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Tactile Contact Exchanges Between Dolphins: Self-rubbing versus Inter-individual Contact in Three Species from Three Geographies

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Self-rubbing and social-rubbing (pectoral fin contact between dolphin pairs) were compared for observations conducted on three dolphin study groups: wild dolphin groups in The Bahamas and around Mikura Island, Japan, and a third group of captive dolphins at the Roatan Institute of Marine Sciences, Roatan, Honduras. A primary aim of this research was to determine whether self-rubbing and social pectoral fin rubbing served overlapping functions. Self-rubbing rates were nearly identical between the three study sites, suggesting that site-specific differences (e.g., environmental conditions, substrate, presence of rocks or coral, social grouping) do not affect the rates at which dolphins rub their bodies against non-dolphin objects. The function of self-rubbing is not entirely clear, and likely involves a combination of factors (e.g., play, pleasure), with functions such as hygiene possibly being shared by both self-rubbing and social-rubbing. Rubbing behavior in general (e.g., rates, body parts used) were similar at all three sites for all three species, suggesting that rubbing is an evolutionarily conserved behavior for delphinid species. Still, subtle and individually distinct differences were documented among our study groups with respect to how often and with whom dolphins exchanged pectoral fin contact or engaged in self-rubbing. Site-specific social pressures and predation risks, as well as individual personality might play a role with respect to the expression of an individual's observed rubbing behavior.

Self-rubbing and object-rubbing have been observed in a number of wild and captive odontocete species, including beluga whales (*Delphinapterus leucas*, Smith, Aubin, & Hammill, 1992), pilot whales (*Globicephala macrorhyncha*, Kritzler, 1952), Guiana dolphins (*Sotalia guianensis*, Rossi-Santos & Wedekin, 2006), dusky dolphins (*Lagenorhynchus obscurus*, Harlin, Würsig, Baker, &

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Markowitz, 1999), and killer whales (*Orcinus orca*, Ford, 2009; Williams, Lusseau, & Hammond, 2006, 2009). These events consisted of rubbing on or otherwise physically touching objects and substrates. Possible functions of these behaviors include hygiene (e.g., parasite removal, sloughing), social (e.g., affiliative, socio-sexual), and sensual (i.e., pleasure). In belugas, the occurrence of rubbing on substrates is thought to facilitate the annual molting process (O'Corry-Crowe, 2009). Kritzler (1952) hypothesized that object rubbing observed in captive pilot whales (including rubbing on a sea turtle) was done for sensual pleasure, but that it might also serve a hygienic purpose in a wild setting. Rubbing on pebble beaches, as observed in killer whales, potentially a cultural trait for specific populations (Whitehead, Rendell, Osborne, & Würsig, 2004), is thought to facilitate parasite removal, or possibly play a social role (Ford, Ellis, & Balcomb, 2000; Williams et al., 2009). For the Guiana dolphin, rubbing contacts with the muddy substrate were likely a consequence of feeding behavior (Rossi-Santos & Wedekin, 2006). Contact with objects such as buoys and seaweed may also be a result of play behavior (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006).

Unlike self-rubbing, social-rubbing (i.e., rubbing involving two or more conspecifics) using the pectoral fin may serve primarily a social or social-sexual function (Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Dudzinski, Gregg, Paulos, & Kuczaj, 2010). Pectoral fin contact (i.e., rubbing or touching involving the pectoral fin) has been observed in both wild and captive odontecete species. Wild delphinids observed to exchange pectoral fin contact behavior include Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, Dudzinski et al., 2009, 2010; Mann & Smuts, 1998, 1999; Sakai, Hishii, Takeda, & Kohshima, 2003, 2006a, 2006b), spinner dolphins (*Stenella longirostris*, Johnson & Norris, 1994), Atlantic spotted dolphins (*Stenella frontalis*, Dudzinski, 1996, 1998; Dudzinski et al., 2009, 2010), belugas (Smith et al., 1992), rough toothed dolphins (*Steno bredanensis*, Kuczaj & Yeater, 2007), and sperm whales (*Physeter macrorhynchus*, Whitehead & Weilgart, 2000). Species of captive dolphins observed to share pectoral fin contact include common bottlenose dolphins (*Tursiops truncatus*, Dudzinski et al., 2009, 2010; Samuels, Sevenich, Gifford, Sullivan, & Sustman, 1989; Tamaki, Morisaka, & Tami, 2006; Tavolga & Esspian, 1957), spinner dolphins (Johnson & Norris, 1994) and Commerson's dolphins (*Cephalorhynchus commersoni*, Johnson & Moewe, 1999).

Dudzinski (1998), Norris, Würsig, Wells, and Würsig (1994), and Sakai et al. (2006) suggested that pectoral fin rubbing is an affiliative behavior serving both social and hygienic functions, similar to grooming behaviors in primates. Tavolga and Essapian (1957) suggested pectoral fin rubbing was a passive form of sexual behavior seen primarily in pre-copulatory situations. Additionally, Norris et al. (1994) observed rubbing of the abdominal and genital area by both wild and captive spinner dolphins and described it as a caressing behavior. Connor, Mann, and Watson-Capps (2006) suggested that contact swimming (defined as one dolphin's pectoral fin touching another dolphin's side) might function to reduce male harassment, assist in locomotion, or reduce stress between female Indo-Pacific bottlenose dolphins. Samuels et al. (1989) hypothesized that social-rubbing may aid in the removal of ectoparasites and old epidermal cells, and noted that one

observed individual dolphin which received infrequent rubbing from other dolphins rubbed its body against objects in order to facilitate this process.

The aim of this investigation was to examine whether self-rubbing behavior might serve similar functions as pectoral fin rubbing. If, as Samuels et al. (1989) suggested, self-rubbing might serve as a proxy for social-rubbing, then similarities in the form of the rubbing behavior should be evident (e.g., body part being rubbed). Self-rubbing and pectoral fin rubbing behaviors from three distinct study populations are described and compared. Pectoral fin rubbing data from wild Atlantic spotted dolphins (Bimini, The Bahamas) are described here for the first time, supplementing data from captive bottlenose dolphins (Roatan Institute for Marine Sciences, Honduras) and wild Indo-Pacific bottlenose dolphins (Mikura Island, Japan), which were previously described in Dudzinski et al. (2009, 2010). Self-rubbing data for all three study sites are presented for the first time. We used the same protocols and sampling techniques to collate both types of behavioral events and then to compare data across study populations and between rubbing event types. In addition to these comparisons, case studies from each population are presented in order to describe similarities and differences between these behaviors as exhibited by individuals from the three study groups.

Method

Data collected on all study populations were part of a long-term, comparative examination of dolphin communication (Beard, 2008; Dudzinski, 1996, 1998; Dudzinski et al., 2003, 2009, 2010; Gregg, 2008; Gregg, Dudzinski, & Smith, 2008; Melillo, 2008; Melillo, Dudzinski, & Cornick, 2009; Paulos, Dudzinski, & Kuczaj, 2007).

