# Homosexual Behaviour in Animals

## An Evolutionary Perspective

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# 4

## Establishing trust: socio-sexual behaviour and the development of male–male bonds among Indian Ocean bottlenose dolphins

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### Introduction

In the popular press, bottlenose dolphins have been characterized as 'sexual' animals who frequently engage in non-reproductive sexual behaviour (Kluger, 1999; CNN, 2002; Begos, 1999; Fahy, 2003; Kyodo News International, 2001), including homosexual encounters. However, actual accounts of same-sex activity in bottlenose dolphins include only a few descriptive studies from captivity (for example, Caldwell and Caldwell, 1972; McBride and Hebb, 1948) and the wild (for example, Herzing and Johnson, 1997); only one quantitative study, which focused on just two captive individuals (Östman, 1991), has been published. Systematic research on homosexual behaviour in other cetaceans is limited to a killer whale dissertation study (Rose, 1992). Even though bottlenose dolphins are one of the best-studied cetaceans, their sexual behaviour has not been quantified in field settings. Given the difficulty in studying marine mammals, and cetaceans in particular, the dearth of research in this area is not surprising. The present study of Indian Ocean bottlenose dolphin calves, followed closely since 1988, is the first to quantify homosexual behaviour in wild cetaceans using focal animal sampling.

Since the start of this research, it became evident that all age–sex classes participate in socio-sexual behaviour, which includes genital contact between opposite-sex and same-sex individuals. However, calves and juveniles engage in higher rates than adults, including homosexual activity. Relative to adults, calf and juvenile socio-sexual behaviour is typically seen in a playful context, and it seems likely that these behaviours fulfil some social function(s). But, with so little previous research on play, development and sexual behaviour in

107

dolphins, specific hypotheses have not been developed other than Östman (1991), who characterized adult male homosexual behaviour among captive dolphins as dominance related.

The study of sexual play or socio-sexual behaviour in calves is of interest because elements of play often reflect components of adult behaviours (for a review of primates see Pereira and Fairbanks, 1993) and informs how sexual behaviour develops. Pre-pubertal sexual behaviour and especially male–male interactions are common in other species, for example, domestic pigs (Berry and Signoret, 1984) or primates (for example, Brown and Dixson, 2000). A fundamental question in the play literature is whether the relative contribution of play behaviours (including socio-sexual play) primarily has current or future utility (for example, Fairbanks, 1993). For example, socio-sexual play may allow calves to practice skills for future courtship, promote bonds of current or future value, have organizational effects on development, or be a by-product of hormonal activity during early development (that is, postnatal surge in testosterone found in some primates, Brown and Dixson, 2000). A profound difficulty in discriminating these functions is that, even in captivity, one cannot manipulate one variable, such as time spent in socio-sexual behaviour, without affecting other important behaviours, such as physical contact and social interaction. Developmental outcomes are multi-determined and it would be extremely challenging to assess the long-term effects of infantile socio-sexual behaviour.

Of particular interest in bottlenose dolphin research is the relationship, if any, between male homosexual behaviour and alliance formation, a crucial part of male mating strategies (Connor et al., 1992a,b, 1996, 1999). Males form first-order alliances (pairs and trios) that cooperate to sequester and maintain exclusive access to a single female for up to six weeks (although typically less than one week), an event known as a consortship. Some first-order alliances appear to remain highly stable for 15–20 years (Connor, unpublished data). They typically pair with one or two other alliances to form second-order alliances. Second-order alliances cooperate by helping each alliance keep their respective females during consortships. Although popular accounts occasionally infer that males coerce copulations on the female, such behaviour has never been observed. Males may also form a super-alliance of up to 14 individuals. Pairings and trios within the super-alliance are labile, with no more than three males consorting with a female at any time. However, if the pair or trio is challenged by an outside alliance, the entire super-alliance may help the pair or trio defend the female. Although adult male pairs (but not trios) have been noted at several research sites (for example, Owen et al., 2002), and not at other bottlenose dolphin research sites, only in Shark Bay, Western Australia are males known to form multi-level alliances (see review by Connor et al., 2000), a pattern otherwise seen only in humans.

We understand little concerning how such intense, prolonged male–male bonds are formed and maintained. The current study from Shark Bay may offer some insights into the mechanisms.

I begin with quantitative description of the patterns and frequencies of socio-sexual and homosexual behaviour in bottlenose dolphins, including sex-differences, preferential partnerships and the role of actor and recipient. In the discussion, hypotheses typically proposed to explain homosexual behaviour in other non-human animals will be examined against the dolphin data.

## Methods

### Bottlenose dolphin society

Three major long-term studies of bottlenose dolphins have been ongoing for more than 15 years, in the Moray Firth, Scotland; Sarasota, Florida, USA; and Shark Bay, Australia. Everywhere they have been studied, bottlenose dolphins (*Tursiops* sp.) live in coastal fission–fusion societies, characterized by sex-segregation and frequent changes in group membership (reviewed in Connor *et al.*, 2000). Adult females tend to associate with other adult females, juveniles and calves. Adult males tend to associate with other males or be solitary. Preferential male–male associations are particularly strong at two long-term study sites, Sarasota, Florida and Shark Bay, Australia (reviewed in Connor *et al.*, 2000). Females form loose networks, with weaker, but consistent associations with other females (Smolker *et al.*, 1992). In Shark Bay, the age at first birth is 12 and females nurse calves for three to six years (Mann *et al.*, 2000) and daughters continue to associate with their mothers after weaning; sons rarely do (Connor *et al.*, 2000). Some females are solitary, and are almost never sighted with other dolphins except their own calves, and some are highly social, almost never sighted without other dolphins (Mann *et al.*, 2000; Gibson and Mann, 2003). Their diet consists mainly of fish and squid (Connor *et al.*, 2000); lactating females spend on average 30% of the day foraging and <2% socializing (Mann and Watson-Capps, 2005; Mann and Sargeant, 2003). Calves tend to socialize for 10–15% of their time (Mann and Watson-Capps, 2005). Activity budgets for juveniles and adult males have not been reported. Both sexes are philopatric and the communities do not appear to be closed (Connor *et al.*, 2000), but males tend to disperse or range more widely than females (Krützen *et al.*, 2004a).

