

Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour

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Summary

Aggressive behaviour is rarely observed, but may have a large impact on the social structure, relationships and interactions in animal societies. Long-term behavioural study of Indian Ocean bottlenose dolphins in Shark Bay, Australia, suggests that males are more aggressive than females, and use sexual coercion during the breeding season, but age and sex-specific patterns of aggression have not been well documented. We analyzed tooth rake marks, an indirect measure of received conspecific aggression, to determine such patterns by age, sex, and adult female reproductive state. Photographs of 224 Shark Bay bottlenose dolphins were examined for tooth rakes and each rake was categorized as new (broken skin), obvious (white rake lines that are clearly visible) or faint (faint evidence of rakes). Rake lines were also coded by each body section visible in the photograph. Cycling females (those that became pregnant within 6 mos. of the photograph date) were significantly more likely to have new tooth rakes than non-cycling females (pregnant or with a dependent calf <20 mos.). Adult males were significantly more likely to have tooth rake marks than adult females, with the same tendency for juveniles. Calves, with far fewer rakes than any age class, showed no significant sex difference. Body coverage of tooth rakes was significantly more extensive for adult males than for adult females, but there were no sex differences on coverage for juveniles or calves. Comparison of tooth rakes at two periods during adulthood (>2 years apart) suggests that the marks are not cumulative. Overall, 83% of the population has tooth rake marks, suggesting that agonistic interactions occur for most individuals at least every two years. Analysis of agonistic interactions for 55 adult focal females (observed for 1960 h) and their 88 calves

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(observed for 1876 h) show that female aggression is extremely rare (occurring every 490 h), but females receive aggression more often (every 61 h), and 84% of received aggression was from juvenile and adult males. Focal adult females were never observed acting aggressively towards juveniles or adults of either sex, suggesting that female bottlenose dolphins are highly tolerant. Of the four observed instances of adult female aggression, all were directed at their dependent offspring. Male calves are significantly more aggressive than female calves, and calves had higher rates of agonistic interactions than their mothers (every 18 h), even though calves had fewer tooth rakes than all other age classes. The patterns of tooth rake presence and prevalence likely result from sexual coercion of adult females by adult males and intra-sexual male competition.

Keywords: intra-specific aggression, female tolerance, sexual coercion, tooth rakes, bottlenose dolphins, *Tursiops* sp.

Introduction

For over three decades, scars and natural markings have been used for photo-identification of cetaceans (Würsig & Würsig, 1977; Hammond et al., 1990; Würsig & Jefferson, 1990). The marks used to distinguish individuals include tears, nicks, tooth rakes, pigmentation patterns, and other marks located on the dorsal fin, flukes, and back (Gill & Fairbairns, 1995). In long-term studies of cetaceans, photo-identification helps researchers obtain information on group structure, life history parameters, site fidelity, movement patterns, and population size in, for example, sperm whales (*Physeter macrocephalus*; Whitehead, 1990; Childerhouse & Dawson, 1996), blue whales (*Balaenoptera musculus*; Sears et al., 1990), minke whales (*Balaenoptera acutorostrata*; Gill & Fairbairns, 1995), bowhead whales (*Balaena mysticetus*; George et al., 1994), bottlenose whales (*Hyperoodon ampullatus*; Gowans & Whitehead, 2001), humpback whales (*Megaptera novaeangliae*; Carlson & Mayo, 1990), humpback dolphins (*Sousa chinensis*; Karczmarski, 1999) and bottlenose dolphins (*Tursiops* sp.; Smolker et al., 1992; Wilson et al., 1997; Durban et al., 2000; Grellier et al., 2003).

However, only a few studies have used conspecific marks or scarring (tooth rakes) in cetaceans to examine relative rates of received aggression according to age and sex, and no studies have examined rake patterns by female reproductive state. Fresh or recent wounds may be used to indicate vulnerability to attacks by season or reproductive status. These measures are important given that, like predation events, agonistic interactions are rarely observed in wild animals, although indirect evidence of predation

(e.g., George et al., 1994; Heithaus, 2001a) and agonism (e.g., MacLeod, 1998) may be prevalent. Both predation and conspecific aggression likely have a large impact on the socio-ecology, social structure and relationships in odontocetes, and rake marks may be one of the best measures of such infrequently observed events. The current study investigates the presence and prevalence of conspecific tooth rake marks in Indian Ocean bottlenose dolphins in Shark Bay (*Tursiops* sp.) across age and sex classes and by adult female reproductive state. We also examine rates of agonism observed in bottlenose dolphin adult females and their calves for comparison, and to exclude the interpretation that female aggression could be the cause of rake patterns for any age or sex class.

Scars and marks can be acquired as a result of aggressive interactions between conspecifics or from predators (McCann, 1974; Heithaus, 2001a), as well as from boat strikes and by-catch in nets (Sears et al., 1990; George et al., 1994; Wells & Scott, 1997; Slooten et al., 2000). Attempted predation can be inferred from scars matching the dentition of predators, such as killer whales (*Orcinus orca*; George et al., 1994), and sharks (Heithaus, 2001a). Scars and wounds inflicted by conspecifics are common throughout odontocetes, including the families Delphinidae, Platanistidae, Physeteridae and Ziphiidae (McCann, 1974). Odontocetes tend to use teeth in aggressive intra-specific interactions, especially between males (Heyning, 1984). Such rake marks are characteristic of the species' dentition, and serve as good indicators of intra-specific aggression (McCann, 1974).