Study Sites and Populations

Data were gathered from three locations over seven years (from 2003 to 2009) near Bimini, The Bahamas, around Mikura Island, Japan, and at RIMS (Roatan Institute for Marine Science), Anthony's Key Resort, Roatan, Honduras. The Atlantic spotted dolphins (*Stenella frontalis*) are believed to be a resident population located near North Bimini, approximately 8-16 km from the coastline, along the northwest edge of the Great Bahama Bank (Melillo, 2008; Melillo et al., 2009). This area ranges from 6 to 12 m in depth with a white sandy bottom and visibility typically at least 30 m. Approximately, 90 individual dolphins have been identified with relative age categories and sex determined for most individuals (Melillo, 2008; Melillo et al., 2009; DCP unpublished data, 2001 - 2010).

Approximately, 165 individual Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were identified within 300 m of Mikura Island, Japan, from 1997 – 2009 (Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004; DCP unpublished data 1995 – 2009). Mikura lies roughly 200 km south of Tokyo, is a dormant volcanic island 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. Both the Mikura and Bimini study sites are adjacent to fish-productive, deep water (Marianas Trench and Gulf Stream, respectively) and include dolphins ranging from calves to adults.

RIMS is located on the northwest coast of Roatan, the center of three Bay Islands approximately 27 miles north of mainland Honduras. The bottlenose dolphin (*Tursiops truncatus*) study group ranges in age from neonate to 30+ years and resides in a natural lagoon with a sea floor consisting of natural coral, sea grass, and sand with depths from shore to 8 m. The enclosure has a surface area of roughly 300 m^2. The age and sex distribution for this study group matches that of most coastal wild bottlenose dolphin study groups (Connor et al., 2006; Kogi et al., 2004).

Data Collection

Data were collected at all sites with a mobile video/acoustic system that permits underwater real-time synchronous video and audio recordings of dolphin behavior and vocalizations (Dudzinski, Clark, & Würsig, 1995). Limiting factors to underwater video-documentation include poor weather, sea, and visibility conditions. Protocols for video data collection from all study groups follow those outlined in Dudzinski et al. (2009, 2010).

Pectoral fin contacts and self-rubbing behaviors were coded only from videotaped data, for reliability. Event sampling for pectoral fin and self-rubbing contact among individual dolphins was conducted from all video data gathered from each study site. Each contact event between one dolphin's pectoral fin and another dolphin's body (including the pectoral fin) was documented. Additionally, each contact event between an individual dolphin's body part and any non-dolphin object (self-rubbing) was documented. These objects could include the sea floor (sand, grass, coral), netting, floating objects. Other relevant, recorded data included date of occurrence, "real" time of contact, initiating dolphin's identification, age and sex, receiving dolphin's identification, age and sex, identity of *rubber*/*rubbee* role, each dolphin's posture, duration of contact, whether contact was a touch or rub (for both pectoral fin and self-rubbing contact), and identification of the departing dolphin (for pectoral fin contact). For self-rubbing events, pertinent information listed above was recorded, and the object type was also noted.

Definitions

Numerous definitions of rubbing behavior exist in the literature (see Sakai et al., 2006a for an overview for pectoral fin contact). For this study, several definitions for pectoral fin contact were employed that have previously been defined in Dudzinski et al. (2009). Pectoral fin contact events 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. The *rubber* is the dolphin whose pectoral fin is the focus of the event, and the *rubbee* is the dolphin whose body is being contacted. 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. The behavior was further described as either a *touch* (i.e., static contact) or a *rub* (i.e., active movement between the *rubber's* pectoral fin and the *rubbee's* body part).

Self-rubbing was defined as a single dolphin contacting one or multiple body parts to something other than another dolphin (e.g., sea grass, garbage, sand). The behavior was described as either a *touch* (i.e., static contact with the object) or a *rub* (i.e., active movement between the dolphin's body part(s) and the object). Self-rubbing exchanges were begun by a dolphin approaching and physically contacting an object in the environment and ended when that dolphin departed or lost contact with the object. For self-rubbing events, the single dolphin involved was by definition both the *rubbee* and the initiator.

For both pectoral fin contact and self-rubbing events, we divided the dolphin's body surface into 11 parts to record the dolphin body part in contact with either a pectoral fin or an object (see diagrams in Dudzinski et al., 2009, 2010). Additionally, definitions for posture, age and sex follow those presented in Dudzinski et al. (2009, 2010).

Statistical Analyses

Even though a single animal might have contributed multiple pectoral fin contacts, or a single animal engaged in multiple self-rubbing episodes in an encounter, we only included one contribution per identified dolphin in the role of *rubber* and *rubbee* per encounter and only included one self-rubbing episode per dolphin per encounter to ensure independence and randomness of the data. Because data of the RIMS study group were collected in 30- or 60-min observation sessions, the data were sub-divided into 3-min samples from which one contribution per identified dolphin as *rubber*, as *rubbee* and per self-rubbing behavior were included. Three minutes was the minimum time definition of an underwater encounter during observations of the wild study groups (Dudzinski, 1998; Dudzinski et al., 2009). Thus, from the total number of pectoral fin and self-rubbing contacts per site per year of study, our sample size was limited to individual adjusted contacts.

Because the return on effort between each of these three field sites differed greatly (~80-85% at RIMS compared with ~5-15% at Bimini or Mikura), self-rubbing and pectoral fin contact rates were calculated by taking the total number of individual adjusted contacts per year per study site divided by the total effort (i.e., minutes of underwater video per site per year). Comparisons of contact rates (both self-rubbing and pectoral contacts) within and between sites were examined (using individual adjusted sample sizes) with a t-test with two samples assuming unequal variances. Body part and posture preference (using individual adjusted sample sizes) for both *rubber* and *rubbee* (for pectoral fin data) and the *rubbee* (for self-rubbing data) within and between sites was examined using Chi-square analysis. When comparing variables for self-rubbing and pectoral fin contact events, only events involving the *rubbee*/initiator from the pectoral fin contact data were used to facilitate a fair comparison insofar as individuals involved in self-rubbing behavior could only be classified as a *rubbee/*initiator. For self-rubbing data, Chi-square analysis was used to compare the proportion of self-rubbing to pectoral fin contact between years and study sites. For pectoral fin contact data, Chi-square analysis was used to compare fin-to-fin versus fin-to-body contact, to assess variation in posture when the initiator was *rubber* versus *rubbee*, to compare the proportion of self-rubbing to pectoral fin contact between years and study sites, 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.

Results

A collective total of 25 years of video data was examined to compare how dolphins from three distinct geographic regions use their pectoral fin(s) to share contact in comparison with how these same dolphins engage in self-rubbing behavior. For pectoral fin data, video data ranged from a total 3,952 minutes from 7 years near Bimini, The Bahamas, 1,208 minutes from 7 years around Mikura Island, Japan, and 4,484 minutes from 6 years of data collected on the RIMS study group. For self-rubbing data, video data ranged from a total 3,952 minutes from 7 years (Bimini), 3,261 minutes from 11 years (Mikura Island), and 5,134 minutes from 7 years (RIMS).

Self-Rubbing Behavior

Dolphins at each of the three field sites included in this study were often observed to engage in self-rubbing, but to a lesser degree than they participated in pectoral fin tactile exchanges. Dolphins at Mikura engaged in self-rubbing a total of 136 times during the study period; dolphins around Bimini engaged in 145 episodes of self-rubbing; and dolphins at RIMS self-rubbed 182 times in total for the study period.

