

# Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp.

S. Gero, L. Bejder, H. Whitehead, J. Mann, and R.C. Connor

**Abstract:** We investigated association patterns of 52 photographically identified, free-ranging bottlenose dolphins (*Tursiops* spp. Gervais, 1855) across four behavioural states (rest, travel, social, and foraging/feeding) to investigate how behavioural state influences patterns of association. Group composition and behavioural data were extracted from 2178 encounter surveys collected over 3 years. Analyses revealed three general types of association: (1) affiliates, which consistently demonstrate preferred associations across all behavioural states; (2) acquaintances, which never form preferred associations but still associate in at least one behavioural state; and (3) behavioural associates, which form preferred associations in at least one, but not all behavioural states. The majority of associations in Shark Bay, Australia, are acquaintance type (38.2%), with affiliates (5.7%, principally between adult males) and behavioural associates (28.9%, principally between juveniles) being relatively rarer. Permutation tests identified behaviourally specific preferred associations during all behavioural states. Although behaviourally specific preferred associations appear to exist within the Shark Bay social structure, it seems that the social organization and mating system constrain the social relationships for the majority of males and females in differing ways which prevent them from having behavioural associates, leaving juveniles free to associate based on short-term expediency and behavioural specific needs.

**Résumé :** Nous avons étudié les patrons d'association entre 52 grands dauphins (*Tursiops* spp. Gervais, 1855) libres en nature et identifiés par photographies pendant quatre états comportementaux (repos, déplacement, interaction sociale et recherche de nourriture/alimentation), afin de déterminer de quelle manière l'état comportemental affecte les patrons d'association. Nous avons tiré les données sur la composition des groupes et sur le comportement de 2178 inventaires de rencontres faits au cours de 3 années. Les analyses indiquent l'existence de trois types généraux d'associés, (1) les affiliés qui exhibent régulièrement des associations préférentielles, indépendamment de leur état comportemental, (2) les connaissances qui ne forment jamais d'association préférentielle, mais qui s'associent tout de même pendant au moins un état comportemental et (3) les associés comportementaux qui forment des associations préférentielles dans au moins un, mais pas l'ensemble, de leurs états comportementaux. La plupart des associés à Shark Bay, Australie, sont du type des connaissances (38,2 %), les autres types, soit les affiliés (5,7 % surtout des mâles adultes) et les associés comportementaux (28,9 % surtout des jeunes), étant relativement plus rares. Des tests de permutation permettent d'identifier des associations préférentielles spécifiques au comportement dans chacun des états comportementaux. Bien que des associations préférentielles spécifiques en fonction du comportement semblent exister dans la structure sociale de Shark Bay, il apparaît que l'organisation sociale et le système d'accouplement imposent des contraintes aux relations sociales chez la majorité des mâles et des femelles de manières différentes, ce qui les empêche d'avoir des associés comportementaux; les jeunes peuvent, par ailleurs, s'associer librement selon les circonstances à court-terme et leurs besoins comportementaux spécifiques.

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## Introduction

The study of the society in which a species lives often gives insight into the behaviour and ecology of the species, as well as into the dynamics of the population under study (Whitehead 1997). A society can be defined as a set of conspecifics that interact more regularly with one another than with members of other societies (Struhsaker 1969; Kappeler and van Schaik 2002). A society is composed of

three interrelated component parts: (1) the social organization, which characterizes society's demographics by describing the size, age composition, sex ratio, and spatiotemporal cohesion of a society; (2) the mating system, which describes both the behavioural and genetic aspects of the reproductive interactions within the system; and (3) the social structure, which refers to the patterning of social interactions and relationships among dyads of society members regardless of their sex, age, and the size of the group (Kappeler

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and van Schaik 2002). According to Hinde's (1976) framework, the type and patterning of social interactions between a pair of individuals define their social relationships and the pattern of dyadic relationships can then be used to characterize the social structure of a society. Thus, to study social structure, one must collect detailed data on the interactions between individuals over time (Hinde 1976).

As cetaceans spend the majority of their time underwater, social interactions are often difficult to observe, let alone quantify (Whitehead 1997; Mann 1999; Whitehead et al. 2000). The spatiotemporal group, or a set of individuals in the same place and time, acts as a proxy and can be used to define association (Whitehead 1997; Whitehead and Dufault 1999; Whitehead et al. 2000). Thus, to understand cetacean social structure it is critical to investigate factors that may determine group formation, including the identity of associates.

