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Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985–1995

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Abstract

Free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, were observed in Bahamian waters from 1985–1995. Interspecific interactions between these two species were documented and are reported here.

Of 1246 encounters with dolphins, over 15% were mixed species activity. Of these encounters, 60% were affiliative 34.9% were aggressive, and 4.8% involved foraging activity. Compared to single species, mixed species encounters were (1) longer in duration and (2) larger in group size. Mixed species encounters that were affiliative in nature were significantly shorter in duration and smaller in group size than aggressive encounters. The ratio of spotted dolphins to bottlenose dolphins was significantly less during foraging activity than it was in other behaviors.

Mating, with penile intromission, was seen between adult male bottlenose dolphins and juvenile spotted dolphins of both sexes. Young adult males of both species engage in interspecific high-energy bouts of sexual play and aggression. The antagonists in these encounters were often conspecific coalitions of spotted dolphins and solitary or small groups of bottlenose dolphins. Mixed-sex, mixed-species adult groups (including pregnant females) were seen foraging together and traveling together. Interspecific coalitions of males were observed during interspecific and interindividual (intraspecific) conflicts. Alloparental behavior, between a young adult female spotted dolphin and an emaciated bottlenose dolphin calf was also observed. The costs and benefits of interspecific associations—including predator protection, competitive and cooperative foraging strategies, shared repertoire of vocal and gestural signals, and the question of species divisions and hybridization are discussed.

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Introduction

Interspecific interactions have been noted between many species of primates (Klein & Klein, 1973; Struhsaker & Leland, 1979; Struhsaker, 1981; Terborgh, 1983; Jolly, 1985; Waser 1982, 1987), cetaceans in captivity (Caldwell *et al*., 1971; Terry, 1984; Wood, 1953), cetaceans in the wild (Norris & Prescott, 1961; Perrin *et al*., 1973; Leatherwood & Reeves, 1978; Norris *et al*., 1978; Saayman & Tayler 1973, 1979; Wursig & Wursig, 1980; Cockeron, 1990; Jefferson *et al*., 1991; Shelden *et al*., 1995; Bearzi, 1996; Ross and Wilson, 1996; Weller *et al*., 1996), and between many terrestrial species, including rodents, carnivores, artiodactyls, pinnipeds, and birds (Fagan, 1981). Interspecific activity between cetaceans and humans has also been reviewed (Lockyer, 1990).

This paper describes interspecific interaction between Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, in the Bahamas over an eleven year period. We describe the behavioral contexts in which inter-species interaction occurs, and the duration, group size, sex composition, and ratio of these two species during such encounters.

Methods

Atlantic spotted dolphins and bottlenose dolphins were encountered over shallow sandbanks, ranging in depth from 6–16 m north of Grand Bahama Island in the Bahamas (Fig. 1). These dolphins have been habituated to human presence in the water and are being tracked as part of a long-term study of their communication and behavior. Observations were made at the surface and underwater a total of 973 field days, from 1985–1995. Several types of

