

A Sex-Specific Affiliative Contact Behavior in Indian Ocean Bottlenose Dolphins, *Tursiops* sp.

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Abstract

A variety of signals are employed by animals to establish, mediate and advertise social bonds. Gentle contact behaviors, such as grooming in primates, are an important class of affiliative signals that may provide direct benefits (e.g. stress reduction, parasite removal) in addition to their signal information. Unlike other kinds of signals (e.g. male displays) examples of affiliative contact behaviors restricted to one sex are rare. Here we describe a strongly sex-biased affiliative behavior 'contact swimming', in female bottlenose dolphins in Shark Bay, Western Australia. Females were more likely to be observed contact swimming than males and the presence of males likely influenced this behavior. This is surprising given that female relationships have been characterized as weak. Female dolphins are sometimes herded and harassed by males and contact swimming occurs most often between females in male-biased groups. Contact swimming may serve as a signal of cooperation between females. Possible direct benefits include stress reduction and assisted locomotion.

Introduction

With the evolution of social living came the problem of forming, maintaining, advertising, and repairing social bonds between individuals (e.g. de Waal 1986, 1993). Affiliative contact behaviors such as grooming and socio-sexual behavior play an important role in the expression and negotiation of social bonds. In rare cases an affiliative contact behavior may be restricted largely to one sex. Perhaps the best known example is found in bonobos (*Pan paniscus*). Female bonobos engage in a behavior, genital-genital or 'G-G' rubbing (Kuroda 1980), where 'usually two, but sometimes more, females clasp each other ventro-ventrally and rapidly rub the anteriors of the external genitalia together with a repeated lateral motion' (White 1996). Genital-genital rubbing is thought to play an important role in conflict mediation and bond formation (Kuroda 1980; de Waal

1987; Hohmann & Fruth 2000). Genital-genital rubbing can be viewed as an extension of male-female ventro-ventro sexual behavior. What might be the male equivalent, 'penis fencing', is apparently much less common (de Waal 1989). Sexual anatomy does not play a role in *contact swimming*, a gentle contact behavior described among bottlenose dolphins in captivity (Tavolga & Essapian 1957; Samuels & Tyack 2000) and in Shark Bay, Western Australia (Richards 1996; Mann & Smuts 1999; Connor et al. 2000a). In contact swimming, one dolphin rests its pectoral fin against the flank of another dolphin, behind the other dolphin's pectoral fin and below or just posterior to the dorsal fin. Contact swimming is a highly distinctive and visible behavior with no relative movement between the two dolphins; this lack of relative motion between the body of one individual and the pectoral fin of the other distinguishes contact swimming from other forms of pectoral fin

contact behavior, such as petting or rubbing (Richards 1996). Contact swimming is not seen nearly as often as petting and rubbing and is qualitatively different, requiring the two individuals to swim synchronously, sometimes for extended periods of time. Richards (1996) did not observe any contact swimming between adult males, but he could not test the sex-specific hypothesis because the data were largely from follows of females in female-biased groups. Using data from focal follows on males and females we test the hypothesis that contact swimming occurs more often between females than between males.

Contact swimming, or any other affiliative behavior, must be understood in the context of the dolphins' social structure, including patterns of grouping, sex specific bonds and mating strategies (Kappeler & van Schaik 2002). The Shark Bay bottlenose dolphin society is a very large (>600) open fission–fusion society. By 'open' we mean that within the ca. 250 km² study area that runs along a 40 km stretch off the east side of Peron Peninsula, we have detected no community boundary. Rather, there appears to be a continuous mosaic of overlapping ranges. Individuals associate in small groups that change in composition, often many times a day (Connor et al. 2000a).

The strongest bonds among adults (at least as reflected by association patterns) are between males that form complex hierarchical alliances in competition over estrus females (Connor et al. 1992a,b, 1999, 2001). Female associations are weaker but variable; some females are relatively solitary while others maintain a wide range of same-sex associates including some of moderate strength (Smolker et al. 1992). Variation in female 'sociability' may be explained, in part, by foraging habits, which vary markedly within the population (Connor et al. 2000a; Connor 2001; Mann & Sargeant 2003). The abundance of large sharks and shark bite scars on the dolphins suggests that predators exert some influence on group and bond formation in both sexes (Connor et al. 2000a; Heithaus 2001).