The strength and stability of an association is likely to be based on socio-ecological benefits in areas such as predator defense, food acquisition, and social support (Hamilton 1964; Alexander 1974; Axelrod and Hamilton 1981; Norris and Schilt 1988; van Schaik 1989). Fission–fusion societies, rare in mammals, present an opportunity to examine the costs and benefits of association. Here, we explore the fission–fusion society of free-ranging Indo-Pacific bottlenose dolphins, *Tursiops* spp. Gervais, 1855, to determine how behavioural state influences patterns of association. We suggest that associates are chosen to maximize efficiency or benefits when carrying out specific behaviours. In a study population which exhibits at least 13 different foraging techniques (Smolker et al. 1997; Connor et al. 2000b; Mann and Sargeant 2003; Krützen et al. 2005), it is likely that individuals would maximize foraging efficiency by associating preferentially with individuals that forage in a similar manner (de Waal and Luttrell 1986). In turn, these foraging associates may not provide equivalent benefits while performing social or resting behaviours. The inherent fluidity in a social structure in which individuals rapidly change group composition and size and the relatively low cost of locomotion (Williams 1999) would allow individuals to maximize behaviourally specific benefits by creating the opportunity for different behaviourally specific preferred partnerships.

Although a fluid social structure allows for many potential social relationships, the social organization and mating system of the society constrain these social options by reducing partner reliability, availability, and quality (Janson 1986; van Schaik 1996; Strier 2000; Kappeler and van Schaik 2002). For example, strong long-term male social bonds are infrequent in species living in a monogamous mating system, whereas strong male–female bonds are likely in this system. Within our study population, contrasting patterns of associations between the sexes have already been identified (Connor et al. 1992; Smolker et al. 1992). Smolker et al. (1992) described the social organization of this population, outlining three types of groups: (1) mature females and their dependent calves tend to group together with other mother and calf pairs, forming a network of relationships as opposed to particular strongly associated subgroups; (2) juveniles of both sexes tend to group inconsistently on their own; and (3) mature males preferentially associate with two or three other males to form alliances. Two distinct alliance strategies have

been identified among mature males in Shark Bay, each with two levels but which differ in their patterns of association and relatedness (Connor et al. 1992, 1999, 2001; Krützen et al. 2002). The social organization and mating system of this dolphin society likely constrain social options for a majority of the adults of both sexes, but in different ways. Mature male relationships are likely constrained by the nature of the alliance mating strategy; female relationships are likely constrained by reproductive status, but non-reproductive juveniles of both sexes are likely constrained to a lesser degree. Thus, we predict that juveniles would be more likely to form behaviourally specific preferred associations.

## Materials and methods

### Field methods

We used group composition and behavioural data collected from 2178 group encounter surveys between February 1999 and November 2001 (effort during 25 months). These data were collected as a part of the ongoing longitudinal field study in Shark Bay, Western Australia (25°47'S, 113°43'E). A survey was completed for each individual or group that was encountered during daylight hours. An individual was deemed a part of the group when it was within 10 m of any other group member (10 m “chain rule”; Smolker et al. 1992). Composition of a group was determined by standard photo-identification techniques (Würsig and Jefferson 1990). Unidentified animals were not used in analyses (6% of surveys contained unidentified animals). Using scan sampling (Altmann 1974), the predominant behavioural state was classified into four mutually exclusive categories based on observed behaviourally specific events following previous work at this field site: foraging/feeding, resting, socializing, and traveling (Smolker et al. 1992; Mann and Smuts 1998). Encounter surveys were only included in the analyses if the predominant behavioural state were unambiguous (i.e., only behaviourally specific events from one behavioural state were observed during the encounter).

### Analyses

Only animals sighted more than 30 times were considered for the analyses (Table 1). Calves were excluded from the analyses because of their unique dependent relationship with their mothers (Mann and Smuts 1999). Animals sighted in the same group were considered associated. We used the half-weight index (HWI) as a measure of association, as it accounts best for observer biases inherent in photo-identification techniques (Cairns and Schwager 1987; following Smolker et al. 1992). We stratified the encounter surveys into one of the four behavioural states and calculated the HWI for each dyad under each behavioural state, as well as over all encounters. Following Whitehead (1997), we plotted the HWI in the different behavioural states for each dyad against each other to determine whether strength of association differed between behavioural states.

