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Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*)

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Abstract

Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas use a variety of signals (contact behaviors, vocalizations, and postures) to exchange information. Affiliative contact was observed more often than other physical contact. Seven specific contact behaviors were most often observed: rubbing (17.6%), simple contact (13%), petting (12.4%), petting/rubbing (8.5%), contact position (7.3%), melon-to-genital contact (5.8%), and sand rubbing (28.3%). Each of these specific contacts varied according to dolphin age, sex, behavioral activity, and group type. Contact among individuals may be modified by posture, behavior, and internal and external referents: posturing by dolphins appeared to function specifically to indicate intent or message meaning in differing contexts. Age and sex differences were documented as related to initiator and receiver roles assumed by the dolphins. For example, dolphins more often exchanged rubs or pets with individuals of the same sex and age class. Physical contact and vocal type varied significantly, but at differing levels, with behavioral activity, group type and age. Tactile and vocal signals could be used concurrently, to maximize or enhance a message, or could be used separately, but with similar functions.

Introduction

An aquatic lifestyle has resulted in the evolution of unique adaptations for signal exchange (communication) among dolphins. Signals may be expressed via physical, acoustic, or visual contact. Signals may be used singly or concurrently depending on the intended message.

The literature is replete with information concerning physical contact—extensive touching—among dolphins (Pryor, 1990; Norris *et al.*, 1994; Östman, 1994). Visual cues may be simple, passive displays of posture, coloration patterns or orientation within the water column, or they may be sequences of behaviors that indicate movement, species, reproductive condition, and more (Herman & Tavolga, 1980; Würsig *et al.*, 1990). Dolphins use both vocal and non-vocal auditory cues. Examples of non-vocal cues include jaw claps, tail slaps, breaches, and leaps (Shane, 1990; Norris *et al.*, 1994). Vocal signals fall into a broad dichotomy of pulsed and non-pulsed sounds (Herman & Tavolga, 1980; Au, 1993). Pulsed sounds include echolocation clicks, squawks, whines and other burst-pulsed sounds. Non-pulsed sounds are frequency-modulated pure-tonal vocalizations and include whistles and chirps.

Assigning particular vocalizations to specific individual dolphins in the wild is difficult at best. For this reason, a wealth of data has been gathered on dolphin vocal behavior as related to general behavioral activity (Weilgart & Whitehead, 1990; Norris *et al.*, 1994). While data gathered on vocalization rates and occurrences is valuable information, it does not yield an examination of communication by the strictest definition. Studies of animal communication require the ability to identify involved individuals as well as the signals used. It is especially important to identify the signal sender and receiver when examining the intricacies of subtle exchanges between social animals.

Until recently, however, cetacean researchers were not able to identify individual vocalizing dolphins within free-ranging groups. Researchers were also limited by water clarity and lack of dolphin habituation to human swimmers in their ability to collect detailed observations of dolphin behavior underwater. Recent technology, coupling video and sound recording devices, has facilitated the collection of in-depth observations of dolphin behavior and vocalizations while underwater (Dudzinski *et al.*, 1995).

The Bahamas' Atlantic spotted dolphins (*Stenella frontalis*) represent a unique research opportunity for the study of dolphin communication.

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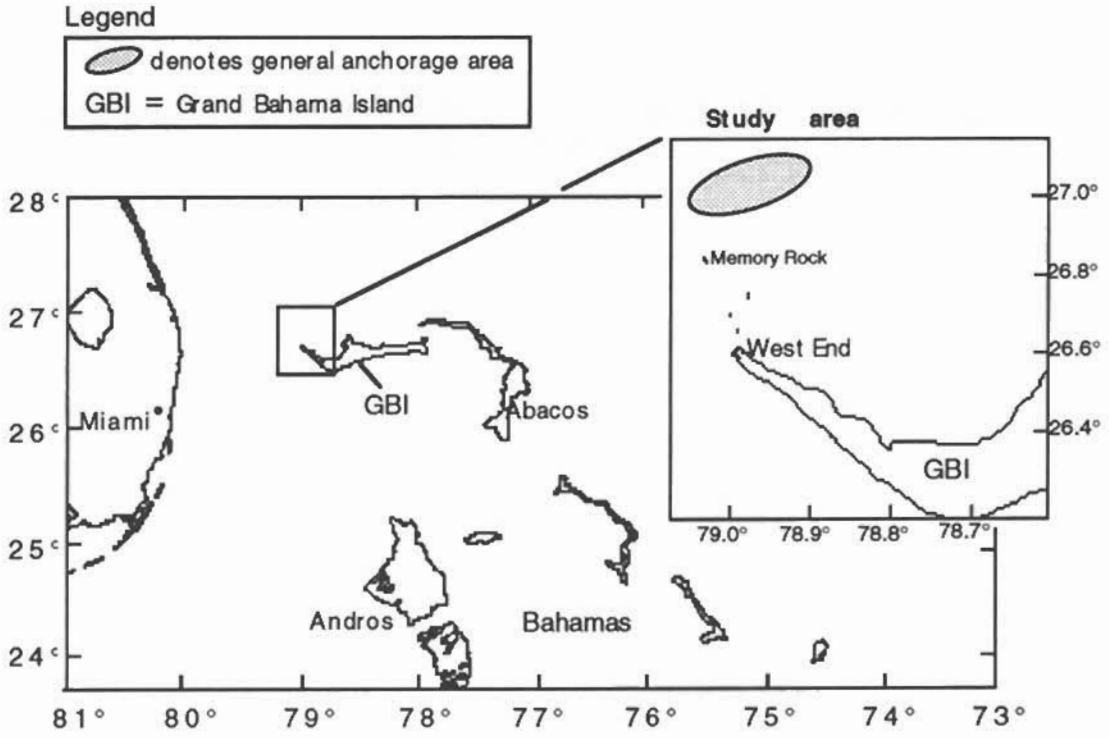

Figure 1. Map of the study area on the Little Bahamas Bank, and geographic location of the study area with regards to the east coast of Florida.

