more sightings in Port Stephens

Social cluster	Individual females																																					
	39	52	11	18	45	1	3	10	36	42	4	17	6	20	54	22	21	29	110	73	61	63	62	64	65	66	67	68	79	83	71	87	75	124	132			
39																																						
52	0																																					
11	0	0.15																																				
18	0	0.14	0.55																																			
45	0.12	0.08	0.54	0.74																																		
1	0.12	0.25	0.16	0.08	0.17																																	
3	0.2	0.29	0.14	0.27	0.3	0.23																																
10	0.08	0.31	0.42	0.41	0.32	0.33	0.18																															
36	0	0.48	0.15	0.22	0.08	0.43	0.07	0.39																														
42	0.24	0.08	0	0.15	0.08	0.17	0.3	0.13	0.08																													
4	0	0.17	0.17	0.24	0.09	0	0.24	0.07	0.09	0.55																												
17	0	0.19	0	0.09	0	0.11	0.26	0.22	0.2	0.4	0.44																											
6	0	0.38	0.15	0.07	0	0.33	0.14	0.31	0.24	0.08	0.09	0.19																										
20	0	0.43	0.14	0.07	0	0.08	0.13	0.24	0.15	0.07	0.08	0.17	0.14																									
54	0	0.24	0.08	0	0	0	0.15	0.06	0	0	0	0	0.16	0.81																								
22	0.22	0.23	0	0.07	0.08	0.17	0.29	0.31	0.16	0.24	0.09	0.29	0.15	0.36	0.24																							
21	0	0.44	0.07	0.07	0	0	0.07	0.12	0.08	0.08	0.17	0.18	0.15	0.62	0.54	0.22																						
29	0	0.33	0.11	0	0	0.12	0.2	0.08	0	0.12	0.13	0.15	0	0.4	0.12	0.11	0.32																					
110	0	0.26	0.08	0	0	0	0.16	0	0	0	0.11	0.11	0.17	0.48	0.55	0	0.5	0																				
73	0.13	0.17	0.08	0	0	0	0.08	0	0	0.09	0.2	0.11	0.17	0.24	0.27	0	0.25	0.13	0.3																			
61	0	0	0	0	0	0	0	0	0	0.11	0	0	0.1	0	0	0	0	0	0	0																		
63	0.12	0	0	0	0	0	0.08	0	0	0.26	0.19	0.11	0	0	0	0	0.12	0	0.1	0.33																		
62	0	0	0	0	0	0	0	0	0	0.11	0	0	0.11	0	0	0	0	0	0	0	0.62	0.35																
64	0	0	0	0	0	0	0	0	0	0.24	0.13	0	0.11	0	0	0	0	0	0	0	0.67	0.5	0.55															
65	0.14	0	0.09	0.08	0.1	0	0	0.07	0	0.1	0	0	0	0	0	0	0	0	0	0	0.38	0.6	0.4	0.29														
66	0	0	0	0	0	0	0	0	0	0.11	0	0	0	0	0	0	0	0	0	0	0.77	0.35	0.67	0.55	0.53													
67	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0.67	0.21	0.43	0.46	0.35	0.57												
68	0.15	0	0	0	0	0	0.09	0	0	0.3	0.22	0.12	0	0	0	0	0.15	0	0.11	0.4	0.74	0.43	0.46	0.59	0.43	0.25												
79	0.17	0.2	0	0.09	0.11	0	0	0.15	0.11	0.11	0.12	0.13	0	0.27	0.11	0.1	0.29	0.17	0.12	0.24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0.14	0	0.17	0.17	0.19	0.1	0.33	0.14	0.19	0.1	0.11	0.12	0.09	0.08	0.1	0.09	0	0.14	0.11	0.11	0	0.1	0	0	0.11	0	0	0	0.12	0								
71	0	0	0	0	0	0	0	0	0	0.2	0.11	0	0.1	0	0	0	0	0	0	0	0.53	0.42	0.29	0.62	0.24	0.43	0.38	0.5	0	0	0	0	0	0	0	0	0	
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0.47	0	0.42	0	0.27	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0.17	0	0	0	0	
75	0	0.17	0.08	0.24	0.09	0	0.24	0.07	0.09	0.36	0.4	0.22	0.17	0.16	0.09	0.09	0.08	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0.12	0.21	0	0	0	0	
124	0.18	0.11	0	0	0.11	0.24	0.1	0.08	0	0.11	0	0.14	0.11	0.19	0.11	0.11	0.1	0.18	0.25	0.12	0	0	0	0	0	0	0	0	0	0	0	0	0.15	0	0	0	0.12	0
132	0	0	0	0	0	0.11	0.09	0	0	0.21	0	0.13	0.1	0	0	0.1	0	0	0	0	0.43	0.33	0.62	0.33	0.38	0.62	0.27	0.27	0	0	0	0.27	0	0	0	0	0	

