



## A comparison of pectoral fin contact between two different wild dolphin populations

Kathleen Maria Dudzinski<sup>a,b,\*</sup>, Justin David Gregg<sup>a</sup>, Christine Ann Ribic<sup>c</sup>, Stan Abraham Kuczaj<sup>b</sup>

<sup>a</sup> Dolphin Communication Project, CT, USA

<sup>b</sup> Department of Psychology, University of Southern Mississippi, Mississippi, MO, USA

<sup>c</sup> US Geological Survey Wisconsin Cooperative Wildlife Research Unit, Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI, USA

### ARTICLE INFO

#### Article history:

Received 4 September 2008

Received in revised form 17 November 2008

Accepted 18 November 2008

#### Keywords:

Altruism

Dolphin

Flipper rubbing

Grooming

Reciprocity

Social behaviour

### ABSTRACT

Contact behaviour involving the pectoral fin has been documented in a number of dolphin species, and various explanations about its function have been offered. Pectoral fin contact can take a variety of forms, and involves a number of body parts and movements, likely differing depending upon social or ecological context. For this study, we compare the pectoral fin contact behaviour of two species of wild dolphins: Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from around Mikura Island, Japan, and Atlantic spotted dolphins (*Stenella frontalis*) from The Bahamas. The two study populations exhibit surprising similarity in the ways in which pectoral fin contacts are used, despite differences in species and environmental conditions at the two sites. Differences in contact rates for calves between the two sites suggest that calf-focused aggression from adult dolphins is more prevalent at Mikura than in The Bahamas. Our results suggest that pectoral fin contact behaviour seems to be driven primarily by social pressures, and may be similar in function to allogrooming described in primates.

© 2008 Elsevier B.V. All rights reserved.

### 1. Introduction

“Flipper rubbing” behaviour, when physical movement occurs between one dolphin’s body or pectoral fin and another dolphin’s pectoral fin, has been observed in wild and captive individuals of various odontocete species. Wild species include Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Mann and Smuts, 1998, 1999; Sakai et al., 2003, 2006a, 2006b) spinner dolphins (*Stenella longirostris*) (Johnson and Norris, 1994), Atlantic spotted dolphins (*Stenella frontalis*) (Dudzinski, 1996, 1998), belugas (*Delphinapterus leucas*) (Smith et al., 1992), rough-tooth dolphins (*Steno bredanensis*) (Kuczaj and Yeater, 2007), and sperm whales (*Physeter macrorhynchus*) (Whitehead and Weilgart, 2000). Captive dolphins observed engaging in flipper rubbing include common bottlenose dolphins (*Tursiops truncatus*) (Tavolga and Essapian, 1957; Samuels et al., 1989; Tamaki et al., 2006), spinner dolphins (Johnson and Norris, 1994), and Commerson’s dolphins (*Cephalorhynchus commersoni*) (Johnson and Moewe, 1999).

However, contact behaviour involving the pectoral fin has not been defined clearly, is labeled in a variety of ways, and is often lumped together with other types of concurrent behaviour (see

Table 1 in Sakai et al., 2006a for an overview). For example, Mann and Smuts (1998, 1999) studied wild Indo-Pacific bottlenose dolphins in Shark Bay, Australia and reported a behaviour they termed “petting”, in which one dolphin rubs another with its flipper or fluke. Johnson and Norris (1994) and Bateson (1974) also documented a similar behaviour in Hawaiian spinner dolphins that they called “caressing” or “pectoral whetting” wherein the pectoral fins of both dolphins are rapidly flicked back and forth over the body surface. Dudzinski (1998) studied contact behaviours among wild Atlantic spotted dolphins in The Bahamas and described “petting” and “petting/rubbing” where one dolphin rubs its pectoral fin over another dolphin’s pectoral fin or body, respectively. Samuels et al. (1989) analyzed and defined “gentle rubbing” in captive bottlenose dolphins where one dolphin rubs the length of its body or a specific body part against the immobile, outstretched pectoral fin of a partner. “Petting” was defined by Samuels et al. (1989) as one dolphin giving a rub to another by moving its pectoral fin back and forth against another’s body, while the term “pec touches” was used by Johnson and Moewe (1999) to describe the use of the leading edge of the pectoral fin to contact any part of another individual’s body for Commerson’s dolphins. In addition to rubbing, static contact behaviour involving the pectoral fin but without rubbing motions has been observed in both captive (Tavolga and Essapian, 1957; Samuels and Tyack, 2000) and wild dolphins (Richards, 1996; Connor et al., 2006; Mann and Smuts, 1999; Connor et al., 2000; Paulos et al., 2007). Connor et al. (2006, p. 631) termed this behaviour “contact swimming”, and described

\* Corresponding author at: Dolphin Communication Project, P.O. Box 711, Old Mystic, CT 06372-0711, USA.

E-mail address: [kdudzinski@dolphincommunicationproject.org](mailto:kdudzinski@dolphincommunicationproject.org) (K.M. Dudzinski).

**Table 1**  
Summary of effort expended and minutes of video collected per year per study site.

Location	Year	# Min. Effort	# Min. video	% yr-old calves
Mikura	1997	2,475	79	4.96
Mikura	1998	5,604	273	7.97
Mikura	1999	1,963	99	5.44
Mikura	2000	1,670	130	6.71
Mikura	2001	1,864	87	8.13
Mikura	2002	2,059	311	1.82
Mikura	2004	2,328	229	5.29
Bahamas	1993	~36,000	148	3.33
Bahamas	1994	~36,000	41	7.07
Bahamas	1995	~21,000	89	2.5
Bahamas	2000	~9,000	13	2.14
Bahamas	2001	~12,000	222	2.14

The minutes of effort relates to time spent looking for dolphins during boat trips. The percent of the total population comprised of calves  $\leq$  one year old for each study site annually is also presented.

the behaviour as follows: “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.” Dudzinski (1996, 1998) labeled this behaviour as “contact position” though the definition was the same as Connor et al. (2006).

Although the literature is still sparse with respect to research on pectoral fin contact exchanges, and the definitions of the behaviours involved are highly variable, possible function(s) for flipper rubbing/touching have emerged. Samuels et al. (1989) analyzed gentle rubbing among four captive bottlenose dolphins and suggested that this contact served both social and hygienic functions. The authors suggested a social function because preferential rubbing relationships persisting for many months were observed between certain individuals. They also speculated that this behaviour could help in the removal of ectoparasites and old epidermal cells based on observations that one particular dolphin, which received infrequent rubbing from other dolphins, often rubbed its body against objects. Norris et al. (1994) who studied Hawaiian spinner dolphins, Sakai et al. (2006a) who studied Indo-Pacific bottlenose dolphins, and Dudzinski (1998) who studied Atlantic spotted dolphins all suggested that flipper rubbing is a kind of affiliative behaviour similar to grooming observed in primates, and so may have both hygienic and social functions. Some researchers have suggested that flipper rubbing is a type of sexual behaviour: Tavolga and Essapian (1957) studied captive bottlenose dolphins and suggested that pectoral fin rubbing is a passive or inactive form of sexual behaviour. They termed what they observed as “stroking” because it appeared primarily as a pre-copulatory behaviour. Norris et al. (1994) also reported that pectoral fin contact among captive spinner dolphins was observed during their “caressing bout” and was oriented specifically to the abdomen and the genital area. Caressing was documented both for captive spinner dolphins and their wild counterparts in Hawaii (Norris et al., 1994) with rubbing by a dolphin’s pectoral fins or flukes observed predominantly when dolphins swam in the mating posture (i.e., belly-to-belly). Norris et al. (1994) also discussed a more active behavioural pattern among spinner dolphins: “pectoral whetting” (originally defined by Bateson, 1974 but cited in Norris et al., 1994) was when two dolphins swim belly-to-belly with mutual pectoral fin rubbing. Connor et al. (2006) discussed a number of hypotheses to explain the function of contact swimming as observed between female dyads within male-biased groups, including reduced male harassment, assisted locomotion and reduced stress.