The mean contact rates for self-rubbing events at each site were: RIMS, 0.03 SRB/min; Mikura, 0.03 SRB/min; Bimini, 0.05 SRB/min. T-tests reveal no significant differences in these rates: Mikura vs. RIMS: $t(15) = -0.067$, $p > 0.05$; Mikura vs. Bimini: $t(14) = -1.194$, $p > 0.05$; RIMS vs. Bimini: $t(9) = -1.338$, $p > 0.05$. The number of self-rubbing episodes by a single individual dolphin had a maximum range of 1-8 at Mikura (tied: TaIDs: 237, 404), 1-22 at Bimini (SfID87) and 1-25 at RIMS (Mika). Median duration in self-rubbing was similar between sites (3 s at Mikura, 4 s at both Bimini and RIMS); however, episodes were longer at Bimini ($\bar{x}$ = 7 s, SD = 10.5 s, range 1-67 s) than RIMS ($\bar{x}$ = 6.52 s, SD = 9.5 s, range 1-91 s) and longer at RIMS than at Mikura ($\bar{x}$ = 4.77 s, SD = 6.3 s, range 1-50 s). At Bimini, touches (N = 96) and rubs (N = 86) were roughly equal in use by dolphins when self-rubbing; however, dolphins at Mikura and at RIMS exhibited

nearly twice as many rubbing (Mikura: touch $N = 48$, rub $N = 88$; RIMS: touch $N = 46$, rub $N = 99$) episodes as touch contact when self-rubbing.

Comparison of self-rubbing across the three study sites revealed no difference in overall frequency of self-rubbing between the three sites ($X^2_2 = 2.03$, $p = 0.36$); however, there were age and sex differences despite the lack of overall site differences (Table 1). An analysis that combined study sites revealed that juveniles were most likely to engage in self-rubbing behavior ($X^2_2 = 113.62$, $p < 0.001$); however, this general finding is a bit misleading in that the relationship between age and self-rubbing behavior varied across study sites. Self-rubbing behavior was most likely among sub-adults at Mikura ($X^2_2 = 71.25$, $p < 0.001$), juveniles at Bimini ($X^2_2 = 87.24$, $p < 0.001$), and juveniles at RIMS ($X^2_2 = 121.47$, $p < 0.001$, Table 1). Adults were more likely to produce self-rubbing behavior at RIMS and Mikura than at Bimini ($X^2_2 = 13.89$, $p < 0.001$, Table 1), while sub-adults were more likely to engage in self-rubbing behaviors at Mikura than at Bimini or RIMS ($X^2_2 = 70.50$, $p < 0.001$). RIMS and Bimini juveniles were more likely to engage in self-rubbing than were Mikura juveniles ($X^2_2 = 41.51$, $p < 0.001$). In addition, Bimini calves produced more self-rubbing behaviors than did RIMS or Mikura calves ($X^2_2 = 50.53$, $p < 0.001$). In fact, Mikura calves were never observed engaging in self-rubbing behavior.

Table 1
Distribution of self-rubbing behavior observed by age and sex at three field sites.

Age	Mikura	Bimini	RIMS
Adult	21	7	30
Sub-adult	57	8	6
Juvenile	18	70	83
Calf	0	37	8
unID	40	60	18
Sex			
Male	26	6	47
Female	52	101	80
unID	58	75	18

Collapsing across study sites, females were more likely than males to engage in self-rubbing bouts ($X^2_2 = 33.81$, $p < 0.001$). This was true for each individual study site as well: Mikura ($X^2_1 = 8.66$, $p < 0.01$; Bimini ($X^2_1 = 84.34$, $p < 0.001$), RIMS, ($X^2_1 = 8.57$, $p < 0.01$). However, the female advantage in self-rubbing was most evident in Bimini, where females produced over 94% of the self-rubbing events where sex was known.

Dolphins from around Bimini assumed postures quite similar to the dolphins from RIMS when engaged in self-rubbing behavior, though dolphins at Mikura seemed to assume both horizontal (HOR, $N = 38$; lOSD[1], $N = 23$; rOSD, $N = 39$) and vertical (HDO, $N = 29$) postures each with similar frequency with the exception of HUP ($N = 1$). Dolphins at Mikura did engage in HOR and rOSD postures more than on their left side.

Collapsing across study sites, dolphins self-rubbed with their rostrum more

[1]Acronyms fully defined in Dudzinski et al. (2009): HOR is horizontal, lOSD is on left side, rOSD is on right side, HDO is vertical head down, HUP is vertical head up, and VTU is belly up, horizontal.

than with all other body parts combined (X^2_1 = 11.10, p < 0.001); however, this general pattern did not hold across all three study sites. RIMS dolphins showed a strong preference for their rostrums during self-rubbing (X^2_1 = 60.03, p < 0.001), and it is their behavior that influenced the overall general trend described above. Bimini and Mikura dolphins used their rostrums more than any other body part during self-rubs, but not significantly more so than all other body parts combined. In fact, Mikura dolphins were more likely to use another body part than to use the rostrum (X^2_1 = 9.22, p < 0.01) despite the fact that the rostrum ranked first in frequency of occurrence during self-rubs.

Pectoral Fin Contact – Bimini Data

Previously, we showed that mean pectoral fin contact rates between dolphins at RIMS were not significantly different from those at Mikura (Dudzinski et al., 2010). In order to compare contact rates for the new Bimini data, the RIMS and Mikura data were pooled. The mean contact rate for the pooled Mikura and RIMS sites was 0.35 contacts/min, while the mean contact rate at Bimini was 0.13 contacts/min. A t-test revealed a significant difference in these rates (t(13) = 3.592, p = 0.003), suggesting that pectoral fin contact at Bimini is less frequent than at Mikura and RIMS.

Pectoral fin to pectoral fin vs. pectoral fin to body. Spotted dolphins observed around Bimini followed the trend of the same species in the northern Bahamas (i.e., the White Sand Ridge study group (see Dudzinski et al., 2009)) and as the Mikura dolphins: they engaged in more pectoral fin to body contact regardless of their role as *rubber* and *rubbee* when identified as the initiating dolphin (X^2_1 = 6.09, p < 0.05).

Initiator vs. receiver. Similarly, spotted dolphins around Bimini exchange pectoral fin contact significantly more often as the initiator in the *rubber* role (X^2_1 = 9.44, p < 0.001). Wild dolphins (Mikura and Bimini) and captive (RIMS) dolphins were similar in that the *rubber* was most likely to initiate contact with the pectoral fin at nearly identical rates.

Body parts contacted. Pectoral fin contacts were scored according to the frequency with which body parts were contacted by the initiator in the role of *rubber* and *rubbee* at Mikura and RIMS (for sample sizes, see Table 1 from Dudzinski et al., 2010) and at Bimini for spotted dolphins during this study. We documented 577 pectoral fin contacts among spotted dolphins at Bimini with respect to body part contacted. To determine if the *rubber* or *rubbee* initiates contact on similar body parts at Bimini as compared with dolphins from the other study sites, body parts were ranked from most to least likely to be contacted for each of these two conditions and compared with body parts contacted at each of the other field sites (Table 2; Dudzinski et al., 2010). *Rubbee* initiators from Bimini and Mikura contacted the same three body parts in the same order: face (B), side (C) and rostrum (A), and even though the order differed from that of the northern Bahamas and RIMS, the body parts were always the same three parts (Table 2). The side was also the primary body part contacted by *rubbers* as initiators, as at all three other sites (Table 2; see also Dudzinski et al., 2009). Dolphins at Bimini contacted the peduncle more than dolphins at the other sites,

but body part preference generally was consistent between dolphins at all four study sites.