Associations significantly higher than expected by chance are shown in bold within a shaded box, and those significantly lower than expected by chance are shown in bold within a nonshaded box

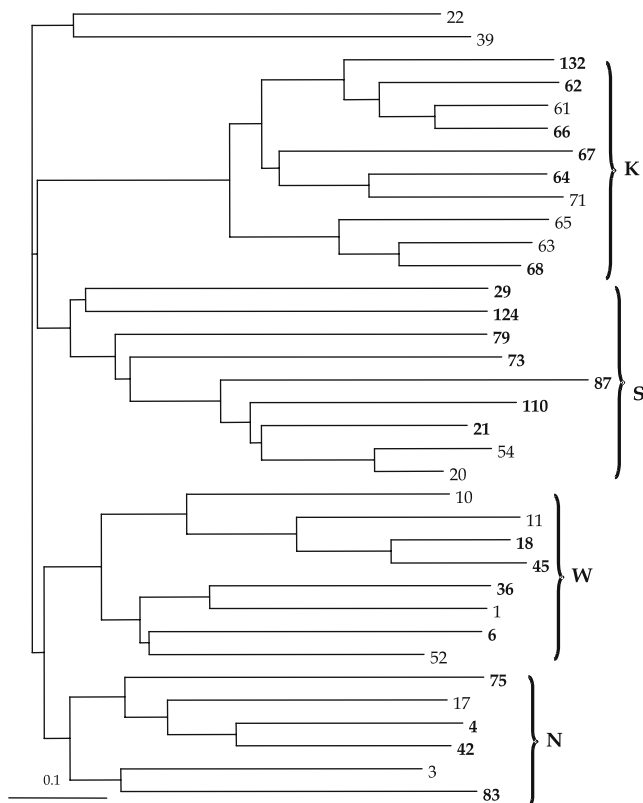


Fig. 1 Neighbor-joining tree of associations between female Indo-Pacific bottlenose dolphins with six or more sightings in Port Stephens. Individuals are denoted by *numbers*. *Numbers* are in **bold** for genotyped females. Main clusters, or social groups, are shown with a *brace* and labeled with *capital letters*. Branches are proportional to distance of associations

consistent with the use of different core areas within the Port by females from the different social clusters [*K* in the west, *S* in the southeast, *W* and *N* in the northeast, but only *W* within the Myall River (Möller 2001)] and therefore does not seem to be an artifact of the data analysis.

Female associations, genetic relatedness, and maternal kinship

Genetic data were available for 21 of the 35 females used for association analysis (Table 2). There was an increase in the degree of genetic relatedness with an increase in the degree of association, but this relationship was not significant (matrix randomization test, $F=2.31$, $N=210$, $P=0.12$) (Fig. 2). Nevertheless, the mean genetic relatedness between pairs of frequent associates was significantly higher than that between pairs of infrequent associates (two-sample randomization test, FA: mean $R=0.29$,

$SD=0.212$, $N=21$; IA: mean $R=0.15$, $SD=0.277$, $N=108$, $P<0.016$). Two mtDNA haplotypes [SEAust1 and SEAust2 (Möller and Beheregaray 2001)] (Table 2) were identified among females used in the association analysis. There was a significant correlation between the mtDNA haplotype sharing and the degree of female association (matrix randomization test, $F=7.32$, $N=210$, $P<0.025$). Among the most frequently associated female pairs, most shared mtDNA haplotype, while pairs that were never sighted together or associated infrequently included pairs sharing and not sharing mtDNA haplotype (Fig. 3).

