

FLIPPER RUBBING BEHAVIORS IN WILD BOTTLENOSE DOLPHINS (*TURSIOPS ADUNCUS*)

MAI SAKAI

Department of Biological Sciences,
Graduate School of Bioscience and Biotechnology,
Tokyo Institute of Technology, 2-12-1-W3-43,
Ookayama, Meguro-Ku, Tokyo 152-8551, Japan
E-mail: msakai@bio.titech.ac.jp

TORU HISHII

Mikura-jima Iruka Kyoukai,
Mikura Island, Tokyo 100-1301, Japan

SHOHEI TAKEDA

Department of Comparative Psychology,
Division of Humane & Social Studies for Man-Nature Relations,
Faculty of Agriculture, Tokyo University of Agriculture and Technology,
3-5-8, Saiwai-cho, Fuchuu-city, Tokyo 183-8509, Japan

SHIRO KOHSHIMA

Department of Biological Sciences,
Graduate School of Bioscience and Biotechnology,
Tokyo Institute of Technology, 2-12-1-W3-43,
Ookayama, Meguro-Ku, Tokyo 152-8551, Japan

ABSTRACT

“Flipper rubbing” behavior was quantitatively analyzed in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Tokyo, Japan. We observed two types of flipper rubbing: (1) F-B rubbing; one dolphin (Rubber) rubbed its flipper over various parts of a partner’s (Rubbee) body, and (2) F-F rubbing; both dolphins rubbed each other’s anterior flipper edge in alternating shifts. F-B rubbings tended to be initiated by the Rubbee and were terminated by the Rubber. The Rubbee often moved actively its body part that was in contact with the Rubber’s flipper, and assumed side-up, upside-down, or other postures while the Rubber remained horizontal in most cases. These facts suggest that the Rubbee engaged in F-B rubbing more actively than the Rubber, and might receive some benefit from the frictional contact during F-B rubbing. Dolphins often switched their roles as Rubber and Rubbee between episodes of flipper rubbing bout. Adults and sub-adults exchanged F-B rubbing and F-F rubbing most often with individuals of the same sex in the same age class. F-B rubbing was frequent in mother-and-calf dyads. Our results suggest that flipper rubbing is an affiliative behavior which could be a quantitative measure of social relationships among individuals of this species in future studies.

Key words: Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, social behavior, contact behavior.

“Flipper rubbing” behavior, in which one dolphin rubs another dolphin with its flipper (pectoral fin) has been reported in various cetacean species; the wild individuals include Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, Mann and Smuts 1998, 1999), spinner dolphins (*Stenella longirostris*, Johnson and Norris 1994), Atlantic spotted dolphins (*Stenella frontalis*, Dudzinski 1998) and sperm whales (*Physeter macrocephalus*, Whitehead and Weilgart 2000), captive individuals include bottlenose dolphins (*Tursiops truncatus*, Tavolga and Essapian 1957), spinner dolphins (Johnson and Norris 1994), and Commerson’s dolphins (*Cephalorhynchus commersoni*, Johnson and Moewe 1999). However, we still have no precise studies on this behavior. In addition, this behavior has not previously been defined clearly and has been called by various names often together with other types of behavior (see Table 1).

Some researchers have discussed possible function(s) for pectoral fin rub exchanges. Norris (1991) and Dudzinski (1998) both pointed out that flipper rubbing may be a kind of affiliative behavior, similar to grooming in primates. Other researchers have suggested that flipper rubbing is a kind of sexual behavior. Tavolga and Essapian (1957) studied captive bottlenose dolphins and suggested that flipper rubbing represents a passive or inactive form of sexual behavior because it appears primarily as a precopulatory behavior. To clarify the potential functions for flipper rubbing, more precise data, especially those on wild dolphins, are needed.

In this study we examined the flipper rubbing behavior of wild Indo-Pacific bottlenose dolphins. We video-recorded 561 flipper rubs and quantitatively analyzed them to clarify the precise characteristics of flipper rubbing and to discuss the possible functions for this contact behavior.

METHODS

Study Area and Study Period

The study was conducted at Mikura Island (19.62 km²) located about 220 km south of Tokyo, Japan. All observations were conducted in an area within 300 m from the coastline, at water depths of 2–45 m during spring to early autumn between June 2000 and October 2002.