Table 2
Rank order (from most to least likely) of body parts contacted for the initiator in the role of rubber and rubbee for dolphins at Bimini, The Bahamas.

Rubber	Rubbee
C	B
K	C
F	A
H	M
B	E, F
D	D
L, E	L
A	H, K
G, M	

Note: G was not contacted when the *rubbee* was initiator at Bimini.

Body postures. Similarly, spotted dolphins at Bimini significantly more often assumed the HOR posture as *rubber* or *rubbee* when exchanging pectoral fin contacts ($X^2_5 = 16.245$, $p < 0.01$). Unlike results from either wild site, but similar to RIMS, when the HOR position, which accounts for 59.04% of postures observed at Bimini, is removed from the dataset, a strong preference for specific positions is still observed ($X^2_4 = 14.223$, $p < 0.01$): HDO = 35.25%; HUP = 31.97%; lOSD = 14.75%; rOSD = 12.29%; VTU = 5.74%, suggesting dolphins at Bimini are vertical more often than on one side or the other when exchanging pectoral fin contacts.

As with our study at Mikura, White Sand Ridge (northern Bahamas) and RIMS, we examined Bimini data to determine whether two dolphins involved in a pectoral fin contact episode assumed either same or different postures. Observations from Bimini are similar to results for the Mikura dolphins but not those from White Sand Ridge or RIMS (Dudzinski et al., 2010): the initiating dolphin as the *rubber* did result in both dolphins in the same posture more often than was the case when the initiating dolphin was the *rubbee* ($X^2_1 = 3.996$, $p < 0.05$).

Sex and age. Dolphins at all field sites were categorized into four age classes: adult (A), subadult (S), juvenile (J) and calf (C). There was no significant difference in the rate with which spotted dolphins at Bimini assumed the initiator role as *rubber* or *rubbee* for the four age classes ($X^2_3 = 6.97$, *ns*); however, more juveniles and calves assumed the role of *rubbee* ($X^2_3 = 28.18$, $p < 0.0001$) when receiving pectoral fin contact at Bimini (Table 3). Still, juveniles did assume the role of *rubber* as initiator more than twice that of adults or sub-adults (Table 3), and only marginally more than calves. While females assumed the role of *rubber* initiator almost three times as often as males, and also the role of *rubbee* receiver about 3.5 times that of males, these numbers were not significantly different from

what was expected (Table 3). Still, the trend seems to be similar to that observed at the other sites, with spotted dolphins at Bimini more often preferring same-sex, same-aged rubbing partners when sharing pectoral fin contact.

Table 3
Pectoral fin contacts by age class and sex for spotted dolphins at Bimini, the Bahamas.

Role	Adult	Subadult	Juvenile	Calf
INI.*Rubber*	49	32	114	82
INI.*rubbee*	17	8	27	9
rec.*Rubber*	23	6	24	6
rec.*rubbee*	33	50	108	75
	Female	Male		
INI.*Rubber*	133	50		
INI.*rubbee*	25	14		
rec.*Rubber*	34	8		
rec.*rubbee*	155	38		

Note: INI is initiator; rec is receiver

Self-Rubbing Behavior vs. Pectoral Fin Contact

Self-rubbing contact occurred less frequently than pectoral fin contact for all three study sites. Significant differences in rates between the two contact types were found at RIMS ($t(5) = -6.178$, $p = 0.002$), Mikura ($t(6) = -3.893$, $p = 0.008$), and Bimini ($t(7) = -3.794$, $p = 0.003$). Mean rates for the study period for each contact type at each site were RIMS: 0.03 SRB/min, 0.29 PEC/min; Mikura: 0.03 SRB/min, 0.40 PEC/min; Bimini: 0.05 SRB/min, 0.99 PEC/min.

The age class and sex of dolphins (when known) involved in self-rubbing events were compared to pectoral fin contact events for each study site. For these comparisons, only pectoral fin contacts involving the *rubbee* in the initiator role were used because self-rubbing events could only ever involve a dolphin classified as both *rubbee* and initiator. No significant difference was found in the proportion of males vs. females for the two rubbing event types for Mikura or RIMS. For Bimini, however, a significant difference in the proportions was found ($X^2_1 = 100.52$, $p < 0.001$), with 94% of self-rubbing events being performed by females, but just 21% of females involved in pectoral fin contact exchanges as the *rubbee* and initiator. A significant difference in the proportion of age classes involved in the two rubbing event types was observed at RIMS ($X^2_3 = 25.55$, $p < 0.001$), Mikura ($X^2_3 = 13.2$, $p = 0.004$) and Bimini ($X^2_3 = 18.42$, $p < 0.001$). At RIMS, subadults were more than twice as often involved in self-rubbing (47%) than pectoral fin contact (21%). At Mikura, calves were involved in 13% of pectoral contact exchanges as the *rubbee* and initiator, but were never observed self-rubbing. In contrast, at Bimini, calves were involved in 30% of self-rubbing events, but just 10% of pectoral fin contact exchanges as *rubbee* and initiator.

Dolphins at all sites seemed to preferentially use three body parts when engaged in self-rubbing as compared to pectoral fin contact: the three body parts contacted most during self-rubbing included the rostrum (A), pectoral fin (H) and fluke (M). Body parts that *rubbers* contacted when initiating tactile interaction were used when comparing these social contacts with self-rubbing. Combining all sites, dolphins were more likely to use their rostrums to rub when self-rubbing than when rubbing another animal ($X^2_1 = 139.92$, $p < 0.001$). Dolphins at RIMS ($X^2_1 =$

47.26, $p < 0.001$), Mikura ($X^2_1 = 20.57$, $p < 0.001$) and Bimini ($X^2_1 = 78.04$, $p < 0.001$) were all more likely to use their rostrums during self-rubs than during social (pectoral fin exchanges) rubs. When considering the pectoral fin as used during contact – self-rubbing and pectoral fin contact exchanges – combining all sites, dolphins were equally likely to use their pectoral fins to rub when self-rubbing and when rubbing another animal ($X^2_1 = 0.143$, *ns*), although the results at each site individually presented three unique situations. Dolphins at RIMS were more likely to use their pectoral fins during social rubs than during self-rubs ($X^2_1 = 13.09$, $p < 0.001$). Dolphins at Mikura were equally likely to use their pectoral fins during social rubs and during self-rubs ($X^2_1 = 1.96$, *ns*). Dolphins in Bimini were more likely to use their pectoral fins during self-rubs than during social rubs ($X^2_1 = 10.25$, $p < 0.01$). Combining all sites, dolphins were more likely to use their flukes to rub when self-rubbing than when rubbing another animal ($X^2_1 = 19.26$, $p < 0.001$), though there was a slight difference between the sites. Dolphins at RIMS were more likely to use their flukes during social rubs than during self-rubs ($X^2_1 = 7.14$, $p < 0.001$), while dolphins at Mikura Island ($X^2_1 = 5.44$, $p < 0.05$) and in Bimini ($X^2_1 = 37.00$, $p < 0.001$) were more likely to use their flukes during self-rubs than during social rubs.

