

Interactions Between Atlantic Spotted (*Stenella frontalis*) and Bottlenose (*Tursiops truncatus*) Dolphins off Bimini, The Bahamas, 2003-2007

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Abstract

Interspecific interactions have been observed in a variety of social animals. Functional explanations include foraging, anti-predatory, and social advantages. These behaviors are poorly understood in marine mammals but are increasingly studied phenomena in sympatric populations. Resident Atlantic spotted dolphins (*Stenella frontalis*) off Bimini, The Bahamas, have been the subject of ongoing photo-identification and behavioral studies since 2001. A lesser-known population of bottlenose dolphins (*Tursiops truncatus*) has been observed interacting with these *S. frontalis* since 2003. To examine the functional significance of these interactions, interspecific behaviors were documented with underwater video using focal animal sampling. Mating or sexual play were the primary activities observed in nearly 50% of interactions, with male *T. truncatus* as the initiators. Therefore, the most likely functional explanation for these interactions is social. We hypothesize that male *T. truncatus* which lack access to *T. truncatus* females because of sexual immaturity or low social status seek copulations with *S. frontalis* females as an alternative.

Key Words: Atlantic spotted dolphin, *Stenella frontalis*, bottlenose dolphin, *Tursiops truncatus*, Bimini, interspecific interactions, mating

Introduction

Interspecific interactions occur between a variety of species in both terrestrial and marine habitats (Stensland et al., 2003). The primary functions of interspecific interactions are increased foraging efficiency and/or an anti-predation strategy in mixed species of primate groups (Hardie & Buchanan-Smith, 1997; Mendes-Pontes, 1997; McGraw & Bshary, 2002), an anti-predation strategy in ungulates (Keast, 1965; Sinclair, 1985), foraging efficiency in terrestrial carnivores

(Kilian et al., 1991; Minta et al., 1992), and possibly a social function in pinnipeds (Kerley, 1983; Kovacs et al., 1997; Lancaster et al., 2006). Among cetaceans, the functional explanations are less clear (Shelden et al., 1995; Herzing & Johnson, 1997; Frantzis & Herzing, 2002; Herzing et al., 2003). However, combinations of foraging, anti-predatory and social functions have been suggested (Norris & Døhl, 1980; Scott & Chivers, 1990; Corkeron, 1990; Kenney, 1990; Baraff & Asmutis-Silva, 1998; Scott & Cattanach, 1998; Stensland et al., 1998; Acevedo-Gutierrez et al., 2005; Kristiansen & Forestell, 2007).

Mixed genera and higher taxa groups, including pantropical spotted dolphins (*Stenella attenuata*) or spinner dolphins (*S. longirostris*) that associate with yellowfin tuna (*Thunnus albacares*) to feed on smaller prey in the eastern tropical Pacific Ocean (ETP) led Scott & Cattanach (1998) to suggest both foraging efficiency and potential anti-predatory benefits to these gatherings. The dolphins might follow the tuna, which regularly drive dolphin prey to the surface, or the tuna could be following the dolphins for the same purpose. However, both tuna and dolphins are at risk from shark predation, so their associations potentially reduce their individual risk via the Dilution Effect, Confusion Effect, or Detection Effect (Krebs & Davies, 1993; Scott & Cattanach, 1998).

S. longirostris have been observed approaching groups of *S. attenuata* during the former's daytime rest periods in the ETP. In this case, *S. attenuata* were alert and feeding in the open ocean, and they potentially provided respite from vigilance for the resting *S. longirostris* (Norris & Døhl, 1980). The function of these mixed-species groups was suggested as a likely anti-predation strategy on the part of *S. longirostris* (Norris & Døhl, 1980; Scott & Cattanach, 1998).

Immature Indo-Pacific bottlenose dolphin males (*Tursiops aduncus*) have also been observed mating with female Indo-Pacific humpback dolphins (*Sousa chinensis*) off the coast of Zanzibar

(Stensland et al., 2003). While it is unknown if these interactions resulted in hybrid offspring, the young age of the *T. aduncus* involved suggests the practice of adult behaviors and, thus, a social rather than a reproductive function (Stensland et al., 2003).

This paper describes interactions between *Stenella* and *Tursiops* off the coast of Bimini, The Bahamas, from 2003 to 2007. Duration of observations and interactions, environmental conditions, group composition, individual reoccurrence, and behavioral contexts are reported, and potential functional explanations are considered. Of the three potential explanations for interspecific interactions, we hypothesize that social advantages are the most likely explanation for the *Stenella*/*Tursiops* groups observed in this study.

Materials and Methods

Study Area

The study was conducted west and north of North Bimini Island, The Bahamas. The survey area, the northwest portion of the Great Bahama Bank directly adjacent to the Gulf Stream, is bounded north/south from 25° 42' N to 25° 54' N and east/west from 79° 11' W to 79° 16' W (Figure 1). Although there are scattered ledges and coral heads present, the study area consists primarily of 6 to 12 m depths with a white sandy sea floor.

Surveys were conducted from aboard local eco-tour vessels (12.8 m *Stapleton*, 11.6 m *Delta*, or 12.8 m *Hatteras*) typically during the 4 to 5 h prior to sunset. A total of 233 boat trips were completed during this 5-y period (2003 to 2007; 33, 40, 44, 55, and 61 trips, respectively), resulting in 996 h searching for dolphins. Sightings were defined as time with dolphins in view, beginning with initial surface observation, through any underwater encounters and any surface observations that followed. Encounters were defined as underwater observations > 3 min in duration with dolphins in visual range (Dudzinski, 1996).

Study Animals

S. frontalis have been the focus of long-term behavioral ecology studies conducted by the Dolphin Communication Project (DCP) around Bimini, The Bahamas, since 2001 (DCP, unpub. data). They were classified by age according to the development of pigmentation along their bodies. Each individual's spot pattern is unique and, along with nicks and scars, can be used to identify individual animals over time (Table 1; Perrin, 1970; Dudzinski, 1996; Herzing, 1997). Sexual dimorphism in *S. frontalis* is too subtle for field use. There are 89 individual *S. frontalis* cataloged in Bimini. The sex ratio for individuals of

identified sex is estimated 2:1 (female:male). The sex is unconfirmed for 37 individual *S. frontalis*; therefore, the sex ratio estimate should be viewed with caution considering that the number of individuals with uncategorized sex is equal to roughly a third of the study population.