Scars from conspecifics have been used to provide indirect measures of aggression among black salamanders (*Aneides flavipunctatus*; Staub, 1993), leopard seals (*Hydrurga leptonyx*; Rogers & Bryden, 1997), cervids (*Alces alces andersoni*, *Cervus elaphus nelsoni*; Geist, 1986) and cetaceans (e.g., Kato, 1984; MacLeod, 1998). Kato (1984) observed tooth scars on the heads of 48 out of 70 male sperm whales as evidence of intrasexual fighting. Tusk-inflicted head scars on narwhals (*Monodon monoceros*) indicated a significant difference in head scarring between males and females, with females and immature males having fewer scars (Gerson & Hickie, 1984). In addition, MacLeod (1998) suggests that unpigmented intra-specific scarring acts as an indicator of male dominance and/or victory in aggressive social interactions in 18 species of odontocetes, including the narwhal, sperm whale, Risso's dolphin (*Grampus griseus*) and the family Ziphiidae. These species

have both dental weaponry dedicated to intra-specific confrontation and reduced re-pigmentation of scars, thus allowing permanent scars to accumulate (MacLeod, 1998). MacLeod (1998) hypothesized that battle scars advertise male quality in terms of dominance and/or fitness to other males during aggressive social interactions. Bottlenose dolphins, however, have fewer scars because their intra-specific rake marks regain pigmentation over time (Lockyer & Morris, 1990; MacLeod, 1998). Thus, rake marks in bottlenose dolphins may not indicate male age or quality (MacLeod, 1998), but could indicate relative rates and timing of received aggression. The current study focuses on the link between tooth rake marks and aggressive behaviour.

Bottlenose dolphins express aggression through posture, movement, and sound, with the most severe forms involving contact through body slamming, ramming, and biting (Samuels & Gifford, 1997; Connor et al., 2000a). Biting refers to the abrupt and forceful contact between one dolphin's teeth and another dolphin's body, usually resulting in long, thin, parallel, or nearly parallel tooth rake marks on the skin (Samuels & Gifford, 1997). Bottlenose dolphins continue to acquire both temporary marks and permanent scars throughout their lives; however, wounds tend to heal rapidly on dolphin integument due to the relative absence of a 'scab' once a wound is inflicted. Instead, a buffer layer of degenerating cells replaces the open wound, and protects the underlying new growth of tissue (Lockyer & Morris, 1990). Tooth rake wounds penetrate the skin and often harm the underlying blubber layer; scars of this nature disappear after 5 to 20 months (Lockyer & Morris, 1990). Melanocytes reside deep in the epidermis and give rise to columns of pigmented cells. Since tooth rakes tend not to damage deep tissue, re-pigmentation eventually occurs, causing such scars to become indistinguishable over time (Lockyer & Morris, 1990). Major wounds that result in a significant loss of tissue, such as shark bites, can heal completely, but leave permanent scars and loss of pigmentation (Lockyer & Morris, 1990; Heithaus, 2001a).

Common contexts of conspecific aggression are intrasexual competition (Andersson & Iwasa, 1996; Cunningham & Birkhead, 1998) and intersexual conflict (i.e., sexual coercion, Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995). Sexual coercion is defined as 'use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female' (p. 3, Smuts &

Smuts, 1993). Male sexual aggression appears to be most common in gregarious and polygynous species, such as pinnipeds (e.g., Cox & Le Boeuf, 1977; Le Boeuf & Mesnick, 1990) and bottlenose dolphins (Connor et al., 1996), in which females do not form long-term bonds with a single male but encounter several that compete for access to her (Smuts & Smuts, 1993). Males in several species, including chimpanzees (*Pan troglodytes*; Goodall, 1986) and Japanese macaques (*Macaca fuscata*; Soltis et al., 1997) exert more aggression toward estrous females than anestrus females, thus providing further support that males use aggression to obtain matings. Other studies do not show a relationship between male attacks and female reproductive state (e.g., Black-handed spider monkey, *Ateles geoffroyi*; Campbell, 2003). Black spider monkey (*Ateles paniscus*; Symington, 1987), bottlenose dolphin (Connor et al., 1992a, b, 1996), and chimpanzee (Watts, 1998) males use coalitionary aggression against single females. We will examine whether tooth rake marks on bottlenose dolphin females provides evidence for intersexual aggression.

Everywhere they have been studied, bottlenose dolphins live in a flexible fission-fusion social system, characterised by frequent changes in group membership (Connor et al., 2000a). Adult male-female bottlenose dolphin associations are infrequent, and tend to occur only when the adult female is cycling (Connor et al., 1992a; Smolker et al., 1992; Owen et al., 2002). In Shark Bay, first-order alliances of males cooperate to consort with individual cycling females (Connor et al., 1992a, b, 1996). The minimum interbirth interval for females with surviving infants in Shark Bay is four years (Mann et al., 2000), meaning that the operational sex ratio is highly skewed, with very few receptive females at any given time despite a socioeconomic sex ratio that is 54% female (Mann & Sargeant, 2003). Given the high density and rate of interaction among males in Shark Bay, this skew likely drives male cooperative alliance formation and intense intrasexual competition over access to cycling females (Connor et al., 2000a; Connor & Whitehead, 2005).