When comparing the proportion of touches vs. rubs within the same site for self-rubbing vs. pectoral contact, no significant difference was found for Mikura or RIMS. A difference in the proportion of touches vs. rubs was found for Bimini, however ($X^2_1 = 47.06$, $p < 0.0001$), with 38% of self-rubbing events involving touches, but just 4% of pectoral fin contacts involving touches.

Select Case Studies Per Study Site

From each study population, we identified individual examples, which were unique in their presentation of both pectoral fin contact and self-rubbing behaviors. We present two examples from each field site to illustrate the individual character traits present in these tactile actions.

Bimini, The Bahamas: Nemo, Tina. SfID#76 (Nemo) and SfID#14 (Tina) are two young female Atlantic spotted dolphins. Both are gregarious and particularly curious about human swimmers. At her first observation, Nemo did not have a right pectoral fin: the limb was amputated seemingly at the shoulder joint as suggested by photographic and video evidence (Figure 1). Nemo participated in 31 pectoral fin exchanges with eight identified and nine unidentified spotted dolphins ranging from 1 to 6 contacts per partner. Of the identified partners, six were female and two were male, ranging in age from juvenile to adult, though her preference seemed to be to exchange pectoral fin contacts with same-aged, same sexed individuals as herself (35.48% juvenile, 29.03% subadult, 6.45% adult partners, 54.84% female, 16.13% male partners). As the *rubber (*$N = 13$, 1 unidentified pairing*)*, Nemo shared pectoral fin contact with similar frequency as the initiator (53%) and receiver (38%); however, as the *rubbee* ($N = 18$), Nemo was significantly more often in the role of receiver (67%) than initiator (11%). The lack of a pectoral fin did not seem to affect Nemo's involvement in pectoral fin contact exchanges with her peers.

Figure 1. Nemo, a female Atlantic spotted dolphin resident to the sea around Bimini, The Bahamas. Note her lack of a right pectoral fin. Nemo always used her left (intact) pec when making contact as either rubber or rubbee.

Tina is also a young female spotted dolphin who is described as highly social and has a habit of swimming within inches of the camera and researcher, as well as other eco-tour participant swimmers. She was involved in more pectoral fin contact exchanges than any other spotted dolphin documented during this study; Tina participated in 81 pectoral fin exchanges with 14 identified and 22 unidentified partners. Of her identified partners, 10 were female, three were male and one unidentified for sex, ranging in age from calf to sub-adult. Though her preference, like Nemo, was for same-aged, same-sexed partners, the male partners were all younger than Tina, likely calves of adult females in her social group. As the *rubber (N* = 45, 15 unidentified pairings), Tina engaged in significant more pectoral fin contacts as the initiator (53%) as opposed to the receiver (13%) role. When Tina was the *rubbee* (*N* = 36, 19 unidentified pairings), Tina was the receiver (44%) significantly more than she assumed the initiator (2%) role. These results seem to suggest that Tina's exchanges of pectoral fin contact were highly reciprocal with her peers.

Both Nemo and Tina also engaged in self-rubbing behavior episodes. Nemo self-rubbed on four observed occasions while Tina self-rubbed eight times; their longest self-rubbing episode was 13 s and ranged between 1 and 13 s (Nemo) and 3 and 13 s (Tina), though Tina had a slightly longer average duration for self-rubbing actions (Tina $\bar{x}$ = 6.6 s; Nemo $\bar{x}$ = 5.5 s).Both juvenile female spotted dolphins rubbed into the sand, but Tina also rubbed into seaweed while Nemo did not. Nemo only placed her rostrum into the sand, while Tina rubbed her rostrum, side and belly into the sand and seaweed.

RIMS: Ronnie, Bill. When we began our studies at RIMS, Ronnie and Bill were calves; they have aged to sub-adults as we documented their interactions with each other and other members of their social group. Ronnie was an offspring of the alpha female and was quite mischievous: he would often antagonize the

other dolphins and then swim back to the safety of his mother's side. When she weaned him and had her next calf, Ronnie was left to fend for himself and deal with the repercussions of his instigations. Bill's mother died when Bill was 1.5 years old. He was already eating fish and so survived without additional nursing from a surrogate.

Ronnie and Bill participated in significantly more pectoral fin contact exchanges than any of the other dolphins in the RIMS study group. Their roles when engaged in pectoral fin contact, however, differed from each other significantly (Figure 2). Ronnie assumed the role of *initiator* as *rubber* more than twice that of Bill, though they assumed the role of *initiator* as *rubbee* with almost equal frequency (Figure 2, Table 4). As *receivers*, Ronnie and Bill assumed the role of *rubber* again with about equal frequency; however, Bill assumed the role of *rubbee* more than three times that of Ronnie (Figure 2). Ronnie assumed the role of *rubber* more than three times that of *rubbee* while Bill was the *rubbee* almost 1.5 times that he assumed the role of *rubber*.

Both Ronnie and Bill participated in significantly more pectoral fin contacts during 2003, when they were younger (Table 4). As they aged, they were observed to exchange fewer pectoral fin contacts. Ronnie and Bill exchanged 67 pectoral fin contacts with each other with Ronnie in the *rubber* role twice as often as Bill. Ronnie was observed in 2003 to exchange most (N = 206) of his pectoral fin contacts with Tela, his older sister. During these exchanges Ronnie was the *initiator* in the *rubber* role (N = 188) significantly more than the *rubbee*. The remaining pectoral fin contacts in which Ronnie was a participant involved two same-aged females (Maury, N = 17; Mika, N = 24), one younger female (Fiona, N = 8), and five other similarly-aged and one adult males (Anthony, N = 5; Buster, N = 5; Esteban, N = 2; Hector, N = 7; Mateo, N = 1; Ritchie, N = 9). He was also observed to exchange two pectoral fin contacts with his mother and one with another adult female. With females, Ronnie was more often in the *rubber* role, whereas with males his contacts seemed evenly distributed for his role as *rubber* or *rubbee*.

