

The role of touch in select social interactions of Atlantic spotted dolphin (*Stenella frontalis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)

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Received: 10 August 2006 / Accepted: 7 April 2007 / Published online: 5 June 2007
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Abstract In this descriptive study, the potentially communicative functions of non-vocal behaviors produced by two species of dolphin, Atlantic spotted (*Stenella frontalis*) and Indo-Pacific bottlenose (*Tursiops aduncus*), were examined in the context of three focal events: *depart* (one or more dolphins depart company of others), *join* (two or more dolphins come together), and *contact* (dolphin makes contact with another using a part of its body). These particular events were chosen because they involve interactions between dolphins and so provide an opportunity to examine possible precursors or antecedents to specific social behaviors. Non-vocal behaviors occurring before and/or after these focal events were documented and analyzed in an attempt to determine if certain behaviors were consistently associated with the departure (*depart*) or arrival (*join*) of another dolphin, or with physical contact (*contact*) between dolphins in each species. Touch behaviors were found to be significantly related to each of the three focal events so were examined in further detail. Overall, in comparing species, the Indo-Pacific bottlenose and Atlantic spotted dolphins in this descriptive study exhibited more similarities than differences in their use of touch behaviors in potentially communicative situations across five broad

behavioral contexts. However, a difference in the use of touch behaviors produced before departing or after joining a conspecific was noted. Specifically, the spotted dolphins were more likely to use contact after joining than before departing, whereas the bottlenose dolphins were equally likely to use contact in both situations.

Keywords *Stenella frontalis* · *Tursiops aduncus* · Non-vocal communication · Behavioral associations · Contact behavior · Mikura · Japan · Bahamas

Introduction

Communication is an integral part of daily life for social species (Altmann 1967; Cullen 1972; Smith 1977). Without some type of system to exchange information reliably and consistently, social systems could not exist (Marler 1977; Otte 1974). Dolphins are highly social mammals (see examples in: Dudzinski 1998; Rossbach and Herzing 1999; Slooten 1994; Smolker et al. 1992), and the mode of information transmission between individuals may vary. Dolphin communication involves tactile, visual, acoustic, and behavioral signals used individually or synergistically (Caldwell and Caldwell 1977; Connor and Smolker 1996; Dudzinski 1998; Dudzinski et al. 2002; Herman 1980; Herzing 1996; Pryor 1990; Reynolds and Rommell 1999; also see Herzing 2000 for review). Behavioral signals employed by dolphins can be further divided into two categories: actions that produce a sound (e.g., a tail slap or jaw clap) and actions that are not associated with specific sounds (e.g., body rub or pectoral rub). Dolphins produce sounds by an internal exchange of air in the delphinid anterior cranial region (see Popper 1980 for review). Such sounds are often referred to as “vocalizations” (see Reidenberg and Laitman

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1988 for review). For the sake of convenience, all signals that dolphins produce without activating their internal sound production system are referred to as “non-vocal behaviors” in this paper.

Historically, the study of dolphin non-vocal behavior has been hindered in several ways. Much of the comparative work on non-vocal communication involves species that vary their facial expressions (Chevalier-Skolnikoff 1973; Goodall 1986; Hauser 1993; van Hoof 1972), an ability that dolphins lack. In addition, most of the interactions that occur between dolphins take place under water. Only recently have researchers developed technology to simultaneously record both the visual and acoustical aspects of interactions between individual dolphins from the underwater perspective (for more details on employed techniques see: Dudzinski et al. 1995; Herzing 1996; Lammers et al. 2003; Schotten et al. 2005).

Pryor (1990) suggested that gaze cues could be important for information sharing among cetaceans. Recent evidence suggests that bottlenose dolphins (*Tursiops truncatus*) have the capacity to produce and comprehend gaze signals as a type of referential pointing (Xitco et al. 2001). While interacting with humans, the two dolphins being studied by Xitco and colleagues spontaneously produced behavior resembling gaze alternation that was coupled with referential pointing with their rostra. Their gaze alternation/pointing behavior was directed at a human and the dolphins appeared to monitor the human's behavior prior to pointing. Subsequent research demonstrated that the dolphins were sensitive to the perspective of the human observer (Xitco et al. 2004). The spontaneous emergence of pointing behavior in captive animals coupled with their ability to understand the pointing gesture of a human (Herman et al. 1999) suggests a possible communicative capacity for such behaviors among dolphins. Intra-specific activity, comparable to this pointing behavior, was documented from a sub-group of wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in response to a dead conspecific (Dudzinski et al. 2003). Although monitoring behavior was not observed in the two occurrences reported by Dudzinski and colleagues, the positioning of the dolphins' bodies toward the carcass was suggestive of referential pointing.

Non-vocal communicative behaviors are typically visual or tactile signals used to share information among conspecifics. Visual displays such as leaping or the positioning of body parts may help communicate information about the environment or the behavioral state of the sender. For example, dusky dolphins (*Lagenorhynchus obscurus*) leap to indicate prey has been located (Würsig and Würsig 1980). Other visual signals have been associated with aggression or threat, including a direct approach, facing another animal head-on (Dudzinski 1996, 1998; Herzing

1996), shaking of the head, “popping” of the jaws (Connor and Smolker 1996) and opening and closing of the jaws (Dudzinski 1998; Herman and Tavalga 1980; Overstrom 1983). Visual information might also play a role in evaluating potential threats. For example, scarring on an individual may indicate that this animal has been in many fights and may therefore be a potential threat (MacLeod 1998; Pryor and Shallenberger 1990). In contrast, an animal that is facing away may signal appeasement or subordination (Bateson 1965). Caldwell and Caldwell (1977) reported that a submissive posture in which the mouth is closed and the lateral portion of the submissive dolphin's body is presented occurs in some agonistic interactions between animals. Visual signals that have been correlated with submissive encounters in captive dolphins include looking away, flinching, and generally orienting the body away from the other dolphin (Samuels and Gifford 1997; Würsig et al. 1990).

