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Directionality of Sexual Activities During Mixed-Species Encounters between Atlantic Spotted Dolphins (*Stenella frontalis*) and Bottlenose Dolphins (*Tursiops truncatus)*

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In the Bahamas, interspecific groups of Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, have been observed underwater since 1985 on Little Bahama Bank. Mixed-species groups engage in associative behaviors and aggression on a regular basis. Because of their complex cognitive behaviors and large brain encephalization, dolphins are likely capable of complex social interactions, even between species.Between 1993-2003, 177 Mixed-Species Encounters (MSE) were categorized by the age class of male spotted dolphins, the ratio of spotted dolphins to bottlenose dolphins, behavior as Associative (traveling, babysitting, play) or Aggressive (chases, mounting, head to heads) and by directionality of sexual behavior. The majority (68%) of MSE involved adult spotted dolphin. Associative behaviors were observed more than aggressive behaviors in groups where no adult male spotted dolphin, only male calves, or male juvenile spotted dolphins were present. Aggressive behaviors were observed more frequently than associative behaviors in adult male spotted dolphin groups. When groups were unbalanced in favor of one species or the other, differences in social interactions occurred. Male spotted dolphins were never observed attempting to mount male bottlenose dolphin although they chased them. Despite the larger ratio of male spotted dolphins to bottlenose dolphins during MSE, directionality of male-to-male sexual contact was primarily one-way. Male bottlenose dolphin mounted and copulated with male spotted dolphins but not the reverse. Opportunities for cross-species mating and hybridization clearly occurred. Male bottlenose dolphins copulated with female spotted dolphins and male spotted dolphins copulated with female bottlenose dolphins. These sympatric dolphins in the Bahamas have a complex and dynamic relationship that varies with sex and age and revolves around potential reproductive isolation issues.

In the Bahamas, a resident group of Atlantic spotted dolphins have been behaviorally observed underwater on Little Bahama Bank (LBB) since 1985. Life history (Herzing, 1997) and correlations with sound and behavior (Herzing, 1996, 2000, 2006) have been described. In addition bottlenose dolphin distribution (Rossbach & Herzing, 1999), feeding behavior (Rossbach & Herzing, 1997), and social structure (Rogers, Brunnick, Herzing, & Baldwin, 2004) has been documented. Long-term interactions between sympatric Atlantic spotted dolphins and Atlantic bottlenose dolphins in the Bahamas have been observed consistently every year since 1985. These two species have been observed in mixed group interactions and spend 15% of their time engaged in interspecies activities including foraging, traveling, play, alloparental care, aggressive activity and interspecific alliances (Herzing & Johnson, 1997). During these mixed group interactions group size and duration of encounters increased. A variety of mechanisms of information transfer (Herzing, 2005) and specific teaching mechanisms have also been observed (Bender, Herzing, & Bjorklund, 2008) for spotted dolphins suggesting that complex interactions within and between

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species are possible. A close genetic relationship between Atlantic spotted dolphins and bottlenose dolphins has also been reported (LeDuc, Perrin, & Dizon, 1999) suggesting that hybridization may be possible. One example of hybridization, based on morphological observations, has been reported in an adjacent study site (Herzing, Moewe, & Brunnick, 2003) and regular interactions between these species at this secondary site have subsequently been described as primarily social (Melillo, Dudzinski, & Cornick, 2009). A degree of asymmetry of alliance formation between these two species also exists on LBB, suggesting that spotted dolphins regularly form more complex levels of alliance associations than bottlenose dolphins (Elliser, 2010; Elliser & Herzing, in press).

The functional benefits of interspecies interaction between social mammals include not only foraging advantages and predator avoidance but also potential social and reproductive benefits (Bearzi & Standord, 2007). The advantages of group size during aggression in primates have also been reported (Schaffner & French, 1997; Silk 1999). The adaptive significance and evolutionary benefits of complex social interactions for terrestrial species are diverse (Norconk, 1990). Interspecific interactions and mixed-species troops have been reported in other social mammals especially for sympatric primate species and include observations of displacing, grooming, foraging, playing, and mating (Terborgh, 1990; Waser, 1987) and interspecific communication (Windfelder, 2001). It is likely that thoroughly studied terrestrial examples of interspecies interactions may provide insight into cetacean mixed species interactions.