We used a permutation test as in Bejder et al. (1998) with modifications as in Whitehead et al. (2005) to test for preferred association in each of the behavioural states and for all the data combined against the null hypotheses that animals associate randomly with one another. The observed association matrix was randomized 40 000 times with 100

**Table 1.** Mean number of times an individual bottlenose dolphin (*Tursiops* sp.) was sighted in each behavioural state, as well as the range and the age- and sex-class breakdown of the sampled individuals.

|                | Forage       | Rest         | Social      | Travel       |
|----------------|--------------|--------------|-------------|--------------|
| Age class      |              |              |             |              |
| Adult          | 35           | 35           | 33          | 35           |
| Juvenile       | 17           | 17           | 17          | 17           |
| Sex class      |              |              |             |              |
| Male           | 26           | 26           | 26          | 26           |
| Female         | 26           | 26           | 24          | 26           |
| Total <i>N</i> | 52           | 52           | 50          | 52           |
| Mean (SD)      | 19.0 (14.10) | 26.9 (16.58) | 10.2 (9.22) | 17.2 (10.76) |
| Minimum        | 4            | 5            | 0           | 3            |
| Maximum        | 61           | 70           | 38          | 44           |

**Table 2.** Observed and random coefficient of variation (CV) of half-weight indices (HWIs) across the four behavioural states and pooled across all behavioural states.

| Behavioural state  | CV of observed HWI mean | CV of randomized HWI mean | <i>p</i> |
|--------------------|-------------------------|---------------------------|----------|
| Foraging           | 1.89                    | 1.12                      | <0.0001  |
| Rest               | 1.64                    | 0.83                      | <0.0001  |
| Social             | 1.64                    | 1.20                      | <0.0001  |
| Travel             | 1.88                    | 1.08                      | <0.0001  |
| Pooling all states | 1.71                    | 0.92                      | <0.0001  |

flips per permutation for each analysis. Associations were permuted within daily sampling intervals to remove possible demographic effects (i.e., mortality, recruitment, or migration to or from the study area; Whitehead 1999). The resulting *p* values were not considered a formal statistical threshold, but rather as indicating the strength of evidence for nonrandom associations; and thus, a Bonferroni adjustment is not required (Bejder et al. 1998).

We identified a dyad as having a preferred association when their association index was twice the mean index, including all zero values (as in Durrell et al. 2004). This threshold value was chosen because it is approximately twice the expected value if associations were completely random. A total of six separate hypothesis matrices were formed, one for each combination of age (adult–adult, adult–juvenile, juvenile–juvenile) or sex (male–male, male–female, female–female) classes in which a “1” was scored for each dyad with the combination of age or sex classes in question and a “0” for all others. A preferred association matrix was constructed in which a score between 0 and 4 was given to each dyad for the number of behavioural states in which they formed a preferred association (i.e., a zero was given to dyads which never formed preferred associations, a four was given to pairs that formed preferred associations in all behavioural states, and scores of one, two, or three were given to dyads that only formed preferred associations in as many behavioural states). Mantel tests (Mantel 1967; Schnell et al. 1985) and matrix correlation coefficients between the elements of each of the hypothesis matrices and the preferred association matrix were carried out to determine if the relative age and sex of the individuals in a dyad were correlated with the type of association they formed. The statistical significance of each Mantel test was tested against a null hy-

pothesis in which the number of preferred associations was unrelated to the age- or sex-class combination, using 1000 random permutations (see Schnell et al. 1985).

The calculation of the HWI, the Mantel tests, and the Monte Carlo permutation tests were carried out using Socprog version 2.2 (Whitehead 2005) in Matlab® version 6.5 (The Mathworks, Inc. 2002).

