THE ROYAL SOCIETY

Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia

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Bottlenose dolphins are one of only a few mammalian taxa where the males are known to cooperate within their social group in order to maintain mating access to single females against other males. Male bonds in bottlenose dolphins have been hypothesized as evolving through kinship and associated inclusive fitness effects. In this study we tested whether individually identified male bottlenose dolphins preferentially associate and form alliances with kin in a small coastal resident population of southeastern Australia using a combination of behavioural data, genetic sexing, sequences of the mitochondrial DNA control region and nuclear microsatellite markers. Males generally associated significantly more often than expected with one to three other males, with whom they jointly herded females for mating. Associations and alliance membership were not associated with either maternal kinship or genetic relatedness. The majority of male pairs within alliances were randomly related, although high relatedness values were found between males of different alliances in the resident population. These findings indicate that mechanisms other than kin selection may be foremost in the development and maintenance of cooperation between male bottlenose dolphins.

Keywords: alliances; kinship; bottlenose dolphins; *Tursiops aduncus*; mitochondrial DNA control region; microsatellites

1. INTRODUCTION

Kinship is assumed to play a fundamental role in the evolution of cooperation. Inclusive fitness theory explains how individuals may indirectly enhance their own fitness through positive effects on the reproduction of genetic relatives of varying degrees (Hamilton 1964). Cooperation among unrelated individuals may be evolutionarily stable when one party benefits from the interaction while the other receives benefits later through reciprocity (i.e. reciprocal altruism) (Trivers 1971) or when both cooperating parties benefit from the interaction (i.e. by-product mutualism) (Brown 1983). Individuals behave cooperatively when, despite individual costs, they act in such a way as to make possible the achievement of an advantageous outcome for the members of a group of two or more individuals through collective action (Mesterton-Gibbons & Dugatkin 1997). Individuals that cooperate during competitive or aggressive encounters on an opportunistic basis are said to form coalitions, while those displaying enduring cooperative relationships are designated as members of alliances (De Waal & Harcourt 1992).

The males of most mammalian species provide little or no paternal care and, consequently, invest in maximizing their mating opportunities in order to increase their reproductive success (Trivers 1972). In social systems where several breeding females associate within a defensible home range multiple males may cooperate in order

to defend female groups against intruders (Clutton-Brock 1989). However, when the home range of female groups is too large to be defensible, single resident males commonly defend receptive females and compete intensively for them with both resident and intruder males (Clutton-Brock 1989). In a very few species males cooperate within their social group in order to gain and maintain access to single receptive females and prevent other resident males from mating, for example baboons (Packer 1977), bottlenose dolphins (Connor *et al*. 1992*a*) and chimpanzees (Watts 1998).

Coastal bottlenose dolphins (genus *Tursiops*) are long-lived (*ca*. 45 years) mammals that live in fission–fusion societies where individuals associate in groups that often change in both size and composition (e.g. Wells *et al*. 1987; Smolker *et al*. 1992). Ontogeny is prolonged, with juveniles occasionally associating with their mothers after independence and with strong, long-term associations between certain classes of individuals (Wells *et al*. 1987; Smolker *et al*. 1992). Unlike most mammals, both male and female coastal bottlenose dolphins apparently remain in their natal range until adulthood (Connor *et al*. 2000*a*). Among their various vocalizations, bottlenose dolphins produce signature whistles (Caldwell & Caldwell 1965), which are used for identifying individuals and possibly kin (Smolker *et al*. 1993; Sayigh *et al*. 1999).

Male bottlenose dolphins display a large repertoire of mating strategies, from single roving males (Wells 1991) to the most complex cooperative relationships described outside humans (Connor *et al*. 1992*a*,*b*, 1999). Male bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, form a system of multilevel alliances and

coalitions (Connor *et al.* 1992*a,b*, 1999, 2000*a*). Alliances are generally found in long-term, strongly associated pairs and triplets that cooperatively herd single females for mating (Connor *et al.* 1992*a,b*). In addition, male alliances associate at moderate levels with other pairs and triplets with whom they occasionally form coalitions in order to attack other alliances or protect each other from an attack while competing for females (Connor *et al.* 1992*a,b*). Strong and stable bonds have also been reported in pairs and triplets of male bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida (Wells *et al.* 1987). Pairs and triplets have been observed aggressively separating individual females from groups, presumably for mating, and also jointly defending the community boundary against neighbouring males (Wells 1991).