Among captive bottlenose dolphins, male-male agonistic interactions are the most frequent, followed by male-female agonism (Samuels & Gifford, 1997). In the wild, male aggression towards females appears to be related to male attempts to enforce and maintain consortships (Connor et al., 1992a, b, 1996). Such observed aggression includes head jerks (sharp movements of the head), chasing, tail hitting, charging, biting or jawing, and body slamming (Connor et al., 1992a, b). Shark Bay bottlenose dolphin males have

been characterized as aggressive within and between alliances, as well as towards adult females (Connor et al., 1992a, b, 1996). Aggressive behaviour may also be influenced by anthropogenic factors. In Shark Bay, an alliance of adult males that visited a provisioning beach (to receive fish hand-outs from tourists and fishers) in the 1980s, exhibited higher rates of aggression towards females than non-provisioned males, but aggression was clearly a component of consortships (Connor et al., 1996). Female-female interactions are rarely aggressive in captive bottlenose dolphins (Samuels & Gifford, 1997), and a study of mothers and newborn calves in Shark Bay revealed extremely low rates of adult female aggression, with all but one event involving the provisioned females (Mann & Smuts, 1999). With the exception of the provisioned females, adult females have not been observed competing over food, territories or mates.

Despite extensive observations of male consortships and indirect evidence for aggression, agonistic interactions are infrequently observed among wild bottlenose dolphins. Thus, indirect measures of aggression, such as tooth rakes, are important in assessing the levels of intra-specific competition in a population of wild bottlenose dolphins. Since aggression is presumed to be more frequent among adult males, we hypothesize that adult males have more tooth rakes present, and a wider coverage of tooth rakes on their bodies than adult females. We also hypothesize that adult females have more new tooth rake wounds in the year they are cycling than when they are pregnant or with a young offspring. Furthermore, even though tooth rakes on bottlenose dolphins fade over time, both males and females should acquire more tooth rakes as they reach reproductive maturity, since rates of male-female agonism and male-male agonism are expected to increase. We do not expect tooth rake marks to increase during adulthood once dominance relations are more established. Since calves receive low rates of aggression, they are not hypothesized to have many tooth rakes or exhibit sex differences.

Methods

Study site

The study site is located on the east side of Peron Peninsula, which bisects Shark Bay, Western Australia (25°47'S, 113°43'E). A long-term study of the Shark Bay dolphins based on photo-identification was established in 1984

off a fishing camp (now resort) called Monkey Mia (Connor & Smolker, 1985). Shark Bay bottlenose dolphin taxonomic status remains unresolved and are thus referred to as *Tursiops* sp. The main study area currently extends 200 km² off the east side of the Peron Peninsula and includes over 600 animals. The water depth ranges from 0.5 to 15 m. The seafloor is mostly covered with sea grass in shallow areas, large patches of sand in the deeper habitats and sandy coastal flats. Between 3-7 adults have been partially provisioned at the Monkey Mia beach since the 1970s. Currently four adult females are provisioned on a daily basis and the amount of fish fed is strictly controlled by the West Australian Department of Conservation and Land Management (Mann & Kemps, 2003).

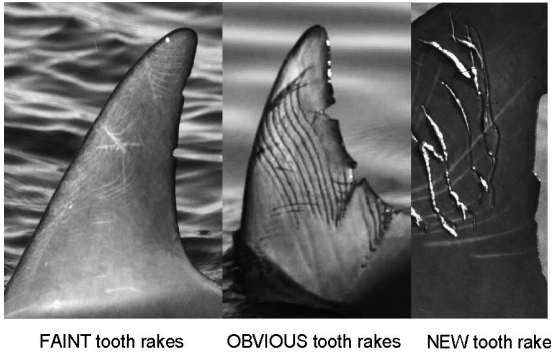
Examining photographs and coding tooth rakes

The first author, EMS, blind to sex, age and reproductive status of specific dolphins, classified tooth rake coverage for 649 photographs of both color slide film and digital images from the Shark Bay Dolphin Project (Table 1) that were taken between 1989-2002. Individual dolphins were chosen based on the quality of the photo-identification images. Only photographs of good quality could be utilized to examine tooth rakes. Such pictures were well focused, well exposed, and front lit. Each photograph was scored by the presence or absence of tooth rake marks in each visible body section. Marks and wounds were considered to be tooth rakes if they were superficial, thin parallel rakes, which are easily distinguished from deeper, crescent-shaped wounds caused by sharks. The dolphin tooth rakes were classified as new (broken skin), obvious (white rake lines that were clearly visible), or faint (faint evidence of rake lines; Figure 1). Although these might be viewed as stages of healing and re-pigmentation, it is important to note that recent rakes are often obvious and rarely show broken skin. Thus, the first category indicates both severity and recency of the wound. If a region of a dolphin's body contained more than one type of tooth rake, the freshest or most obvious one was coded.