## Results

### Randomness of association

Significantly high and low associations were identified in each of the four behavioural states, since the coefficients of variation of the observed HWIs were significantly larger than for the randomly permuted data ( $p < 0.0001$ , Table 2)

### Strength of association and behavioural state

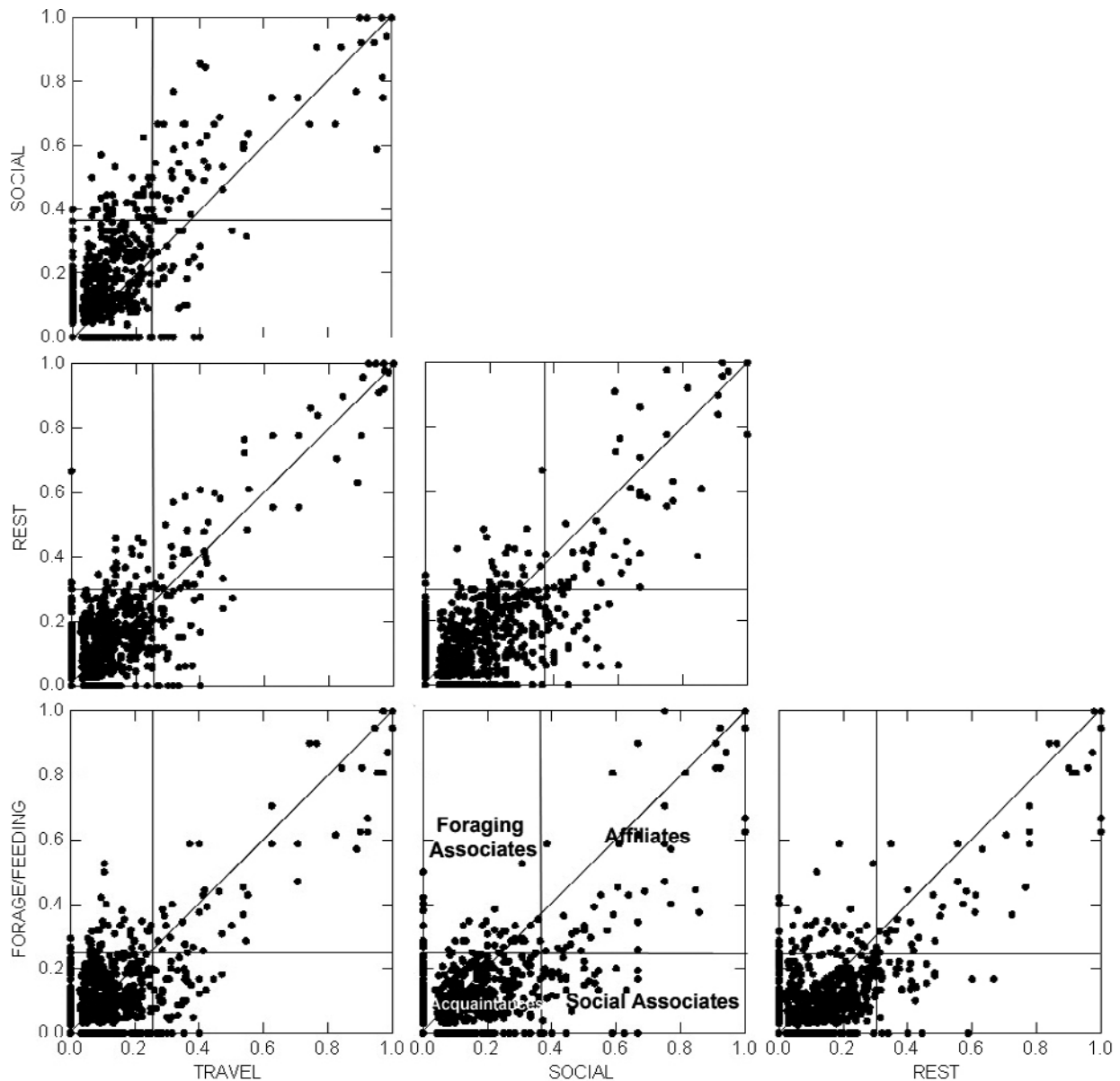
Analyses revealed three general patterns to associations (Table 3): (1) affiliates, which consistently demonstrate preferred associations across all behavioural states; (2) acquaintances, which never form preferred associations but still associated in at least one behavioural state; and (3) behavioural associates, which form preferred associations in at least one, but not all behavioural states (i.e., the strength of association between behavioural associates varied across behavioural states). Figure 1 depicts the HWI of each dyad against itself across behavioural states and is used to illustrate the three types of association. The diagonal represents the 1:1 ratio line on which points would be expected to fall if behavioural state had no relationship with the strength of the association, in which case, the HWI for a given dyad would be equal in both states. The apparent arc in the data points in some panels indicates that dyads with intermediate

