Aquatic Mammals 2013, *39*(4), 335-343, DOI 10.1578/AM.39.4.2013.335

Pectoral Fin Contact Between Dolphin Dyads at Zoo Duisburg, with Comparison to Other Dolphin Study Populations

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Abstract

Tactile exchanges using the pectoral fin have been noted in a variety of dolphin species. In this study, bottlenose dolphins (*Tursiops truncatus*) at Zoo Duisburg in Germany were seen to exchange pectoral fin contact much like both wild and captive dolphins. The rate of overall contact (touches and rubs) was slightly larger among the Zoo Duisburg dolphins than for three other study sites, although relative rates for contact via rubs and touches by Zoo Duisburg dolphins appears similar to that of dolphins at the other study sites. Pectoral fin contact between Zoo Duisburg dolphins was more similar to that of dolphins at the Roatan Institute for Marine Sciences in that there was no difference in whether the dolphin was *rubber* or *rubbee* when initiating pectoral fin contact, although at all sites, including Zoo Duisburg, the *rubber* was more often the initiator of a pectoral fin contact. More similar to both wild groups, but not the other captive group of dolphins, Zoo Duisburg dolphins had a strong preference for the horizontal body posture when exchanging pectoral fin contacts. The most striking result is that all dolphins studied have a strong preference for body part contacted: when the *rubbee* is initiator, the top three body parts most contacted by all dolphins include the face, rostrum, and side. Similarly, when in the role of *rubber* initiator, the top most contacted and third most contacted body parts are identical at all four study sites. The exchange of contact via the pectoral fin seems to be a conserved action with respect to form and function across dolphin species regardless of the environment in which the dolphins reside.

Key Words: pectoral fin contact, dolphin, social behavior, tactile exchange

Introduction

There are relatively few peer-reviewed studies that report on observations of captive delphinid behavior outside of experimental contexts. These studies have focused on stress (Waples & Gales, 2002); mother-calf interactions (Gubbins et al., 1999) and calf development (Fellner et al., 2012), including the development of whistle (Fripp & Tyack, 2008) and echolocation production (Favaro et al., 2013); and dolphin/human interactions, particularly during interactive programs (Frohoff & Packard, 1995). Studies investigating social, affiliative, and communicative behavior of captive dolphins are scarce (e.g., Tamaki et al., 2006; Dudzinski et al., 2010); and research that compares wild and captive dolphin social behavior are even more uncommon (Caldwell et al., 1965; Brown et al., 1966; Mann & Smuts, 1999; Dudzinski et al., 2010; Greene et al., 2011). Still, a few comparative reports document differences in social behavior between captive and wild animals (see "Maternal Behaviour" in Mann & Smuts, 1999), while others presented similarities (e.g., Gubbins et al., 1999). In general, quantitative comparative studies of wild and captive delphinid populations are rare, particularly when it comes to investigating differences in social behavior.

There are numerous reasons to compare the social behavior of wild and captive dolphins, including (1) supplying guidelines for those working in rehabilitation and husbandry; (2) evaluating the legitimacy of extrapolating results and interpretation of research on wild species to captive populations and vice versa; (3) establishing the external validity of captive studies; and (4) assessing the physical and mental health of captive animals via comparisons with behavior displayed by their wild counterparts. Using these goals as a guide, this study centered on one aspect of delphinid social interaction—pectoral fin contact—in order to compare the social behavior of captive dolphins in a manmade structure to that of captive dolphins in a natural lagoon as well as dolphins in the wild.

The exchange of tactile behavior (touching or rubbing) via the pectoral fin is an affiliative behavior that involves contact between one dolphin's