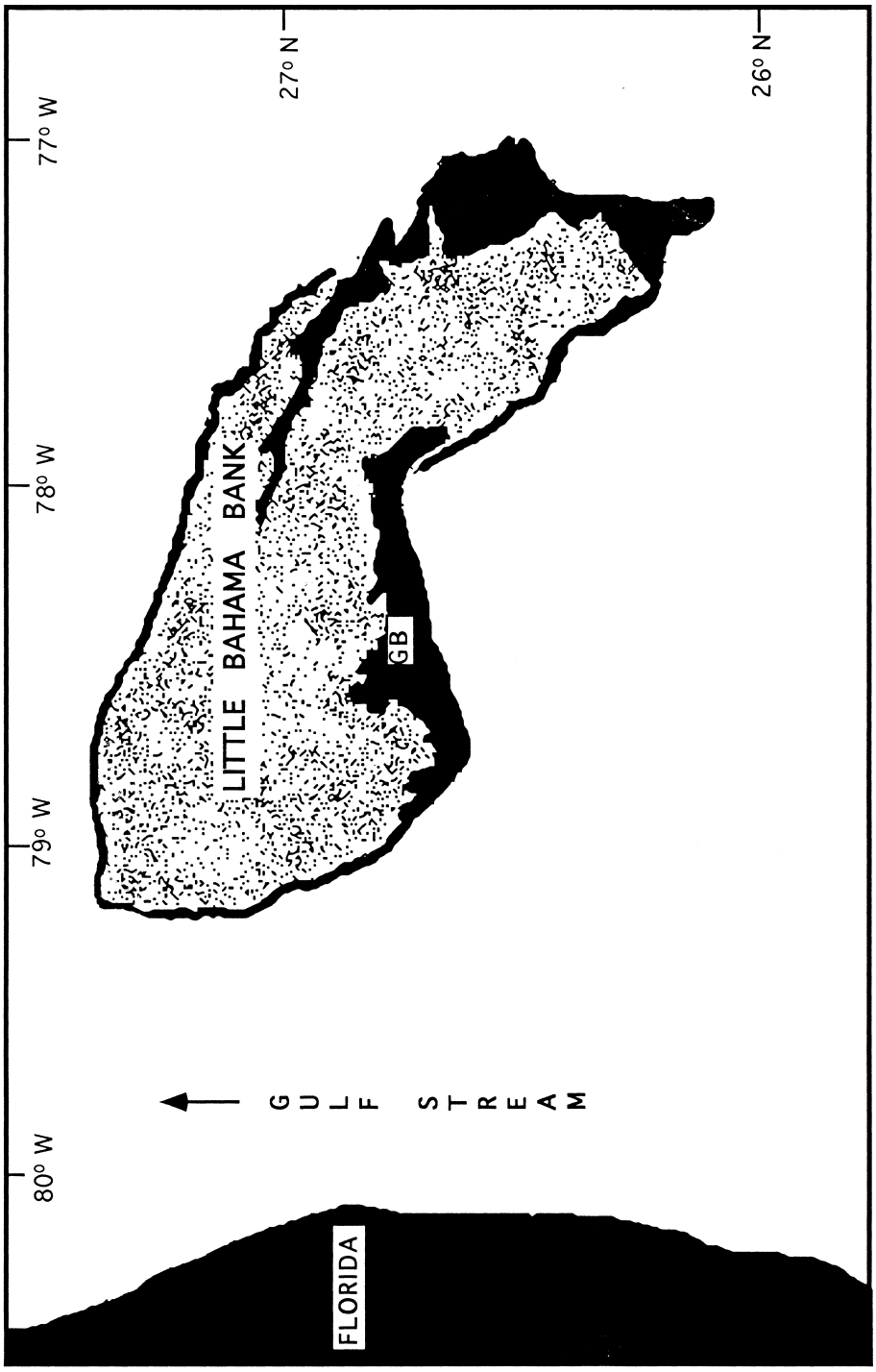

Figure 1. Chart of study area. Darkened area represents land masses and shaded area represents the submerged sandbank outlined by the 20 m depth contour. GB=Grand Bahama Island.

Table 1. Comparative aspects of single species vs mixed species encounters for Atlantic spotted and bottlenose dolphins in the Bahamas, 1985–1995

	Spotted dolphins (n=963)	Bottlenose dolphins (n=94)	Mixed-species (n=189)
% of all encounters	77.3	15.2	7.5
Mean duration of encounters (minutes)	28.4 (S.D.=6.62)	29.0 (S.D.=24.41)	47.0 (S.D.=19.77)
Mean group size of encounters	7.7 (S.D.=1.35)	7.5 (S.D.=3.72)	13.7 (S.D.=8.59)

vessels were used during this study, including a 4 m whaler and a 20 m catamaran for stability during anchorage offshore.

Dolphins were individually identified using surface and underwater photo identification techniques documenting natural marks on their dorsal fins, flukes, and spot patterns. Pictures were taken using a Nikonos III or V with a 35-mm lens. An underwater video camera, Sony CCDV9 8 mm or Yashica KXV1u Hi8 mm, with attached hydrophone, Labcore 76, was used for acquiring both identifications and simultaneous behavior and vocalizations. encounter data collected included individuals present, group size, age classes, time of day, environmental factors, and behavioral activity.

Each encounter was also scored as to the predominant sex of the dolphins engaged in the behavior (females, males, or undetermined). Sex was determined by direct observation of the genital area (mammary slits or penile slit/erection) in both species. Although the presence of bottlenose dolphins in mixed species encounters was noted, their exact group composition and life history parameters were only occasionally known in detail at the time of this report. Since sex and age class categories were established for spotted dolphins during this study (Herzing, in press) age or sex specific descriptions for spotted dolphins within mixed species encounters were used. Mixed species activities were categorized as foraging, aggressive (which often included sexual behavior), and affiliative (which included travel, play, and neutral associations). The term 'coalition' (De Waal & Harcourt, 1992) is used here to refer to the joining of forces by two or more parties during a conflict of interest with other parties.

Results

Duration, group size and species ratios

Out of 1246 total encounters with dolphins, over eleven years, bottlenose dolphins were observed with spotted dolphins over 15% of the time (Table 1). The mean duration (x=47.00, S.D.=19.77) of mixed species encounters were significantly longer (P=0.0001 for spotteds, P=0.0345 for bottlenose) than either single species encounters. The mean group size (x=13.7, S.D.=8.59) of mixed species encounters was also significantly larger (P=0.0001 for spotteds, P=0.0002 for bottlenose) than either single species encounters. In addition, the mean group size of bottlenose dolphins was smaller, and spotted dolphins larger, in mixed groups than during single species encounters. Over 30% of all mixed species encounters were clearly of an aggressive/sexual nature and over 60% were affiliative (Fig. 2).

Of the three behavioral categories in mixed species activity, aggressive encounters were significantly longer in mean duration (x=67.54, P=0.0061) (Fig. 3) and larger in mean group size (x=19.56, P=0.0001) (Fig. 4) than the average for all mixed species encounters. Aggressive behavior had the highest mean (spotted to bottlenose dolphin) ratio (x=5.59), and the largest ratio ranges (0.13–38.00), of the three behavioral activities. The mean ratio of spotted to bottlenose dolphins during

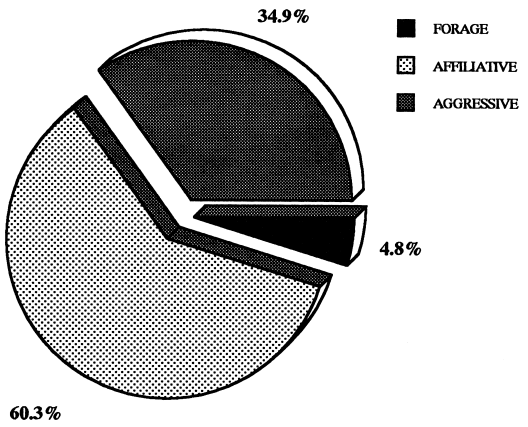

Figure 2. Percentage of behavior in mixed species encounters 1985–1995 (n=189).

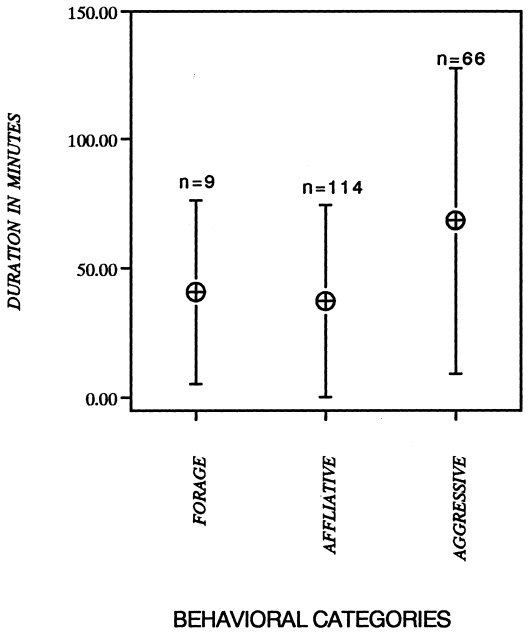

Figure 3. Mean duration of mixed species encounters for three behavioral categories 1985–1995.