**Table 3.** Frequency of dyadic associations by type.

|   | Never observed associated | Acquaintances | Behavioural associates |            |            |            | Affiliates |
|---|---------------------------|---------------|------------------------|------------|------------|------------|------------|
|   |                           |               | Total                  | 1          | 2          | 3          |            |
| Mean (SD) number of dyads per individual ( <i>n</i> = 52) | 16.3 (9.68)               | 17.0 (5.50)   | 14.2 (6.81)            | 7.2 (4.55) | 4.4 (2.73) | 2.6 (2.15) | 3.5 (2.91) |
| Total number of dyads                                     | 361                       | 506           | 383                    | 194        | 119        | 70         | 76         |
| Percentage of possible dyads                              | 27.2                      | 38.2          | 28.9                   | 14.6       | 9.0        | 5.3        | 5.7        |

**Note:** The breakdown for behavioural associates into one, two, or three of the four behavioural states is shown.

**Fig. 1.** Plots comparing dyadic half-weight index (HWI) of bottlenose dolphin (*Tursiops* sp.) pairs between behavioural states. The diagonal represents the 1:1 ratio line on which points would be expected to fall if behavioural state had no relationship with strength of association. Horizontal and vertical lines mark the threshold value defining preferred associates.



**Table 4.** Frequency of behaviourally specific preferred associations across behavioural states.

|   | Forage     | Rest       | Social     | Travel     |
|---|------------|------------|------------|------------|
| Mean (SD) number of dyads per individual ( $n = 52$ ; except $n = 50$ for social) | 5.9 (6.02) | 5.9 (4.67) | 6.4 (3.45) | 5.8 (3.59) |
| Total number of dyads   | 153        | 154        | 159        | 152        |
| Percentage of possible dyads  | 11.5       | 11.6       | 12.0       | 11.5       |

**Table 5.** Relative age and sex breakdown of associations by type as a percentage of dyads,  $N$ .

|                   | $N$ | Never observed associated | Acquaintances | Behavioural associates |      |      |      | Affiliates | $p^*$  |
|-------------------|-----|---------------------------|---------------|------------------------|------|------|------|------------|--------|
|                   |     |                           |               | Total                  | 1    | 2    | 3    |            |        |
| <b>Age class</b>  |     |                           |               |                        |      |      |      |            |        |
| Adult             | 595 | 28.1                      | 40.3          | 26.7                   | 12.3 | 9.4  | 5.0  | 4.9        | 0.875  |
| Adult-juvenile    | 595 | 28.2                      | 37.5          | 28.6                   | 15.8 | 8.4  | 4.4  | 5.7        | 0.373  |
| Juvenile-juvenile | 136 | 19.1                      | 31.6          | 39.7                   | 19.8 | 9.6  | 10.3 | 9.6        | <0.001 |
| <b>Sex class</b>  |     |                           |               |                        |      |      |      |            |        |
| Male-male         | 325 | 23.4                      | 29.6          | 33.8                   | 15.7 | 11.1 | 7.1  | 13.2       | <0.001 |
| Male-female       | 676 | 33.0                      | 40.4          | 24.4                   | 14.1 | 6.6  | 3.7  | 2.2        | 0.001  |
| Female-female     | 325 | 19.1                      | 42.2          | 33.2                   | 14.8 | 11.7 | 6.7  | 5.5        | 0.062  |

\*The  $p$  value is from the Mantel test comparing age class or sex class to all others.

strength associations were stronger in only one of the behavioural states, or that the strength of association varied with behaviour. Behaviourally specific associations appear to be strongest when engaging in social or foraging behaviours and weaker when traveling or resting. All animals formed acquaintance-type associations, but only 51 possessed behavioural associates and only 42 formed affiliate-type associations.

### Preferred associations

Although one animal did not form any behaviourally specific preferred associations, all 52 individuals formed at least one preferred association. A total of 459 preferred associations were identified out of a possible 1326 dyads, i.e., they had association indices above twice the mean index. Out of the possible 51, the average individual was observed associated with 34.7 (SD = 9.68) individuals, of which 17.7 (SD = 7.52) were preferred (i.e., had a HWI greater than twice the mean). For two dolphins, 62.7% of their associations are preferred (32 preferred associations of a possible 51), while one individual only formed one preferred association, which was of the affiliate type.

We repeated the analysis after changing the arbitrary threshold value to be identified as a preferred association to any dyad with an HWI above twice the mean of non-zero indices, thereby doubling the threshold value. Patterns and results were similar, but the frequencies of each type of association differed slightly.