The year they conceive, females are consorted by male alliances for periods ranging from minutes to weeks. Many consortships are established or maintained with aggression or the threat of aggression (Connor et al. 1992a,b, 1996, 2000a). Over a breeding season, females are typically consorted by a number of alliances at different times over several months. These observations accord with captive findings that females are seasonally polyestrous (Kirby & Ridgway 1984; Yoshioka et al. 1986; Schroeder 1990; Schroeder & Keller 1990). Male testes are

large compared to mammals of similar size (but small for a delphinid) indicating an important role for sperm competition (Kenagy & Trombulak 1986; Connor et al. 2000b). Multiple cycles may reflect a female counterstrategy to male coercion to minimize the risk of infanticide and/or preserve a degree of mate choice (Connor et al. 1996).

Gentle contact (affiliative) behaviors play an important role in dolphin bonds as is typical of many terrestrial mammals (Aureli et al. 2002; DeVries et al. 2003). Both males and females engage in petting and gentle rubbing, terms that apply to a general class of affiliative behavior that involve contact between the pectoral fin of one individual and any part of the body of another (Tavolga & Essapian 1957; Mann & Smuts 1999; Connor et al. 2000a). One dolphin may actively move its pectoral fin against another or a dolphin may rub against another dolphin's stiffly held pectoral fin. These behaviors have in common relative motion between one individual and the pectoral fin of another. In contrast, contact swimming is characterized by a lack of relative motion between the two individuals (Richards 1996).

Methods

Shark Bay is located 25°47'S, 113°43'E in Western Australia; a long-term study of the Shark Bay dolphins was established in 1984 off of a fishing camp called Monkey Mia. The main study area currently extends 250 km² off the east side of the Peron Peninsula and includes over 600 animals that are identified by dorsal fin shape and markings. The habitat consists mostly of embayment plains (5–13 m), shallow sand flats (0.5–4 m), and shallow seagrass beds (0.5–4 m), bisected by deeper channels (7–13 m).

Data on *contact swimming* were extracted from *surveys* and *follows*. Surveys are typically brief (5–15 min), but sometimes longer (up to 1 h), encounters with dolphin groups where we record group composition, predominant group activity, location, environmental variables and all occurrences of specific behaviors. During follows, an individual dolphin or mother–infant pair was tracked for periods of 1 h or longer. Data on contact swimming were taken from surveys and follows on females and males. The duration of contact swimming events was recorded during male follows. Contact swimming is not a common behavior but is very striking when it occurs and it is easily distinguished from petting or rubbing. We define contact swimming as follows: one dolphin (actor) rests its pectoral fin against the flank of

another dolphin behind the other dolphin's pectoral fin and below or just posterior to the dorsal fin. The actor is positioned alongside and just above the other within 1/3 of a meter and 1/3–1/2 m behind the tip of the other's rostrum. As Richards (1996) noted 'The extreme closeness of two animals in a staggered position is immediately obvious even at some distance'. We recorded all occurrences of contact swimming in the focal dolphin's group during 535 h of follows on 21 males and 1752 h following 58 females.

We used two methods to count new cases of contact swimming between the same two individuals. To estimate the duration of contact swimming events, we counted a new case if (1) at least 5 min had elapsed since the previous case, or (2) during an interim of <5 min one member of the pair had engaged in contact swimming with another individual or (3) the individuals switched roles. The 5 min rule, roughly equivalent to two surfacing bouts, allows us to reliably ascertain whether two animals have broken off contact swimming, given that the dolphins are not continuously visible. To test for sex differences in contact swimming we employed a more conservative definition. We counted one case for any pair of individuals per day unless two events were separated by at least 5 min and there was a group composition change. With this restriction there were only six cases where the same pair was counted twice on one day.

For 53 contact swimming events using the conservative definition, there was at least one adult male and one adult female present. In five of the 53 events, only one adult female was present. In all five cases the female engaged in contact swimming with an immature female. These five cases were not used for the analysis. The remaining subset ($n = 48$) was used to determine the likelihood of two females contact swimming given the group composition of males and females. If there are more adult males present, the probability that a female would contact swim decreases if the behavior was randomly distributed between males and females. We calculated the probability that two adult females would contact swim for each event. This was done by taking the number of possible F:F pairs in the group and dividing it by the total possible number of pairs in the group (M-M, M-F, F-F). For example, in a group of three adult males and two adult females the probability of observing two females contact swim is 0.10 by random chance. We then tested if the observed number of F-F contact swimming pairs differed from expected.

Results

Using the less conservative definition, 62 contact swimming events were recorded during focal follows on males. Most were brief, lasting for a few surfacings to <5 min (Fig. 1). The longest bouts approached 20 min in duration (see also Richards 1996). During focal follows on females we recorded the longest bout in our records; a 34 min bout between two adult females.