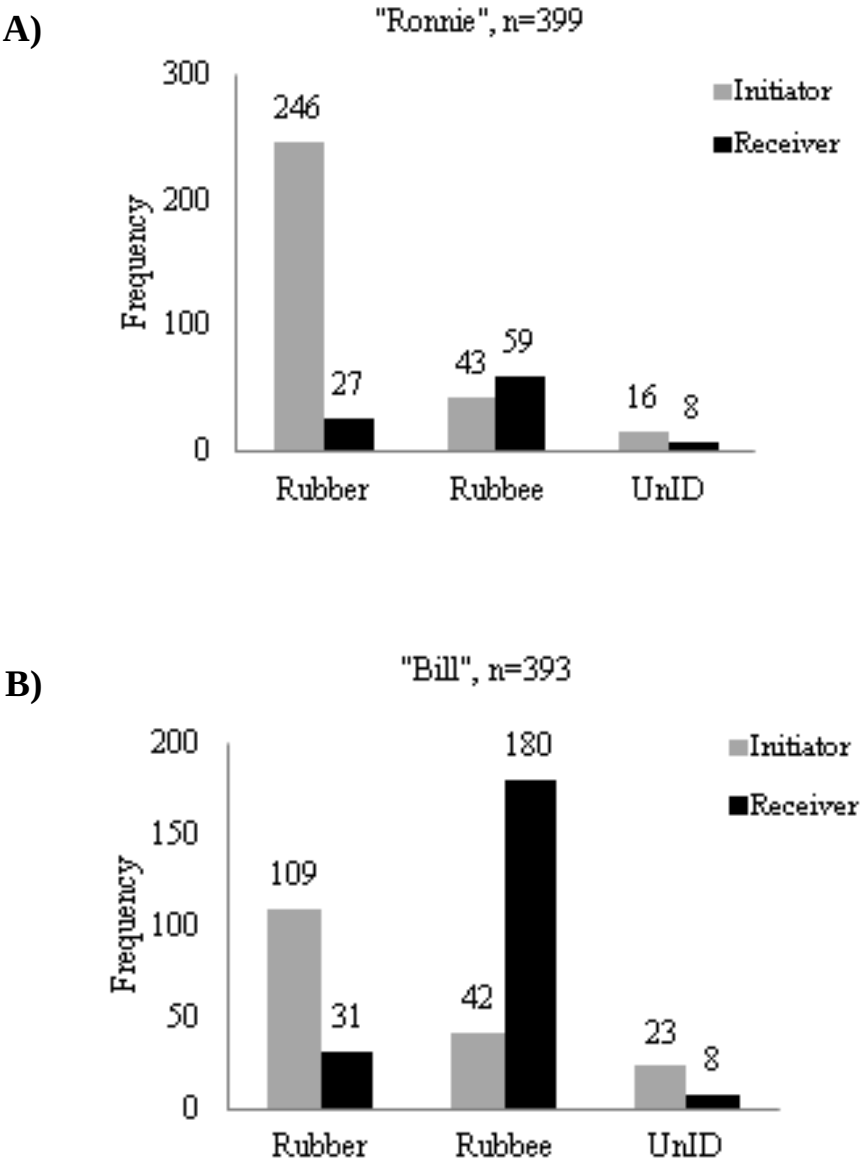

Figure 2. Distribution of pectoral fin contacts by Ronnie **(A)** and Bill **(B)** in the roles of *rubber* and *rubbee*. Initiator role is gray, receiver role is black.

Table 4
Pectoral fin contact exchanges involving Ronnie or Bill by year and in their role as rubber or rubbee.

Year of study	Ronnie as *Rubber*	Ronnie as *Rubbee*	Ronnie age	Bill as *Rubber*	Bill as *Rubbee*	Bill Age
2003	248	42	Calf	115	170	Juvenile
2004	18	19	Juvenile	10	10	Juvenile
2005	24	20	Juvenile	22	22	Juvenile
2008	15	13	Subadult	27	17	Subadult

Note: No data are available for 2006 and 2007 as both of these two young males were housed as a different facility.

Bill's pectoral fin contacts were more evenly distributed between his roles of *rubber* and *rubbee* and with several members of the social group at RIMS. Similar to Ronnie, Bill engaged in significantly more pectoral fin contact when he was younger, in 2003; however, he assumed the role of *rubbee* slightly more than as *rubber* (Table 4). With the exception of Maury, a similarly aged female to Bill with whom he exchanged 71 pectoral fin contacts during this study, Bill exchanged pectoral fin contact primarily with other males (N = 230) in the group: the adult males (Esteban, N = 8; Paya, N = 1), sub-adult males (Buster, N = 16; Dexter, N = 12; Hector, N = 56; Ritchie, N = 32), and juvenile, same-aged, or younger males (Anthony, N = 9; French, N = 6; Jack, N = 2; Mateo, N = 21). Interestingly, both Ronnie and Bill showed a similar body part preference when in the role of *rubber* and *rubbee* for their rostra, followed by their faces.

While Ronnie and Bill were involved in a majority (45%) of the pectoral fin contacts documented at RIMS, together they were only involved in 11% (Ronnie, N = 3, 2%; Bill, N = 13, 9%) of the total observed self-rubbing episodes. Bill's self-rubbing episodes ($\bar{x}$ = 6.7 s, 1-38 s) were slightly longer than Ronnie's ($\bar{x}$ = 7.9 s, 3-11 s). As with pectoral fin contact, both Ronnie and Bill showed a preference for their rostra in self-rubbing episodes. Ronnie was observed to rub on wood twice (67%) and a length of rope (33%) once. Bill rubbed on seaweed (39%), grass (46%) and the fence (15%).

Mikura Island, Japan: adult female (065FA), male sub-adult (043MS). Because our sample sizes and time spent per individually-identified dolphin from the group around Mikura Island is not as large as for dolphins observed near Bimini or at RIMS, we present details on the sub-groups of adult females and sub-adult males from Mikura. We use two individuals (TaID#065FA and TaID#043MS) for whom our samples were largest to illustrate trends for these two groups. ID065FA, as with most of the adult females, was more often the *initiator* versus *receiver* and more often the *rubbee* as opposed to the *rubber* (Figure 3). ID043MS, and most sub-adult males, engaged in pectoral fin contacts with about equal frequency as *initiator* or *receiver*, but was more often the *rubber* as opposed to the *rubbee* (Figure 3).

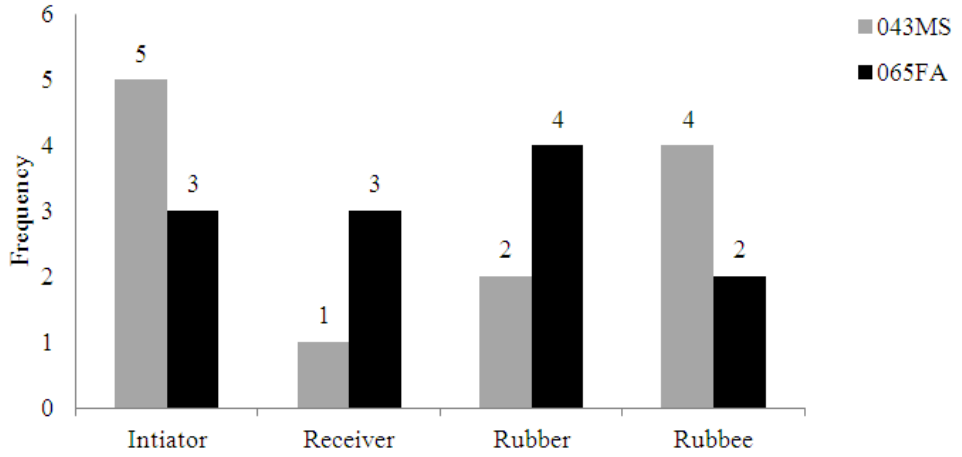

Figure 3. Distribution of pectoral fin contacts for ID065FA and ID043MS in their roles as *initiator*, *receiver*, *rubber* and *rubbee*.

ID043MS (50%) and ID065FA (33%) both showed a preference for their sides (body part C) and then their backs (E, both at 17%) to be contacted when engaged in pectoral fin tactile behavior. While ID043MS also showed a preference for the peduncle side for pectoral fin contact (17%), ID065FA favored her belly (17%) and face (17%). Both ID043MS and ID065FA exhibited a strong partner preference for same-age, same-sex individuals: ID043MS exchanged pectoral fin contact only with other male sub-adults, while 065FA shared pectoral fin contacts mostly with other adult females (50%) but also with individuals of all other age/sex classes with equal frequency (~17%).