Female social clusters, genetic relatedness, and maternal kinship

Mean genetic relatedness of female pairs within and between social clusters was not significantly different (two-sample randomization test, within: mean $R=0.16$, $SD=0.272$; between: mean $R=0.13$, $SD=0.296$; $N=210$, $P=0.29$) (Table 3).

The proportion of female pairs with the same and with different mtDNA haplotypes within and between clusters was also not significantly different (randomized chi-square test, random $\chi^2=22.13$, $N=210$, $P=0.4$) (Table 3).

Discussions

This study demonstrates that associations among female Indo-Pacific bottlenose dolphins can be related to kinship. Both genetic relatedness and maternal kinship were correlated with associations of female *T. aduncus* in Port Stephens, southeastern Australia. Genetic relatedness based on microsatellite markers was significantly higher among frequent female associates than among infrequent associates. Additionally, maternal kinship was a good predictor of female associations, with frequent associates usually sharing mtDNA haplotype. Nevertheless, there were also many closely related females that were not seen to associate, suggesting that other factors must also be involved.

Association patterns of female *T. aduncus* in Port Stephens resembled, in many respects, those found in two other coastal bottlenose dolphin populations [reviewed in Connor et al. (2000a,b)]. In Sarasota and Shark Bay, female *T. truncatus* and *Tursiops* sp., respectively, usually associate at moderate levels with a stable subset of females and infrequently with others and display considerable flexibility in the degree of sociability (Connor et al. 2000a). In Port Stephens, females generally associated at low to moderate levels with other females, associated more closely with

Table 2 Genetic data for female bottlenose dolphins with six or more sightings in Port Stephens

Individual females																					
Band	73 ^a	4 ^b	132	64	66	79	45	21	29	87	83	42	75	18	68	67	36	6	110	62	124
<i>S</i>	<i>N</i>	<i>K</i>	<i>K</i>	<i>K</i>	<i>S</i>	<i>W</i>	<i>S</i>	<i>S</i>	<i>S</i>	<i>S</i>	<i>N</i>	<i>N</i>	<i>N</i>	<i>W</i>	<i>K</i>	<i>K</i>	<i>W</i>	<i>W</i>	<i>S</i>	<i>K</i>	<i>S</i>
73 ^a	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0
4 ^b	0.04	1	1	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1
132	-0.29	-0.10	1	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1
64	-0.10	0.51	0.22	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1
66	0.00	0.30	0.54	0.49	1	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1
79	0.42	0.00	-0.10	0.17	-0.18	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0
45	0.47	0.16	0.12	0.38	0.20	0.19	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0
21	0.05	0.05	0.27	0.17	0.23	-0.29	0.46	0	0	1	0	0	1	0	0	0	0	1	0	0	
29	0.02	0.46	0.10	0.45	0.17	0.25	0.24	0.40	1	0	1	1	0	1	1	1	1	1	0	1	1
87	0.16	0.69	0.33	0.47	0.65	0.03	0.27	0.08	0.14	0	1	1	0	1	1	1	1	1	0	1	1
83	0.72	0.15	-0.38	0.02	-0.18	0.51	0.47	0.06	0.32	-0.03	0	0	1	0	0	0	0	0	1	0	0
42	0.23	0.25	0.30	0.23	0.60	-0.05	0.44	-0.03	-0.13	0.67	0.06	1	0	1	1	1	1	1	0	1	1
75	0.46	0.51	-0.01	0.12	0.39	0.08	0.14	-0.11	-0.11	0.79	0.24	0.62	0	1	1	1	1	0	1	1	
18	0.25	-0.05	0.33	0.04	0.56	-0.06	0.06	0.31	0.24	0.17	0.16	0.24	0.26	0	0	0	0	0	1	0	0
68	0.07	-0.14	0.43	0.16	0.56	0.11	0.07	0.09	0.05	0.27	-0.12	0.33	0.16	0.54	1	1	1	0	1	1	
67	0.35	0.39	0.22	0.25	0.49	0.36	0.14	0.03	0.34	0.47	0.25	0.43	0.50	0.47	0.58	1	1	0	1	1	
36	-0.06	0.42	0.55	0.31	0.67	-0.23	0.32	0.36	0.29	0.66	-0.06	0.68	0.41	0.48	0.40	0.41	1	0	1	1	
6	-0.49	-0.24	0.02	0.22	-0.16	-0.06	-0.15	-0.05	0.12	-0.37	-0.30	-0.42	-0.66	-0.28	-0.10	-0.36	-0.21	0	1	1	
110	-0.19	-0.09	0.12	0.13	0.40	-0.37	-0.09	0.05	-0.10	0.16	-0.29	0.24	0.01	0.16	0.06	0.01	0.32	0.33	0	0	
62	-0.05	0.09	0.20	0.12	0.51	-0.37	0.14	0.33	-0.10	0.41	-0.21	0.53	0.28	0.04	0.15	0.26	0.36	-0.22	0.29	1	
124	-0.29	-0.33	-0.10	0.01	-0.31	0.28	-0.33	0.06	0.13	-0.36	-0.17	-0.71	-0.48	-0.05	-0.14	-0.23	-0.47	0.05	-0.34	-0.33	