### Field site

Shark Bay is located at 25°47′S, 113°43′E in Western Australia. After an initial visit in 1982, a long-term study of the Shark Bay dolphins was established

in 1984 off of a fishing camp (now resort) called Monkey Mia (Connor and Smolker, 1985). The habitat consists mostly of embayment plains (5–13 m in depth) and shallow seagrass beds (0.5–4 m) bisected by deeper channels (7–13 m). Observations are in 6 m depth on average, making near continuous follows possible. The study area currently extends, 250 km$^2$ off the east side of the Peron Peninsula and includes over 600 animals that are monitored annually. Over 250 are observed in several long-term studies using focal follow methods. Most of the dolphins are well habituated to small boats (4–5 m), allowing us to follow individuals for many hours (Smolker et al., 1993; Mann and Smuts, 1998). Based on genetic haplotypes, the Shark Bay bottlenose dolphin species classification remains unresolved and the animals are hence referred to as Tursiops sp. (M. Krützen, unpublished).

### Age–sex class determination

Calves are defined as still nursing, with an average weaning age of four years (Mann et al., 2000). Juveniles are weaned but still pre-reproductive (for females up to age 12, for males up to age 14). Adult females are age 12 or older and adult males age 14 or older (when males begin to form stable long-term alliances). Physiological data from captivity and the field suggest that males are capable of fathering offspring as early as eight to ten years of age (Schroeder, 1990; Wells et al., 1987), but in Shark Bay their access to reproductive females is limited until they have formed stable alliances (Krützen et al., 2004b). Although birth years are not known for most dolphins born prior to 1982, all dolphins could be classified into an age class based on ventral speckling (Smolker et al., 1992), age of first reproduction (for females, see Mann et al., 2000) or body size.

### Subjects and dataset

A long-term study of bottlenose dolphin mothers and calves was initiated in 1988 (Mann and Smuts, 1998; Mann and Smuts, 1999; Mann et al., 2000; Mann and Sargeant, 2003; Mann and Watson-Capps, 2005). Between 1989 and 1999, 46 focal calves born to 26 mothers were observed for 1349 hours during the first four years of life (27 females for 725 hours 19 males for 624 hours). Focal mothers and calves were observed from 1 to 9 hours per day depending on weather conditions. The median and average follow duration is three hours. Most calves were observed for 10–15 hours per year or age class.

The population is residential and female home ranges are well known, minimizing the search effort required to find specific individuals. Group size and membership was determined by scan sampling the number of animals within

a 10 m chain (see Smolker *et al.*, 1992) at either five or one minute intervals. For example, every minute we scan every individual that surfaces within 10 m of any individual in the group. Any individual who surfaces more than 10 m outside of any group member is considered to have left the group. Average and median group size for adult females is 4–5 individuals (Mann *et al.*, 2000). Maternal and calf behaviours were observed continuously but scored by either point sampling (1 min intervals) or predominant activity sampling (2.5 min intervals, Mann, 1999). Social events were noted continuously (frequency sampling) when possible for the focal dyad and on an *ad libitum* basis for non-focal individuals. For the latter, the direction of interactions (actor–recipient) were used, but rates of socio-sexual interactions were not calculated. For focal mothers and calves, the type of social behaviour was indicated every minute (sexual behaviour, various types of play, petting, rubbing, etc.), while event frequencies (mounts, body parts involved in petting) were recorded continuously or when observed. Activity budgets are fairly accurate, but event rates are an underestimate since some sub-surface activities were not observed or because participants could not be readily identified during some polyadic interactions.

### Socio-sexual behaviour

Vasey (1995) defines homosexual behaviour as genital contact and/or manipulation involving same-sex individuals. The current study defines four behaviours – 'mounting', 'goosing', 'push-ups', 'petting' – as 'socio-sexual' when genital contact is involved. These activities are considered to be 'homosexual' when between same sex partners.

- *Mounting* is observed in three basic forms: dorso–ventral (Figure 4.1a), lateral–ventral and ventral–ventral. During lateral–ventral mounts, the mountee turns on-side, facilitating the mount. During ventral–ventral mounts, the mounter swims belly-up under the mountee. Mounts were mostly dorso–ventral.
- *Goosing* occurs when the actor brings his or her beak into contact (gently or not so gently) with the genital area of the recipient (Figure 4.1b). This has also been called 'beak to genital propulsion'.
- *Push-ups* occur when one dolphin pushes up the genital area of another with his or her head, usually so it clears the water.
- *Socio-sexual petting* is defined by pectoral fin-to-genital contact, when one dolphin either strokes the genital area of another dolphin with his or her pectoral fin (Figure 4.1c), or inserts the pectoral fin into the genital slit of another dolphin. Genital contact is one type of petting,
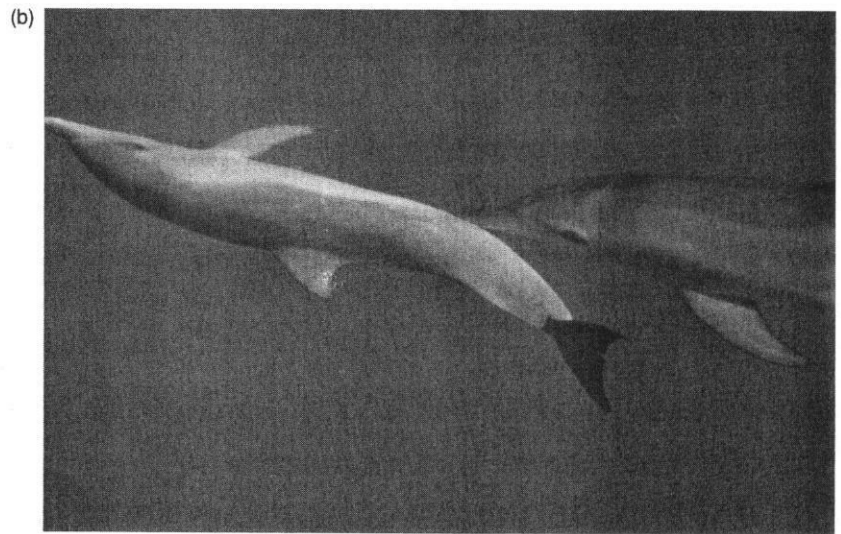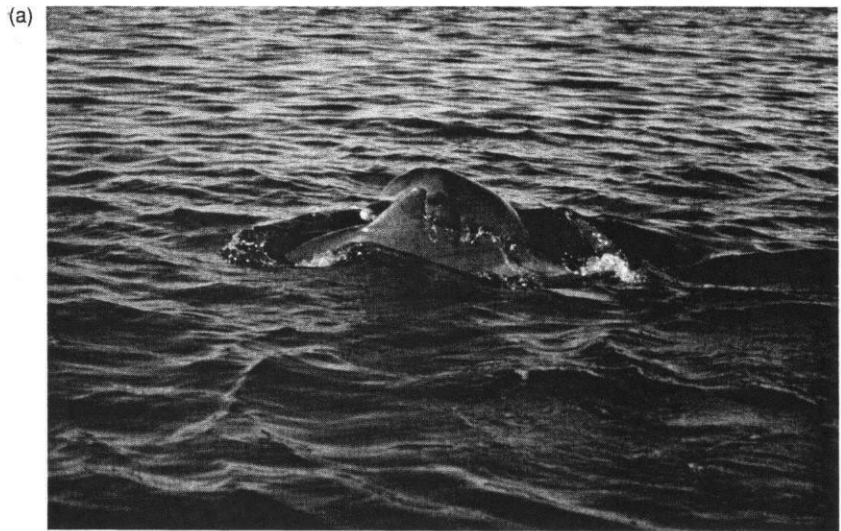
**Figure 4.1.** Socio-sexual behaviour in bottle-nosed dolphins. (a) Typical dorsal–ventral mount position. (b) Juvenile female with her beak to the genital area of a female calf (gentle goosing). (c) Pectoral fin petting of the genital area. (d) Interactions in a group of 11 immature males. As illustrated by the photograph, the actors and recipients are difficult to identify. At least four males were involved in the current interaction. The owner of the erection was not identified.