T. truncatus were also observed within the study area. Individuals were recognized by the shape of and nicks or scars present on the dorsal fin (Würsig & Würsig, 1977) as well as by any distinguishing markings observable elsewhere on the body. Age estimates were based on length and girth relative to adult females (Table 2; Shane et al., 1986). The age class of an individual was considered unknown if the proximity of the individual or water clarity made classification uncertain; however, in all cases during this study, unknown age classification for *T. truncatus* indicated an inability to distinguish between subadult and adult. Size varies between inshore and offshore populations, but males tend to be larger among all *T. truncatus* groups (Reeves et al., 2002). As with *S. frontalis*, this sexual dimorphism is too subtle for field use. The size, sex ratio, and range of the Bimini *T. truncatus* are unknown at this time.

Stenella in this area is in frequent contact with and is habituated to the presence of boats and human swimmers because they are the primary subjects of commercial swim-with-dolphin programs as well as DCP's long-term research studies. *Tursiops* appears less tolerant than *Stenella* of boats or human swimmers within close proximity; however, both species were observed throughout the study period.

Data Collection

Photographic and behavioral data were collected using digital video cameras encased in underwater housings. Two different underwater housings (a TopDawg by Light in Motion, Monterey, CA, USA, and a custom-built mobile video/acoustic system [Dudzinski et al., 1995] with two omnidirectional hydrophones) were used. Video data were collected employing a focal-animal-follow sampling protocol (Altman, 1974; Mann, 1999) in which the first, random animal in view is the focal animal and was recorded until it went out of the camera's field of view. However, when mixed-species encounters began with a group of dolphins in the video-frame, rather than a focal individual, effort was biased toward *Tursiops* as the focal animal to document as many *Tursiops*' behaviors as possible.

Individual dolphins were identified opportunistically using underwater digital still photographs. A Canon Rebel XT digital camera (8 megapixels) with a 55- to 200-mm lens was used above water to photograph *Tursiops*' dorsal fins for identification

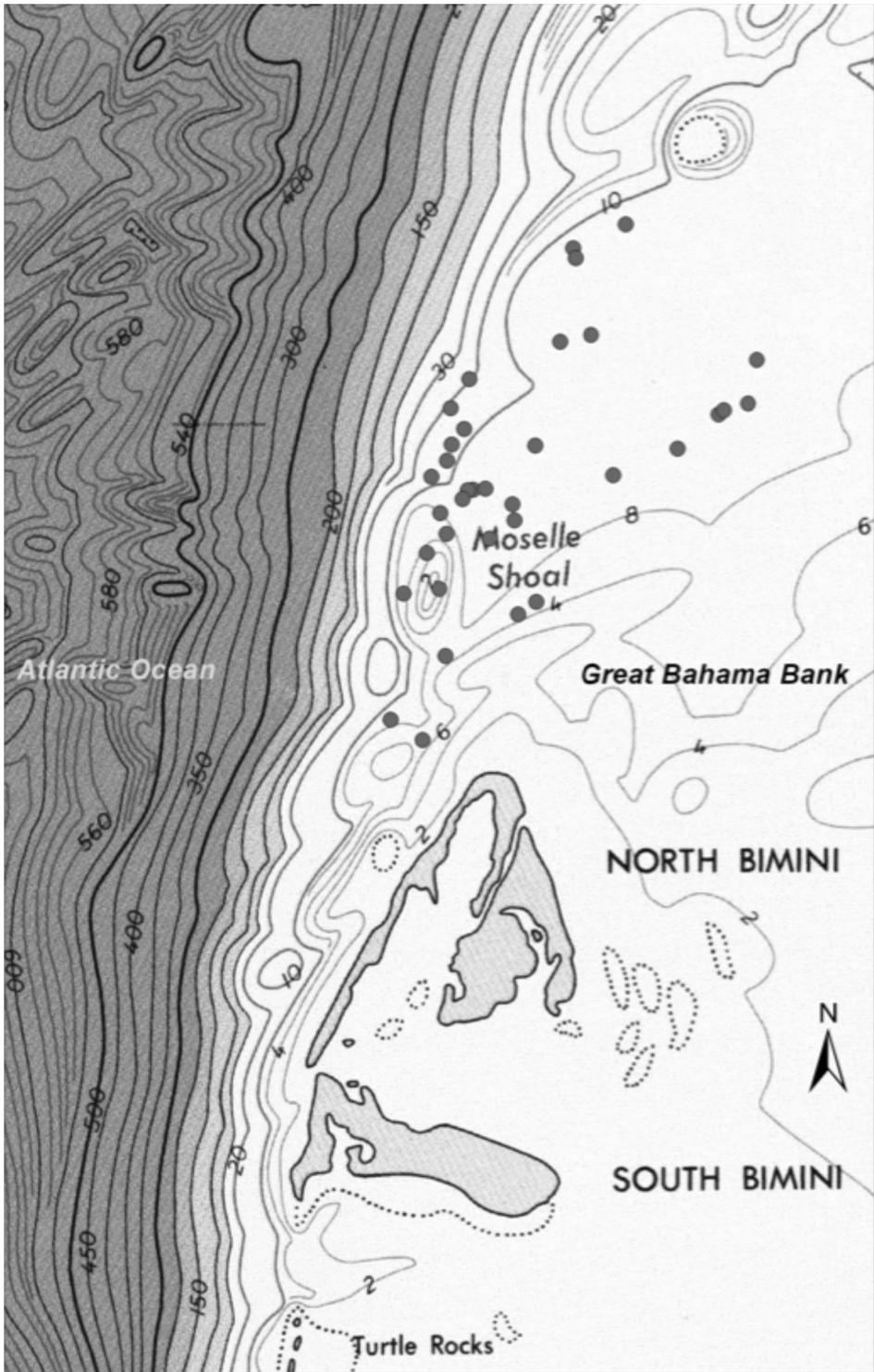


Figure 1: Mixed-species observations were distributed throughout the study area along the western edge of the Great Bahama Bank. Map credit: NOAA