We investigated flipper contact behaviours in two populations of wild dolphins: Indo-Pacific bottlenose dolphins from Mikura Island, Japan, and Atlantic spotted dolphins from Little Bahama Bank, The Bahamas. A comparison between the two sites allowed us to discuss in more detail the possible function of pectoral fin contact

behaviour by considering the similarities and differences between two species in two disparate geographic locations. These two populations were chosen because each research site allowed access to long-term video data collected in water that allowed for consistently good visibility, where each population was habituated to the presence of researchers and their recording equipment. We investigated the type, quantity, frequency, and location of flipper contact between the two sites, as well as the body parts, postures, age, gender, and individual identification of the dolphins involved in these behavioural exchanges.

## 2. Materials and methods

Data collected on both study populations were part of a long-term, longitudinal and comparative examination of dolphin communication and signal exchange (e.g., Dudzinski, 1996, 1998; Dudzinski et al., 2003; Gregg et al., 2008).

### 2.1. Study sites and populations

Data were gathered at two locations over a total of 12 years on the Little Bahama Bank, The Bahamas and around Mikura Island, Japan. The Atlantic spotted dolphins were found near the White Sand Ridge of the Little Bahama Bank, located ~64.5 km north of West End, Grand Bahama Island. This area ranges from 6 to 10 m in depth with a white sandy bottom and good visibility to at least 30 m. Dolphins are most often sighted in the northwest section of this sand bar. Data for this study on this group of dolphins were collected from 1993–1995 and 2000–2001. Approximately 150 individual spotted dolphins were identified with relative age categories and sex determined for all individuals (Dudzinski, 1996; Herzing, 1997; Brunnick, 2000). The Indo-Pacific bottlenose dolphin group is a population resident to the area within 300 m of Mikura Island, Japan. Mikura Island is a dormant volcanic island roughly 200 km south of Tokyo with a circumference of 16.4 km, and is characterized by a boulder-strewn seafloor with depths ranging from 2 to 60 m at 2 to 250 m from shore, respectively. DNA analysis confirms that the dolphins around Mikura are *aduncus*-type (Kakuda et al., 2002). The Mikurajima Bandouiruka Kenkyukai (M.B.K.) conducted a photo-identification research study on this group of dolphins between 1994 and 2004 (Kogi et al., 2004): the identified population consisted of approximately 165 dolphins. Video data from 1997 to 2002 and from 2004 were used to examine pectoral fin contact between dolphins in this study group. Both study sites are adjacent to fish-productive, deep waters (Gulf Stream for The Bahamas and Marianas Trench for Mikura Island, Japan).

### 2.2. Data collection

Dolphin behaviours and sounds were recorded with a mobile video/acoustic system that permits real-time synchronous video and audio recordings under water (Dudzinski et al., 1995). Underwater swims were video-documented opportunistically with limiting factors including poor weather, sea, and visibility conditions. Behavioural data were collected using focal animal and all-occurrence sampling (Altmann, 1974). Identified individuals were opportunistically observed, based upon which dolphins were near the vessel. Follows and recordings of individual dolphins began as soon as the video camera and observer were in a favorable underwater position and group composition was assessed. An individual was selected and recorded until it was no longer within the field of view. Pectoral fin contact behaviour was coded only from videotaped segments (for reliability and repetition).

Event sampling for pectoral fin contact between individual dolphins was conducted from all video data gathered during 1993 to 1995, 2000, and 2001 from The Bahamas on spotted dolphins

and from 1997 to 2002 and 2004 for Indo-Pacific bottlenose dolphins around Mikura Island, Japan. Each contact event between one dolphin's pectoral fin and another dolphin's body (including the pectoral fin) was documented. Other relevant, recorded information included: date of occurrence, "real" time of contact, initiating dolphin identification, age and sex, receiving dolphin identification, age and sex, each dolphin's posture, duration of contact, whether contact was a touch or rub, group behaviour and composition, and identification of the departing dolphin. In addition, whether the initiating and receiving dolphins were the *rubber* or *rubbee* and which body part was contacted on the *rubbee* were documented.

### 2.3. Definitions

Definitions of rubbing behaviour in general or the contact between pectoral fins or a pectoral fin and the body of a second dolphin more specifically vary considerably in the published literature (see Sakai et al., 2006a for an overview). For this study, we defined *rubbing* as the active movement between one dolphin's (i.e., the *rubber*'s) pectoral fin and another dolphin's body (i.e., the *rubbee*). We defined *petting* as pectoral fin-to-pectoral fin rubbing where active movement between pectoral fins of two dolphins is observed. *Touchees* were defined as physical contact between the pectoral fin of one dolphin and another dolphin's body without active movement of either the pectoral fin or the area of the body being touched. The term *contact* is used to denote all pectoral fin contact behaviour including *rubbing*, *petting* and *touching*.

Pectoral fin tactile exchanges were begun by one dolphin (either the *rubber* or *rubbee*) approaching and physically contacting another dolphin and were ended by one of the dolphins departing from the other. We defined this behaviour unit between the start of contact and the departure as a flipper contact episode. In addition, either the *rubber* or the *rubbee* can be the *initiator* or the *receiver* of the contact. For example, the *rubbee* may initiate contact with the *rubber* by approaching the *rubber* and soliciting a rub by placing part of its body in contact with the *rubber*'s pectoral fin. Subsequently, the *rubber* in this scenario is considered the *receiver*, and the *rubbee* is the *initiator*.

To record the dolphin body part in contact with a pectoral fin, we divided the body surface of the dolphin into 11 parts (Fig. 1). Dolphin posture during pectoral fin contact exchange was categorized into the following types: horizontal (HOR), side-down left (IOSD), side-down right (ROSD), upside down (VTU), head down (HDO) and head up (HUP). Horizontal was defined as a posture in which the dolphin's ventral side is parallel to the sea floor and "facing" down. A posture in which one pectoral fin is kept up and the other is parallel to the sea floor was classified as side-down. An upside down posture was defined as the dolphin horizontal with the ventral side up and the dorsal side toward the sea floor. Head down or head up postures related to the dolphin in a vertical position in the water column with its head down or up, respectively.

Four dolphin age classes (i.e., adult, subadult, juvenile and calf) were identified and used to categorize dolphins at each study site.

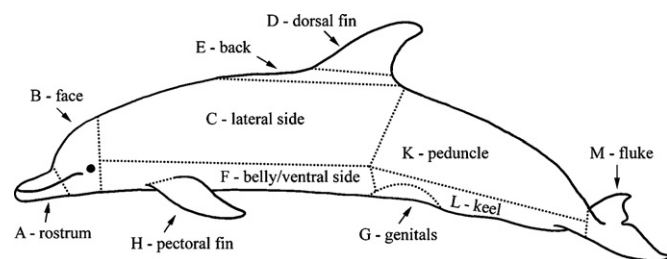


Fig. 1. Illustration depicting the 11 body part categories on a dolphin used to quantify potential contact preference by *rubber* and *rubbee*.

