

# Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)

Joanna Wiszniewski<sup>1\*</sup>, Shannon Corrigan<sup>1</sup>, Luciano B. Beheregaray<sup>2</sup> and Luciana M. Möller<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Macquarie University, NSW 2109, Australia; and <sup>2</sup>School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia

## Summary

1. Determining the extent of variation in male mating strategies and reproductive success is necessary to understand the fitness benefits of social and cooperative behaviour.
2. This study assesses the reproductive success of male Indo-Pacific bottlenose dolphins in a small embayment population where different behavioural strategies of males have previously been identified. Parentage for 44 sampled calves was examined using 23 microsatellite loci and one mitochondrial DNA marker. Our candidate parent pool of 70 males and 64 females contained individuals sampled from both the embayment and adjacent coastal populations.
3. A moderate level of polygyny was detected in our sample. We assigned paternity of 23 calves to 12 males at the strict 95% confidence level and an additional nine calves to two males at the 80% confidence level. The majority (92%) of successful males were identified as residents to the embayment, and 46% of offspring were located within the same social group or community as their father.
4. Our results suggest that the size of alliances was the best predictor of reproductive success for males in this population, while the strength of association among allied males, alliance stability and male ranging patterns had little influence. In line with predictions for male alliances formed between unrelated individuals, we found that reproductive skew within alliances was not large.
5. Together, our genetic and behavioural analyses demonstrate that alliance formation between male dolphins is a successful strategy to enhance reproductive output.

**Key-words:** alternative reproductive strategies, cetaceans, coalitions, cooperation, paternity analysis, relatedness, sociality

## Introduction

Characterizing the mating system of a population and the degree of reproductive skew is fundamental to the understanding of social evolution, maintenance of cooperative relationships among individuals and population-level processes such as inbreeding, gene flow rates and dispersal patterns (Keller & Reeve 1994; Clutton-Brock 1998; Frankham, Ballou & Briscoe 2003). A great diversity of male reproductive strategies has evolved, including the formation of close male bonds in coalitions or alliances, tactical associations with females prior to breeding, infanticide, mate-or resource guarding and strategic ranging patterns (Olson & Blumstein 2009; Smuts 1985; Boyko & Marshall 2009; Watts 1998; Lancaster, Goldsworthy & Sunnucks 2007; Schubert *et al.* 2009; Haenel, Smith & John-Alder 2003). The set of male reproductive strategies in a population is generally shaped by the spatial and temporal distribution of receptive females, which in turn depends on ecological conditions (Whitehead

& Connor 2005; Ostner, Nunn & Schülke 2008; Emlen & Oring 1977). Within-population variation in male mating behaviour and reproductive success, on the other hand, can usually be attributed to differences in individual characteristics, such as social rank, age and mating experience (Harcourt *et al.* 2007; Spong *et al.* 2008; Rodriguez-Llanes, Verbeke & Finlayson 2009; Rasmussen *et al.* 2007). As a result, considerable variation in reproductive strategies and mating systems has been found within and between closely related species (e.g. swift foxes, *Vulpes velox*, Kamler *et al.* 2004; harbour seals, *Phoca vitulina richardsi*, Hayes *et al.* 2006).

Coalitions or alliances of males cooperate to obtain access to receptive females and engage in aggressive interactions with other males to defend territories or females (Packer *et al.* 1991; Caro 1994; Connor 1996). Strong male associations have been described in a diverse range of species, including lions, *Panthera leo* (Packer *et al.* 1991), bottlenose dolphins, genus *Tursiops* (reviewed in Gowans, Würsig & Karczmarski 2008), lance-tailed manakins, *Chiroxiphia lanceolata* (DuVal 2007), chimpanzees, *Pan troglodytes* (Watts 1998) and horses, *Equus caballus* (Feh 1999). When

\*Correspondence author. E-mail: jo.wiszniewski@gmail.com

alliances are formed between closely related individuals, reproductive success within alliances may be skewed because unsuccessful individuals would still attain inclusive fitness benefits through kin selection if their partners are successful (Keller & Reeve 1994; Packer *et al.* 1991; Krützen *et al.* 2004). For other populations with unrelated male alliances, reproductive success is generally skewed towards the dominant male. Subordinate males can be successful, however, if their cooperation and assistance in defending territories or females increases their mating opportunities (e.g. Feh 1999; Kays, Gittleman & Wayne 2000).