Table 1. Age class designations and descriptions of *Stenella*, after Perrin (1970)

Age class	Age group	Coloration	Pattern type
1	Neonate (< 3 wks)	Gray and ivory, with fetal folds	Neonatal
2	Calf (3 wks < 4 y)	Dark gray dorsal and light gray ventral	Two-tone
3	Juvenile (4 < 7 y)	Dark dorsal, light ventral, and few spots	Speckled
4	Subadult (7 < 10 y)	Entire body spotted	Mottled
5	Adult (10+ y)	Black mask, heavily spotted, spots fused, and faded ventrally	Fused

Table 2. Age class designations and descriptions of *Tursiops* (Shane et al., 1986)

Age class	Age group	Description
1	Neonate (< 3 wks)	¼ length of adult; fetal folds present
2	Calf (3 wks < 4 y)	Approximately ½ length of adult; no fetal folds, slender
3	Juvenile (4 < 7 y)	Approximately ¾ length and slender
4	Subadult (7 < 10 y)	¾ to similar length as adult, but girth < adult
5	Adult (11+ y)	Largest girth; female often with calf

beginning in 2006. Individuals were added to photo-identification catalogs after both sides of the animal were documented (*Stenella*) or clear, high-resolution photographs of the complete dorsal fin were obtained (*Tursiops*). Individual identification from video and still pictures was confirmed by at least two trained DCP researchers. A hand-held Garmin GPS was used to mark the dolphins' location at each sighting. Depth and environmental data (Table 3) were also recorded for each dolphin sighting.

Data Filtering and Analyses

Video segments with clear focal and affiliate animals and positively identified species were examined for species confirmation, age class, sex of individuals, and whether known individuals were present. Affiliates were defined as non-focal animals visible in the video-frame and were numbered by proximity to the focal animal at the time they appeared in the frame (i.e., affiliate1, affiliate2, etc.). Animals were not renumbered if they changed position during the sequence. Sex was determined by clear observation of the genital

area (i.e., presence or absence of mammary slits) or penile erection.

Behaviors were classified according to Dudzinski (1996, 1998) and are applicable to both species. A subset of behaviors, including actions related to body position of two or more dolphins and their behavioral interactions (e.g., slow swimming, rubbing, or one dolphin pushing another into the sand), was used to investigate interspecific interactions. Behaviors were categorized as sexual, aggressive, affiliative (e.g., travel, play, and neutral associations; Herzing & Johnson, 1997), investigative (e.g., head scanning or echolocation clicks), or foraging. Video segments were broken into focal observations to allow for frequency analysis. Each time (1) the focal animal changed, (2) the behavior of a focal or affiliate animal changed, or (3) a new affiliate animal entered the video-frame, a new focal observation was designated.

SPSS, Version 15, for Windows was used to calculate means for environmental data and determine frequencies of behaviors and group composition (i.e., species, age class, sex, and individuals) of focal groups. Even when species was confirmed, not all individuals could be identified with respect to a specific number in the photo-ID catalog; therefore, a subset of video data, where all individuals were identifiable to the catalog level, was analyzed for the reoccurrence of individuals in mixed-species groups over time. Results are reported as mean \pm 1 standard error unless otherwise stated.

Results

Sighting and Encounter Summary

From June 2003 to September 2007, a total of 451 sightings of and 262 encounters with *Stenella* and/or *Tursiops* in single- or mixed-species groups

Table 3. Environmental variables

Underwater visibility	Estimated and grouped in increments of 3 m (< 3 m, 3-9 m, 9-12 m, 12+ m)
Cloud cover	Estimated percent cloud cover within visible sky
Sea state	Based on Beaufort scale (1 = ripple-like scales; 2 = small wavelets; 3 = large wavelets, scattered whitecaps; 4 = small waves, fairly frequent whitecaps)

were recorded. Of these observations, 40 (8.87% of 451) were sightings of mixed-species groups and 34 (12.98% of 262) were encounters with mixed-species groups. Sightings of and encounters with mixed-species groups were distributed throughout the study area (Figure 1). Mean durations of mixed-species sightings and encounters were 27.24 ± 3.53 and 15.35 ± 2.88 min, respectively. Mean group size of mixed-species groups observed from the boat was 12 animals. Of the 34 mixed-species encounters, 15 yielded useable video data segments, totaling 73 min 32 s ($\bar{x} = 5$ min 15 s \pm 68 s), which were used in the remaining analyses. Mixed-species observations occurred an average of 98.33 ± 13.28 min before sunset, in mean water depth of 13 ± 2 m, most frequent underwater visibility of 3 to 9 m, cloud cover of 50%, and Beaufort sea state of 2.

Photo-Identification

A total of 89 reliably recognizable individual *Stenella* and 24 individual *Tursiops* were identified and cataloged during the 5-y study period (Table 4). *Tursiops* identified thus far around Bimini match the description (e.g., size, coloration) for the coastal ecotype (Rossbach & Herzing, 1999; Reeves et al., 2002; Parsons et al., 2006), although offshore *Tursiops* were observed on at least one occasion off Bimini during this study period (Melillo, pers. obs.) and once previously by another team of researchers in the same study area (Herzing et al., 2003).

Group Size and Composition

Within the 15 segments of video data, there were 284 separate focal observations. The maximum number of both *Stenella* and *Tursiops* in each mixed-species group was four individuals per species. The total number of animals in the video-frame at one time ranged from one to five individuals (22.9%, 27.8%, 19.0%, 21.1%, and 9.2%

of observations, respectively). Most commonly, there was one *Stenella* (36.6%) and one *Tursiops* (58.8%) per focal observation.