body and another dolphin's pectoral fin (for an overview, see Sakai et al., 2006a; Dudzinski et al., 2009). Tactile behavior via the pectoral fin has been studied in both captive and wild odontocete populations: captive dolphins documented include bottlenose dolphins (*Tursiops truncatus*; Tavolga & Essapian, 1957; Samuels et al., 1989; Tamaki et al., 2006), spinner dolphins (*Stenella longirostris*; Johnson & Norris, 1994), and Commerson's dolphins (*Cephalorhynchus commersonii*; Johnson & Moewe, 1999). Pectoral fin contact has been observed among the following wild odontocetes: Indo-Pacific bottlenose dolphins (*Tursiops aduncus*; Mann & Smuts, 1998, 1999; Sakai et al., 2003, 2006a, 2006b; Dudzinski et al., 2009), spinner dolphins (Johnson & Norris, 1994), Atlantic spotted dolphins (*Stenella frontalis*; Dudzinski et al., 2012), belugas (*Delphinapterus leucas*; Smith et al., 1992), rough-tooth dolphins (*Steno bredanensis*; Kuczaj & Yeater, 2007), and sperm whales (*Physeter macrorhynchus*; Whitehead & Weilgart, 2000).

In order to further investigate the similarities and differences between the social behavior of wild and captive dolphin populations, pectoral fin tactile exchanges observed in a group of captive dolphins housed at Zoo Duisburg were compared to similar behavior reported for dolphins housed at the Roatan Institute for Marine Sciences (RIMS), Honduras; Mikura Island, Japan; and Little Bahama Bank (LBB) and Grand Bahama Bank (GBB), The Bahamas (Dudzinski et al., 2009, 2010). The primary aim of this investigation was to examine whether dolphins housed in a man-made structure use their pectoral fins to exchange contact with each other in the same manner as do wild dolphins or captive dolphins in natural lagoons with respect to select body parts, assumed postures, contact rates, and partner preference.

Methods

Study Sites and Populations

Behavioral observations of dolphin-dolphin interactions were collected at Zoo Duisburg (ZD), Germany, from 28 November to 3 December 2012. At this time, there were nine bottlenose dolphins: one adult male, three adult females, two juvenile females, one female calf, and two male calves. The adult male ("Ivo") and one adult female ("Pepina") were wild caught and transferred to ZD from other institutions in 1994 and 1999, respectively, while the other seven individuals were born at ZD (Table 1).

The ZD pectoral fin contact data were compared to observations collected at four other study sites (Dudzinski et al., 2009, 2010, 2012). Data from the other study sites were gathered over a total of 18 y collectively at RIMS, Anthony's Key Resort, Roatan, Honduras; around Mikura Island, Japan; and on the LBB and GBB, The Bahamas (Table 2).

Atlantic spotted dolphins are found along the White Sand Ridge of the LBB (study group of about 150 identified dolphins), located ~64.5 km north of West End, Grand Bahama Island, with a second group (of about 100 identified dolphins) studied roughly 8 to 16 km from Bimini Island (Table 2; Dudzinski, 1996; Herzing, 1997; Brunnick, 2000; Melillo, 2008). Both groups are primarily observed in depths ranging from 6 to 12 m (e.g., Melillo et al., 2009).

A group of roughly 165 identified Indo-Pacific bottlenose dolphins are resident to the area within 300 m of Mikura Island, Japan, a dormant volcanic island roughly 200 km south of Tokyo with a circumference of 16.4 km (Table 2; Kogi et al., 2004). The sea floor is characterized by boulders and depths ranging from 2 to 60 m at 2 to 250 m from shore, respectively.

RIMS is located on the northwest coast of Roatan, approximately 43.5 km north of

Table 1. Zoo Duisburg (ZD) study population

Name	Ivo	Pepina	Delphi	Daisy	Donna	Dolly	Diego	Darwin	Dörte
Age (y)	~33	~31	20	16	5.5	5.5	1.5	1.5	1.5
Sex	Male	Female	Female	Female	Female	Female	Male	Male	Female

Table 2. Summary of years of study and data collected at all study sites for which pectoral fin contact data have been analyzed; study group size for The Bahamas and Mikura group averaged over years presented. For The Bahamas, 1993-1994 represents the Little Bahama Bank (LBB) group and 2003-2009 represents the Grand Bahama Bank (GBB) group. Study group size for the Roatan Institute for Marine Sciences (RIMS) is presented as average for years included.