Dolphin Population

In this study, only underwater video-recorded behaviors were analyzed. We also used video data recorded by members of Mikura-jima Bandouiruka Kenkyukai (M.B.K, a group for underwater video-identification of dolphins from 1994 to 2003). From 2000 to 2001, M.B.K. estimated that about 160 Indo-Pacific dolphins are resident around this island (Kogi *et al.* 2004). The sex of observed dolphins was determined by examining the genital slit. We classified dolphins into four age classes as defined by M.B.K: adult, subadult, juvenile, and neonate (Kogi *et al.* 2004). M.B.K. defined a mother-and-calf dyad as a pair including an adult female and a calf observed together for more than 50% of the total observations for the adult female. We define calves as juveniles or neonates.

Table 1. Definition of flipper rubbing behavior in previous studies.

Species	Source	Term	Suggested functions	Category
Bottlenose dolphin	Tavolga and Essapian (1957)	Stroking	Precopulatory behavior	FsBx, FFB, FmBx
	Mann and Smurs (1998, 1999)	Petting	Grooming	FmBx
Atlantic spotted dolphin	Connor <i>et al.</i> (2000)	Petting	Affiliative	FE, FmBx
	Connor (2002)	Petting	Affiliative and hygienic	FF, FmBx
	Dudzinski (1998)	Petting	Social grooming	FE, FmBx
	Johnson and Norris (1994); Norris (1991)	Petting/Rubbing	Reaffirmation of relationships	FsBx
		Caressing		FmBx
Hawaiian spinner dolphin	Johnson and Norris (1994)	Wuzzles		FmBx
		Pectoral whetting (Bateson 1974)		FFFF, FFB
Hawaiian spinner dolphin	Bateson (1974)	Flipper rubbing		FmBx, FsBx
		Pat-a-cake		FFFF
Commerson's dolphin	Johnson and Moewe (1999)	Flipper-to-body rubbing		FmBx
			Flipper-to-flipper rubbing	
Sperm whale	Whitehead and Weilgart (2000)			FF
Indo-Pacific bottlenose dolphin	This study			

FmBs; F-B rubbing, moving flipper back and forth, static body.

FsBm; F-B rubbing, static flipper, moving body back and forth.

FmBm; F-B rubbing, moving flipper back and forth, moving body back and forth.

FmBx; F-B rubbing, moving flipper back and forth, body movement was not described.

FsBx; one dolphin contact with static flipper on the other's body, and swim along or across the other's body produced a stroking effect.

FF; F-F rubbing.

FFB; one dolphin rubs the other's body with both flippers.

FFFF; two dolphins facing belly to belly F-F rub with both flippers at the same time.

Data Collection

A researcher entered the water and recorded dolphin behavior using a digital camcorder (Sony) in a waterproof housing (DIV or Sony). The sampling method adopted was an *ad lib* protocol (Altmann 1974). To minimize the disturbance by our presence, we followed a noninvasive approach to observation *i.e.*, only when dolphins approached us could we closely observe them. Dolphins did not show any unusual behavior during observations in most cases. We did not use scuba tanks. We also never attempted to touch the dolphins and never fed them.

Definition of Flipper Rubbing Behavior

We defined “flipper rubbing” as the behavior in which one dolphin contacts another dolphin with its pectoral fin (flipper) and either or both dolphins actively move the touching body parts back and forth. During this behavior, the dolphin whose flipper was in contact with a second individual’s body was labeled the Rubber while the dolphin whose body was physically touching the partner’s flipper was called the Rubbee. Flipper rubbing exchanges were begun by a dolphin making physical contact to another dolphin and were terminated when one of the dolphins broke contact from the other. We defined this behavior unit between the making and breaking of actual contact as a flipper rubbing “episode.” A flipper rubbing episode was often repeated several times with short interruptions. During the interruption, the dolphins did not physically touch each other but they remained engaged in the same behavioral activity such as parallel swimming and synchronized surfacing for respiration. We defined flipper rubbing episodes with interruptions as a flipper rubbing “bout.”