(c)

(d)
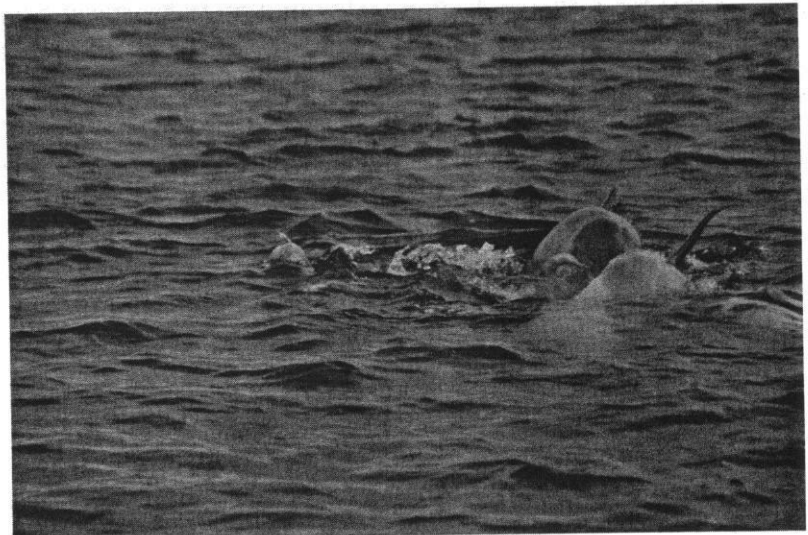
**Figure 4.1.** (*cont.*)

although other body parts are frequently involved during petting interactions. We can often observe petting, but not always specify the body parts involved. Thus, only those including specific contact with the genital area are included in this study.

*Rubbing* of the genital area on the body part of another dolphin is also a form of sexual contact, but this was infrequently observed except during mounts, push-ups or gooses and is therefore not considered a separate act. Because both

male and female dolphins have genital slits, males can easily achieve penile intromission with other males. However, this was so rarely observed that it was not included in our analysis. Intromission is generally difficult to confirm because it lasts for a few seconds only, is underwater, and the body of the mounter is pressed against the mountee. Genital inspections, when the inspector brings his/her beak close to the genital area of another dolphin without touching, often occur, but are not considered sexual by this definition.

Each mount, petting of genital area, goose or push-up was considered one socio-sexual event. Events were considered part of a socio-sexual bout when they occurred within 5 min of the last event, involved at least one of the same participants and were not interrupted by non-social behaviour (for example, forage). Rates, calculated only for focal individuals, are underestimates because not all events were recorded, especially during long bouts of socio-sexual behaviour, which typically involved all or mostly male participants.

Several factors lead to potential underestimates. During long bouts, the dolphins tend to change direction often, making it difficult for observers to identify the actor and recipient (Figure 4.1d). Another bias concerns petting, which was classified as socio-sexual only if the observer was able to determine contact with the genital area. However, this was not always possible because of the difficulty in viewing which body parts are involved. Since females tended to engage in more petting interactions than males, the rate of female–female socio-sexual behaviour might also be underestimated.

### Partner availability

Fission–fusion social systems such as in Shark Bay are difficult to quantify because the group composition is fluid and ever-changing. Since individuals who interact are likely to be together in social groups in the first place, preferential grouping is correlated with preferential relationships. For example, during or just prior to socio-sexual interactions, the participants often segregate themselves into a separate group for varying periods of time. Calves are not like most mammals with extensive parental care in that they venture hundreds of meters from their mothers and join groups without them. Compared with terrestrial mammals, the costs of locomotion are low for dolphins (Williams et al., 1993), facilitating these separations and associations with others. Theoretically, a calf has numerous social options, for at least brief periods of time when away from the mother.

I computed the bias in interactions between individuals of different sex–age classes, the proportion of female and male calves, juveniles and adults in the entire population of frequently sighted individuals (>20 times) whose sexes were known for a nine-year period (1991–1999). The entire pool of 305 individuals

varied depending on births and deaths, ranging from 253 to 197 in a given year. The proportion of each sex class varied little from year to year, no more than 2%. On average, the population consisted of 6.7% (SD = 0.2) female calves, 8.8% male calves (SD = 0.5), 17.9% juvenile females (SD = 0.4), 16.0% juvenile males (SD = 0.9), 27.0% adult females (SD = 0.8) and 23.5% adult males (SD = 0.6).

