



Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins

C.H. Frère^{a,*}, M. Krützen^{a,b,1}, J. Mann^{a,c,2}, J.J. Watson-Capps^{d,3}, Y.J. Tsai^{c,2}, E.M. Patterson^{c,2}, R. Connor^{a,e,4}, L. Bejder^{f,5}, W.B. Sherwin^a

^aSchool of Biological Earth and Ecological Sciences, University of New South Wales

^bAnthropological Institute and Museum, University of Zürich

^cDepartments of Biology and Psychology, Georgetown University

^dBiology Department, Metropolitan State College of Denver

^eDepartment of Biology, UMASS-Dartmouth

^fCentre for Fish and Fisheries Research, Division of Science and Engineering, Murdoch University

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Few studies of kinship in mammalian societies have been able to consider the complex interactions between home range overlap, association patterns and kinship, which have created a critical gap in our understanding of social evolution. We investigated the association patterns of female bottlenose dolphins, *Tursiops aduncus*, in the eastern gulf of Shark Bay, Western Australia and found that they depended upon the complex interplay of at least three factors: home range overlap, matrilineal kinship and biparental kinship. While home range overlap was positively correlated with female association patterns, preferred associations were found between females showing as little as 27% home range overlap, and some pairs showed avoidance despite 100% home range overlap. Furthermore, on average, both casual and preferred associations took place between females that were more closely biparentally related than expected by chance and this pattern varied depending upon whether or not pairs of females shared the same matriline.

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The influence of inclusive fitness on affiliative behaviour has been extensively studied in species ranging from eusocial insects (Reeve et al. 1990; Seger 1991; Bourke 1997) to long-lived mammals such as primates (Chapais 2001; Clutton-Brock 2002; Perry et al. 2008; Langergraber et al. 2009), lions, *Panthera leo* (Packer et al. 1991), elephants (Fernando & Lande 2000; Archie et al. 2006) and cetaceans (Whitehead & Baird 2000; Krützen et al. 2003;

Parsons et al. 2003; Gero et al. 2009). Owing to practical difficulties in data collection, however, few studies of kinship in mammalian societies have been able to consider the complex interactions between home range overlap, association patterns and kinship (Maher 2009). This represents a critical gap in our understanding of social evolution.

Biparental relatedness (genetic relatedness measured from nuclear DNA) is clearly an important factor in affiliative behaviour and is central to the theory of kin selection (Hamilton 1964a, b). There is also good reason to study maternal relatedness (genetic relatedness measured from mitochondrial DNA), especially when focusing on female association. For instance, Archie et al. (2006) found that groups of African savannah elephants, *Loxodonta africana*, that shared mtDNA haplotypes were more likely to fuse than groups that did not. Female bottlenose dolphins, *Tursiops aduncus*, in Port Stephens, Australia, were found to associate more with other females that shared the same mtDNA haplotype (Möller et al. 2006). In the eastern gulf of Shark Bay, mtDNA analysis revealed that a particular foraging technique shared by several females and their offspring occurred almost exclusively within the same

* Correspondence: C. H. Frère, School of Biological Earth and Ecological Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

E-mail address: c.frere@unsw.edu.au (C.H. Frère).

¹ M. Krützen is at the Anthropological Institute and Museum, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

² J. Mann, Y. J. Tsai and E. M. Patterson are at the Departments of Biology and Psychology, Georgetown University, Washington DC 20057-1229, U.S.A.

³ J. J. Watson-Capps is at the Biology Department, Metropolitan State College of Denver, Denver, CO 80217, U.S.A.

⁴ R. Connor is at the Department of Biology, UMASS-Dartmouth, Dartmouth, MA 02747, U.S.A.

⁵ L. Bejder is at the Centre for Fish and Fisheries Research, Division of Science and Engineering, Murdoch University, South Street, Murdoch, WA 6150, Australia.

matriline (Mann & Sargeant 2003; Krützen et al. 2005; Sargeant et al. 2005; Mann et al. 2008). Thus, the interpretation of the results can depend upon whether biparental or matrilineal kinship is investigated.

When data are available, nongenetic factors, such as home range overlap, should be included when investigating the role that matrilineal and biparental kinship play in mammalian societies. Space use and ranging patterns of individuals have commonly been used to investigate social structure. This is because the amount of spatial overlap between individuals provides indirect information about the probability of social interactions (Clutton-Brock 1989). For instance, association patterns among tent-making bats, *Artibeus watsoni*, correlate with roosting and foraging home range overlap (Chaverri et al. 2007). The degree of spatial overlap between female and male marmots, *Marmota monax*, correlates with kinship (Maher 2009). Home range overlap, however, does not always explicitly account for association patterns. Association patterns among female grey kangaroos, *Macropus giganteus*, were not exclusively predicted by their patterns of spatial overlap (Carter et al. 2009). Similarly, no correlation was found between female elephant core areas and their association patterns (De Villiers & Kok 1997).