	ZD	RIMS	Bahamas	Mikura
Years in field	2012	2003-2009	1993-1994, 2003-2009	1997-2008
Video data (min)	272	4,484	512	1,208
Study group size	9	19 (16-24)	~125, ~95	~165

Honduras. This facility, located inside a fringing reef of a natural lagoon, is an enclosure that encompasses about 300 m^2 in surface area. Age and sex distribution for this group of captive bottlenose dolphins matches that of most coastal wild bottlenose dolphin groups (Table 2; Kogi et al., 2004; Connor et al., 2006).

Data Collection

Data collection protocols for ZD were identical to those established for observations of both captive and wild dolphins at the other study sites (for protocol details, see Dudzinski, 1998; Dudzinski et al., 2012). Video data were collected either through underwater viewing ports or using a camera array (Dudzinski et al., 1995) while in the water among the dolphins, using non-invasive focal animal and all-occurrence sampling (Altmann, 1974; Mann, 1999). Follows and recordings of dolphins began as soon as the video camera/observer were in a favorable position (in front of viewing port or under water). An individual dolphin was selected and recorded until it was no longer within the field of view.

Event sampling for pectoral fin contact was conducted from all video data for each dolphin study group; contacts between one dolphin's pectoral fin and another dolphin's body (including the pectoral fin) were documented. Other relevant 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, and identification of the departing dolphin. Also, whether the initiating and receiving dolphins were the *rubber* or *rubbee* and which body part was contacted on the *rubbee* were documented.

Definitions

Rubbing and static contact between one dolphin's body and another's pectoral fin are defined in the literature (see Sakai et al., 2006a, for an overview). During this study, we followed definitions applied to our previous research of both wild and captive dolphins (see Dudzinski et al., 2009, 2010, 2012). Tactile exchanges via a pectoral fin were begun by one dolphin (either the *rubber* or *rubbee*) approaching and physically contacting another dolphin, and were ended when one dolphin departed from the other. This behavior unit (i.e., between the start of contact and a departure) was defined as a pectoral fin contact episode. As in Dudzinski et al. (2009), *rubbing* was defined as active movement between the *rubber*'s pectoral fin and the *rubbee*'s body. *Petting*, one type of rubbing, was defined as the active movement between two dolphins' pectoral fins while in contact. *Touches* were defined as physical contact of one dolphin's pectoral fin with another's body in the absence of active movement from any of the body parts involved. The term *contact* is used to refer to rubbing, petting, and/or touching.

A dolphin's body was divided into 11 sections in order to document which specific body part came into contact with a pectoral fin (see Dudzinski et al., 2009, Figure 1, for body diagram). Dolphin posture was categorized as horizontal (HOR), side-down left (lOSD), side-down right (rOSD), upside down (VTU), head down (HDO), and head up (HUP) (Dudzinski et al., 2009, 2010).

Statistical Analyses

Because data from ZD represent one observation session (272 min of data collected over 5 d), all pectoral fin contacts were included in contrast to the individually adjusted pectoral fin contact data from the other three study sites (for sampling protocols, see Dudzinski et al., 2009, 2010). A comparison by location of exchanged pectoral fin contact behavior was examined with a *t*-test with two samples assuming unequal variances. Body part preference for both *rubber* and *rubbee* in the role of *initiator* was examined with Spearman Rank Order Correlation. Chi-square analysis was used to examine fin-to-fin vs fin-to-body contact and to assess variation in posture assumed when the *initiator* was *rubber* vs *rubbee* and *initiator* vs *receiver* roles, and a Fischer's Exact Test was used to determine if the initiating dolphin engaged in more rubbing than petting behavior.

Results

A total of 272 min of video observations of the Zoo Duisburg (ZD) dolphins were collected during a visit to the facility in 2012. A total of 153 pectoral fin contacts were exchanged between dolphin dyads during these documented video observations.

Comparison of Contact Frequency Among Research Sites

The relative rate of contact events appears stable between four field sites (n = 139 contact episodes at The Bahamas, n = 450 at Mikura, and n = 1,478 at RIMS; Dudzinski et al., 2010); however, because only 1 y of data are currently available from observations of the ZD study group, a mean rate value was not calculable. The rate of overall contact (touches and rubs) was slightly larger among the ZD dolphins than for the other three study sites (Figure 1), although relative rates for contact via rubs, touches, and overall contacts by ZD dolphins appears similar to that of the other three study sites (Figure 1). Dolphins

at ZD exchanged touches (0.194 touches/min) that were almost identical to touches by dolphins at Mikura (0.192 touches/min), while ZD dolphins exchanged rubs (0.364 rubs/min) about 1.5 times more than dolphins at the other three sites (0.210 rubs/min at Mikura, 0.224 rubs/min at The Bahamas, and 0.209 rubs/min at RIMS).