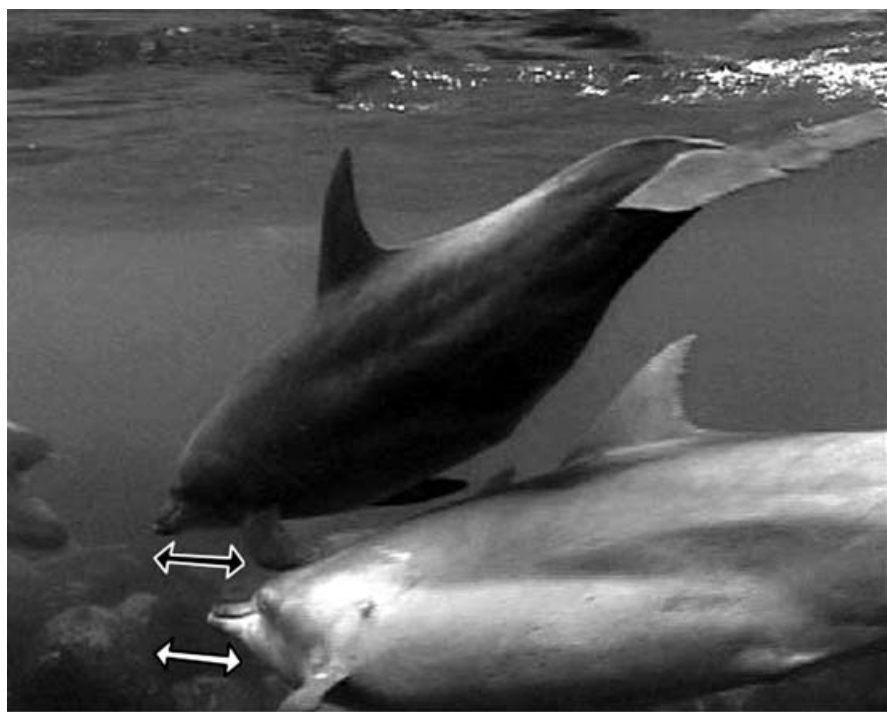
Flipper rubbing behavior was categorized as “flipper-to-body rubbing” (F-B rubbing) and “flipper-to-flipper rubbing” (F-F rubbing). In F-B rubbing, one dolphin (Rubber) rubbed some part of its partner’s body excluding the Rubbee’s flipper edge (Fig. 1A). In F-F rubbing, both dolphins rubbed each other’s leading edge of their flippers—moving their flippers back and forth similar to grinding one knife against another (Fig. 1B).

Analysis of Flipper Rubbing Behavior

For each video-documented flipper rubbing event, we identified the sex and age class of the dolphins involved and recorded their posture, part of the body in contact with the flipper, and movement of the flipper or body of each dolphin.

To record the body part in contact with the flipper, we divided the body surface of the dolphin into 11 surface areas (Fig. 2). The percentage of surface area of each body part to the total body surface area was estimated by measuring the body of a dead

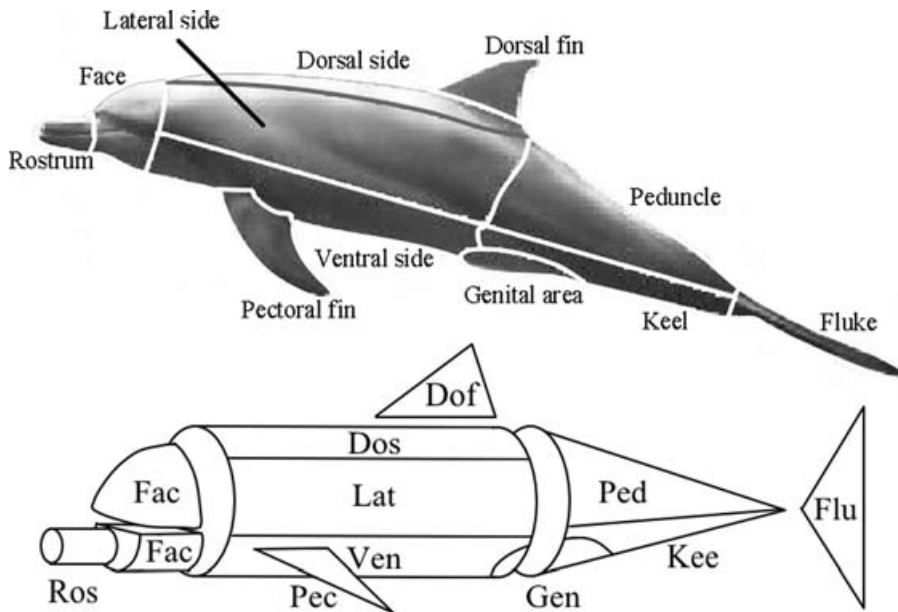
Figure 1. Flipper-to-body rubbing and flipper-to-flipper rubbing. (A) #036 (sub-adult male, Rubber, above) rubbed the face of #012 (sub-adult male, Rubbee, below) moving its pectoral fin back and forth (indicated by a black arrow). #012 moved its face horizontally (indicated by a white arrow) and reciprocally to the movement of Rubber’s pectoral fin. (B) A pair of subadult males (#360; left and #271; right) conducting flipper-to-flipper rubbing. They rubbed the frontal edge of the flipper with each other similar to grinding one knife onto another knife moving their pectoral fin back and forth.