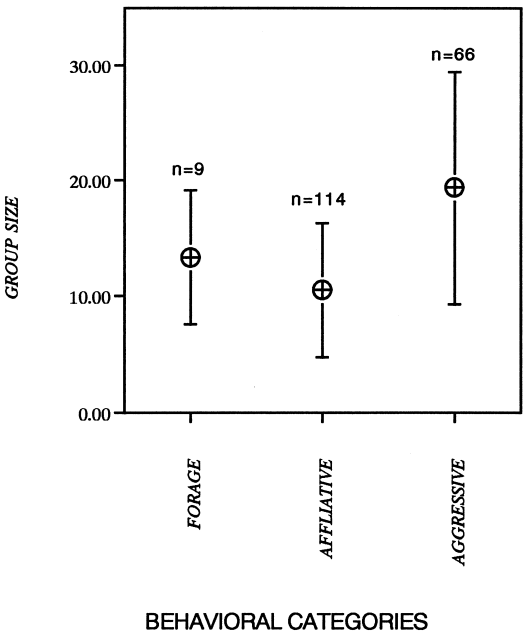

Figure 4. Mean group size of mixed species encounters for three behavioral categories 1985–1995.

foraging behavior (x=2.07) was significantly less (P=0.0031) than the other categories (Fig. 5).

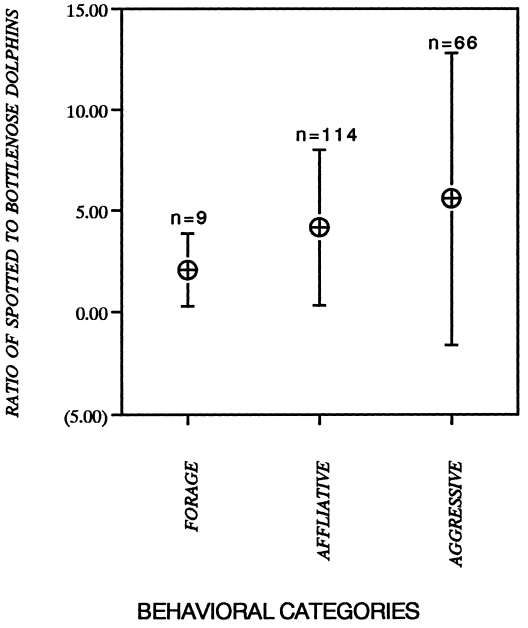

Figure 5. Mean ratio of spotted to bottlenose dolphins mixed species encounters for three behavioral categories 1985–1995.

The predominant sex of spotted dolphins that were active during each behavioral activity varied, with males predominantly active in aggressive/sexual categories. Although sex was undetermined for over half of the dolphins in affiliative interactions, among the dolphins whose sex was known, they were three times as likely to be female as male.

Group composition

Bottlenose dolphins have been observed in the following subgroup structures with spotted dolphins: traveling groups tended to consist of adult bottlenose dolphins with adult spotted dolphins (males, pregnant females and mixed sexes). Sexual interactions included adult male bottlenose dolphins with juvenile female spotted dolphins (mating), adult female bottlenose dolphins with juvenile male spotted dolphins (social, aggressive/sexual), juvenile male bottlenose dolphins with juvenile male spotted dolphins (social, aggressive/sexual), and adult male bottlenose dolphins with adult male spotted dolphins (social, aggressive/sexual) Fig. 6.

Descriptions of interspecific social interactions

While the above results capture general trends in interspecies interactions, they are insufficient to convey the subtlety and complexity of those