Individuals of this group have swum with skin divers since the late 1970s and are habituated to the presence of people and boats. The waters of the Bahamas are clear and warm with visibility often more than 30 m. Combined, these factors facilitate lengthy underwater observations of dolphin social behavior and interactions with associates. The aim of this paper is to examine, evaluate, and describe signals that are used by spotted dolphins and how signal exchange varies given dolphin age, sex, group type, and behavioral activity.

Methods

Study site

The Little Bahamas Bank is a sandbar, roughly 45 km^2, approximately 64.5 km north of West End, Grand Bahama Island, Bahamas (Fig. 1). Depths (at mean high tide) range from 3–10 m, with an average depth of 6 m. From May to September, 1992 to 1995, four to five consecutive days each year were spent at anchor, weather-permitting, while observing and documenting dolphin behavior and vocalizations.

Dolphin population

Visual inspection of the genital area was used to identify a dolphin's sex. Females have one external urogenital opening, while males have a genital slit and a shorter, posterior anal opening. The study population consists of at least 95 recognizable individuals, with an approximately 1:1 sex ratio (Dudzinski, 1996; Herzing, 1997). Spotted dolphins are categorized into five relatively distinct age classes (also known as spot classes) denoted by amount of body pigmentation (Table 1, Perrin, 1970; Herzing, 1997). Neonates (class 1) were sighted rarely and thus were not included in analysis of signals and signal exchange. An adult female and calf were identified as a mother/calf dyad if the adult was identified as female and was seen with the calf alone; the dyad was observed frequently swimming in echelon when in the company of other adults; or the calf was observed to nurse from the same female.

Individual spotted dolphins were observed within five different group types: adult female(s) with juveniles (AFjuv), all juveniles, mixed sex and aged groups (mixed), same sex and aged groups (same), and mother/calf groups (Mc).

Table 1. Color pattern changes with age and spot class designations in Atlantic spotted dolphins

Spot class	Age group[a]	Coloration	Pattern type
1	Neonate 1<3wks	Gray and ivory	Neonatal
2	Calf 3 wks<4yrs	Dark gray dorsal, light gray ventral	Two-tone
3	Juvenile 4<7yrs	Dark dorsal, light ventral, few spots	Speckled
4	Subadult 7<10yrs	Entire body spotted	Mottled
5	Large adult 10^{+} yrs	Black mask, heavily spotted, spots fused and faded ventrally	Fused

[a]Age estimates are based on Perrin (1970) and Herzing (1997). Age categories are probably not mutually exclusive at the range ends.

Data collection

Hi-8 video (Sony CCD-FX710 stereo camera) and 35-mm still-photography (Nikonos IV and V with 20 mm lens) were used to document underwater spotted dolphin behaviors. Encounters (defined as a swim with dolphin(s) in visual range underwater for 3 min or more) were documented with video opportunistically with limiting factors including poor weather, sea, and visibility conditions. Use of a mobile video/acoustic array facilitated identification of selected individual spotted dolphins, their behaviors, and vocalizations (Dudzinski *et al.*, 1995). Real-time observations were recorded to classify the behavioral activity of swim encounters, and to supplement and clarify video data.

Behavioral data was collected using focal animal and all-occurrence sampling (Altmann, 1974). Identified individuals were opportunistically observed, based upon which dolphins approached the vessel. All videotaped dolphins were included in analysis of variation of specific behaviors according to individual age and sex within each behavioral activity and according to group type. Data for behavior analyses was limited to videotaped segments (for reliability and repetition). Follows and recordings of individual dolphins began as soon as the video-camera and observer were in a favorable position and group composition was assessed. An attempt was made to have even representation among all spot classes and both sexes for focal follows. An individual was selected and recorded until it was no longer within the field of view.

All-occurrence sampling of contact behaviors, including contact with conspecifics, the sand, and other objects was conducted from all videotaped encounters by the author and two independent observers with experience observing dolphin behavior underwater. Comparisons of samples from each observer were made to determine reliability in documentation of contact behaviors. Identification of specific contact behaviors and the frequency of occurrence of contact behaviors, documented from all three observers, matched at a level of 90%, on average; therefore encounters where independent observers matched at 90% or better represent data used in analysis.

Behavioral activities

Observed behavioral activities were classified into five major categories: foraging, inquisitive, travel, play, and social. Foraging was dolphins chasing fish, ingesting fish, a dolphin digging in the sand with its rostrum (see Rossbach, 1998 for details). Fast circle swims around snorkelers, apparent mimicry of human postures and movements, direct approaches to people, click vocalizations apparently directed at people, and physical contact with swimmers were classified as inquisitive. Dolphins moving steadily in one general direction, not varying more than 45° from each other when more than one individual was present, were considered to be traveling. Play was defined as swift movements, fast and circular swimming, chases among individuals, and pushing or pulling objects (e.g., fish, sea cucumbers, sea weed) or associates. During play, dolphins approach conspecifics at oblique angles. Social activity was much physical contact among group members. Individuals were usually oriented toward one another and moving slowly, but not in one specific direction (as when traveling). Social activity included genital-oriented behaviors. Much rubbing and contact behavior among individuals characterized social affiliations, while aggressive interactions were represented by much biting, hitting, body-slamming, raking, jaw displaying, and also by intense, loud vocalizations. No affiliative rubbing behavior was recorded during aggressive social activity. Approaches were at direct angles or head-on between individuals.