Social bonds between male bottlenose dolphins first appear when they are juveniles and strengthen with maturity (Wells 1991; Connor *et al.* 2000*a*). There is limited evidence that bonds may form between males born to related females (Duffield & Wells 1991), which suggests that male bonds may be based on kinship and benefit through inclusive fitness (Wells 1991). However, because genetic relationships remain largely unknown within bottlenose dolphin societies, the role of kinship in male bonds has never been explicitly tested.

In this study we used a combination of behavioural data, genetic sexing, sequences of the mitochondrial DNA (mtDNA) control region and nuclear microsatellite markers for testing whether individually identified male bottlenose dolphins (*T. aduncus*) preferentially associate and form alliances with kin in a small coastal resident population of southeastern Australia.

2. MATERIAL AND METHODS

(a) *Study area and population*

Port Stephens (32°42′ S, 152°06′ E) is a shallow, predominantly sandy bay of *ca.* 140 km^2 in New South Wales, southeastern Australia. Bottlenose dolphins are observed in Port Stephens throughout the year, with an estimated 160 recognizable individuals, of which 87 are regularly sighted within the port (Möller 2001). A molecular phylogenetic analysis recently indicated that this population belongs to the species *T. aduncus* (Möller & Beheregaray 2001).

(b) *Behavioural data and biopsy sampling*

The compositions of 158 temporary dolphin groups were determined by photographic identification of individuals (photo-identification) during 38 boat surveys conducted between December 1998 and April 2000. Dolphins were defined as part of the same group if they were within a 100 m radius (Irvine *et al.* 1981) with coordinated activities. Individuals in a group were usually found within a 10–20 m radius, although they were more widespread when feeding. Group size ranged from one to 30 individuals, with a mean of 6.75 ± 0.37 dolphins (Möller 2001). Dolphins were individually recognized by the pattern of the natural marks on their dorsal fins (Würsig & Jefferson 1990; Möller & Harcourt 1998).

Small skin samples were collected from 87 free-ranging dolphins using a PAXARMS.745 biopsy system (PAXARMS N.Z. Ltd, Timaru, New Zealand) during 26 additional boat surveys between March 1999 and April 2000. The biopsies were preserved in a salt-saturated solution of 20% dimethyl sulph-

oxide (Amos & Hoelzel 1991). We identified individuals during sampling by either photo-identification as they were biopsied or through visual recognition by one of the authors (L.M.M.).

Behavioural observations of female herding by males were collected *ad libitum* (Altmann 1974) during all surveys. Individuals were considered herding if we observed a 'captured female', a 'capture attempt' or an 'escape attempt' (Connor *et al.* 1992*b*). Males with a captured female usually travelled tightly positioned on either side of her and/or behind her. Capture attempts involved males chasing a female from the sides and behind her or rushing up and around her. An escape attempt was characterized by a captured female bolting away from the males.

(c) *Genetic analyses*

DNA was extracted from the biopsy samples following the salting-out protocol described in Sunnucks & Hales (1996). The sex of the sampled dolphins was determined by amplification of the genes *ZFX* and *SRY* through the polymerase chain reaction (PCR) using the protocol developed by Banks *et al.* (1995). Nine cetacean microsatellite loci were amplified by the PCR according to Beheregaray & Sunnucks (2000): these were Ev1 and Ev37 (Valsecchi & Amos 1996), Mk5, Mk6, Mk8 and Mk9 (Krützen *et al.* 2001), D8 (Shinohara *et al.* 1997) and Kw2 and Kw12 (Hoelzel *et al.* 1998). A fragment of *ca.* 460 bp of the mtDNA control region was amplified by the PCR according to Möller & Beheregaray (2001). Samples from males that were positively identified at the time of biopsying were sequenced with an ABI 377 DNA sequencer (Perkin-Elmer, Applied Biosystems, Foster City, CA, USA). Alignment of the resultant sequences was performed by eye, with distinct haplotypes within a 403 bp segment identified using the editor in the program PAUP v.4.0b4 (Swofford 2000).