While the marine environment provides significant challenges for parentage analysis, bottlenose dolphins are an ideal system to investigate cetacean mating systems given that several long-term behavioural studies have been conducted on these species (*Tursiops truncatus* and *Tursiops aduncus*) in a diverse range of ecological and social environments (reviewed in Connor *et al.* 2000; Gowans, Würsig & Karczmarski 2008). Considerable inter- and intra-specific variation in social behaviour and male reproductive strategies has also been described. Male dolphin alliances are generally found in populations where the availability of receptive females is limited and where little sexual dimorphism exists because of difficulties in monopolizing females in a three-dimensional environment (Whitehead & Connor 2005; Möller *et al.* 2001; Parsons *et al.* 2003). Male dolphins provide no parental care and appear to mate promiscuously (Krützen *et al.* 2004). For these reasons, males that form alliances and guard single females at various times through the breeding season may have greater reproductive success than single roving males (e.g. Krützen *et al.* 2004). Owen, Wells & Hofmann (2002) hypothesized that males in alliances may also have a higher reproductive success as a result of their larger home ranges and spatial overlap with more females compared with non-allied males. Understanding the relationship between paternity success and alliance formation and behaviour in these populations will increase our understanding of the evolution and maintenance of alternative reproductive strategies.

This study examines the mating system and male reproductive strategies in a population of Indo-Pacific bottlenose dolphins (*T. aduncus*) inhabiting the Port Stephens embayment in southeastern Australia. The population is small and genetically distinct from bottlenose dolphins on the adjacent Hunter coast (Möller, Allen & Harcourt 2002; Möller *et al.* 2007; Wiszniewski *et al.* 2010). The low to moderate level of gene flow that occurs between the Port Stephens and Hunter coast populations is mainly mediated by males and is directionally biased towards the Hunter coast population (Möller & Beheregaray 2004; Wiszniewski *et al.* 2010). Most males in this population have been found in randomly related alliance partnerships and observed in consortships with females (Möller *et al.* 2001). However, over an 8 year study period, considerable intra-specific variation in alliance size, stability and ranging patterns has been found (Wiszniewski, Brown & Möller 2012). In particular, three different types of association patterns were identified: (i) males that form strong and highly stable social bonds with one to three other males; (ii)

males that form weaker and/or more labile partnerships; and (iii) males that are solitary or allied for only a short period of time (Wiszniewski, Brown & Möller 2012). In this study, we aimed to determine the frequency of calves sired by males that are resident to the embayment and within the two socially and spatially defined communities in this population. Secondly, we aimed to assess the level of polygyny in the population and assess whether paternities were evenly distributed within alliances. Finally, we investigated the success of various male mating strategies, including alliance size, alliance stability and ranging patterns. These results provided new and important insights into the evolution and maintenance of cooperative mating strategies in male dolphins.

## Materials and methods

### STUDY SITE AND POPULATION

The Port Stephens embayment is located 200 km north of Sydney on the New South Wales coast in eastern Australia and covers c. 166 km<sup>2</sup> of surface area. While the Port Stephens' dolphins are genetically distinct from the Hunter coastal population, there is evidence of some gene flow occurring between the two populations (Möller & Beheregaray 2004; Möller *et al.* 2007; Wiszniewski *et al.* 2010). As a result, our parentage analysis included genetic samples from the two closest communities in the Hunter coast population (see Möller *et al.* 2007 for more details).

The Port Stephens population is spatially and socially segregated into two mixed-sex communities (eastern and western, Wiszniewski, Allen & Möller 2009). Low but significant levels of genetic differentiation have also been found between the two communities (Wiszniewski *et al.* 2010). The smaller western community consists of around 30 adults of both sexes, while the larger eastern community consists of around 90 adults of both sexes. This eastern community is further subdivided into three smaller social groups that have largely overlapping home ranges. Within these social groups, associations are often temporarily stable among individuals of the same sex, as well as between males and females (Wiszniewski, Lusseau & Möller 2010).