Genetic relatedness [*R* of Queller and Goodnight (1989)] is shown in the lower matrix, while haplotype sharing is shown in the upper matrix. Pairs with a value of 1 had the same haplotype, while pairs with value of 0 had different haplotypes

^aHaplotype SEAust1

^bHaplotype SEAust2

certain females and formed distinct groups of associates. Females from these social clusters use different core areas

within the Port (Möller 2001) and therefore are likely to be equivalent to Sarasota’s female bands (Wells et al. 1987).

Wells et al. (1987) hypothesized that reproductive condition may play the predominant role in determining associations within bands of female *T. truncatus*, while

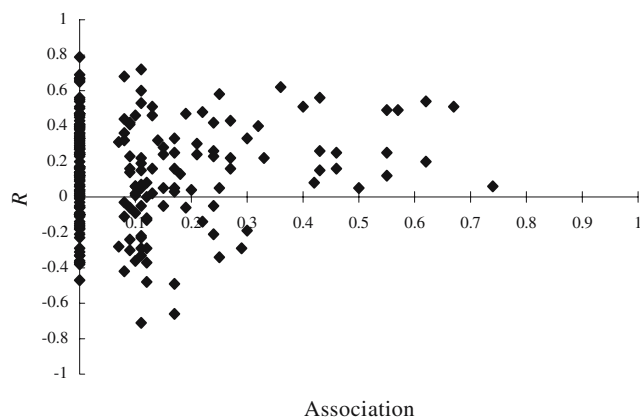


Fig. 2 Relationship between association and genetic relatedness (*R*, Queller and Goodnight 1989) for female Indo-Pacific bottlenose dolphins in Port Stephens

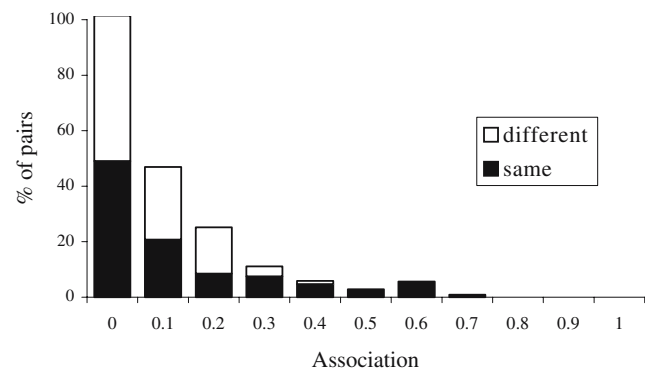


Fig. 3 Associations between female Indo-Pacific bottlenose dolphins with the same and different mtDNA control region haplotypes