(d) *Statistical analyses and definitions*

Dolphins that were individually identified by photographs on at least seven occasions, excluding recognized females and calves, were selected for calculating pairwise associations using the half-weight index (Cairns & Schwager 1987). Individuals were considered associated if found together in a group within a given survey day. These associations range from zero for two dolphins never seen together in the same group to unity for two individuals that were always sighted together. Individuals were classed as females if they were sampled and genetically sexed as such or from association with a dependent calf. The association coefficients were converted to distance measures by subtracting them from unity, and a neighbour-joining tree (Saitou & Nei 1987) was then constructed in order to display the relationships of the associations graphically. Thus, these distances range from zero for two individuals always sighted together to unity for two dolphins that were never seen together. Neighbour joining was used instead of a classical cluster analysis following Mitani *et al.* (2000), because the former is more informative as it provides both the topology and distance separating individuals. Overall and pairwise associations were tested for departures from randomness within the program SOCPROG 1.2 (Whitehead 1999*a*) using the permutation procedure developed by Manly (1995), which was adapted for association data by Bejder *et al.* (1998) and then refined by Whitehead (1999*b*) in order to account for demographic effects. The tests were two-tailed (with $\alpha = 0.05$) and based on 10 000 permutations. Significant pairs (i.e. non-random associates) were defined by emerging every time across 10 tests.

Alliance membership was identified by three additive criteria: (i) by an association criterion, (ii) by significantly non-random associations, and (iii) by behavioural observations of individuals jointly herding females. The association criterion considered individuals to be members of a grouping if (i) they were reciprocal closest associates or (ii) when individuals did not have a reciprocal closest associate, they were the second closest associate of a pair that were each other's closest associate and their coefficient of association was within 20% of that of both individuals (Connor *et al.* 1992*b*). If individuals of a grouping defined by the association criterion were associated significantly more often than expected by chance and were also observed at least once jointly herding a female, they were then considered alliance partners.

The microsatellite loci were tested for Hardy–Weinberg equilibrium and for pairwise linkage disequilibrium using the program GENEPOP v.3.1 (Raymond & Rousset 1995). The multilocus genotypes of all sampled dolphins were used for estimating symmetrical pairwise genetic relatedness within the program KINSHIP 1.2 (Goodnight *et al.* 1998). The relatedness coefficients for a sample satisfactorily representing a population in Hardy–Weinberg equilibrium should average 0.5 for full-siblings, 0.25 for half-siblings and zero for randomly related individuals (Queller & Goodnight 1989).

A matrix of pairwise genetic relatedness was then constructed in order to include only individuals that (i) were identified at the time of sampling, (ii) were genetically sexed as males, and (iii) had previously qualified for association analysis. A matrix of mtDNA haplotype identity was also constructed for these individuals, including values of unity for pairs with identical haplotypes and values of zero for pairs with different haplotypes. Each of these matrices were correlated with an association matrix containing the same individuals using a Mantel matrix randomization procedure (Manly 1997*a*). Manly's (1997*a*) Mantel matrix randomization determines the significance of the correlation by making a direct comparison of the test statistic with the randomization distribution.

We also compared the mean genetic relatedness and frequency of haplotype sharing within and between alliances considering only males from alliances from which we had sampled at least two individuals. The mean difference between the pairwise genetic relatednesses within and between alliances was evaluated using the two-sample randomization test (Manly 1997*a*). The frequencies of the pairwise mtDNA haplotype identity and non-identity within and between alliances were compared using a randomized χ^2-analysis (Manly 1997*a*). These tests were conducted within the program RT 2.1 (Manly 1997*b*) with 10 000 randomizations.

3. RESULTS

Associations were calculated for 38 individuals and are displayed in a neighbour-joining tree (figure 1). The mean association was not significantly different from the random mean (real mean = 0.12, random mean = 0.12 and $p = 0.459$). However, the standard deviation was significantly higher than the random standard deviation (real s.d. = 0.165, random s.d. = 0.113 and $p < 0.001$). The dolphins had zero to three non-random associates, with 20 pairs associating significantly more often than expected by chance (figure 1).