A



B



Body part	Code	Surface area (%)	Number of episodes	Expected number	Binominal test
Lateral side	Lat	26.0	67	54	+
Face	Fac	8.9	50	19	++
Ventral side	Ven	17.3	18	36	--
Peduncle	Ped	15.4	16	32	--
Dorsal side	Dos	8.7	22	18	+
Fluke	Flu	5.5	8	11	-
Pectoral fin	Pec	3.4	8	7	+
Genital area	Gen	2.6	10	5	+
Keel	Kee	5.1	8	11	-
Dorsal fin	Dof	4.7	1	10	--
Rostrum	Ros	2.3	0	5	-

Figure 2. Definitions of body parts, their estimated percent area to the total body surface, and amount of flipper-to-body rubbing oriented to each part. Signs indicate a rub greater (+), less (-), than expected number of F-B rubbing significant at $P < 0.05$ (++ or --, binominal test).

individual (see Dudzinski *et al.* 2003) to create a simplified model of the dolphin body (Fig. 2). When flipper rubbing was directed to several body parts during an episode, we separately counted it for each body part in the analysis of contacted body parts.

Dolphin posture during flipper rubbing was categorized into the following four types. "Horizontal" was defined as a posture in which the dolphin's ventral side was

parallel to the sea floor. A posture in which one pectoral fin was kept up toward the sea surface and the other was directed to the sea floor was classified as “side-up.” “Upside-down” postures were defined as a dolphin with its ventral side facing up and the dorsal side parallel to the sea floor. Postures other than the above three types and instances when a dolphin(s) changed posture during flipper rubbing were classified as “other.”

Statistics

We used only the episodes performed by identified dolphins in the statistical analyses. Differences in the role as initiator or departer by a Rubber and Rubbee during flipper rubbing were evaluated using a binominal test. Differences in the posture assumed by Rubber and Rubbee during flipper rubbing was evaluated using a Kolmogorov–Smirnov test. In both cases, we used individual dolphins as the unit of analysis, including only one episode (the first one) for each identified individual to avoid a possible effect of pseudo-replication by analyzing many data from the same individual repeatedly. These analyses included a total of 322 episodes of F-B rubbing performed by identified individuals and involved 100 individuals as Rubber with an average (\pm SD) of 3.22 ± 2.76 episodes per individual, and 121 individuals as Rubbee with average of 2.65 ± 2.28 episodes per individual. A binominal test was used to compare differences between actual observed numbers of rubs and the expected number for each body part. Here we used dyads as the unit of analysis, including only one episode (the first one) for each combination of individuals to avoid a possible effect of pseudo-replication by analyzing many data from the same dyad. This analysis included a total of 184 dyads of F-B rubbing that involved 100 individuals as Rubbers with an average (\pm SD) of 1.84 ± 1.08 episodes per individual, and 119 individuals as Rubbee with an average of 1.55 ± 0.94 episodes per individual. Biases in the F-B rubbing exchange between a mother and a calf were evaluated using a Wilcoxon signed rank test. Differences in duration between F-B rubbing and F-F rubbing were evaluated using a Mann–Whitney *U* test. All the tests were two-tailed at $P < 0.05$. It is possible that our findings are biased by prevalence of subadult males in our data set (31.7% of 145 individuals, 42.9% of 322 episodes, Table 2).