### Behaviourally specific preferred associations

A total of 383 behaviourally specific associations were identified out of the possible 1326 dyads. The average dolphin has approximately six behavioural associates in all behavioural states, although the standard deviations (SDs) varied between the states (Table 4).

### Relative age and sex of preferred partners

Table 5 summarizes the frequencies of the types of associations formed between dyad members stratified based on relative age and sex. Mantel tests did not reject the null hypothesis that distribution of types of association was different from the population distribution for adult-adult or mixed-age associations. However, there were relatively more juvenile-juvenile behavioural associates than in the general population. Juveniles also associated with most other juveniles so that juvenile-juvenile dyads had the lowest probability of never having been observed associated (Table 5).

When comparing relative sex (both males, both females, opposite sex; Table 5), two tests against the distribution of preferred associates in the general population were significant. Associations between males have a relatively higher percentage of affiliates (13.2%), while having a low number of acquaintances (29.6%). Females show the opposite pattern, in which 42.2% of their associations are acquaintances while only 5.5% are affiliates (Table 5). Associations between the sexes have relatively high percentage of acquaintances.

### Discussion

The principal goals of this study were to identify whether dolphins form behaviourally specific preferred associations and to describe patterns of their occurrence among age and sex classes. By this we mean, for example, that some dolphins preferentially associate with certain individuals when foraging and others when socializing. Results shown here demonstrate that preferred associations are formed within each of the four behavioural states. Based on this, dolphin associations can be divided into three general categories: (1) affiliates, which consistently demonstrate preferred associations across all behavioural states; (2) acquaintances, which never form preferred associations but still associated

in at least one behavioural state; and (3) behavioural associates, which form preferred associations in at least one, but not all behavioural states. Of the 1326 possible dyads, 383 were behavioural associates. It appears that a large number of individuals have different preferred partners in different behavioural states. In what follows, we discuss possible factors that limit the social options of older individuals and suggest theoretical benefits incurred by individuals that are able to form behaviourally specific preferred associations. Further work is needed to elucidate the functional aspects of behaviourally specific preferred associates in the network of individuals that make-up this dolphin society.

### Factors influencing behaviourally specific preferred associations

Mantel tests revealed significant relationships in dyadic associations among the sex classes. This finding likely reflects the fact that social options of males and females are limited in different ways by the social organization and mating strategy of their society. Two distinct alliance strategies have been identified among male alliances in Shark Bay (Connor et al. 1992, 1999, 2001). In the predominant strategy, first-order alliances are long-term, strong associations between pairs and trios of usually related individuals (Krützen et al. 2002) that can last for up to 18 years in Shark Bay (R.C. Connor, unpublished data). Stable, long-term alliance members spend the majority of their time together, independent of behaviour, even when not herding oestrous females (Connor et al. 1992, 1999). Association preferences of individuals are likely to differ, and so an individual's behaviourally specific preferred group composition will rarely, if ever, occur (Newton-Fisher 1999). This may be a possible factor driving mature adult males to form alliances with preferred affiliates, instead of multiple groups with different behavioural associates. The social organization of the Shark Bay society creates a situation where the importance for males of having long-term social alliance partners that maximize reproductive success regardless of behavioural state outweighs the potential short-term benefits of forming behaviourally specific preferred associations.

In females, it has been suggested that association may follow the similarity principle (de Waal and Luttrell 1986), such that it is advantageous for females of the same reproductive state to associate (Wells et al. 1987; Connor et al. 2000a). According to Connor et al. (2000a), adult females benefit by associating with females in similar reproductive states because of similar requirements for food and defence against both males and predators. An adult female may prefer to associate with a specific individual who shares the same foraging or social priorities; however, if their preferred female associate loses her calf, it may become more beneficial to associate with other mothers than with this preferred behaviourally specific associate. This being the case, the social options of adult females may also be constrained by reduced partner availability. Differences in reproductive timing (Barrett and Henzi 2002), calf mortality, and long inter-birth intervals likely result in a lack of preferred partner reliability through time (Mann et al. 2000). Partner reliability is likely most important during the first few months post partum, when predation risk is high and group size is largest (Mann et al. 2000). The timing of association could be critical, even

though mean group size does not predict female reproductive success (Mann et al. 2000). Acquaintance-level associations might suffice in allowing females to meet foraging, reproductive, and social demands. In an analysis such as this one, where the data are across years, it is not surprising that we do not observe adult females forming consistent affiliate or behavioural associate type associations.