Focal and affiliate animals classified by species, age class, and sex are summarized in Table 5. During mixed-species observations, *Tursiops* more commonly (66.2%) represented the focal animal; however, *Stenella* represented the majority of all other positions (affiliate1 through affiliate4; 68.7%, 72.3%, 90.0%, and 75.0%, respectively). The predominance of *Tursiops* as focal animals is an artifact of the bias toward this species in data collection previously described. There were no confirmed *Tursiops* calves or juveniles during mixed-species observations, and the most commonly observed *Tursiops* were subadult (34.0%). All age classes of *Stenella* were observed at least once during mixed-species observations. Both males and females of each species were observed at least once. Confirmed sex observations of *Tursiops* were 64.4% males.

Cataloged individuals observed in mixed-species encounters are summarized in Table 6. Not all videotaped animals could be positively identified as cataloged individuals. There were no confirmed repeat sightings of cataloged *Tursiops* across multiple mixed-species observations; however, some individually identified *Stenella* were seen during more than one mixed-species observation.

Observed Behaviors

In seven of the 15 video segments, mating or sexual play behaviors occurred at least once. Among all focal observations, for both focal and affiliate animals, the most common behavioral category was affiliative. For the focal, affiliate1, and affiliate2 animals, the 2nd, 3rd, and 4th most common behavior categories were sexual, aggressive, and investigative, respectively (Figure 2). Only the focal and affiliate1 animals were ever observed foraging. For affiliate3 animals, aggressive and investigative were the 2nd and 3rd most common behavioral categories. For affiliate4 animals, investigative behaviors were the 2nd most common, with both sexual and aggressive behaviors equally the 3rd most common. (See video hyperlink: www.aquaticmammalsjournal.org/Video/index.htm.)

Discussion

Interactions between *Stenella* and *Tursiops* off Bimini, The Bahamas, were observed only 40 times out of 451 total sightings (281 *Stenella*-only, 110 *Tursiops*-only, 20 species unknown) during the 5-y study period, indicating that mixed-species groups are relatively uncommon. However, these results suggest that mixed *Stenella/Tursiops*

Table 4. Breakdown of age class and sex of known individuals among *Stenella* and *Tursiops*

	<i>Stenella</i>	<i>Tursiops</i>
Total	89	24
Calf	9	0
Juvenile	16	0
Subadult	15	4
Adult	49	1
Unknown age class	0	19
Female	35	1
Male	16	2
Unknown sex	38	21

Table 5. Breakdown of age class and sex by focal or affiliate position and species; Tt = *Tursiops truncatus* and Sf = *Stenella frontalis*

	Calf	Juvenile	Subadult	Adult	Unknown age	Male	Female	Unknown sex
Focal Tt (<i>n</i> = 188)	0.0%	0.0%	34.0%	7.4%	58.5%	64.4%	4.8%	30.9%
Focal Sf (<i>n</i> = 96)	16.7%	56.3%	5.2%	14.6%	7.3%	7.3%	39.6%	53.1%
Affiliate1 Tt (<i>n</i> = 67)	0.0%	0.0%	10.4%	0.0%	89.6%	56.7%	1.5%	41.8%
Affiliate1 Sf (<i>n</i> = 147)	25.9%	56.5%	0.0%	4.8%	12.9%	10.2%	12.2%	77.6%
Affiliate2 Tt (<i>n</i> = 39)	0.0%	0.0%	2.6%	0.0%	97.4%	61.5%	0.0%	38.5%
Affiliate2 Sf (<i>n</i> = 102)	33.3%	52.0%	1.0%	3.9%	9.8%	5.9%	10.8%	83.3%
Affiliate3 Tt (<i>n</i> = 9)	0.0%	0.0%	22.2%	11.1%	66.7%	22.2%	0.0%	77.8%
Affiliate3 Sf (<i>n</i> = 81)	19.8%	58.0%	0.0%	2.5%	19.8%	1.2%	29.6%	69.1%
Affiliate4 Tt (<i>n</i> = 7)	0.0%	0.0%	28.6%	0.0%	71.4%	0.0%	0.0%	100.0%
Affiliate4 Sf (<i>n</i> = 21)	9.5%	61.9%	4.8%	0.0%	23.8%	33.3%	9.5%	57.1%

Table 6. Individual photo-ID code (species, number, Tt = *Tursiops truncatus*, and Sf = *Stenella frontalis*), sex, age class, and the frequency that individual was observed in mixed-species observations during the study period; where age class crosses two classifications, this individual's age class changed during the study period.

Individual ID	Sex	Age class	Frequency observed
Tt02	Female	5	1
Tt04	Unknown	4	1
Tt20	Unknown	4	1
Tt21	Male	4	1
Tt23	Male	4	1
Sf04	Male	4	1
Sf10	Female	¾	2
Sf14	Female	¾	3
Sf17	Male	5	1
Sf36	Female	¾	1
Sf38	Female	4	1
Sf76	Female	¾	3
Sf78	Male	3	2
Sf79	Male	3	2
Sf80	Female	3	2
Sf87	Female	2	1

groups off Bimini are likely social in nature and may also confer some anti-predation advantages.

Social Advantages

The social advantages possible through mixed-species groupings can be divided into at least three categories: (1) reproduction, (2) aggression diffusion, and (3) alloparenting. Nearly 50% of the recorded mixed-species interactions during this study included mating or sexual play, suggesting a reproductive function for these encounters, with some support for aggression diffusion as well.

These behaviors were always initiated by subadult or unknown aged (indicating borderline between subadult and adult) *Tursiops*; however, challenges in determining *Tursiops* sex limits potential discussion of a male *Tursiops* strategy.

Both *Stenella* and *Tursiops* are polygynandrous (both males and females have multiple partners; Dudzinski, 1996; Mesnick & Ralls, 2002); however, variation in observed behaviors among delphinid species supports the idea that mating strategies differ between populations, particularly among *Tursiops* (Parsons et al., 2003). *Tursiops*-only groups are rarely observed mating in the study area, so the role of male alliances and herding of females (Connor et al., 2000, 2001; Möller et al., 2001; Parsons et al., 2003) in this population is unknown. Little is known about *Stenella* mating strategies; however, observations of *Stenella*-only mating groups in Bimini have generally included at least 10 individuals clustered near the surface. The overall movement of a *Stenella* mating group was often too swift to allow for detailed underwater observations.