Although visual signals may play a role in both aggressive and affiliative interactions (see Tyack 2000), the meaning of such signals is affected by the age of the signaler and the angle of approach (Dudzinski 1998). For example, a male dolphin will often assume an S-shaped posture during an agonistic encounter (Caldwell and Caldwell 1977; Defran and Pryor 1980; Tavalga 1966). Consistent with these observations, a display of the “S-posture” by itself may be seen as a threat when produced by an Atlantic spotted dolphin (*Stenella frontalis*); however, if this posture is combined with an oblique angle of approach and presentation of the genital region, it is indicative of a less aggressive and more playful context (Dudzinski 1998). The affects of age on the meaning of the S-posture are clear for this species. Spotted dolphin subadults are more likely to perform the S-posture in the context of aggressive activity, while juveniles are more likely to do so in bouts of rough and tumble play with conspecifics (Dudzinski 1996, 1998; Herzing 1996).

Dolphin skin is highly innervated and hence very sensitive (Palmer and Weddell 1964). Areas around the eye and blowhole are as sensitive to touch as human fingers and lips (Ridgway and Carder 1990). Tactile contact may be affiliative, such as gentle nipping or mouthing prior to sexual activity (Dudzinski 1998; Herman and Forestell 1977; Herman and Tavalga 1980; Norris et al. 1977; Sayaman and Tayler 1973), simple contact, or rubbing or petting while swimming in pairs (Dudzinski 1998; Sakai et al. 2003). Physical contact may also be aggressive and occur when animals attempt to establish or maintain dominance, protect their young, defend resources, or procure sexual partners. Aggressive tactile behaviors include biting, hitting, tooth-raking, and ramming (Brown and Norris 1956; Norris 1967; Östman 1990; Slooten 1994). Such behaviors are often coupled with non-vocal auditory

signals such as jaw claps or tail slaps in agonistic encounters (Mann and Smuts 1999; Östman 1990). Touch clearly serves a variety of communicative and non-communicative functions.

Communication itself is multifaceted (Kuczaj and Kirkpatrick 1993), but one measure of successful communication concerns behavioral changes that it produces (Krebs and Davies 1993). The purpose of this study was to examine the non-vocal communicative behaviors observed during interactions between individuals from two dolphin species: Indo-Pacific bottlenose dolphins around Mikura Island, Japan, and Bahamas' Atlantic spotted dolphins. We investigated behavioral sequences that occurred in specific social contexts, with particular attention to the effects of age and species on identified behavioral associations.

Methods

A subset of underwater video recordings of two dolphin groups, collected in Japan and in the Bahamas during two ongoing longitudinal studies from 1992 to the present, was examined for the study described herein (see Dudzinski 1996, 1998; Kogi et al. 2004 for details on longitudinal studies).

Study groups

The Atlantic spotted dolphins group is a wild population found along the White Sand Ridge of the Little Bahamas Bank, which is ~64.5 km north of West End, Grand Bahamas Island. This area ranges from 6 to 10 m in depth with a white sandy bottom and generally good visibility to at least 30 m. The data used in this study were collected in 1993 and 1994 and were from a longitudinal study on dolphin communication (see Dudzinski 1996, 1998). During the identified subset of data examined, the identified population consisted of approximately 125 individuals with an overall equal male-to-female ratio (Dudzinski 1996). For this study, 22 dolphins were identified in scored video clips from 1993 data (8 males, 14 females) and 21 dolphins from the 1994 data (6 males, 15 females).

The Indo-Pacific bottlenose dolphin group is a population resident to the area within 300 m of Mikura Island, Japan (Kogi et al. 2004). Water depth at this location varied from 4 to 20 m. The seafloor was rocky and visibility was poor (generally less than 15 m) in comparison to the Bahamas. The identified population consisted of approximately 165 dolphins with an overall equal sex ratio (Kogi et al. 2004). For this study, 16 dolphins were identified in scored video clips from 1997 data (7 males, 9 females), 17 individuals from 1998 data (6 males, 11 females), and 72 dolphins from 2002 (38 males, 34 females).

Video recordings

The data were collected using focal animal and all-occurrence sampling (Altmann 1974; Mann 1999). The subset includes data collected during 4-month summer field seasons in 1993 and 1994 in the Bahamas (see Dudzinski 1996, 1998), and during similar length field seasons in 1997, 1998, and 2002 in Japan. The decision to use these data was based on the availability of information regarding confirmed identification of focal dolphins. Restricting analysis to identified dolphins reduced overestimation of a particular behavior in a group because of repeated production by a single individual. However, it also limited group size because of the difficulty inherent in identifying individual dolphins when more than four animals were recorded. Video segments in which the number of dolphins in view affected the ability to accurately identify and follow specific individuals, were eliminated. As a result, analyses were generally restricted to groups in which fewer than four dolphins were in view, which may have influenced the types of interactions that were observed. However, the decision to restrict analyses to videos in which it was possible to identify focal animal(s) resulted in a much clearer picture of the social interactions among focal animals.