In order to assess the occurrence and extent of tooth rake marks, the dolphin's body was divided into 12 zones: jaw, head, throat, anterior, chest/pectoral fins, dorsal fin, mid-flank, belly, anterior peduncle, posterior peduncle, ventral peduncle, and flukes (Figure 2). The majority of the images were lateral views of the dorsal region. The image was coded as left

Table 1. Sample sizes and the number of examined photographs for each age and sex class

Subjects	# of Dolphins	# of Photographs
All dolphins	285	649
Adult males	61	156
Adult females	61	168
Old juvenile males	23	77
Old juvenile females	17	33
Young juvenile males	12	28
Young juvenile females	14	36
Male calves	18	20
Females calves	18	21
Unknown age/sex	61	110

**Figure 1.** Tooth rakes were categorized as faint (faint rake lines), obvious (rake lines that are clearly visible), and new (broken skin). Photographs courtesy of Brooke Sargeant (2 left) and Mike Heithaus (right).

or right lateral side, dorsal or ventral view. Out of the 649 examined photographs, 308 viewed dolphins from the left lateral side, 316 were viewed from the right lateral side, 20 were viewed dorsally, and 5 were viewed ventrally. Each visible body section was coded by the presence or absence of tooth rakes and the type of rake (new, obvious, faint, Table 2).

To quantitatively estimate tooth rake coverage the visibility of each body section was weighted. If more than 75% of a body region was visible, it was scored as ‘1’ or entirely visible. If less than 75% of a body region was visible, it was scored as ‘0.5’ or partially visible. The presence or absence of tooth rakes for each body section was also weighted such that if a section contained

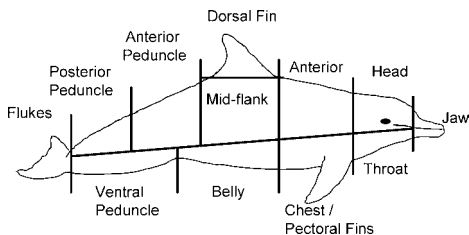


Figure 2. The dolphin's body was divided into 12 sections. Photographs show dolphins from the right and left lateral side, dorsal side, and ventral side. Body sections were either partially or entirely visible in photographs. For distribution of rakes by body section photographs, see Table 2.

Table 2. Proportion of tooth rakes in 12 sections of the dolphin's body. See Figure 2 for locations of body parts

Body part	Jaw	Head	Anterior	Dorsal fin	Mid-flank	Anterior peduncle	Posterior peduncle	Flukes	Throat	Chest	Belly	Ventral peduncle
# of photographs	14	40	125	264	179	183	76	2	6	9	9	7
# of photographs with rakes	3	11	56	185	83	132	58	0	2	2	2	3
Proportion	0.214	0.275	0.448	0.701	0.464	0.721	0.763	0.000	0.333	0.222	0.222	0.429

one or multiple tooth rakes, it was given a value of one. Body sections that did not contain tooth rakes were given a value of zero. The presence of tooth rakes for each individual was summed and divided by the sum of visible body sections. For example, if a dolphin had three body sections completely visible, and one body section partially visible in a photograph, the sum of the visible body sections would equal 3.5. If tooth rakes were present on two of the four visible body sections, then the sum of the presence of tooth rakes would equal 2. The tooth rake coverage for this dolphin would therefore be calculated by dividing 2 by 3.5, which equals 0.571. This rough estimate of the tooth rake coverage yielded values ranging from 0-2 (mean \pm SD = 0.78 ± 0.44 , $N = 285$). Of 285 dolphins, 152 were photographed more than once in our sample. If these photographs were within a two yr period ($N = 76$ dolphins) they were combined to yield one coverage score because tooth rakes tend to heal in 5-20 mo (Lockyer & Morris, 1990). If different

body sections were visible in the combined photographs, their values were added. If the same body sections appeared in more than one photograph the most visible tooth rake type (new, obvious, and faint) was coded to increase certainty that the rakes occurred within a given age class. For 76 individuals photographed more than 2 yrs apart, we used the earlier photograph for this analysis. Therefore, each individual dolphin only had one estimated tooth rake coverage value.

Age and sex classes

Many of the bottlenose dolphins born after 1984 are of known age. Age classes included four categories: calf, young juvenile, old juvenile, adult. Adult females were considered 12 yr of age or older (Mann et al., 2000). Adult males were classified as 14 yr and older when stable alliances begin to form (Connor, unpubl.). Juvenile females were from 4 through 11 yr of age, and juvenile males were classified from 4 through 13 yr of age. The juvenile period was subdivided into young juveniles (4-7 yr for females, 4-8 yr for males) and old juveniles (8-11 yr for females, 9-13 yr for males). Individuals less than 4 yr of age were classified as calves. Ages for each photograph were determined by known birth dates, rates of speckling, and body size estimates. Shark Bay dolphins can live at least until their late 30s (Mann et al., 2000).

The sex of most individuals is based on previous observations of the genital area (the presence of mammary slits or penis), association with a calf that regularly swam in infant position (in contact, under the mother), and in a few cases, by genetic sampling (Mann et al., 2000). Overall this study examined 61 adult males, 61 adult females, 35 juvenile males, 31 juvenile females, 18 male calves, 18 female calves, and 61 individuals of unknown age/sex (Table 1).