Table 2. The seven most commonly observed contact behaviors, and other contact behaviors documented between spotted dolphins. Definitions are listed only for contact behaviors that were most frequently observed and recorded. Codes and behavior names are listed for other contact behaviors. Appendix C in Dudzinski (1996) provides definitions for other behavior codes

Code	Frequency of occurrence	Behavior	Definition
CNT	13%	Contact	Body to body contact, with no movement between bodies
CTP	7%	Contact position	Pectoral fin of one dolphin placed on lateral of another with no movement
MTG	6%	Melon to genitals	One dolphin pushes melon against genitals of another dolphin
PET	12%	Petting	One dolphin moves pec. fin along another's PEC fin
PRB	9%	Petting/rubbing	Placement of PEC. fin on body of another dolphin & rubbing but pec. fin static, moves as part of body
RUB	18%	Rubbing	One dolphin rubs its body on another's body (or body part)
SRB	28%	Sand rubbing	Rubbing all/part of the body in the sand

Code	Behavior	Code	Behavior
BCP	Body contact	MPN	Melon position
BTB	Belly to belly	NDG	Nudging with rostrum
BTG	Bottom grubbing	PDD	Push down another dolphin
FIK	Bury flukes in sand	PUU	Push up another dolphin
KRB	Keel (peduncle) rub	RZZ	Reciprocal nuzzling w/rostra
LOB	Lie on bottom	SPT	Synchronous pet
Mostly aggressive behaviors:			
BOD	Full body rolls	BSL	Body slam
BTE	Bite	RAM	Ram
RHT	Rostrum hit	THT	Tail (flukes) hit
Mostly sexual behaviors:		DSM	Dorsal mount
GOS	Rostrum to genitals	INT	Intromission
IVM	Inverted mount	MFG	Mutual face to genital rub
MNT	Mount	PMT	Pectoral fin mount

All contact behaviors were described operationally for this study (Table 2). A complete catalog of behaviors, that represents a partial ethogram of the underwater behavior of Atlantic spotted dolphins, is available elsewhere (Dudzinski, 1996). Communication was defined as consisting of exchanges of information between a sender and a receiver using a code of specific signals that usually serve to meet common challenges (e.g., reproduction, predator defense, foraging) and in group living species, to promote group cohesiveness (Vauclair, 1996).

Data analyses

Data were examined for variation among individual dolphins, their vocalizations, and their contact behaviors. It was difficult, if not often impossible, to identify specifically which animal received a vocal signal, thus this work focused on exchanges of contact behavior which are observable. Vocal behavior was defined with regard to signal sender and to exchange of contact behaviors among individuals. Contact behavior, vocalizations of focal dolphins, and observable responses from conspecifics were recorded from all video sequences. All contact behaviors were tallied for each individual dolphin and then categorized to dolphin age class and sex. Contact behaviors were also tallied according to activity and group type.

Binomial Z scores were calculated for the most frequently observed contact behaviors according to spot class and behavioral activity (Bakemann & Gottman, 1986). A log-linear statistical test was employed when examining the interactions among spot (age) class, group type, behavioral activity, and the seven most-frequently observed contact behaviors in binomial form (Zar, 1984; C. Ribic, pers. comm., 1996). Matrices were employed to examine data and elucidate potential relationships among spot class, sex, and individually identified dolphins with respect to initiator and receiver roles.

Table 3. Number of minutes of videotaped observations for each dolphin spot class and both sexes

Age	Spot class	Minutes	Sex	Minutes
Calf	2	494.3	Female	952.4
Juvenile	3	514.1	Male	683.7
Subadult	4	431.8		
Adult	5	485.5		

Focal follow lengths: $x = 14.0 \pm 5.2$ min; median = 12.2 min; range = 3.0–33.2 min.

Goodness-of-fit (G^2) test statistics were performed on data to examine if observed numbers of initiator and receiver roles per sex and spot class differed from what would be expected by chance, or as compared with other cells in each matrix (Zar, 1984).

Results

Each spot class was observed equally during recorded encounters (Kruskal–Wallis rank test, $H = 0.16$, $df = 3$, $P = 0.98$) (Table 3). Behavioral activity was not found to be related to spot class ($\chi^2 = 16.56$, $df = 12$, $P < 0.05$). The number of observations of each group type is roughly equal, although group types varied considerably in their distribution according to behavioral activity (Table 4). Mixed groups were observed in social activities more (11.4%) than other groups. AFjuv groups engaged in more play and social activity than other activities, with this group type also exhibiting more play than other groups. Groups of Mc dyads were primarily observed to be traveling. Juvenile groups appeared about equal in the distribution of their recorded behavioral activities (Table 4).

Social activity was consistently characterized by the highest amount and variety of all contact behaviors with the exception of PRB (Table 5). Simple contact (CNT) and sand rubbing characterized play activities. Dolphins exhibited significantly less active physical contact among individual dolphins, especially rubbing and CNT, during inquisitive and foraging activities. Travel was characterized by less petting (PET) and rubbing (RUB) among individuals, however dolphins did exhibit CNT (Table 5).

Certain spot classes exhibited physical contact more than others (goodness-of-fit test = 82.48, $df = 3$, $P = 0.001$). Juveniles (class 3) engaged in the most active contact with PET and RUB. Class 5 dolphins were involved in more CNT and contact position than other age classes. Subadults (class 4) showed the least amount of contact behavior in any form (Table 5). Spot classes 3 and 5 engaged in significantly more SRB as compared with class 2 and 4 dolphins (goodness-of-fit test = 60.37, $df = 3$, $P = 0.001$).

Seven specific contact behaviors were frequently observed, and are presented in descending order of occurrence: sand rubbing (SRB), rubbing (RUB), simple contact (CNT), petting (PET), petting/rubbing (PRB), contact position (CTP), and melon-to-genital contact (MTG) (see Table 2 for code definitions). SRB does not involve contact between dolphins; therefore, this behavior was not included in analyses of intraspecific interactions. Other physical contact (22%) included hits, rams, bites, pushes with the rostrum, or tail hits.