These proportions were used as the pool of available partners for focal calves and were contrasted with the sex difference for each age class. Using the average number of animals across all years, this meant that each year a focal calf had, on average, 19 potential male calf partners, 35 potential juvenile male partners, 52 potential adult male partners, 15 potential female calf partners, 39 potential juvenile female partners and 60 potential adult female partners. The mother was excluded from the analysis.

A likelihood score for each bout was then computed, taking into account the number of partners in each age and sex class involved for each bout, and the number of individuals in each age and sex class for the population. Basically, the expected likelihood of an interaction given the group composition is subtracted from the observed. The resulting value is between 1 and −1, where a positive value means that a male was more likely to be the partner than expected and a negative value means that a female was more likely to be the partner. This was contrasted within age class but between sexes to see if male or female calves preferred male or female calves, juveniles or adults as partners. These were averaged for each focal calf to compute an overall score. The sample size refers to the number of focal calves that interacted with either a male or female in each age class. Values could not be computed for calves who did not interact with individuals in a given age class. For example, if a calf did not interact with any juveniles, then a preference score for male vs. female juveniles could not be calculated. The Mann–Whitney U test was used to examine sex differences. The average value was also converted to binary scores for chi-square analysis of overall preference. Even though calves associate with far fewer individuals (averaging 34, range = 0–82; Gibson and Mann, 2003) than the total population available to them, the difference between observed and expected would not be affected by total number of associates, only by relative number of males and females within an age class.

## Results

### Events and bouts of socio-sexual behaviour

Data for focal calves and mothers included 1597 events during 245 bouts of socio-sexual behaviour. Focal calves or their mothers were involved in all but 11 bouts which were *ad libitum* and not used to calculate rates. Of the 1545

## Socio-sexual Events
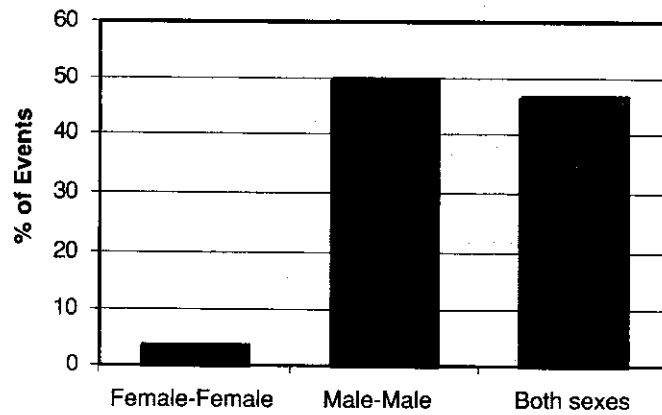
Figure 4.2. Proportion of socio-sexual events ($n = 1597$) that were homosexual or bisexual.

## Socio-sexual bouts
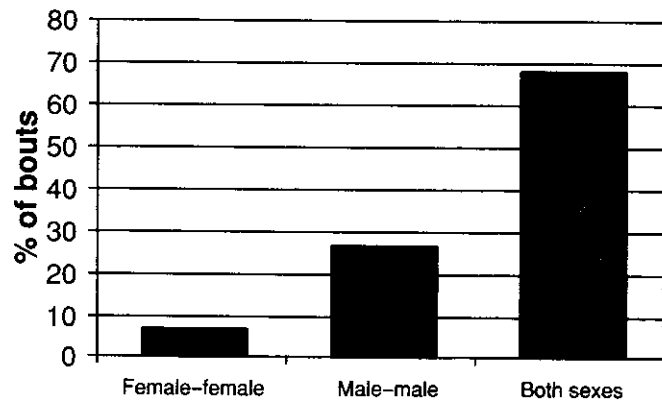
Figure 4.3. Proportion of bouts that were exclusively female, exclusively male or bisexual. Bout = events clustered within 5 min intervals ($n = 245$).

events involving males, at least one of the male participants was observed with an erection 15.5% of the time; this is an underestimate since erections are brief and difficult to see when the genital area is underwater or pressed against another individual. Most socio-sexual events were mounts (66.5%) and gooses (25.3%). Push-ups (3.7%) and petting (4.6%) were least common.

Half of all socio-sexual events were homosexual (Figure 4.2). This can largely be attributed to the fact that male–male interactions were more common. Out of 245 bouts (Figure 4.3), the majority (67.4%) involved both males and females; 26.1% involved males only and 6.5% involved females only. The types of socio-sexual interactions differed between the sexes. Nearly half of female–female

Table 4.1 *Sex-ratio percentages of actors to recipients for each socio-sexual event (n = 1597). M = male, F = female*

| | Recipient | | | | |
|---|---|---|---|---|---|
| Actor | F | FF | M | MM | Events (n) |
| F | 47.6 | 1.0 | 51.4 | 0.0 | 105 |
| FF | 0.0 | 0.0 | 100.0 | 0.0 | 3 |
| MF | 68.8 | 0.0 | 31.2 | 0.0 | 16 |
| M | 47.6 | 0.0 | 52.1 | 0.3 | 1037 |
| MM | 28.1 | 0.0 | 71.7 | 0.2 | 424 |
| MMM | 60.0 | 0.0 | 40.0 | 0.0 | 10 |
| MMMM | 100.0 | 0.0 | 0.0 | 0.0 | 2 |

bouts involved socio-sexual petting (43.8%). In contrast, none of the male–male bouts involved socio-sexual petting. Of all petting interactions involving the genital area (21 events), seven were female–female (33.3%) and 14 were male–female (67.7%). Six of the seven petting interactions between females were between four mother–daughter pairs. Five of the 14 male–female interactions involved a single male calf with his mother.

Although females participated in socio-sexual bouts, males were likely to continue the interaction after the female left and be more active. Sex ratios of actors versus recipients did also reveal a greater participation of males (Table 4.1). In a total of 1597 events, there were only five where two individuals were the recipients at the same time (all same-sex interactions), but males commonly acted together against a single individual. Females were the recipients in 683 of all events (42.8%), whereas male recipients constituted 914 events (57.2%). Females were actors in 8.1% of events and males in 94.4%. Males were both actors and recipients in the majority of events. In all cases, male–male interactions were more common than male–female for both dyadic and triadic interactions. Synchronized acts with more than one actor were recorded in 455 events (28.5%).