Thirty-one individuals qualified under the association criterion as members of 13 groupings, including nine

pairs, three triplets and one quadruplet (figure 1). Of these, 20 individuals from eight groupings qualified as significant non-random associates (figure 1). All of those individuals were observed herding females exclusively with members of their groupings and, therefore, qualified as alliance partners (figure 1). The herding observations included 10 capture attempts, five captured females and two capture attempts followed by a captured female, with between one and six herding events per alliance.

Samples were obtained from 20 of the 38 individuals selected for calculating associations. All these individuals were genetically sexed as males. The microsatellite loci amplified between four and nine alleles per locus (mean = 6.6 ± 0.6) and the expected heterozygosities ranged from 0.32 to 0.84 (mean = 0.55 ± 0.05). The exact tests for linkage disequilibrium revealed no significant locus comparison at the 5% level. None of the loci showed significant departures from Hardy–Weinberg equilibrium and probability tests did not detect an excess or deficiency of heterozygotes at any locus.

There was no significant correlation between the pairwise genetic relatedness and associations between males ($F = 1.94$, $p = 0.17$ and $n = 190$ pairs). There was also no significant correlation between the mtDNA haplotype identity and associations when considering the same individuals ($F = 0.14$, $p = 0.70$ and $n = 190$ pairs).

Eighteen of the 20 males sampled were considered as members of alliances (figure 1). We obtained samples from at least two individuals from seven of the eight alliances, including all individuals of two pairs, one triplet and one quadruplet. The mean genetic relatedness of male pairs within alliances was not significantly different from the mean genetic relatedness of male pairs between alliances (mean genetic relatedness within alliances = 0.01, s.d. = 0.26 and $n = 14$ and mean genetic relatedness between alliances = 0.09, s.d. = 0.24 and $n = 139$) ($p = 0.334$). Pairs within alliances were in general randomly related, even though several males in different alliances proved to be highly related ($R > 0.4$ and $n = 13$) (table 1).

The frequencies of male pairs with identical and different mtDNA haplotypes within alliances were not significantly different from the respective frequencies for male pairs between alliances (random $\chi^2 = 18.93$ and $p = 0.81$) (figure 2). Nine out of 14 pairs within alliances had different haplotypes (figure 2).

4. DISCUSSION

Male bottlenose dolphins in Port Stephens generally associated more often than expected with one to three other males and herded females with these males. These associations are similar to those of male pairs and triplets seen in other bottlenose dolphin populations and the herding behaviour is analogous to that reported for male alliances in Shark Bay, Western Australia (reviewed in Connor *et al.* 2000*a*).