Atlantic spotted dolphins age classes were defined according to the development of pigmentation along their bodies (Perrin, 1970; Dudzinski, 1996; Brunnick, 2000), as well as girth and length. For spotted dolphins, calves have no spots and are roughly half the size of an adult. Juvenile spotted dolphins have begun to develop spots ventrally, have reached one half to two-thirds the size of an adult, and no longer regularly associate with their mothers. Subadult spotted dolphins have spot pigmentation over the entire body, except the pectoral fins, flukes and dorsal fin, and have reached two-thirds to equal size of an adult spotted dolphin. Adult spotted dolphins are covered in spot pigmentation and are roughly 2 m in length. Age classification of the Indo-Pacific bottlenose dolphins from Mikura follows from the definitions outlined by Kogi et al. (2004). Calves are roughly half the size of an adult, have no spots, minimal to no scarring, and are regularly observed in the company of their mothers. Juveniles are roughly two-thirds the size (length and girth) of an adult, have not yet begun to develop spots, have begun to acquire scars, are frequently observed with their mothers, and are a light-gray color. They are classified as juveniles typically one year after first being observed. Subadults are roughly similar in length to an adult but with less girth, have begun to develop spots ventrally, and no longer associate with their mothers. Adults have larger girth, spots covering the ventral area, possess many scars, and are a darker gray color. Female adults are classified as such once they have given birth to a calf.

### 2.4. Statistical analyses

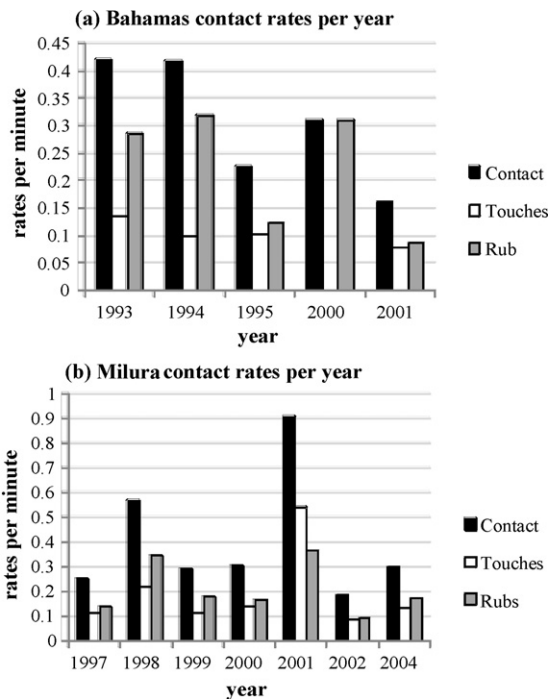
In order to ensure independence and randomness of the data, we only included one contribution per identified dolphin in the role of *rubber* and one contribution per identified dolphin in the role of *rubbee* per encounter, even though a single animal might have contributed multiple pectoral fin contacts in an encounter. Thus, from the total number of pectoral fin contacts per site per year of study, we limited our examined sample size to individual adjusted contacts as defined above. Sampling in this way facilitated an avoidance of pseudo-replication of the data. Comparison of the stability of pectoral fin contacts between sites was compared as rates where the total number of individual adjusted contacts per year per study site was divided by the total effort (i.e., minutes of underwater video per site per year). A comparison by location of exchanged pectoral fin contact behaviour was examined (using individual adjusted sample sizes) with a t-test with two samples assuming unequal variances. Body part preference for both *rubber* and *rubbee* in the role of initiator (using individual adjusted sample sizes) was examined with Spearman's rank correlation. Chi-square analysis was used to examine fin-to-fin versus fin-to-body contact, to assess variation in posture assumed when the initiator was *rubber* versus *rubbee*, to examine identification of sex/age in partner preference during contacts, rubbing versus touching for contacts, and initiator versus receiver roles. All chi-square analyses were conducted with individual adjusted contact data.

## 3. Results

Twelve years of video data were examined to understand how dolphins use their pectoral fins in the exchange of contact behaviour (Table 1). A total of 512 min of video data provided the basis for analyses from 5 years of data collected from The Bahamas and 1208 min from 7 years of data from Mikura Island, Japan.

### 3.1. Comparison of contact frequency between research sites

A total of 139 contact episodes were recorded from The Bahamas, and 450 from Mikura. The mean rate of contact (rubs, including petting, and touches) per minute for each year were calculated for

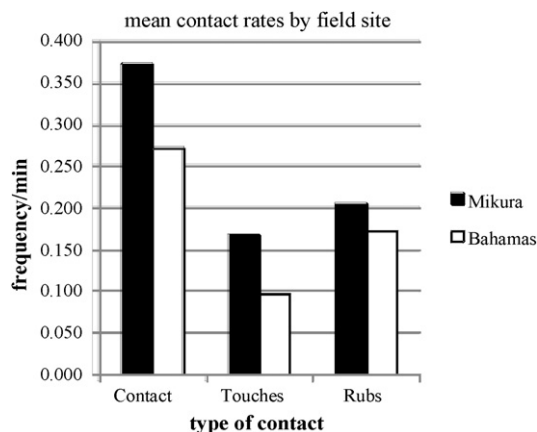


**Fig. 2.** Mean contact rates per minute for each year for (a) The Bahamas and (b) Mikura Island. Note that frequency of contacts for The Bahamas and Mikura Island are on different scales.

each site (Fig. 2). Contact rate values were determined by dividing the number of observed contacts by the total number of hours of video data for each year. A comparison of the mean rates for contacts across the entire sampled period for each of the two sites is provided in Fig. 3: mean contact rates in The Bahamas data were 0.271 contacts per minute, while mean contact rates at Mikura Island were 0.372 contacts per minute. In order to determine if rate of contact differed between sites, a *t*-test was performed using mean contact rates per year for each site. No significant difference between contact rates was found: contacts ( $t_9 = 3.89, P = 0.4$ ); rubs (including *petting*) ( $t_8 = 1.71, P = 0.13$ ); touches ( $t_8 = 0.21, P = 0.84$ ), which suggests that both study populations of dolphins engage in contact behaviours at similar rates.

3.2. Pectoral fin to pectoral fin vs. pectoral fin to body

We examined the data to determine if the dolphin initiating contact prefers *petting* (i.e., pectoral fin to pectoral fin contact) or



**Fig. 3.** Mean contact rates per minute across both field sites.

*rubbing* (i.e., pectoral fin to body contact) while in the role of either the *rubber* or the *rubbee*. For The Bahamas, the dolphin initiating contact was more likely to engage in *rubbing* behaviour, than *petting* behaviour ( $X^2_1 = 6.09, P = 0.014$ ). A similar trend was found at Mikura, where the dolphin initiating contact was more likely to engage in *rubbing* behaviour, than *petting* behaviour ( $X^2_1 = 4.40, P = 0.036$ ).

3.3. Initiator vs. receiver

In contrast to the results reported by Sakai et al. (2006a), we found that the *rubber* was significantly more often the initiator of contact episodes at Mikura Island, Japan ( $P < 0.001, 74.41\%$  of 340 episodes), as well as in The Bahamas ( $P < 0.001, 73.73\%$  of 118 episodes). There was no significant difference found between the two sites in terms of how often the *rubber* was also the *initiator* ( $X^2_1 = 0.001, P = 0.98$ ), suggesting that in our study the *rubber* tends to initiate contact behaviour at nearly identical rates for both study populations.