The broad behavioral context (bbc) of the dolphins being recorded was determined at the time of data collection based on the activity of the majority of the dolphins present from within the group being videotaped. The bbc is not a specific behavior, but a general classification of group activity. Five broad behavioral contexts were considered: general social, foraging, play, travel and inquisitive (see Dudzinski 1996, 1998, with general social here equating to "social" in Dudzinski).

The number and gender of dolphins identified at each study site and the proportion of dolphins represented by each age class were also noted.

Behaviors studied

Video recordings were analyzed in an attempt to determine if behaviors were occurring in a particular sequence or if certain behaviors were likely to elicit specific responses from other dolphins. Behaviors that were consistently associated with a particular broad behavioral context and that elicited similar responses when they occurred were viewed as possible communicative exchanges (see Goodall 1986; Struhsaker 1967; Tschudin et al. 2001, for more detailed considerations of this notion).

To reduce the potential ambiguity involved in determining the beginning or ending of a potential behavior chain, specific behaviors were chosen to be "focal events." In this study, the focal events are italicized to

avoid confusion with other behaviors. These focal events were: *depart* (one or more dolphins depart company of others), *join* (two or more dolphins come together), and *contact* (dolphin makes contact with another using any part of its body); they marked the beginning (in the case of *join* or *contact*) or the end (in the case of *depart* or *contact*) of a chain of behaviors. More specifically, *join* could only mark the beginning of a sequence because one or more of the dolphins was not present prior to their joining. *Depart* could only represent the end of a chain due to the absence of a dolphin after departing. *Contact*, however, could occur at any point two or more dolphins are together so could be used to mark the beginning or the end of a chain of behaviors. Furthermore, the *depart* and *join* focal events are each comprised of the singular behavior after which they are named. However, the *contact* focal event is actually an aggregate and is comprised of several touch behaviors (Table 1).

These three particular focal events were chosen because they involve interactions between dolphins and so provide an opportunity to examine possible precursors or antecedents to specific social behaviors. Although *depart*, *join*, or *contact* do not represent the entire repertoire of potentially communicative actions, they do mark a change in the dynamics of the social environment at a given time and provide an observable point at which to mark the beginning or end of a potentially communicative exchange between dolphins. Although this method does not completely eliminate ambiguity, the use of focal events helps to determine where a communicative sequence may start or end by focusing on specific events likely to elicit signal exchange between interacting dolphins.

Statistical analyses

Segments of continuous video of identified focal dolphins were scored using an observational data computer program

Table 1 List of behaviors that each focal event is comprised of (adapted from Dudzinski 1996)

<i>Depart</i>	<i>Join</i>	<i>Contact</i>
Depart	Join	Touch dorsal back
		Touch fluke
		Touch lateral
		Touch melon
		Touch mouth
		Touch pectoral fin
		Touch peduncle
		Touch rostrum
		Touch ventral surface
		Reciprocal nuzzle

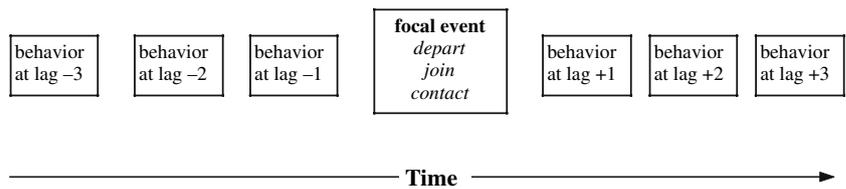
(The Observer[®] v5.0). After being scored with Observer[®], the data were tabulated and exported for further statistical analyses, including the calculation of conditional probabilities. The Z-score binomial test was used to determine if there was a significant association between focal events and other identified behaviors (Bakeman and Gottman 1986). As the total number of paired transitions (N) increases, the binomial distribution approximates the normal distribution with $p < 0.05$. However, the problem of type 1 error occurs when performing sequential analyses, especially as the number of behavioral codes and pair-wise comparisons increases (Bakeman and Gottman 1986). Given the large number of pair-wise comparisons in this study, a smaller p value ($p < 0.001$) for determination of significance of conditional probabilities was chosen to reduce the possibility of a type 1 error. Where Z tests for proportions were conducted, the standard p value of 0.05 was used.

State-lag analyses were performed and were based on event sequences (Bakeman and Gottman 1986) rather than event duration. State-lag analyses rather than time-lag analyses were chosen because the coding scheme employed included both state- and event-type behaviors. The use of a time-lag analysis (which considers all behaviors that occur within a specific time) might be misleading as it may overestimate the importance of state behaviors at the expense of the shorter (but critical) event behaviors. In contrast, state-lag analyses consider all behaviors occurring within a designated number of behaviors (state or event) before and after the event of interest.

Transitions at lags (positions) -1 , -2 , and -3 or $+1$, $+2$, and $+3$ (depending upon the focal event) were calculated and transformed into Z-scores using a macro written for Excel. These Z-scores were examined for significance at the $p < 0.001$ level. This analysis provided information regarding which behaviors occurred significantly more often than would be expected by chance at positions one, two, and three behaviors prior to or after a focal event (Fig. 1, for other studies using sequence analysis see Nowacek 2002; Slooten 1994).