Males were not likely to associate or form alliances preferentially with either their maternal kin or genetically related individuals. This was not due to a lack of opportunity; all males of alliances had male relatives present in the resident population, but they were typically in different alliances. Under most circumstances, males
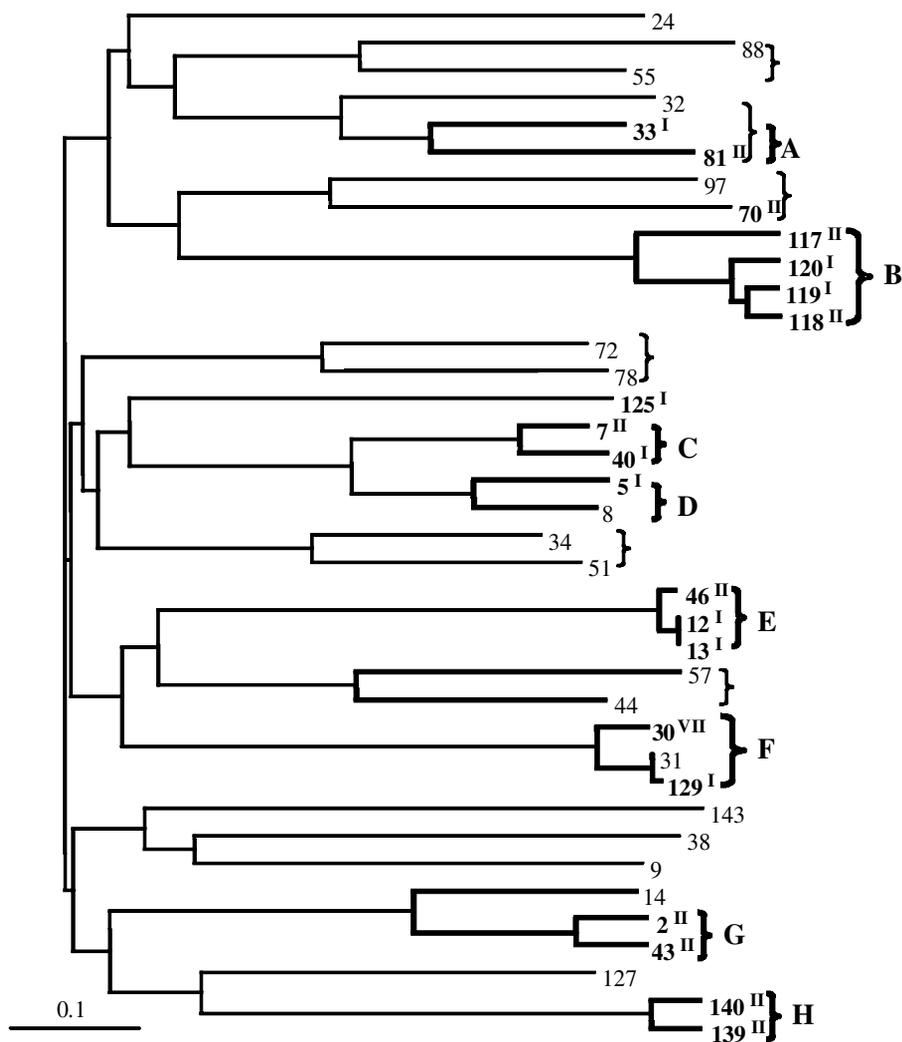
Figure 1. Neighbour-joining tree of the associations between bottlenose dolphins (excluding recognized females and calves). Individuals are denoted by numbers. The numbers are in bold for biopsy-sampled dolphins. Mitochondrial DNA haplotypes are denoted by superscript Roman numbers. All sampled individuals were genetically sexed as males. Branches in bold represent associations that are significantly higher than expected by chance. Groupings based on the association criterion are shown with a brace. Alliances are shown with a brace in bold and are labelled with upper case letters.

might be predicted to gain more from forming an alliance with a close relative than with unrelated animals. The key question is therefore why male dolphins at Port Stephens do not preferentially form alliances with kin.

It might be that bottlenose dolphins are unable to identify kin. However, kin recognition is likely to occur. Juvenile bottlenose dolphins usually remain loosely associated with their mothers and associate more closely with them when their siblings are born (Wells 1991). Bottlenose dolphins are also known to produce signature whistles, which are used for communicating identity, for contacting individuals and for group cohesion (Smolker *et al.* 1993; Janik & Slater 1998; Sayigh *et al.* 1999; Janik 2000). Signature whistles develop over the first few months *postpartum*, with male calf whistles sharing similar features with their mothers' whistles (Sayigh *et al.* 1995). Accordingly, there is both a mechanism for identifying individuals (including kin) and also opportunities for dolphins to become familiar with at least siblings of adjacent cohorts. Yet alliances usually do not revolve around kin.

Male dolphins may form alliances with males other than their maternal brothers for a number of reasons. The minimum age difference between consecutive maternal brothers will be between 2 and 3 years if the interbirth interval in the Port Stephens bottlenose dolphin population is similar to that found elsewhere (Wells *et al.* 1987; Mann *et al.* 2000). The mean age difference between maternal brothers is therefore likely to be even greater. This probably results in substantial differences in physical maturity between brothers during the period when adolescent males form bonds with other males. The length, girth and body mass of male *T. truncatus* asymptote at *ca.* 20–25 years of age (Read *et al.* 1993), 10–13 years after the onset of sexual maturity (Wells *et al.* 1987). Body mass influences dominance relationships between males in captivity, with an older, heavier male usually winning agonistic interactions until the younger male attains a similar body mass (Samuels & Gifford 1997). This suggests that physically mature males have superior competitive ability compared with younger, not yet fully grown males. Male–male aggression in both *T. truncatus* and *T. aduncus* is