Interspecies interactions have been documented in over 33 cetacean species (Bearzi, 2005; Frantzis & Herzing, 2002, Querouil et al., 2008). Recently the dynamics of vocalization use between two species of sympatric dolphins in Costa Rica has been reported, suggesting that interspecies interactions are both complex and negotiated on a consistent basis (May-Collado, 2010). In addition to interspecific group interactions, individuals have been documented in complex situations including an individual common dolphin (*Delphinus delphis*) with bottlenose dolphins (*Tursiops truncatus*) by Bearzi (2005), an individual long-finned pilot whale (*Globicephala melas*) with Atlantic white-sided dolphins (*Lagenorhynchus acutus*) by Baraff and Asmutis-Silvia (1998), and an individual Risso's dolphin (*Grampus griseus*) with striped dolphins (*Stenella coeruleoalba*) and common dolphins (Frantzis & Herzing, 2002).

The objective of this study was to first describe the features of sexual activity and aggression during Mixed Species Encounters (MSE) of Atlantic spotted and bottlenose dolphins in the Bahamas relative to sex, age class, and directionality of mounting and copulation, and secondly to test if there was a significant difference in 1) the ratio of species (to determine any unbalanced species advantages) when adult male spotted dolphins were present, 2) the occurrence of aggressive vs. associative behavior when adult male spotted dolphins were present, and 3) the directionality (which species mounted the other) of mounting/copulation behavior between the two species.

Method

Since 1985 Atlantic spotted dolphins and bottlenose dolphins have been observed every summer for approximately 100 days, May through September, on the Little Bahama Bank (LBB). These two species are resident and sympatric and have a clear physical size difference: an adult bottlenose dolphin is approximately 1 m larger than an adult spotted dolphin. This is an area of shallow water, ranging approximately 6 to 16 m in depth, 480 km^2 in size. Underwater visibility averages 30 m. Observations were conducted using a 20-m motor-powered catamaran.

When dolphins were encountered researchers entered the water to obtain underwater video and simultaneous sound using various cameras (e.g., Sony TRV PC110, Sony XR550) with attached hydrophones. Sampling included *ad libitum*, focal, and behavioral events (Altmann, 1974). All dolphins were identified using standard photo identification

techniques using underwater cameras, and determination of sex was accomplished by underwater visual observation of the genital area. Age classes for spotted dolphin were classified using Herzing (1997) modified after *S. attenuata* (Perrin, 1970) and the life history, reproductive activity, association patterns, and underwater sound and behavior of these resident dolphins have been well documented for over 28 years, spanning three generations. Bottlenose dolphins were classified as adults, juveniles, and calves.

Other data recorded include date, time, location, associations, environmental information, and general behavioral activity. Video information was logged and reviewed every evening on board the research vessel and included detailed notes and scoring of underwater behaviors and vocalizations. This long-term data set of audio and visual information has been archived since 1985 and is accessible for detailed analysis based on individuals (220 spotted dolphins, 200 bottlenose dolphins), age classes, and behavior categories (e.g., aggression, courtship).

A total of 177 MSE were reviewed in the long-term database from 1993 to 2003. MSE aggressive interactions were similar in duration to spotted dolphin intraspecific interactions but had a greater maximum duration and range (*Interspecies* - 82.7 hrs. avg duration = 62.05 min, SD 56.75 min, range 5 - 300 min; *Intraspecies* - 85 hrs, avg duration 57.93 min, SD 42.70, range 5 – 180 min).

MSE were scored as to the 1) age class of male spotted dolphins present (no males, male calves, juvenile males, or adult males, 2) the ratio of spotted to bottlenose dolphins, 3) general behavioral activity as either *Associative* (traveling, babysitting or play) or *Aggressive* (chases, mounts with erections, or head to head postures) for each age class, and 4) direction of the sexual activity (which species was mounting and copulating with the other) by species, sex, and age class.