Table 3 Mean and range of associations (HWI, Cairns and Schwager 1987) and genetic relatedness (R , Queller and Goodnight 1989), and proportion of pairs with same and different mtDNA haplotypes within female social clusters in Port Stephens

Social cluster	Association			Relatedness			mtDNA haplotype	
	N 1	Mean	Range	N 2	Mean	Range	Same (%)	Different (%)
<i>K</i>	45	0.46	0.21–0.77	15	0.35	0.12–0.58	100	0
<i>S</i>	36	0.27	0–0.81	21	0.01	–0.37–0.42	42.9	57.1
<i>W</i>	28	0.28	0–0.74	6	0.04	–0.28–0.48	33.3	66.7
<i>N</i>	15	0.29	0.1–0.55	6	0.31	0.06–0.62	50	50

Only females sighted six or more times were included. N 1 is the number of pairs for associations, while N 2 is the number of pairs for the genetic data

kinship may play an important role in determining band membership. In Port Stephens, reproductive state also seems to affect associations between females, with females with same aged calves within social clusters usually showing strong association coefficients (Möller 2001). In Sarasota, field observations and preliminary mtDNA analysis suggest that female bands may include multiple generations of females from more than one matriline (Duffield and Wells 1991). Mean genetic relatedness and the proportion of mtDNA haplotype sharing within and between Port Stephens' social clusters were not significantly different, suggesting the dispersal of females between social groups. However, one of the clusters (*K*) was composed exclusively of one matriline and closely related females, which indicates that the kinship composition of social clusters can be variable. This might be related to ecological differences because the core area of *K* females is the only one located in the estuarine waters of the Port (Möller 2001), or to demographic differences between the matriline.

Similarities in association patterns of female bottlenose dolphins *T. aduncus* and *T. truncatus* inhabiting widely separated coastal areas suggest that similar forces may be acting on female sociality. It has been hypothesized that fission–fusion grouping patterns in bottlenose dolphins reduce feeding competition by allowing individuals to disperse (Connor et al. 2000b). This seems to be the case in Port Stephens, where feeding groups are generally smaller in size compared to those engaged in other activities (Möller et al. 2002). If female bottlenose dolphins decrease food competition with other females by splitting into smaller groups to feed, then association with kin may not be essential. Females are predicted to form groups and associate with kin when resources such as food or territories can be defended against other females (e.g., Wrangham 1980). Female bottlenose dolphins, however, have not been observed

cooperating with other females to defend resources (Connor et al. 2000b). Nonetheless, if protection from predators and male harassment is an important factor promoting the formation of female bottlenose dolphin groups (Connor et al. 2000a), then association with kin should still be preferred, as related individuals usually make more reliable cooperators (Wrangham 1980). In addition, if assistance for infant rearing is of importance, kin should also be preferred due to the potential gains through inclusive fitness (Hamilton 1964).

The emerging picture from this study is that kinship correlates with associations between female Indo-Pacific bottlenose dolphins, but that kinship relations are not a prerequisite for social cluster membership. Connor et al. (2000b) proposed that a model for social bonds of female bottlenose dolphins should take into account not only persistent associations with a relatively small number of associates that may be mostly kin but also the relatively large number of associates that are unlikely to be kin. This study revealed that persistent associations may occur between related and unrelated individuals (although to a different extent) and that relatives may be either members of the same social cluster or not. Because relatives occur in different clusters, these individuals could function as the channel that mediates social bonds across social clusters and between unrelated individuals.