Sexual behaviors in *Stenella/Tursiops* groups more closely resembled *Tursiops* herding behavior as the activity generally progressed toward the sea floor with one to two *Tursiops* males in pursuit of a single *Stenella*. The sex and age of *Stenella* in these encounters varied, and other *Stenella* were typically within close proximity. It is possible that the size advantage of *Tursiops* predisposes them toward dominant behaviors; however, the lack of retaliation or retaliation attempts by *Stenella*, despite their ability to do so (Herzing & Johnson, 1997; Dudzinski, unpub. data) suggests that *Stenella* might not perceive the *Tursiops* as a threat. Male *Stenella* were never observed instigating sexual interactions (indicated by erections) with *Tursiops*, although Herzing et al. (2003) reported a single such observation off Bimini. *Stenella* may therefore instigate sexual interactions

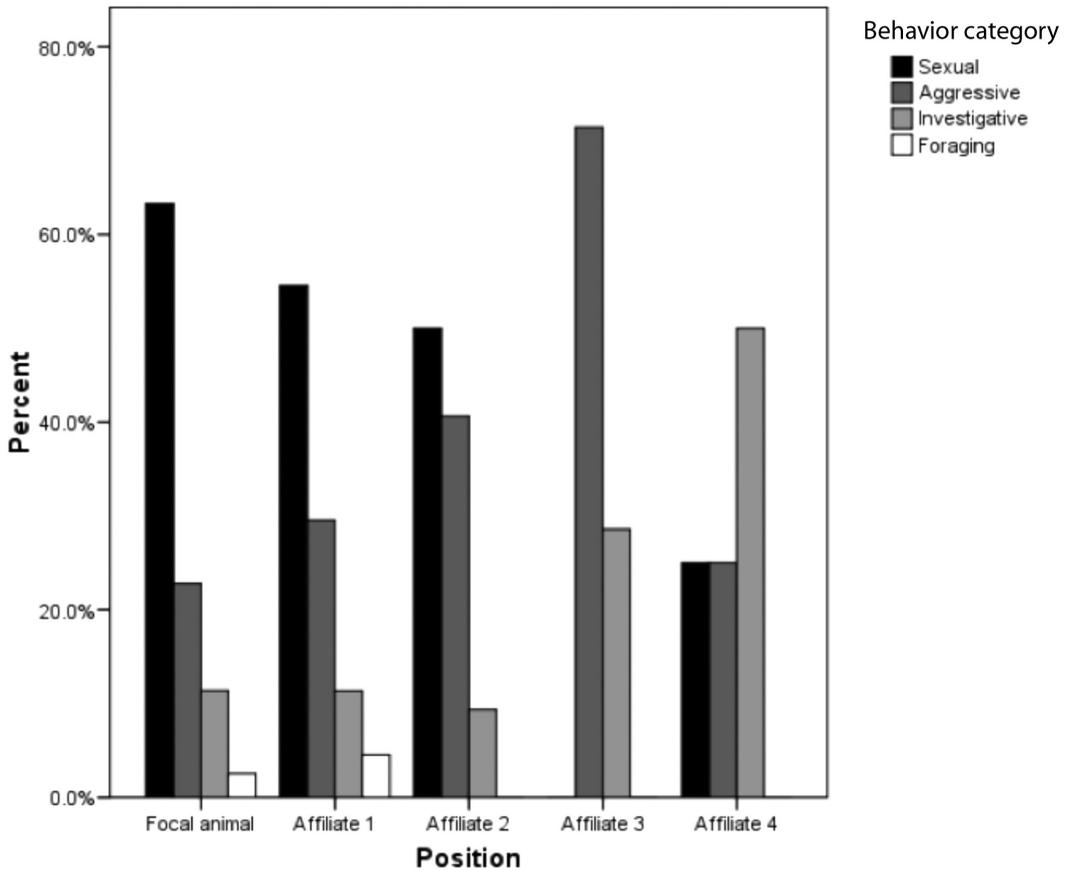


Figure 2. Removing affiliative behaviors from consideration, the most common behavior category among focal, affiliate1, and affiliate2 animals was sexual; aggressive behavior among these individuals appears inversely related to sexual behaviors with a peak in aggression among affiliate3 animals. Sample sizes are as follows: focal, $n = 284$; affiliate1, $n = 213$; affiliate2, $n = 141$; affiliate3, $n = 90$; and affiliate4, $n = 28$.

with *Tursiops*, but this is not the typical scenario observed in Bimini. Herzing & Johnson (1997) also reported two adult female *Tursiops* soliciting sexual interactions from two juvenile male *Stenella* in the Little Bahama Bank population. However, only one female *Tursiops* was observed in mixed-species groups in the Bimini population during this study; therefore, interspecific sexual interactions may be a *Tursiops* male strategy at this site. More data with confirmed bottlenecked sex are required.

Individuals of both species might gain from these interactions given the social role of sex in delphinids (Norris & Døhl, 1980; Wells, 1984; Connor et al., 2000) and if immature sexual behavior is considered in the context of play. Immature animals' behavior is more plastic than that of adults; and play behaviors, including interspecific play, could help shape adult behaviors (Spinka et al., 2001; Stensland et al., 2003). The high frequency

of reproductively immature *Stenella* and *Tursiops* in the mixed-species groups in this study supports this possibility. The high frequency of immature animals also suggests that *Tursiops* genes are not being successfully passed on; however, the possibility of hybrids cannot be ruled out.

Although territoriality is rare in cetaceans (Miller, 2002) and observed behaviors within this study group do not suggest territoriality (Mitani & Rodman, 1979; Grant et al., 1992), it is possible for conflicts to arise when the two species encounter each other in overlapping areas of their range. Interspecific sexual interactions might serve to diffuse tensions in mixed-species groups. When examining behavioral patterns without the neutral category of "affiliative," an inverse relationship between sexual and aggressive behaviors emerges as animals are further removed in the group from the focal and affiliate1 individuals (Figure 2). The diffusion of aggression through sexual

behaviors is common within pygmy chimpanzee (*Pan paniscus*) groups (de Waal, 1997). *Stenella* and *Tursiops*, like *P. paniscus*, both have complex, fission-fusion social systems (Wells et al., 1980; Dudzinski, 1996; Bearzi & Stanford, 2007) and engage in sex with multiple partner combinations (de Waal, 1997; Hohmann & Fruth, 2003), including those incapable of reproduction (e.g., non-ovulating female-male, male-male, female-female, adult-juvenile). Perhaps, like *P. paniscus*, *Stenella/Tursiops* groups substitute sexual behaviors for rivalries (de Waal, 1997) as indicated by the spike in aggression as individual dolphins become further removed from sexual interactions (Figure 2).