Table 4. Distribution of group types according to behavioral activities. Percentages of the total number of encounters ($n = 185$) given in parentheses

Group type	Behavioral activities					
	Social	Play	Inquisitive	Travel	Forage	Totals
AFjuv	12 (6.5%)	11 (5.9%)	3 (1.6%)	8 (4.3%)	2 (1.1%)	36 (19.5%)
M/calf	6 (3.2%)	6 (3.2%)	3 (1.6%)	16 (8.6%)	3 (1.6%)	34 (18.4%)
Juvenile	7 (3.8%)	7 (3.8%)	4 (2.2%)	7 (3.8%)	5 (2.7%)	30 (16.2%)
Same	12 (6.5%)	7 (3.8%)	6 (3.2%)	11 (5.9%)	4 (2.2%)	40 (21.6%)
Mixed	21 (11.4%)	3 (1.6%)	2 (1.1%)	12 (6.5%)	7 (3.8%)	45 (24.3%)
Totals	58 (31.4%)	34 (18.4%)	18 (9.7%)	54 (29.2%)	21 (11.4%)	

Table 5. Calculated Z score for the seven most-frequently recorded contact behaviors for each spot class and behavioral activity. Values are totaled for 1993–1995

	Contact behaviors‡						
	CNT	CTP	MTG	PET	PRB	RUB	SRB
Spot class							
2	−0.21	−2.62†	6.73*	−2.47*	−1.55	−1.99†	−1.26
3	−1.68	−0.92	−1.26	3.04*	1.05	3.64*	1.92
4	−1.59	−2.08†	−2.89†	0.43	0.54	−0.62	−0.62
5	3.31*	5.26*	−2.69†	−1.13	−0.06	−1.32	−0.24
Activity							
Social	4.79*	4.07*	4.41*	2.72*	1.31	5.87*	5.87*
Play	3.71*	−0.49	1.23	0.57	1.40	0.21	2.73*
Inquisitive	−6.74†	−3.39†	−2.80†	−0.05	−0.87	−2.74†	−4.10†
Travel	−0.18	0.77	−2.54†	−1.21	−0.90	−2.35†	−4.34†
Forage	−4.92†	−3.00†	−2.35†	−3.34†	−1.80	−3.55†	−2.93†

*identifies cells with significantly more observations of contact.
†denotes cells with significantly less observations.
‡abbreviations for contact behaviors and definitions are given in Table 2.

Of 46 recorded MTG behaviors, 39 (84.8%) were directed by a calf to an adult female while swimming in echelon. Two or three MTG were usually followed by two nursing episodes. The remaining 15.2% (7/46) MTG occurred between two class 3 juveniles ($n=6$ cases) and between a juvenile and an adult female ($n=1$ case) during travel. MTG contact was not recorded between adults or subadults. MTG was observed mainly during social activity and significantly less during inquisitive, travel, and foraging activities (Table 5).

Log-linear analysis indicated that the best fit model of the data was that contact behaviors differed significantly with group type, activity, and spot class. Six of the most-frequently observed contact behaviors (CNT, CTP, PET, PRB, RUB, and SRB) were not independently or randomly distributed across the categories of spot class, group type, or behavioral activity (Log-linear analyses, resulting best fit model $G^2=109.67$, $df=107$; at alpha=0.05, the critical value was 132.144 [Zar, 1984]). MTG were not included in this analysis because this behavior was almost exclusively associated with mother/calf dyads. According to the model, the observed numbers of each of these six behaviors were significant according to spot class, behavioral activity, and group type (Table 6; Zar, 1984; C. Ribic pers. comm., 1996). For example, class 5 dolphins participated in twice as many CNT as other spot classes. This trend in CNT according to the different age categories is also evident in the group type categories: adult female with juvenile (AFjuv) and mixed groups showed more CNT than juvenile, mother/calf, or same groups (Table 6). CNT was observed primarily in social and play contexts, as well as during travel—mostly between same sex, age individuals. Class 2 and 4

Table 6. Occurrences of six most frequently observed behaviors among spotted dolphins from video analysis. Log-linear analyses render these values significant. (a) behaviors according to spot class; (b) behaviors according to behavioral activity (BBC); and (c) behaviors according to group type. Abbreviations for behaviors are provided in Table 2. AFjuv denotes adult female with juveniles groups

	Contact behaviors					
	CNT	CTP	PET	PRB	RUB	SRB
(a) *Spot class*						
2	36	9	15	10	27	82
3	37	20	47	23	68	123
4	20	7	21	13	25	28
5	60	42	24	17	35	105
(b) *BBC*						
Social	168	50	44	19	108	121
Play	98	16	20	12	40	61
Inquisitive	0	0	10	3	10	6
Travel	59	18	11	5	21	14
Forage	10	1	0	1	6	11
(c) *Group type*						
AFjuv	64	39	50	26	55	116
Juvenile	12	8	16	5	23	3
Mother/calf	3	0	0	0	0	4
Mixed	70	42	90	47	144	258
Same	3	0	4	7	3	15