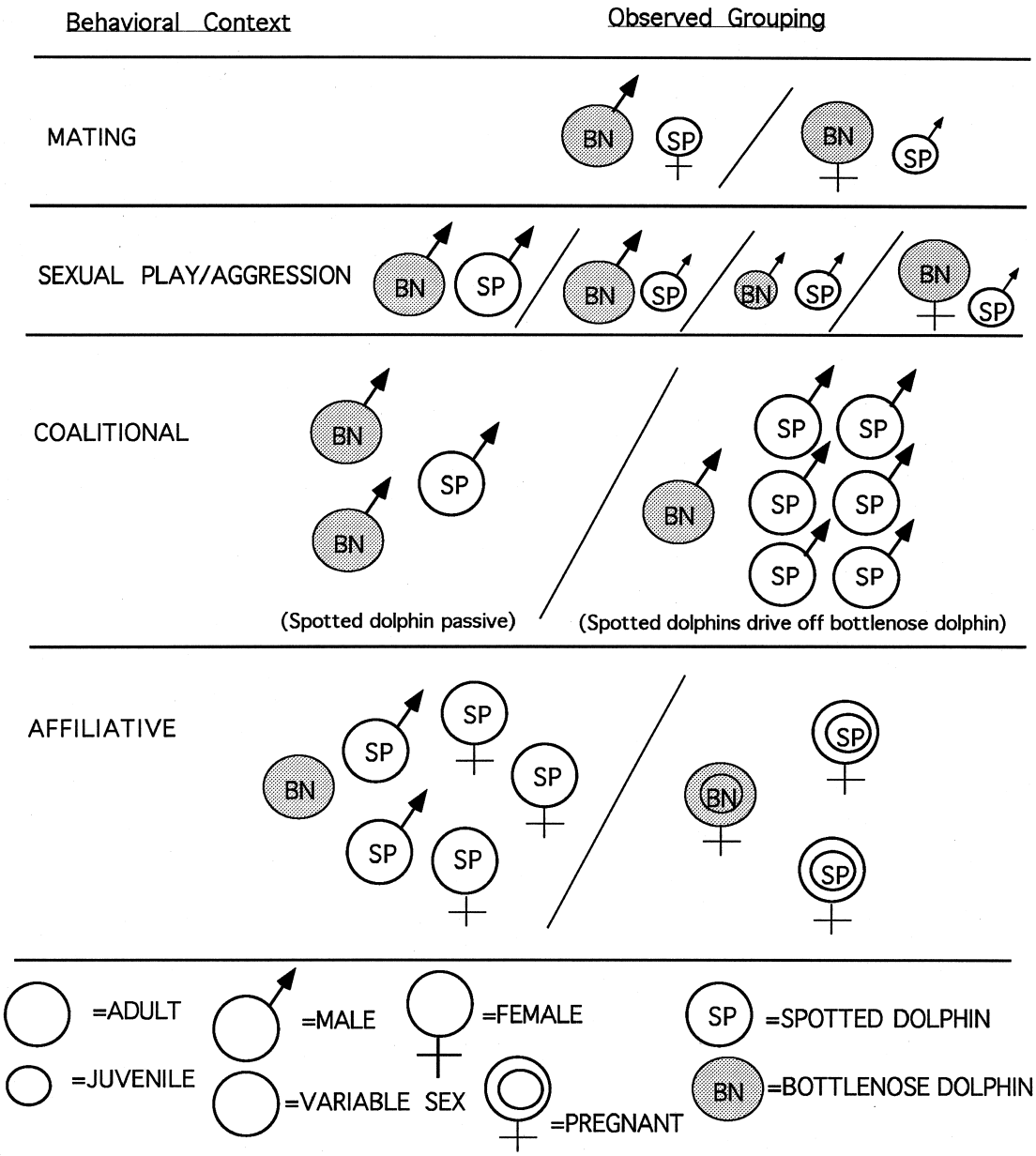

Figure 6. Mixed species and sex groupings of spotted and bottlenose dolphins in different behavioral contexts.

interactions. They also provide little information on the signals that the dolphins use to mediate such interactions. In the next section, we will describe particular encounters between bottlenose and spotted dolphins that either typify a class of interactions or portray unique incidents. By providing the actual sequences of behavior, including both similarities and differences in signaling, we hope to add to our understanding of the mechanisms of interspecies communication.

Interspecific mating/sexual solicitation

Adult male bottlenose dolphins/juvenile female spotted dolphins. On 20 June 1986 (1200–1300 h) copulation was observed between an adult male

bottlenose dolphin, GE, and a juvenile female spotted dolphin, RM, estimated at six years of age. RM and a second juvenile female spotted dolphin were engaged in reciprocal genital stimulation. GE approached the female spotted dolphins and positioned himself, at first without an erection, beneath and ventral to RM. GE then laid on the ocean floor near the females, on his side with an obvious erection. GE then approached RM, attempted intromission and eventually copulated with RM. No resistance was observed from RM. This event was the only incident of interspecific mating, between male bottlenose dolphins and female spotted dolphins, that we have verified. However, frequent observations of copulation between male bottlenose and male spotted dolphins are described below.

Adult female bottlenose dolphins/juvenile male spotted dolphins. On 30 April 1990 (1630–1700 h) two adult female bottlenose dolphins were observed soliciting genital contact from two juvenile male spotted dolphins. The female bottlenose dolphins solicited pectoral flipper rubs, including head and genital rubs, from the young males. The bottlenose dolphins then held the smaller spotted dolphins between their pectoral flippers, thrusting against the spotted dolphins' genital area. No penile erections of the young males were observed during this behavior. The females then propelled the males through the water with their rostra on the spotted dolphins' tail flukes. Some head to head postures and squawks were also observed but appeared playful in nature and were not observed to escalate into aggression.

Interspecific aggression/sexual interaction

Adult male bottlenose dolphins/adult male spotted dolphins. Interspecific male sexual interactions were first observed on 12 July 1991 (1800–1900 h). Two adult male bottlenose dolphins and fifteen spotted dolphins were observed together. The bottlenose dolphins began to chase and mount two male spotted dolphins within a larger coalition of male spotted dolphins. Erection, penile rubbing, and copulation (by the bottlenose only) were observed during this encounter. Bottlenose dolphins initially focused on the youngest male spotted dolphin in the coalition during mounting behavior. The other spotted dolphins present did not defend, distract, or otherwise engage the bottlenose dolphins. The spotted male dolphin that was initially the focus of the bottlenose dolphins, floated passively in the water while the bottlenose dolphins positioned themselves to each side of him. After copulating with this dolphin, the two male bottlenose dolphins then pursued and engaged another young adult male spotted dolphin. Similar sexual behavior occurred between these individuals. During this encounter head-to-head posturing, squawking, and other aggressive displays (by both species) were observed. The bottlenose dolphins were successful in mounting and copulating with the spotted male dolphins and reciprocal sexual behavior was not observed. Throughout the next four years, these types of interspecies encounters between males were observed dozens of times (Figs 7 and 8). Typically, interactions, which included penile intromission attempts or actual intromission, involved the young spotted dolphins taking a passive role, floating without resistance while the adult bottlenose dolphin actively arched and rubbed its body and genitals against the young spotted dolphin. While the above is fairly typical for interspecies sexual encounters, these interactions actually varied considerably in both sequence and outcome. For example, as described above, in many initial encounters, bottlenose dolphins dominated and sexually manipulated the passive male spotted dolphins. However, if during a given event, the number of spotted male dolphins increased and outweighed the number of bottlenose, interspecific copulatory events would cease, and aggressive chasing of the bottlenose dolphins by the spotted dolphin males would ensue. In many cases the spotted dolphins actually drove the bottlenose dolphins to leap out of the water and often chased them out of the area.