Pectoral Fin to Pectoral Fin vs Pectoral Fin to Body

Previously, Dudzinski et al. (2009, 2010) found that at both wild study sites (The Bahamas and Mikura), the initiating dolphin engaged in more rubbing than petting behavior while in the role of the *rubber*. For the ZD dolphins, like the dolphins at RIMS (Dudzinski et al., 2010), there was no difference in the proportion of rubbing vs petting behaviors when in the role of the *rubber* vs *rubbee* according to a Fischer's Exact Test ($p = 0.582$).

Initiator vs Receiver

Dolphins initiate contact as the *rubber* two to three times more often as compared to the *rubbee*, and this trend is not significantly different between the four sites ($X^2_3 = 4.9$, $p = 0.1793$). That is, there was no significant difference found between the ZD dolphins and the other dolphin study groups with respect to how often the *rubber* was the initiator. If the data from RIMS, Bimini, and Mikura are pooled and compared to the ZD data, no significant difference was found between the latter group and the other dolphin groups with respect to how often the *rubber* was the initiator ($X^2_1 = 1.51$, $p = 0.22$). At ZD, similar to each of the other study sites, the *rubber* was also significantly more often the initiator of contact episodes ($p < 0.001$, 79.57% of 142 episodes).

Participation in pectoral fin contact exchanges by identified individuals followed trends documented in our other study groups (Figure 2). The majority of the contacts were shared between mother-calf dyads ($n = 80$ pectoral fin contacts, 56.7%), while same-aged females shared contact with each other more than with other dolphins (outside of mother-calf dyads; Figure 2). Additionally, similar to results from The Bahamas and RIMS, but not from Mikura (Dudzinski et al., 2009, 2010), calves exchanged pectoral fin contact with other calves and with non-related adults (Figure 2).

Body Parts Contacted

Similar to our previous studies (Dudzinski et al., 2009, 2010), pectoral fin contact exchanges were scored according to the body part that was contacted by the initiating dolphin as *rubber* or *rubbee*: the dolphin body was sectioned into 11 identified areas (see Dudzinski et al., 2009, for body plan). For analysis, the first body part contacted represented episodes with multiple body parts that were contacted during a single episode. Dolphins at the other three study sites (The Bahamas, Mikura, and RIMS) exhibited