The more active role of males is also evident, if events are broken down by age and sex class (Table 4.2). The 42 events that involved both a calf and juvenile as actors simultaneously were added to the juvenile–juvenile category, whereas five cases of more than one recipient in an event were excluded.

Median partner number for heterosexual and male same-sex bouts was three, but all cases of female same-sex bouts involved two individuals. Male–male socio-sexual bouts never involved more than four participants, but dyadic and triadic interactions were equally common. Heterosexual bouts were typically dyadic, but groups of 3–4 were also common (Table 4.3).

Table 4.2 *Proportion of socio-sexual events by age and sex class (divided by the total for a specific age-sex class of actor) (n = 1572). M = male F = female*

| Actor | F calf | F juvenile | F adult | M calf | M juvenile | M adult | Events (n) |
|---|---|---|---|---|---|---|---|
| | | | Recipient | | | | |
| F calf | 22.9 | 2.1 | 31.3 | 41.7 | 2.1 | 0.0 | 48 |
| F juvenile | 19.2 | 7.7 | 11.5 | 53.9 | 7.7 | 0.0 | 26 |
| F adult | 36.7 | 6.7 | 0.0 | 56.7 | 0.0 | 0.0 | 30 |
| M calf | 17.8 | 10.0 | 20.1 | 42.3 | 4.8 | 5.0 | 926 |
| M juvenile | 23.6 | 9.0 | 16.9 | 49.4 | 1.1 | 0.0 | 89 |
| M adult | 10.5 | 10.5 | 10.5 | 57. 9 | 0.0 | 10.5 | 19 |
| MM calves | 7.7 | 8.0 | 8.4 | 65.0 | 10.5 | 0.3 | 323 |
| FF calves | 18.6 | 6.9 | 21.6 | 34.3 | 18.6 | 0.0 | 102 |
| MM adult | 5.9 | 11.8 | 11.8 | 70.6 | 0.0 | 0.0 | 17 |

Table 4.3 *Percentage of socio-sexual bouts involving females (F) only, males (M) only, and both sexes*

| Sex | Socio-sexual bouts | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Overall |
|---|---|---|---|---|---|---|---|---|---|
| | | Number of participants | | | | | | | |
| FF | n | 16 | | | | | | | 16 |
| | Mean duration (min) | 2.0 | | | | | | | 2.0 |
| | SD duration (min) | 1.6 | | | | | | | 1.6 |
| MM | n | 30 | 32 | 3 | | | | | 65 |
| | Mean duration (min) | 9.0 | 17.1 | 20.3 | | | | | 13.6 |
| | SD duration (min) | 9.2 | 10.2 | 19.6 | | | | | 10.9 |
| MF | n | 78 | 45 | 25 | 11 | 3 | 1 | 1 | 164 |
| | Mean duration (min) | 3.1 | 9.7 | 17. 8 | 18.6 | 39.0 | 75.0 | 8.8 | 9.3 |
| | SD duration (min) | 4.5 | 10.1 | 12.0 | 18.2 | 20.7 | – | – | 12.7 |
| Total | n | 124 | 77 | 28 | 11 | 3 | 1 | 1 | 245 |
| | Mean duration (min) | 4.3 | 12.8 | 18.1 | 18.6 | 39.0 | 75.0 | 8.8 | 9.9 |
| | SD duration (min) | 6.3 | 10.7 | 12.5 | 18.2 | 20.7 | – | – | 12.1 |

Bouts involving one male and one female were typically short, but with more participants they were longer (usually because more males were involved). The average bout length was 9.9 mins (SD = 12.1; median = 5.0; range = 0.1–75.0). These bouts often involved multiple dolphins and partner exchanges. Up to eight individuals participated in socio-sexual bouts and up to five in a single event. The maximum for one event was four juvenile males simultaneously mounting or attempting to mount an adult female.

*divided by the total for*

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| M adult | Events (n) |
| --- | --- |
| 0.0 | 48 |
| 0.0 | 26 |
| 0.0 | 30 |
| 5.0 | 926 |
| 0.0 | 89 |
| 10.5 | 19 |
| 0.3 | 323 |
| 0.0 | 102 |
| 0.0 | 17 |

*males (M) only,*

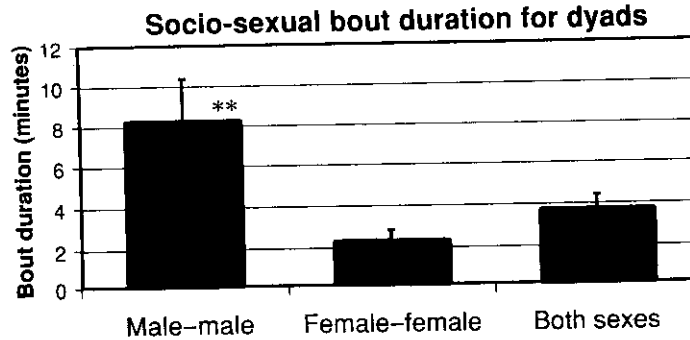| 8 | Overall |
| --- | --- |
| | 16 |
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Figure 4.4. Mean bout durations and SE for dyads: male–male, female–female, male–female.

To increase statistical independence of bouts for comparison of bout length, only one bout per day that involved the same participants was used. If there were two such bouts, the one with longer duration was chosen. This method reduced the sample to 187. If we compare dyadic bouts only (thus controlling for the number of partners; Figure 4.4), male homosexual bouts lasted significantly longer than female homosexual bouts ($t = 2.06$, df $= 34$, $p = 0.047$) and heterosexual bouts ($t = 2.53$, df $= 72$, $p = 0.014$). However, female homosexual bouts were not significantly longer than heterosexual bouts ($t = 0.95$, df $= 62$, $p = 0.34$). For bouts that involved three individuals, male homosexual bouts (17.6 min, SD 2.1) were significantly longer than heterosexual bouts (10.9 min, SD $= 1.6$; $t = 2.31$, df $= 54$, $p = 0.025$).