3.4. Body parts contacted

We documented 141 rubs and touches between dolphins from The Bahamas, and 370 from Mikura with respect to identification of body part contacted. These episodes were scored according to the frequency with which body parts were contacted by the *initiator* in the role of the *rubber* and the *rubbee* (Table 2). In order to determine if the *rubber* and the *rubbee* initiate contact on similar body parts between the two research sites (see Fig. 4 for contact rates), the body parts were rank ordered from least to most likely to be contacted for each of these two conditions for each site; a Spearman rank correlation was performed. Episodes where multiple body parts were contacted throughout the episode were eliminated from this test. When the *initiator* was in the role of the *rubber*, a significant correlation was seen between the two sites ( $r_s = 0.66, N = 91, P < 0.05$ ). Similarly, when the *initiator* was in the role of the *rubbee*, a significant correlation was seen between the two sites ( $r_s = 0.71, N = 308, P < 0.01$ ). These correlations demonstrate that the identified preferential choice of body part to contact (touches and rubs) by the *rubber* and the *rubbee* is consistent between the two species at each of the field sites.

3.5. Body postures

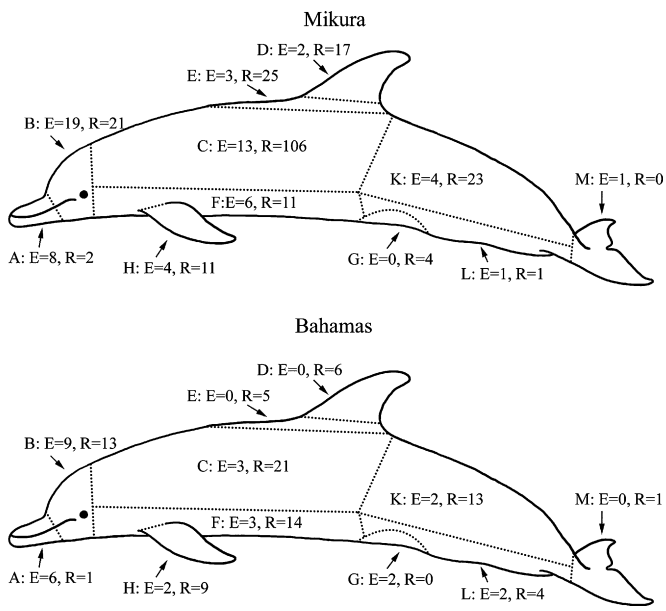
Body posture assumed by the *initiator* in both the *rubber* and *rubbee* roles was examined for each field site. For both Mikura Island and The Bahamas, a strong preference was shown for the HOR position for both the *rubber* and *rubbee* roles when combined for all contact types (Japan:  $X^2_5 = 804.77, P < 0.001$ ; The Bahamas:

**Table 2**

Rank order (from most to least likely) of body parts contacted for the *initiator* in the role of *rubber* and *rubbee* for both Mikura Island and The Bahamas.

Mikura Island		The Bahamas	
Rubbee	Rubber	Rubbee	Rubber
B	C	B	C
C	E	A	F
A	K	C	K
F	B	F	B
H	D	K	H
K	H	G	D
E	F	H	E
D	G	L	L
L	A	D	A
M	L	E	M
G	M	M	G

See Fig. 1 for definition of body part codes.



**Fig. 4.** Frequency of pectoral fin contact by *rubber* (R) and *rubbee* (E) for each body part from The Bahamas and Mikura Island.

$X^2_5 = 192.49, P < 0.001$ ). When HOR was removed from the analyses to assess relative preferences for the remaining five postures, there were no significant differences in preferences for these five postures at either Mikura Island or The Bahamas.

We examined the data to determine whether the two dolphins involved in a contact episode assumed either the same or different postures. At Mikura Island, dolphins were found in the same posture significantly more often than a different posture during a rubbing episode when the *initiator* was in the role of *rubber* ( $X^2_1 = 22.58, P < 0.001$ ). Touching episodes at Mikura Island when the initiating dolphin was the *rubber* did not result in both dolphins in the same posture more often than was the case when the initiating dolphin was the *rubbee* ( $X^2_1 = 2.17, NS$ ). The pattern for The Bahamas was the exact opposite. Rubbing episodes in The Bahamas when the initiating dolphin was the *rubber* did not result in both dolphins in the same posture more often than was the case when the initiating dolphin was the *rubbee* ( $X^2_1 = 0.87, NS$ ). However, the dolphins were found in the same posture significantly more often during a touching episode when the initiator was in the role of *rubber* ( $X^2_1 = 12.04, P < 0.001$ ).

**3.6. Sex and age**

For both Mikura Island and The Bahamas, strong preferences for same-sex rubbing partners were found for both the *rubber* and *rubbee* (Table 3). Same sex preferences occurred when the *initiator* was the *rubber* ( $X^2_1 = 45.94, P < 0.001$ ) and when the initiator was the *rubbee* ( $X^2_1 = 24.81, P < 0.001$ ). The same trend was found

**Table 3**  
Differences in gender for the partner chosen by the *initiator* while in the role of *rubber* and *rubbee* for both Mikura Island and The Bahamas.

Initiator	Mikura Island		Bahamas	
	Male receiver	Female receiver	Male receiver	Female receiver
Male <i>rubbee</i>	<b>29</b>	4	6	2
Female <i>rubbee</i>	9	<b>24</b>	7	<b>24</b>
male <i>rubber</i>	<b>60</b>	22	17	6
Female <i>rubber</i>	15	<b>62</b>	6	<b>38</b>

Values in bold font highlight the same sex/same age partner preferences.

**Table 4**

Age partner preferences for the initiating dolphin (noted in the far left column) in the role of *rubber* and *rubbee* for Mikura Island and The Bahamas for all contact types.

	Mikura				Bahamas			
	A	S	J	C	A	S	J	C
<i>Rubber</i>								
A	43	12	19	12	6	2	1	5
S	12	78	3	2	1	5	7	2
J	9	2	10	0	4	2	16	1
C	35	3	0	0	22	3	6	15
<i>Rubbee</i>								
A	19	4	2	1	3	0	1	10
S	7	34	0	0	0	1	2	0
J	7	0	10	0	0	5	8	4
C	12	0	0	0	5	0	0	4

A: Adult, S: Subadult, J: Juvenile, C: Calf.

in The Bahamas: *rubber* ( $X^2_1 = 24.34, P < 0.001$ ), *rubbee* ( $X^2_1 = 7.86, P = 0.005$ ). No differences were observed between Mikura Island and The Bahamas when examining the rate at which males choose other males in the role of *rubber* ( $X^2_1 = 0.11, P = 0.74$ ) or *rubbee* ( $X^2_1 = 2.81, P = 0.094$ ), nor when females choose other females in the roles of *rubber* ( $X^2_1 = 1.98, P = 0.16$ ) or *rubbee* ( $X^2_1 = 0.11, P = 0.14$ ) (Table 3). There was no difference in the rates at which males or females were found in the role of *rubber* vs. *rubbee* as either the *initiator* or *receiver* for the two sites: both genders were found in these roles (i.e., *rubber* or *rubbee*) at the same frequency for each condition (*initiator* or *receiver*) for both Mikura Island and The Bahamas.