Except for the study by Möller et al. (2006) on the association patterns and kinship of female bottlenose dolphins in Port Stephens, interactions between relatedness and association patterns have generally focused on male dolphins (e.g. Möller et al. 2001; Krützen et al. 2003, 2004a). Female bottlenose dolphins reportedly form loose social bonds with other females of various ages and degrees of kinship (Wells et al. 1987; Smolker et al. 1992; Möller et al. 2006). In the eastern gulf of Shark Bay, the affiliation patterns of female dolphins can be characterized as 'resident-egalitarian' (in the sense of Sterck et al. 1997) based on the scarcity of contest competition among females (Scott et al. 2005). While female dolphin affiliation patterns do not show the same group structure as those of males, they have a more labile open fission–fusion grouping pattern (Smolker et al. 1992). In contrast, males form long-term alliances of up to 14 animals (Connor et al. 1992a, b, 2000, 2001) that sexually coerce females and compete to prevent other alliances from gaining access to females (Scott et al. 2005; Connor et al. 2006).

In this study, we used a combination of behavioural and genetic data to explore the influence of both home range overlap and kinship on the affiliative behaviour of female bottlenose dolphins in the eastern gulf of Shark Bay, Western Australia. In particular, we tested whether female–female association patterns are influenced by matrilineal and biparental kinship.

METHODS

Association Patterns Analysis

Group composition and behavioural data were collected from 9851 group encounter surveys (1994–2004). These data were used to assess the general female social structure and individual-specific associations of 46 females that overlapped for the whole study period (postweaning; age 4 years and older). Data were collected as part of a long-term field study in the eastern gulf of Shark Bay, Western Australia (25°47'S, 113°43'E) initiated in the mid-1980s (Connor & Smolker 1985; Smolker et al. 1992). Surveys were completed for each group that was encountered, and group composition was assessed using standard photo-identification methods (Würsig & Jefferson 1990). Unidentified individuals as well as ambiguous identifications (ca. 10%) were removed from the analyses. Variation in effort between years could also bias the data, and such biases were addressed in several ways. First, we generated

the association estimates between pairs of females using the half-weight index (HWI), which is the most appropriate association index when members of each possible pair are more likely to be scored when separate than when together (Cairns & Schwager 1987). The half-weight index is defined as $HWI = x / \{x + y_{ab} + 0.5(y_a + y_b)\}$, where x = number of encounters for which both dolphin 'a' and 'b' were in the same group; y_a = number of encounters including dolphin 'a' but not dolphin 'b' in the same group; y_b = number of encounters including dolphin 'b' but not dolphin 'a' in the same group; and y_{ab} = number of encounters including dolphin 'a' and 'b' in different clusters of groups at the same time (Cairns & Schwager 1987). The HWI index ranges from 0 (never seen together) to 1 (never seen apart). HWI estimates were calculated in SOCPROG 2.2 (Whitehead 1999). Second, only females sighted more than 30 times were included in the analysis. A high sighting number increases the chance of having captured all possible associates within a female's social network. In our data set, we found that the percentage of HWI equal to zero reached a plateau above 30 sightings. This indicates that zero HWI estimates between pairs of females that have been sighted at least 30 times are more likely to be real 'avoidances' rather than the result of not having sampled those two females together.

The standard deviation and the coefficient of variation of HWI, based on the observed distribution of HWI, were used as indication of the level of structure within the female social system (Whitehead 1999, 2009). Overall pairwise associations were tested for departures from randomness using the permutation procedure developed by Manly (1995) and available in SOCPROG 2.2. This permutation procedure (referred to as the MBFB method) was adapted for association data by Bejder et al. (1998) and redefined by Whitehead (1999) to account for demographic effects. We ran 20 000 permutations with 1000 flips per permutation for each analysis, and significant variations from random were tested using a two-tailed test ($\alpha = 0.05$). The sampling period was set to 1 day to avoid replication of association within the same day.

To investigate further the interaction between associations and biparental kinship, we subdivided HWI association estimates of each females into three categories: avoidance (A), casual (C) and preference (P). Pairwise association estimates at or below the 2.5% percentile were considered as avoidance (A). Pairwise association estimates at or above the 97.5% percentile were considered as preference (P). Casual associations (C) were defined as having a HWI pairwise estimate between the lower (2.5%) and the higher (97.5%) percentiles. We used a conservative cutoff value to increase the probability of capturing real preferred associations (most often seen with) and avoidances (never seen with). While we investigated other methodologies to categorize association indices, we found that they were more appropriate for male alliances or did not account for individual variation in the degree of sociality (e.g. Möller et al. 2006). For instance, some females are more solitary than others; thus a solitary female's preferred associate might be a nonsolitary female's casual associate.