Table 2. Difference in F-B rubbing partner with sex and age class.

Sex and age class	Partner of F-B rubbing				Juvenile	Neonate
	Adult male	Subadult male	Adult female	Subadult female		
Adult male (9)	<u>2</u>	4	6†	1†	0	0
Subadult male (46)	—	<u>109</u>	10†	14†	1	0
Adult female (36)	—	—	<u>31</u>	3	77*	25*
Subadult female (19)	—	—	—	<u>32</u>	0	0
Juvenile (26)	—	—	—	—	<u>0</u>	0
Neonate (9)	—	—	—	—	—	<u>0</u>

Underlined figures; dolphin pairs of the same sex in the same age class.

*all of adult female and calf pairs in F-B rubbing were mother and her calf dyads.

†intersexual F-B rubbing.

Parenthetic figures are number of individuals that performed F-B rubbing.

RESULTS

General Characteristics of Flipper Rubbing

We video-recorded 561 flipper rubbing episodes that included 108 multiple-episode bouts and 300 single-episode rubs in total. During the study period we video-recorded 535 episodes of F-B rubbing (Fig. 1A) and 26 episodes of F-F rubbing (Fig. 1B). The sex ratio and age class composition of the observed dolphin population was almost the same during each year of the study (Kogi *et al.* 2004). Flipper rubbing was performed by 145 identified individuals (Table 2).

The duration of F-B rubbing episodes ranged from 2 to 53 s with an average (\pm SD) of 8.9 ± 9.2 ($n = 120$ episodes in which both dolphins were identified and we could record the episode from beginning to end). The duration of F-F rubbing episodes ranged from 2 to 5 s with an average of 3.43 ± 1.27 ($n = 7$ episodes which we could record from beginning to end).

Each flipper rubbing bout contained 2–6 flipper rubbing episodes with an average of 2.42 ± 0.91 episodes/bout. The duration of a flipper rubbing bout was 7–140 s with an average of 42.3 ± 41.8 s ($n = 26$ bouts for which we could record the beginning and end of the bout). F-F rubbing often occurred with F-B rubbing in the same bout (15 of 26 episodes). Following an interruption during F-B rubbing, dolphins often switched their roles as Rubber and Rubbee in the subsequent episodes (57.6% of 132 interruptions between F-B rubbings).

Characteristics of Flipper-to-Body Rubbing

Individuals that initiate or terminate F-B rubbing—Dolphins that initiated F-B rubbing (*i.e.*, starters) by making contact with a rubbing partner tended to assume the Rubbee role during that rubbing episode ($P < 0.05$, 73.1% of 67 individuals, only the first episode in which each individual involved as the starter was analyzed). In contrast, dolphins that ended F-B rubbing (*i.e.*, the enders) by separating from a partner tended to be the Rubber in that episode ($P < 0.005$, 66.7% of 81 individuals, only the first episode in which each individual involved as the ender was analyzed). In other words, F-B rubbings were initiated more by the Rubbee and were terminated by the Rubber.

Movement of the Rubber's flipper and the Rubbee's body during F-B rubbing—During F-B rubbing, the Rubbers usually moved their flippers back and forth, and Rubbees also often moved their bodies back and forth as if they rub their bodies against Rubber's flippers (Fig. 1A). F-B rubbings could be divided into the following three types: F-B rubbings with moving flipper and moving body (FmBm type, 68.1% of 166 dyads, only the first episode recorded for each dyad was analyzed); F-B rubbings with moving flipper and static body (FmBs type, 22.2% of 166 dyads); and F-B rubbings with static flipper and moving body (FsBm type, 9.6% of 166 dyads). This means that for most F-B rubbing (77.7% of 166 dyads), the Rubbee moved the part of its body touching the Rubber's flipper, and they rubbed their body even against the static flipper in FsBm type.