The more conservative definition, which counts a new event between the same two individuals only if 5 min had intervened and there was a group composition change, produced 96 contact swimming events (36 from female focal follows, 36 from male focal follows and 24 from surveys). The overwhelming majority of contact-swimming events were between females and most of these were observed in male-biased groups (Fig. 2). In three events (3.1%) the sex of one partner was not known and the other was female. Adult males were present in 60 (62.5%) events and in 92 (95.8%) events adult females were present. As the total adult age structure of the population is 53% female and 47% male (Mann & Sargeant 2003), this represents an obvious sex bias.

Male-Male

Contact swimming between males was rare in our sample, accounting for only seven (7.3%) of the 96 events. Two cases involved two adult males. In one other event, an adult male contact swam with a juvenile. The remaining events involved juvenile/infant males but in all of these instances adult males were also present.

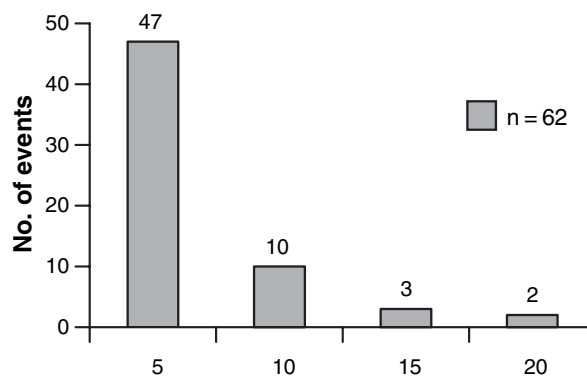


Fig. 1: Most contact swimming events lasted less than 5 min. The distribution of the durations (minutes) of 62 contact swimming events observed during 535 focal follow hours on males

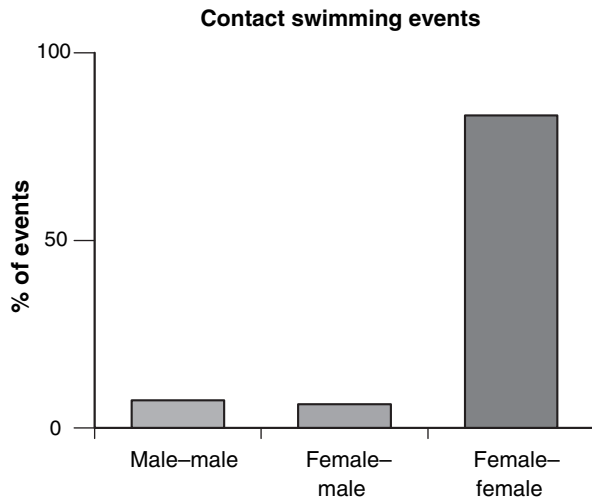


Fig. 2: Most contact swimming events occurred between two adult females. The percentage of contact-swimming events ($n = 96$) between adults that involved two males, a male and a female or two females

Female-Male

All six cases between males and females involved juvenile males, but three involved adult females (50% of female-male contact swimming) and three involved immature females (50% of female-male contact swimming).

Female-Female

The 80 events between two females accounted for 83.3% of the total. Of these, 19 female-female events (23.8%) involved an adult and juvenile female and 54 (67.5%) were between two adult females. Considering only contact swimming events

between two adults, 54 of 56 (96.4%) were between females. Of all contact swimming events involving adult females, 25 different adult females participated including 10 who were not part of the focal dataset.

To evaluate the sex difference in contact swimming we included only the 53 contact swimming events that occurred in groups with at least one adult male and female present and where at least one participant was an adult. Each of the 53 events had two participants for a total of 106 participants of which 94 were adults, including 92 females and only 2 males ($\chi^2 = 86.17$, $df = 1$, $p < 0.001$). This significantly greater participation by females in contact swimming occurred in substantially male biased groups (Fig. 3). To account for the bias, or number of adult males and females in each group, we used the 48 cases with two adult females available and at least one adult male available and calculated the mean expected probability of two adult females contact swimming. Based on the number of adult males and adult females present in each case the mean probability of two adult females contact swimming was $19.4 \pm 2.5\%$. In 40 cases (83.3%) two adult females contact swam; in seven cases (14.6%) an adult female contact swam with an immature female, and in one case an adult male contact swam with an immature female (2.10%). In sum, adult females were significantly more likely to contact swim with each other than expected ($\chi^2 = 125.48$, $df = 1$, $p < 0.001$).