Behaviors at lags one, two, and three behaviors prior to the focal event *depart* were identified (lags -1 , -2 , and -3); therefore, this part of the analysis proceeded in a “backwards” fashion from this focal event. Behaviors after *depart* were not examined because of the absence of one or more of the dolphins. For the focal event *join*, behaviors at positive lags one, two, and three were examined. In most cases, the dolphins that joined were not both visible on the video prior to the act of coming together, thereby preventing coding of their behavior preceding their joining. Significant behaviors may have occurred prior to the joining of animals, but because of the unavailability of data during this pre-join period, we could not include this

Fig. 1 A visual description of where in time behaviors at lags 1, 2, and 3 before and after a focal event occur



information in our analyses. The analysis of the focal event *contact* included examination of both negative (-1, -2, and -3) and positive (+1, +2 and +3) lag behaviors. Behaviors leading up to as well as behaviors occurring after a *contact* focal event might assist in determining whether the contact behavior itself has a communicative effect. A change in behavior is an indication that communication may have occurred; therefore, significantly occurring behaviors that are produced prior to the contact might in some way be eliciting the contact. Similarly, behaviors that are produced after the focal event *contact* might be a result of the contact occurring. [Note: The focal event *contact* is an aggregation of all touch behaviors, which were grouped because they were varied in number and scope (Table 1).]

Inter-observer reliability

To assess inter-observer reliability, video segments were divided into four groups based on length in seconds. Interrater reliability was determined using Cohen’s kappa (Cohen 1960). From each video segment group, a second observer scored 10% of the video clips; the overall value of kappa was found to be 0.89, indicating a high degree of agreement between observers (Fleiss 1981).

Results

The data were parsed into video clips called ‘observations’ for ease of scoring and digital storage. A total of 18,070 s of video data was used: overall, observations ranged in length from 3.3 to 813.2 s (overall mean = 92.7 s and median = 53.1 s; bottlenose dolphins: 3.3 to 402.3 s, mean = 64.3 s, and median = 41.2 s; spotted dolphins: 11.5 to 813.2 s, mean = 185.6 s, and median = 101.9 s). The variation in observation length was a result of dolphins being in view of the camera lens (and hence on tape) for unpredictable and varied duration(s).

A total of eight behaviors from Dudzinski (1996) were found to have occurred significantly more often than chance ($p < 0.001$) either prior to *depart* (lags -1, -2, and -3), after *join* (lags +1, +2, or +3) or before or after *contact* (lags -1, -2, -3, +1, +2, or +3) (Table 2 for the behavior list). (Remember that the focal event *contact* is an aggregate and is defined as any touch between dolphins.)

The number of dolphins identified at each study site and the proportion of dolphins represented by each age class were noted. All age classes except calves were represented in each year. The proportion of dolphins in each age class varied between sites (Table 3). The number of focal events (*depart*, *join*, or *contact*) also varied by species (Table 4).

Depart: Several touch behaviors were found to be significantly associated with *depart* in both spotted and bottlenose dolphins. In the spotted dolphins the four significant touch behaviors were: touch with lateral ($Z = 3.76$; $p < 0.001$), touch with melon ($Z = 7.58$; $p < 0.001$), touch with pectoral fin ($Z = 4.37$; $p < 0.001$), and touch with rostrum ($Z = 5.13$; $p < 0.001$). In the bottlenose dolphins, there were two significantly associated touch behaviors: touch with melon ($Z = 7.56$; $p < 0.001$) and touch with pectoral fin ($Z = 4.92$; $p < 0.001$). Because significant associations between *depart* and touch behaviors were observed within species in both dolphin groups, we examined the associations between the initiation of the touch behaviors and departures (see Fig. 2). In 4 of 14

Table 2 List of touch behaviors identified as occurring significantly more often than chance ($p < 0.001$) at lags -1, -2, -3, +1, +2, or +3 around the focal events *depart*, *join*, or *contact* (adapted from Dudzinski 1996)

Behavior name	Description
Touch fluke	Contact with another using its fluke
Touch lateral	Contact with another using the lateral portion of its body
Touch melon	Contact with another using the melon
Touch mouth	Contact with another using its mouth
Touch pectoral fin	Contact with another using its pectoral fin
Touch rostrum	Contact with another using its rostrum
Touch ventral surface	Contact with another using its ventral surface
Reciprocal nuzzle	Dolphins rubbing rostrums against each others’ bodies

Table 3 Proportion of dolphins in each age class by year for each species with the total number of dolphins identified per species in parentheses

	Adult	Sub-adult	Juvenile	Calf
Atlantic spotted (43)	0.35	0.09	0.47	0.09
Indo-Pacific bottlenose (105)	0.39	0.51	0.09	0.01

Table 4 Number of focal events for Atlantic spotted dolphins in the Bahamas and Indo-Pacific bottlenose dolphins around Mikura Island, Japan, by broad behavioral context