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Appendix

Social cluster membership, reproductive state, and number of sightings of female Indo-Pacific bottlenose dolphins with six or more sightings in Port Stephens, southeastern Australia

Female ID	Social cluster	Reproductive state	Number of sightings
39		≥1 year	6
52	W	≥1 year	16
11	W	≥1 year	16
18	W	≥1 year	20
45	W	No calf	12
1	W	≥1 year	11
3	N	≥1 year	17
10	W	New 1	22
36	W	No calf	13
42	N	No calf, new 2	15
4	N	≥1 year, new 2	11
17	N	≥1 year	9
6	W	New 1	15
20	S	≥1 year	19
54	S	≥1 year	18
22		≥1 year	13
21	S	≥1 year	17
29	S	No calf	6
110	S	≥1 year	13
73	S	≥1 year	11
61	K	New 1	7
63	K	No calf, new 2	14
62	K	≥1 year	6
64	K	≥1 year, new 2	6
65	K	New 1	9
66	K	New 1	6
67	K	≥1 year	8
68	K	No calf, new 2	10
79	S	No calf	8
83	N	No calf	11
71	K	≥1 year	9
87	S	No calf	6
75	N	≥1 year	11
124	S	≥1 year	6
132	K	No calf	7

Reproductive state refers to estimated age or absence of calf at beginning of study, and summer of parturition thereafter. Females with no social cluster membership are those that were not classified as member of any particular main cluster.

New 1 Newborn in Austral Summer 1, 1998/1999, New 2 Newborn in Austral Summer 2, 1999/2000.

References

Alexander RD (1974) The evolution of social behaviour. *Ann Rev Ecol Syst* 5:325–383

- Amos W, Hoelzel AR (1991) Long term preservation of whale skin for DNA analysis. *Rep Int Whal Comm (Special issue 13)*:99–104
- Bejder L, Fletcher D, Bräger S (1998) A method for testing association patterns of social animals. *Anim Behav* 56:719–725
- Cairns SJ, Schwager SJ (1987) A comparison of association indices. *Anim Behav* 35:1454–1469
- Cockcroft VG, Cliff G, Ross GJB (1989) Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. *S Afr J Zool* 24:305–310
- Connor RC, Wells RS, Mann J, Read AJ (2000a) The bottlenose dolphin: social relationships in a fission–fusion society. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean societies: field studies of dolphins and whales*. The University of Chicago Press, Chicago, pp 91–126
- Connor RC, Read AJ, Wrangham R (2000b) Male reproductive strategies and social bonds. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean societies: field studies of dolphins and whales*. The University of Chicago Press, Chicago, pp 247–269
- Corkeron PJ, Morris RJ, Bryden MM (1987) Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquat Mamm* 13:109–113
- Duffield D, Wells RS (1991) The combined application of chromosome, protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. *Rep Int Whal Comm (Special issue 13)*:155–169
- Gilson A, Syvanen M, Levine KF, Banks JD (1998) Deer gender determination by polymerase chain reaction: validation study and application to tissues, bloodstains, and hair forensic samples from California. *Calif Fish Game* 84:159–169
- Goodnight KF, Queller DC (1998) Relatedness 5.4. Goodnight software. Available at <http://www.gsoftnet.us/GSoft.html>
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:140–162
- Hamilton WD (1964) The genetical evolution of social behavior. *J Theor Biol* 17–52
- Hoelzel AR, Potter CW, Best PB (1998) Genetic differentiation between parapatric ‘nearshore’ and ‘offshore’ populations of the bottlenose dolphin. *Proc R Soc Lond B* 265:1177–1183
- Irvine AB, Scott MD, Wells RS, Kaufmann JH (1981) Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fish Bull* 79:671–678
- Krützen M, Valsecchi E, Connor RC, Sherwin WB (2001) Characterization of microsatellite loci in *Tursiops aduncus*. *Mol Ecol Notes* 1:170–172
- Krützen M, Barré LM, Möller LM, Heithaus MR, Simms C, Sherwin WB (2002) A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. *Mar Mamm Sci* 18:863–878
- Manly BFJ (1995) A note on the analysis of species co-occurrences. *Ecology* 76:1109–1115
- Manly BFJ (1997a) RT, a program for randomization testing, version 2.1. Centre for applications of statistical and mathematics. University of Otago, Otago, New Zealand
- Manly BFJ (1997b) *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman and Hall, London, UK
- Mann J, Barnett H (1999) Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: defense and reactions by the mother. *Mar Mamm Sci* 15:568–574
- Möller LM (2001) Social organisation and genetic relationships of coastal bottlenose dolphins in southeastern Australia. Ph.D. thesis, Macquarie University, Australia
- Möller LM, Beheregaray LB (2001) Coastal bottlenose dolphins from southeastern Australia are *Tursiops aduncus* according to sequences of the mitochondrial DNA control region. *Mar Mamm Sci* 17:249–263