Relatedness

Since 1994, skin biopsy samples have been collected using a system especially designed for small cetaceans to minimize short- and long-term impacts (Krützen et al. 2002). Biopsy tissues were stored in a saturated solution of 5 M NaCl/20% (v/v) dimethyl sulphoxide solution (Amos & Hoesel 1991). Genomic DNA was extracted from skin biopsies using standard methods (Davis et al. 1986). The sex of the animals was genetically assessed following the protocol of Gibson et al. (1998).

As described in detail in Krützen et al. (2002), dolphins were only darted when they were travelling at slow to moderate speed

parallel to the vessel at a distance of at least 5 m. Conditions for biopsying are best during travelling, because dolphins dive and move in predictable patterns. Juveniles under 3 years of age (estimated by date of birth if known, or by their overall body length being smaller than 50% of an adult) were not darted. Wounds produced by the darting system heal quickly and without complications (Krützen et al. 2002). The research was carried out under a permit issued by Conservation and Land Management. Ethics approval was given from The University of New South Wales.

To estimate pairwise biparental relatedness between females, we used 12 hypervariable polymorphic dinucleotide microsatellite loci: MK3, MK5, MK6, MK8, MK9 (Krützen et al. 2001); EV1, EV14, EV37 (Valsecchi & Amos 1996); KWM12 (Hoezel et al. 1998); 199/200 (Amos et al. 1993); and D14, D22 (Shinohara et al. 1997). The 12 loci used in this study showed no linkage disequilibrium, null alleles or departure from Hardy–Weinberg equilibrium (Krützen et al. 2003, 2004b). Furthermore, there was no need to partition the data set to accommodate population structure within the eastern gulf of Shark Bay owing to high nuclear gene flow between areas minimizing subdivision (Krützen et al. 2004b). Biparental relatedness (R) was calculated from genetic data for each pair or group of individuals within the population. On the basis of its high level of precision, accuracy and ease of computation (Krützen et al. 2003), we chose the Queller & Goodnight's (1989) relatedness index to assess biparental pairwise relatedness estimates between females.

To study matrilineal relatedness, a 355 base pair fragment of the maternally inherited mitochondrial DNA control region was sequenced following Krützen et al. (2003). In total, four unique haplotypes (Krützen et al. 2004b) were identified among the 46 females, each representing a different maternal lineage (frequency of haplotype among the 46 females: H = 10%, D = 7%, E = 40% and A = 43%). Based on these data, we defined whether associating pairs of females belonged to the same matriline or not. Pairs of females with the same mtDNA haplotype and thus belonging to the same matriline were coded as Mt1, and pairs of females with a different mtDNA haplotype were coded as Mt0.

Home Range Analysis

There is still much dispute concerning how best to measure home ranges (Seaman et al. 1999; Calenge 2006; Horne & Garton 2006; Row & Blouin-Demers 2006). Here, we chose the commonly used minimum convex polygons (MCP) rather than the probability density function home range estimate for two reasons. First, the MCP home range estimate generates a conservative area by connecting the outermost points recorded for an animal, describing the maximum known extent of area it uses. In comparison, fixed kernels and other probability function home range estimates are based on probability density, and thus describe the activity space most frequently used within the study region based on the number of detections in a location. In this study, we wanted to investigate whether female dolphins showed preferred association based on kinship rather than home range overlap. Thus we needed a home range estimate, such as MCP, to investigate all possible interactions regardless of spatial behaviour. Second, neither MCP nor fixed kernels avoid the problem of including areas never used by the animal (Horne & Garton 2006).

Home ranges (km^2) were determined by using the last sighting of each female per day. These points were restricted to well-surveyed areas, as determined by GPS logs of boat tracks (a proxy for search effort). Total home range area and overlap areas were calculated using 100% minimum convex polygons (Universal Transverse Mercator projection 1983, zone 49S; ESRI, Redlands, CA, U.S.A., ArcGIS version 9.3, Hawth's Tools extension). We then

calculated the percentage of home range overlap between pairs of females (HRO). Because pairs of females probably had different home range sizes (MCP), the percentage of home range overlap of female 'X' to female 'Z' might be different from the percentage of home range overlap of female 'Z' to female 'X'. For example, if female X's home range is 50 km^2 , and female Z's home range is 10 km^2 , and their overlap is 5 km^2 , then $\text{HRO-XZ} = 10\%$, but $\text{HRO-ZX} = 50\%$. Last, we conducted a second set of analyses in which home range overlap was measured using the grid cell (500 m) method (White & Garrott 1990). Core areas were measured by selecting grid squares that included 75% of group location points (Watts 1998; Robbins & McNeilage 2003). All analyses presented in this study were repeated. In every case, the second analyses gave the same patterns of significance and nonsignificance as the full data set (data not shown).