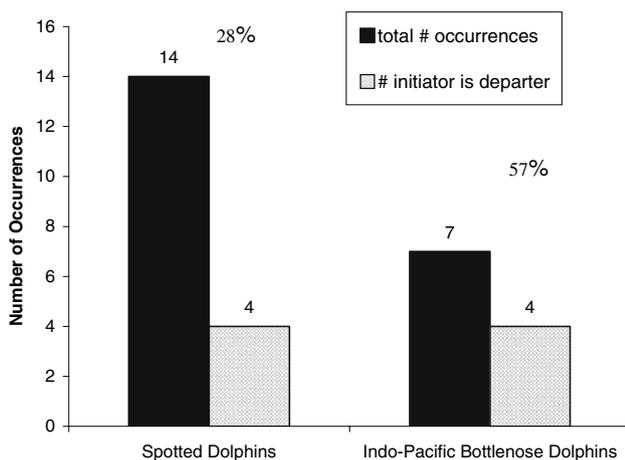
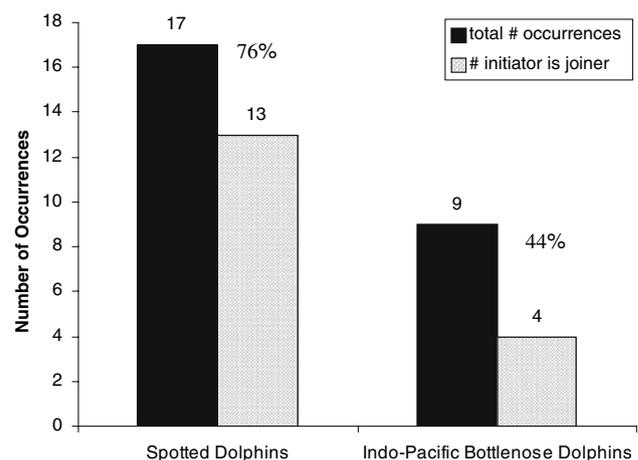
	General social	Travel	Forage	Play	Inquisitive	Totals
Atlantic spotted dolphins						
Contact	43	15	1	29	1	89
Join	25	16	7	19	4	71
Depart	17	11	2	18	5	53
Totals	85	42	10	66	10	213
Indo-Pacific bottlenose dolphins						
Contact	24	7	5	12	8	56
Join	9	8	2	17	8	44
Depart	6	5	1	6	11	29
Totals	39	20	8	35	27	129

instances (28.6%) of touch occurring prior to departure for spotted dolphins, the initiator (3 females, 1 male) was also the departing individual. For bottlenose dolphins, the initiating dolphin (2 females, 1 male, 1 dolphin of undetermined sex) was the departer during four of seven cases (57.1%). There were no significant species differences (spotted vs. bottlenose dolphins) in this regard. Nonetheless, touch behaviors were related to subsequent departures. The difference between this study's spotted and bottlenose dolphin groups' use of this behavioral combination (touch–depart) was not significant ($Z = 1.27$; $p > 0.05$). For spotted dolphins, 26.4% of all *depart* events were preceded (within three lags) by a touch behavior. For bottlenose dolphins, 24.1% of all *depart* events were preceded by a touch behavior.

Join: Certain touch behaviors were significantly associated with *join* in both species. Four touch behaviors were

exhibited routinely by spotted dolphins after a joining of individuals occurred: touch with fluke ($Z = 5.03$; $p < 0.001$), touch with melon ($Z = 5.73$; $p < 0.001$), touch with pectoral fin ($Z = 4.17$; $p < 0.001$), and touch with rostrum ($Z = 4.08$; $p < 0.001$). In bottlenose dolphins, only two touch behaviors (the same behaviors significantly associated with *depart*) were significantly associated with *join*: touch with melon ($Z = 4.07$; $p < 0.001$) and touch with pectoral fin ($Z = 4.32$; $p < 0.001$). Because significant associations between *join* and touch were observed in both dolphin groups, these associations were examined in further detail. For example, was the *joiner* also the initiator of physical contact? In 13 of 17 observations (76.5%) of touch following *join* in spotted dolphins, the touch-initiator (11 females, 6 males) was also the joiner. In four of nine instances (44.4%) of touch following *join* in bottlenose dolphins, the touch-initiator (3 females, 1 male) was also the dolphin that joined another (Fig. 3). The difference in use of this behavioral combination between species was not statistically significant ($Z = 1.82$; $p > 0.05$). In spotted dolphins, 23.9% of all *joins* were followed (within three lags) by a touch behavior. In bottlenose dolphins, 20.5% of all *joins* were followed by a touch behavior.

When comparing species' use of touch after *join* on a context-by-context basis, only the forage context resulted in a significant difference between species (Fig. 4) ($Z = -1.98$; $p < 0.05$). No significant differences were found in the other four contexts: inquisitive ($Z = 0.140$; $p > 0.05$), general social ($Z = 0.942$; $p > 0.05$), play ($Z = -0.586$; $p > 0.05$), and travel ($Z = 1.0$; $p > 0.05$). No significant difference was found between species' use of touch after *join* when all behavioral contexts were pooled ($Z = 0.435$; $p > 0.05$).