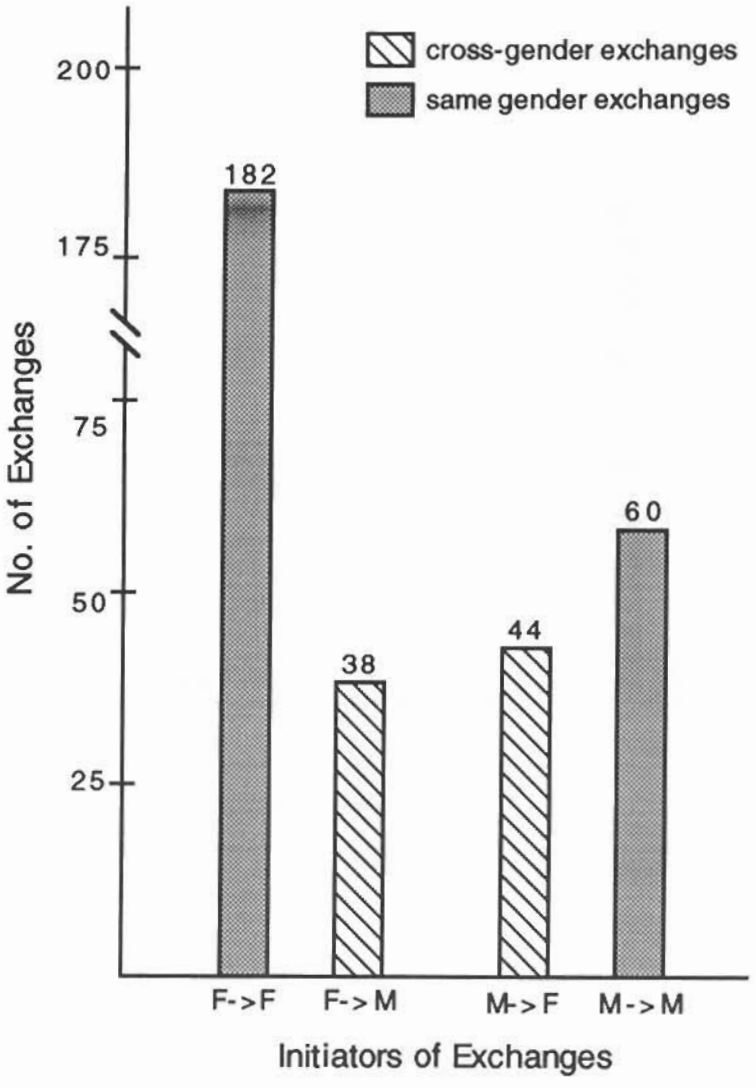

Figure 2. Number of exchanges of contact behaviors with both females and males acting as initiators. 'F' means female, 'M' means male, and '>' indicates direction of contact.

dolphins exhibited significantly less CTP than class 3 and 5 dolphins (Table 6). PET behaviors were relatively evenly distributed among classes with juveniles exhibiting about 1.5 times as many PET as other classes (Table 6). Social activities contained significantly more PET, as did AFjuv and mixed group types (Table 6). SRB was exhibited more by juveniles and adult dolphins, and significantly more during social activities as compared with other modes (Table 6). AFjuv and mixed groups engaged in significantly more SRB behaviors than juvenile, mother/calf or same group types (Table 6).

Exchanges of contact behavior

Females and males both engage in more contact with individuals of the same sex (Fig. 2). Cross-gender exchanges of contact behavior were roughly equal (female initiator-male receiver=17.3%; male initiator-female receiver=19.5%, Fig. 2).

Exchange of physical contact varied depending on age of both dolphins involved. Class 2 dolphins

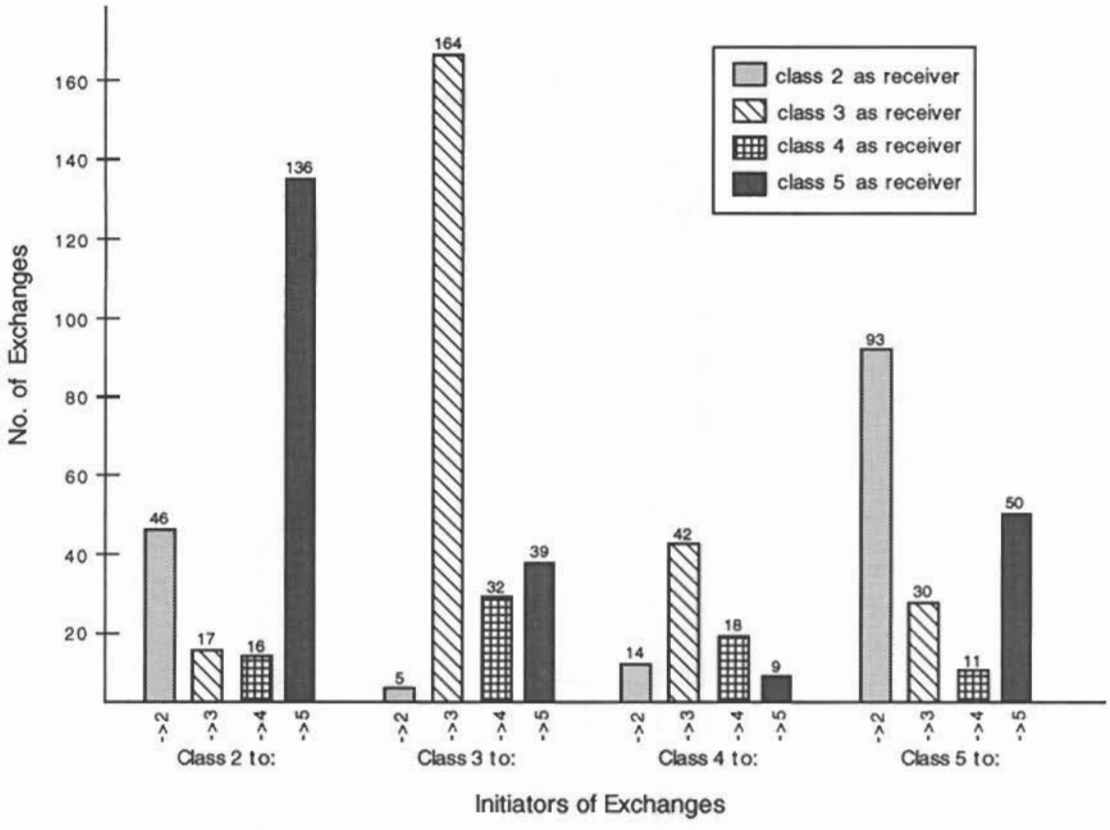

Figure 3. Number of exchanges of contact behaviors with each spot class occupying the role of initiator. Blocks indicate class of receiving dolphin. Sample sizes given above bars.

(calves) initiated and received more contacts with adults than with any other age classes (Fig. 3). It is possible that the mother/calf dyad observations might bias these results, since mother/calf dyads tended to travel together. When other adults were observed in close proximity with calves, there was physical contact, although not nearly the numbers documented between adult females and their calves.

The majority of contact behavior exchanges were between dyads of the same sex and age. Juvenile dolphins initiated (68.3%) and received (64.8%) contacts primarily with other juveniles (Fig. 3). Subadults initiated and received few exchanges of contact behavior when compared with the other three spot classes (Fig. 3). Subadult dolphins, however, did initiate more behaviors to juveniles and received more from juveniles.