Posture of the Rubber and Rubbee during F-B rubbing—During F-B rubbing, the Rubber's posture was significantly different from that of the Rubbee (Kolmogorov–Smirnov test, $D = 0.470$, $P < 0.05$). Most of the Rubbers (97.0%, $n = 100$ individuals) kept a horizontal posture while Rubbees tended to assume various postures, including a horizontal posture (62.0%, $n = 124$ individuals), side-up (29.0%), upside-down (14.5%), or other posture (6.5%).

Body parts rubbed during F-B rubbing—In F-B rubbing, the lateral side (32.2% of 208 episodes by 180 dyads), face (24.0% of 208 episodes), and dorsal side (10.6% of 208 episodes) of the Rubbee were rubbed often (Fig. 2). In this behavior, the face (50 episodes) was rubbed significantly more frequently than expected based on its percentage to the total body surface area (binominal test, $P < 0.05$, Fig. 2). The dorsal fin, ventral side, and peduncle were rubbed significantly less frequently (binominal test, $P < 0.05$, respectively, Fig. 2). We observed F-B rubbing between a mother (#027) and her calf (#500) whose fluke was encircled by a thin wire (less than 5 mm in diameter). In six of eight episodes, the mother rubbed the wire with her flipper as if trying to remove it, while the fluke was not rubbed often in F-B rubbing.

F-B rubbing between mothers and calves—All of the observed F-B rubbing between adult females and calves occurred in mother-and-calf dyads. In 84.4% of 32 mother-and-calf dyads that we observed, the mothers more often assumed the “Rubber” role than the calves (Wilcoxon signed rank test, $R = 37.50$, $n = 32$ dyads, $P < 0.001$).

Combinations of sex and age classes in F-B rubbing pairs—The majority of the F-B rubbing observed occurred in pairs of adults or sub-adults of the same sex in the same age class (56.2% of 322 episodes by 145 individuals, Table 2). Other pairings included mother-calf pairs (31.7%) and heterosexual pairs of adults or sub-adults (9.6%). Calves (neonates and juveniles) F-B rubbed with their mothers almost exclusively (Table 2).

Three dolphins (two subadult males and one subadult female) with more than 10 records F-B rubbed with at least five to seven different partners during the study period. However, these subadult males (#012 and #014) conducted about half of the bouts with the same partner.

F-B rubbing between male and female—We observed F-B rubbing from 22 male-female dyads including 12 subadult male and subadult female dyads, 5 subadult male and adult female dyads, 4 adult male and adult female dyads, and 1 adult male and subadult female dyad. In 81.8% of 22 dyads, the males more often assumed the “Rubber” role than the females while only in 9% (two subadult male and subadult female dyads) were the females more often “Rubbers” (Wilcoxon signed rank test, $R = 22.00$, $n = 22$ dyads, $P < 0.005$).

Characteristics of Flipper-to-Flipper Rubbing

In all F-F rubbing observed ($n = 26$ episodes), at least one of the dolphins kept a horizontal posture. In about half of the F-F episodes the other dolphin assumed a different posture (53.8% of 26 episodes).

Dolphins of the same sex in same-age classes tended to exchange F-F rubbing most often (85.7% of 21 episodes by 24 individuals in which both dolphins were identified). We observed only three episodes of F-F rubbing by male-female dyads. This result was comparable to that observed for F-B rubbing. We never observed F-F rubbing between a mother and her calf while F-B rubbing was frequent between these pairs. We never observed F-F rubbing by a calf.

DISCUSSION

Our results suggested that the Rubbee engaged in F-B rubbing more actively than the Rubber, in contrast with prior reports (Table 1). The Rubbee tended to initiate the

F-B rubbing while the Rubber tended to terminate it. The Rubbees often assumed unusual postures during the F-B rubbing while the Rubbers remained horizontal in most cases. These results suggest that the Rubbee receives some benefit during the F-B rubbing. The fact that mothers more often assume the "Rubber" role than their calves during F-B rubbing also suggests that this behavior can be seen as a kind of caring behavior, benefiting the Rubbees (calves).