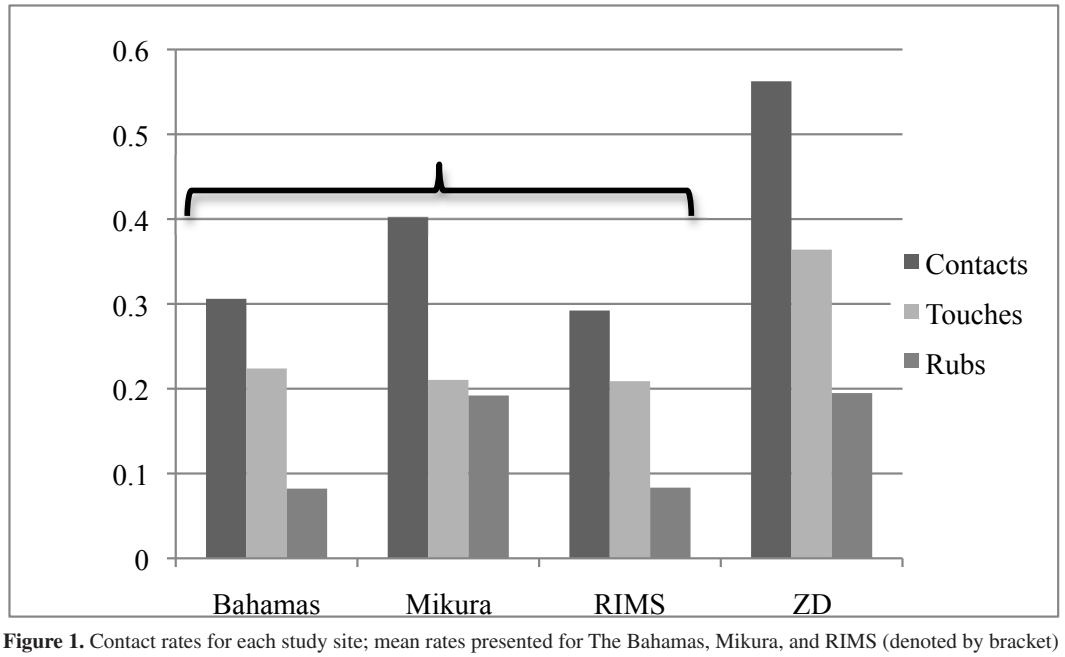

Figure 1. Contact rates for each study site; mean rates presented for The Bahamas, Mikura, and RIMS (denoted by bracket) and single rate value for 1 y of data from Zoo Duisburg (ZD)

	Initiator		Receiver	
Dolphin ID	R	E	R	E
Ivo	3	1	0	6
Pepina	17	1	13	18
Delphi	5	1	2	6
Daisy	13	1	3	14
Dolly	9	0	1	13
Donna	9	0	0	8
Diego	28	17	4	26
Darwin	16	4	1	14
Dörte	12	3	6	7

		Receiver							
		Ivo	Pepina	Delphi	Daisy	Dolly	Donna	Diego	Darwin	Dörte
Initiator	Ivo		1					3		
	Pepina							18		
	Delphi		2		1			1		3
	Daisy					2		2	10	
	Dolly				1		6		2	
	Donna					9				
	Diego	4	28	1					2	10
	Darwin				15	3	2			
	Dörte	2		6				7		

Figure 2. Sample size per dolphin as initiator and receiver of pectoral fin contacts in role of *rubber* (R) and *rubbee* (E, top chart) and exchanges between specific dyads in the group (bottom chart); boxes shaded in black denote mother-calf pairs, and boxes shaded in dark gray denote same-aged female dyad exchanges. Sample sizes given per cell. Cells with no value indicate no documented pectoral fin contact.

consistent body part preference (Dudzinski et al., 2010), and this trend was also documented among the dolphins at ZD (Table 3). When the initiator was in the role of *rubber*, a significant correlation between role and body part was found between ZD and the dolphin groups at our other study sites (ZD and RIMS: $r_s[11] = 0.97$, $p < 0.000001$; ZD and The Bahamas: $r_s[11] = 0.86$, $p < 0.0003$; ZD and Mikura: $r_s[11] = 0.88$, $p < 0.0002$). Similarly, when the initiator assumed the role of *rubbee*, a significant correlation between role and body part was documented between ZD and the dolphin groups at our other study sites (ZD and RIMS: $r_s(11) = 0.66$, $p < 0.014$; ZD and The Bahamas: $r_s(11) = 0.55$, $p < 0.038$; ZD and Mikura: $r_s[11] = 0.67$, $p < 0.012$).

What is striking is that the top three body parts most contacted by the *rubbee* as initiator are the same at all four study sites (Table 3). Similarly, when in the role of *rubber* initiator, the top most contacted and third most contacted body parts are identical at all four study sites (Table 3). Comparing ZD dolphins as *rubber* vs *rubbee* for body part preference confirms, as with our previous study on contact between dyads at RIMS, The Bahamas, and Mikura (Dudzinski et al., 2010), that these dolphins have a general preference for body part(s) used during tactile interactions involving pectoral fin contact (ZD *rubber* initiator vs *rubbee* initiator: $r_s[11] = 0.43$, NS [using $p < 0.05$ level]). These preferences reflect the initiator role and are consistent across study sites.