Female reproductive status

To determine whether cycling females had more fresh or new rakes than non-cycling, the reproductive status of each adult female was assessed on the date of the photograph after her tooth rakes were coded. A female was considered to be cycling if the date of the photograph was within 6 mos pre-conception. Females were classified as not cycling if they were pregnant, or with a young calf (≤ 20 mo). Most of the females (55 out of 75) easily fell into these two categories. However, the reproductive status for 20 females was less

certain, because they were either lactating with an older calf (>20 mo), or without a calf at the time of the photograph, but were not seen with a calf the following year. These females could have become pregnant but may have lost their offspring before researchers sighted them. For each of these 20 females, we examined the long-term survey record to determine if the females were sighted with adult males more than twice, or being consorted. If the females were not sighted or associated with adult males less than two times, they were grouped with non-cycling females ($N = 11$). If they associated with adult males two times or more, they were classified as cycling even though a subsequent pregnancy was not detected. Each adult female was represented only once in this analysis.

Rates of aggressive behaviour in adult females and calves

Agonistic interactions involving adult females were determined through 1,960 focal hours on 55 adult females. Details concerning focal observations are reported elsewhere (see Mann & Watson-Capps, 2005). Nearly all females followed had dependent calves ($N = 88$; 24 male calves observed for 714 h, 35 female calves observed for 960 h, 29 calves of unknown sex observed for 222 h). Therefore, we also report rates of aggression for male and female calves and test for sex differences. Since aggressive interactions tend to be obvious, we can document most, but not all such interactions for focal dolphins. Subtle agonistic interactions, especially those involving submissive behaviour only (e.g., flinch, see Samuels & Gifford, 1997) would often escape observation. Although agonism is typically defined as including either aggressive or submissive behaviour, we focus only on events with clear examples of aggression, including open jaw (including jawing and jaw clapping), charge, chase, hit, slam, and head-to-head tiff. Since chases also occur during playful interactions, especially among calves, we considered these events as agonistic only if other aggressive or submissive behaviours occurred. Agonistic events were defined as those involving the same individuals that were not separated by more than five minutes. Only agonistic events that included aggression were included. The actors and recipients of aggressive acts were indicated when focal subjects were involved. The age and sex class of participants was noted. These analyses were designed to help interpret the results on tooth rakes.

Analyses

The data were analyzed using SPSS 11.5 to determine: (1) whether cycling females were more likely to have new tooth rakes than non-cycling females (Pearson Chi-Square test); (2) whether scars or marks accumulated or faded during adulthood (Wilcoxon Matched-Pairs Signed-Ranks test); (3) the age and sex class differences in tooth rake presence (Pearson Chi-Square test); (4) the age and sex class differences in tooth rake prevalence or coverage (Mann-Whitney U-test and ANOVA); and, (5) if male and female calves differ in the rates of agonism, including rates of receiving or exhibiting aggression (Student *t*-test). For the first analyses, females were classified as with or without new tooth rakes. For all other analyses, all types of tooth rakes (new, obvious, faint) were used.

To determine if tooth rake marks increased or accumulated during adulthood, we compared adults who were photographed more than 2 years apart. This analysis tests two non-exclusive hypotheses: (1) adults receive more aggression as they age; (2) scars are cumulative and do not fade or disappear with time. If there was no difference in rakes over time, then neither hypothesis would be supported and the difference between rake marks by age class could not be attributed to simple accumulation of scars with age. If adults had more marks as they aged, then either hypothesis could be supported and a detailed analysis of rake location would be needed to see if specific rakes faded with time.

To determine age and sex class differences in tooth rake presence, we compared the absence and presence of tooth rakes for adult males and females, juvenile males and females, and male and female calves. Dolphins were placed in the 'absence' category if they had a tooth rake value of zero. Those with a value greater than zero were placed in the 'presence' category.

To determine the sex differences in overall tooth rake prevalence, we compared tooth rake coverage values for males and females within each age class (adults, juveniles and calves) using a Mann-Whitney U-test. We collapsed old and young juveniles into a single category for this analysis to increase the juvenile sample size. To examine developmental patterns in more detail, a two-way Analysis of Variance (ANOVA) was also used to analyze age, sex, and interaction effects in mean tooth rake coverage values for males and females across four age classes: calves, young juveniles, old juveniles and adults. Differences between age classes were examined using

post-hoc comparisons with a Bonferroni correction to account for the use of multiple statistical tests.

Results

Proportion of body sections viewed

One to nine body sections were surveyed on 285 dolphins with typically three body sections per individual (mean \pm SD = 2.86 ± 1.19). More tooth rakes were observed on the dorsal fin, anterior peduncle and posterior peduncle compared to other body sections (Table 2). Overall, 83.1% of all the dolphins in this study had tooth rakes present on at least one body section.

Presence of new tooth rakes on adult females: cycling vs non-cycling

Twenty-one cycling females and 54 non-cycling females were tested for the presence of new vs obvious or absent tooth rakes. Cycling females had significantly more new tooth rakes than non-cycling females ($\chi^2 = 5.69$, $df = 1$, $p = 0.017$, $N = 75$). Nine of 21, or 42.9% of cycling females had new tooth rakes, while only 16.7% (nine of 54) non-cycling females had new tooth rakes.