Results

Of 177 MSE, the majority of encounters involved adult male spotted dolphin (68% adult males, 14% juvenile males, 7% male calves, 11% no males present). In all but one category of age class (when no males were present) the ratio of spotted dolphin to bottlenose dolphin was greater than 1:1 (Figure 1). When tested for a species advantage during MSE, the ratio of spotted dolphins to bottlenose dolphins was greater than 1:1 significantly more often when adult male spotted dolphins were present than when all other age class categories were combined (Pearson's $X^2(1, n = 177) = 18.29, p < 0.001$).

In 3 of the 4 age-class categories (no males present, male calves, juvenile males) associative behavior was more common than aggressive behavior. The adult male age class category showed over twice the frequency of aggressive behavior as associative behavior during MSE (Figure 2). When tested, significantly more aggressive behavior occurred when adult male spotted dolphins were present than when all other age class categories were combined (Pearson's $X^2(1, n = 195) = 25.67, p < 0.001$).

Although male spotted dolphins occasionally chased and mounted female bottlenose dolphins, they never mounted (although they chased) male bottlenose dolphins (Figure 3). When tested, male bottlenose dolphins mounted male spotted dolphins significantly more often than male spotted dolphins mounted male bottlenose dolphins (Pearson's $X^2(1, n = 49) = 49.00, p < 0.001$). Juvenile male spotted dolphins also occasionally mounted and copulated with each other. Female bottlenose dolphins solicited young male spotted dolphins on at least one occasion.

Figure 4A and B shows all possible directions of copulation/sexual activity between the two species. Although male dolphins of both species chased, mounted, or copulated with female dolphins of the opposite species, male bottlenose dolphins directed the majority of their sexual activity (primarily mounting and copulation) to male spotted dolphins (Figure 5). To a lesser degree, adult female bottlenose dolphins sexually solicited male juvenile spotted dolphins.

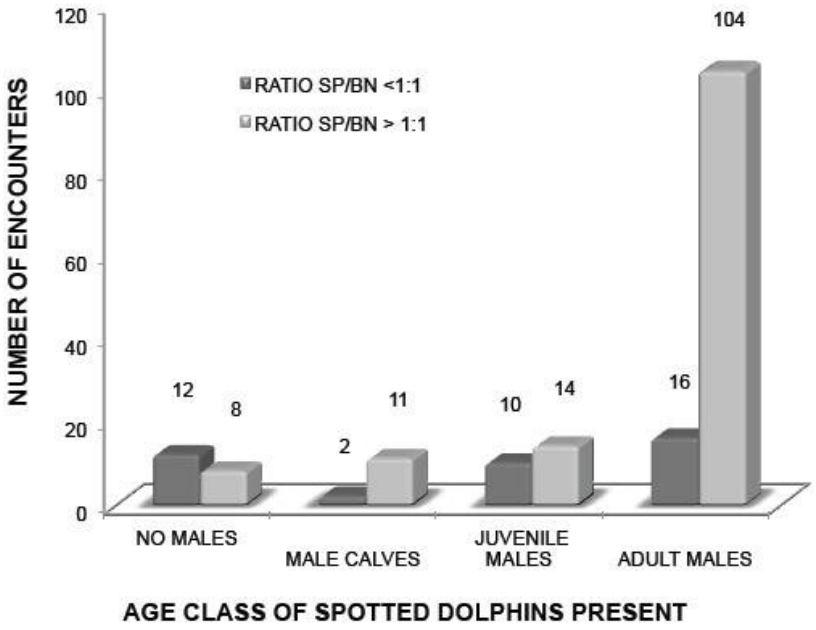

Figure 1. Ratio of spotted dolphins to bottlenose dolphins during Mixed Species Encounters (MSE) from 1993 – 2003 in the presence of adult male, juvenile males, male calves, and when no males were present.