Body Postures

Like Japan, The Bahamas (Dudzinski et al., 2009) and RIMS (Dudzinski et al., 2010), a strong preference was shown for the horizontal (HOR) position (i.e., adopted in 81% of contact events) for both the *rubber* and *rubbee* roles when combined for all contact type ($X^2_5 = 125.00$, $p < 0.001$). Unlike the other captive site at RIMS, but similar to Japan and The Bahamas, when the HOR position is removed from the ZD dataset, a strong preference for specific positions is still not observed ($X^2_4 = 6.58$, NS).

We also examined the ZD dataset to determine whether two dolphins involved in a pectoral fin contact episode assumed the same or different postures. Overall, the initiator, whether *rubber* or *rubbee*, assumed the same posture (72.5%) as compared to a different posture (27.5%) with the receiver. Additionally, when initiating rubs vs

Table 3. Rank order (from most to least likely) of body parts contacted for the *initiator* in the role of *rubber* and *rubbee* for ZD, Mikura Island, The Bahamas, and RIMS (data for Mikura Island, The Bahamas, and RIMS from Dudzinski et al., 2010)

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

Note: A = rostrum, B = face, C = lateral side, D = dorsal fin, E = back, F = belly/ventral side, G = genitals, H = pectoral fin, K = peduncle, L = keel, and M = fluke (Dudzinski et al., 2009)

touches as a *rubber*, ZD dolphins did not differ significantly with respect to same or different postures ($X^2_1 = 2.46$, NS), and the same was true for rubs vs touches by the *rubbee* when initiator ($X^2_1 = 0.17$, NS). These results are similar to the RIMS and Mikura dolphins more so than both spotted dolphin groups in The Bahamas (Dudzinski et al., 2010, 2012).

Sex and Age

Differences in partner preference for pectoral fin contact exchanges were identified among the ZD dolphins. For example, males hardly ever contacted each other and mostly initiated contacts as *rubbees* to females, which is quite different to what was observed at our other field sites; however, on closer examination of the raw data, it is clear that all but six contacts involved the male calves and their mothers. Because there is only one adult male in this group and three mother-calf pairs, a direct sex/age comparison to results at the other sites with respect to pectoral fin contact is not possible.

Discussion

A number of trends consistent among all of the research sites involved in our study of pectoral fin contact behavior are beginning to paint a picture of a class of social tactile behavior that might well be universal for delphinid species. The following is a list of observations of pectoral fin contact behavior that are identical across the five field sites and three species we have investigated so far:

- The *rubber* is more often the initiator of a contact episode.
- Rubs are observed more often than touches.
- The majority of contact episodes are observed within mother-calf dyads.
- Dolphins are most likely to rub the lateral side of their partner when initiating contact as the *rubber*.
- Dolphins are most likely to solicit a rub to the face when initiating contact as the *rubbee*.
- Dolphins prefer to maintain a horizontal body position during contact events.
- Individuals within each dolphin dyad were more often in the same posture than in different postures during a contact event.

In addition, rubbing rates for each of the five field sites are roughly similar (ranging from 0.209 rubs/min at RIMS to 0.364 rubs/min at ZD). Also, the top three body parts most contacted by all dolphins at all sites include the face, rostrum, and side. This suggests that these aspects of pectoral fin contact behavior are both conserved with respect to form for a number of delphinid species and might constitute the norm for which affiliative social contact behavior involving the pectoral fin is concerned.

Bottlenose dolphins at Zoo Duisburg, exchanged pectoral fin contact much like dolphins at our other research sites. There were, however, a handful of differences worth noting. The rate of overall contact (touches and rubs) was slightly higher among the ZD dolphins than for the other study sites, although relative rates for contact via touch by ZD dolphins were nearly identical to touch exchanged by dolphins around Mikura. Active contact between ZD dolphins was more similar to that of dolphins at RIMS in that when the initiating dolphin was either the *rubber* or the *rubbee,* that individual engaged in petting vs rubbing in similar proportions for each condition (i.e., with a preference for rubbing). More similar to both wild groups, but not to dolphins at

RIMS, ZD dolphins had a strong preference for the horizontal body posture when exchanging pectoral fin contacts. Also, like the wild dolphin groups but not the RIMS dolphins (Dudzinski et al., 2009, 2010), when the horizontal posture was removed, ZD dolphins did not exhibit a strong preference for any of the remaining postures.