For each of the two field sites, dolphins were categorized according to four age classes: adult, subadult, juvenile and calf. At Mikura Island, no differences were found for the rates at which animals in each of the four age classes assumed the role of *rubber* vs. *rubbee* as either the *initiator* ( $X^2_3 = 6.28, P = 0.099$ ) or the *receiver* ( $X^2_3 = 5.10, P = 0.165$ ) (Table 4). In The Bahamas, no difference was found for the rates at which animals in each of the four age classes assumed the role of *rubber* vs. *rubbee* as the *receiver* ( $X^2_3 = 6.18, P = 0.103$ ), but significant differences were observed for the *rubber* vs. *rubbee* when in the role of the *initiator* ( $X^2_3 = 14.55, P = 0.002$ ) (Table 4). For The Bahamas, the *initiator* was the *rubber* 50% of the time for adults, 83% for subadults, 58% for juveniles and 84% for calves. This suggests that subadults and calves tend to initiate rubs in the role of the *rubber* in The Bahamas more frequently than is observed for other age classes and conditions; as *rubber*, juvenile and calf spotted dolphins initiated pectoral fin contact more with other juveniles ( $n = 16$ ) and calves ( $n = 15$ ) (respectively) than with the other age classes, excluding mother/calf pairs (Table 4). As *rubber*, calves initiated pectoral fin contact with adult females ( $n = 22$ ), likely their mothers, almost twice as often as with other calves (Table 4). As a *rubber initiator*, calves at both sites initiated more contact with adults than with all other age classes, even calves (Table 4). Similarly, as *rubbee*, adults in The Bahamas initiated much more pectoral fin contact with calves ( $n = 10$ ) than with adults, subadults or juveniles (Table 4); also in the role of *rubbee*, calves initiated more contact with adults than with other calves, and not at all with subadults or juveniles (Table 4).

When the frequency at which each age class assumed each role (i.e., *rubber* vs. *rubbee*) for each condition (i.e., *initiator* or *receiver*) was compared between the two sites, the only significant difference found was between adults as *initiators*: in The Bahamas, the adult *initiator* was the *rubber* in 50% of episodes, whereas around Mikura Island the adult *initiator* was the *rubber* in 75% of episodes ( $X^2_2 = 5.55, P = 0.019$ ). Overall, this suggests similarity within and between field sites in terms of the rate at which animals of different age classes assume various roles (i.e., *rubber*, *rubbee*, *initiator*, *receiver*), with a significant exception in The Bahamas where it appears that adults tend to assume the role of *rubber/rubbee* more uniformly

when initiating contact than is observed for other age classes, and when compared to their counterparts around Mikura Island.

When comparing the frequency with which the four different age classes initiated contact with each of the other four age classes in both the role of rubber and rubberee (Table 4), significant differences between contact rates were observed for both sites: Mikura Island with the *initiator* as the *rubber* ( $X^2_9 = 168, P < 0.001$ ); Mikura Island with the *initiator* as the *rubberee* ( $X^2_9 = 92.7, P < 0.001$ ); The Bahamas with the *initiator* as the *rubber* ( $X^2_9 = 41.7, P < 0.001$ ); and The Bahamas with the *initiator* as the *rubberee* ( $X^2_9 = 32.1, P < 0.001$ ). These trends suggest that the *initiators* (of any age class) appear to have strong preferences for individuals of specific age classes when choosing a receiver. It should be noted that some of these trends are likely to be explained by bias in the proportion of animals of a certain age class observed at each study site. For example, the majority of animals observed around Mikura Island are subadults (Kogi et al., 2004; Dudzinski, unpublished data 1997–2004): this would bias the number of observations of subadult-to-subadult contacts around Mikura Island. Still, in the role as *rubber*, adults initiated two to three times more pectoral fin contact with other adults, than with all other age classes (Table 4). Similarly, subadult *rubbers* at Mikura initiated contact with other subadults five to 25 times more than with all other age classes (Table 4). When subadults were in the role of *rubberee*, they initiated contact five times more with other subadults than with adults and never with juveniles or calves (Table 4). Juvenile dolphins at Mikura initiated flipper contact with other juveniles when acting as *rubber* or *rubberee* more than with adults, subadults or calves. In fact, juveniles at this location never initiated pectoral fin contact with subadults or calves when in the role of *rubberee* (Table 4). One observed trend, however, cannot be explained by age class bias, namely the scarcity of calf-to-calf contacts observed around Mikura Island. The average proportion of calves less than a year old from within the study population observed at Mikura Island was 5.76%, while calves of the same age range at The Bahamas represented an average 3.44% of that population (see Table 1 for annual percentages per study site). Even given the larger percent of calves within the population recorded around Mikura Island, no calf-to-calf contacts were observed in either the role as *rubber* or *rubberee*. In The Bahamas, the number of calf-to-calf contacts was much greater. When the rate at which calves initiate contact with each of the four age classes is compared between the two sites (with the calf as *rubberee*), significant differences between the two sites are observed ( $X^2_3 = 23.4, P < 0.001$ , Table 4). Calves around Mikura Island were significantly less likely to seek contact with other calves when compared to calves in The Bahamas. Rates per site were as follows: Mikura Island—calf-to-adult 92%, calf-to-subadult 8%, calf-to-juvenile 0% calf-to-calf 0%; The Bahamas—calf-to-adult 48%, calf-to-subadult 6%, calf-to-juvenile 13%, calf-to-calf 34%.

### 3.7. Individual dolphin IDs

A complete examination of the individual pairs and reciprocity of pectoral fin contact exchanges is beyond the scope of this paper (though it is being examined for future discussion of individual variation); however, several dolphin pairs are included to illustrate the nature of the age and sex partner preferences previously presented.

#### 3.7.1. The Bahamas

Three sets of individual pairings were examined in greater detail; these pairings represented one adult male (SfID018) with two subadult males (SfID055, SfID025), a juvenile female (SfID061) with several peers of varying age class representing both sexes (e.g., juvenile females: SfID109, SfID111; subadult female: SfID030; calf male: SfID112), and three juvenile males (SfID084, SfID094, SfID103). For the adult/subadult males, SfID018 initiated both touch

and rubbing contacts as the *rubber* with SfID025 along the lateral side, belly and pectoral fin for durations lasting between 3 and 17 s. SfID025 reciprocated by rubbing the lateral side of SfID018 and also initiating contact to SfID055's pectoral fin and belly about a minute after contact with SfID018. After these observations, all three males swam out of the observer's view. These three males were traveling together across the shallow sandbar of the White Sand Ridge on two consecutive afternoons in July 1993. On the second day of our observations, we documented SfID055 initiating a 4 s rub to SfID025's belly. The underwater observations of these 3 males over these 2 days totaled 31 min and it is likely that we did not record all of the reciprocal pectoral fin or other rubbing contact exchanged between these individuals as they traveled through the study area.