Dolphins around Mikura were rarely observed to rub on inanimate objects: over seven years of observation only 136 observations of self-rubbing were documented and from this total, adult females engaged in seven self-rubs (19% of total) while male sub-adults conducted 10 self-rubs (27% of total). The average duration for all self-rubbing episodes was 2.65 s; adult females spent slightly longer (3.29 s) involved in self-rubbing that male sub-adults (2.2 s). Dolphins involved in self-rubbing mostly rubbed their sides into some substrate that included rocks (N = 3), rocks with seaweed (N = 3), seaweed (N = 8) and three unidentified objects. Interestingly, in a departure from observations of pectoral fin contact among all dolphin groups studied and self-rubbing behavior at Bimini and RIMS, dolphins at Mikura assumed a posture on their right side when engaged in self-rubbing (total: 53%; FA = 44%; MS = 56%).

Discussion

Self-rubbing rates were nearly identical between the three study sites, suggesting that site-specific differences (e.g., environmental conditions, substrate, presence of rocks or coral, social grouping) do not affect the rates at which dolphins rub their bodies against non-dolphin objects. It could have been the case that the presence of an object like soft sand in the Bahamas, seemingly an object dolphins would prefer to rub against (as opposed to rocks or coral), would cause

the animals to produce more self-rubbing than at the study sites where soft sand is less common (e.g., Mikura). The fact that this was not observed coupled with the fact that social-rubbing rates are also similar across all three study sites leads us to conclude that the motivation for self-rubbing is unrelated to the natural environment. Rubbing behavior in general (e.g., rates, body parts used) were similar at all three sites for all three species, suggesting that rubbing in dolphins is an evolutionarily conserved behavior for delphinid species.

The function of self-rubbing is not entirely clear, and likely involves a combination of factors. Nonetheless, the results of this study suggest that self-rubbing and social-rubbing are likely to be triggered by different factors. Self-rubbing is unlikely to fulfill any of the social functions that have been attributed to social-rubbing, including maintenance of social bonds, social grooming, conflict resolution, stress reduction, assisted locomotion or pre-copulatory behavior. It has been suggested that beach rubbing in killer whales serves a social function (Ford et al., 2000), although the details of the hypothesized social function for this behavior have not been discussed in detail. Consequently, only the following proposed functions are potentially likely to be shared by self- and social-rubbing: hygiene (e.g., sloughing, parasite removal), play, sensual pleasure, and a consequence of feeding or foraging behavior. If, as Samuels et al. (1989) suggested, self-rubbing might serve as a proxy for social-rubbing for hygienic purposes (e.g., sloughing skin, parasite removal), then similarities in the form of the rubbing behavior should be evident (e.g., body part being rubbed).

This study found that self-rubbing involved the rostrum and flukes significantly more often than social-rubbing events. If dolphins were self-rubbing those body parts requiring hygienic attention because a suitable rubbing partner was not available, one would expect the same body parts to be involved in social- and self-rubbing, something which was not observed in this study. The preferential use of the rostrum during self-rubbing events is possibly a consequence of feeding or foraging behavior at the Bimini field site, where crater feeding [involving the dolphin pushing its rostrum into the sand while foraging for buried prey, Rossbach & Herzing, (1997)] was included as a self-rubbing event. Still, this type of feeding behavior was not observed at Mikura or RIMS (though RIMS dolphins participating in the Scuba Dive programs outside of their enclosure do rub their rostrums into the sand, Eldon and Teri Bolton, RIMS, personal communication to KMD, 2003) where the rostrum was also more likely to be used in self-rubbing events. Another possibility is that the use of the rostrum and the flukes is often observed in the context of play – where a dolphin carries an object in a game of ‘catch and release’, a behavior that was also categorized as a self-rubbing event. This behavior was observed at all three field sites and could account for the preferential use of the rostrum and flukes for self-rubbing. The preference for the rostrum and flukes does not fit well with the hygiene function unless there is a reason why a social partner would be less likely to rub these particular body parts. Perhaps the flukes are avoided during a social-rubbing event given that they are often in motion in order to propel a dolphin through the water. This would make it harder for a rubbing partner to access the flukes for purposes of skin-sloughing or parasite removal, which might then lead the animal to rub on a non-dolphin object to facilitate this process.

Despite the overall similarity in contact rates between the three sites, some important differences were observed in terms of which sex and age classes were involved in the rubbing events. Females were more likely to be involved in self-rubbing events than males, with 94% of the self-rubbing events involving females at Bimini. Perhaps males' social interactions provide sufficient amounts of tactile stimulation to preclude significant amounts of self-rubbing behavior. Or it may be the case that females self-rub more often than males because of the control that a self-rubbing experience provides – control that may be lacking in female-male social interactions. Dolphins of different ages engaged in self-rubbing and social-rubbing at different rates, with the most striking finding that calves at Mikura were never observed self-rubbing or to engage in same-age social contact, while calves at Bimini were involved in 30% of the self-rubbing events and 27% of social-rubbing. In our previous study of social-rubbing involving the Mikura dolphins (Dudzinski et al., 2010), we found that calves and juveniles at RIMS initiated social-rubbing at far greater rates than their wild counterparts at Mikura and White Sand Ridge in The Bahamas, and suggested that reduced male aggression (directed at younger dolphins) at RIMS might have contributed to these rates. That is, young dolphins would be less likely to seek out social contact in the wild for fear of agonistic encounters with conspecific males, resulting in lower rates of social-rubbing for young, wild dolphins. It seems this hypothesis cannot be applied to the findings from this study given the significant difference in the self-rubbing rates for calves at the two wild sites. Social groupings (i.e., relative number of males/females and age classes) are similar at the two sites, meaning this difference in calf self-rubbing behavior cannot be explained by social interaction alone, nor can it be explained by differences in environmental conditions given that overall self-rubbing rates are the same at each site. There are no data on rates of adult male aggression directed at calves for either of the two sites, making it difficult to determine if calf behavior is influenced by adult male behavior.

Self-rubbing and social-rubbing are likely to have different functions, with evidence from this study suggesting that play, hygiene, and a consequence of feeding/foraging behavior are likely functions of self-rubbing. Analysis of rubbing data from other species in other environmental conditions will help confirm the hypothesis that rubbing behavior in dolphins is conserved for delphinid species. It is still not understood how social or other conditions specific to individual populations might influence the display of some rubbing behavior (e.g., the non-existent self-rubbing behavior for calves at Mikura). Factors like male conspecific aggression or predation risk might influence the rubbing behavior of younger animals who might 'stick close' to their mothers in Mikura, but stray farther from their mothers in Bimini or RIMS. This idea could be tested by measuring the rates at which calves separate from their mothers at each of the three sites. These data contribute to a larger picture that is currently emerging suggesting that rubbing behavior is widespread and consistent in form for dolphin species, and that differences in observed form and rates of these behaviors could reveal unique population-specific social pressures.