Table 1. Pairwise relatedness (Queller & Goodnight 1989) between sampled male bottlenose dolphins (*T. aduncus*).
(*R*-values within alliances are marked with an asterisk.)

alliance	individual	46	12	118	117	120	70	7	30	40	125	140	5	33	119	2	129	13	81	43	139
E	46	—																			
E	12	−0.11*	—																		
B	118	0.21	0.13	—																	
B	117	0.12	−0.41	0.49*	—																
B	120	−0.05	0.17	0.11*	−0.25*	—															
	70	0.04	0.22	0.32	0.18	0.13	—														
C	7	0.48	0.36	0.58	0.07	0.14	0.19	—													
F	30	−0.15	0.35	−0.11	−0.30	0.25	0.18	−0.05	—												
C	40	−0.25	−0.15	0.20	0.36	0.43	0.03	−0.07*	0.24	—											
	125	−0.12	−0.13	0.06	0.18	0.13	0.18	−0.28	0.30	0.46	—										
H	140	−0.11	0.04	0.27	0.50	−0.12	0.35	−0.03	−0.18	0.17	0.22	—									
D	5	0.21	0.23	0.36	0.13	0.20	0.13	0.46	0.02	0.20	0.24	0.28	—								
A	33	−0.06	0.26	0.26	0.08	0.15	0.34	0.22	0.21	0.16	0.08	0.11	0.27	—							
B	119	−0.40	−0.40	−0.02*	0.21*	−0.12*	−0.05	−0.27	0.07	0.47	0.30	0.10	0.03	0.08	—						
G	2	−0.07	0.35	0.11	−0.01	0.07	0.43	0.00	0.13	0.09	−0.01	0.35	0.08	0.67	−0.15	—					
F	129	−0.28	−0.10	0.36	0.23	0.18	0.10	−0.02	−0.03*	0.42	0.36	−0.01	0.06	0.12	0.11	−0.13	—				
E	13	−0.28*	−0.25*	0.11	0.08	−0.09	−0.43	−0.36	−0.34	−0.23	−0.09	0.04	−0.12	−0.10	−0.33	−0.19	0.05	—			
A	81	−0.52	−0.07	0.01	−0.20	0.05	−0.12	0.00	−0.01	0.17	−0.01	−0.37	−0.04	−0.26*	0.33	−0.37	0.39	−0.05	—		
G	43	0.51	−0.06	0.48	0.41	0.37	0.17	0.29	−0.08	0.12	0.17	0.21	0.23	0.33	−0.07	0.27*	0.22	0.23	−0.25	—	
H	139	0.09	0.04	0.39	0.64	0.11	0.40	0.29	−0.08	0.34	0.16	0.47*	0.45	0.32	−0.07	0.26	0.21	−0.23	−0.26	0.39	—
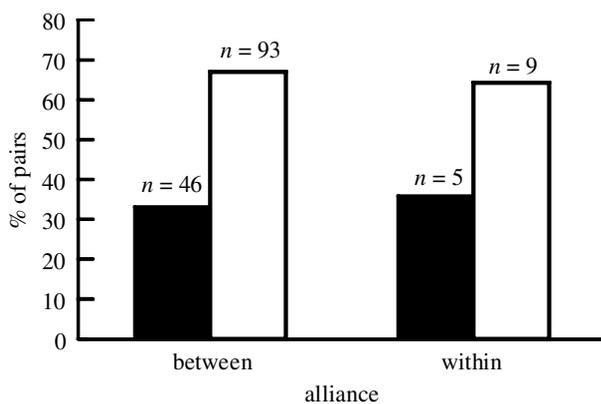
Figure 2. Proportion of bottlenose dolphin male pairs with identical and different mtDNA haplotypes within and between alliances (the numbers of pairs are indicated by the *n*-values). Shaded, identical; unshaded, different.

important in competition for females (Connor *et al.* 1992*a*,*b*; Tolley *et al.* 1995). Therefore, a younger, smaller brother may not be a preferred alliance partner. Fighting abilities have been proposed as affecting partner choice in coalitions of male savannah baboons (Nöe 1992) and in chimpanzees the lack of male bonds between maternal brothers may also be explained by a lack of equivalent social maturity (Goldberg & Wrangham 1997).