### Focal calves

Socio-sexual behaviour ('sex play') was often observed but significantly more common among male calves (mean $= 2.4$, SD $= 0.7$ events per hour, median $= 1.1$, range $= 0.0$–10.1) than female calves (mean $= 0.1$, SD $= 0.1$ events per hour; median $= 0.0$, range $= 0$–1.3; Mann–Whitney U $= 398.5$, $p < 0.001$, $n = 46$ calves).

The focal male was the actor in 79.8% of the events (SD $= 5.1$%, median $= 80.4$%). The focal female was the actor in 38.2% of events (SD $= 12.6$%, median $= 29.9$%), but the event rate was extremely low for most females. The three females who were actors more than recipients had only three or fewer events each. Even so, the difference in ratios between actor and recipient was significant between sexes (Mann–Whitney U $= 111.5$, $p = 0.015$, $n = 24$). Of 46 focal calves, 30.4% were not seen engaging in any socio-sexual behaviour. Nine of the 14 abstainers were females (34.6% of females), and five were males (26.3% of males).

### Focal mothers and kin

Focal mothers were much less sexually active than their calves, but if they did engage in socio-sexual behaviour, their calf was almost always the partner. Average adult female (lactating) rate of socio-sexual interactions was 0.06 per hour (SD = 0.10, range = 0–0.34). In other words, one would have to observe a lactating (non-cycling female) for 17 hours, on average, before observing a single socio-sexual interaction. Fourteen of 26 mothers were not seen engaging in any socio-sexual behaviour. Of the 126 events (63 bouts) that involved a focal mother, nearly all, 91.3% of events and 92.0% of bouts, involved her offspring exclusively as either the actor or recipient. Only 0.8%, one event (petting of the genital area) involved an adult male with the focal adult female and ten socio-sexual events (7.9%) were between the focal female and unrelated juveniles or calves.

Fifty-eight socio-sexual bouts involved mothers with their calves only. Five focal female calves engaged in ten bouts with their mothers. All 13 male calves observed engaging in any form of sexual behaviour also mounted their mothers (44 bouts). The remaining four bouts also involved mother–calf pairs, but not during focal observations for that dyad. On average, female calves had socio-sexual interactions with their mothers once every 72.5 hours. Male calves had socio-sexual interactions with their mothers once every 14.2 hours.

Socio-sexual behaviour also occurred with other kin. For example, one male calf mounted his grandmother 67 times and another mounted his maternal sister five times. Eight maternal brother–sister pairs were never observed engaging in sexual behaviour. One pair of maternal brothers mounted each other 27 times, but five maternal brother dyads were not observed mounting each other. One female had a daughter by her own father, although in-breeding is generally quite low in the population (Krützen et al., 2004b).

Paternity is known for 16 offspring in the population (Krützen et al., 2004b). Adult males rarely mount calves, but one recently weaned juvenile male was mounted frequently by his father during one bout of socio-sexual behaviour. Several juveniles had been socializing and the juvenile was on the periphery of the group and not directly involved. Two adult males joined the group and the juvenile's father mounted his son (achieving intromission) repeatedly for several minutes, while his son lay passively on his side.

### Socio-sexual interactions between same-sex partners

Only 3.7% of all socio-sexual events (n = 51 events, 16 bouts) involved only females (cf. Tables 4.1, 4.2). Nearly all events were dyadic, but one event

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involved three females. In eight bouts, adult females were the actors (either mounting, goosing or petting the genital area of another female). In all cases, a juvenile or calf female was the recipient. No homosexual interactions involving two adult females were observed in this study. In four of the eight bouts, the recipient was also the young daughter of the actor. Calves also directed socio-sexual behaviour towards immature and adult females in 12 bouts. Five of those involved daughter–mother pairs. Roughly half of all female homosexual interactions involved mothers and daughters, but such interactions were infrequent.

Male homosexual interactions typically involved more than two individuals (cf. Tables 4.1, 4.2). Another striking aspect of these interactions is that dolphins of all age and sex classes direct most of their socio-sexual interactions towards male calves. Male calves were the most common actors and recipients in socio-sexual events.

### Synchronous socio-sexual behaviour

In 28.9% of 1572 events, two or more dolphins simultaneously acted on a third (cf. Tables 4.1, 4.2). Nearly all of the actors were male (95.8% of 455 events), with only three cases where females acted synchronously (all involved juvenile females mounting or goosing a male calf, 0.7%) and 16 where a male and female synchronously acting on a third (3.5%). Of the 436 events in which two males acted simultaneously in mounting, goosing or pushing-up (but never petting) a third, a male, was the recipient in 70.4% of the events. Most synchronized behaviour involved pairs of male (93.2%) with 12 cases (2.6%) when three or four males attempted syncronized matings, gooses or push-up of a single individual. Thus, most synchronized socio-sexual interactions involved males exclusively.

### Partner preferences

Preferences within each age class were examined to determine if male or female calves biased their interactions towards calves, juveniles or adults by sex, given their availability in the population. For an individual to be included in the analysis, s/he had to interact with at least one member of the age class. First, mean scores for observed minus expected (see Methods) were ranked to test for calf sex differences in partner preferences. Male and female calves did not significantly differ in their preferences (Mann–Whitney U, all NS). Second, these scores (positive score = male preference and negative score = female preference) were converted to binary scores to examine whether calves interacted significantly more with males than females within an age class. Calves of both sexes showed a significant preference for interacting with male calves than

with female calves (chi-square = 8.9, df = 1, $p$ = 0.003, $n$ = 22). For 20 calves that interacted with either a male or female juvenile, there were no significant preferences (chi-square = 1.8, df = 1, $p$ = 0.18). Similarly, for ten calves that interacted with adults (excluding the mother), there was no significant sex preference (chi-square = 1.6, df = 1, $p$ = 0.21).

### Symmetry of male–male socio-sexual relationships

Most male–male interactions among calves were symmetrical (2.7 dyads, SD = 1.5), with regular role exchanges between the pair in terms of actor and recipient (Table 4.4). All calves had at least one symmetrical relationship. Male calves averaged 1.7 asymmetrical relationships (SD = 1.3). Individual differences were obvious; for example, COO had six symmetrical relationships and no asymmetrical, whereas SMO and SRY had more asymmetrical relationships than symmetrical. Overall, male calves who interact regularly with other males tend to form socio-sexual relationships (defined as males they mounted with more than five times) with up to seven males (average 4.2 males, SD = 1.8).