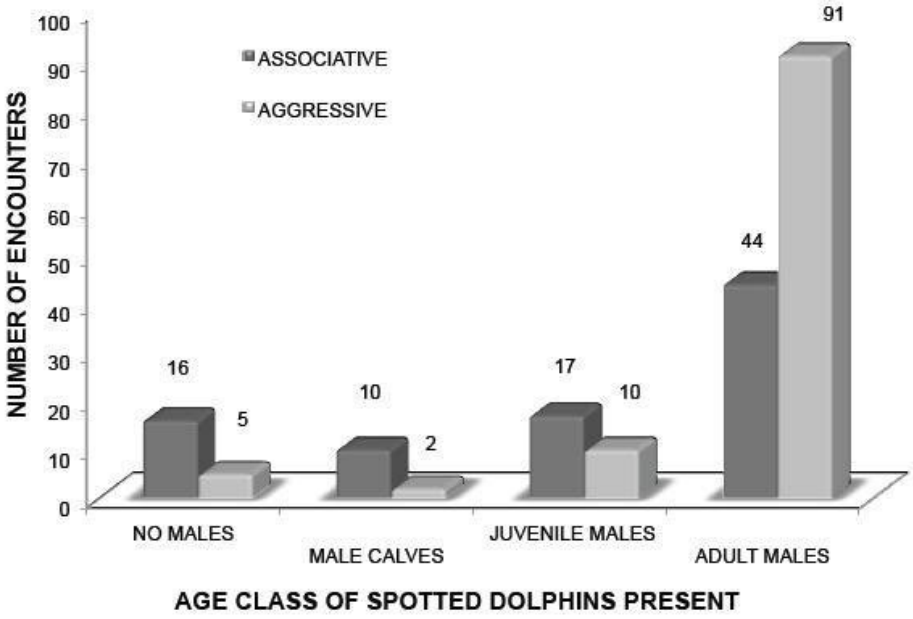

Figure 2. Associative behavior (traveling, babysitting, play) and Aggressive behavior (chases, mounts with erections, head to head postures) during Mixed Species Encounters (MSE) from 1993 – 2003 when adult male, juvenile males, male calves, and when no males were present.

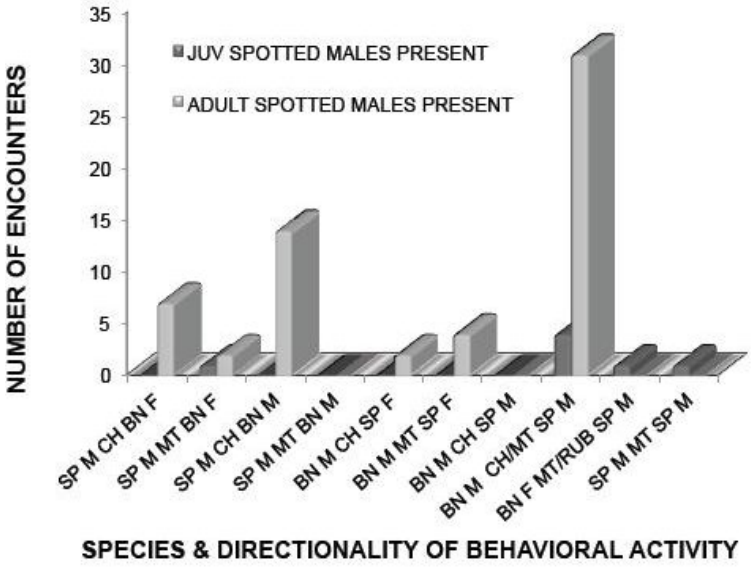

Figure 3. Occurrence and directionality of specific chases and sexual aggressive behaviors of spotted and bottlenose dolphins during Mixed Species encounters (MSE) from 1993 – 2003. All combinations of chases, mounts, and head to heads are broken down in either the presence of juvenile spotted males or adult spotted males. SP = spotted dolphin, BN = bottlenose dolphin, M = male, F = Female, CH = chase, MT = mount, DIS = discipline.