Since adult associations included both males and females, it is to be expected that a Mantel test would find no significant correlation between type of association and adult age categories, as the sexes tend to form opposing types of association. A significant relationship is found between type of association and juvenile associations (Table 5). A higher frequency of behavioural associates is observed between juveniles than among any other relative age category. Juveniles would be less constrained by the mating system and social organization than adults, and are thus able to associate based on behaviourally specific needs before reaching maturity at which point being with other females of similar reproductive status or alliance members outweighs those needs. These findings appear to contrast results from Sarasota, Florida, where juvenile bottlenose dolphin males begin alliance formation during the juvenile period (Wells 1991; Owen et al. 2002). However, 9.6% of the Shark Bay juvenile associations are of the affiliate type, a value higher than that observed between adults (Table 5). These affiliate relationships in the juvenile period are likely to represent the early stages of alliance formation.

### Preferred associations while foraging and socializing

Results of the permutation tests show that there are dyads with higher HWI than expected by chance in each of the four behavioural states. This would suggest that some associations in all behavioural states are nonrandom, and therefore, preferred. Preferred associations are strongest when either socializing or foraging.

Even though Smolker et al. (1992) describe the spatio-temporal structure of foraging groups as ephemeral, the results of this study suggest that preferred associations are indeed formed between individuals while foraging. Foraging individuals likely receive by-product benefits by coordinating their behaviours (Brown 1983; McDonald and Potts 1994). Partner preferences are expected in by-product mutualisms in which individuals differ in the ability to provide or use by-product benefits (Wrangham 1982; Connor 1995). In Shark Bay, these differences may relate to varying foraging techniques (Smolker et al. 1997; Connor et al. 2000b; Mann and Sargeant 2003; Krützen et al. 2005). According to the similarity principle (de Waal and Luttrell 1986), it is likely more beneficial to forage with individuals that share similar foraging tactics, as by-product benefits are likely higher between individuals that forage in the same manner and habitat.

In a social context, individuals may prefer to associate with animals which provide different benefits reaped in situations other than foraging and feeding. Females often associate with individuals who do not share their foraging tactic (Mann and Sargeant 2003; Sargeant et al. 2005). There are many benefits to a varied social experience; here we will briefly discuss two classes of benefit: (1) predator defence and the development and maintenance of allies and (2) short- and long-term gain in skills.

Social interdependence and the establishment of preferred social associations may be important in active defence against predators. While antipredator tactics such as detection, dilution, and confusion can successfully be accomplished by groups of random individuals (e.g., Krebs and Davies 1993), active defence such as mobbing (Wood et al. 1970) may be more effective among individuals possessing preferred social ties as well as among kin. Mann and Barnett (1999) describe an incident in which both related and unrelated bottlenose dolphins in Shark Bay came to the defence of a calf under attack by a shark. In the weeks following the attack, the calf's mother increased the amount of time spent in the area where the attack occurred and associated only with her grandson and individuals that aided in her calf's defence (Mann and Barnett 1999).

Behaviourally specific social associates may also be important in the development of parenting skills. Mann and Smuts (1998) found that calves engaged in social associations during most mother-calf separations. The authors suggest that kinship influences the identity of experienced escorts, but that more often unrelated inexperienced younger females escort the calves. Juvenile females may benefit from associating preferentially with calves and their mothers during social periods under the learning-to-parent hypothesis (Lancaster 1972; Mann and Smuts 1998). However, these benefits are difficult to quantify in the wild (Mann and Smuts 1998).

### Conclusion

This is the first study to show that behaviourally specific preferred associations exist in any cetacean population. It appears, however, that the social organization and mating system of this dolphin society limit social options for the majority of both adult males and adult females, but in different ways, each which prevent them from developing behaviourally specific preferred associations. These constraints result in females primarily forming acquaintance-type associations and the males developing affiliate-type relationships with long-term alliance members, leaving only the juveniles free to form behaviourally specific partnerships. Overall, it appears that juveniles are free to associate based on short-term expediency and behaviourally specific needs, rather than being constrained to social options of a fully mature individual that are focused on reproduction and the rearing of young. Future work should focus on elucidating what role behaviourally specific preferred associations play in the social organization of these animals.

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