Coalitional behavior by the spotted dolphins was, in fact, critical in determining the outcome of several interspecies interactions. Coalitions of male spotted dolphins often demonstrated certain ritualized behaviors during aggressive interactions. They synchronized their swimming movements and vocalizations and faced off, head-to-head with their opponents while producing loud vocalizations. If the situation escalated the spotted dolphins used open mouth displays, snapped their jaws, arched their backs, and finally charged, body slamming and raking the others with their teeth.

One particular series of encounters, taking place over two days, illustrates how the 'balance of power' can shift in such situations, depending on the activity of spotted coalitions. On 21 June 1994 (1600–1620 h), ten spotted dolphins, including two mother/calf pairs, two juveniles, and a coalition of four adult male spotted dolphins (ST, FL, CS, U) were observed with four bottlenose dolphins, including at least two known males. While the mother/calf pairs were foraging, two male bottlenose dolphins with erections approached the oldest male spotted dolphin (ST) in the coalition and attempted penile intromission. The male spotted dolphin became passive while the bottlenose dolphins rolled him around and

Figure 7. Male spotted dolphin and bottlenose dolphin in head to head confrontation during interspecies sexual and aggressive behavior.

attempted to position themselves in a sidemount orientation. Actual copulation was not observed, nor did any of the other male spotted dolphins attempt to intercede or fend off the bottlenose dolphin. At 1820 h the same spotted dolphins were encountered without the bottlenose dolphins but with two additional adult male spotted dolphins that were long-time associates of ST.

On the following day, 22 June (1230–1440 h) the same group of spotted dolphins were encountered but now the group included nine male spotted dolphins, comprised of two coalitions that had a long-term associations with each other over the years. This 'supercoalition' (Conner *et al*, 1992) formation was tightly aggregated, with males often in prolonged body contact with each other. Four bottlenose dolphins were also present including the two individuals that had mounted ST on the previous day. (One of these bottlenose dolphins (SL) was specifically identifiable by his deformed left pectoral flipper.) Initially SL and another male bottlenose dolphin approached ST and began to sidemount him. ST broke from them and returned to his male coalition who were within visual proximity. When SL and the second male bottlenose dolphin attempted to approach and mount another male spotted dolphin, the coalition of spotted dolphins rapidly accelerated and chased the bottlenose dolphins away.

During the course of this observation period, the male spotted dolphins formed and reformed into their groups and traversed the area, in tight formation, with ST positioned slightly ahead of the group. At one point, after the above-described copulation attempts, the spotted dolphins approached the bottlenose dolphins foraging on the bottom and ST accelerated away from the coalition and swam directly towards SL, followed by the other spotted dolphins. The supercoalition chased SL around and out of the water, posturing and squawking intensely. SL eventually broke off and returned to the bottom to forage. At this time, the supercoalition of male spotted dolphins engaged in rapid pectoral flipper rubbing and squawking, and swam in a tight-knit formation with their mouths slightly open. When this activity subsided they began, once again, to cruise the area. As the afternoon wore on, the spotted male dolphins repeatedly approached SL, and once again charged and chased him. These cyclic chases and cessation of behavioral activity continued over a two-hour period. Meanwhile, other bottlenose dolphins that were present were left alone to forage on the bottom and were not pursued by the spotted dolphins. In addition,

Figure 8. Two male bottlenose dolphins with erections attempt to side-mount a male spotted dolphin.

mother/calf spotted dolphin pairs swam on the periphery of the activity and did not interact with the bottlenose dolphins.

Adult bottlenose dolphins/juvenile male spotted dolphins. In addition to the above interactions involving adults, interspecific sexual interactions also occurred between juvenile groups of both species, and between adult bottlenose dolphins (males and females) and juvenile male spotted dolphins. Although similar behavior patterns were observed during juvenile activity, behaviors rarely escalated and intensified to the degree that they did during adult behavior. Some sequences are described below.

On 5 August 1993 (1900–2000 h), two adult female bottlenose dolphins were observed alternately side mounting a two year old male spotted dolphin calf (with his mother present) and then tail-slapping him in the head. This was followed by the young male spotted dolphin rubbing the fluke of the female bottlenose with his pectoral flipper. Penile erection was not observed.

On 27 July 1994 (1600–1640 h), one female bottlenose dolphin and eleven juvenile male spotted dolphins were observed together. The bottlenose dolphin chased, bit, and threatened the juvenile male spotted dolphins, especially the oldest one. The male juvenile spotted dolphins then synchronized their inverted swimming behavior and chased the bottlenose dolphin away.

On 19 September 1995 (1145–1245 h) four adult bottlenose dolphins and seven juvenile male spotted dolphins were observed together. Juvenile male spotted dolphins coordinated their swimming behavior and chased and nipped at the male bottlenose dolphins. This behavior escalated until one of the bottlenose dolphins began to rapidly chase one of the juvenile male spotted dolphins.

Cooperative interaction

Interspecific coalition formation—males. In addition to the intraspecific coalition cooperation during interspecies competition described above (see also Herzing, 1996), interspecific coalition formation has also been observed. In one example, juvenile male spotted dolphins joined a bottlenose coalition against an intruding bottlenose. This sequence began on 17 May 1993 (1630–1800 h) when two juvenile male spotted dolphins (GS, OR) were observed with nine bottlenose dolphins; two were known adult males, two were female, and the sex of the rest was unknown. The two male bottlenose dolphins repeatedly mounted GS as he floated passively. GS then swam behind them in an

arched posture while the bottlenose dolphins took turns tail-slapping GS on the head. Then the second juvenile male spotted dolphin, OR, joined GS, and they swam together as the male bottlenose dolphins pursued them. A new bottlenose dolphin (a particularly scarred up and thus easily identified individual) came in on the periphery of this activity. The two male spotted dolphins and two male bottlenose dolphins immediately synchronized their surfacing and swimming behavior. This interspecific coalition joined with the other bottlenose dolphins and confronted the intruding bottlenose dolphin in a head-to-head face-off. The interspecific group then chased the lone bottlenose away. They then pursued one of the female bottlenose dolphins in the group. However, unlike the male bottlenose dolphins, the spotted dolphins were not thereafter observed to mount or copulate with the pursued female.