**Fig. 2** Number of total occurrences of a touch behavior occurring prior to a dolphin departing and the number of occurrences in which the dolphin is both the initiator of touch and the 'departer' for both study species**Fig. 3** Number of total occurrences of a touch behavior occurring after dolphins join and the number of occurrences in which the dolphin is both the initiator of touch and the 'joiner' for both study species

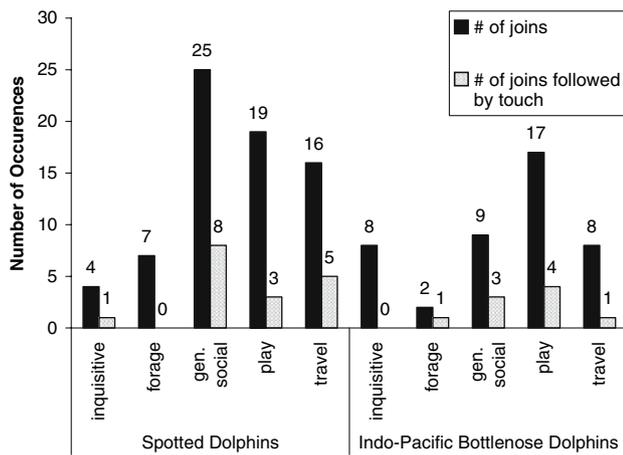


Fig. 4 Total number of *join* events by broad behavioral context and the number of times that touch followed those *join* events for both study species

In comparing *depart* and *join* within species, it was determined that spotted dolphins were more likely to touch another individual after joining (76.5%) than before departing (28.6%) ($Z = 2.58$; $p < 0.01$), whereas the Indo-Pacific bottlenose dolphins were equally likely to touch another after joining as before departing (44.4 vs. 57.1%) ($Z = 0.504$; $p > 0.05$).

Contact: In both dolphin study groups, touch behaviors were significantly associated with the focal event *contact*: i.e., touch behaviors followed one another. For example, a pectoral fin rub by one dolphin might elicit a pectoral fin rub from another dolphin. In spotted dolphins, behaviors significantly associated with *contact* included touch with the lateral surface, the melon, mouth, pectoral fin, ventral surface, and rostrum (observed in 4 females, 3 males). Bottlenose dolphins exhibited less variety of touch behaviors around this focal event with only touch with the melon or pectoral fin emerging as significantly associated (Table 5) (observed in one female, two males, and one dolphin of undetermined sex).

If touch truly is a solicitation of further contact (for whatever purpose), it should be reciprocated in a successful conveyance of the signal (assumes the dolphin solicited is willing to reciprocate). To address this issue, the data were analyzed to determine how often touch was reciprocated. In spotted dolphins, there were seven cases of reciprocated touch with seven different animals participating (one adult, one sub-adult, five juveniles). All of these cases occurred in general social or play contexts. For bottlenose dolphins, there were only three cases of reciprocation with four different dolphins participating (three sub-adults, one calf). These cases also all occurred in general social or play contexts. Reciprocation of touch behavior occurs similarly in both study groups ($Z = 0.8819$; $p > 0.05$) and represents

Table 5 List of touch behaviors significantly associated within three lags prior (before focal event *contact*) or within three lags after another touch behavior

Before <i>contact</i>		After <i>contact</i>	
Behavior	Z	Behavior	Z
Atlantic spotted dolphins			
Touch lateral	6.09	Touch lateral	3.54
Touch melon	10.64	Touch melon	3.70
Touch mouth	8.97	Touch pec fin	6.13
Touch rostrum	4.31	Touch rostrum	4.50
Reciprocal nuzzle	6.48	Touch ventral	13.29
		Reciprocal nuzzle	5.72
Indo-Pacific bottlenose dolphins			
Touch melon	3.90	Touch melon	3.88
Touch pec fin	5.37	Touch pec fin	5.33

Z scores are given; all p values are < 0.001 . (Reminder: the focal event *contact* is defined as any touch between dolphins)

31.3% of all interaction events in the general social context from spotted dolphins and 16.7% for bottlenose dolphins. The two study species also exhibit similar reciprocation patterns in the play context ($Z = 0.3042$; $p > 0.05$) with 20.0% of all interaction events during play for spotted dolphins representing reciprocal touch and 14.3% for bottlenose dolphins.

Discussion

Every perceivable behavior that an organism exhibits can convey information to conspecifics intentionally or unintentionally. This descriptive study revealed a variety of behaviors that were significantly associated with situations that might precipitate the conveyance of information. These situations included the *departing* or *joining* of dolphins, as well as *contact* between dolphins. The decision to more closely examine certain behaviors that were significantly associated with these focal events was based on previous research into possible functions of touch between dolphins (Dudzinski 1996, 1998; Saayman and Tayler 1972; Sakai et al. 2003) and on the occurrence of certain behaviors across both study species, different age classes, and different broad behavioral contexts (Dudzinski 1996, 1998; Herzing 1997).

Depart: In both the Atlantic spotted and Indo-Pacific bottlenose dolphins studied, touch behaviors were significantly associated with the focal event *depart*. Four touch behaviors in spotted dolphins were evidenced in three of the five broad behavioral contexts (forage, travel and play). In the bottlenose dolphins, only two touch behaviors were significantly associated with *depart* and were observed in

three of the five potential broad behavioral contexts (general social, inquisitive, and play). Both species exhibited this behavioral association between *depart* and touch in the play context. The incidence of touch occurring prior to the departure of a dolphin in these contexts could be a signal that the dolphin is about to depart. This was examined by determining how many times the dolphin that departed was also the same one that initiated the touch. In spotted dolphins, 28.6% (4 out of 14) of the cases involving touch before departure also involved the same dolphin initiating both behaviors. In the bottlenose dolphins, 57.1% (four of seven) of the cases were represented by a dolphin playing both touch initiator and departer roles. Even though slightly above chance, it may be more important for bottlenose dolphins around Mikura Island to use touch to confirm attention from a peer that it is about to depart because water visibility may deter them from maintaining visual contact after departure. In contrast, underwater visibility in the Bahamas is better (for both distance and particulate matter) than around Mikura, thus providing greater opportunity for prolonged visual contact after departure among spotted dolphins. That is, Bahamas' spotted dolphins may be better able to use a visual signal to coordinate activity post departure. However, given the small sample size of this study, further research into this possibility is warranted. Furthermore, vocal signals were not analyzed in this study so their role cannot be assessed.