### SAMPLE COLLECTION AND GENETIC PROFILING

Biopsy samples of bottlenose dolphins in the Port Stephens embayment were collected as part of a long-term and intensive sampling effort that took place between 1999 and 2008. We conducted 102 boat sampling trips and amassed a sample of 89 adults and 46 calves and juveniles, which represents c. 77% of the resident Port Stephens adult population (Appendix S1) and 62% of calves observed during the study period. Calves were sampled only after 2 years of age. The age of calves was determined by direct observation in the year that the calf was born, or if the calf's mother was unknown, the age of the calf was estimated when sampled based on body size. Seventy-six per cent of individuals were identified during sampling surveys using standard photo-identification techniques. Accordingly, these dolphins have both genetic- and photo-identification numbers assigned. In addition, we sampled 47 individuals from communities on the adjacent Hunter coast (an open marine environment). All coastal individuals were considered adults at the time of sampling (based on body size) and were therefore considered potential parents. Samples were obtained using a Paxarms (Timaru, New Zealand) biopsy rifle (Krützen *et al.* 2002) or a biopsy pole (Bilgmann *et al.*

2007) and were preserved in 20% dimethyl sulphoxide saturated with sodium chloride (Amos & Hoelzel 1991) or 100% ethanol.

DNA was extracted from biopsy samples using a salting-out protocol (Sunnucks & Hales 1996), and the sex of each individual was determined by amplifying fragments of the SRY and ZFX genes using the polymerase chain reaction (PCR; Gilson *et al.* 1998). The nuclear DNA microsatellite loci amplified in this study included KW2, KW9 and KW12 (Hoelzel *et al.* 2002), MK5, MK6, MK8 and MK9 (Krützen *et al.* 2001), EV1, EV14 and EV37 (Valsecchi & Amos 1996), D8 (Shinohara, Domingo-Roura & Takenaka 1997), TG20 (Caldwell, Gaines & Hughes 2002), Tur4\_80, Tur4\_87, Tur4\_91, Tur4\_105, Tur4\_141, Tur4\_142, Tur4\_E12, Tur4\_F10, Tur\_111, Tur\_128 (Nater, Kopps & Krützen 2009), Ttr11 and Ttr63 (Rosel, Forgetta & Dewar 2005). Detailed genetic methodology is provided as Supporting Information. Because the genotypes at Ttr63 deviated significantly from Hardy-Weinberg equilibrium (HWE) and null alleles were detected, this locus was removed from the data set. Thus, the parentage and relatedness analyses described below are based on the 23 loci that did not deviate from HWE and had no null alleles detected with MICRO-CHECKER v. 2.2.3 (Van Oosterhout *et al.* 2004). A 460-bp fragment of the mitochondrial DNA control region was also amplified with primers Dlp-1.5 and Dlp-5 (Baker *et al.* 1993) following the protocol described in Möller & Beheregaray (2001).

#### PARENTAGE ANALYSIS

Parentage analysis was conducted for 44 calves sampled in Port Stephens (including 20 known mother–calf pairs) using the maximum-likelihood approach in (i) CERVUS (Kalinowski, Taper & Marshall 2007) and (ii) COLONY v. 2.0 (Wang & Santure 2009). All adult males sampled in the Port Stephens embayment and the two adjacent Hunter coastal communities were included. Because males as young as 6 years old have sired offspring in another bottlenose dolphin population (Krützen *et al.* 2004), males that were sampled as calves or juveniles in 1999 and 2000 ( $N = 5$ ) were included as candidate fathers when they were at least 6 years of age.

Simulations in CERVUS were first conducted to estimate the critical values of  $\Delta$  [the difference between log likelihood (LOD) scores of the two most likely candidate parents] associated with a strict (95%) and relaxed (80%) levels of statistical confidence in assignment (Kalinowski, Taper & Marshall 2007). Parameters used in the simulations are presented in Appendix S1.