A similar incident occurred on 5 August 1994 (1430–1520 h) thirty spotted dolphins and seven bottlenose dolphins were observed together. Two of the bottlenose dolphins were engaged, intraspecifically, in aggressive behavior, including a head-to-head stand-off. One of the bottlenose dolphins broke away, joined a coalition of male spotted dolphins that were approaching from another direction, and the interspecific group then chased the other bottlenose dolphin away.

In a third example, on 9 August 1994 (1445–1815 h), an adult male bottlenose dolphin was observed to join a male spotted dolphin coalition in the pursuit of a female spotted dolphin. The bottlenose dolphin did not engage in copulation attempts but was actively engaged in the chase. This chase occurred in the context of foraging, following an incident of interspecific-male-to-male aggressive/sexual play (as described above), between that same bottlenose male and the spotted coalition.

In a fourth incident, on 3 June 1993 (1550–1630 h) eleven spotted dolphins and four bottlenose dolphins were observed together. A juvenile male spotted dolphin was engaging in aggressive/sexual play with a male bottlenose dolphin. The coalition of male spotted dolphins confronted with the young spotted dolphin and began chasing and buzzing him in a disciplinary manner (Herzing, 1996). The young spotted dolphin was then joined by the group of bottlenose dolphins and pursuit by the spotted male coalition ceased.

Interspecific travel—pregnant females. While mixed-species traveling could consist of single or mixed-sex groups, of particular interest were groups of females of similar reproductive status. For example, on 20 July 1993 (1900–1930 h), pregnant females of both species were observed traveling together. Three late pregnant adult spotted dolphins (two with their older offspring present), and two pregnant female bottlenose dolphins swam along together. Although each species stayed closest to its conspecifics, they traveled as a group in the same direction. Interestingly, traveling is the only behavioral activity in which visibly pregnant females (estimated at the six month stage) of the two species have, as yet, been observed together.

Interspecific alloparental care. On 19 March 1989 (0900–0930 h), ten spotted dolphins and one bottlenose calf were observed together. Four of the spotted dolphins, including two males and two females were identified as part of our regular study group. Among these was a young adult female spotted dolphin (WP) who was swimming with the yearling bottlenose dolphin calf. The calf appeared emaciated and appeared to have a sunken melon/blowhole area (Fig. 9). The calf swam underneath WP in a position similar to intraspecific mother/calf formation. No nursing was observed but WP and the calf swam together for most of the encounter. No other bottlenose dolphins were observed in the area that day. Interestingly, WP has not yet given birth herself (as of 1996), and she has been visibly pregnant only once, although she is an estimated age of 16, well into the age of sexual maturity for spotted dolphins (Herzing, in press). During WP's interactions with conspecifics, she has repeatedly been observed care-taking young spotted dolphins and has consistently shown high coefficients of association with offspring of two to three years of age, from various mothers in the spotted dolphin group (D. Herzing & B. Brunnick, unpublished data).

A similar incident occurred in July 1996 where a young adult female spotted swam with a bottlenose calf in echelon position for over an hour. In this instance, there were bottlenose dolphins present in addition to spotted dolphins and the calf eventually returned to the bottlenose group.

Interspecific foraging behavior. On two sequential days in 1991, thirty spotted dolphins and one and two (respectively) bottlenose dolphins were observed foraging together on a concentrated patch of loose sand, 20 m × 20 m. This was an unusual event because of the density of dolphins in such a small area of bottom. On the first day, one bottlenose dolphin engaged in foraging behavior with the spotted dolphins for an hour without any apparent conflict. On the second day, bottlenose dolphins were observed foraging with the spotted dolphins. Five minutes into this observation, an escalated and aggressive fight broke out between the two species. The two bottlenose dolphins, who were foraging approximately five meters away from each other, joined up and synchronized their swimming activity, leaping out of the water as the

Figure 9. Young adult female spotted dolphin (WP) with an emaciated bottlenose dolphin calf beneath.

spotted dolphins chased them. Head-to-head posturing and various vocalizations were recorded during this bout, and continued as the spotted dolphins chased the bottlenose dolphins out of the area.

Discussion

Given the amount of time and effort these animals invest in interspecific interactions, one has to wonder what, if any, biological payoffs are involved. Is this simply a case of two species incidentally, as it were, extending behaviors that have adaptive repercussions within their own species to the other dolphins that happen to share their habitat? Or does this extension also feed back on the fitness of these animals? One could speculate that there might be a variety of possible benefits to developing close social ties across species. These might include increased predator protection, modified competition for food resources, and—in as much as the animals do share a repertoire of vocal and gestural signals—the extension of parenting and/or coalitional strategies across species boundaries. Let us consider each of these in turn.

Predation

The issue of cooperation against predators must remain the most speculative, as we, like most dolphin observers in the field, have never witnessed an incident of predation. However, based on demographic data on infant mortality (Scott *et al*., 1996; Richards 1993; Herzing, in press), and the presence of severe sharkbites, both the spotted and the bottlenose dolphins appear subject to significant predation pressure from sharks. From the spotted dolphins' point of view, the fact that bottlenose dolphins are significantly larger (spotted dolphins have a maximum length of 2.2 meters while the bottlenose can reach 3.9 meters) might make them a useful ally against large sharks. In turn, the bottlenose could also benefit from such an association since, as our data indicate, interspecies groups are larger than single-species groups, and the greater combined mass of the mixed groups could be more effective at detecting, deterring or repelling predators.