Our estimate, that over 96% of contact swimming events among adults occur between females, is conservative. The analysis of contact swimming among adults excluded many more female than male participants. The analysis excluded same sex groups or groups with only one adult female. As a result, we excluded one event with two adult male participants

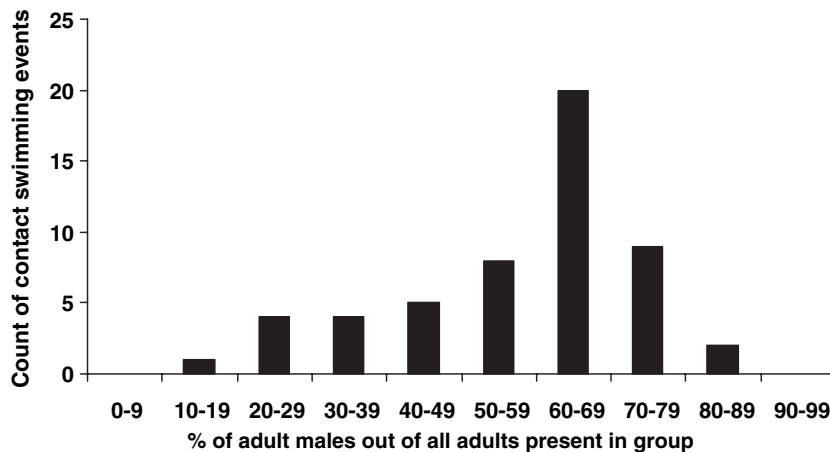


Fig. 3: Most contact swimming between females occurred in male biased groups. The proportion of adults that were males in each group for the 53 contact swimming events where at least one adult male and one adult female were present

and 22 events involving a total of 30 adult female participants. Further female bias was concealed by our conservative definition, allowing a pair to count only once a day unless separated by at least 5 min and a group composition change.

Discussion

Our analysis of focal data on females and males demonstrate that contact swimming is a behavior that occurs almost entirely between females, often in male biased groups (see also Richards 1996). We do not exclude the possibility that females vary in the extent to which they engage in contact swimming. We also found that males do, on rare occasions, engage in contact swimming (contra Richards 1996).

The lack of male participation in contact swimming is not because males do not touch each other. In a sample of 449 h of focal follows on 17 adult males, using the same 'less conservative' 5 min rule used to distinguish contact-swimming events, we recorded 302 cases of petting between identified adult males (= 0.67/h) but no cases of contact swimming.

What is the function of contact swimming? We suggest that contact swimming is a general affiliative signal, found mostly in females. Such a signal may occur in any context where it is important for one female to signal to another a willingness to establish, maintain or strengthen their bond. Male harassment represents a common, but not exclusive, context for the expression of such a signal between females. In this context contact swimming may also signal the females' cooperation to the males. Immediate costs and benefits may be required to maintain the honesty of a general signal of affiliation (Zahavi 1977, 1995). Here we consider three benefits (with associated costs) that might accrue to one or both females engaged in contact swimming, (1) reduced male harassment, (2) assisted locomotion and (3) reduced stress.

Richards (1996) favored the hypothesis that contact swimming represents cooperation between females to thwart male harassment. This hypothesis follows from the large number of contact swimming events that occurred with males present, the coercive tactics of males toward cycling females, and a few cases where the initiating of contact swimming was associated with the approach or aggressive behavior of males (Richards 1996). One might question whether the male bias in groups with contact swimming (Fig. 3) reflects a bias in the groups we observe, but in fact the opposite is true. We have

many more hours of follows on females and such groups contain a much higher percentage of females than males (Smolker et al. 1992). Richards (1996) also reported that cycling and pregnant females were over-represented in contact swimming events and that lactating females were under-represented. This likely reflects greater costs for females already burdened by lactation and a hitch-hiking calf. Further, cycling females participated in contact swimming more often than pregnant females (Richards 1996).

As Richards (1996) noted, some of his data do not support the male harassment hypothesis. For example, males were not present in one-third of his cases involving adult females of known reproductive state. Richards' solution to this discrepancy was to generalize the 'cooperation against males' hypothesis to include the need for females to practice contact swimming when males were absent. However, it seems unlikely that adult females would need to practice this relatively simple behavior. The two other immediate benefits we consider, assisted locomotion and stress reduction, have the advantage of not limiting benefits from contact swimming to the presence of harassing males.