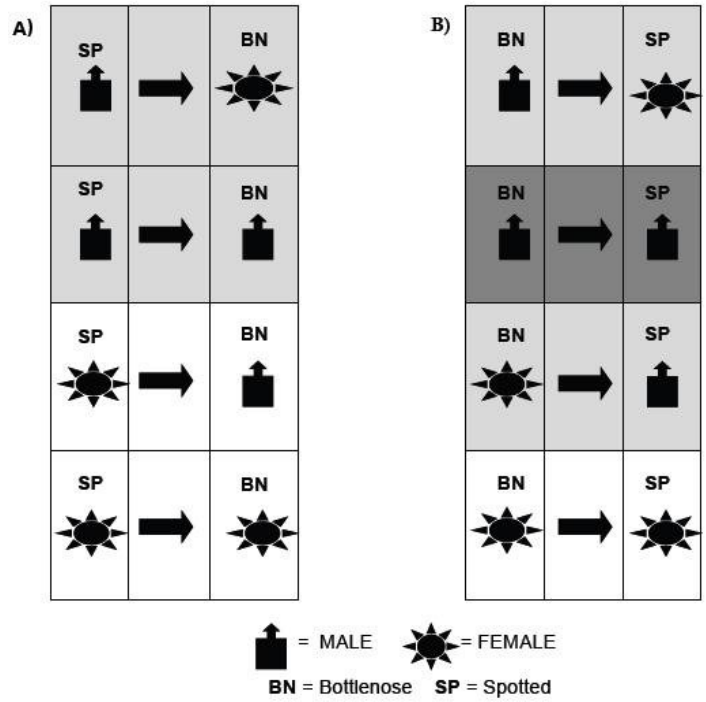

Figure 4. **A)** Directionality of sexual (mounting/copulation) behavior for spotted dolphins during Mixed Species encounters (MSE) from 1993 – 2003. **B)** Directionality of sexual (mounting/copulation) behavior for bottlenose dolphins during Mixed Species encounters (MSE) from 1993 – 2003. Dark gray depicts the major directionality by species and sex of spotted dolphins (SP) or bottlenose dolphins (BN). Light gray depicts occasional direction of sexual activity. White depicts no sexual activity.

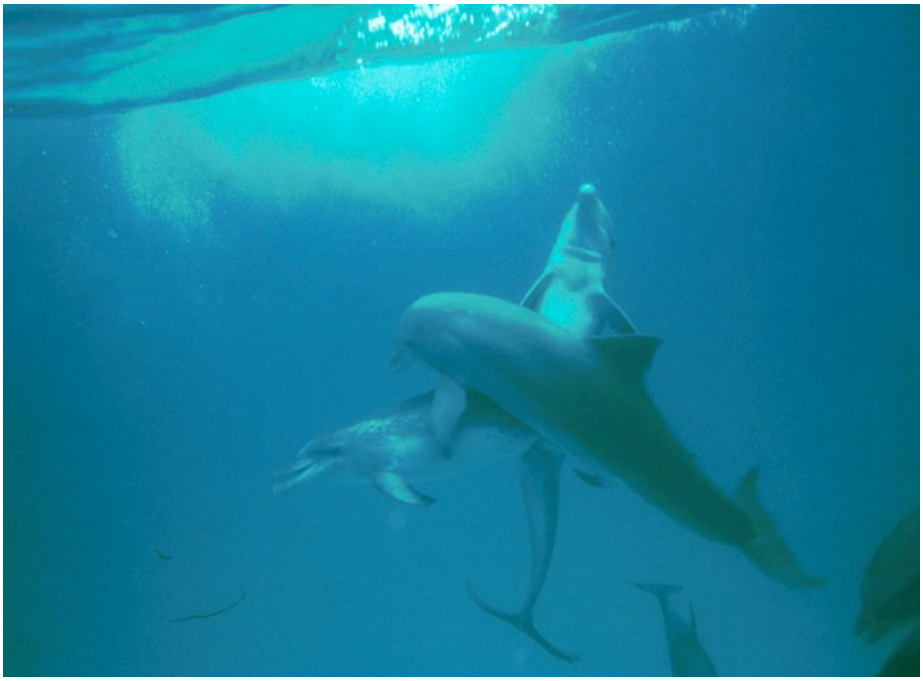

Figure 5. Two male adult bottlenose dolphins side mount and copulate with a young male spotted dolphin in the Bahamas (Photo credit: Wild Dolphin Project).