### Discussion

In bottlenose dolphins, male calves engage in higher rates of both socio-sexual and homosexual behaviour than female calves and adults. Male homosexual bouts were also significantly longer than either female–female or male–female socio-sexual bouts and male calves were more often actors than recipients. Female homosexual interactions were infrequent, characterized by petting and were typically dyadic. Male socio-sexual behaviour among immatures (calves and juveniles) was characterized by mounting, goosing, synchrony and multiple participants (typically involving three or more individuals), not unlike adult male alliance behaviour. This suggests that these behaviours help mediate the development of male–male bonds. In addition, polyadic, particularly triadic interactions, are likely to help males practice adult courtship and sexual behaviour.

Bottlenose dolphin calves engage in very high rates of socio-sexual contact. The event rate for males (2.38/h) is nearly 40 times that for wild female bonobos (0.06–0.03 /h, Hohmann and Fruth, 2000), a species already characterized as hypersexual. Female calves engage in lower rates of socio-sexual contact (0.15/h), but still more than twice as often as that reported for bonobo females. In addition, the rate of bottlenose dolphin calf socio-sexual behaviour is higher than that reported for wild and captive primates during comparable developmental periods (for example, Brown and Dixson, 2000).

Table 4.4 Symmetry and asymmetry patterns of mounts for ten male calves and their primary male sexual partners. Only individuals with 10 or more mounts are shown. For each pair with at least five interactions, the proportion that were in one direction determined a symmetry score. For example, COO mounted SMO 110 times which represents 59% of the mounts involving SMO. Symmetrical dyads = scores of 25–75% (bold); assymetrical dyads = scores of 0–24% or >75% (underlined and italicized)

| | | Recipients | | | | | | | | | | | | | | | | | | Relationships (n) that are | |
| | | M calves | | | | | | | | | | M juveniles | | | | | | M adults | | M adults | |
| Actors | | COO | DIN | JBO | JSE | NOM | QUA | RAB | SMO | SRY | URC | ARC | BOO | DAG | EDG | LAN | LIN | SHA | WAV | Symmetrical dyads | Asymmetrical dyads |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M calves | COO | | 13 | | | | | 35 | 110 | | | 3 | | 8 | | | | 11 | 5 | 6 | 0 |
| | DIN | | | 16 | | | | | | _22_ | | | | | | | | | | 1 | 1 |
| | JBO | 1 | | | | 19 | | | | 42 | | | | | | | | | | 2 | 1 |
| | JSE | 27 | | | | | | 67 | _44_ | _24_ | | 14 | | _7_ | _1_ | | | | | 3 | 3 |
| | NOM | 1 | | 23 | | | | | 43 | | | 14 | | | | _11_ | | | | 2 | 1 |
| | QUA | | | | | 12 | | | 14 | | | | | | | | | | | 2 | 0 |
| | RAB | 52 | | | 37 | | | | _44_ | 13 | | 2 | | _13_ | | | 6 | | _29_ | 4 | 3 |
| | SMO | 75 | | | | | | | | _0_ | | 17 | | | | | | | | 2 | 3 |
| | SRY | | | 26 | | | 29 | _7_ | _0_ | | _9_ | | | _0_ | _11_ | | | 1 | | 2 | 3 |
| | URC | _5_ | | _3_ | | | | 1 | | 19 | | | | | | | | | | 1 | 2 |
| M juveniles | ARC | | | | | | | 28 | | | 5 | | | | | | 3 | | | 1 | 0 |
| | BOO | 2 | | | 7 | | | 1 | 11 | | | | | | | | | | | 2 | 0 |
| | DAG | 9 | | | _0_ | | | _1_ | | | | | | | | | | | | 1 | 2 |
| | EDG | _5_ | | | | | | | _14_ | | | | | | | | | | | 0 | 2 |
| | LAN | | | | _0_ | | | 2 | | | | | | | | | | | | 0 | 1 |
| | LIN | | | | | | 4 | | | | | | | | | | | | | 1 | 0 |
| M adults | SHA | 12 | | | | | | | | 1 | | | | | | | | | 3 | 1 | 0 |
| | WAV | 11 | | | | | | _2_ | | 1 | | | | | | | | 1 | | 1 | 1 |

A number of hypotheses have been proposed to explain homosexual behaviour in animals (review in Vasey, 1995), such as group stability, tension reduction, reconciliation, dominance assertion, bond/alliance formation and mating practice. Little is known about hormonal or other proximate factors that might correlate with the hypersexual activities of male dolphin calves. But the patterning of male behaviour, including partner selection and synchronicity with other males, suggests that male homosexual behaviour is more than a hormonal by-product.

One functional explanation maintains that socio-sexual behaviour could enhance *group stability* or solidarity. However, with a fission–fusion social structure, groups are typically unstable, except between members of a stable adult male alliance. Homosexual behaviour is therefore unlikely to enhance group stability or solidarity but – as will be discussed below – may help foster and strengthen long-term alliance formation and maintenance between certain individuals.

*Tension-reduction* around food, other resources or during social conflict, is also an unlikely explanation, since socio-sexual behaviour rarely occurs in connection with hunting activities, which in Shark Bay is a solitary endeavour (though more than one dolphin may be attracted to large schools of fish) and dolphins do not share prey.

Similarly, *reconciliation* does not seem to be a likely function explanation. Although there seem to be competitive elements to socio-sexual interactions, most occur in a playful context and agonistic interactions involving calves are rare (Scott *et al.*, 2005).