Statistical Analyses

Correlation of matrices (HWI with HRO, Mt and R)

Partial Mantel tests were used to investigate interactions between female–female association patterns (HWI) with percentage of home range overlap (HRO), matrilineal (Mt) and biparental relatedness (R). A partial Mantel test is an extension of the two-way Mantel test, which allows for the correlation of two variables while controlling for a third (Smouse et al. 1986; Manly 2001). Ideally, we would use a test that would allow us to control for more than one variable at a time, but such tests are not suitable for data with pairwise estimates such as HWI, Mt and R . Thus, we first investigated the correlation between HWI and HRO while separately controlling for Mt and R ($r_{(\text{HWI-HRO})\text{Mt}}$ and $r_{(\text{HWI-HRO})\text{R}}$). Second, we investigated the correlation between HWI and Mt while separately controlling for HRO and R ($r_{(\text{HWI-Mt})\text{HRO}}$ and $r_{(\text{HWI-Mt})\text{R}}$). Third, we investigated the correlation between HWI and R while separately controlling for HRO and Mt ($r_{(\text{HWI-R})\text{HRO}}$ and $r_{(\text{HWI-R})\text{Mt}}$). The level of significance for our tests was set at 0.0167 (Bonferroni correction; i.e. $0.05/3$, where 3 represents the number of tests performed for a given data set for a given hypothesis). For all six partial Mantel tests, we ran a total of 1000 randomizations.

Between-groups comparisons

To investigate further the relationship between associations (HWI) and biparental relatedness (R), we examined how the degree of biparental relatedness between pairs of females might differ depending on the type of individual-specific association. To do so, we subdivided the data set into nine groups (Table 1), each accounting for differences in the strength of association and the degree of matrilineal relatedness (Mt1 and Mt0). We used the Monte Carlo randomization procedure to determine whether members of the same group, according to Table 1, were significantly more closely biparentally related to each other than random pairs

Table 1

Grouping structure showing subdivisions used in the correlation between patterns of associations (HWI) and biparental relatedness

HWI	Subdivision		
	All female pairs	Pairs with shared MtDNA	Pairs with unshared MtDNA
Avoidance (A)	All-A	Mt0-A	Mt1-A
Casual (C)	All-C	Mt0-C	Mt1-C
Preference (P)	All-P	Mt0-P	Mt1-P

For each category the mean biparental relatedness estimates were calculated and significant departures from random expectations were assessed using random Monte Carlo analyses ($\times 1000$). See Methods for details on how association types were measured.

of females drawn from across the population ($N = 1035$). This procedure randomly shuffles observed pairwise relatedness estimates into newly assigned groups, while keeping each group size constant (e.g. Mt1-C = 607 and Mt1-A = 800). We then measured the within-group mean biparental relatedness estimate of these new randomly assigned groups. This procedure was repeated 1000 times to generate distributions of expected association estimates if group composition was random with respect to associations. To assess significance, the observed within-group mean biparental relatedness of nine groups (Table 1) was compared to their relevant expected distributions of 1000 randomized biparental relatedness means. The Monte Carlo randomization procedures used in this study were carried out in PopTools version 3.0.3 (G. M. Hood, <http://www.cse.csiro.au/poptools>).

RESULTS

Association Patterns and Home Range Overlap

Relative to random expectations, the association between females was low and variable. The observed mean association (HWI) between females was slightly but significantly lower than expected if association patterns were random (MBFB test ($\times 20\,000$): observed HWI = 0.0186, random HWI = 0.023, $P = 0.001$). The observed standard deviation and coefficient of variation were significantly higher than the randomized standard deviation and coefficient of variation (MBFB test: 20 000 iterations; observed SD = 0.056, random SD = 0.0376, $P = 0.001$; observed CV = 2.44, random CV = 1.986, $P = 0.001$).

Female–female association patterns (HWI) and percentage of home range overlap between pairs of females (HRO) showed a significant positive correlation when we controlled for the effect of either matrilineal (Mt) or biparental relatedness (R; partial Mantel test ($\times 1000$): $r_{(\text{HRO-HWI})_{\text{Mt}}} = 0.291$, $P = 0.0001$; $r_{(\text{HRO-HWI})_{\text{R}}} = 0.276$, $P = 0.0001$). Moreover, preferred associations were found between females showing as little as 27% home range overlap, while some pairs showed avoidance despite 100% home range overlap (Fig. 1). This indicates that female association patterns were not solely dictated by the extent of their home range overlap.