Two approaches were used to conduct parentage analysis. First, we assigned maternity for all known calves (i.e. mother was identified from behavioural observations) without prior information on maternity ( $N = 20$ ). This was conducted to assess the reliability of the CERVUS assignments and confirm field observations. Second, we used the ‘parent-pair’ approach to assign both parents simultaneously to each of the 44 calves sampled. For this analysis, maternal information was included for the 20 known mother–calf pairs. A parent-pair was accepted at two levels of statistical confidence: (i) a strict 95% confidence level and (ii) a relaxed 80% confidence level. For both levels, a parent-pair was accepted only if two or fewer loci were mismatching for the trio (i.e. a genotypic inconsistency between the offspring and one or both parents based on Mendelian patterns of inheritance), and no other parent was assigned parentage in COLONY. Any mismatches between calves and putative parents were scored again and if an inconsistency between genotypes could be attributed to a scoring error, the genotype was adjusted accordingly. If the program COLONY could not assign a parent at the 95% confidence level, the assigned parent discrepancy from CERVUS result was accepted. For parent-pairs that did not meet either criterion, a single

parent was chosen in the same manner as parent-pairs (95% and 80% confidence level, one or no mismatching loci between the parent and offspring, and confirmation of assignment with COLONY). If two parents were assigned separately to a calf with high statistical confidence, but did not meet the parent-pair assignment criteria, both parents were rejected. We accepted parents with two or fewer mismatching loci to reduce the chance of rejecting true parents because of null alleles and/or genotypic errors. For the four cases where the known mother of a calf was not genetically sampled, the mother’s identity was certain from behavioural observations, and no other candidate mother was assigned by either CERVUS or COLONY, the mother’s photo-identification information was used in the analysis of male reproductive strategies. In addition to assigning parentage, COLONY was also used to examine potential full- and half-sibships among calves.

#### DISTRIBUTION OF PATERNITIES

To assess the level of male polygyny in this population in relation to other populations/species, we calculated the standardized variance in paternity success (variance divided by the mean) for all males assigned to at least one calf (Coltman, Bowen & Wright 1998). To assess whether reproductive success was skewed within alliances, we calculated the binomial skew index ( $B$ ), in which the observed group variance is corrected by the expected variance if each member has the same probability of gaining reproductive success (Nonacs 2000). This index was adjusted for males being in alliances for differing lengths of time. We also chose this index given the reliable results produced under a wide range of conditions, including variance in group size and group productivity (Nonacs 2000, 2003). We calculated the  $B$  index, which ranges from  $-1$  to  $1$ , and the 95% confidence intervals (CI) in SKEW CALCULATOR v. 1.2 (Nonacs 2003). Only alliances in which at least two males had been sampled and at least two paternities had been assigned over the study period were included in the analysis. Significance was assessed using 10 000 simulations.

#### HOME RANGE SIZE AND OVERLAP ANALYSIS

To assess the influence of spatial patterns on male reproductive success, we used school membership data collected from 1999 to 2008 to estimate core area use and home range size for each individual. Analyses were restricted to schools sighted at least 12 h apart to minimize spatial autocorrelation of data points (Swihart & Slade 1985), and only adults sighted more than 10 times over the study period were included in the analysis (following Ingram & Rogan 2002; Fury & Harrison 2008). We used the fixed kernel density estimator (KDE, Worton 1989) to estimate each individual’s 50% and 95% utilization distributions using 50% and 95% volume contours. The 50% contour represents core area use, while the 95% contour represents home range. All KDE contours were calculated using a  $100 \times 100$  m grid, and bandwidth was calculated with an adjusted smoothing factor ( $h_{adj}$ ) that was obtained by multiplying the  $h_{ref}$  smoothing factor with the average ratio of  $h_{srid\ cv}/h_{ref}$  (see Wauters *et al.* 2007 for further details). The KDE<sub>adj</sub> method was used because it has been shown to perform as well as the minimum convex polygon, and better than KDE with either the least squares cross validation method or reference smoothing factor ( $h_{ref}$ ) (Wauters *et al.* 2007). All landmasses were excluded from utilization distributions before core area and home range sizes were calculated. These areas, and the percentage of core area and home range overlap between males and females, were calculated using the package ‘ADEHABITAT’ (Calenge 2006) developed

for the R v. 2.2 software (R Development Core Team 2005). To assess the influence of spatial overlap on male reproductive success, we compared the mean overlap between mated and unmated pairs using a two-sample randomization test in RT v. 2.1 (Manly 1997). Significance at the 5% level was assessed using 10 000 randomizations. For unmated pairs, only adults that were present at the same time were included in the analysis (Hazlitt, Goldizen & Eldridge 2006).