SfID061 was often observed exchanging tactile contact with other spotted dolphins: as *rubber*, she initiated 7 and received 3 pectoral fin contacts during 4 underwater sessions with a subadult female, a male calf and 2 juvenile female (SfID109 and SfID111) spotted dolphins. As *rubberee*, SfID061 initiated or received an additional 14 pectoral fin contacts with SfID109 and SfID111. Contacts with the subadult female and male calf were brief, averaging 1 or 2 s, primarily along the side, dorsal fin, or face and were seemingly not reciprocated; however, pectoral fin contact exchanged between SfID061, SfID109 and SfID111 was strongly reciprocal ( $n = 38$  exchanges between these 3 individuals), longer in duration (median = 3 s, range between 1 and 24 s), and covered more of the body (e.g., dorsal fin, rostrum, face, side, belly, pectoral fin). In comparison, the 3 juvenile male spotted dolphins all exchanged relatively brief pectoral fin contacts (only 1 or 2 s) only with other male juveniles, which were only mildly reciprocal (2 sets of exchanges between SfID084 and SfID103). Also, these 3 juvenile males exchanged touches and rubs with equal frequency whereas the juvenile and calf females exchanged primarily rubbing contact.

#### 3.7.2. Mikura island

Interactions between a few subadult male bottlenose dolphins highlight the significance in same-sex, same-age partner preferences observed among individuals around Mikura Island. TaID053 and TaID240 initiated ( $n = 5$ ) and received ( $n = 5$ ) an equal amount of pectoral fin rubs with each other during our observations, which ranged from 1 to 7 s (median = 1 s) and focused on their faces (40% of rubs) and backs (40%). TaID053 also exchanged pectoral fin contact with four other subadult males (TaID043, TaID230, TaID263, TaID358) in reciprocal fashion; both rubs and touches were exchanged and the body focus for contact was the side, back and belly during these exchanges. Most contacts were 1 s in duration though exchanges of 2–8 s were recorded. TaID240 also initiated and received pectoral fin contact with 2 other subadult male bottlenose dolphins that we documented: 5 contacts with TaID263 and 4 contacts with TaID226. More rubs ( $n = 6$ ) than touches ( $n = 3$ ) were recorded but the duration (median = 1 s, range 1–7 s) and body part (67% to lateral side) were consistent with the other exchanges observed between subadult males from this study population.

## 4. Discussion

This study has revealed a number of similarities between the two study sites in terms of contact behaviour involving the pectoral fin. The rates of observed contacts between sites are nearly identical. Species at both sites engage more frequently in *rubbing* than *petting*, and the *initiator's* order of preference of initial body part to contact is nearly identical between the two sites. Dolphins at both sites appear to prefer the horizontal (HOR) position when engaging in contact behaviours, and both species prefer same sex rubbing partners.

Contrary to the findings of Sakai et al. (2006a), we found that the *rubber* is significantly more likely to be the *initiator* than the *receiver* for both Mikura and The Bahamas. Sakai et al. found that for Mikura dolphins, 73.1% of *initiators* (of 67 episodes) were the *rubbee*. For this study, we found that 74.41% (of 340 episodes) of *initiators* were the *rubber*, not the *rubbee*. This discrepancy in findings is surprising given that both studies used similar definitions, and coded data in a similar fashion. The frequency of observed dolphins from the defined age classes and gender involved in each study were roughly similar as well. It is not the case that the differences between the two studies reflect the fact that Sakai et al. (2006a) focused on active rubbing, while we included all forms of pectoral fin to body contact in our analyses (e.g., touches). When we only include active rubbing in our analyses, the *rubber* was still more likely to initiate a contact event than was the *rubbee* ( $X^2_1 = 6.99$ ,  $p < 0.01$ ). One possible explanation is the difference in sampling sizes:  $N = 67$  for Sakai et al. (2006a), whereas  $N = 340$  for this study.

Overall, there is much similarity within and between each field site in terms of the rate at which animals of different age classes assume various roles (i.e., *rubber*, *rubbee*, *initiator*, *receiver*). The *initiators* (of any age class) appear to have strong preferences for individuals of specific age classes when choosing a *receiver*. For both sites and for all roles, adults tend to primarily contact other adults, and occasionally calves and juveniles, and subadults almost exclusively tend to contact other subadults. The only exception appears to be that in The Bahamas, subadults and calves tend to initiate rubs in the role of the *rubber* more frequently than do the other age classes. An important and striking difference between the two sites is the observation that calves in Mikura are significantly less likely to seek contact with other calves when compared to calves in The Bahamas. This suggests that calves (and to some extent the other ages classes) in The Bahamas are less inhibited when seeking a rubbing partner, and often leave their mother's side to seek contact with other individuals. Calves in Mikura on the other hand were never observed leaving their mother's side to seek out contact with another calf or juvenile. Perhaps there are social or ecological pressures in Mikura that are absent in The Bahamas that require a calf to 'stick close' to its mother during the first few years of its life. These pressures may include increased predation from sharks, or the increased likelihood of aggressive behaviour from adult and subadult males. Incidents of adult and subadult male aggression toward young calves have been recorded from around Mikura, and infanticide has been suggested as a possible cause of calf mortality at this site (Dudzinski, personal observation, 2003) and for bottlenose dolphins in the Moray Firth (see Patterson et al., 1998).

With the exception of the notable differences in rates of contact among calves, the majority of contact behaviours we investigated were similar across the two sites despite some environmental differences: Mikura consists of a rocky, boulder-strewn sea floor and has poor average water clarity; The Bahamas site consists of a calcium carbonate sandy bottom and much clearer water. Although one might expect contact rates to be higher at Mikura given the relatively poor visibility, which may result in dolphins seeking physical contact with one another given the decreased ability to stay in visual contact, such was not the case for the dolphins observed in this study. If reduced water clarity does increase the incidence of dolphin contact behaviours, then the waters around Mikura Island are not sufficiently murky to produce such an effect. One might also expect that if dolphins rub their bodies for hygienic reasons (e.g., to remove parasites, sloughing skin), contact rates would be higher at Mikura Island where there is less opportunity to rub in the sand, a behaviour often witnessed in The Bahamas (Dudzinski, 1996, 1998). However, we did not document differing amounts of contact at these sites for these dolphins.

These observations, coupled with the observations of Sakai et al. (2006a) concerning the lack of evidence for a parasite removal

function of rubbing behaviour, suggest that the primary function of rubbing is not hygienic. In addition, if rubbing were a behaviour whose primary goal was self-stimulation, we would expect to observe decreased rubbing rates in The Bahamas, where rubbing in the sand should produce pleasurable stimulation and reduce the need for tactile stimulation resulting from contact with conspecifics. Moreover, the observation that the *rubber* is the initiator of contacts in the majority of cases for both sites is inconsistent with the notion that the primary function of contact is self-stimulation. The fact that dolphins engage in contact behaviours at similar rates despite differences in water clarity suggests that the function of contact behaviour has a social component. In addition, the *initiators* of contact behaviour generally tend to choose same sex partners and partners of the same age class, which suggests that rubbing behaviour has a strong social component. However, given that the vast majority of contact occurs with same sex partners, it is unlikely that rubbing is a pre-copulatory behaviour, as has been previously suggested (e.g., Tavolga and Essapian, 1957). Furthermore, as has been pointed out by Sakai et al. (2006a), the reciprocal nature of rubbing bouts (i.e., switching *rubber/rubbee* roles during a bout) suggests that rubbing serves an affiliative function.