Wells (1991) suggested that the male bonds in Sarasota *T. truncatus* were potentially based on kinship because some bonds were formed between males born to the same female bands. Female bands are composed of adult females and their more recent offspring and may be largely composed of related females (Duffield & Wells 1991). We do not know whether males in Port Stephens form bonds within their mother's bands. We do know that, in this area, female bands may include both related and unrelated females (Möller 2001). Thus, male calves are likely to have a long period when they associate with and possibly become familiar with both related and unrelated young dolphins

and may later form alliances with them. Alternatively, males may form bonds independently of their mothers' bands. For instance, male lions either disperse together from their natal pride, forming coalitions composed of siblings and related similar-aged cohort individuals or join together subsequent to dispersal, forming coalitions with unrelated animals (Packer *et al.* 1991).

The large numbers of randomly related male pairs within Port Stephens' alliances suggest that other mechanisms may be foremost in the development and maintenance of cooperation between male bottlenose dolphins *T. aduncus*. Cooperation between these males may have evolved through reciprocal altruism or mutualism. Reciprocal altruism has been invoked as accounting for coalition formation between unrelated male baboons (Packer 1977), although the evidence is equivocal (Bercovitch 1988). If alliance formation in male bottlenose dolphins were based on reciprocal altruism, one would expect males alternately to forego mating with individual females in successive herding events and for paternity to be evenly distributed within alliances. Nonetheless, limited behavioural evidence from elsewhere indicates otherwise. Dolphin alliance partners in Shark Bay have been reported synchronously mounting a herded female from either side (Connor *et al.* 1992*b*). If males increase their chances of mating success by forming an alliance and all males within the alliance gain potential access to the female, males would then receive by-product mutualistic benefits. This has been reported for pairs and triplets of top-ranking male chimpanzees, which cooperate in order to mate guard receptive females from lower-ranking males but tolerate each other's mating activities (Watts 1998). Social bonds between male chimpanzees were previously thought to reflect kinship ties (Goodall 1986), but genetic analyses have demonstrated that frequent male associates and coalition partners are not maternally related (Goldberg & Wrangham 1997; Mitani *et al.* 2000).

Herding of females by males in bottlenose dolphins has been suggested to be as much a strategy for preventing

females from mating with rival males as preventing rival males from having access to the female (Connor *et al*. 1995). Males of *T. truncatus* are larger and more robust than females (Read *et al*. 1993; Tolley *et al*. 1995), which may facilitate monopolization of females by single males. Male pair formation in this species might be restricted to middle- or low-ranking males that can only monopolize females in alliances (Connor *et al*. 2000*a*). In contrast, male pairs and triplets and cooperative herding of females predominate in *T. aduncus* in both the Port Stephens and Shark Bay populations. There is less pronounced sexual dimorphism in this species (Ross & Cockcroft 1990), which might make it more difficult for males to monopolize females on their own.

Male bottlenose dolphins have large testes relative to their body mass, which suggests multimale mating and sperm competition (Connor *et al*. 2000*b*). Multimale mating by female bottlenose dolphins may be a strategy for confusing paternity and reducing the risk of infanticide by males (Connor *et al*. 1995). However, another explanation is that females may receive genetic benefits from multiple mating (Jennions & Petrie 2000). One such benefit might be the accumulation of genetically diverse sperm in order to avoid incompatibility between genomes (e.g. Zeh *et al*. 1998). In this scenario, female bottlenose dolphins, which are spontaneous ovulators and seasonally polyoestrous (Schroeder 1990), could favour sperm competition of alliances formed by unrelated males. More comprehensive behavioural observations on the role of both males and females in herding and mating, together with paternity analyses, may elucidate which mechanism explains the cooperative relationships of these males as well as characterizing the mating system of this species.

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