#### FACTORS AFFECTING MALE REPRODUCTIVE SUCCESS

To identify factors affecting male reproductive success, all parents assigned at the 80% confidence level were included in the analyses. While using these results increases the chance of type I error, in all but one case, parentage assignments were confirmed at the 95% confidence level in COLONY (see Results). Because CERVUS did not assign another candidate father and no mismatches were observed among this particular parent-calf trio, it is likely that the parent-offspring relationship is true.

To determine factors affecting male reproductive success, we used backward-stepwise multiple regression analysis using the number of calves assigned to each male as the response variable. The following explanatory variables were used: alliance size, average strength of association with top associates, alliance stability index ranging from one (no stability) to four (highest stability) based on an 8-year photo-identification data set (Wiszniewski, Brown & Möller 2012) and 95% home range size. When the year of birth for a calf was not known, we used the average alliance size that the male was sighted in over the 8 years. To avoid multicollinearity among explanatory terms (Graham 2003), the 50% core area size was excluded from the analysis (correlation with 95% home range size:  $r = 0.969$ ,  $N = 29$ ,  $P < 0.001$ ). Further, because some calves were born prior to the start of the photo-identification study (1998/1999), we assumed that alliance size and strength of association among allies was similar in these earlier years. However, given the potential error, we re-analysed the data set using calves that were born only within the study period. In this restricted model, we included the number of years a male was sighted as an additional variable because a number of males were not observed over the entire study period. For both analyses, all explanatory variables were included into the model to examine the combined effect of the variables. Starting with the weakest predictor (identified by the highest  $P$ -value), variables were then removed in a stepwise fashion, and the regression was re-calculated at each step. We conducted an analysis of variance (ANOVA) to assess the significance of the most parsimonious model chosen using Akaike Information Criterion. All analyses were performed in the R package.

## Results

#### GENETIC VARIATION

After the removal of duplicate samples ( $N = 20$ ), reliable genotypes were available for 128 adults (64 males and 64 females) and 44 calves. These included 68 individually recognized adults from the 89 samples collected in Port Stephens and 40 adults from the adjacent Hunter coast population (Newcastle and Broughton Island communities). Tests for linkage disequilibrium demonstrated independent assortment of the 23 loci. Levels of genetic variation and frequencies of null alleles as estimated by CERVUS are provided in Table S1 for the remaining 23 loci.

#### PARENTAGE ASSIGNMENT

The overall probability of parental exclusion over the 23 loci was 0.996 for the first parent, and the probability of full-sib identity was  $1.9 \times 10^{-7}$ . Maternity analysis in CERVUS without prior information of parentage resulted in 16 accurate assignments for the 20 known mother-calf pairs in the data set. One calf's mother was not assigned with confidence because of few loci compared ( $N = 13$ ); one calf did not have a candidate mother assigned because of the presence of two closely related females in the data set that had compatible genotypes with the calf; the remaining two calves had the same mother identified in the field, but another female was assigned maternity to both calves because of a mismatch at one locus (Ttr11). We accepted the mothers identified in the field for two reasons. First, in the latter case, the field-identified mother seems to have had a null allele at the mismatching locus (Ttr11) given that this locus had a null allele frequency of 0.0316, and the mother was a homozygote for an allele not present in either of the two calves. Second, mothers identified in the field were only accepted if the mother-calf pair was observed in close spatial proximity multiple times by two independent observers. It is therefore unlikely that an error was made twice for the same mother.

Using the strict 95% confidence criteria, parentage was resolved for 16 of the 44 calves sampled (36%) (Table 1; Table S3). When both parents could not be identified, maternity and paternity was resolved separately for five and seven calves, respectively. At the relaxed 80% confidence level, an additional seven calves had both parents assigned (52% in total), and two had only fathers assigned (Table 1). The reduced statistical support for these assignments was generally because of the presence of a second candidate parent that had a moderate likelihood of parentage. However, we accepted the assignments since in each case, the selected parent had fewer (or no) mis-matching loci and obtained a higher delta score (i.e. difference in likelihood between two candidate parents). Results from CERVUS were strongly supported by analyses in COLONY, with the exception of seven trios that were assigned with 95% confidence and two trios assigned with 80% confidence in CERVUS, in which one parent was not identified by COLONY. Given that the program did not

**Table 1.** Success in parentage assignment for 44 calves and variation in reproductive success among male dolphins at the 80% and 95% confidence levels

	80% confidence	95% confidence
Parentage assignment for 44 calves		
Calves assigned both parents	52%	36%
Calves assigned mother	11%	11%
Calves assigned father	20%	16%
Male reproductive skew		
Calves assigned paternity	32	23
Successful males in population	20	19
No. of paternities/successful male	Mean = 2.30; range: 1–7	Mean = 1.77; range: 1–5
Standardized variance	1.04	0.67

assign another candidate parent to the calf, we accepted the parentage results from CERVUS (Table S3).