The assisted locomotion hypothesis posits that the actor enjoys an energy benefit by traveling in the slipstream of the recipient (Norris & Prescott 1961; Richards 1996). Here the actor is essentially 'hitching a ride'; much like a young calf does swimming under or above its mother (Norris & Prescott 1961). Newborn calves typically swim in 'echelon' for more than 40% of the time in the first months of life, but rarely thereafter (Mann & Smuts 1999). This behavior, with the calf often resting the pectoral fin on the mother's flank, is similar to contact swimming described here. Richards (1996) did not include assisted locomotion in the extensive list of hypotheses he attempted to test because, 'although pairing probably offered the potential for riding' he never saw contact swimming animals 'go very far together' in the contact swimming position. Large costs and benefits are not required by our signaling hypothesis; they must be sufficient only to maintain the 'honesty' of the signal in female-female bonding.

The stress reduction hypothesis derives from the frequent occurrence of contact swimming during male harassment or herding and studies demonstrating that some types of affiliative contact reduce heart rate (macaques, Boccia et al. 1989; Aureli et al. 1999) or suppress the hypothalamic-pituitary-adrenal (HPA) axis in a variety of mammals (DeVries et al. 2003). In this regard contact swimming is similar to G-G rubbing in bonobos which is found most

often, but not exclusively, in potentially competitive feeding contexts. Genital–genital rubbing is thought to reduce tension but also to promote female–female bonding (Kuroda 1980; de Waal 1987; White 1996; Hohmann & Fruth 2000). Likewise, we suggest that contact swimming might reduce stress during male harassment and in other contexts, and also promote female–female bonding as a general signal of affiliation.

It is difficult to predict a priori whether one or both contact swimming participants would enjoy reduced stress (and, if only one, if it is the actor or receiver). In contrast, the hitch-hiking hypothesis predicts clearly that the actor enjoys a benefit and the recipient a cost. A combination of heart rate and HPA axis measures might be used to test the stress and locomotion hypothesis. We emphasize, however, that the stress reduction and assisted locomotion hypotheses are not mutually exclusive. A hitch-hiking individual might enjoy reduced stress in addition to lower locomotor costs and the two benefits could, in theory, be exchanged simultaneously (reduced stress for a ride). All three hypotheses suggest an additional cost borne by non-consorted females that remain in the group and participate in contact swimming with consorted females: an increased risk of aggression from males (see Richards 1996).

Why does contact swimming exist? More specifically, what benefit does contact swimming provide that the more commonly observed affiliative behavior, petting, does not? A possible answer is suggested by the assisted locomotion hypothesis. The energetic benefit derived from riding in the slipstream of another individual would not likely be obtained during petting. It also seems unlikely that the benefits posited for the stress reduction or reduced male harassment hypotheses would be similarly exclusive to contact swimming. However, contact swimming may also communicate more specific information about the quality of the bond or the nature of affiliative intent in a particular context, e.g. support during male harassment. Why is contact swimming rare among males? One answer can be derived from the assisted locomotion hypothesis. Assisted locomotion is a normal part of maternal care but there is no evidence for paternal care in bottlenose dolphins. It is perhaps not surprising that females, who normally assist in the locomotion of their offspring, would employ this behavior as a signal in bond formation with other adult females.

An interesting contrast with G–G rubbing in bonobos is that contact swimming is found in the sex

with weaker same-sex bonds (in bonobos the G–G rubbing females have stronger bonds than are found between males). Further, contact swimming has been observed between females that associate rarely as well as females that associate often (Richards 1996). We suggest that these observations make sense in view of the dolphins' social structure. It is a nearly universal rule in birds and mammals that one sex disperses or disperses further than the other; in mammals males are typically the dispersing sex while in birds females more often leave home (Greenwood 1980). Many cetaceans, however, may habitually violate this rule because members of both sexes may be philopatric (reviewed in Connor 2001). An important variable emerging in cetacean studies is not which sex emigrates but the extent to which the members of each sex continue to associate with their mothers (Connor et al. 2000a). Thus, in resident killer whales, *Orcinus orca*, both sexes continue to associate strongly with their mothers in 'matrilineal units' (Baird 2000). In contrast, bottlenose dolphin males do not maintain strong associations with their mothers but females do, to varying degrees (Connor et al. 2000a). Females may continue to associate with their mothers and other maternal kin as well as a coterie of unrelated same sex associates that they experience from infancy through old age. Thus, while foraging strategies may disfavor persistent high levels of association between individual females, it is not surprising that females would have signals to mediate bonds with individuals that they may not associate with often, but who may be valuable social partners when viewed in the context of a 35+ yr life-span.

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