Association Patterns and Maternal Relatedness

Female–female association patterns (HWI) and matrilineal relatedness (Mt) showed a significant positive correlation when we controlled for the effect of either percentage of home range overlap

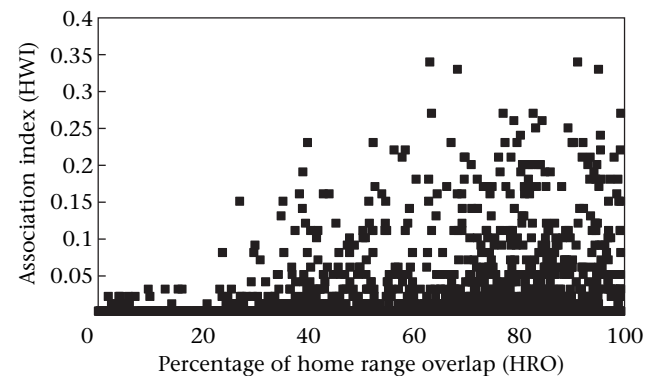


Figure 1. Relationship between percentage of home range overlap (%) and association index (HWI) between female bottlenose dolphins.

(HRO) or biparental relatedness (R; partial Mantel test ($\times 1000$): $r_{(\text{HWI-Mt})_{\text{HRO}}} = 0.156$, $P = 0.0001$; $r_{(\text{HWI-Mt})_{\text{R}}} = 0.202$, $P = 0.0001$).

Association Patterns and Biparental Relatedness

Overall, female–female association patterns (HWI) and biparental relatedness (R) showed a weak but significant positive correlation when we controlled for the effect of percentage of home range overlap (HRO; partial Mantel test ($\times 1000$): $r_{(\text{HWI-R})_{\text{HRO}}} = 0.058$, $P = 0.014$). In contrast, we found that when we controlled for the effect of matrilineal relatedness (Mt), the positive correlation between female–female association patterns (HWI) and biparental relatedness (R) was no longer significant after correcting for multiple testing (Bonferroni correction; $r_{(\text{HWI-R})_{\text{Mt}}} = 0.047$, $P = 0.032$). This suggests that matrilineal relatedness influenced the relationship between female–female association patterns and biparental relatedness. In addition, we did not find a nonlinear relationship between association and biparental relatedness. When we subdivided the data set into nine female–female association types (Table 1), based upon differences in the strength of association (A, C and P) and the degree of matrilineal relatedness (Mt1 and Mt0), randomization tests ($\times 1000$) showed that, on average, pairs of females that showed either casual (C) or preferred association types (P) had significantly higher biparental relatedness than would be seen in female pairs under random association patterns (Table 2). When we further subdivided each of the female–female association types according to matrilineal relatedness (Mt1 and Mt0), we found that Mt1 pairs of females that showed preferred association types (P) had, on average, significantly higher biparental relatedness than would be seen in female pairs under random association patterns (Table 2). Mt1 pairs of females showing either avoidance or casual association were not linked to biparental relatedness (Table 2). For pairs of females that did not share the same matriline (Mt0) we found several patterns. First, similar to Mt1 pairs, avoidance was not linked to biparental relatedness. Second, and unlike Mt1 pairs, preference between Mt0 female pairs was not linked to biparental relatedness. Third, casual encounters showed higher biparental relatedness estimates than would be seen in female pairs under random association patterns (Table 2).

DISCUSSION

Female Association Patterns

Nonrandom associations are common in many mammals that exhibit fission–fusion grouping patterns (e.g. zebra, *Equus grevyi*, and onager, *Equus hemionus*; Sundaresan et al. 2007; spotted hyaenas, *Crocuta crocuta*; Smith et al. 2007), but few studies have investigated the effect of spatial overlap on association patterns (De Villiers & Kok 1997; Carter et al. 2009). In this study, we demonstrated that female–female bottlenose dolphin association patterns in the eastern gulf of Shark Bay depend on at least three factors: home range overlap, matrilineal kinship and biparental kinship. Given that associating females must overlap in home range to some degree, it is not surprising that the percentage of home range overlap and female association were found to correlate. However, we found preferred associations between females showing as little as 27% home range overlap, while some pairs showed avoidance despite 100% home range overlap. The incorporation of home range overlap in future studies of kinship in mammalian societies would enable us to determine whether the relationship between home range overlap and association patterns suggested in our study is a characteristic of other fission–fusion grouping patterns, or unique to bottlenose dolphins.

Table 2Mean biparental relatedness values ($R \pm SD$) for all possible female pairwise combinations (PC), according to Mt and HWI as per Table 1

	All	Mt0	Mt1
Avoidance (A)	0.00017±0.17 (1444; 0.86)	0.0078±0.17 (1036; 0.145)	0.0003±0.16 (326; 0.16)
Casual (C)	0.0152±0.17 (1114; 0.0001)	0.025±0.16 (607; 0.0001)	0.0146±0.18 (442; 0.059)
Preference (P)	0.053±0.22 (99; 0.0001)	0.016±0.19 (44; 0.169)	0.08±0.25 (53; 0.0001)

In parentheses are the number of pairs followed by the P values generated from Monte Carlo randomization procedures ($\times 1000$) described in the *Methods*. Bold P values indicate significantly higher degrees of biparental relatedness than random expectations.