Changes in tooth rake coverage during adulthood

Mean tooth rake coverage values did not differ for individuals that were represented more than once (>2 yrs apart) in their adulthood (Matched-Pairs Signed-Ranks test, $z = -1.08$, $p = 0.28$, $N = 39$). Coverage values for 17 adults decreased over time periods greater than 2 yr, while 19 adults increased their tooth rake coverage values. Three individuals maintained the same coverage values during both time periods.

Age and sex class differences in tooth rake presence

Male bottlenose dolphins were significantly more likely to have tooth rakes than females when all age classes were combined ($\chi^2 = 5.10$, $df = 1$, $p = 0.02$, $N = 224$). Most of the males examined in this study possessed tooth rakes (101 of 114, 88.6%), as did the majority of females (85 of 110, 77.3%). By age class, adult males were significantly more likely to have

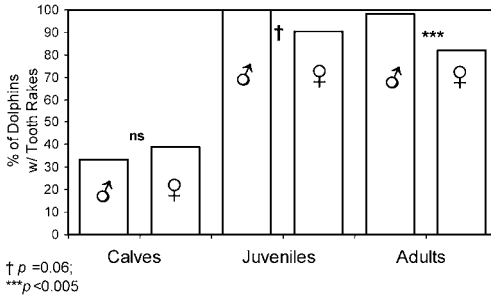


Figure 3. Percent of males and females that have tooth rakes in three age classes. Adult males were significantly more likely to have tooth rakes than adult females ($\chi^2 = 9.24$, $df = 1$, $p = 0.002$, $N = 122$). Juvenile males tended to have more tooth rakes than juvenile females ($\chi^2 = 3.55$, $df = 1$, $p = 0.06$, $N = 66$). Tooth rake presence did not differ significantly between male and female calves ($\chi^2 = 0.12$, $df = 1$, $p = 0.73$, $N = 36$).

tooth rakes than adult females ($\chi^2 = 9.24$, $df = 1$, $p = 0.002$, $N = 122$). Sixty of 61 adult males had tooth rakes (98.4%), while 50 of 61 adult females had tooth rakes (82.0%, Figure 3). The presence of tooth rakes was highest for juvenile males, with 100% having tooth rakes present on at least one body section ($N = 35$). Juvenile males tended to have more tooth rakes than juvenile females (28 of 31, 90.3%; $\chi^2 = 3.55$, $df = 1$, $p = 0.06$, $N = 66$). However, there were no significant differences in tooth rake presence between male and female calves ($\chi^2 = 0.12$, $df = 1$, $p = 0.73$, $N = 36$). Six of 18 male calves (33.3%) had tooth rakes present, while seven of 18 female calves (38.9%) had visible tooth rakes (Figure 3).

Age and sex class differences in tooth rake coverage

Estimated tooth rake coverage values for the individuals of known sex ranged from 0-2 (mean \pm SD = 0.78 ± 0.44 , $N = 254$). Adult males had a significantly more widespread coverage of tooth rakes than adult females (Mann-Whitney U-test, $z = -4.19$, $N_1 = 61$, $N_2 = 61$, $p < 0.001$). The median tooth rake coverage value was 1.00 for adult males, and 0.94 for adult females. Tooth rake coverage values were not significantly different among juvenile males and females ($z = -1.58$, $N_1 = 35$, $N_2 = 31$, $p = 0.12$). The median values for juvenile males and females were 1.00 and 0.82 respectively. As expected, the tooth rake coverage of male and female calves did not differ significantly ($z = -0.09$, $N_1 = 18$, $N_2 = 18$, $p = 0.93$). The median tooth rake coverage value for both male and female calves was zero.

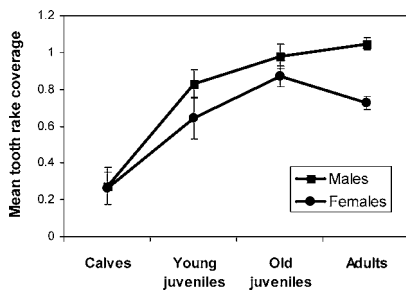


Figure 4. Sex and age differences in the prevalence of tooth rakes. Means \pm SE for each age and sex class are shown. ANOVA indicates significant sex and age effects (sex: $F_{1,223} = 7.87$, $p = 0.005$; age: $F_{3,223} = 30.76$, $p < 0.001$; interaction: $F_{3,223} = 2.18$, $p = 0.09$). Post-hoc comparisons show that calves had significantly fewer tooth rakes than juveniles and adults (see text).

In comparing mean tooth rake coverage values for males and females across the four age classes (calves, young juveniles, old juveniles, and adults), we found age and sex effects (ANOVA: sex: $F_{1,223} = 7.87$, $p = 0.005$; age: $F_{3,223} = 30.76$, $p < 0.001$; interaction: $F_{3,223} = 2.18$, $p = 0.09$; Figure 4). Using post-hoc comparisons with a Bonferroni correction, we found several differences between age classes. Calves had significantly lower tooth rake coverage values than young juveniles (mean difference \pm SE = 0.46 ± 0.09 , $p < 0.001$), old juveniles (mean difference \pm SE = 0.66 ± 0.09 , $p < 0.001$) and adults (mean difference \pm SE = 0.62 ± 0.07 , $p < 0.001$). No other age classes were significantly different from each other. The mean difference between young and old juveniles was 0.20 ± 0.09 ($p = 0.140$). Young juveniles and adults differed on average by 0.16 ± 0.08 ($p = 0.248$) and old juveniles differed from adults by 0.056 ± 0.06 ($p = 1.0$).