#### REPRODUCTIVE SKEW

All males that were assigned paternity were considered adults at the beginning of the study. Using the strict 95% confidence criteria, 13 males were assigned paternity to 23 calves, representing 19% of males sampled (Table 1; Table S2). With the relaxed criteria, one more male was assigned paternity, and paternity was resolved for an additional nine calves. Only one of the 23 sampled males from the Hunter coast population was assigned paternity (to one calf at 95% confidence and an additional calf at 80% confidence). At the relaxed confidence level, 75% of eastern males that were assigned paternities ( $N$  males = 12) were to calves of eastern females, with just over half of the successful matings occurring within one of the three smaller social groups (i.e. among close, long-term associates). For the successful western males ( $N$  males = 13), 54% of successful matings were with western females. Because only one social group is present in the west, 48% of parentage assignments were between members of the same social group. In total, 64% of paternities were sired by males within their communities (Table S2).

To test whether paternities were evenly distributed among alliance partners, we examined reproductive skew within five alliances using paternities assigned at the 80% confidence level, and within four alliances using paternities assigned at the strict 95% level. For each alliance at the two significance levels, the binomial index of reproductive skew was not significantly different from random expectations (Table 2). Therefore, reproductive skew within alliances was not large when reproductive success was averaged over the 10-year study period.

#### MATE FIDELITY

At the 80% confidence level, we had six instances where females were assigned maternity to at least two calves and the calves' fathers were also identified. The two calves of the one western female were sired by the same western male, while the other five eastern females had their calves sired by different males. The males that sired calves with one female were also members of different alliances and different communi-

ties. Together, there were 17 cases of multiple calves having at least one common parent (females:  $N = 8$ ; males:  $N = 9$ ), and only one of these calf pairs was identified as full-sibs based on the assignment of the same parent-pair (Table S3). These results suggest that bottlenose dolphins do not display mate fidelity, and females do not exhibit 'alliance fidelity'. However, the full-sibship analysis in COLONY highlighted the presence of another two sets of potential full-sibs, in which one parent was not sampled (Table S2). Two of the calves were born to the same western female, while the other two calves assigned to the same western male were sampled within the western community's core area. No other western female was assigned maternity to multiple calves, and thus, we cannot exclude the possibility of female mate fidelity in the western community.

#### FACTORS AFFECTING MALE REPRODUCTIVE SUCCESS

Analyses of male reproductive strategies were conducted using parentage assignments accepted at the 80% confidence level. We found no significant difference in the mean core area overlap between mated and unmated pairs (mated:  $N = 16$ ; mean  $\pm$  SE =  $0.39 \pm 0.06$ , unmated:  $N = 657$ ; mean =  $0.41 \pm 0.01$ ;  $P = 0.378$ ) or the mean home range overlap (mated mean =  $0.55 \pm 0.07$ , unmated mean =  $0.59 \pm 0.01$ ;  $P = 0.294$ ).

The most parsimonious model to explain variance in male reproductive success included alliance size only (coefficient estimate =  $0.97 \pm 0.29$ ,  $t = 3.28$ ,  $P = 0.003$ ; overall model significance: adjusted  $R^2 = 0.26$ ,  $F_{1,27} = 10.56$ ,  $P = 0.003$ ; Fig. 1). A restricted model that examined variance among males that sired calves only during the photo-identification study period (1999–2008) and controlled for differences in sighting rates among males was also explained by alliance size only (coefficient estimate =  $0.65 \pm 0.20$ ,  $t = 3.19$ ,  $P = 0.004$ ; overall model significance: adjusted  $R^2 = 0.25$ ,  $F_{1,27} = 10.16$ ,  $P = 0.004$ ).