Discussion

Age Classes and Ratio of Species

Adult male spotted dolphins were the most likely to be involved in interspecies interactions with bottlenose dolphins. In addition, ratios of spotted dolphins to bottlenose dolphins were greater that 1:1 when adult male spotted dolphins were present. There is a documented degree of asymmetry of alliance formation between these two species on LBB. Spotted dolphins form more complex levels of alliance associations than bottlenose dolphins (Elliser, 2010; Elliser & Herzing, in press) similar to two levels of alliance formation of bottlenose dolphins in Shark Bay, Australia (Connor, Watson-Capps, Sherwin, & Krutzen, 2011), however bottlenose dolphins on LBB only form the first level of alliance structure (Rogers et al., 2004). The behavior of large coalitions of spotted dolphins, that showed ritualized behaviors (including a ratio of six spotted dolphins chasing one bottlenose dolphin (Herzing & Johnson, 1997), could be related to asymmetries of both alliance formation and their physical size differences.

Behavior, Asymmetry, and Directionality of Behaviors

Associative behavior was observed more frequently during interspecies interactions in younger age class dolphins whereas aggressive behavior dominated the activity of adult male spotted dolphins when with adult male bottlenose dolphins. During aggressive behavior, there was also an asymmetry and directionality of sexual activity between male bottlenose dolphins and

male spotted dolphins. Adult male bottlenose dolphins chased and mounted both adult male spotted dolphins and juvenile male spotted dolphins. Although other combinations of sexual activities were observed, adult male bottlenose dolphins predominantly mounted and copulated with male spotted dolphins. Juvenile and adult male spotted dolphins occasionally chased and mounted female bottlenose dolphins, but they never mounted male bottlenose dolphins even though they chased them. Occasionally, male spotted dolphins copulated with female bottlenose dolphins and both male and female bottlenose dolphins solicited sexual stimulation or copulated with spotted dolphins of the opposite sex.

In reports of other cetacean species, the larger of the species has tended to dominate such interactions including bottlenose dolphins to harbour porpoises (*Phocoena phocoena*) by Ross and Wilson (1996) and Patterson et al. (1998), bottlenose dolphins to estuarine dolphins (*Sotalia guianensis*) by Wedekin, Daura-Jorge, and Simoes-Lopes (2004), Hawaiian spinner dolphins (*Stenella longirostris*) to Pantropical spotted dolphins (*Stenella attenuata*) by Psarakos, Herzing, and Marten *(*2003), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) to harbor porpoise by Baird, Willis, Guenther, Wilson, and White (1998).

Hybridization Potential

Although mixed-species associations for protection from predators has been theorized and described for a few tropical species of delphinids (Kiszka, Perrin, Pusineri, & Ridoux, 2011), others have proposed a social advantage theory to mixed groups (Stensland, Angerbjorn, & Berggren, 2003). In the Bahamas both social behavior and predatory defenses occur during mixed-species interactions suggesting that these two theories are not mutually exclusive. However, the possibility that competition for reproductive advantage may potentially drive interspecies breeding is supported by both the genetic relationship between these species and history of bottlenose dolphin interbreeding in captivity.

In nature, reproductive isolation between species is accomplished by three mechanisms: geographical isolation, physical isolation, or behavioral isolation. These sympatric species in the Bahamas have no geographical or physical barriers to block interbreeding. In captivity bottlenose dolphins have mated with thirteen other dolphin species (Sylvestre & Tanaka, 1985) sometimes producing fertile offspring. Behavioral isolation is the only mechanism left to discourage hybridizing between these free-ranging species.