- Möller LM, Beheregaray LB (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Mol Ecol* 13:1607–1612
- Möller LM, Beheregaray LB, Krützen M, Harcourt RG (2001) Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proc R Soc Lond B* 268:1941–1947
- Möller LM, Allen SJ, Harcourt RG (2002) Group characteristics, site fidelity and abundance of bottlenose dolphins (*Tursiops aduncus*) in Jervis Bay and Port Stephens, southeastern Australia. *Aust Mammal* 24:11–21
- Patterson IAP, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proc R Soc Lond B* 265:1167–1170
- Pope TR (2000) Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behav Ecol Sociobiol* 48:253–267
- Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney D, Seyfarth R, Wrangham RW, Struhsaker T (eds) *Primate societies*. University of Chicago Press, Chicago, pp 250–266
- Pusey AE, Packer C (1994) Non-offspring nursing in carnivores: minimizing the costs. *Behav Ecol* 5:362–374
- Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution* 43:258–275
- Randall JA, Rogovin K, Parker PG, Eimes JA (2005) Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship and ecological constraints. *Behav Ecol* 16:961–973
- Ross HM, Wilson B (1996) Violent interactions between bottlenose dolphins and harbour porpoises. *Proc R Soc Lond B* 263:283–286
- Rossiter SJ, Jones G, Ransome RD, Barratt EM (2002) Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Behav Ecol Sociobiol* 51:510–518
- Rusu AS, Krackow S (2004) Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice. *Behav Ecol Sociobiol* 56:298–305
- Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* 4:406–425
- Shane (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island. In: Leatherwood S, Reeves R (eds) *The bottlenose dolphin*. Academic, San Diego, pp 245–265
- Shinohara M, Domingoroura X, Takenaka O (1997) Microsatellites in the bottlenose dolphin *Tursiops truncatus*. *Mol Ecol* 6:695–696
- Silk JB (2002) Kin selection in primate groups. *Int J Primatol* 23:849–875
- Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123:38–69
- Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Adv Stud Behav* 22:1–63
- Sunnucks P, Hales DF (1996) Numerous transposed sequences of mitochondrial cytochrome oxidase I–II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). *Mol Biol Evol* 13:510–523
- Valsecchi E, Amos W (1996) Microsatellite markers for the study of cetacean populations. *Mol Ecol* 5:151–156
- van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87:120–144
- van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) *Comparative socioecology: The behavioral ecology of humans and other mammals*. Blackwell, Oxford, pp 195–218
- Wells RS (1991) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Pryor K, Norris KS (eds) *Dolphin societies, discoveries and puzzles*. University of California Press, Berkeley, pp 199–226
- Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In: Genoways HH (ed) *Current mammalogy*. Plenum, New York, pp 247–305
- Whitehead HP (1999a) Testing association patterns of social animals. *Anim Behav* 57:F26–F29
- Whitehead HP (1999b) Socprog 1.2 (for matlab 5.1): programs for analysing social structure. Available at <http://myweb.dal.ca/~hwhitehe/social.htm>
- Williams GC (1966) *Adaptation and natural selection*. Princeton University Press, Princeton, New Jersey
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–292
- Wrangham RW, Rubenstein DI (1986) Social evolution in birds and mammals. In: Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution in birds and mammals*. Princeton University Press, Princeton, New Jersey, pp 452–470
- Würsig B, Würsig M (1977) The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198:755–756