Posture and approach behaviors

During play and social activities, spotted dolphins were often observed to assume a posture similar to an 'S' shape: head 'up', anterior ventral surface (i.e. chest) 'down', peduncle 'up', and flukes 'down'. This 'S' posture was recorded from dolphins while swimming horizontally in the water column, or just below the surface; from dolphins positioned vertically, head up while swimming to the surface; and while inverted (i.e., belly up) and either stationary or swimming in the horizontal plane. Class 3, 4, and 5 dolphins were observed in this posture during play and socially aggressive encounters. One adult was recorded using an 'S' posture while chasing fish just below the water's surface, with no other dolphins in view. Calves were observed occasionally in an 'S' posture while swimming in echelon with an adult; however, these situations did not involve overt actions with conspecifics. During this play, this 'S' posture was exhibited between juveniles and accompanied by open jaw movements or just prior to rubbing exchanges. At these times, dolphins were positioned at oblique angles to one another. Subadults and adults exhibited 'S' postures associated with direct approaches, loud intense vocalizations, bubble emissions and aggressive contact behaviors.

Table 7. Samples of frequency-modulated pure-tones for identified, vocalizing individual spotted dolphins. For 21 whistles, the vocalizer was too close to the camera to determine spot class

	Whistles	Chirps
Females	161	64
Males	97	19
Total:	258	83
Class 2 (calves)	38	24
Class 3 (juveniles)	123	37
Class 4 (subadults)	36	5
Class 5 (adults)	40	17
Total:	237	83

Vocal exchanges

During approximately 14 h of videotaped swim encounters, 1247 whistles and chirps (n=934 and 313, respectively) were recorded. Only pure tones where spot class, sex and identification were positively identified are included in these results (Table 7). Individual dolphins were identified as producing 341 frequency-modulated pure-tones: 258 whistles and 83 chirps. For 257 other frequency-modulated sounds, either spot class or sex was determined, although specific dolphin identity was not confirmed.

Recipients of vocal exchanges were difficult to identify except in cases where only two individuals were exchanging physical contact or were posturing toward one another while vocalizing. Click trains, squawks and whines occurred mostly during investigative behaviors (e.g., approaches and head scanning). Trends in the use of two types of vocal exchanges, as associated with specific behaviors, were evident. Concurrent with a click train was an approach, accompanied by head scanning in the horizontal plane, from the approaching dolphin toward a second individual. When the approaching dolphin was within 3 m of the second animal, it changed direction while simultaneously producing a chirp. This sequence of behaviors was observed with each role occupied by both sexes and by juveniles and adults. The role of initiator or receiver, however, did not appear specific to age or sex. It is possible that this sequence might also be produced by subadults; however, no observations of subadults in either role were witnessed.

The second example of vocal type(s) potentially correlated with behavior(s) involves whistles, squawks and whines and behaviors observed during play and socially aggressive activities. Whistles were often recorded from individuals exchanging rubbing behaviors, or between bouts of aggressive exchanges, but also while rubbing one another. Squawks and whines were recorded from dolphins exchanging aggressive contact behaviors (e.g., hits, bites and jaw claps), although whines were also often recorded from juveniles or calves during play activities. Whistles were recorded during play and aggression when dolphins were interacting, though not necessarily in physical contact. During these activities, whistles were often accompanied by bubble emissions and other behaviors. It is probable that whistles in these situations are modified by context and thus indicate different usage and meaning.

Discussion

Spotted dolphins use a system of different levels of signals to exchange information among individuals about activities and relationships. Signal repertoires may include visual displays and postures, vocalizations, natural markings, and various physical contact behaviors either displayed to or exchanged between individuals.

Physical contact among conspecifics is a defining factor in many social interactions. Individuals may inadvertently touch one another; however, active rubbing or grooming is often observed and can be used as an indicator of the relationship between individuals in a group that cannot always be predicted by dominance or kin relations chimpanzees, *Pan troglodytes*, (Goodall, 1986); vervet monkeys, *Cercopithecus aethiops*, (Seyfarth & Cheney, 1984); jackals and other wild dogs, *Canis* sp., (Moehlman, 1987). In general, rubbing between conspecifics (often described as 'grooming') can serve several functions including ectoparasite removal (Goodall, 1986; Hart *et al.*, 1992), tension reduction among individuals (Goodall, 1986), appeasement or reconciliation after agonistic interactions (de Waal & Roosemalen, 1979; Bernstein, 1993), or establishment and maintenance of close social bonds (Seyfarth, 1980; Moehlman, 1987).

Spotted dolphins preferentially initiated physical contact with certain individuals. Females engaged in more contact with other females; male dolphins displayed similar same-sex initiator-receiver preferences. An age preference was evident; same aged dolphins interacted more on average with each other than with different aged individuals. Overall, contact behavior for all spotted dolphin ages (regardless of group type) occurred more frequently during social activity. Mixed and adult female and juveniles group types exhibited more contact than other groups. Contact was dictated by the general behavioral activity; age and number of conspecifics are also factors for intraspecific interactions among these dolphins.

Dolphins were observed coming together while swimming in most any spatial orientation and

making physical contact. Active and affiliative contact behaviors included petting, rubbing, and contact position. Petting and rubbing behaviors involved two or more conspecifics; however, these actions could be directed at objects, people, or the sea floor. Most petting was directed towards the melon, pectoral fins, or lateral regions. It was difficult at times to discern who initiated and received the pet, but this behavior appeared to be reciprocal. Within encounters, petting was often observed when dolphins had been separated by time or distance, and may represent a greeting or a familiarizing mechanism among individuals. Petting may also be a form of appeasement used to quiet excited or startled individuals. On several occasions, adult dolphins were observed petting calves or juveniles that had just been engaged in much fast and erratic swimming, or even heightened play among conspecifics. Use of the pectoral fin may indicate a specific message that is likely to be context dependent when used to rub a companion. Dolphin petting behavior, while having somewhat different proximate functions due to anatomical differences, may share some functional aspects with the social grooming of many terrestrial species, especially primates (e.g., Seyfarth, 1980; Seyfarth & Cheney, 1984).