Age specificity for touch prior to *depart* was not detected: in spotted dolphins, two adults, one sub-adult, and one juvenile were the initiators, while among bottlenose dolphins the initiators were one adult, two sub-adults, and one juvenile. With so few cases, however, it is difficult to determine with certainty if age plays a factor in tactile contact with a peer before departing. Although no significant difference between these species' use of touch before departing was found during this study, the small sample size may again be a factor. Future studies should aim to increase the sample size to determine if a different picture exists for these two species in diverse habitats.

Join: For both the Atlantic spotted and Indo-Pacific bottlenose dolphins studied, a variety of touch behaviors were significantly associated with the focal event *join*. The occurrence of touch after dolphins joined was further examined for its role as a signal in potentially communicative exchanges. This was accomplished by determining how many times the dolphin that joined was also the individual that initiated a touch. In spotted dolphins, in 76.5% of the instances of touch that occurred after dolphins joined, the dolphin that joined was also the initiator of the touch. Age classes of spotted dolphin initiators engaged in *join* and followed by touch varied (four adults, one sub-adult, four juveniles, one calf), but directly mirrored the demographics of the population for the two years repre-

sented in this study [12 adults, three sub-adults, 12 juveniles, three calves (Dudzinski 1996)]. Therefore, equal distribution of this behavioral association (*join* followed by touch) across spotted dolphin age classes resulted. For Indo-Pacific bottlenose dolphins, in 44.4% of the cases of *join*-touch, the dolphin that joined was also the one that initiated the touch. In all cases ($n = 4$), the dolphin pairs were comprised of two sub-adults (four different sub-adults). It would seem that both species use the *join*-touch behavioral combination in a similar manner; however, again, the small sample size makes a definite determination impossible.

The high percentage of occurrence of *join*-touch (76.47%) coupled with the potential uniform distribution across age classes among spotted dolphins suggests that a touch behavior after joining may be a regular part of the signal repertoire of these spotted dolphins. The response of the receiver, however, is neither consistent enough to consider it a stimulus-response chain, nor is the sample size of this study large enough to make conclusive claims. Touch after joining has been documented in other delphinid species [e.g., bottlenose dolphins, Saayman and Tayler 1972; Würsig and Würsig 1979; and killer whales (*Orcinus orca*) Jacobsen 1986], and it may function as a form of greeting, especially when involving the pectoral fin (Dudzinski 1998; Sakai et al. 2003).

Contact: For both species, an analysis of behaviors occurring up to three lags before or three lags after *contact* between dolphins revealed significant associations between this focal event and a variety of touch behaviors (i.e., touch was preceded or followed by another touch behavior). Touch from one dolphin to another may have several communicative functions: It may function as the solicitation of reciprocated touch for grooming or in the establishment, maintenance, or advertisement of social bonds (Kaplan 2005; Norris et al. 1994; Östman 1990; Pryor 1990). The part of the body touched could also contribute to the signal's meaning (Sakai et al. 2003).

Touch as a potential solicitation of reciprocated touch was examined in further detail and revealed that the two study species did not differ in their use of reciprocal touch (as measured by the percentage of all interaction events that included touch in which reciprocated touch occurred). These results do not strongly support the hypothesis that touch may possess a communicative function solely as a solicitor of reciprocated touch. The literature on cetacean tactile contact suggests that dolphins use this type of signal as a means to maintain social bonds, as well as in other situations such as aggression, courtship, or sex (Caldwell and Caldwell 1977; Connor and Smolker 1996; Dudzinski 1998; Evans and Bastian 1969; Herzing 1996; Pryor 1986; Sakai et al. 2003). Still, these situations do not always require a behavioral response from the receiver and hence

make determining communicative function for the observer more difficult. Furthermore, other factors (e.g., context, associates, and internal motivators) should be weighed when considering potential signal meaning; for example, the willingness of a touch receiver to reciprocate should be considered, if not measured. It is possible that touch was used as a communicative signal, but that the signal receiver chose to ignore it (or the human observer was unable to perceive it). Moreover, this analysis looked only at the six (three negative and three positive) lags surrounding *contact*. Reciprocation of touch might not have occurred immediately, but possibly later in the behavioral chain of events.

Another factor to be considered is that dolphins frequently move in and out of the camera's view. Reciprocation of touch could have occurred outside of the observer's field of view. Indeed, these factors should be considered limitations to this descriptive study. Despite the overall paucity of support for touch as a request for reciprocal behavior arising from this study, the consistency of occurrence in the more social of the behavioral contexts suggests that it may serve some function in dolphin sociality.