Size variation may be a factor in juvenile spotted interactions with bottlenose dolphins, as well as in the directionality of sexual mounting behavior. Directional hybridization has been observed in the porpoise family, Family *Phocoenidae*, between Dall's porpoise (*P. dalli*) and harbour porpoise (*P. phocoena*) by Baird et al. (1998). Here the maternal species was the smaller Dall's porpoise and paternal species was the larger harbour porpoise, which produced fertile offspring.

On Great Bahama Bank (GBB) hybridization (maternal spotted dolphin, paternal bottlenose dolphin) has been reported (Herzing et al., 2003). However, Herzing et al. (2003) also noted that on GBB, a secondary study site for the same two sympatric species (although with more restricted observation time), winter time observations suggest that male spotted dolphins mount and copulate with male bottlenose dolphins, the reverse of LBB, suggesting that directionality may be site specific, seasonal, or community specific. Female bottlenose dolphins on LBB have been reported to migrate around the entire sandbank (Parsons et al., 2003), potentially reducing or complicating access to female bottlenose dolphins by resident male bottlenose dolphins. To complicate interbreeding issues more, the offshore bottlenose dolphin

ecotype has been observed on LBB with resident inshore ecotype bottlenose dolphins described here, and evidence for their hybridization also exists (Parsons, Durban, & Claridge, 2006).

In addition, on LBB a small subset of resident bottlenose dolphins have spots on their ventral areas and these individuals display behavioral traits more similar to spotted dolphins than the resident bottlenose dolphins, suggesting that reverse mating may also occur. Such mixed behavioral as well as morphological features is not unknown in hybrid baboons. Directional mating behavior and hybridization (driven by habitat disturbance) for two species of baboon has been described (Sugawara, 1979) in the Awash valley in Ethiopian East Africa, for the Olive baboon (*Papio anubis*) and the Hamadryas baboon (*Papio hamadryas*). Matrilineal (multi-male, multi-female) olive baboon society mated and produced fertile offspring with the "cross-migrant" young bachelors and deposed older hamadryas males.

Like baboon hybridization issues, it is also possible that individual dolphins with low social status or socially deposed males within the larger community drive these interspecific dynamics on LBB. The emerging importance of the individual, including delphinds, in complex social societies has been examined (Lusseau & Newman, 2004).

The detailed life history and genetic aspects of ongoing hybridization and the evolutionary significance in defining reproductive isolation has been described (Alberts & Altmann, 2001; Tung, Charpentier, Garfield, Altmann, & Alberts, 2008). Even mate choice dynamics among sympatric fur seals has been observed (Goldsworthy, Boness, & Fleischer, 1999). Aspects of interspecies mating in the Bahamas suggest that competition and access to females, by both species, in the area may lead to similar issues and dynamics over time.

In the Bahamas a complicated relationship exists between two sympatric species of dolphins, Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*). Previous observations have shown a variety of regular affiliative and aggressive behaviors (Herzing & Johnson, 1997). A closer look at age class, sex, and species roles on LBB during aggressive sexual activity suggests that male sexual mounting and copulation behavior is highly directional, with male bottlenose dolphins primarily copulating with male spotted dolphins, even though males of both species chase and copulate with females of the opposite species. The sexual activities between male dolphins of both species suggest either a dominant sexual dynamic exists or there is female resource competition between the species. Cusick (2012) recently described detailed video analysis of the dynamic process, including directional mounting behavior and synchrony, during these interspecies interactions on LBB that may yield a better understanding of the relative power and dominance mechanisms between these two species. Interspecies interactions may not only be valuable for predator protection and interspecies cooperation, but may also be advantageous for reproductive resources between two closely related species. This study was limited by seasonal observations and lack of genetic evidence for hybridization. Future research during non-summer months and assessing the amount of female resource competition that exists, by obtaining genetic evidence of hybridization, would be fruitful areas for research. With shrinking habitats in the ocean we should expect to see reproductive resource competition as species are driven together with climate change and habitat alterations.

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