Case Studies

Generally, while both self- and social-rubbing behavior is widespread and consistent in form for the studied dolphin species, the observed differences in age or gender rates might be more readily explained by individual variation or expression of these actions. As such, three case study sets were presented for each included study population. At Bimini, Nemo and Tina are best described as gregarious, socially interactive dolphins who often make close approaches to other dolphins and to human swimmers during observations. Both are juvenile females who have been observed since they were calves (Nemo, since 2003; Tina, since 2001). Nemo was first observed without a right pectoral fin (Figure 1), yet she engaged in social-rubbing slightly more often as initiator than receiver, and when in the role of receiver, Nemo was more often the *rubbee*. It might be that she compensates slightly for her lack of two pectoral fins but using her body to initiate some social-rubbing. Still, Nemo engaged in social-rubbing with the observed trend for all dolphin groups – preferring same-aged, same-sex partners, suggesting that her missing fin does not impact her social contacts with peers.

Tina was involved in more pectoral fin contact than any other spotted dolphin documented during this study, also exhibiting a preference for same-aged, same-sex partners. The few males with which Tina did share social-rubbing via the pectoral fin were younger than her, possibly calves of adult females. Thus, Tina might have been practicing her alloparenting skills in preparation for her eventual role as a mother. Indeed, alloparenting behavior from juvenile and subadult females has been documented for a variety of dolphin (and other mammal) species in both wild and captive settings (Simard & Gowans, 2004). Overall, Tina seemed to engage in initiator/receiver roles with relatively equal frequency when engaging in social-rubbing actions, suggesting she engaged in much reciprocal contact. Reciprocal exchanges among chimpanzees for social grooming behavior has been documented (Hemelrijk & Ek, 1991), and the concept of reciprocal altruism as expressed by dolphins is not new (Connor & Norris, 1982); pectoral fin contact among peers might be a tactile signal soliciting a reciprocal action request for some future interaction among dolphin pairs. For example, placement of the pectoral fin on the flank of a second dolphin seems to indicate a request of solicitation for "something," often a context-dependent topic (Dudzinski, 1998; Dudzinski et al., 2009).

Both of these Bimini female spotted dolphins also engaged in self-rubbing behavior, though Tina was observed to self-rub twice as often as Nemo. Nemo seemed only to engage in self-rubbing behavior as related to crater feeding while Tina rubbed in the sand and on seaweed. It is possible that Tina was more involved in playful self-rubbing behaviors, especially considering that young dolphins were nearby during all of her self-rubbing events. These self-rubbing actions by Tina could have been part of her alloparenting activity or used to engage younger dolphins when their mothers were otherwise involved.

At RIMS, Ronnie was born to the alpha female of the group and had also an older sister within the group during our first year of study. Bill's mother died when he was 1.5 years old and he had no siblings. Bill was not "adopted" by any adult females, but he was already consuming fish and thus did not require dietary

nourishment from the other dolphins. Ronnie and Bill were observed while calves and juveniles, but were moved from the RIMS population for two years during which they became subadults. Though Ronnie and Bill engaged in more social-rubbing when they were younger, as opposed to when they aged to subadults, their self- and social-rubbing behavior was still consistent with respect to partner preference, posture and body part contacted during both pre-move and post-move periods.

Ronnie initiated more pectoral fin contacts than any other dolphin in the RIMS group during 2003, with most of these social-rubs exchanged with his older sister, Tela. Ronnie also assumed the role of *rubber* much more often than any other dolphin. Ronnie was precocious: he was described by trainers as a bit of bully and quite pushy (Eldon and Teri Bolton, personal communication to KMD, 2003-2009). As a calf and young juvenile, he would instigate aggressive interactions with other dolphins and then hide behind his mother (alpha female). Ronnie would insert himself into social situations between other dolphins and was routinely covered in fresh rake marks. Once weaned, Ronnie was unable to use the status of his mother's role in the group as a shield; he might have shifted his social-comfort solicitations to his older sister, Tela. Young animals might transfer social contact from their mother to another individual, likely an older sibling, during the weaning process. Observations of Ronnie in 2010 and 2011 suggest that his personality has remained stable – he continues in his role of bully more often than not (KMD personal observation, January 2010, May 2011). Additionally, Ronnie seems to spend more time with male calves in the social group as opposed to conspecifics of similar age of either sex. It is possible that the older individuals have little tolerance for Ronnie's more routinely aggressive actions while younger dolphins might not have the exposure or experience of Ronnie's behavior to avoid it (KMD personal observation, Jan 2010, May 2011; Teri Bolton, personal communication to KMD, May 2011).

Bill and Ronnie were born within 15 months of one another, and while they were calves at the same time, they possess very distinct personalities. Even though Bill lost his mom at 1.5 years old, he was not alloparented by any of the adult females in the RIMS study group. Rather, Bill seemed to spend more time with other male dolphins of either the same age or older, even the alpha males in a given year. Males from several groups of bottlenose dolphins have been shown to form stable bonds (Shane, Wells, & Würsig, 1986). It is possible that Bill commenced the development of his social relationships with the other males in the RIMS social group much earlier than would be expected because of his mother's death. Before 2005 and between 2007 and 2009, Ronnie seemed to fill the role of Bill's partner/alliance pair. The male hierarchy and partnerships shifted considerably in late 2009 and early 2010 after a new male dolphin joined the group[2] and several younger males became subadults. In 2011, Bill did not seem to possess one specific pair bond with another male dolphin in the group, but rather

[2]An adult male bottlenose dolphin joined the RIMS captive study population by his choice. Named Han, this male spent 3-4 weeks immediately outside the RIMS pens and once into the group, began eating dead fish within one week, and began stationing and following hand signals within two weeks (KMD personal observations, May, 2009; Teri and Eldon Bolton, personal communication to KMD, May, 2009).

had a more fluid, changing association pattern with most of the adult and subadult males in the RIMS study group.

Sample sizes and time spent per dolphin in observations were much lower for our study of the Mikura Island dolphins as compared to the other study sites. Still, a few trends seemed apparent: adult females spent more time with their calves or other females than with males or juvenile groups. It is possible the maternal strategy within the study group around Mikura is more conservative than at our other study sites, possibly because of the proposed presence of infanticide in this group (see Patterson et al., (1998) for a discussion of infanticide in bottlenose dolphins). That is, females might not permit their calves to stray far or play in "youth groups" because of the potential for young adult males to attempt to kill the calves, or alternatively the calves might be more at risk from sharks or other predators around Mikura Island. Specific data on infanticide or predation are not available to confirm the extent these might significantly affect maternal strategies. But, the fact that self-rubbing was also not witnessed by Mikura calves is further circumstantial evidence that male-aggression or predation represent strong influences on the maintenance of close proximity between mothers and their calves.

We have documented a number of similarities in the tactile behavior of diverse dolphin populations; however, as noted in the earlier discussion of individual dolphins, it is not the case that all dolphins are the same. Dolphins exhibit consistent and distinct personalities (Highfill & Kuczaj, 2007), and these individual differences are reflected in their tactile behaviors. For example, the dolphin Bill is more cautious than the dolphin Ronnie, and as a result Bill initiated far fewer tactile interactions than did Ronnie. In addition to the individual differences that we see within a population, there may also be meaningful differences between populations. For example, it seems that dolphin calves in Bimini are more adventurous than are dolphin calves in Mikura. Such cultural differences may be driven by social or habitat characteristics, or some combination of the two. Although the study of dolphin personality is in its infancy, our results demonstrate the need to incorporate both individual and cultural differences into explanations of dolphin behavior.

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