What kind of benefit the Rubbees receive during the F-B rubbing is still unclear. However, the Rubbees seem to seek frictional contact with the Rubber's flipper during F-B rubbing because they often actively moved the part of its body touching the Rubber's flipper. The Rubbees seemed to determine the body part that was rubbed by assuming various postures other than normal horizontal posture. One of the possible benefits that the Rubbees receive from the frictional contact during F-B rubbing is the care of body surface. F-B rubbing seems effective to remove the old skin from the body surface. We could see many small, whitish fragments of the old skin coming off like smoke from the part of the body surface that was F-B rubbed in our direct observation and in a video record.¹ The fact that the F-B rubbing between a mother and her calf with the fluke entangled by a thin wire were mainly oriented to the wire also suggests that F-B rubbings serve to remove undesired or harmful objects from the body surface. However, we have never seen the dolphins rubbing parasites on the body surface during F-B rubbing and F-F rubbing, while we often observed soft-bodied barnacles (*Xenobalanus* sp.) and remoras (*Echeneis* sp.) attached to the body surface of the dolphins in the study area. Another possibility is that dolphins conduct F-B rubbing to exchange body contact that simply feels good. It has been reported that stroking of the body can be an effective reward in the training of bottlenose dolphins (Defran *et al.* 1975, see Herman and Tavalga 1980) and many captive species solicit stroking from their handlers (Defran and Pryor 1980). Because dolphins have been reported to have acute tactile sensitivity especially in their face (Ridgway 1986, Supin *et al.* 2001), it is possible that they often F-B rub the face (Fig. 2) because it is a body part most sensitive to such contacts. It is also possible that dolphins conduct F-B rubbing only to attract the partner's attention. However, the long duration of the frictional contact, posture, and movement of the Rubbees suggest that the Rubbees receive not only the attention from the partners, but also some other proximate benefits during the F-B rubbing.

Frequent exchange of the roles as the Rubber and the Rubbee observed within the flipper rubbing bouts suggests that the F-B rubbing is an affiliative social behavior in which the dolphins exchange some benefit in turns. Adults and subadults tended to F-B rub with dolphins of the same sex in the same age class, and calves F-B rubbed almost exclusively with their mothers. It has been reported that adult male bottlenose dolphins form tight associations with particular individuals of the same sex (Connor *et al.* 1992), females have large networks with other females (review in Connor *et al.* 2000), and mother and calves are each other's most common associate (Mann and Smuts 1999). Records of F-B rubbing exchange by three subadults showed that they F-B rubbed with various partners and some individuals frequently F-B rubbed with a particular individual, though the sample size is still extremely small. These results suggest the possibility of F-B rubbing exchange as a measure of affiliative relationship between individuals.

¹ Personal communication from M.B.K., Mikura Island, Tokyo 100-1301, Japan. 1999.

In heterosexual F-B rubbings, males were more often “Rubbers” than females, suggesting that the males gave some proximate benefits to the females during these F-B rubbings. It is possible that some F-B rubbings are used in sexual context between males and females. Tavolga and Essapian (1957) also described stroking (FsBx, FFB, FmBx, Table 1) as a precopulatory behavior in captive bottlenose dolphins.

Since the F-F rubbings often occurred with F-B rubbings in the same bout and were observed between the individuals of the same sex and the same age class, it is possible that the F-F rubbing have functions similar to those of the F-B rubbing. However, all F-F rubbing were observed in adult or subadult pairs and no F-F rubbing by calves were observed. Therefore, F-F rubbing may have a function different from that of F-B rubbing and/or it may contain elements that must be learned by the calves.

Some characteristics of F-B rubbing clarified in this study are similar to those of social grooming behavior of terrestrial mammals. In these behaviors, the groomees also receive some benefit during the behavior. Exchange of the roles as the groomer and the groomee are also observed within a grooming bout. Mothers tend to take the groomer role in mother/calf dyads (see review in Spruijt *et al.* 1992; *e.g.*, impala, *Aepyceros melampus*, Hart and Hart 1992; Mooring and Hart 1992; Japanese macaques, *Macaca fuscata*, Muroyama 1991, 2001; patas monkeys, *Erythrocebus patas*, Muroyama 1994).

The results of this study suggest that flipper rubbing behavior could be used as a quantitative measure of social relationships among individuals of this species in future studies. However, to understand the social functions of the flipper rubbing behavior, we should analyze the exchange of this behavior among individuals with known relationships and examine the behavioral sequence before and after this behavior.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:
Supplementary Movie S1