Rubbing conspecifics is similar to petting behaviors both proximately and functionally. It has been observed in dolphins that have joined, suggesting a form of greeting (e.g., for bottlenose dolphins *Tursiops truncatus*, Saayman & Tayler, 1972; Würsig & Würsig, 1979; for killer whales *Orcinus orca*, Jacobsen, 1986). Specifically in spotted dolphins, rubbing is seen mostly during social and play contexts by all age classes and both sexes, and appears to be symmetrical in use. Rubbing may function to strengthen social bonds among interacting dolphins, or to indicate to others that the rubbing pair have a close association, at least for that time. Rubbing likely functions as a form of social contact to assist animals living in fission-fusion societies in maintaining the cohesion and integrity of their groups.

Contact position (CTP) was observed between dolphins seemingly without regard to age or sex. It is possible that spotted dolphins use CTP to solicit or express short-term strong associations between individuals. Contact position has been observed for wild (Saayman & Tayler, 1972; Saayman *et al.*, 1973; Connor, 1990) and captive (Defran & Pryor, 1980; Rhind, 1991) delphinids. For spotted dolphins, CTP may simply be a re-affirmation of bonds between two individual dolphins that have been separated for some time, or might be a signal to conspecifics that these dolphins are tightly paired for this given period of time. That is, CTP might indicate to conspecifics that two dolphins exchanging a CTP behavior are 'acting as a team'. This explanation is supported by observations of alternately aggressive and affiliative bouts of behavior observed from spotted dolphins during the course of this study. CTP has also been referred to as 'bonding'; and it has been suggested this behavior is indicative of dominance relationships (Rhind, 1991). [Caution should be taken with use of the term 'bonding', as it implies intent on the part of the soliciting dolphin that is not currently measurable.]

In the Bahamas, spotted and bottlenose dolphins rub their bodies in the sandy bottom. Rubbing against objects (sand, tank, and floor) has been documented for captive dolphins (Defran & Pryor, 1980; Rhind, 1991). Killer whales have rubbing beaches in British Columbia (Matkin & Saulitis, 1994); while bottlenose dolphins rub on boulders found in shallow waters off Mikura-jima, Japan (pers. observ., 1995, 1997, 1998). Sand or bottom rubbing behaviors may have another hygienic function similar to self-grooming in other animals to remove ectoparasites (Halloran & Beckoff, 1995), or dead skin, such as for belugas (*Delphinapterus leucas*) during their annual molt (Smith *et al.*, 1992). Rubbing may also simply 'feel good'.

Anecdotal evidence for contact position function

One swim encounter warrants mention because it exhibited distinct correlations between vocal, behavioral, and postural activity among dolphins. The encounter, on 6 July 1994, at about noon, was 12 min in length, involving at least 20 dolphins. The animals were sighted splashing at the surface approximately 150 m to the northeast of our anchored vessel. Once underwater, dolphin vocalizations were audible for approximately 70 s before visual contact was made. Dolphins appeared to ignore swimmers and focused on hitting, biting, ramming, and swimming directly at one other. Loud, intense vocalizations (e.g., loud squawks, whistles and pops) and bubbles (streams, trails, and singletons) were produced during exchanges of aggressive behaviors, modified by fast swims and 'S' and head-to-head postures. The witnessed aggressive displays alternated with bouts of affiliative contact (much rubbing, petting, and contact position) within subgroups of three to four dolphins. Vocalizations and bubble production all but ceased during the affiliative bouts, yet resumed with aggressive actions. Each individual in the sub-group was in contact position with its neighbor; all individuals were synchronous in every aspect of their behavior. Synchrony may act to facilitate the affinity of short-term associations between two (or more) associates, as well as demonstrate these associations to opponents. During affiliative exchanges, the subgroup swam around each other,

then a minute later, resumed aggressive activity. Contact position in this context could be an indicator to others that the touching dolphins are supporting each other. Of course, this explanation does not rule out the dominance hypothesis; it does, however, suggest a broader functional base for this behavior given the varying ecological and social constraints on a species.

Mother/calf interactions

Adult (class 5) females and class 2 (calves) dolphins (presumed mother/calf dyads) had extensive contact between one another. Mother/calf dyads spend most of their time in each other's company which could account for the preference of exchanges between individuals in these dyads. However, lack of contacts exchanged among adult females within mother/calf groupings, even though swimming in close proximity, suggests the preference in exchange of physical contacts between mothers and calves is intentional. Added support is garnered from observations of one particular trio of spotted dolphins. An adult female was observed with two calves, one approximately three years older. While the older calf continued to initiate contact with the mother, the reciprocal was not evident. Preferential treatment and care of young offspring has also been observed in social terrestrial species (Goodall, 1986). Directing the majority of her physical contact toward a calf is a likely mechanism for an adult female to insure her offspring's well-being.

The usual swimming position for a mother/calf dyad is in echelon (Tavolga & Essapian, 1957). The most prevalent contact between mothers and calves while swimming in echelon was the calf's melon to the mother's genital area. While it is possible that melon-to-genital (MTG) contact between mother/calf dyads simply represents accidental touches during close-proximity, directed swimming, it is more likely that MTG contacts are intentional by both mothers and calves to be assured of the other's presence. An alternative explanation is suggested by several incidents of MTG alternating with nursing by class 2 dolphins; the calf may be 'kneading' the mammary area of the mother to stimulate milk let-down, as has been witnessed in the young of some terrestrial mammals (Hart *et al.*, 1992; Rowell, 1993). Most probably, as with other contacts described, there is not one exclusive explanation or function for MTG contact.