Relatedness

The influence of kinship on association patterns and the frequency of social interactions among females has been documented in a wide range of mammalian species (e.g. bottlenose dolphins: Möller et al. 2006; lions: Packer et al. 1991; primates: Dunbar 1980; elephants: Vodya & Sukumar 2005; Archie et al. 2006; spotted hyaenas: Holekamp et al. 1997; bushbuck, *Tragelaphus scriptus*: Wronski & Apio 2006). In this study, while female association patterns and home range overlap were positively correlated, we also found clear support for a positive relationship between female association and both matrilineal (Mt) and biparental relatedness (R). More importantly, we showed that the extent of biparental kinship changed depending on the type of female–female association (avoidance, casual and preferred) and on whether or not pairs of females shared the same matriline. In particular, one group of female pairs showed high association and high maternal and biparental relatedness, while another group, which although maternally unrelated, had casual associations with biparental relatives. The first pattern seems to be true for other mammals in which fully mature daughters stay with their mothers forming matrilineal or natal breeding groups (e.g. longtailed macaques, *Macaca fascicularis*: de Ruiter & Geffen 1998; bushbuck: Wronski & Apio 2006). However, the additional evidence of association between maternally unrelated individuals suggests more complex association patterns.

The higher extent of biparental kinship found between pairs of females showing casual associations outside their matriline is unusual. There are two possible means by which this might occur. First, this pattern might be the result of geographical overlap between a set of females and a set of males. Generally, females that overlap geographically tend to associate with an overlapping set of males. Thus associating females would be expected to have a higher probability than nonassociating females of mating with the same set of males, and consequently their offspring would probably show higher paternal relatedness than females with nonoverlapping home ranges. If this persisted over generations, it could produce the patterns seen in our results. However, if this scenario were true we would expect a similar trend in pairs of females that show casual associations within their matriline, which we did not find. Paternal kin recognition is another explanation for the higher biparental kinship found between casual female associates outside of the matriline. Paternal kin recognition has been documented in female rhesus macaques, *Macaca mulatta*, with Widdig et al. (2001) providing evidence that adult females associate more frequently with paternal half-sisters than with nonkin. The evidence of paternal kin bias and the mechanisms responsible for paternal kin discrimination are important for our understanding of the evolution of social behaviour (Silk 2002; Widdig 2007), but remain to be tested in this population.

While the small but significant microsatellite variation found between mitochondrial clades in the eastern gulf of Shark Bay (Krützen et al. 2004b) might influence the patterns of biparental relatedness, it is unlikely for two reasons. First, only 5.25% of this variation was found between mitochondrial clades (see Table 4 in Krützen et al. 2004b), suggesting that mitochondrial haplotypes do

not have much of an effect on which microsatellite alleles an individual will have. Second, the extent of biparental relatedness within and outside matrilineal classes suggests that the microsatellite variation between mitochondrial clades does not drive the patterns of biparental relatedness.

In conclusion, this study demonstrates that female–female bottlenose dolphin association patterns in the eastern gulf of Shark Bay depend on home range overlap, matrilineal kinship and biparental kinship. This indicates that investigations of sociality should carefully consider interactions between home range overlap, association patterns and kinship in mammalian societies. Future analyses on the specific context of female kin associations (e.g. behavioural context, habitat, female reproductive state, season and age) will help us better understand why kin relationships are important in open fission–fusion social systems.

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References

- Amos, B. & Hoebel, A. R. 1991. Long-term preservation of whale skin for DNA analysis. In: *Genetic Ecology of Whales and Dolphins* (Ed. by A. R. Hoebel & G. P. Donovan), pp. 99–103. Cambridge: International Whaling Commission.
- Amos, B., Schlotterer, C. & Tautz, D. 1993. Social structure of pilot whales revealed by analytical DNA profiling. *Science*, **260**, 670–672.
- Archie, E. A., Moss, C. J. & Alberts, S. C. 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B*, **273**, 513–522.
- Bejder, L., Feltcher, D. & Brager, S. 1998. A method for testing association patterns of social animals. *Animal Behaviour*, **56**, 719–725.
- Bourke, A. F. G. 1997. Sociality and kin selection in insects. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 203–227. Oxford: Blackwell.
- Cairns, S. & Schwager, S. 1987. A comparison of association indices. *Animal Behaviour*, **35**, 1454–1469.
- Calenge, C. 2006. The package 'adehabitat' for the R software: a tool for the 17 analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Carter, A. J., Macdonald, S. L., Thomson, V. A. & Goldizen, A. W. 2009. Structured association patterns and their energetic benefits in female eastern grey kangaroos, *Macropus giganteus*. *Animal Behaviour*, **77**, 839–846.
- Chapais, B. 2001. Primate nepotism: what is the explanatory value of kin selection? *International Journal of Primatology*, **22**, 203–229.
- Chaverri, G., Gamba-Rios, M. & Kunz, T. H. 2007. Range overlap and association patterns in the tent-making bat *Artibeus watsoni*. *Animal Behaviour*, **73**, 157–164.
- Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proceedings of the Royal Society B*, **236**, 339–372.
- Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, **296**, 69–72.
- Connor, R. C. & Smolker, R. A. 1985. Habituated dolphins (*Tursiops* sp.) in Western Australia. *Journal of Mammalogy*, **66**, 398–400.
- Connor, R. C., Smolker, R. A. & Richards, A. F. 1992a. Dolphin alliances and coalitions. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. De Waal), pp. 419–440. Oxford: Oxford University Press.