Delphinid rubbing behaviour is potentially analogous to grooming behaviour observed in terrestrial mammals. The grooming of other individuals (termed 'allogrooming' or simply 'grooming') has been documented in many primate species (e.g., chimpanzees (*Pan troglodytes*) (Hemelrijk and Ek, 1991), patas monkeys (*Erythrocebus patas*) (Muroyama, 1994), Japanese macaques (*Macaca fuscata*) (Muroyama, 1991), as well as other mammalian species (e.g., squirrels (Halloran and Bekoff, 1995) and horses (*Equus caballus*) (Rho et al., 2007)). Grooming in primates leads to increased support during future agonistic encounters (Seyfarth and Cheney, 1984), as well as increased food sharing (de Waal, 1997). These kinds of exchanges involve a system of reciprocal altruism where individuals' behaviour toward conspecifics is based upon a history of interaction with that individual or the individual's close kin (Seyfarth and Cheney, 2007). de Waal (1997) describes the trade-off of grooming 'services' for food sharing 'services' a 'service economy' in chimpanzees. In these studies, the recipient of the grooming (i.e., the groomee) was shown to alter/increase sharing and aid giving behaviour as a result of the grooming. Consequently, the groomee could be considered to have accumulated a 'social debt' for the grooming services provided that would be re-paid during future interactions with the groomer.

This 'services' model may help explain our observation that the majority of dolphin rubbing episodes involved same sex partners. In many documented dolphin societies, agonistic encounters between the sexes involves mate guarding (Willis and Dill, 2007), herding (Connor et al., 1992), and infanticide (Dunn et al., 2002). As a result, long-term social bonds between same sex partners have developed (Connor, 1992). In the absence of 'grooming' as the currency in the dolphin services economy, rubbing may be a commodity that is traded for future assistance in agonistic encounters, such as male conflicts. This possibility is consistent with the notion of reciprocal altruism (Connor and Norris, 1982).

Recent research, however, has challenged the notion that grooming in primates should always be considered a 'service' that benefits the groomee. In a study of stress in Barbary macaques (*Macaca sylvanus*), individuals who spent more time grooming in the role of the groomer had reduced stress hormone levels in their feces, whereas the groomee's stress hormone levels were unaffected by the amount of grooming they received (Shutt et al., 2007). This finding suggests that the groomer may receive assurance of his/her position within a social network by engaging in grooming behaviours directed at conspecifics, leading to a drop in stress levels. For this explanation, the potential benefits received by the groomee (e.g., parasite removal) play a less important role in the

function of the interaction, and a discussion of future agonistic support or other forms of reciprocal altruism must be re-focused on the groomer. If we apply a similar explanation to rubbing behaviour in dolphins, then it may be that the *rubber* receives the greatest benefit during a rubbing bout, which may partly explain why in this study the *rubber* tends to initiate such bouts. For this explanation, it would then be the *rubber* who has accumulated a 'social debt', and would be expected to reciprocate to the benefit of the *rubbee*—either by allowing him/herself to be rubbed in the future, or to come to the *rubbee's* aid during agonistic encounters.

There are potential pitfalls in suggesting an analogy between grooming in primates and rubbing in dolphins. Unlike primate grooming, the *rubbee* seems to more actively participate in the rubbing act, often by moving the body part being rubbed—it is not a case that the *rubbee* should be understood as exclusively 'receiving' the behaviour in question. The *rubbee* often moves the body part being rubbed in conjunction with the movement of the *rubber's* flipper (Sakai et al., 2006a). In such cases, the *rubbee* is participating in the rubbing act. For dolphin rubbing then, both animals could be considered as active participants in the act.

For dolphin rubbing, it is not yet clear which of the individuals is receiving the most benefit in the case of an imbalanced 'social debt' (i.e., the *rubber* or the *rubbee*), or if any social debt arises at all. Especially in the case of *petting*, the behaviour itself does not necessarily provide clues as to its social significance for each of the participants, making the distinction between mutualism and reciprocal altruism difficult to establish. If the benefits of rubbing are not weighted toward either the *rubber* or the *rubbee*, then rubbing may itself be an act of mutualism, and not altruism. A study by Tamaki et al. (2006) suggests that contact behaviour may be used by dolphins to restore alliances, and reduce tensions in post-conflict encounters for bottlenose dolphins, similar to one of the proposed functions of genito-genital rubbing in bonobos (Blount, 1990). If we assume that there may be multiple functions and manifestations of rubbing behaviour within dolphin societies, then explaining the function of rubbing behaviour in dolphins requires that we determine who exactly is receiving benefits from the acts involved.

This study provides only an initial direct comparison of the pectoral fin contact behaviour of two species at two study sites. Continued long term study of wild dolphin populations, as well as the addition of new focus species at other study sites are required to form a consistent picture of the kinds of rubbing behaviours used by various dolphin species. Comparison of environmental and ecological factors between sites, as well as the social structure of the species involved will shed further light on the likely function and ontogeny of pectoral fin contact behaviour. For this to be accomplished, and to allow for easier meta-analysis of the results reported in the literature by different research groups, we urge that rubbing nomenclature conventions be adopted. Currently, the evidence points toward a social component being the driving force behind the evolution of rubbing behaviour, possibly similar in function to grooming in primates, but further study is required to confirm this hypothesis.

## Acknowledgements

Financial support for data collection during the Dolphin Communication Project's longitudinal studies of the Bahamas' Atlantic spotted dolphins and the Indo-Pacific bottlenose dolphins around Mikura Island, Japan was obtained from numerous sources: the National Science Foundation, International Women's Fishing Association, Houston Underwater Club's SeaSpace Foundation, Cetacean Society International, Lerner-Gray Fund of the American Museum of Natural History, Texas A&M University at Galveston (TAMUG), Marine Mammal Research Program at TAMUG, the National Geographic Society (grant #4851–92), the Japanese Society for the

Promotion of Science, Casio's Eco-Research Fund, and a Kaken-Hi grant from the Japanese government. All data were collected during ecotour-format boat trips that were partially sponsored by Oceanic Society Expeditions (in The Bahamas), the Miyake Fishermen's Cooperative (from Miyake Island), and the Mikura Iruka Kyoukai (at Mikura Island). More than a dozen boats and boat captains supported data collection, and they are collectively thanked here. Permission to collect data around Mikura Island was provided by the village office and conducted in collaboration with the Mikura Iruka Kyoukai. Permission to collect data on the spotted dolphins in The Bahamas was granted in the form of permits to K.M. Dudzinski (1993–2005) and to the Dolphin Communication Project (2000 and 2001) from the Department of Fisheries (Marine Resources), Ministry of Agriculture, The Bahamas. Mention of trade names or products does not constitute endorsement for use by the U.S. government. This paper represents contribution #102 of the Dolphin Communication Project.