Predator defense in mixed-species groups has been reported in several primate species (Struhsaker, 1981; Terborgh, 1983; Jolly, 1985, Waser, 1987), and in dolphins (Norris *et al*., 1978; Wursig, 1986; Corkeron, 1990; Pryor & Kang-Shallenberger, 1991) who also maintain overlapping ranges. These interactions can be either exploitative (e.g. one species responding to the alarm calls of another (Gautier & Gautier-Hion, 1969; Wiley, 1980; Munn, 1986), or allowing a species to attack the common predator) or more collaborative (e.g. interspecies mobbing of the predator). Either or both of these may occur in dolphins as well. In the Eastern tropical Pacific, for example, it has been suggested (Perrin *et al*., 1973) that the sympatric spinner dolphins, *Stenella longirostris*, and pantropical spotted dolphins,

Stenella attenuata, alternate periods of rest and activity, mutually benefiting from the alertness of the other species. Corkeron (1990) reported mixed-species activity and differences in group size during varying activity. In addition, evidence, from both captivity and the field, of cross species epimeletic or helping behavior in dolphins (Connor & Norris, 1981), further supports the possibility of cooperative defense, especially in the case of individuals with long-standing social ties.

Foraging

Our data on foraging relations between these two species is also limited, in that mixed groups were least often observed (4.8% of encounters) in the foraging context. Spotted dolphin foraging takes place both during the day on the shallow sandbanks (Herzing, 1996) and at night in deep, offshore areas (D. Herzing, B. Brunnick & N. Matlack, unpublished data). Bottlenose foraging has only been observed during daylight hours on the shallow sandbanks (Herzing, 1996; Rossbach & Herzing, in press). It seems apparent that the dolphins are practising distinct foraging strategies, and are likely feeding on different prey species. In our relatively few observations of mixed-species foraging, some cases involved dolphins feeding independently and undisturbed in one another's proximity, while other incidents were interspersed with aggression or displacement activity. However it is unclear whether the latter should be considered a direct response to feeding competition or the incidental continuation of ongoing social interactions.

The question of whether these dolphins ever feed cooperatively remains unanswered. Atlantic spotted dolphins (Fertl & Würsig, 1995) and bottlenose dolphins (Leatherwood, 1975; Shane, 1990; Bel'kovich, 1991) have been documented as collaborating with conspecifics to herd, contain, and share a school of prey fish. In addition, multiple examples of apparent cooperative fishing between *Tursiops* sp. and humans have been reported (Lockyer, 1990). While we have no data that directly addresses whether this occurs between spotted dolphins and bottlenose dolphins in the Bahamas, our observations of a mixed group of these animals cooperating in socio-sexual aggression against another group does provide some precedent for interspecies cooperation in these animals.

Social behavior

In such similar species, who encounter one another on a regular basis in clear waters, a variety of gestural signals may be recognized and even co-opted across species boundaries (Tavolga, 1966; Norris, 1967; Caldwell & Caldwell, 1977; Johnson & Norris, 1994). Signal co-optation and interspecific acoustic signal recognition has been described in songbirds (Baptista & Morton, 1981), humans and dogs (McConnel, 1990), and in many bird, fish, and insect species (Smith, 1977; Hart, 1996). Friendly associations between primates have also been described (Klein & Klein, 1973; Waser, 1982, 1987; Jolly, 1985). In dolphins in particular, the streamlining of their form, through evolution, for hydrodynamic efficiency, has limited their range of gestural signals relative to other mammals (Johnson & Norris, 1986). Such limitations converge across delphinid species, increasing the likelihood of a shared gestural repertoire. In fact, signal recognition has already been described between the two species observed in this study, for both acoustic signals (Caldwell *et al*., 1971) and behavioral cues (Wood, 1953). On the other hand, differences across species may also tell us something about differences in temperament, in mating or competitive strategies, in the meaning of signals within a specific context, and perhaps even in the propensity to imitate. Let us consider some of the cross-species social interactions reported in this and other delphinid studies.

Alloparental care

One advantage to similarities in anatomy and behavior may be the occasional incidence of interspecies alloparenting. In addition to the incidents reported here of alloparental care and pregnant female interspecific travel, Leatherwood & Reeves (1978) described a captive bottlenose dolphin calf pairing with a female spotted dolphin while its mother performed in shows. Other examples from the wild include Bearzi's (1996) description of alloparental care by a common dolphin (*Delphinus delphis*, toward a bottlenose calf in northern Adriatic waters and, in French Polynesia, M. Poole (pers. comm., April 1996) has observed a young spinner dolphin, *S. longirostris*, less than three years of age, regularly associating with a bottlenose dolphin community.

Aggression

Shared aggressive behaviors, including open-mouth threats, squawks, and head-to-head posturing, have been described for various delphinid species, including *Tursiops truncatus* (Caldwell & Caldwell, 1967; Overstrom, 1983; Herzing, 1988) and *Stenella plagiodon* (Wood, 1953). Aggressive behavior between intraspecific male coalitions has also been reported in bottlenose dolphins, *Tursiops aduncus* (Connor *et al*., 1992), in pantropical spotted dolphins, *Stenella attenuata*, in tuna purse-seine nets (Pryor & Kang-Shallenberger, 1991) and in Atlantic spotted dolphins, *Stenella frontalis* (Herzing, 1996). Given these similar repertoires, it is

not surprising that such interactions have also been observed across species.

In addition to the interspecies aggression reported here, similar observations have also been made between *Tursiops* and *Stenella* in captivity (Wood, 1953). Aggressive bottlenose dolphins have also been reported actually killing harbor porpoise, *Phocoena phocoena*, in the Moray Firth, Scotland (Ross & Wilson, 1996). Harassment of a neonate harbor porpoise, *Phocoena phocoena*, by a Pacific white-sided dolphin, *Lagenorhyncus obliquidens*, has been reported (R. Baird, pers. comm., January 1997). Aggressive encounters between other sympatric delphinids include Risso's dolphins, *Grampus griesus*, and pilot whales, *Globicephala macrorhyncus*, in southern California waters (Shane, 1995). All of the above groups have also, at times, been observed to coexist without overt aggression. Understanding the conditions that elicit such agonism poses a challenge to future dolphin research.