- Connor, R. C., Smolker, R. A. & Richards, A. F. 1992b. Two levels of alliance formation among bottlenose dolphins (*Tursiops*) sp. *Proceedings of the National Academy of Sciences, U.S.A.*, **89**, 987–990.
- Connor, R. C., Wells, R. S., Mann, J. & Read, A. 2000. *The Bottlenose Dolphin: Social Relationships in a Fission–Fusion Society*. Chicago: University of Chicago Press.
- Connor, R. C., Heithaus, M. R. & Barre, L. M. 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society B*, **268**, 263–267.
- Connor, R. C., Mann, J. & Watson-Capps, J. J. 2006. A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Ethology*, **112**, 631–638.
- Davis, L. G., Dibner, M. D. & Battey, J. F. 1986. *Basic Methods in Molecular Biology*. New York: Elsevier.
- De Villiers, P. A. & Kok, O. B. 1997. Home range, association and related aspects of elephants in the eastern Transvaal Lowveld. *African Journal of Ecology*, **35**, 224–236.
- Dunbar, R. I. M. 1980. Determinants and evolutionary consequences of dominance among female gelada baboons. *Behavioral Ecology and Sociobiology*, **7**, 253–265.
- Fernando, P. & Lande, R. 2000. Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus*). *Behavioral Ecology and Sociobiology*, **48**, 84–91.
- Gero, S., Engelhaupt, D. & Whitehead, H. 2009. Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology*, **63**, 143–151.
- Gibson, A., Syvanen, M., Levine, K. & Banks, J. 1998. Deer gender determination by polymerase chain reaction: validation study and application to tissues, blood-stains, and hair forensic samples from California. *California Fish and Game*, **84**, 159–169.
- Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, **7**, 1–16.
- Hamilton, W. D. 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, **7**, 17–52.
- Hoezel, A. R., Potter, C. W. & Best, P. B. 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. *Proceedings of the Royal Society B*, **265**, 1177–1183.
- Holekamp, E., Cooper, S. M., Katona, C. I., Berry, N. A., Frank, L. G. & Smale, L. 1997. Patterns of association among spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy*, **78**, 55–64.
- Horne, J. S. & Garton, E. O. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *Journal of Wildlife Management*, **70**, 641–648.
- Krützen, M., Valsecchi, E., Connor, R. C. & Sherwin, W. B. 2001. Characterization of microsatellites in *Tursiops aduncus*. *Molecular Ecology Notes*, 170–172.
- Krützen, M., Barre, L. M., Moller, L. M., Heithaus, M. R., Simms, C. & Sherwin, W. B. 2002. A biopsy system for small cetaceans: darting success and wound healing on *Tursiops* spp. *Marine Mammal Science*, **18**, 863–878.
- Krützen, M., Sherwin, W. B., Connor, R. C., Barre, L. M., Van de Castele, T., Mann, J. & Brooks, R. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society B*, **270**, 497–502.
- Krützen, M., Barre, L. M., Connor, R. C., Mann, J. & Sherwin, W. B. 2004a. 'O father: where art thou?' Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Molecular Ecology*, **13**, 1975–1990.
- Krützen, M., Sherwin, W. B., Berggren, P. & Gales, N. J. 2004b. Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (*Tursiops* spp.) in Shark Bay, Western Australia. *Marine Mammal Science*, **20**, 28–47.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bedjer, L. & Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 8939–8943.
- Langergraber, K., Mitani, J. & Vigilant, L. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, **71**, 840–851.
- Maher, C. R. 2009. Genetic relatedness and space use in a behaviourally flexible species of marmot, the woodchuck (*Marmota monax*). *Behavioral Ecology and Sociobiology*, **63**, 857–868.
- Manly, B. F. J. 1995. A note on the analysis of species co-occurrences. *Ecology*, **76**, 1109–1115.
- Manly, B. F. J. 2001. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. London: Chapman & Hall.
- Mann, J. & Sargeant, B. L. 2003. *Like Mother, Like Calf: the Ontogeny of Foraging Traditions in Wild Indian Ocean Bottlenose dolphins (Tursiops sp.)*. Cambridge: Cambridge University Press.
- Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R. & Patterson, E. 2008. Why do dolphins carry sponges? *PLoS ONE*, **3**, e3868. doi:10.1371/journal.pone.0003868.
- Möller, L. M., Beheregaray, L. B., Harcourt, R. G. & Krützen, M. 2001. Alliance membership and kinship in wild bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society B*, **268**, 1941–1947.
- Möller, L. M., Beheregaray, L. B., Allen, S. J. & Harcourt, R. G. 2006. Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of Southeastern Australia. *Behavioral Ecology and Sociobiology*, **61**, 109–177.