Alloparental care (Riedman, 1982) has been observed in both captive and wild mixed-species groups (Bearzi, 1996; Stensland et al., 2003). In the present study, no *Tursiops* calves were observed in mixed-species groups. There was a single observation of an adult female *Tursiops* that appeared to be pregnant (ventral posterior area visibly swollen) in the midst of a *Stenella* group. This is the only confirmed female *Tursiops* in a mixed-species group in this study, and the female exhibited only affiliative behaviors.

Foraging Advantages

Throughout the study period, only two mixed-species focal groups were observed in close proximity to potential prey. During the first of these sessions, two *Tursiops* were actively bottom-grubbing (crater-feeding). There was no feeding on the part of the two *Stenella*. The second mixed-species observation in close proximity to potential prey involved a single adult *Tursiops* (unknown sex) approaching a mixed-age group of *Stenella*, which was investigating a school of jacks (Carangidae). No dolphins of either species made any attempt to capture fish; therefore, neither observation was indicative of foraging advantages. Interspecific foraging behaviors have been observed in the more northern Little Bahama Bank population of *Stenella* (Herzing & Johnson, 1997). The lack of observed foraging behaviors in mixed-species groups in Bimini could be related to the small sample size of mixed-species observations in the Bimini study population relative to the Little Bahama Bank population. Although a comparison in prey abundance between the two locations is not available, single-species groups have been observed foraging at both sites.

Anti-Predation Advantages

Predatory sharks (e.g., bull [*Carcharhinus leucas*], tiger [*Galeocerdo cuvier*], and hammerhead [*Sphyrna mokarran*, *S. lewini*]) are a likely source of injury and mortality for dolphins as indicated

by the presence of scars on both *Stenella* and *Tursiops* in the study area (Dudzinski & Melillo, pers. obs.). *Stenella* may encounter reduced predation risk from sharks in the presence of larger *Tursiops*, and both species may benefit from the increased size of mixed groups (Norris & Schilt, 1988; Herzing & Johnson, 1997). However, shark predation attempts were never observed during the study nor was the strategy of predator avoidance by alternating resting/active periods as seen in other mixed-species dolphin groups (Norris & Døhl, 1980). Both species may benefit from the Dilution Effect when in larger groups (Norris & Schilt, 1988), while individual *Tursiops* might gain added protection from joining a larger *Stenella* group. However, mixed-species groups in the study area were not observed in greater numbers than those of single-species groups. The smaller group sizes observed under water (vs the average mixed-species group size observed from the boat) are a factor of the limitation of the camera viewfinder and the fact that the groups were often dispersed over an area greater than the available underwater visibility.

Orange Cay

An exploratory research trip was conducted from 20 to 25 July 2007 to Orange Cay, The Bahamas (approximately 96 km south of Bimini), during which a *Stenella/Tursiops* group was observed. This single observation, however, did not fit the typical mixed-species observations off Bimini. Here, four *Stenella* (subadult and adult) entered a group of at least 10 *Tursiops* (mixed ages and sex) vs *Tursiops* joining young *Stenella* in Bimini. Off Orange Cay, slow swimming, interspecific rubbing, circleswims, teeth-raking, *Tursiops* erections, and interspecific intromission attempts were observed. Further population and behavioral studies are needed in this area to provide a more thorough comparison between populations; however, it is possible that interspecific interactions may vary within short distances.

Future Directions

The function of the relatively infrequent, but regular, interactions described herein is likely a social advantage. Immature *Tursiops* may pursue *Stenella* in an attempt to diffuse sexual energies when denied access to conspecific mates; however, more data with confirmed sex of *Tursiops* are needed. Rowe & Dawson (2009) have recently developed a method for sexing *Tursiops* using dorsal fin photographs. This method could be tested on the Bimini population and would provide additional data about these interactions. Populations should be monitored via behavioral and, ultimately, genetic sampling for potential hybrids. *Tursiops* have

successfully reproduced with other odontocete species in captivity (Døhl et al., 1974; Nishiwaki & Tobayama, 1982; Zornetzer & Duffield, 2003) and possibly in the wild (Fraser, 1940; Herzing et al., 2003; Acevedo-Gutierrez et al., 2005; Kristiansen & Forestell, 2007); the potential for hybridization with *Stenella* cannot be ruled out. Genetic studies would be useful to confirm potential hybrids, particularly given that hybrid individuals (*Stenella/Tursiops*; based on morphology and coloration patterns) are suspected from observations collected on both the Little Bahama Bank (Dudzinski, unpub. data) and in the Bimini *Stenella* populations (Herzing et al., 2003). Although the Bimini *Stenella* population is considered stable, its relatively small size makes it more vulnerable to introgression over time (Lehman et al., 1991). If hybridization is successful, then any population stresses would increase this vulnerability as seen in coyote (*Canis latrans*) and North American gray wolf (*C. lupus*) populations (Lehman et al., 1991).

The interactions in this study occurred over time and between populations; therefore, continued observations are required to determine whether interspecific interactions represent a significant exchange between species, particularly in the context of potential cultural transmission of behavior in species with complex social structures. There does not appear to be mixing between the Little Bahama Bank and Bimini *Stenella* populations (Herzing, pers. comm., 2007; Dudzinski & Melillo, pers. obs.), so transmission of information between *Stenella* groups in the region is unlikely unless both populations are mixing at the southern and northern (respectively) bounds of their ranges. Range of and mixing between *Tursiops* populations is unknown at this time.