Rates of aggression

During 1,960 focal hours of observation on adult females and calves, adult females were aggressive actors on only four occasions, at a rate of 0.002 aggressive acts per h or one aggressive act every 490 h. All four of these events involved female aggression towards their own calves. Adult females were recipients of aggressive acts during 32 events, or 0.016 times per h or every 61 h. In 12.5% of those events, adult females received aggression from their calves (2 male, 2 of unknown sex). In 84.4% of those events, adult females received aggression from juvenile or adult males. In only one

case (3.1%), an unrelated female calf was aggressive towards the focal adult female. There were no instances of aggression observed between the focal adult female and either adult or juvenile females. Only 16 (29%) of 55 adult females were observed in agonistic interactions.

Similarly, only 25% of calves (22 of 88) were observed in agonistic interactions (36% of male calves and 29% of female calves), but the rate of agonism was higher for calves than for their mothers, with a total of 103 events at an overall rate of 0.054 times per h, or every 18 h. Calves were aggressive during 58 of these events (56.3%) at a rate of 0.031 per h or once every 32.7 h, and were recipients of aggression in 44 events (43.7%) at a rate of 0.023 per h or once every 43.1 h.

Male calves were involved in agonistic interactions at a higher rate (mean \pm SE = 0.052 ± 0.017 events per h, $N = 25$ males) than female calves (0.015 ± 0.004 events per h, $N = 34$ females; $t = 2.35$, $p = 0.024$). Male calves exhibited significantly higher rates of aggression (mean \pm SE = 0.044 ± 0.016 events per h) than female calves (mean \pm SE = 0.008 ± 0.003 ; $t = 2.59$, $df = 57$, $p = 0.012$). Put another way, male calves were aggressive every 15.5 h, whereas female calves were aggressive every 82.4 h. In contrast, the rate of receiving aggression was no different for male calves (mean \pm SE = 0.019 ± 0.008 events per h) than female calves (mean \pm SE = 0.007 ± 0.003 ; $t = 1.56$, $df = 57$, $p = 0.12$). Most agonistic interactions involving female and male focal calves involved other male calves, totaling 43% of all interactions (Figure 5). Only 12% of focal calf agonistic interactions involved female calves. A smaller proportion of calf agonistic interactions involved juveniles, 24%, and adults, 20%. Notably, female focal calves had only one agonistic interaction with an adult female and none with adult males (Figure 5). Female calves were observed more than male calves (960 h vs 714 h respectively), so the difference cannot be attributed to differences in observation time.

The high proportion of male calf involvement was typically related to play behaviours that turned aggressive. These numbers should be interpreted with caution because they are not corrected for the proportion of time calves spend with these age-sex classes (e.g., adult and juvenile males are rarely present in mother-calf groups).

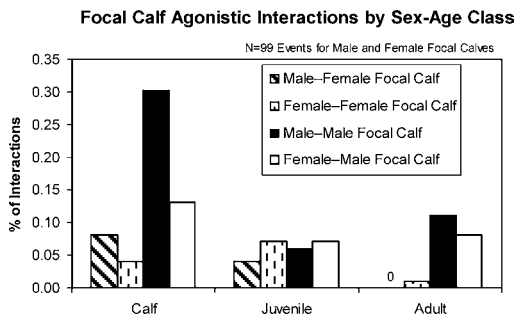


Figure 5. Distribution of agonistic interactions by age and sex class for focal calves. Because there were 99 events, the actual number of events is roughly equivalent to the percent value. For example, 30% of calf agonistic interactions were between the focal male calf and another male calf (30 of 99). Female focal calves had no agonistic interactions involving adult males. Mother-calf agonistic interactions were excluded from this summary.

Discussion

Most bottlenose dolphins in Shark Bay (83.1%) have tooth rake marks, suggesting that aggressive encounters are common among conspecifics, occurring at least every two years beyond infancy. Most of our hypotheses were supported in that males had more rakes than females, cycling females had more new rakes than non-cycling females, and calves had fewer rakes than juveniles and adults. The focal data on adult females and calves show that adult female aggression is virtually non-existent, juvenile and adult males are responsible for the majority of attacks on adult females, and male calves already show higher rates of aggressive behaviour than female calves. Based on these data, we infer that juvenile and adult males were responsible for the widespread rakes on juveniles and adults of both sexes. Adult females were most likely to receive attacks when they were cycling compared to other reproductive states, a finding consistent with the contention that sexual coercion plays a part in the bottlenose dolphin mating system. Rake marks on calves most likely occur in the context of play that turns agonistic, particularly involving male calves. Finally, the absence of female aggression towards other juvenile and adult females suggests that females are extremely tolerant and do not compete aggressively for resources.

Calves

Although calves had the fewest tooth rakes, sex differences were already apparent, with higher rates of both agonism and aggression among males

compared to females. For calves, there were no sex differences in rake marks or in the likelihood of receiving aggression. The difference in tooth rakes for calves compared to juveniles and adults may be attributed to the number of years available to acquire marks (some calves were under one year of age whereas all juveniles and adults would have had at least two years to show rake marks) or that they are protected by their mothers. In addition, juveniles and adults may be more likely to receive elevated aggression that results in visible rakes or injury, unlike the initially playful context characteristic of calf agonistic interactions.