## References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.
- Bateson, G., 1974. Observations of a cetacean community. In: McIntyre, J. (Ed.), *Mind in the waters*. Charles Scribner's Sons, New York, NY, pp. 146–165.
- Blount, B.G., 1990. Issues in bonobo (*Pan paniscus*) sexual behavior. *American Anthropologist* 92, 702–714.
- Brunnick, B.J., 2000. Social Structure of Atlantic Spotted Dolphins in the Bahamas (*Stenella frontalis*). Union Institute, Cincinnati, OH.
- Connor, R.C., 1992. Dolphin alliances and coalitions. In: Harcourt, A.H., de Waal, F. (Eds.), *Coalitions and Alliances in Humans and Other Animals*. Oxford University Press, Oxford, pp. 415–443.
- Connor, R.C., Mann, J., Watson-Capps, J., 2006. A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Ethology* 112, 631–638.
- Connor, R.C., Norris, K.S., 1982. Are dolphins reciprocal altruists? *American Naturalist* 119, 358–374.
- Connor, R.C., Smolker, R.A., Richards, A.F., 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America* 89, 987–990.
- Connor, R.C., Wells, R., Mann, J., Read, A., 2000. The bottlenose dolphins: social relationships in a fission fusion society. In: Mann, J., Connor, R., Tyack, P., Whitehead, H. (Eds.), *Cetacean Societies: Field Studies of Whales and Dolphins*. University of Chicago Press, Chicago, pp. 91–126.
- de Waal, F.B.M., 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior* 18, 375–386.
- Dudzinski, K.M., 1996. Communication and Behavior in the Atlantic Spotted Dolphins (*Stenella frontalis*): Relationships Between Vocal and Behavioral Activities. Texas A&M University, Galveston, TX, p. 128.
- Dudzinski, K.M., 1998. Contact Behavior and signal exchange in Atlantic Spotted Dolphins (*Stenella frontalis*). *Aquatic Mammals* 24, 129–142.
- Dudzinski, K.M., Clark, C.W., Würsig, B., 1995. A mobile video/acoustic system for simultaneous recording underwater recording of dolphin interactions. *Aquatic Mammals* 21, 187–193.
- Dudzinski, K.M., Sakai, M., Masaki, K., Kogi, K., Hishii, T., Kurimoto, M., 2003. Behavioural observations of bottlenose dolphins towards two dead conspecifics. *Aquatic Mammals* 29, 108–116.
- Dunn, D.G., Barco, S.G., Pabst, D.A., McLellan, W.A., 2002. Evidence for infanticide in bottlenose dolphins of the Western North Atlantic. *Journal of Wildlife Diseases* 38, 505–510.
- Gregg, J.D., Dudzinski, K.M., Smith, H.V., 2008. 3D MASC: a method for estimating relative head angle and spatial distance of dolphins from underwater video footage. *Animal Behaviour* 75, 1181–1186.
- Halloran, M.E., Bekoff, M., 1995. Cheek rubbing as grooming by Albert Squirrels. *Animal Behaviour* 50, 987–993.
- Hemelrijk, C.K., Ek, A., 1991. Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour* 41, 923–935.
- Herzing, D., 1997. The life history of free-ranging Atlantic Spotted Dolphins—(*Stenella frontalis*): age classes, color phases, and female reproduction. *Marine Mammal Science* 13 (4), 576–595.
- Johnson, C.M., Moewe, K., 1999. Pectoral fin preference during contact in Commerson's dolphins (*Cephalorhynchus commersonii*). *Aquatic Mammals* 25, 73–77.
- Johnson, C.M., Norris, K.S., 1994. Social Behavior. In: Norris, K.S., Würsig, B., Wells, R.S., Würsig, M. (Eds.), *The Hawaiian Spinner Dolphin*. University of California Press, Berkeley, pp. 243–286.
- Kakuda, T., Tajima, Y., Arai, K., Kogi, K., Hishii, T., Yamada, T.K., 2002. On the resident "Bottlenose Dolphins" from Mikura Water. *Memorandum of the Natural Science Museum of Tokyo* 38, 255–272.
- Kogi, K., Hishi, T., Imamura, A., Iwatani, T., Dudzinski, K.M., 2004. Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science* 20, 510–526.



- Kuczaj, S.A., Yeater, D.B., 2007. Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras. *Journal of the Marine Biological Association of the United Kingdom* 87, 141–148.
- Mann, J., Smuts, B., 1998. Natal attraction: allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour* 55, 1097–1113.
- Mann, J., Smuts, B., 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136, 529–566.
- Muroyama, Y., 1991. Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). *Behaviour* 119, 161–170.
- Muroyama, Y., 1994. Exchange of grooming for allomothering in female patas monkeys (*Erythrocebus patas*). *Behaviour* 128, 103–119.
- Norris, K.S., Würsig, B., Wells, R.S., Würsig, M., 1994. *The Hawaiian Spinner Dolphin*. University of California Press, Berkeley.
- Patterson, I.A.P., Reid, R.J., Wilson, B., Grellier, K., Ross, H.M., Thompson, P.M., 1998. Evidence for infanticide in bottlenose dolphins: An Explanation for violent interactions with harbour porpoises? *Proceedings: Biological Sciences* 265, 1167–1170.
- Paulos, R.D., Dudzinski, K., Kuczaj, S., 2007. The role of touch in select social interactions of Atlantic spotted dolphin (*Stenella frontalis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). *Journal of Ethology* 26, 153–164.
- Perrin, W., 1970. Color patterns of the eastern Pacific spotted porpoise (*Stenella graffmani Lönnbeg*) (Cetacea, Delphinidae). *Zoologica (NY)* 54, 135–149.
- Rho, J.R., Srygley, R.B., Choe, J.C., 2007. Sex preferences in Jeju pony foals (*Equus caballus*) for mutual grooming and play-fighting behaviors. *Zoological Sciences* 24, 769–773.
- Richards, A.F., 1996. *Life History and Behavior of Female Dolphins (Tursiops sp.) in Shark Bay, Western Australia*. University of Michigan, Ann Arbor.
- Sakai, M., Hishii, T., Takeda, S., Kohshima, S., 2003. Quantitative analyses of flipper rubbing behavior in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). In: 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC.
- Sakai, M., Hishii, T., Takeda, S., Kohshima, S., 2006a. Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science* 22, 966–978.
- Sakai, M., Hishii, T., Takeda, S., Kohshima, S., 2006b. Laterality of flipper rubbing behaviour in wild bottlenose dolphins (*Tursiops aduncus*): caused by asymmetry of eye use? *Behavioural Brain Research* 170, 204–210.
- Samuels, A., Sevenich, M., Gifford, T., Sullivan, T., Sustman, J., 1989. Gentle rubbing among bottlenose dolphins. In: 8th Biennial Conference on the Biology of Marine Mammals, Monterey.
- Samuels, A., Tyack, P., 2000. Flukeprints: a history of studying cetacean societies. In: Mann, J., Connor, R., Tyack, P., Whitehead, H. (Eds.), *Cetacean Societies: Field Studies of Whales and Dolphins*. University of Chicago Press, Chicago, pp. 9–44.
- Seyfarth, R.M., Cheney, D.L., 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308, 541–543.
- Seyfarth, R.M., Cheney, D.L., 2007. *Baboon Metaphysics: The Evolution of a Social Mind*. University of Chicago Press, Chicago.
- Shutt, K., MacLarnon, A., Heistermann, M., Semple, S., 2007. Grooming in Barbary macaques: better to give than to receive? *Biological Letters* 3, 231–233.
- Smith, T.G., Aubin, D.J.S., Hammill, M.O., 1992. Rubbing behaviour of belugas, *Delphinapterus leucas*, in a high Arctic estuary. *Canadian Journal of Zoology* 70, 2405–2409.
- Tamaki, N., Morisaka, T., Taki, M., 2006. Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioral Processes* 73, 209–215.
- Tavolga, M.C., Essapian, F.S., 1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother–infant behavior. *Zoologica* 42, 11–31.
- Whitehead, H., Weilgart, L., 2000. The sperm whale: social females and roving males. In: Mann, S., Connor, R.C., Tyack, R.L., Whitehead, H. (Eds.), *Cetacean Societies*. The University of Chicago Press, pp. 154–173.
- Willis, P.M., Dill, L.M., 2007. Mate guarding in male dall's porpoises (*Phocoenoides dalli*). *Ethology* 113, 587–597.