Vocal exchanges

Vocalizations appeared to be used in lieu of contact between individuals or concurrently with certain tactile exchanges suggesting that dolphins may use different signals to convey similar messages, or to modify or enhance specific information. Examples of both concurrent and separate uses of vocal and tactile behaviors by spotted dolphins were observed. Some individuals, separated by distance, exhibited one or two distinct behavioral exchanges when approaching each other: one vocal and one tactile. Typically, one dolphin approached a second individual while swimming horizontally and slowly. When within 2 m of contact, the approaching dolphin would either: (1) commence head-scanning movements directed at the second dolphin while producing a click train followed by a chirp emission at about one meter separation, and then, abruptly turn and swim off, or; (2) the approaching dolphin would swim at the second individual and at about one meter separation would angle into a parallel position and begin rubbing pectoral fin to pectoral fin. Often this action was reciprocated. Both types of exchanges were expressed during similar contexts and, to the observer, appeared to indicate a form of greeting, a method of reacquainting the individuals, or a reaffirming of pre-existing social bonds.

Concurrent use of vocal and tactile behaviors is exemplified by the socially aggressive encounters witnessed. Vocal behavior paralleled the actions of individuals: loud, intense sounds (e.g., squawks) accompanied aggressive contact, 'S' postures, frequent bubble releases, and direct approaches; while silence or multi-looped whistles and chirps were recorded with bouts of affiliative contact alternating with aggression. Taken individually, each of these behaviors do not necessarily indicate irritation or anger from a dolphin. This is evident when examples of such behaviors are documented during play activities or from single individuals engaged in inquisitive or foraging contexts. Combined, however, these behaviors most definitely send a synergistic message of agitation, irritation.

Signal repertoires and modifying referents

Repetition of various interactions between individual dolphins was low, but anecdotal accounts suggest that these dolphins possess a set of signals that vary in repertoire. Observations of these same signals within different activities, as well as accompanied by external and internal referents indicate that dolphins have the ability to adjust their signals to modify intended messages depending on context.

Approaches at right angles or directly at another dolphin were observed only during aggressive interactions. During play, juveniles were never observed to approach cohorts directly or at right angles. It is likely that behaviors (e.g., jaw claps) are not specific to particular expressions of irritation or aggression, unless modified or coupled with a direct or perpendicular approach. Play is often characterized by mock fighting behaviors that are modified with subtle cues reminding conspecifics that the intent of

ongoing activities is not truly aggressive (Fagen, 1981; Bekoff, 1984). As in other mammals, young engage in play more than adults (Fagen, 1981; Bekoff, 1984). Play among young may represent time for the formation of long-term social attachments, as well as the development of skills required later in life (Bekoff, 1984).

Spotted dolphins were observed, at times, to assume a position closely resembling the 'S'-posture reported for humpback whales (*Megaptera novaeangliae*, Helweg *et al.*, 1992) and delphinids (Defran & Pryor, 1980; Norris *et al.*, 1994). In these studies, the posturing animal, usually male, was engaged in aggressive displays towards conspecifics. The 'S'-shaped posture is suggested to be an aggressive stance in many cetaceans (Defran & Pryor, 1980), and may be similar to the arched back and neck position observed in many terrestrial mammals during aggressive displays (Lorenz, 1967; Bekoff,1984). While spotted dolphin subadults assumed an 'S- posture during aggressive activity, juveniles were observed using 'S'-postures in conjunction with 'aggressive' actions during play with cohorts.

Subadult spotted dolphins were least interactive in tactile exchanges. When observed in physical contact, subadults exchanged highly aggressive behaviors. Interestingly, these behaviors were alternated with bouts of affiliative contact. The dolphins might alternate affiliative contact with hits, or direct attacks, to minimize direct physical damage to associates. A different, but related, explanation is that the dolphins will display aggressively at 'foes' for a few minutes and then become very tactile with friends to display another slightly different but related message. This message would tell other subgroups that the three to four dolphins in physical contact and swimming synchronously are tightly bonded and will support each other in a fight. Thus, both aggressive and affiliative bouts might convey similar messages.

Subadult dolphins were observed to wave and flare their pectoral fins while vertical in the water. At this time, they directed head snaps, jaw claps and bubble releases to other dolphins also vertical in the water. These signals may be used concurrently by dolphins to create an illusion that they are larger than actual size and possibly to intimidate the intended recipient(s). Conversely, bubbles may function to camouflage or disguise the bubble-producer from conspecifics, as has been proposed for male humpback whales (Helweg *et al.*, 1992). This might cause the intended recipient to misjudge the actual size of the emitter. Another explanation for bubble release is that they may simply be non-intentional indicators of an individual's internal agitation. These alternative explanations do not negate the potential for bubbles to be used as defensive reflectors, or for other reasons. How these signals are all related depends on context. More observations of the same signals, both separately and combined, are needed to establish potential meanings behind the use of each signal.

Posture can often signal intent and demeanor of a signal sender, as well as provide insight to the meaning concluded by a recipient (Östman, 1985; Helweg *et al.*, 1992; Würsig *et al.*, 1990). In spotted dolphins, posture may also represent a patterned combination of signal units: posture may alter the representation of the spot patterns on older individuals. Their spots become complex, intricate patterns of various sizes. The overall differences in the amount of spotting are potentially informative among conspecifics for age and identification. It is probable that varying degrees of spotting coupled with certain postures or behaviors provides information on meanings for particular signals. For example, the same approach behavior directed at an adult spotted dolphin will be received differently whether the approaching dolphin is another adult or a calf. The fact that juveniles initiated more tactile contact than they received and subadult dolphins received more contact than they initiated suggests that spotted dolphins recognize relative ages of conspecifics.

Besides vocal and tactile signals, terrestrial social mammals communicate much information through subtle and overt kinesic and non-linguistic expression, including changes in facial expressions, irregularities in respiration, and carriage of the overall form. Adaptation to life in the ocean has removed from delphinids the use of facial expression; evolution has streamlined the body and limited the applicability of much kinesic communication in cetaceans. Nonetheless, posture and contact as well as sound are used effectively among spotted dolphins for information exchange.

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