Juveniles

Tooth rakes increased on both sexes with age, largely due to the shift from infancy to the juvenile period. Male juveniles tended to have tooth rakes more often than female juveniles, but the degree of body coverage, or prevalence of rake marks was not significantly different for males and females. While juvenile females tend to associate with other females and calves (Mann & Smuts, 1999), juvenile males leave their mother and often associate with other juvenile males in small groups, although both sexes remain residents of their natal area (Connor et al., 2000a). Juvenile males appear to avoid adult males; therefore, adult males are not thought to be responsible for the majority of tooth rakes observed on juvenile males. Instead, playful and competitive bouts, as well as frequent sexual practice behaviours among juvenile males probably result in the high presence and prevalence of tooth rakes observed.

Similar tooth rake patterns for juvenile and adult females suggest that females might receive more aggression when they near the onset of cycling from either juvenile or adult males, and this aggression continues periodically throughout adulthood. Juvenile females may be less experienced in avoiding aggressive encounters. In one captive study where adult and subadult bottlenose dolphins were housed together, a subadult male and subadult female had the highest rates of conflicts although the aggressor and recipient were not indicated in this study (Weaver, 2003). Detailed study of male and female juvenile behaviour and associates will shed light on the factors related to high levels of aggression during this period.

Adults

The high presence and prevalence of tooth rakes observed on adult males is not surprising. Competition for mates, both within and outside of an alliance, results in aggressive intrasexual encounters (e.g., Connor et al., 1992a, b, 1996). In addition, sociosexual behaviour, which is commonly aggressive, occurs in non-reproductive contexts among males (Connor et al., 1996). As predicted, adult females had a significantly lower presence and prevalence of tooth rakes than adult males. However, a large number of adult females, 82%, had tooth rakes. This might be expected given that most adult females would have fertile periods averaging every 2.6 years (calculation based on reproductive data in Mann et al., 2000). Thus, a high proportion of females would have fresh or fading marks even if males only jawed them when they were cycling. The fact that focal adult females were never observed acting aggressively towards juveniles or other adults, but received aggression primarily from juvenile and adult males, suggests that males are almost exclusively responsible for the rake patterns we have documented.

Our finding that cycling females had more fresh or new rakes than non-cycling females suggests that males used aggression to either intimidate or coerce females. Because we only considered females to be cycling if they definitely became pregnant or in a few cases, associated regularly with adult males, our analysis was very conservative. Some cycling females might have been in the non-cycling group, but the reverse was unlikely. In addition, new tooth rakes are good indicators of the severity of aggression received. Obvious tooth rakes might also, in fact, be recent.

Tooth rake marks are a good indicator of relative rates of aggression; but the jawing or biting that leaves such marks are likely milder than other forms of aggressive contact. Other forms of intra-specific aggression, such as body slamming and ramming with the rostrum, would result in more lethal internal damage (Connor et al., 2000b), but we are not likely to find dead animals given the uninhabited coastline and high density of sharks (Heithaus, 2001a, b). Lethal aggression has been documented at other bottlenose dolphin study sites, but is largely restricted to infanticide (Patterson et al., 1998; Dunn et al., 2002). The calves examined from both Moray Firth, Scotland and Virginia died from severe blunt-force trauma (Patterson et al., 1998; Dunn et al., 2002). All 18 calves from Moray Firth bore new tooth rakes (Patterson et al., 1998), while only three of nine stranded calves from Virginia had external evidence of aggression in the form of tooth rakes (Dunn

et al., 2002). Although biting is a common form of aggression, it does not occur in all aggressive encounters. Therefore, this study includes dolphins that received and survived a subset of aggressive encounters.

Our study supports but does not provide definitive evidence for sexual coercion. Since both matings and aggressive behaviour were rarely observed in adult Shark Bay bottlenose dolphins, we cannot determine whether male attacks on females increased their chances of mating. Females may mate with non-aggressive males within an alliance or favor alliances that are less aggressive. Further, juvenile or subadult males may be responsible for a large proportion of attacks on females. Sex differences in aggressive behaviour emerge early and adult females show remarkably low rates of aggression, even towards their calves. The latter finding provides insights into the nature of female social relationships, suggesting that female bottlenose dolphins may be characterized as tolerant (cf. Sterck et al., 1997), where females appear to have low contest competition, form egalitarian relationships and rarely form coalitions. Since females individually hunt for mobile prey that are typically swallowed quickly and whole, they neither compete for nor share food (Mann & Sargeant, 2003). In contrast, males are clearly in direct reproductive competition.

Future studies should investigate the seasonal rates of new tooth rakes among adult and juvenile males to see if males encounter more aggression during the breeding season or if rake marks are related to transitions in male status within or between alliances. Further, the factors associated with attacks on juvenile females are not well-understood. Intra-specific rates of rake marks on bottlenose dolphins in other locations should also be examined, especially where adult males do not form aggressive coalitions. Such comparative studies would be of great value, as they would reveal how social structures relate to the amount of aggressive behaviour exerted toward conspecifics.

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