Socio/sexual activity

In spotted dolphins, both male-to-male and female-to-male coupling nearly always occurs in the ventro–ventro position. In contract, the male bottlenose dolphins typically attempt to mount the spotted dolphins in a 'sidemount' orientation during interspecific copulation. Such sidemounts have also been observed in intraspecies interactions between bottlenose dolphin males (McBride & Hebb, 1948; Tavolga & Essapian, 1957, 1966; Caldwell & Caldwell, 1967, 1977; Osman, 1991). Interestingly, in July 1996, D.H. observed an exception to the above-described pattern for spotted dolphins. Shortly after a male spotted dolphin had been sidemounted by a male bottlenose dolphin, that spotted male was one of two individuals observed sidemounting a female spotted dolphin. This incident appeared to be an example of mimicry of the sidemount behavior, as this sequence lacked any of the normal foreplay activity characteristic of spotted dolphin mating behavior.

Interspecies coalitions

Among the most remarkable and unexpected findings reported in this study was the occurrence of interspecies coalitions. Intraspecific coalitions of bottlenose males have been observed elsewhere both pursuing females and engaging in intercoalitional aggression (Connor *et al*., 1992), and in herding females (Wells *et al*., 1987). Coalitional behavior of male spinner dolphins (Johnson & Norris, 1994) and male pantropical spotted dolphins (Pryor & Kang-Shallenberger, 1991) have also been described. Similar behavioral types of interspecific (vs intraspecific) interactions were observed across species in our study. In one case, male spotted dolphins joined male bottlenose dolphins pursuing a female bottlenose dolphin and, in another, one bottlenose dolphin joined a male spotted dolphin coalition pursuing a female spotted. It is interesting to note, however, that in both cases, the subsequent mating behavior was only intraspecies.

Participating in such cross-species pursuits, along with repeated incidents of interspecies aggressive/sexual play, may be a means of helping to forge bonds between familiar males of these two species. Such bonds apparently came into play in the other cross-species coalitional interactions. In one of these, a pair of bottlenose dolphins joined a male spotted dolphin coalition to chase off an unfamiliar bottlenose dolphin and, in the other, one of a fighting pair of bottlenose dolphins joined a spotted dolphin coalition to chase off their conspecific opponents. Similarly, a male juvenile spotted dolphin, after engaging in aggressive/sexual play with a bottlenose dolphin, was able to avoid more serious harassment from a coalition of adult spotted dolphins when joined by that bottlenose dolphin and its conspecific cohorts. Thus, while the relationship between male spotted dolphins and bottlenose dolphins is often antagonistic—with the bottlenose dolphins dominating the spotted dolphins unless the spotted dolphins significantly outnumber them—there is apparently, at times, a kind of balance struck between them, where they may also come to one another's aid. Such agonistic aid across species may be an additional example of reciprocal altruism in these animals (Connor & Norris, 1981; Nishida & Hiraiwa-Hasegawa, 1986; De Waal & Harcourt, 1992).

The question of species boundaries

Despite their overlapping behavioral repertoires, hybrids between bottlenose and spotted dolphins in the Bahamas have not yet been observed. Isolating mechanisms, geographical or behavioral, are apparently successful in keeping these free-ranging species reproductively separate. For example, although bottlenose males seem to have many opportunities to mate with receptive female spotted dolphins proximity-wise, behaviorally these females are usually monopolized by coalitions of male spotted dolphins. It may be that intraspecies coalitional behavior among males not only serves to maximize the reproductive success of potential sires, but may serve to ward off and intercept any inappropriate mating activity between the species.

That such isolating mechanisms are required is supported by the occurrence of delphinid hybrids in captivity. For example, captive bottlenose dolphins have been successfully crossed with many species including the rough-toothed dolphin, *Steno bredanensis* (Dohl *et al*., 1974), the false killer

whale, *Pseudorca crassidens* (Nishiwaki & Tobayama, 1982), and both the Risso's dolphin, *Grampus griseus*, and pilot whales, *Globicephala macrorhyncus* (Leatherwood & Reeves, 1983; Sylvestre & Tanaka, 1985). At least one of these crosses (*Tursiops*/*Pseudorca*), has itself been successfully recrossed with a *Tursiops*, producing two second generation offspring.

Other cetacean hybrids have also been reported in the wild. For example, a fertile hybrid has been documented between a blue whale, *Balaenoptera musculus*, and fin whale, *Balaenoptera physalus*, in Norwegian waters (Arnason *et al*., 1991). The first known hybrid fetus in the porpoise family, between Dall's porpoise, *Phocoenoides dalli*, and the harbor porpoise, *Phocoena phocoena*, has been documented from waters in British Columbia, Canada (Guenther *et al*., 1995). And most recently a possible hybrid of the long-snouted common dolphin, *Delphinus capensis*, and dusky dolphin, *Lagenorhynchus obscurus*, has been reported in Peruvian waters (Reyes, 1996). A breakdown of interspecific sexual behavior isolating mechanisms between pinniped species has also been observed in the wild (Miller, 1996) and may suggest that this could occur in other species.

In addition to the above, recent anatomical (Perrin *et al*., 1987) and genetic (LeDuc & Dizon, 1993) studies have suggested that the Atlantic spotted dolphin, *Stenella frontalis*, may be closer to the bottlenose dolphin, *Tursiops aduncus* and *T. truncatus*, and common dolphin, *Delphinus delphis*, than to other *Stenella* species. This is interesting in light of the multiple affiliative interactions reported between *Stenella*, *Tursiops* and *Delpinus*. Thus, while no obvious hybrids have been observed in the current study and behavioral mechanisms that may serve to preclude cross-species reproduction seem to be in effect, the dividing line between these species may be more tenuous than has previously been supposed.

Conclusion

In the Bahamas, bottlenose dolphins and spotted dolphins have been observed using both intra- and interspecific cooperation for both interspecific and interindividual (intraspecific) conflicts. For social and cultural animals, such as primates and cetaceans, intragroup cooperation and competition may involve the fine art of sharing and co-opting signals and may include the necessity of establishing long-term relationships and patterns of familiarity with conspecifics as well as interspecific neighbors.

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