Both study species engaged in reciprocated touch behaviors during general social and play contexts. Although these two contexts contained the majority of *contact* events for both species, general social and play also include more socialization compared with forage, inquisitive, and travel. During foraging, the focus is on procuring food. Travel features movement from one area to another. Within the inquisitive context, the dolphins' attention is turned away from each other and is on something else in their environment (i.e., humans). This suggests that touch exchanges and socialization are associated with each other, supporting the hypothesis that touch could be a solicitation for something (here reciprocated touch) from the signal receiver.

Although touch behaviors were significantly associated with all three focal events in both species, the spotted dolphins in this study used a wider variety of touch behaviors. This was consistently seen when touch occurred prior to a dolphin departing, after dolphins joined, and when touch occurred after another touch behavior. Perhaps for these spotted dolphins, touch serves a more communicative function than for the dolphins around Mikura. The Bahamas' study area is surrounded by an expansive, sandy seafloor environment with exceptional underwater visibility (~30 m on average). Thus, spotted dolphins live in a habitat that likely facilitates the use of a more visual mode of communication with touch secondary and acoustic signals tertiary in the priority of information exchange systems. Conversely, while the setting around Mikura Island is characterized by similar water depth to that of the

Bahamas, it is represented by drastically different environmental conditions: boulders of varying size cover the seafloor and comparatively mediocre underwater visibility averages 10–12 m on a good day. This suggests that these Indo-Pacific bottlenose dolphins live in an environment where an acoustic (i.e., vocal) communicative repertoire may be more beneficial than visual or tactile signals because of reduced underwater visibility.

In summary, the study of non-human (and human) animal communication is difficult. We cannot know for certain what the internal affective state of the non-verbal animal is, be it human infant or non-human animal. We cannot absolutely attribute motivation, nor infer intentionality; however, we can look at behavior from an external viewpoint and attempt to ascribe behavioral changes as potential signals for sharing information. This descriptive study provided information on what behaviors were significantly associated with specific, potentially communicative situations and could serve as the basis for further study.

Overall, touch behaviors were significantly associated with *joining* and *departing* for both the Atlantic spotted and Indo-Pacific bottlenose dolphins. The spotted dolphins, however, were more likely to use touch after *joining* than before *departing*, whereas the bottlenose dolphins were equally likely to use touch in both situations. This could indicate that overall, touch is involved throughout their behavioral repertoire and does not necessarily play a more important role in *departing* than in *joining*. Touch may not have a specific communicative function such as a greeting behavior, but may function more in establishing and maintaining social bonds throughout the population, as for some terrestrial species (e.g., Moehlman 1987; Seyfarth 1980; Seyfarth and Cheney 1984). For example, long-tailed macaques (*Macaca fascicularis*) are more likely to provide support to another who has recently groomed it than to one who has not (Hemelrijk 1994). Therefore, who initiates the touch may not *always* be important. One caution to this interpretation is reflected in the methodological elimination of large groups of dolphins from this dataset, which may have contributed to the decreased occurrence of touch after *joining* seen among the Indo-Pacific bottlenose dolphins. Nonetheless, the data from these Indo-Pacific bottlenose dolphins and the Atlantic spotted dolphins indicate more similarities than differences between these species in their use of specific behaviors in potentially communicative situations.

In contrast, individual spotted dolphins were more likely to use touch after *joining* than before *departing* and made use of a wider variety of touch behaviors than did the studied bottlenose dolphins. The wider variety of touch behaviors exhibited by the spotted dolphins may be an indication that physical contact serves a more communicative function in

this group of animals as compared with the bottlenose dolphins around Mikura Island. The Bahamas' environment (good visibility) likely facilitates a communicative repertoire that emphasizes visual and tactile signals. The Indo-Pacific bottlenose study group produces three times as many vocal sounds as compared with the Atlantic spotted dolphin study group (Dudzinski, unpublished data 1992–2004). Therefore, these bottlenose dolphins may rely more on an auditory-based signal system because of reduced underwater visibility as well as other environmental factors.

The ultimate goal of this project was to increase our understanding of non-vocal communication in the social lives of dolphins by examining communicative behaviors across age classes and between two species. By documenting and describing the behaviors exhibited in specific situations identified as likely to elicit some communicative exchange, we were able to provide a foundation for future research into the communication systems of these species. Although this study was limited by a small sample size, continued research into this subject area with these and other species (both in human care and in the wild) may provide information about the importance of environmental versus genetic influences on the use and development of signals appropriate for the exchange of information between individuals and groups.

Acknowledgments Financial support for data collection during DCP's longitudinal studies of the Bahamas Atlantic spotted dolphins as well as 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 and M University at Galveston (TAMUG), Marine Mammal Research Program at TAMUG, the National Geographic Society (grant #4851–92), the Japanese Society for the Promotion of Science, Casio's Eco-Research Fund, and a Kaken-Hi grant from the Japanese government. All data were collected during ecotour-format boat trips that were partially sponsored by Oceanic Society Expeditions (in the Bahamas), the Miyake Fishermen's Cooperative (from Miyake Island), and the Mikura Iruka Kyoukai (at Mikura). More than a dozen boats and boat captains supported data collection, and they are collectively thanked here. Thanks also to Andrew Wright and Peter Sugarman for their programming assistance. This work was conducted in partial fulfillment of Paulos' Master's Degree thesis. This paper represents contribution 154 of the Sea Research Foundation.

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