#### Discussion

This study revealed several important aspects of the mating system of Indo-Pacific bottlenose dolphins that contributes to our general understanding about male reproductive strategies and the fitness benefits of social and cooperative

**Table 2.** Tests for reproductive skew within alliances using the binomial skew index,  $B$ . Per capita reproductive success (PC) is given for each alliance at the 80% and 95% confidence levels. Significance was determined using one-sided  $P$ -values based on 10 000 simulations and 95% confidence intervals (CI)

Photo-ID of allies	80% confidence level				95% confidence level			
	PC	$B$	95% CI	$P$	PC	$B$	95% CI	$P$
12, 13, 46	1.00	0	-0.22, 0.44	0.770	1.00	0	-0.22, 0.44	0.770
30, 129	2.50	-0.08	-0.10, 0.32	1.000	1.50	-0.11	-0.12, 0.32	1.000
117, 118, 119, 120	3.25	0.09	-0.06, 0.33	0.053	2.25	0.07	-0.08, 0.37	0.134
139, 140	1.00	-0.20	-0.21, 0.43	1.000	1.00	-0.204	-0.21, 0.42	1.000
7, 15, 40	0.67	0.20	-0.29, 0.20	0.346				

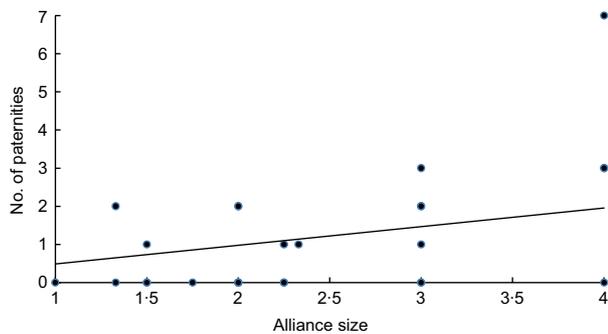


Fig. 1. Effect of alliance size on the reproductive success of male Indo-Pacific bottlenose dolphins in Port Stephens, southeastern Australia.

behaviour. First, resident male dolphins from the Port Stephens embayment fathered the majority of calves in this population, which is consistent with findings of restricted gene flow between the Port Stephens and Hunter coast populations (Möller *et al.* 2007; Wiszniewski *et al.* 2010). Second, we revealed a higher level of polygyny in these animals relative to many other aquatically mating mammals, including baleen whales and seals (Cerchio *et al.* 2005; Frasier *et al.* 2007; Hayes *et al.* 2006; Harcourt *et al.* 2007). Substantial variation in reproductive success among male alliances and individuals was also observed. Alliance size was the best predictor of paternity success in this population, while alliance stability and strength of association within alliances as well as their ranging patterns had little effect in comparison. Finally, we found that reproductive skew was not large within alliances, which is the outcome predicted for alliances composed of unrelated males with similar social ranks.

Substantially lower levels of polygyny have been observed in aquatically mating marine mammals compared to terrestrial species (reviewed in Frasier *et al.* 2007). These findings are most likely due to the three-dimensional marine environment that prevents males from fully controlling females or the resources that are required by them (Fabiani *et al.* 2004; Hayes *et al.* 2006; Harcourt *et al.* 2007; Cerchio *et al.* 2005). In Port Stephens' dolphins, variance in male reproductive success was considerably higher than in other studied aquatically mating populations. Moderate levels of polygyny could be expected based on the diffuse breeding season in bottlenose dolphins (Schroeder 1990) and patterns of mate-guarding within the breeding season, where male alliances may control single receptive females for up to a few weeks at a time (Connor, Smolker & Richards 1992b; Möller *et al.* 2001; J. Wiszniewski, unpublished data). Indeed, similar levels of polygyny were also found in the large Shark Bay bottlenose dolphin population in Western Australia (Krützen *et al.* 2004), where mate-guarding by 2–3 male allies occurs frequently (Connor *et al.* 2000). Thus, the greater number of paternities assigned to males in larger alliances in Port Stephens suggest that cooperative alliance formation is a suc-

cessful strategy to monopolise female dolphins provided a certain number of males are present.