The differences noted here between the ZD dolphins and the other field sites, as well as the difference previously noted between the RIMS dolphins and The Bahamas and Mikura dolphins (Dudzinski et al., 2010) do not suggest that the distinctive environmental conditions of wild vs captive dolphins result in obvious changes to the form (and possibly function) of pectoral fin contact behavior. The only difference between wild vs captive sites that was consistent for both RIMS and ZD dolphins was that petting vs rubbing behaviors occurred with similar proportions when dolphins engaged their partner either in the role of *rubber* or *rubbee*. Thus, for the wild sites, we find that when an animal solicits contact as the *rubbee*, it will engage in more petting behavior than if it were in the role of the *rubber* when it initiated contact. Dolphins at ZD and RIMS, however, continue to solicit rubbing vs petting contact in similar proportions for both roles, with a preference for rubbing. It is not immediately obvious as to what might be the cause of this difference or whether it indicates a difference in function for petting behavior for wild vs captive sites as we have previously discussed (Dudzinski et al., 2010).

Because there was only one adult male in the ZD population, we were unable to directly test for any differences in form or function of contact behavior as it relates to male/female aggression or infanticide—factors that might explain some of the captive vs wild differences found in previous studies (see Dudzinski et al., 2010, for a discussion). The differences in form of pectoral fin contact behavior between captive vs wild sites do not appear to be a product of either social or environmental conditions that are specific to a captive environment. It remains to be seen if the slightly increased contact rate at ZD will be maintained once more data are collected.

It is too early to suggest that similarities between our four field sites in pectoral fin contact behavior indicate universals in form that can be extrapolated to all delphinid species (Dudzinski et al., 2010). Similarly, the differences observed between the five sites could result from any number of individual or combinations of factors, including species, social conditions, or environmental conditions, none of which are immediately obvious based on the results so far. With the completion of this study, however, a consistent pattern of similarities in the form of pectoral fin contact behavior is emerging which suggests that (1) these behaviors might well be conserved between species and that (2) difference in environmental and social conditions do not appear to change the form or rate of the observed behaviors in any obvious ways. The continued analysis of our current research archive together with the addition of future research years and research sites will allow for stronger conclusions to be drawn and might well reveal that affiliative pectoral fin contact is a social behavior that is consistent in form and function between many delphinid species living in a variety of environmental conditions.

Acknowledgments

Zoo Duisburg provided access to the dolphins and financial support for collection of observational data on the dolphins housed in their dolphinarium. Financial support for data collection during the Dolphin Communication Project's (DCP) longitudinal studies of The Bahamas' Atlantic spotted dolphins (both LBB and GBB) 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), At-Sea Processors' Association Pollock Conservation Cooperative Fund at Alaska Pacific University, the Japanese Society for the Promotion of Science, Casio's Eco-Research Fund, and a Kaken-Hi grant from the Japanese government. The Galindo Family and Anthony's Key Resort (AKR) provided logistical support that includes lodging, food, and access to the dolphins during all data collected on the dolphins at the Roatan Institute for Marine Sciences (RIMS) over the seven-year period. All data on wild dolphins were collected during ecotour-format boat trips that were partially sponsored by Oceanic Society Expeditions (in the northern Bahamas), boat trips with donated research space run by Bill and Nowdla Keefe's Wild Dolphin Adventures and Al Sweeting, Jr. at Sea Crest Hotel & Marina (Bimini, The Bahamas), the Miyake Fishermen's Cooperative (from Miyake Island), and the Mikura Iruka Kyoukai (at Mikura Island). DCP-organized ecotours brought volunteers to AKR to assist with additional funding for our data collection of the RIMS dolphins. 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 to 2005) and to DCP (2000 and 2009) from the Department of Fisheries (Marine Resources), Ministry of Agriculture, The Bahamas. Bimini data collection and photo-identification processing was assisted by K. DeStefano (2003, 2004), D. Blanding (2005, 2006), and several interns (2007 to 2009). Eldon Bolton, Director of RIMS, provided access to records for the dolphins under his supervision. The trainers of Zoo Duisburg and RIMS provided much insight and discussion during observation sessions of their dolphins. This paper represents contribution #114 of the DCP.

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