Subtle formation of *dominance relationships* between males may occur during this early play period, but such relationships would be difficult to detect. Physical asymmetries would be reinforced during socio-sexual play and male socio-sexual behaviour may acquire more pronounced rank-related functions at later stages of development. Whether those mounted are generally subordinate to the mounter or actor is unknown and needs further study. Several male calves were mounted more often than other male calves. The receiver of mounts, especially when more than two males were involved, frequently displays with slaps of various body parts on the water, and belly-ups to avoid being mounted. The actors frequently chase the receiver who attempts to reverse roles by swimming behind the others. These attempts sometimes result in circle swimming, with two trying to remain behind a third, and the third trying to swim behind the others. Being the receiver appears to be the less desirable position for males, although females are sometimes observed swimming in front of males, apparently inviting males to chase and mount. Gooses and push-ups on the genital area can be forceful and calves clearly compete for the 'behind' position. The sequence of these interactions needs to be more systematically quantified. This is difficult

given that dolphins move very quickly in the water, go in and out of view, and identification of dorsal fins needs to be rapid for determining who is the actor and who is the receiver (see Figure 4.1d). In non-human primates, the literature is equivocal regarding the relationships between mounting and rank, with some studies finding a correlation, others not (reviewed by Vasey, 1995). In the single quantitative study of captive adult male bottlenose dolphins, the more dominant male mounted the subordinate more often than reverse (Östman, 1991).

Similar to the view presented by Smuts and Watanabe (1990) for savanna baboons, *Papio anubis*, bottlenose dolphin male–male socio-sexual interactions appear to be more like negotiation rather than dominance assertion, especially given the duration and frequent role exchanges. Although rank within eventual alliances may be important, rank between alliances is likely to be equally important. The development of alliances would be facilitated by establishing reciprocity or 'trust' (cf. Zahavi, 1977) through repeated interactions and by providing an opportunity to assess the manoeuvrability and social skills of potential partners. For example, male partnerships in socio-sexual activities and *long-term bonds* could be established through taking turns as actor and recipient (symmetrical relationships, as above) and practicing synchronous movement in chasing, mounting, displaying and goosing other males or females. Trust is crucial to these interactions, because the recipient of socio-sexual behaviour is vulnerable by exposing the belly and genital area to one or more males in the advantaged rear position. Role exchanges may therefore be important for establishing trusted allies. A more detailed longitudinal study of male–male relationships across the lifespan is needed to understand how same-sex interactions relate to *bond* or *alliance formation*. Relationship negotiation, mediated by socio-sexual behaviour, may be particularly significant when there is multi-level alliance formation (alliances of alliances), a pattern found only in humans and Shark Bay bottlenose dolphins (Connor *et al.*, 1992a).

Most of the bonds that develop during infancy remain strong post-weaning, up to 16 years of age, when alliances begin to stabilize (Connor, unpublished data). Males may change their associations throughout development, but clearly male social relationships begin to form at a very early age, long before the formation of stable alliance partnerships. The number of symmetrical socio-sexual bonds formed in infancy averaged 2.7, approximating the typical size of first-order alliances (Connor *et al.*, 1992a).

A longitudinal study of alliance development in males with varying degrees of social experience as calves would provide insights concerning the importance of early male–male interactions. Early social experience is influenced by the sociality of the mother and the local cohort available, particularly male calves of the same age. All four calves whose mothers were sponge-carriers (a specific

foraging strategy where the mother carries a marine sponge on her beak and uses it to ferret fish from the seafloor; Mann and Sargeant, 2003) were fairly solitary, spending over 80% of their time alone with their mothers and had no socio-sexual interactions. Solitary females, such as the sponge-carriers, may afford few social opportunities for their calves. Although calves have associates independent from their mothers, the pattern of calf sociality (number of associates and proportion of time in social groups away from the mother) is predicted by the mother's sociality (Gibson and Mann, 2003) However, calves vary in their tendency to separate from the mother (Mann and Watson-Capps, 2005), even though potential social partners may be a few hundred meters away. This could have long-term consequences for calves. As Crews (1998) points out, animals age as they gain socio-sexual experience, but do not necessarily gain such experience with age. Without experimental manipulation, it would be difficult to assess the effects of age and socio-sexual experience separately, or what determines male alliance size, stability, kinship and structure.

Bottlenose dolphin homosexual behaviour differs from that of most other mammals. Few species have homosexual interactions as often as heterosexual (Vasey, 1995). Bottlenose dolphin male calves have higher rates of same-sex interactions than opposite sex interactions. In contrast to primates and virtually all reports of mammalian sexual behaviour, a high proportion of sexual interactions included multiple partners and synchronous mountings, in which two individuals mount a third. Synchronous gooses and push-ups were also observed, as were leaps and displays. Male trios or two males with a female as the mountee, were the most common combinations.

The fact that males were typically acting in pairs or trios is consistent with the patterning of adult male consortships, in which the males mate with and defend a female for a period of time (Connor et al., 1992a,b, 1996). Four or more males have never been known to consort with an individual female. Males do, however, form second-order alliance relationships with more than three males or form more labile first-order relationships with larger groups of males (Connor et al., 1999).

Socio-sexual interactions are also likely to benefit males by providing opportunities for practice mating, which may be critical to male reproductive success. Practice may be more important in dolphins than terrestrial mammals because cetaceans are constantly in motion and females can easily turn belly-up or away from males during mating attempts. Despite the fact that adult males clearly coerce females to stay with them during some consortships and despite hundreds of hours of intensive observation of females in consortships by my colleagues Richard Connor and Jana Watson-Capps, a successful copulation (intromission), forced or cooperative, has not been observed. During mounts, it is nearly

impossible to see if intromission occurs. Since synchronous behaviour and mounts are characteristic of adult courtship, synchronous socio-sexual practice may therefore be important.

Although relations between members of an alliance are clearly cooperative, with males cooperating to capture and retain cycling females, while keeping competing alliances away from the female, males are also in direct competition over fertilizations within an alliance. Thus, Shark Bay dolphin males are cooperating and competing at multiple levels in a fluid, three-dimensional environment, placing additional demands on socio-sexual practice not found in terrestrial animals. Females may need to practice avoiding unwanted matings, but this would favour more heterosexual than homosexual interactions. Most female homosexual interactions were between mothers and daughters, were dyadic and involved petting – possibly analogous to primate grooming. This would suggest that female same-sex interactions were less 'sexual' in nature and more affiliative.

Thus, homosexual interactions in bottlenose dolphins are expected to be much more common amongst males. They seem to serve multiple functions, although the exact fitness consequences, if any, are unknown. Our understanding of the social structure and relationships in a larger context would suggest that male–male socio-sexual interactions are significant for the development of close bonds or alliance formation, negotiating dominance relations within and between eventual alliances, and practicing courtship behaviours for adulthood.

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