- Packer, C., Gilbert, D. A., Pusey, A. E. & O'Brien, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature*, **351**, 562–565.
- Parsons, K. M., Durban, J. W., Claridge, D. E., Balcombs, K. C., Noble, L. R. & Thompsons, P. M. 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, **66**, 185–194.
- Perry, S., Manson, J. H., Muniz, L., Gros-Louis, J. & Vigilant, L. 2008. Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Animal Behaviour*, **76**, 187–199.
- Queller, D. C. & Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.
- Reeve, H. K., Westneat, D. F., Noon, W. A., Sherman, P. W. & Aquadro, C. F. 1990. DNA 'fingerprinting' reveals high levels of inbreeding in colonies of eusocial naked mole-rat. *Proceedings of the National Academy of Sciences, U.S.A.*, **87**, 2496–2500.
- Robbins, M. M. & McNeilage, A. 2003. Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, **24**, 467–491.
- Row, J. R. & Blouin-Demers, G. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia*, **4**, 797–802.
- de Ruiter, J. R. & Geffen, E. 1998. Relatedness of matrilineal, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proceedings of the Royal Society B*, **265**, 79–87.
- Sargeant, B. L., Mann, J., Berggren, P. & Krutzen, M. 2005. Specialization and development of beach hunting, rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, **83**, 1400–1410.
- Scott, E. M., Mann, J., Watson, J. J., Sargeant, B. L. & Connor, R. C. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male–male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, **142**, 21–44.
- Seaman, D. E., Millsbaugh, J. J., Kernohan, B. J., Brundige, G. F., Raedeke, K. J. & Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, **63**, 739–747.
- Seger, J. 1991. Cooperation and conflict in social insects. In: *Behavioural Ecology* (Ed. by J. Krebs & N. Davies), pp. 338–373. Oxford: Blackwell.
- Shinohara, M., Domingo-roua, X. & Takenaka, O. 1997. Microsatellites in the bottlenose dolphin *Tursiops truncatus*. *Molecular Ecology*, **6**, 695–696.
- Silk, J. B. 2002. Kin selection in primate groups. *International Journal of Primatology*, **23**, 849–875.
- Smith, J. E., Memenis, S. K. & Holekamp, K. E. 2007. Rank-related partner choice in the fission–fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, **61**, 753–765.
- Smolker, R. A., Richard, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, **123**, 38–69.
- Smouse, P. E., Long, J. C. & Sokal, R. R. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology*, **35**, 627–632.
- Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, **41**, 291–309.
- Sundaesan, S. R., Fischhoff, I. R., Dunshoff, J. & Rubenstein, D. I. 2007. Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. *Behavioral Ecology*, **151**, 140–149.
- Valsecchi, E. & Amos, B. 1996. Microsatellite markers for the study of cetacean populations. *Molecular Ecology*, **5**, 151–156.
- Vydyia, T. N. C. & Sukumar, R. 2005. Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *Journal of Ethology*, **23**, 1439–1444.
- Watts, D. P. 1998. Long-term habitat use by mountain gorillas (*Gorilla gorilla beringei*). I. Consistency, variation, and home range size and stability. *International Journal of Primatology*, **19**, 651–680.
- Wells, R. S., Scott, M. D. & Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy* (Ed. by H. H. Genoways), pp. 247–306. New York: Plenum.
- White, G. & Garrott, R. 1990. *Analysis of Wildlife Radio Tracking Data*. San Diego: Academic Press.
- Whitehead, H. 1999. Testing association patterns of social animals. *Animal Behaviour*, **57**, F26–F29.
- Whitehead, H. 2009. SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, **63**, 765–778.
- Whitehead, H. & Baird, R. W. 2000. Social organisation of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, **78**, 2096–2105.
- Widdig, A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. *Biological Reviews*, **82**, 319–334.
- Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J. & Bercovitch, F. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 13769–13773.
- Wronski, T. & Apio, A. 2006. Home-range overlap, social vicinity and agonistic interactions denoting matrilineal organisation in bushbuck, *Tragelaphus scriptus*. *Behavioral Ecology and Sociobiology*, **59**, 819–828.
- Würsig, B. & Jefferson, T. A. 1990. Methods of photoidentification for small cetaceans. Individual recognition of cetaceans. *Report of International Whaling Commission*, **12**, 43–52.