This study is limited by a bias created by the subset of individuals visible in the camera's viewfinder. However, the long-term nature of these observations should reduce this bias as more individuals and interactions are observed. The bias toward *Tursiops* as focal animals likely has little influence given that one *Tursiops* and one *Stenella* were most commonly observed together. Affiliative behaviors were also most common regardless of focal species. The high proportion of unknown sex and age classes among *Tursiops* in the photo-ID catalog is a result of identification from above-water dorsal fin photographs, which do not include a view of the genital region or consistent distinction between subadult and adult age classes. The lack of confirmed sex among *Tursiops* from underwater observations is an artifact of the photo-ID catalog's limitation and the infrequency of *Tursiops* orienting their genital region toward the camera. In most cases, a visible erection was the only indicator of male *Tursiops*. It is also

important to note that the *Stenella* in this area are habituated to humans and boats. However, because the animals are not pursued but, rather, allowed to approach the boat only if they choose to do so, we do not consider this a source of bias. In fact, habituation may result in the display of more natural behaviors than might otherwise be observed.

Despite these limitations, understanding the subtleties of these populations' behavioral ecology and the interactions between them will become increasingly important as The Bahamas recently enacted a Marine Mammal Protection Act (2005) amidst a growing ecotourism industry. These data, as well as those from ongoing studies throughout The Bahamas, serve as baseline information with which to inform the scientific, governmental, and public communities as well as for long-term monitoring.

Acknowledgments

Major funding and support were provided by the Dolphin Communication Project (DCP), Mystic Aquarium & Institute for Exploration, the At-Sea Processors' Association Pollock Conservation Cooperative Fund at Alaska Pacific University, Bill & Nowdla Keefe's Bimini Undersea, and Al Sweeting, Jr. Permits to conduct scientific study on the dolphins around Bimini were obtained annually from the Department of Fisheries (Marine Resources), Ministry of Agriculture, Fisheries and Local Government, Nassau, The Bahamas. Animal care and use were reviewed and approved by the Institutional Review Board at Alaska Pacific University. E. Nielsen provided insight during the developmental and writing stages of this study. Data collection and dolphin identification were completed with K. DeStefano and D. Blanding and assisted by J. Gregg, M. Baetti, and T. Baker. K. Beard provided logistic support while in the field. The quality of the manuscript was greatly improved by the comments of anonymous reviewers. This work represents contribution #103 of the Dolphin Communication Project.

Literature Cited

- Acevedo-Gutierrez, A., DiBaradinis, A., Larkin, S., Larkin, K., & Forestell, P. (2005). Social interactions between Tucuxis and bottlenose dolphins in Gandoca-Manzanillo, Costa Rica. *Latin American Journal of Aquatic Mammals*, 4, 49-54.
- Altman, J. (1974). Observational study of behavior: Sampling methods. *Behavior*, 49, 227-267.
- Baraff, L. S., & Asmutis-Silvia, R. A. (1998). Long-term association of an individual long-finned pilot whale and Atlantic white-sided dolphins. *Marine Mammal Science*, 14, 155-161.

- Bearzi, G. A. (1996, March). A "remnant" common dolphin observed in association with bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Proceedings of the Tenth Annual Conference of the European Cetacean Society*. Lisbon, Portugal.
- Bearzi, M., & Stanford, C. B. (2007). Dolphin and African apes: Comparisons of sympatric socio-ecology. *Contributions to Zoology*, 76, 235-254.
- Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin "super-alliance." *Proceedings of the Royal Society of London B*, 268, 263-267.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann (Ed.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91-126). Chicago: University of Chicago Press. 433 pp.
- Corkeron, P. J. (1990). Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 285-293). San Diego: Academic Press. 653 pp.
- de Waal, F. (1997). *Bonobo: The forgotten ape*. Berkeley: University of California Press.
- Dohl, T. P., Norris, K. S., & Kang, I. (1974). A porpoise hybrid: *Tursiops* × *Steno*. *Journal of Mammalogy*, 55, 217-221.
- Dudzinski, K. M. (1996). *Communication and behavior in the Atlantic spotted dolphin (Stenella frontalis): Relationships between vocal and behavioral activities*. Ph.D. dissertation, Texas A&M University, College Station. 218 pp.
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, 24(3), 129-142.
- Dudzinski, K. M., Clark, C. W., & Würsig, B. (1995). A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals*, 21(3), 187-193.
- Frantzis, A., & Herzog, D. L. (2002). Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea). *Aquatic Mammals*, 28(2), 188-197.
- Fraser, F. C. (1940). Three anomalous dolphins from Blacksod Bay, Ireland. *Proceedings of the Royal Irish Academy*, 45, 413-455.
- Grant, J. W. A., Chapman, C. A., & Richardson, K. S. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology*, 31, 149-161.
- Hardie, S. M., & Buchanan-Smith, H. M. (1997). Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). *International Journal of Primatology*, 18, 217-234.
- Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): Age classes, color phases, and female reproduction. *Marine Mammal Science*, 13, 576-595.
- Herzing, D. L., & Johnson, C. M. (1997). Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquatic Mammals*, 23(2), 85-99.
- Herzing, D. L., Moewe, K., & Brunnick, B. J. (2003). Interspecific interactions between Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*, on Great Bahama Bank, Bahamas. *Aquatic Mammals*, 29(3), 335-341.
- Hohmann, G., & Fruth, B. (2003). Intra- and inter-sexual aggression by bonobos in the context of mating. *Behaviour*, 140, 1389-1413.
- Keast, A. (1965). Interrelationships of two zebra species in an overlap zone. *Journal of Mammalogy*, 46, 53-66.
- Kennedy, R. D. (1990). Bottlenose dolphins off the north-eastern United States. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 369-386). San Diego: Academic Press. 653 pp.
- Kerley, G. I. H. (1983). Relative population sizes and trends, and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at Prince Edwards Islands, Southern Ocean. *South African Journal of Zoology*, 18, 388-392.
- Kiliaan, H. L., Mamo, C., & Paquet, P. C. (1991). A coyote, *Canis latrans*, and badger, *Taxidea taxus*, interaction near Cypress Hills provincial-park, Alberta. *Canadian Field-Naturalist*, 105, 122-123.
- Kovacs, K. M., Lydersen, C., Hammell, M. O., White, B. N., Wilson, P. J., & Malik, S. (1997). A harp seal × hooded seal hybrid. *Marine Mammal Science*, 13, 460-468.
- Krebs, J. R., & Davies, N. B. (1993). *An introduction to behavioural ecology*. Oxford, UK: Blackwell Science.
- Kristiansen, R. E., & Forestell, P. (2007, November). Interspecific interactions between marine Tucuxi (*Sotalia guianensis*) and bottlenose dolphins (*Tursiops truncatus*) in Costa Rica. *Proceedings of the Seventeenth Biennial Conference on the Biology of Marine Mammals*. Cape Town, South Africa.
- Lancaster, M. L., Gemmill, N. J., Negro, S., Goldsworthy, S., & Sunnucks, P. (2006). Ménage à trois on Macquarie Island: Hybridization among three species of fur seal (*Arctocephalus* spp.) following historical population extinction. *Molecular Ecology*, 15, 3681-3692.
- Lehman, N., Eisenhawer, A., Hansen, K., Mech, L. D., Peterson, R. O., Gogan, P. J. P., et al. (1991). Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution*, 45, 104-119.
- Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, 15, 102-122.
- McGraw, W. S., & Bshary, R. (2002). Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: Experimental evidence for the effects of reduced ground predator pressure on habitat use. *International Journal of Primatology*, 23, 311-325.