Connor *et al.* (2000) hypothesized that lower- or mid-ranking males may be forming alliances rather than males with greater competitive ability who are able to control and mate with females without assistance. This pattern of alliance formation has been documented in baboons (Noë 1994), horses (Feh 1999) and humans (Benenson *et al.* 2009), although it has not been tested in bottlenose dolphins given the lack of knowledge about dominance relationships outside captivity (Samuels & Gifford 1997). In Port Stephens, paternities within most alliances were relatively evenly distributed, which is the expected result if cooperating males are unrelated and have similar competitive abilities and/or social rankings (e.g. Packer *et al.* 1991). If alliances were composed of lower- or mid-ranking males and higher-ranked males chose a more solitary strategy because of their ability to out-compete allied males or control females alone (e.g. Bissonnette, de Vries & van Schaik 2009), we would expect a relatively even number of paternities assigned to males in stable and unstable/unallied alliance categories. Interestingly, we found that males in larger alliances had a higher success rate compared with more solitary males or those with more fluid association patterns. Therefore, these results suggest that alliances in Port Stephens may be formed by higher-ranking males who choose their partners based on similar competitive abilities. Examples of high-ranking male alliances in animal societies are scarce, although in at least one community of chimpanzees, coalitions of two to three top-ranking males that cooperatively mate-guard females were found to mate more frequently with receptive females and experienced lower aggression rates compared with solitary males (Watts 1998).

Previous analysis of male reproductive strategies in Port Stephens found variation in the stability and strength of male alliance partnerships (Wiszniewski, Brown & Möller 2012). Because age (based on scarring rates and year of appearance in the population) does not appear to be influencing either of these two correlated factors, it was hypothesized that differences among males may represent alternative mating strategies (Wiszniewski, Brown & Möller 2012). However, here, we show that neither strength nor stability of alliances significantly influenced paternity success. Given the apparent fitness benefits of forming large alliances, the question remains why all males do not associate in three- or four-male alliances. The first potential explanation is based on the understanding that alliance formation is a highly complex and long-term process that involves a high level of mutual tolerance, cooperation and coordination (Connor, Smolker & Bejder 2006; Olson & Blumstein 2009). In this case, males in unstable alliances may be in a transitional stage of finding the optimal alliance partner. The second possibility is based on a modelling study by Whitehead & Connor (2005), which showed that the maximum size of an alliance is constrained when significant costs are involved in forming close associations. These costs may relate to decreased foraging efficiency

or increased probability of disease transmission (Krause & Ruxton 2002).

Males in alliances may also achieve greater reproductive success through female mate choice or post-copulatory mechanisms. For instance, females may prefer mating with allied males because they use the synchronous male displays as an indicator of male quality (Connor, Smolker & Richards 1992a; Trainer & McDonald 1995; Connor *et al.* 2000). Alternatively, given that male alliances in Port Stephens are generally composed of non-kin, Möller *et al.* (2001) hypothesized that females may prefer to mate with unrelated male alliances to obtain genetically diverse sperm that will reduce the probability of genome incompatibility (e.g. Zeh, Newcomer & Zeh 1998; Jennions & Petrie 2000). Regardless of alliance composition, females may also prefer to mate with larger alliances to facilitate paternity confusion and thus decrease the risk of infanticide (Connor 1996).

To our knowledge, only one other study to date has found a similar distribution in paternity success among unrelated alliance partners. In this study, Packer *et al.* (1991) found that alliances consisting of two unrelated male lions shared similar reproductive success, while a skewed distribution was found in all larger alliances that contained close kin.

In conclusion, our genetic and behavioural analysis of male mating strategies and reproductive success strongly suggests that alliance formation in dolphins is a successful strategy to enhance reproductive output. Given that home range size, alliance stability and strength did not affect reproductive success, intra-specific variation in association patterns most likely represents differential tactics adopted by males to maximize reproductive success in a social and ecological environment that is both complex and highly dynamic. In addition, our finding of shared reproductive success among most alliance members provides important empirical data that contributes to the evolutionary framework explaining the mechanisms of cooperative behaviour among non-kin. Most importantly, this study shows that male Indo-Pacific bottlenose dolphins in larger alliances have greater reproductive success than males in smaller alliances or unallied males.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Genotype data for each microsatellite locus.

**Table S2.** Parentage results for calves that had both parents assigned based on maximum-likelihood analysis.

**Table S3.** Parentage assignments using CERVUS and COLONY and relationship between parent-calf pairs estimated using ML-relate.

**Appendix S1.** Detailed methodology.

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