- Mendes-Pontes, A. R. (1997). Habitat partitioning among primates in Maraca Island, Roraima, northern Brazilian Amazonia. *International Journal of Primatology*, *18*, 131-157.
- Mesnick, S. L., & Ralls, K. (2002). Mating systems. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 726-733). San Diego: Academic Press. 1,414 pp.
- Miller, E. H. (2002). Territorial behavior. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 1235-1243). San Diego: Academic Press. 1,414 pp.
- Minta, S. C., Minta, K. A., & Lott, D. F. (1992). Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). *Journal of Mammalogy*, *73*, 814-820.
- Mitani, J. C., & Rodman, P. S. (1979). Territoriality: The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology*, *5*, 241-251.
- Möller, L. M., Beheregaray, L. B., Harcourt, R. G., & Krützen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London B*, *268*, 1941-1947.
- Nishiwaki, M., & Tobayama, T. (1982). Morphological study on the hybrid between *Tursiops* and *Pseudorca*. *The Scientific Reports of the Whales Research Institute*, *34*, 109-121.
- Norris, K. S., & Dohl, T. P. (1980). Behavior of the Hawaiian spinner dolphins, *Stenella longirostris*. *Fishery Bulletin*, *77*, 821-849.
- Norris, K. S., & Schilt, C. R. (1988). Cooperative societies in three-dimensional space: On the origins of aggregations, flocks and schools, with special reference to dolphins and fish. *Ethology and Sociobiology*, *9*, 149-179.
- Parsons, K. M., Durban, J. W., Claridge, D. E., Balcomb, K. C., Noble, L. R., & Thompson, P. M. (2003). Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, *66*, 185-194.
- Parsons, K. M., Durban, J. W., Claridge, D. E., Herzing, D. L., Balcomb, K. C., & Noble, L. R. (2006). Population genetic structure of coastal bottlenose dolphins (*Tursiops truncatus*) in the northern Bahamas. *Marine Mammal Science*, *22*, 276-298.
- Perrin, W. F. (1970). Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnerberg (Cetacea, Delphinidae). *Zoologica*, *54*, 135-142.
- Reeves, R. R., Stewart, B. S., Clapham, P. J., & Powell, J. A. (2002). *National Audubon Society guide to marine mammals of the world*. New York: Chanticleer Press.
- Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology*, *57*, 405-435.
- Roszbach, K. A., & Herzing, D. L. (1999). Inshore and offshore bottlenose dolphins (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas. *Canadian Journal of Zoology*, *77*, 581-592.
- Rowe, L. E., & Dawson, S. M. (2009). Determining the sex of bottlenose dolphins from Doubtful Sound using dorsal fin photographs. *Marine Mammal Science*, *25*, 19-34.
- Scott, M. D., & Cattanach, K. L. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. *Marine Mammal Science*, *14*, 401-428.
- Scott, M. D., & Chivers, S. J. (1990). Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 387-402). San Diego: Academic Press. 653 pp.
- Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphins: A review. *Marine Mammal Science*, *2*, 34-63.
- Shelden, K. W., Baldridge, A., & Withrow, D. E. (1995). Observations of Risso's dolphins *Grampus griseus* with gray whales *Eschrichtius robustus*. *Marine Mammal Science*, *11*, 231-240.
- Sinclair, A. E. (1985). Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology*, *54*, 899-918.
- Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *The Quarterly Review of Biology*, *76*, 141-168.
- Stensland, E., Angerbjorn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, *33*, 205-223.
- Stensland, E., Berggren, P., Johnstone, R., & Jiddawi, N. (1998). Marine mammals in Tanzanian waters: Urgent need for status assessment. *Ambio*, *27*, 771-774.
- Wells, R. S. (1984). Reproductive behavior and hormonal correlates in Hawaiian spinner dolphins, *Stenella longirostris*. In W. F. Perrin, R. L. Brownell, Jr., & D. P. DeMaster (Eds.), *Reproduction in whales, dolphins and porpoises: Proceedings of the Conference on Cetacean Reproduction, Estimating Parameters for Stock Assessment and Management* (pp. 465-472). Cambridge, UK: International Whaling Commission.
- Wells, R. S., Irvine, A. B., & Scott, M. D. (1980). The social ecology of inshore odontocetes. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 263-317). Malabar, India: Robert E. Krieger Publishing Company. 480 pp.
- Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *American Association for the Advancement of Science*, *198*, 755-756.
- Zornetzer, H. R., & Duffield, D. A. (2003). Captive-born bottlenose dolphin × common dolphin (*Tursiops truncatus* × *Delphinus capensis*) intergeneric hybrids. *Canadian Journal of Zoology*, *81*, 1755-1762.